## Title

# Cylindrical, pylon-like structures with helix recesses enhance coral larval recruitment

## Authors

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## Keywords

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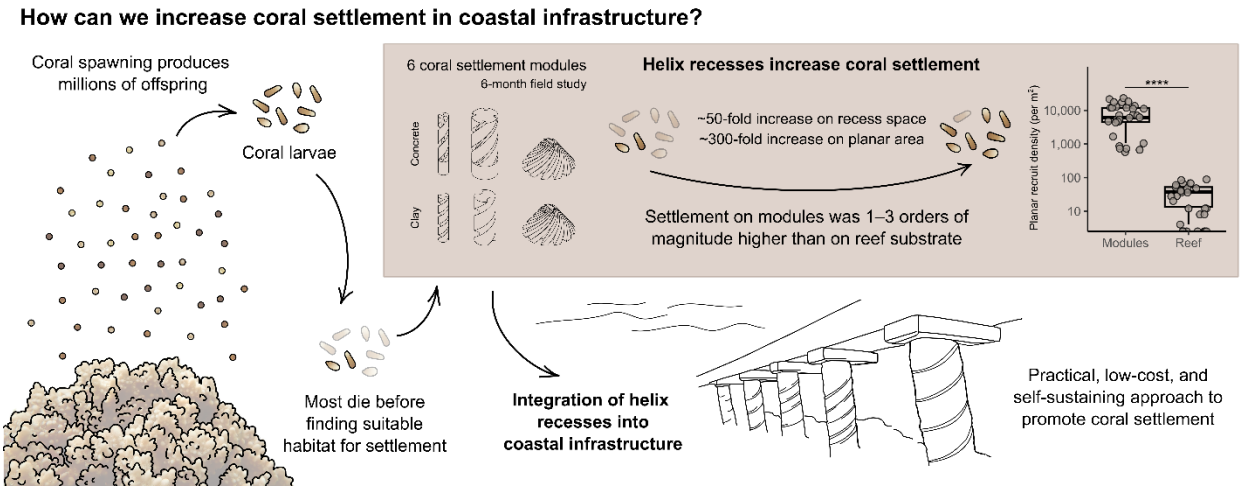
## Graphical abstract




## Abstract

The decline of coral reefs requires scalable restoration strategies that enhance natural recovery processes such as coral larval recruitment. Previous work has shown that 3D-printed clay domes with helix recesses significantly increase settlement and survival of coral recruits compared to control designs without recesses. To examine the broader applicability of these findings for engineering applications, we tested whether the helix microhabitat design could be transferred to space-efficient pylon-like, cylindrical geometries and evaluated its performance across different materials and fabrication methods (cast concrete vs. 3D-printed clay). In a field experiment in Kāneʻohe Bay, Hawaiʻi, coral recruitment was monitored over six months on four cylindrical rod types (varying in diameter and material) and two conical superdome modules, featuring recesses based on the previously optimized helix profile. Cylindrical rods had similar recruitment densities to those on superdome designs, indicating a successful transfer of the design. Most recruits settled inside the recesses across all structures, while outer surfaces consistently supported fewer recruits. Settlement was initially higher on concrete modules, but this difference disappeared over time. The large clay rods, which had wider recesses, maintained the highest recruit densities after six months, suggesting enhanced post-settlement survival. Compared to natural reefs, planar recruit densities on the structures were ~300 times higher. These results indicate that helix design is functionally robust across geometries and materials, with recess size influencing post-settlement outcomes. Cylindrical structures with integrated helix recesses represent a practical, low-cost method that can be implemented in coastal engineering to enhance coral settlement.

## 1. Introduction

Coral reefs are degrading worldwide due to the impacts of climate change and local stressors (Hughes et al., 2017). While lowering global carbon emissions is our best way to combat this trend globally, more effective and scalable restoration strategies are needed to address this trend locally (Edwards et al., 2024; Hughes et al., 2023). Scaling up restoration by utilizing the natural capacity of corals to generate millions of larvae through sexual reproduction presents a promising approach (Boström-Einarsson et al., 2020). The transition from planktonic larvae to settled polyps is a crucial bottleneck in the coral life cycle, as it is characterized by high mortality rates and is strongly reliant on the presence of suitable settlement habitats (Martinez and Abelson, 2013; Nozawa and Harrison, 2008). Designing artificial structures that provide optimal microhabitats for coral settlement can therefore significantly enhance recruitment and restoration success.

