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Optimized recess design in artificial structures dramatically enhances coral settlement and survival

Authors

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Keywords

3D printing, artificial reefs, coral settlement habitat, hydrodynamics, Kāne‘ohe Bay Hawai‘i, scalable restoration

Abstract

The rapid decline of coral reefs prompts the need for new, scalable restoration approaches. Focusing on coral larvae has a great potential for scalability, as a single coral colony can release many thousands of offspring of which the vast majority do not find suitable habitat and die. Here, we designed a range of adaptable modules with distinct geometric features hypothesized to enhance coral settlement and survival. In tank and field experiments, we explored the properties and dimensions of the most successful modules and structural features, and examined the influence of hydrodynamics. Modules with spiral recesses outperformed others, increasing settlement by about 80-fold and post-settlement survival over a year by 20–50-fold compared to controls. Settlement was greatest on cryptic edges with 17 mm deep and 15 mm wide recesses with ~56 µmol m^{-2} s^{-1} photosynthetic active radiation (i.e., ~28% of the incoming light). Settlement was more pronounced under high-flow conditions, suggesting a crucial role of micro-scale hydrodynamics in entraining settling coral larvae. Integrating spiral recesses of informed dimensions into restoration modules or engineering structures can provide a novel, scalable, cheap, and self-sustaining approach to reef restoration.

1 Introduction

Coral reefs are increasingly threatened by global climate change and local disturbance events (Hughes et al., 2018). Lowering carbon emissions is our best chance to mitigate coral decline, however, local efforts can support degrading ecosystems through restoration approaches (Randall et al., 2020; Suggett and Van Oppen, 2022). While small-scale efforts to restore reefs have been successful, the overall scale of reef restoration has not kept pace with the widespread and rapid decline of coral reefs. This is because the effectiveness, scalability, and costs of restoration methods remain challenging (Boström-Einarsson et al., 2020; Hein et al., 2017). Restoration approaches often focus on transplanting reared or fragmented coral colonies to degraded reefs (Boström-Einarsson et al., 2020). These methods have been successful on small local scales (< 1 km^2), but their propagation is labor-intensive and sacrifices healthy corals. A more cost-effective and feasible propagation method is to use sexual propagules obtained during spawning (Randall et al., 2020). A few coral colonies can release hundreds of thousands of individuals during a single spawning event (Madin et al., 2016). Therefore, restoration approaches increasingly collect and move coral larvae to degraded reef areas (Cruz and Harrison, 2017; Harrison et al., 2021; Suzuki et al., 2020). Other approaches focus on collecting and settling larvae onto seeding units that are then outplanted in target areas (Chamberland et al., 2017). Using coral larvae yields high numbers of individuals while maintaining a high genetic diversity comparable to natural populations (Zayasu and Suzuki, 2019).

The process of shifting from motile planula larvae to sessile polyps includes the selection of a suitable substrate, the attachment to it, and the metamorphosis (Randall et al., 2020). While the primary mode of transportation for planktonic larvae is through ocean currents, the larvae can modulate their vertical position in the water column to get in contact with the reef (Tay et al., 2011). Once they are in proximity to the reef, coral larvae can detect a variety of physical, chemical, and biological cues, which guide them to specific locations and influence and trigger settlement (Edmunds, 2023). Biochemical cues from certain crustose coralline algae (CCA) or

bacteria are considered strong settlement cues (Gómez-Lemos et al., 2018; Harrington et al., 2004; Jorissen et al., 2021). Furthermore, material composition, surface topography, and water flow (Gysbers et al., 2024; Hata et al., 2017; Levenstein et al., 2022b, 2022a; Whalan et al., 2015) can affect larvae settlement. Overall, settlement preferences of coral larvae are governed by a trade-off between the need for light, so they can rapidly grow to overcome size-escape thresholds, at the same time high light environments make these early coral life stages prone to overgrowth by competitively superior algae. A successful strategy for larvae is to settle in crevices and near underside edges, protecting them from predation, grazing, and strong physical impacts while still receiving sufficient light to grow (Cruz and Harrison, 2017). However, after settlement, coral recruits undergo an early-life bottleneck, and only a fraction of the larvae that initially settled survive (Martinez and Abelson, 2013; Nozawa and Harrison, 2008). Thus, improving early life survival can have a disproportionately large impact on population dynamics and ultimately coral cover, presenting a scalable tool for coral restoration efforts.

A novel approach to boost restoration efforts is the integration of settlement habitat for coral larvae into coastal structures, such as artificial reefs (AR); a similar vein to creating habitat for other reef organisms to restore biodiversity (Harrison et al., 2021; Lima et al., 2019; Loke et al., 2015). Different methods have been applied to build artificial reefs, deploying for example modular concrete structures like *MARS* or hexagonal rod constructions covered with resin and coral sand like *Reef Stars* (Higgins et al., 2022). Recently, 3D printing has been applied as a versatile method for creating modules to rebuild the structural complexity of reefs (Berman et al., 2023; Levy et al., 2022). Using ceramic 3D printing to build complex modules that include spiral recesses enhances the settlement and survival of coral recruits (Schiettekatte et al. in prep) and can offer new scalable opportunities for restoration. However, it remains unclear which structural elements and microhabitat features should be integrated into artificial reefs to maximize settlement and survival of coral recruits.

Here, we identify the structural features promoting coral settlement and survival on complex ceramic modules. Based on *in situ* observations of coral settlement on natural reef, we I) design and compare different structural features that can be integrated into modules as settlement structures for coral larvae, II) identify the properties and dimensions of the most successful structural features, and III) assess the influence of hydrodynamics on the settlement and survival of coral recruits.

2 Results

2.1 Settlement and survival of coral recruits on different module designs

Seven conical coral settlement modules were designed with distinct structural features mimicking coral reef surfaces that were deployed at two locations in Kāneʻohe Bay and coral settlement and survival were monitored over one year (Figure 1).