Coral larval settlement and survival depend on physical, chemical, and biological factors such as light, substrate properties, hydrodynamics, cues, predation, and competition. Light intensity and turbidity affect the photosynthesis of recruits, algal fouling, and shape the composition of CCA, green, and brown algae, which in turn impacts recruit survival (Ramsby et al., 2024). Coral larvae usually settle in cryptic, low-light habitats (<500 µmol photons $m^{-2}$ $d^{-1}$), yet survival is reduced under very low light (<100 µmol photons $m^{-2}$ $d^{-1}$), (Brunner et al., 2022). Water flow and hydrodynamics shape larval dispersal, transport, and settlement. Coral larvae, which are poor swimmers, often settle in millimeter-scale ridges on substrates, where microtopography creates microenvironments with reduced flow and support settlement (Hata et al., 2017; Levenstein et al., 2022a). Therefore, habitat shape and surface topography strongly influence larval settlement and survival. Coral larvae commonly settle in cryptic microhabitats such as crevices (Brunner et al., 2022; Mundy and Babcock, 1998). Crevice size and geometry (aperture and depth) are key factors influencing coral recruitment (Doropoulos et al., 2016; Nozawa, 2008). Different coral taxa exhibit varying settlement preferences and survival rates across different depths and microhabitats (exposed, vertical, cryptic), (Edmunds et al., 2004). In addition, surface microtopography strongly influences larval settlement. Coral larvae often prefer recess-shaped microtopographies, but preferences differ among species (Nozawa, 2008; Petersen et al., 2005). Further, porous surfaces with specific pore sizes and morphologies provide additional settlement microhabitats for coral larvae (Hoog Antink et al., 2018). Additionally, specific microtopographies (e.g., micro-sized sine wave recesses or the Sharklet AF™ pattern) can reduce biofouling (Erramilli and Genzer, 2019; Myan et al., 2013). Biological cues also play a crucial role for coral larval settlement. For example, the presence of a biofilm is essential for coral larval settlement

(Petersen et al., 2005). Also, CCA are well-known inducers of coral larval settlement (Harrington et al., 2004). Their chemical compounds, such as glycoglycerolipids and betaine lipids, and associated bacterial communities, act as settlement cues for coral larvae (Gómez-Lemos et al., 2018; Jorissen et al., 2021; Tebben et al., 2011). Also, the material of the settlement substrate can influence coral recruitment as well as the development of early benthic communities (Levenstein et al., 2022b). However, site-specific factors often outweigh substrate material in shaping benthic communities and coral recruitment (Burt et al., 2009). The presence of other early benthic communities, which involve competition, such as bryozoans, can negatively impact post-settlement survival of corals (Doropoulos et al., 2016). Predation, although difficult to quantify directly in the field, is considered the primary reason for post-settlement mortality (Cooper et al., 2014). Grazers may feed indiscriminately on recruits, especially on exposed surfaces, while corallivores and cryptic predators also target recruits in sheltered areas (Brandl et al., 2014, Doropoulos et al., 2016). Protective microhabitats are therefore crucial for recruit survival.

Given the importance of the structural complexity coral reefs provide, current restoration approaches increasingly attempt to create artificial reefs through 3D printing, using different materials such as ceramic, cement, and geopolymer mortars (Hoog Antink et al., 2018; Yoris-Nobile et al., 2023). 3D printing enables structures tailored to restoration goals, mimicking the complex architecture of natural reefs (Berman et al., 2023; Chamberland et al., 2017; Levy et al., 2022; Perricone et al., 2023). Large-scale reef-mimicking modules include MARS units by Reef Design Lab, Ørsted, and WWF's limestone reef blocks in the Kattegat Sea, and 3D-printed concrete structures in Florida and Louisiana. At smaller scales, 3D-printed substrates for coral settlement include SECORE's ceramic seeding units, Archireef's terracotta tiles, and Reef Balls.

In line with these developments, our previous research identified optimal microhabitats using 3D-printed clay modules deployed in Kāneʻohe Bay, Hawaiʻi (Reichert et al., 2024). We tested seven conical designs incorporating different surface features (holes, pockets, and recesses) across a range of sizes. We found that specific helix recesses dramatically enhanced settlement (by ~80-fold) and post-settlement survival (by 20-50-fold over one year) of the dominant spawning coral *Montipora capitata*, compared to control domes lacking these features. The most successful 'superdome' design incorporated 12 narrow recesses that created microhabitats with low light levels (~50-60 µmol $m^{-2}$ $s^{-1}$) where recruits preferentially settled along cryptic inner edges. While conical domes provided a good test case, practical application depends on adapting the designs to scalable and infrastructure-ready geometries. Cylindrical pylon-like elements offer potential advantages for use in reef frameworks (Higgins et al., 2022) or for (retro-)fitting coastal

engineering structures, such as pilings. However, transferring microhabitat designs between macro-geometries (cone vs. cylinder) is challenging, since shape affects hydrodynamics and light regimes, which affect microhabitat performance (Koehl, 2007; Levenstein et al., 2022a). In addition, the impact of alternative materials on coral settlement, such as concrete, which offers greater scalability and durability than fired clay, needs to be evaluated.

Therefore, this study aimed to I) adapt and apply the optimized helix recess design, originally developed on conical domes, to cylindrical rods and compare their recruitment performance to concurrently deployed conical 'superdomes', and II) evaluate the influence of material (cast concrete vs. 3D-printed clay) on coral recruitment across both cylindrical and conical geometries.

## 2. Materials and Methods

### 2.1 Experimental design

We conducted a field experiment to evaluate the suitability of these helix microhabitat designs on rod-shaped structures. The experiment compared coral recruitment and survival on six types of settlement modules: four cylindrical rod designs (‘small clay rod’, ‘large clay rod’, ‘small concrete rod’, and ‘large concrete rod’) and two conical superdome designs (‘superdome clay’ and ‘superdome concrete’), (Figure 1). Modules (n = 6 per rod design, n = 4 per superdome clay, and n = 3 per superdome concrete) were deployed at Reef 13 in Kāneʻohe Bay, Oʻahu, Hawaiʻi, one week prior to the predicted *Montipora capitata* mass spawning in June 2024. Recruitment was monitored at 1 week, 2 months, and 6 months post-spawning.

### 2.2 Module design and production

Six types of settlement modules were fabricated with two different geometries (cylindrical rods and conical domes), different diameters (small and large rods), and two materials (cast in concrete and 3D-printed in clay), (Figure 1A, B). 'Small rods’ had a base of 40 mm in diameter. 'Large rods’ had a base of 80 mm (clay) or 100 mm (concrete) in diameter. All rods featured continuous spiral helix recesses (four recesses in the large concrete module, two recesses in all other modules) designed to mimic the successful 'superdome' recesses (Reichert et al., 2024). All cylindrical rods shared a height of 200 mm and featured a continuous spiral helix recess (Figure 1A). The conical modules were based on the 'superdome' modules used in previous studies (20 cm base diameter, 10 cm height, 12 helix recesses across four depths; Reichert et al., 2024) and were produced in

both concrete ('Superdome concrete') and clay ('Superdome clay'). The helix features on the rod modules were intended to mimic the successful microhabitats identified in the superdomes (i.e., recesses with 17 mm depth and 15 mm width, Reichert et al., 2024).

The concrete modules (‘small concrete rod’, ‘large concrete rod’, and ‘superdome concrete’) were fabricated through casting. For both concrete rod models, the recess profiles were designed as trapezoidal shapes at ~98° angle and 20 mm width and depth (Figure 1A). Modules were designed in Autodesk Fusion 360 and master patterns were 3D printed in PLX material (PLA-derived bio-performance filament, BigRep GmbH, Germany) on a BigRep ONE.4 printer (BigRep GmbH), (Figure S1). Flexible molds were created from these master patterns using Mold Star™ 30 platinum-cure silicone rubber (Smooth-On, Inc., USA). The final concrete modules were cast within these silicone molds using a high-strength concrete mix (Quikrete® Concrete Mix No. 1101). An attachment rod was embedded centrally during casting to facilitate underwater deployment. Following demolding, the cast modules were cured for at least two days before deployment. The ‘superdome concrete’ modules were fabricated in the same way, with the master pattern being a clay-printed and fired superdome.

The clay modules (‘small clay’, ‘large clay’, and ‘superdome clay’) were fabricated using 3D printing. Designs from Autodesk Fusion 360 were exported as .stl files and processed using Simplify3D slicing software. Modules were printed using a Delta Wasp 40100 3D printer (Wasp, Italy) with mid-fire pottery clay (Soldate 60, Aardvark Clay and Supplies, United States), prepared using a pugmill (Pugmill/Mixer NVS-07, Nidec, Japan). All clay modules were printed at 110% scale to compensate for shrinkage during drying and firing. Clay was extruded through a 4 mm diameter nozzle, creating a distinct horizontal layer microstructure on surfaces (Figure S1, microstructure clay). The modules were printed as hollow structures using the spiral vase mode, following the procedures developed in previous studies (Reichert et al., 2024). However, printing the target recess profile on the cylindrical clay rods was structurally unstable, so the recess profile for the clay rods was modified to a more rounded shape. Notably, the ‘large clay’ design was printed with wider recesses (40 mm) compared to the target dimensions. After printing, all clay modules were air-dried for 7-10 days in a stable environment until bone-dry and subsequently fired in a kiln (Jupiter Sectional Kiln, L&L Kilns, United States) at ~2030 °F (≈1100 °C) with a 2-hour hold (setting: cone 8).