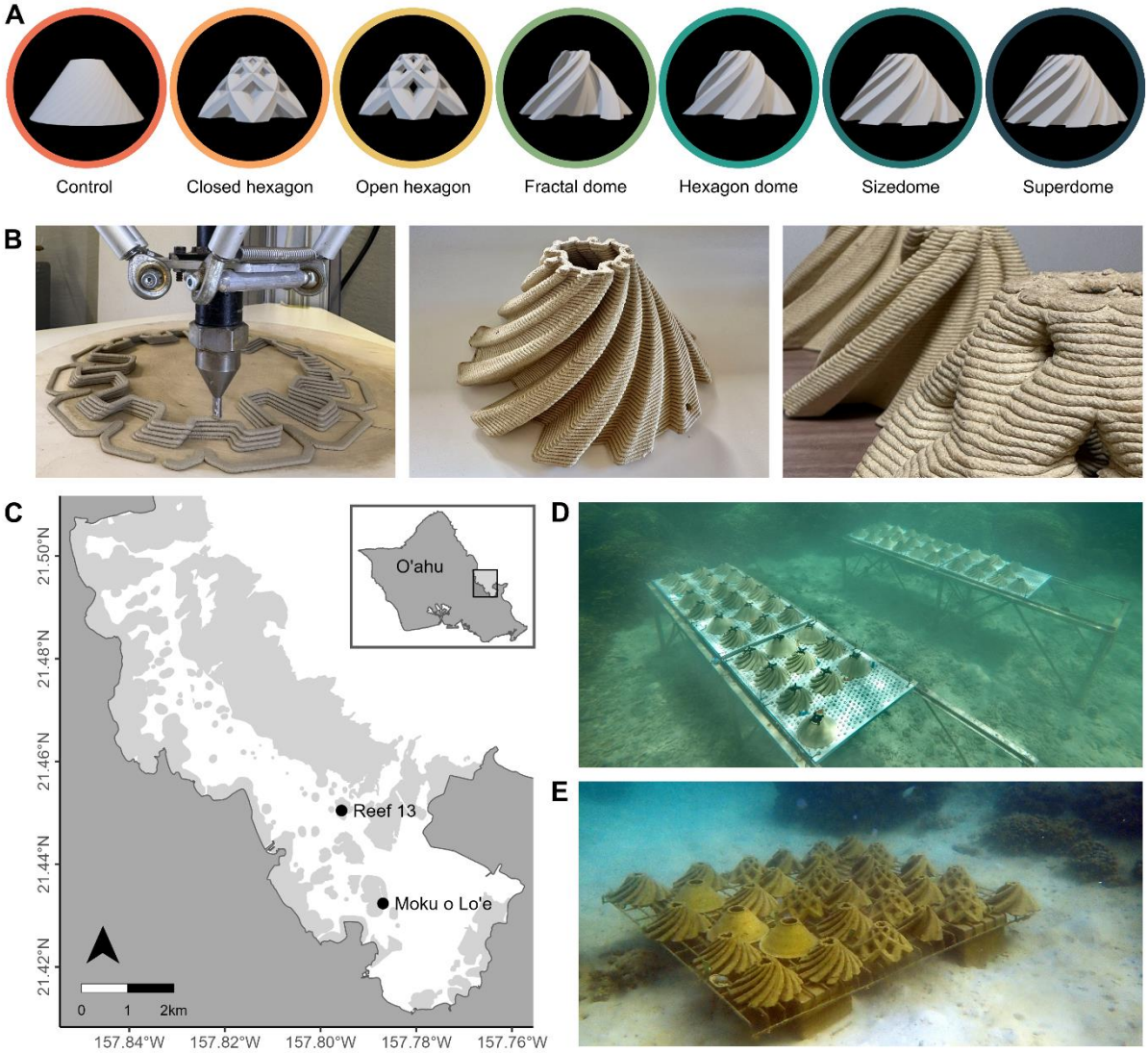

Figure 1: Larvae settlement module designs and production. (A) Seven different designs (control, open hexagon, closed hexagon, fractal dome, hexagon dome, sizedome, and superdome) with different structural features were compared. (B) The conical larvae settlement modules were built with a 3D clay printer. The close-up shows the horizontally caved microscale structure on the surface of the fired modules, created through the 3D printing process. (C) Map of Kāneʻohe Bay, Oʻahu, Hawaiʻi, showing the study location patch reef 13 and Moku o Loʻe. Light grey areas show the presence of reefs. The settlement modules were deployed at underwater tables at (D) reef 13 and (E) Moku o Loʻe.

Throughout the experiment, the highest numbers of recruits and recruit densities were found on modules with spiral recesses (i.e., fractal dome, hexagon dome, sizedome, and superdome; Figures 2A and S1, Wilcoxon tests, $p < 0.05$, Tables S1, S2, and S3). Control domes

consistently had the lowest number of recruits and recruit densities. One week after coral spawning, remarkably high numbers of recruits were found, with up to 1089 recruits on a single sizedome and 1049 on a single superdome, resulting in densities of ~1 recruit per cm^2 (Tables S2 and S3). Recruit densities on modules with spiral recesses decreased during the initial post-settlement mortality and stabilized at ~0.02 recruits per cm^2 after the first two months. Much lower numbers of recruits were found on modules at Moku o Lo‘e, compared to patch reef 13. There, densities increased over time to levels greater than patch reef 13 until they dropped again at the one year mark. Nonetheless, the overall preference for spiral recesses was similar at both sites.

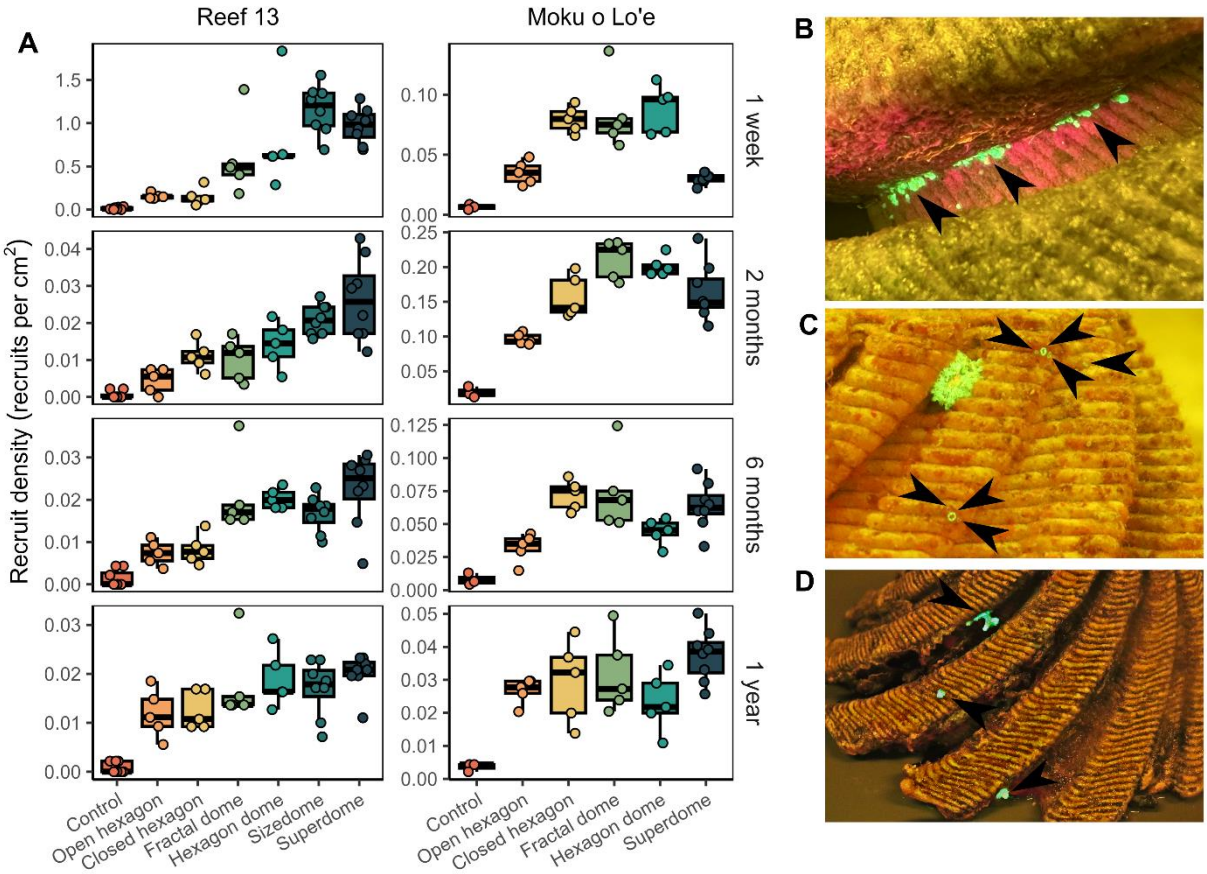

Figure 2: Coral larvae settlement and survival on different settlement modules. (A) Recruit densities (recruits per cm^2) on the seven different designs (control, open hexagon, closed hexagon, fractal dome, hexagon dome, sizedome, and superdome) at the two study locations: patch reef 13 and Moku o Lo‘e after one week, two months, six months, and one year. Data are displayed as box-and-whisker plots with raw data points; lines indicate medians,

boxes indicate the first and third quartile, and whiskers indicate ± 1.5 IQR. (B) *M. capitata* recruits on superdome design from reef 13 after one week. Recruits were mainly found in the corner of the cryptic edge and the inside of spiral domes. (C) *M. capitata* recruits on superdome design from reef 13 after two months. (C) *Pocillopora* sp. recruits on superdome design from Moku o Loʻe after one year. Arrows indicate recruits (fluorescent green), highlighted using blue lights and photographed through a yellow filter.