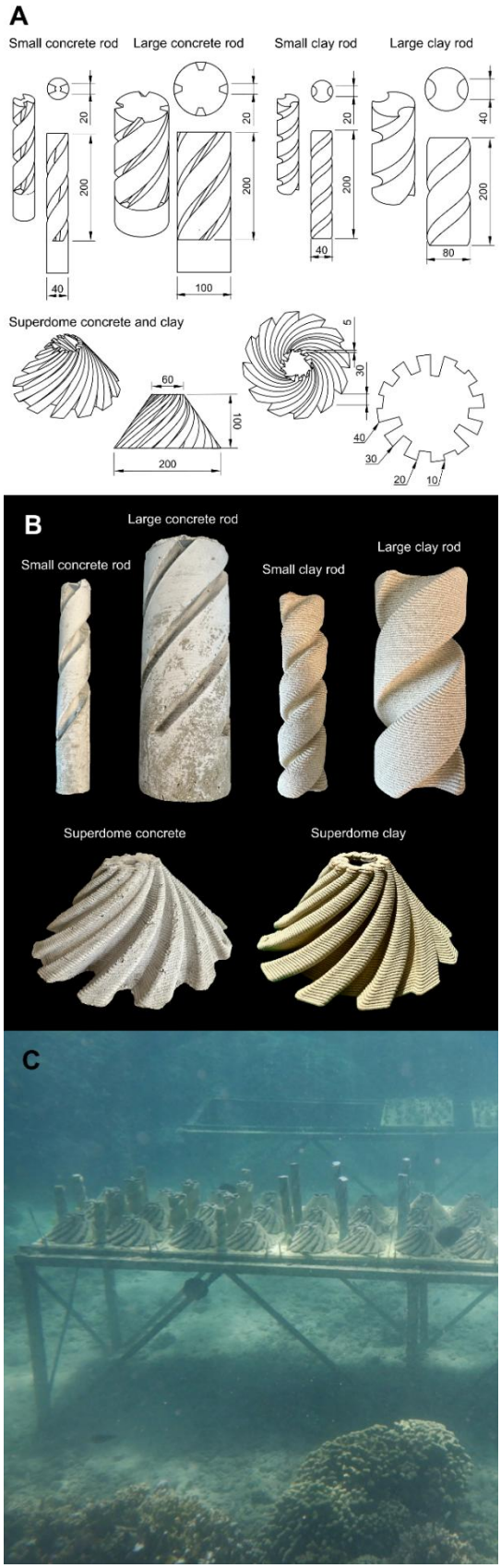



**Figure 1: Designs of coral settlement modules and deployment.** The designs demonstrate that recessed microhabitats can be implemented across both dome and rod shapes, enabling comparative testing of settlement performance. (A) Dimensions of the six tested coral settlement modules (small concrete rod, large concrete rod, small clay rod, large clay rod, superdome concrete, and superdome clay) are presented in technical drawings (unit: mm). Designs were produced in concrete and clay. Rod designs all shared a height of 20 cm with varying diameters and recess dimensions. Superdomes had a conical shape with a base diameter of 20 cm, a height of 10 cm, and decreasing recess sizes towards the top. Recesses had four different depths decreasing towards the top with maximal depths of 1 cm, 2 cm, 3 cm, and 4 cm, respectively. (B) Photos of coral settlement modules in the six different designs tested. (C) Modules were deployed on tables at patch reef 13, Kāneʻohe Bay at ~2 m depth.

### 2.3 Deployment and monitoring

Coral settlement modules were deployed on tables at patch reef 13, in Kāneʻohe Bay, Oʻahu, Hawaiʻi, at ~2 m depth on 21 June 2024, one week before the anticipated mass spawning of *M. capitata* corals, to allow for biofilm conditioning on the structures. Modules were deployed in an upright position onto experimental tables (Figure 1C). Coral recruitment on the modules was assessed at 1 week, 2 months, and 6 months post-spawning. For this, modules were transported back to the lab at Moku o Loʻe, where recruits were counted via fluorescence detection (Sola Nightsea Blue Light, blue-light-blocking glasses). After counting, the modules were brought back to the field site. The number of recruits was counted separately on outside surfaces and surfaces inside the recesses. Recruit counts were converted to recruit densities (per $cm^2$) by standardizing to the location-specific surface area of each module type, determined in the 3D model designs. Further, to determine the planar recruit density, total numbers per module were standardized to the planar area of each module.