2.2 Recess properties of settlement locations of coral recruits

The properties of the recesses where coral recruits were found were analyzed in detail on the high performing superdome modules at reef 13 (Figure 3A, i.e., depth, width, light levels, and positions within the recess). The total number of recruits differed between the recess depths (Figure 3B, Wilcoxon tests $p < 0.05$, Table S4). Specifically, significantly more recruits settled in recesses with depths of 2, 3, and 4 cm than with a depth of 1 cm (depth measured at the bottom of the module). Initially, most recruits were found in recesses with a depth of 3 cm. Long-term survival was highest in recesses of 4 cm depth. Recruit densities, standardized to the surface area of the respective recesses, showed the same patterns, yet did not yield significant differences between recess depths (Wilcoxon tests $p \geq 0.05$, Table S4).

Overall, most recruits were found at an average recess width of 1.45 ± 0.62 cm (Figure 3C). Specifically, coral larvae settled primarily in recess areas with 1.40 ± 0.64 cm width at depths of 1.91 ± 0.82 cm, (Figure 4, Figure S2B, Table S5). Long-term survival shifted towards larger recess sizes and was highest in recess areas with widths of 1.52 ± 0.63 cm and depths of 1.74 ± 0.79 cm. Relative light levels (based on a light level of ~200 µmol m^{-2} s^{-1} PAR at the top of the dome) in which coral larvae settled were rather low and coral recruits were found in areas with light levels of 51.8 ± 48.2 µmol m^{-2} s^{-1} PAR (Figure 3D, Figure S3). Long-term survival revealed a larger distribution across light levels and recruits were mainly found in slightly brighter areas with 59.9 ± 48.2 µmol m^{-2} s^{-1} PAR.

Further, the total number of recruits differed between the positions (cryptic edge, inside, exposed edge, and outside; Figure 3D, Wilcoxon tests $p < 0.05$, Table S6). Independent of recess depth, most recruits were found in the inside corner of the cryptic edge of the recess (Figure 2B and 3E). In contrast, recruits were rarely found on the exposed edge or the outside of the recess. The same patterns were observed for recruit densities, standardized to the area of the respective recess sides (Wilcoxon tests $p < 0.05$, Table S6).

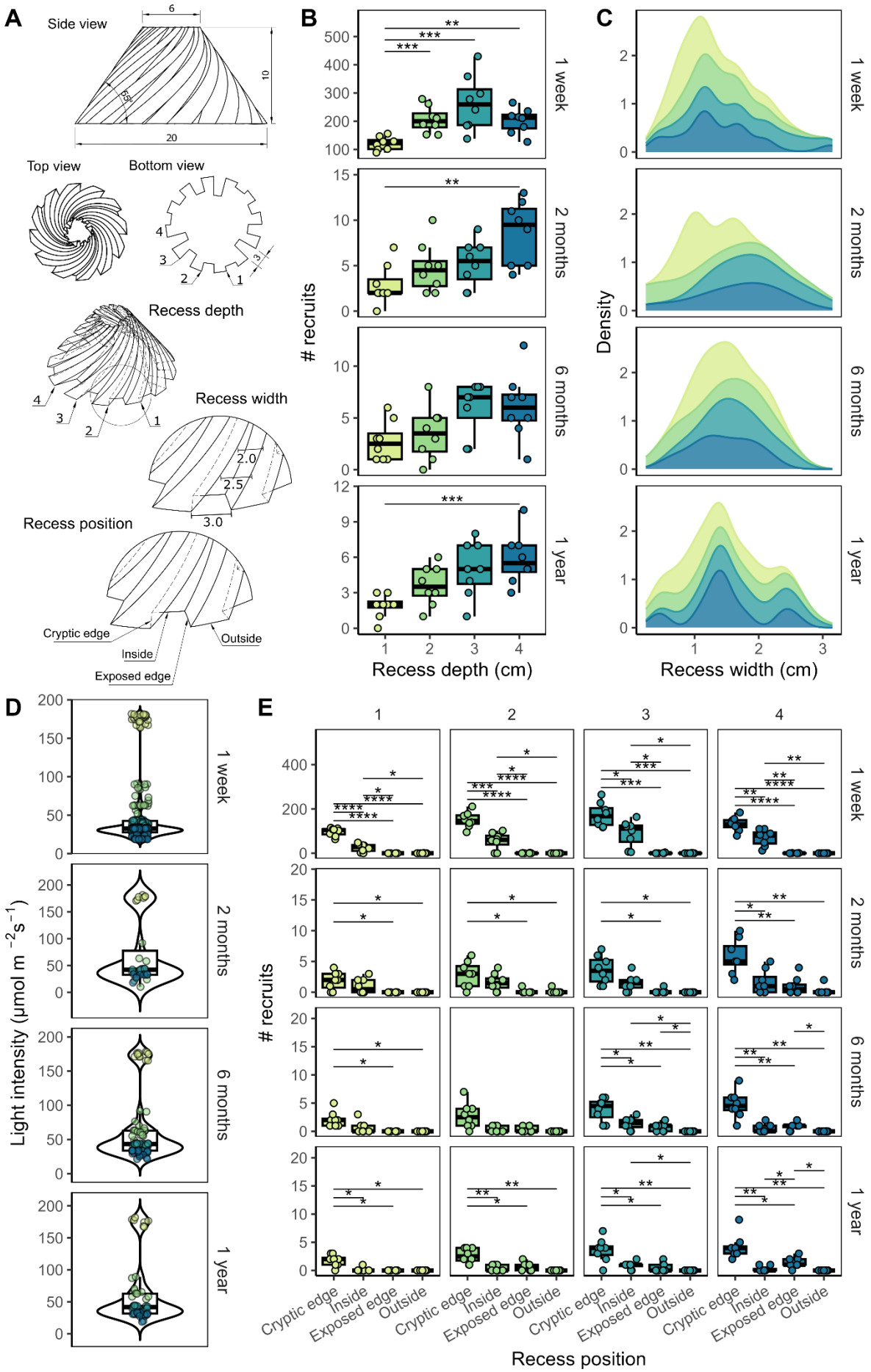
A
Side view
Top view
Bottom view
Recess depth
Recess width
Recess position
Cryptic edge
Inside
Exposed edge
Outside
B
recruits
1 week
2 months
6 months
1 year
Recess depth (cm)
C
Density
Recess width (cm)
D
Light intensity (µmol m⁻²s⁻¹)
E
recruits
Recess position

Figure 3: Recess properties of the superdome modules. Recess properties (recess depth, recess width, light levels, and positions within the recess) of the superdome module affecting coral settlement and survival were compared at reef 13 after one week, two months, six months, and one year. Colors indicate the four recess depths (1, 2, 3, and 4 cm depth, measured at the bottom of the module). (A) Detailed drawing of superdome design, basic dimensions of the settlement modules (diameter, height, angles, unit: cm) and the recess properties studied. (B) Total number of recruits in different recess depths (1, 2, 3, and 4 cm). Data are displayed as box-and-whisker plots with raw data points; lines indicate medians, boxes indicate the first and third quartile, and whiskers indicate ± 1.5 IQR. Asterisks indicate levels of statistical significance, derived from Wilcoxon tests followed by holm-adjustment for multiple testing: * $p \leq 0.05$, ** $p \leq 0.01$, ***$p \leq 0.001$. (C) Recess widths where recruits were found on a subset of superdomes. Data are displayed as smoothed density estimates, stacked from the different recess depths. (D) Light levels (µmol m^{-2} s^{-1}, PAR) at which recruits were found on a subset of superdomes. Data are displayed as violin plots with inset box-and-whisker plots and raw data points. (E) Total number of recruits at the different positions within the recesses (CE: cryptic edge, I: inside, EE: exposed edge, O: outside), split by recess depths (1, 2, 3, and 4 cm). Data are displayed as box-and-whisker plots. Asterisks indicate levels of statistical significance as above.

2.3 Recruit growth and genera found on settlement modules

After one year, coral recruits had grown to a diameter of 3.40 ± 1.91 mm (1–11 mm, min–max here and in the following) on superdome settlement modules at reef 13 and 2.89 ± 1.63 mm (1–12 mm) at Moku o Lo‘e (Table S7). This translated to planar surface areas of 11.40 ± 12.4 mm^2 (0.79– 55 mm^2) on superdomes at reef 13 and 8.38 ± 11.50 mm^2 (0.79–104 mm^2) at Moku o Lo‘e. The volume of coral recruits was estimated to be 29.5 ± 47.8 cm^3 (0.79–220 cm^3) at reef 13 and 23.7 ± 83.2 cm^3 (0.79–933 cm^3) at Moku o Lo‘e. Recruit sizes on superdomes did not show a clear trend for being larger or smaller than those on control domes (Wilcoxon tests, Table S8).

We identified coral recruits of the genera *Montipora*, *Pocillopora*, *Leptastrea*, and *Porites* on the settlement modules (Figure 2B–D). However, coral genera could only be assigned to a fraction of the recruits (~5%, mainly fast-growing *Pocillopora* spp.), as most recruits were too small to be confidently identified. Given this bias, coral genera were not further evaluated. We noted that the initial recruitment was dominated by *Montipora capitata* at reef 13, later followed by additional recruitment by other species, such as *Pocillopora* spp. (observational). At Moku o Lo‘e, recruitment was dominated by *Pocillopora* spp. and *Leptastrea purpurea*, independent of time.

2.4 Coral settlement and survival under different flow regimes

In a separate tank experiment, we compared the effects of three different flow regimes (no, low, and high flow; flow speed of 0, 10, and 15 cm s^{-1}, respectively) on settlement and survival rates of *M. capitata* on coral settlement modules of the superdome and control design. Recruit densities on superdomes increased significantly with higher flow conditions one week after spawning (Linear model, $p = 0.0006$, $R^2 = 0.433$). Specifically, recruit densities were

significantly higher in the ‘medium’ and the ‘high flow’ treatments compared to the ‘no flow’ treatment (Figure 4, Wilcoxon test, p = 0.0410 and p = 0.0110, respectively). Flow had no impact on recruit densities on superdomes after two months or six months. Recruit densities on control domes were not affected initially during settlement but were higher on domes from the ‘high flow’ treatment after two months (Kruskal test, p = 0.0340, Table S9, Figure S4).

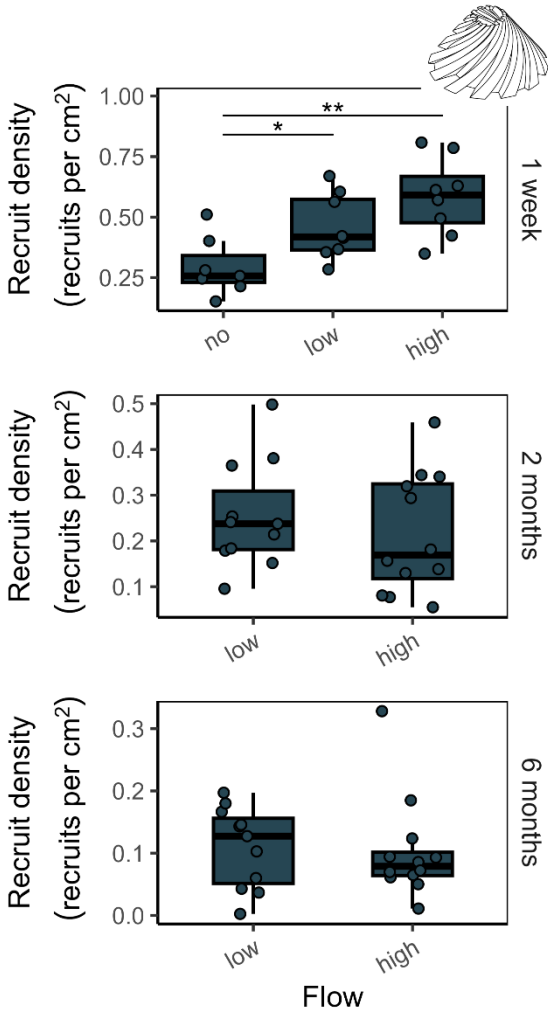

Figure 4: Coral settlement and survival on superdome modules under different flow conditions. Recruit densities (recruits per cm^2) were assessed on the domes in the experimental tanks after one week, two months, and six months. Settlement was studied under three different flow regimes (no flow, low flow, and high flow) after one week. Survival was studied under two different flow regimes (low flow and high flow) after two months and six months. Data are displayed as box-and-whisker plots with raw data points; lines indicate medians, boxes indicate the first and third quartile, and whiskers indicate ± 1.5 IQR. Significant differences are marked with

asterisks, defined as $p < 0.001$ (***), $p < 0.01$ (**), and $p < 0.05$ (*), and derived from Wilcoxon tests followed by holm-adjustment for multiple testing (one week) and Kruskal test (two months and six months).

3 Discussion

3.1 Spiral designs promote settlement and survival of coral recruits

In this study we developed novel designs that increase coral settlement by 80-fold, and post-settlement survival by 20–50-fold, when compared with controls. These results confirm that spiral recesses, as opposed to vertical and horizontal recesses (Schiettekatte et al, in prep), provide a suitable settlement substrate and also sheltered space for survival of the recruits, similar to the micro-scale complexity of benthic substrata (in the scale of 1–10 mm) in reefs (Brandl et al., 2014; Doropoulos et al., 2016; Edmunds et al., 2004). Notably, our settlement modules revealed also dramatically higher densities of recruits (on average 0.03 recruits per cm^2 on a superdome after one year ≙ 300 recruits per m^2) than what can be found on natural substrates in Hawai‘i (1–2 recruits per m^2, (Brown, 2004)). In comparison, settlement on control domes was much lower, indicating that the flat surface presents a less attractive settlement substrate, which is more exposed to external impacts, such as grazing and competition with benthic algae (Doropoulos et al., 2016). Modules with holes and pockets (open and closed hexagon) revealed lower settlement than modules with recesses, yet higher long-term survival rates. Reasons for these differences might be the higher light levels in these spaces (compare Figure S3), and the lower presence of sessile invertebrates and algae competing for space with the coral recruits (Chadwick and Morrow, 2011). Also, holes may allow for better water circulation, which is crucial for gas exchange, nutrient, and food supply (Mass et al., 2010; Sebens et al., 1997), while recesses may have more restricted water flow. Thus, future design iterations might incorporate recesses providing higher light levels and increased flow.

Although the overall trends between the designs were mostly maintained over time, strong differences in the total numbers of recruits were observed. The initially extremely high recruit numbers (up to > 1000 recruits per settlement module) were substantially reduced through post-settlement mortality. These early-life bottlenecks are inherently part of the life history strategy of spawning corals, following a Type III survivorship curve where mortality is highest immediately after settlement (Gosselin and Qian, 1997; Martinez and Abelson, 2013; Nozawa and Harrison, 2008). Future developments can include mitigation methods improving post-settlement mortality. For example, by pre-seeding settlement modules with CCA to prevent the growth of stronger competitors such as fleshy algae (Vermeij et al., 2011).