Recruitment on settlement structures was compared to recruitment on natural reef substrate. After two months, coral recruits were counted in 32 randomly selected 0.5x0.5 m quadrats in the Barrier Reef in Kāneʻohe Bay (21.458853° N, 157.798046° W), using blue light fluorescence. The percent cover of benthic components (CCA, live coral, and rubble/sand) was visually estimated. The three-dimensional structure of each quadrat was reconstructed using photogrammetry from approximately 2500 overlapping images captured in a spiral pattern, following established procedures (Pizarro et al., 2017). Orthomosaics were built in Agisoft Metashape photogrammetric software (Roach et al., 2021). Recruitment density was then standardized to the available surface area by subtracting non-settlement areas (live coral, sand). Recruit density in the reef was similarly standardized to the three-dimensional surface area available, as well as to the planar surface area.

### 2.4 Statistical Analysis

Data were analyzed in R (v.4.5.0, R Core Team, 2025). Differences in recruit densities among the six structure types were assessed using Kruskal-Wallis tests followed by pairwise Wilcoxon rank-sum tests with Holm correction. Comparisons between locations ('Inside' vs. 'Outside') within each structure type were performed using Wilcoxon rank-sum tests. To assess how structural and material features influenced coral recruit density over time, generalized linear models were fitted separately for each timepoint using a Tweedie distribution with a log link function in the glmmTMB

package (Brooks et al., 2017). The Tweedie family is well-suited for modeling continuous, non-negative data with a large proportion of zeros and a right-skewed distribution, such as coral recruit densities (recruits per cm²). Models included the fixed effects of shape (rod vs. superdome), recruit location (inside vs. outside), material (clay vs. concrete), diameter (large vs. small), and recess size (large vs. small). Model diagnostics were performed with the DHARMa package (Hartig, 2025). Estimated marginal means (EMMs) and pairwise contrasts were calculated using the emmeans package (Lenth, 2025).

## 3. Results

### 3.1 Overall recruitment dynamics

Coral recruitment occurred on all deployed structure types featuring helix designs. While early settlement varied significantly among designs, long-term recruitment success was comparable across all module types (Figure 2, Table S1). In particular, initial settlement densities at 1 week post-spawning differed significantly between the structures (Wilcoxon rank-sum test, $p<0.05$). Recruit densities on the overall structures were highest, particularly on concrete structures, reaching densities up to 1.59 ± 0.66 recruits per cm² on the whole module (including inside and outside surfaces) in the concrete superdome design (Figure 2A). Following this, a significant decline in recruit numbers was observed after 2 months due to post-settlement mortality. Recruit densities stabilized equally across all designs to around 0.06 ± 0.03 recruits per cm² (Wilcoxon rank-sum test, $p>0.05$). Between months 2 and 6, densities showed slower declines on most structures, leading to values around 0.03 ± 0.02 recruits per cm² at the 6-month mark. Notably, recruit densities shifted compared to the initial settlement. In particular, the large clay design, which had the lowest initial recruitment, had the highest recruit densities after six months. Recruit densities inside the recesses were considerably higher (Figure 2B), as only few recruits settled on the outside (Figure S2, Table S3, Figure 4B). Trends between different shapes remained the same. Planar recruit densities revealed significantly higher densities on the rod-shaped designs compared to the superdome designs, with the highest densities found on the small concrete rod design (Figure 2C).

**Figure 2**: Coral recruitment on the six tested coral settlement modules (small concrete rod, large concrete rod, small clay rod, large clay rod, superdome concrete, and superdome clay) after 1 week, 2 months, and 6 months reveals that while early settlement varied significantly among designs, long-term recruitment success was comparable across all module types. (A) Recruit densities (recruits per $cm^2$) on the full structure. (B) Recruit densities (recruits per $cm^2$) inside the recesses of the structure. (C) Recruit densities (recruits per $cm^2$) per planar area of the structure. 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 rank-sum tests followed by Holm adjustment for multiple testing: * $p \leq 0.05$, ** $p \leq 0.01$, ***$p \leq 0.001$.

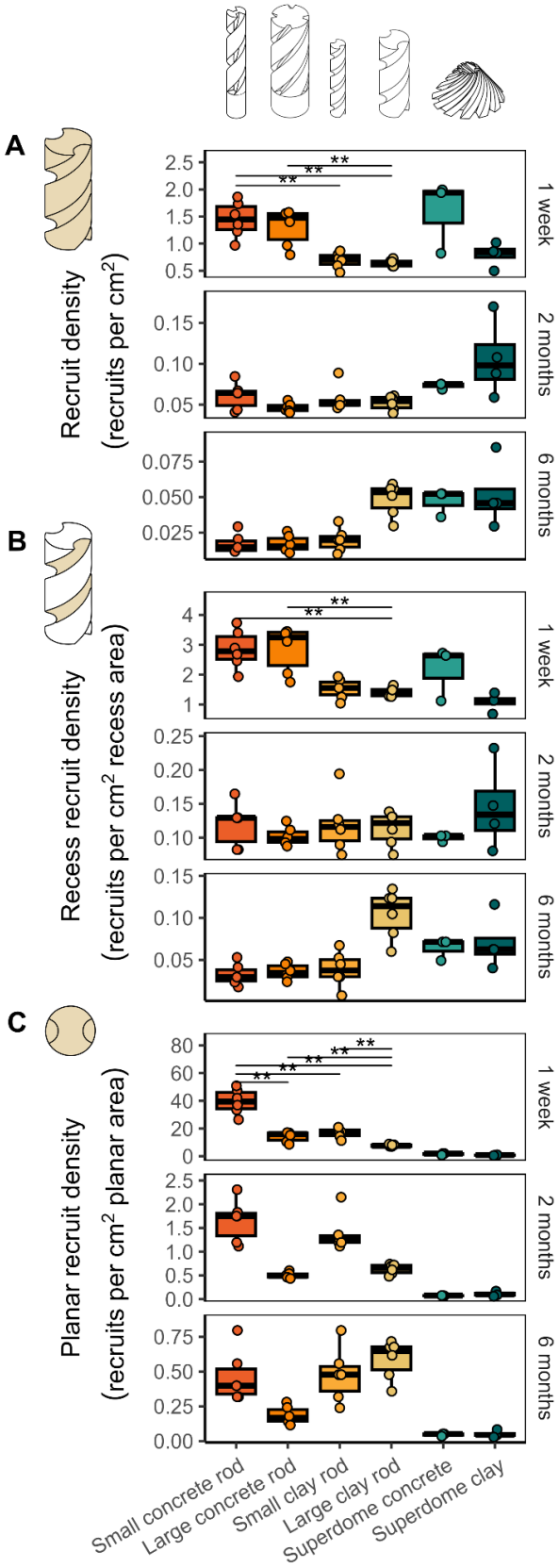


**Table 1**: Statistical results of Tweedie generalized linear models assessing the effects of shape, recruit location, material, diameter, and recess size on coral recruit density (recruits per cm²) after 1 week, 2 months, and 6 months. Model-estimated coefficients (log scale), standard errors, z-values, and p-values are given for each predictor. Significant effects ($p < 0.05$) are highlighted in bold.

| Timepoint | Predictor | Estimate | Std. Error | z value | p value |
|---|---|---|---|---|---|
| 1 week | Intercept | -2.852 | 0.169 | -16.90 | **<0.0001** |
| | Shape (superdome) | -0.349 | 0.144 | -2.43 | **0.0152** |
| | Recruit location (inside) | 3.912 | 0.158 | 24.81 | **<0.0001** |
| | Material (clay) | -0.624 | 0.114 | -5.50 | **<0.0001** |
| | Diameter (small) | -0.002 | 0.120 | -0.02 | 0.9883 |
| | Recess size (large) | -0.097 | 0.180 | -0.54 | 0.5925 |
| 2 months | Intercept | -5.908 | 0.262 | -22.59 | **<0.0001** |
| | Shape (superdome) | 0.073 | 0.181 | 0.40 | 0.6880 |
| | Recruit location (inside) | 3.608 | 0.241 | 14.95 | **<0.0001** |
| | Material (clay) | 0.175 | 0.129 | 1.36 | 0.1750 |
| | Diameter (small) | 0.115 | 0.162 | 0.71 | 0.4780 |
| | Recess size (large) | -0.039 | 0.213 | -0.19 | 0.8530 |
| 6 months | Intercept | -6.382 | 0.312 | -20.46 | **<0.0001** |
| | Shape (superdome) | 0.458 | 0.241 | 1.90 | 0.0571 |
| | Recruit location (inside) | 3.067 | 0.274 | 11.19 | **<0.0001** |
| | Material (clay) | 0.178 | 0.177 | 1.00 | 0.3160 |
| | Diameter (small) | -0.058 | 0.234 | -0.25 | 0.8030 |
| | Recess size (large) | 0.876 | 0.271 | 3.23 | **0.0013** |

Tweedie generalized linear models revealed factors that influence coral settlement and survival (Table 1). The recruitment location (inside vs. outside) was by far the most consistent and influential factor across all time points. Recruits were significantly more abundant inside the structures than on the exposed outside surfaces at 1 week, 2 months, and 6 months (all $p < 0.0001$). The effect was strongest at one week, showing a consistent preference for the protected microhabitats inside recesses. Recruit densities after one week were higher on rods than on superdomes, showing an early effect of module shape ($p = 0.0152$). However, the effect weakened over time and was not visible after 2 or 6 months. Material affected early settlement, with concrete supporting higher recruit densities than clay after 1 week ($p < 0.0001$). However, this difference disappeared at 2 months and 6 months, suggesting that while concrete may promote initial settlement, clay supports comparable long-term outcomes. Recess size had no detectable effect at month 1 or 2, but became a significant factor after 6 months. Larger recesses supported higher recruit densities ($p = 0.0013$), indicating a delayed benefit of larger microhabitats for post-settlement survival and persistence. Rod diameter had no significant effect at any time point. Although larger rods often showed slightly higher densities, the effect was minimal and not significant, indicating that module diameter played only a minor role.