Additionally, we observed differences between the two field study locations that converged over time. At patch reef 13, the total number of recruits per module was much higher. There, settlement modules were exposed to a medium flow environment located at the channel of Kāneʻohe Bay, promoting a high availability of coral larvae in the water column during spawning. The initial recruitment was dominated by *Montipora capitata*, followed later by additional recruitment by other species, such as *Pocillopora* spp. This presents an example of a high seeding event after the mass spawning of *M. capitata*, leading to an initial high recruitment followed by high post-settlement mortality, but maintained trends between shapes over time. In contrast, initial recruitment at Moku o Loʻe was comparatively low. There, settlement modules were exposed to a more shallow water environment, with higher daily temperature fluctuations (compare Figure S5) and lower water flow. The recruitment was dominated by more hardy, brooding coral species, such as *Pocillopora* spp. and *Leptastrea purpurea* (Bahr et al., 2016), which release larvae in repetitive spawning events during the summer months. This presents an example of a successive seeding event, with low initial but continuous recruitment over time and fluctuations in mortality, yet, similarly maintained trends between shapes.

3.2 Recess properties affect settlement and survival of coral recruits

Positions at which recruits have settled within the recess were measured to identify preferred recess dimensions. We found recess widths of ~15 mm with depths of ~17 mm as recess dimensions preferred for coral settlement at reef 13 in this study. Light levels in these areas were comparably low ~56 µmol m^{-2} s^{-1}, corresponding to ~28% of the incoming light on top of the module. Coral larvae prefer moderate light exposure, avoiding overly shaded or extremely bright locations. Similar recess sizes and low light levels have been observed to be beneficial for the survival of coral recruits (Doropoulos et al., 2016; Rahnke et al., 2022; Ramsby et al., 2024). However, the response of recruits to light intensity can be mixed, with other studies showing evidence of faster growth or higher survival under high light intensity (Hancock et al., 2021; Koch et al., 2022). Over time, initial settlement and survival only differed in the mm scale, shifting from slightly smaller recess areas during initial settlement towards larger recess sizes for long-term survival. Similarly, coral recruits were found to have settled in areas with lower light levels of ~ 50 µmol m^{-2} s^{-1}, but survival was higher under higher light levels of ~60 µmol m^{-2} s^{-1}. This is likely due to the presence of competitors such as sessile invertebrates (i.e., sponges or oysters) in larger and darker areas of the recesses (Chadwick and Morrow, 2011). The settlement preferences of coral larvae are a trade-off between light-capture, potential to be overgrown by competitive algae in early life stages and the avoidance of grazing (Doropoulos et al., 2016). Thus, a successful strategy is to settle in recesses near underside edges where they are protected from predation, grazing and strong physical impacts but still receive sufficient light to grow, and from which they then grow out into brighter, more open spaces (Cruz and Harrison, 2017). This corresponds well with the positions at which we found recruits inside the recess: independent of the depth of the recess, most recruits were found in the inside corner of the cryptic edge of the recesses, which provide shelter and lower exposure. In contrast, recruits were rarely found on the exposed edge and the outside of the recess, where they might be more exposed to predation, high light, and competition with fleshy algae.

3.3 Coral settlement on spiral modules is increased under higher flow

We found that settlement on superdomes was significantly increased under higher flow conditions. This suggests that settlement inside the recesses can be strongly influenced by hydrodynamics. Hydrodynamics play an important role in the distribution and settlement of coral larvae, potentially trapping coral larvae through the formation of turbulent flow and micro-eddies (Gysbers et al., 2024; Reidenbach et al., 2009). The millimeter-scale topography of ridges, formed through the layered printing of the clay, might have additionally aid coral settlement in the sheltered areas of the complex modules, by increasing areas of recirculation, directing larvae toward the structure and increasing the window of time for the larvae to settle (Levenstein et al., 2022a). However, given the low levels of settlement on control modules and the outside surfaces of other modules, the small-scale topography alone did not greatly enhance settlement and may only be beneficial in the presence of meso-scale features such as recesses. Regarding survival, flow had no impact on recruits on superdomes, where recruits are rather sheltered inside the recesses. In contrast, on control domes, survival was higher under higher flow, which is in accordance with previous studies that found positive impacts of water flow for the survival of coral recruits (Hancock et al., 2021; Rahnke et al., 2022). On the control domes, recruits are more directly exposed to flow conditions, and the positive effects of increased flow on coral physiology, such as gas exchange, nutrient supply, and food availability, become more evident (Mass et al., 2010; Sebens et al., 1997). These results suggest that flow has an important impact on settlement on the meso- to micro-scale (m to mm range). In this study, we tested a rather narrow flow range (i.e., 0, 10 and 15 cm s^{-1}), corresponding to average conditions in coral reefs (Roik et al., 2016). Higher flow speeds, occurring in high-flow environments of coral reefs, with peak speeds of 30–40 cm s^{-1} (Lentz et al., 2017), might have a negative impact on settlement (Koehl, 2007), resulting in a hump-shape relationship between flow and coral recruitment, and need to be further explored.

3.4 Conclusions

We demonstrate that artificial structures with spiral recesses can dramatically promote coral settlement and survival. We show that modules should be designed with recesses balancing moderate light exposure, shelter from grazing and competition, and identify suitable recess dimensions and light levels. Further, our results highlight that hydrodynamics play a vital role in coral settlement on the meso- to micro-scale, which should be considered. Future design iterations and biological interventions should target post-settlement survival; for example, by incorporating recesses providing higher light and flow levels or interventions decreasing benthic competitors. We conclude that spiral recess designs, which can be easily integrated into local restoration projects or cast into large-scale coastal protection structures, can greatly enhance coral restoration efforts, allowing for the development of more effective, scalable, and self-sustaining artificial or hybrid reefs, supporting the recovery of degraded coral reef ecosystems.

4 Material and Methods

4.1 Design and production of larvae settlement modules

Larvae settlement modules were designed as conical shapes with different structural features in seven designs (Figure 1A). Modules all shared the same base dimensions and had a diameter of 20 cm and a height of 10 cm. Two designs included holes (‘open hexagon’) or pockets (‘closed hexagon’) of different sizes (i.e., 10x12 mm, 16x24 mm, and 26x36 mm diameter). Four designs included various kinds of spiral recesses (‘hexagon dome’, ‘fractal dome’, ‘sizedome’, and ‘superdome’), which decreased in size towards the top and inclined at a constant angle of 45° around the module. The ‘hexagon’ shape held six open recesses of 24–5 mm depth and 48–9 mm width (bottom to top) framed by wide-angled sidewalls (120°). The ‘fractal dome’ shape was designed to provide three exposed, sheltered, and cryptic recesses, each, of 17–3 mm depth and 32–5 mm width (bottom to top), with the same wide-angled walls (120°) as the hexagon

control. The ‘sizedome’ held ten narrow recesses of 20–5 mm depth and 31-8 mm width (bottom to top), framed by narrow-angled sidewalls (100°). The ‘superdome’ held 12 narrow recesses of four different depths (10–2 mm, 20–5 mm, 30–8 mm, and 40–11 mm, referring to as depths 1, 2, 3, and 4 respectively), all with 30–6 mm width (bottom to top), framed by narrow-angled sidewalls (98°). All modules were designed as hollow cones with an open hole to ease production, handling, and attachment. As a control shape, a flat cone sharing the same base dimensions was created.

All shapes were designed in Blender v3.4. Their planar circular base design was replicated in 200 lines, stacked on top of each other, scaled to 30% of the original size, and rotated by 60 degrees (from bottom to top) so that a conical shape with equally inclining angles of the recesses was created by bridging the edge loops of the lines. For two designs cones were mirrored and combined to create holes (from six basic hexagon shapes) and pockets (from the hexagon design, a circular shape with recesses). The resulting meshes were exported as .stl files and converted to a 3D print path using the slicing software Simplify3D. Modules were printed with the Delta Wasp 40100 3D printer (Wasp, Italy) in clay (mid-fire pottery clay, Soldate 60, Aardvark Clay and Supplies, United States). The clay feed material was prepared using a pugmill (Pugmill/Mixer NVS-07, Nidec, Japan). Modules were printed in 110 % of the target size to account for the shrinking of the material, as hollow conical shapes (setting: spiral vase mode). The material was extruded with a 4 mm diameter nozzle, which created a microstructure of horizontal layers on all modules (Figure 1B). Printed modules were air-dried in a stable, airconditioned environment for 5–10 days until they were bone-dry and then fired in a kiln (Jupiter Sectional Kiln, L&L Kilns, United States) at 2030 °C, held for 2 h (setting: cone 8).

4.2 Field experiment

4.2.1 Experimental design and deployment

Larvae settlement modules of the seven different shapes were deployed at two locations in the field (Reef 13 and Moku o Loʻe) in proximity to patch reefs in Kāneʻohe Bay, Oʻahu, Hawaiʻi (Fig. 1E–G, n ≥ 5 per shape and location, see Table S10 for detailed number of replicates). Reef 13 is a rather exposed patch reef with medium flow, located at the channel of Kāneʻohe Bay. The site at Moku o Loʻe is a more sheltered, shallow water environment, with higher daily temperature fluctuations (Figure S5) and lower water flow. The modules were attached to tables one week before coral spawning to allow for a biofilm to form on the surface. A temperature logger (HOBO Pendant MX2201 Water Temperature Data Logger, HOBO, USA) was attached to each table, logging in intervals of 5 min (Figure S5).

4.3 Tank water flow experiment

4.3.1 Experimental design and tank setup

To study the impact of different flow speeds on coral settlement and survival, we performed a tank experiment. We first assessed the effects of flow on larvae settlement. For this, larvae settlement modules of superdome and control shapes were seeded with coral larvae under three different flow speeds: no, low, and high (0, 10, and 15 cm s^{-1}, respectively). The experiment was conducted in three 230 L tanks (180 cm x 56 cm x 23 cm), with a different flow speed treatment established in each tank. The tanks were equipped with two wavemaker pumps each (Nero 7, Aquaillumination, USA), positioned at opposite short sites. The flow was established as an oscillating wave (from full intensity to no intensity) with an interval of 10 seconds, resulting in 0, 10, and 15 cm s^{-1}, respectively. Larvae settlement modules of superdome and control shapes (n = 8 and n = 6 per treatment, respectively) were placed in tanks at equal flow (10 cm s^{-1}) one week before the seeding to allow for biofilm formation on the surface. Then, flow speeds were adjusted to the treatment conditions, and larvae were seeded (for details on

collection and seeding, see sections 2.3.2 and 2.3.3). Recruit numbers were assessed one week after seeding.

We then assessed the impacts of flow on recruit survival. For this, the seeded settlement modules were exposed to two different flow speeds: low flow and high flow (10 and 15 cm s^{-1}, respectively). The seeded settlement modules were distributed equally in two tanks (n = 12 superdomes and n = 9 control domes), originating from the three seeding treatments. Recruit survival was monitored 2 and six months after seeding. Coral growth was assessed six months after seeding.

4.3.2 Collection and rearing of coral larvae

Coral larvae were collected during the mass spawning of *M. capitata* on June 18, 2023, from near Reef 11 in Kāneʻohe Bay, Oʻahu, Hawaiʻi following established best practices (Hancock et al., 2021). Larvae were returned to HIMB, fertilized and reared over 4 days to settlement competency at ambient temperatures in 1 µm filtered seawater following established best practices (Rahnke et al., 2022).

4.3.3 Seeding of coral settlement modules in tanks

Coral larvae were added to the tanks 3 days after spawning. Specifically, 3 l larvae in suspension (concentration: 10.2 ± 1.4 larvae per ml, n = 3 measurements) were scooped out of a stirred, homogenized larvae-rearing bucket and added to each tank. Larvae were added in the afternoon (5:30 pm) and left in the tanks for 24 h to allow for settlement on the modules. Water inflow was turned off during the first 18 h to facilitate an undisturbed water flow within the tanks. For the following 6 h, the tanks were equipped with 65 µm mesh sieves at the outflow to reestablish water inflow during the daytime but retain larvae within the tank. Sieves were gently rinsed every hour using a pipette to bring adhering larvae back in suspension. To ensure that the pumps of the flow treatments had no negative impact on the survival of the coral larvae, the number of

dead larvae was assessed 18 h after seeding. We found no significant difference between the three tanks (Pairwise Wilcoxon test, $p > 0.005$).

4.3.4 Water parameters and tank maintenance

The tank experiment was conducted at the Hawai‘i Institute of Marine Biology (HIMB). The tanks were connected to a permanent saltwater supply from the reef and were provided with filtered saltwater (Pentair Triton II, TR60 sand filter, Pentair Aquatic Eco-Systems Inc., USA). Water parameters of the tank system were measured every other week using a multiparameter photometer (H197115 Hanna Labs Marine Master Multiparameter Photometer, Hanna Instruments, USA) in alternating tanks (salinity: 33.9 ± 0.4, magnesium: 1381 ± 105 ppm, phosphate: 0.2 ± 0.1 ppm, nitrate: 0.33 ± 0.35 ppm, and nitrite: 1 ± 3 ppb). Additional water parameters were measured at the beginning and the end of the experiment (calcium: 476 ± 25 ppm, ammonia: 0.03 ± 0.02 ppm, alkalinity: 6.4 ± 0.1 dKH, and pH: 7.8 ± 0). Temperature was logged with HOBO data loggers positioned in each tank, logging in intervals of 5 min (Figure S6). To avoid tank effects, modules and flow conditions were switched between tanks every other week.

4.4 Monitoring of larvae settlement and recruit survival

Larvae settlement and recruit survival were monitored in both field and tank experiments. Larvae settlement was assessed one week after spawning of *M. capitata* (06.07.2023), and early-life survival 2 and six months (30.08.2023 and 15.01.2024, respectively) after seeding. In the field, an additional timepoint was added at approximately one year after settlement (23.05.2024), before the next anticipated spawning of *M. capitata*.

4.4.1 Assessment of total numbers and densities

The total numbers of recruits were assessed on all settlement modules. For size- and superdomes, the numbers per recess and recess part were additionally assessed (outside, exposed edge, inside, cryptic edge, see Figure 3A). Coral recruits were detected through

fluorescence, using underwater blue lights (Sola Nightsea Blue Light, Light & Motion, USA) and blue-light-blocking glasses (Amazon Basics, Amazon USA). Total numbers were converted to recruit densities by standardizing to the surface area of the module. For size- and superdomes, numbers in recess parts were standardized to the respective area of the recess parts. To determine surface areas of the modules, one dome per design was 3D scanned using the HandySCAN 3D with VX elements (Creaform, Canada) at a resolution of 0.5 mm.

4.4.2 Documentation and modeling of recruit position and recess properties

Recruit position was assessed in a subset of recruits on settlement modules of the superdome shape in the field experiment at reef 13. The recess width at locations with recruits were documented in three superdomes: four recesses each at one week, twelve recesses each at two months, six months, and one year – compensating for the initial high post-settlement mortality. The recess depth and light level at which the recruit was found were modeled as follows. Recess widths and depths were assessed at five positions for each recess depth on two printed and fired superdomes: the base of the module, 2 cm height, 4 cm height, 6 cm height, and the top of the module. The relationship between width and depth was determined for each recess (linear model, Figure S2A). The superdome modules provided a recess width-depth space of 0.9–1.3 cm width and 0.7–1.3 cm depth (Figure S2B). Light levels were measured (LI-250A Light meter, LI-COR, USA) at four positions inside the recesses, excluding the top of the module: the base of the module, 2 cm height, 4 cm height, and 6 cm height. For this, the modules were positioned under an artificial light source with ~200 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR) at the top of the modules to allow for an equal comparison under moderate light exposure, comparable to levels found at the reef. The relationship between light levels and recess width was determined for each recess depth (1, 2, 3, and 4 cm) using general additive models (GAMs) with spline-based smoothed regressions in the gam function of the R package mgcv (Wood, 2017). These were then used to predict light levels at the positions where the recruits were found. Additionally, light levels of other shapes were measured at potential

settlement areas, i.e., inside the recesses at the same heights (hexagon dome, fractal dome, and sizedome) or inside the holes (open and closed hexagon), respectively. For the control dome, light levels were assessed at the same heights at three positions around the module.