### 3.2 Post-settlement survival

Despite slight differences in the recess design between concrete rods (designed to optimal dimensions) and clay rods (rounded recesses constrained by 3D clay printing), the convergence of recruit densities by 2–6 months suggests that the overall helix design concept is robust and most designs showed similar survival rates (Figure 3). Only the large clay rod design stood out. While having wider recesses, this specific design showed minimal decline in recruit density between the 2-month and 6-month time points, indicating enhanced recruit survival during this phase compared to other designs (Figure 3B, Wilcoxon rank-sum test, p=0.0320, Table S4).

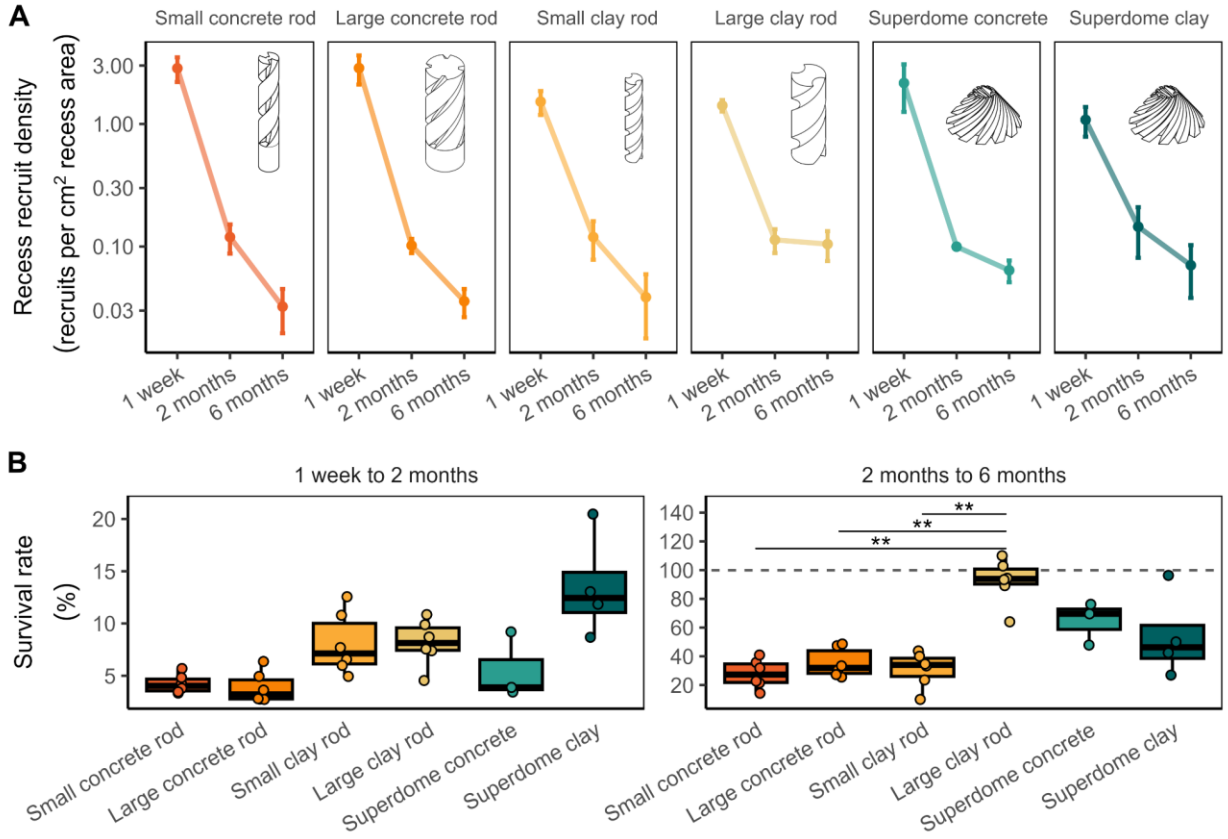



**Figure 3: Coral recruit survival on different settlement modules.** Survival rates suggest that the overall helix design concept is robust and most designs showed similar survival rates. (A) Declines in recruit densities (recruits per $cm^2$ inside the recesses) on different designs in concrete and clay (small concrete rod, large concrete rod, small clay rod, large clay rod, superdome concrete, and superdome clay) from 1 week to 2 months, and to 6 months. Data are displayed as line plots with mean ± standard deviation. (B) Survival rate of recruits on the six different shapes from 1 week to 2 months, and from 2 months to 6 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. Asterisks indicate levels of statistical significance, derived from Wilcoxon rank-sum tests followed by Holm adjustment for multiple testing: * $p \leq 0.05$, ** $p \leq 0.01$, ***$p \leq 0.001$.