4.4.3 Measurement of coral growth, biomass, and genus

Coral growth and genus were assessed in larvae settlement modules of control and superdome shape one year after spawning at both locations the field experiment in the same subset assessed for recruit position. For this, coral length and width were measured, and surface area was calculated assuming an oval shape. Coral length, width, and recruit height were used to calculate the coral volume, approximated as a cylinder. The coral genus was assigned visually after one year, where possible.

4.5 Quantification of recess properties

4.6 Statistical analyses

We performed all data processing and analyses in the R statistical environment (v.4.3.1; R Core Team, 2023). Differences in recruit densities between the different shapes (control, open hexagon, closed hexagon, fractal dome, hexagon dome, sizedome, and superdome) after one week, two months, six months, and one year were derived from Wilcoxon tests followed by holm-adjustment for multiple testing. Differences in recruit numbers (total numbers summarized from three replicate recesses of the same depth on one dome) and recruit densities (number of recruits per cm^2) between the different recess depths (1, 2, 3, and 4 cm) and between the different positions within the recesses (CE: cryptic edge, I: inside, EE: exposed edge, O: outside), split by recess depths (1, 2, 3, and 4 cm) after one week, two months, six months, and one year were derived accordingly. Similarly, differences in coral size and biomass parameters (diameter per recruit, planar surface area per recruit, volume per recruit, total planar surface area per dome, and total volume per dome) on control domes and superdomes at reef 13 and Moku o Loʻe one year were assessed.

The overall impact of flow on coral settlement (recruit density) was assessed using a linear model with flow as a continuous variable, separately for each dome type. Differences in recruit densities between the different flow treatments (no, low, and high) on superdomes and control domes after one week, two months, six months, and one year were derived from Wilcoxon tests followed by holm-adjustment for multiple testing. One dome was excluded from the analysis of the tank experiment (initially in the no flow treatment, later in the low flow treatment) as it was a sizedome, which was included accidentally instead of a superdome.

4.7 Data Availability

Data and scripts will be made available from https://github.com/JessiReichert/Mesoscale_complexity. The designs are included in the patent application no.: PCT/US2024/051295.

5 References

Bahr, K.D., Jokiel, P.L., Rodgers, K.S., 2016. Relative sensitivity of five Hawaiian coral species to high temperature under high-pCO2 conditions. Coral Reefs 35, 729–738. https://doi.org/10.1007/s00338-016-1405-4

Berman, O., Weizman, M., Oren, A., Neri, R., Parnas, H., Shashar, N., Tarazi, E., 2023. Design and application of a novel 3D printing method for bio-inspired artificial reefs. Ecol Eng 188. https://doi.org/10.1016/j.ecoleng.2023.106892

Boström-Einarsson, L., Babcock, R.C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S.C.A., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P.J., Vardi, T., McLeod, I.M., 2020. Coral restoration – A systematic review of current methods, successes, failures and future directions. PLoS One 15. https://doi.org/10.1371/journal.pone.0226631

Brandl, S.J., Hoey, A.S., Bellwood, D.R., 2014. Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. Coral Reefs 33, 421–430. https://doi.org/10.1007/s00338-013-1110-5

Brown, E.K., 2004. Reef coral populations: Spatial and temporal differences observed on six reefs off west Maui. University of Hawai‘i at Manoa.

Chadwick, N.E., Morrow, K.M., 2011. Competition among sessile organisms on coral reefs, in: Coral Reefs: An Ecosystem in Transition. Springer Netherlands, pp. 347–371. https://doi.org/10.1007/978-94-007-0114-4_20

Chamberland, V.F., Petersen, D., Guest, J.R., Petersen, U., Brittsan, M., Vermeij, M.J.A., 2017. New Seeding Approach Reduces Costs and Time to Outplant Sexually Propagated Corals for Reef Restoration. Sci Rep 7, 18076. https://doi.org/10.1038/s41598-017-17555-z

Cruz, D.W.D., Harrison, P.L., 2017. Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. Sci Rep 7. https://doi.org/10.1038/s41598-017-14546-y

Doropoulos, C., Roff, G., Bozec, Y.M., Zupan, M., Werminghausen, J., Mumby, P.J., 2016. Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecol Monogr 86, 20–44. https://doi.org/10.1890/15-0668.1

Edmunds, P., Bruno, J., Carlon, D., 2004. Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. Mar Ecol Prog Ser 278, 115–124. https://doi.org/10.3354/meps278115

Edmunds, P.J., 2023. Coral recruitment: patterns and processes determining the dynamics of coral populations. Biological Reviews 98, 1862–1886. https://doi.org/10.1111/brv.12987

Gómez-Lemos, L.A., Doropoulos, C., Bayraktarov, E., Diaz-Pulido, G., 2018. Coralline algal metabolites induce settlement and mediate the inductive effect of epiphytic microbes on coral larvae. Sci Rep 8. https://doi.org/10.1038/s41598-018-35206-9

Gosselin, L.A., Qian, P.-Y., 1997. Juvenile mortality in benthic marine invertebrates, MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser.

Gysbers, D., Levenstein, M.A., Juarez, G., 2024. The effect of surface topography on benthic boundary layer flow: implications for marine larval transport and settlement. https://doi.org/https://doi.org/10.48550/arXiv.2401.17216

Hancock, J.R., Barrows, A.R., Roome, T.C., Huffmyer, A.S., Matsuda, S.B., Munk, N.J., Rahnke, S.A., Drury, C., 2021. Coral husbandry for ocean futures: Leveraging abiotic factors to increase survivorship, growth, and resilience in juvenile Montipora capitata. Mar Ecol Prog Ser 657, 123–133. https://doi.org/10.3354/meps13534

Harrington, L., Fabricius, K., De'ath, G., Negri, A., 2004. Recognition and selection of settlement substrata dertermine post-settlement survival in corals. Ecology 85, 3428–3437. https://doi.org/10.1890/04-0298

Harrison, P.L., dela Cruz, D.W., Cameron, K.A., Cabaitan, P.C., 2021. Increased Coral Larval Supply Enhances Recruitment for Coral and Fish Habitat Restoration. Front Mar Sci 8. https://doi.org/10.3389/fmars.2021.750210

Hata, T., Madin, J.S., Cumbo, V.R., Denny, M., Figueiredo, J., Harii, S., Thomas, C.J., Baird, A.H., 2017. Coral larvae are poor swimmers and require fine-scale reef structure to settle. Sci Rep 7. https://doi.org/10.1038/s41598-017-02402-y

Hein, M.Y., Willis, B.L., Beeden, R., Birtles, A., 2017. The need for broader ecological and socioeconomic tools to evaluate the effectiveness of coral restoration programs. Restor Ecol. https://doi.org/10.1111/rec.12580

Higgins, E., Metaxas, A., Scheibling, R.E., 2022. A systematic review of artificial reefs as platforms for coral reef research and conservation. PLoS One. https://doi.org/10.1371/journal.pone.0261964

Jorissen, H., Galand, P.E., Bonnard, I., Meiling, S., Raviglione, D., Meistertzheim, A.L., Hédouin, L., Banaigs, B., Payri, C.E., Nugues, M.M., 2021. Coral larval settlement preferences linked to crustose coralline algae with distinct chemical and microbial signatures. Sci Rep 11. https://doi.org/10.1038/s41598-021-94096-6

Koch, H.R., Matthews, B., Leto, C., Engelsma, C., Bartels, E., 2022. Assisted sexual reproduction of Acropora cervicornis for active restoration on Florida's Coral Reef. Front Mar Sci 9. https://doi.org/10.3389/fmars.2022.959520

Koehl, M.R.A., 2007. Mini review: Hydrodynamics of larval settlement into fouling communities. Biofouling. https://doi.org/10.1080/08927010701492250

Lentz, S.J., Davis, K.A., Churchill, J.H., DeCarlo, T.M., 2017. Coral reef drag coefficients - Water depth dependence. J Phys Oceanogr 47, 1061–1075. https://doi.org/10.1175/JPO-D-16-0248.1

Levenstein, M.A., Gysbers, D.J., Marhaver, K.L., Kattom, S., Tichy, L., Quinlan, Z., Tholen, H.M., Kelly, L.W., Vermeij, M.J.A., Wagoner Johnson, A.J., Juarez, G., 2022a. Millimeter-scale topography facilitates coral larval settlement in wave-driven oscillatory flow. PLoS One 17. https://doi.org/10.1371/journal.pone.0274088

Levenstein, M.A., Marhaver, K.L., Quinlan, Z.A., Tholen, H.M., Tichy, L., Yus, J., Lightcap, I., Wegley Kelly, L., Juarez, G., Vermeij, M.J.A., Wagoner Johnson, A.J., 2022b. Composite Substrates Reveal Inorganic Material Cues for Coral Larval Settlement. ACS Sustain Chem Eng 10, 3960–3971. https://doi.org/10.1021/acssuschemeng.1c08313

Levy, N., Berman, O., Yuval, M., Loya, Y., Treibitz, T., Tarazi, E., Levy, O., 2022. Emerging 3D technologies for future reformation of coral reefs: Enhancing biodiversity using biomimetic structures based on designs by nature. Science of The Total Environment 830, 154749. https://doi.org/10.1016/j.scitotenv.2022.154749

Lima, J.S., Zalmon, I.R., Love, M., 2019. Overview and trends of ecological and socioeconomic research on artificial reefs. Mar Environ Res. https://doi.org/10.1016/j.marenvres.2019.01.010

Loke, L.H.L., Ladle, R.J., Bouma, T.J., Todd, P.A., 2015. Creating complex habitats for restoration and reconciliation. Ecol Eng 77, 307–313. https://doi.org/10.1016/j.ecoleng.2015.01.037

Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., Darling, E.S., Diaz, M., Falster, D.S., Franklin, E.C., Gates, R.D., Harmer, A.M.T., Hoogenboom, M.O., Huang, D., Keith, S.A., Kosnik, M.A., Kuo, C.-Y., Lough, J.M.,

Lovelock, C.E., Luiz, O., Martinelli, J., Mizerek, T., Pandolfi, J.M., Pochon, X., Pratchett, M.S., Putnam, H.M., Roberts, T.E., Stat, M., Wallace, C.C., Widman, E., Baird, A.H., 2016. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci Data 3, 160017. https://doi.org/10.1038/sdata.2016.17

Martinez, S., Abelson, A., 2013. Coral recruitment: The critical role of early post-settlement survival. ICES Journal of Marine Science 70, 1294–1298. https://doi.org/10.1093/icesjms/fst035

Mass, T., Genin, A., Shavit, U., Grinstein, M., Tchernov, D., 2010. Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. Proceedings of the National Academy of Sciences 107, 2527–2531. https://doi.org/10.1073/pnas.0912348107

Nozawa, Y., Harrison, P.L., 2008. Temporal patterns of larval settlement and survivorship of two broadcast-spawning acroporid corals. Mar Biol 155, 347–351. https://doi.org/10.1007/s00227-008-1034-8

R Core Team, 2023. R: A language and environment for statistical computing [WWW Document]. URL http://www.r-project.org/

Rahnke, S.A., Hancock, J.R., Munk, N.J., Caruso, C., Drury, C., 2022. Optimizing sexual reproduction of Montipora capitata for restoration: effects of abiotic conditions and light acclimation on juvenile survival and growth. Mar Ecol Prog Ser 691, 41–54. https://doi.org/10.3354/meps14064

Ramsby, B.D., Emonnot, F., Flores, F., Schipper, S., Diaz-Pulido, G., Abdul Wahab, M.A., Severati, A., Negri, A.P., 2024. Low light intensity increased survival of coral spat in aquaculture. Coral Reefs 43, 627–640. https://doi.org/10.1007/s00338-024-02489-6

Randall, C.J., Negri, A.P., Quigley, K.M., Foster, T., Ricardo, G.F., Webster, N.S., Bay, L.K., Harrison, P.L., Babcock, R.C., Heyward, A.J., 2020. Sexual production of corals for reef restoration in the Anthropocene. Mar Ecol Prog Ser. https://doi.org/10.3354/MEPS13206

Reidenbach, M.A., Koseff, J.R., Koehl, M.A.R., 2009. Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wavedriven flow. Limnol Oceanogr 54, 318–330. https://doi.org/10.4319/lo.2009.54.1.0318

Roik, A., Röthig, T., Roder, C., Ziegler, M., Kremb, S.G., Voolstra, C.R., 2016. Year-long monitoring of physico-chemical and biological variables provide a comparative baseline of coral reef functioning in the central Red Sea. PLoS One 11. https://doi.org/10.1371/journal.pone.0163939

Sebens, K.P., Witting, J., Helmuth, B., 1997. Effects of water flow and branch spacing on particle capture by the reef coral Madracis mirabills (Duchassaing and Michelotti). J Exp Mar Biol Ecol 211, 1–28. https://doi.org/10.1016/S0022-0981(96)02636-6

Suggett, D.J., Van Oppen, M.J.H., 2022. Horizon scan of rapidly advancing coral restoration approaches for 21st century reef management. Emerg Top Life Sci. https://doi.org/10.1042/ETLS20210240

Suzuki, G., Okada, W., Yasutake, Y., Yamamoto, H., Tanita, I., Yamashita, H., Hayashibara, T., Komatsu, T., Kanyama, T., Inoue, M., Yamazaki, M., 2020. Enhancing coral larval supply and seedling production using a special bundle collection system “coral larval cradle” for large-scale coral restoration. Restor Ecol 28, 1172–1182. https://doi.org/10.1111/rec.13178

Tay, Y.C., Guest, J.R., Chou, L.M., Todd, P.A., 2011. Vertical distribution and settlement competencies in broadcast spawning coral larvae: Implications for dispersal models. J Exp Mar Biol Ecol 409, 324–330. https://doi.org/10.1016/j.jembe.2011.09.013

Vermeij, M.J.A., Dailer, M.L., Smith, C.M., 2011. Crustose coralline algae can suppress macroalgal growth and recruitment on hawaiian coral reefs. Mar Ecol Prog Ser 422, 1–7. https://doi.org/10.3354/meps08964

Whalan, S., Abdul Wahab, M.A., Sprungala, S., Poole, A.J., De Nys, R., 2015. Larval settlement: The role of surface topography for sessile coral reef invertebrates. PLoS One 10. https://doi.org/10.1371/journal.pone.0117675

Zayasu, Y., Suzuki, G., 2019. Comparisons of population density and genetic diversity in artificial and wild populations of an arborescent coral, Acropora yongei: implications for the efficacy of "artificial spawning hotspots." Restor Ecol 27, 440–446. https://doi.org/10.1111/rec.12857

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7 Author Contributions

JR, HJ, NMDS, and JSM conceived the ideas and designed the methodology. JR, HJ, CD, JH, CH, AN, and LR performed the experiment and collected the data. JR analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.