## Comparison to natural reef recruitment

To assess the performance of the tested coral settlement structures in comparison to natural reef conditions, recruit densities after two months were compared with recruitment on natural substrate at a nearby reef site. Mean recruit density on the reef was 25 ± 24 recruits per m² relative to its 3D surface and 30 ± 28 recruits per m² planar area, calculated based on available benthic settlement surface area (Figure 4A). In contrast, recruit densities on the modules were significantly higher (Wilcoxon rank-sum tests, $p < 0.001$, Holm-corrected; Table S2). Recruit densities inside the helix recesses of all tested module types were ~50-fold higher at 1163 ± 345 recruits per m². Recruit densities on planar areas were ~300-fold higher, with 8269 ± 6443 recruits per m² observed.

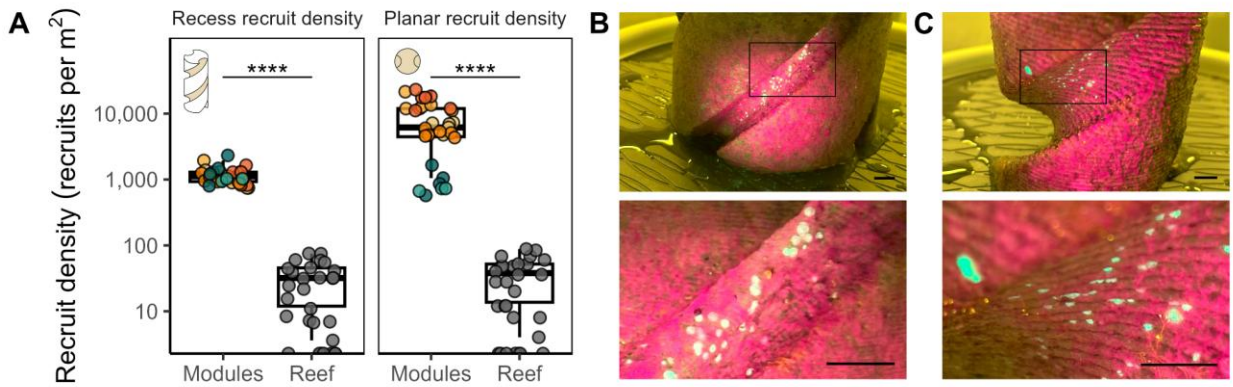



**Figure 4**: Coral recruitment on coral settlement modules was higher than recruitment on natural reef substrate in an adjacent reef after 2 months. (A) Recruit densities (recruits per $m^2$) in the recesses and the 3D reef structure derived from photogrammetry and planar recruit densities are compared. Data are displayed as box-and-whisker plots with raw data points; lines indicate medians, boxes indicate the first and third quartiles, and whiskers indicate ± 1.5 IQR. Asterisks indicate levels of statistical significance, derived from Wilcoxon rank-sum tests: * $p \leq 0.05$, ** $p \leq 0.01$, ***$p \leq 0.001$. (B) Photos of 1-week-old recruits inside the recesses of the large concrete design. Scale bars represent 1 cm. Recruits are green-fluorescent, excited via blue light, and visualized through yellow filters. (C) Photos of 1-week-old recruits inside the recesses of the large clay design, respectively.

## 4. Discussion

This study evaluated the transfer of optimized helix-shaped microhabitat designs to pylon-like, cylindrical rods and examined the influence of geometry and material on coral recruitment. Our findings confirm the effectiveness of the helix design on cylindrical structures, demonstrate the robustness of the design across different materials, and provide new insights into how recess dimensions affect post-settlement survival.

### 4.1 Successful design transfer to cylinders

Similar recruitment densities on cylindrical rods and conical superdomes, especially after initial mortality, show that the helix design transfers successfully to a different macro-geometry. Helix features likely promote larval entrainment by creating small recirculation zones and reducing flow inside recesses, conditions that favor settlement (Hata et al., 2017). These processes seem to work equally well in the recesses of the cylindrical rods and conical domes tested here. The recess dimensions of 1–10 mm match those preferred by coral larvae in other experiments (Doropoulos et al., 2016; Rahnke et al., 2022; Ramsby et al., 2024) and on natural reefs (Brandl et al., 2014; Edmunds et al., 2004). Recruits preferred inner recess surfaces over outer exposed areas, underlining that these features provide crucial and suitable microhabitats on cylindrical structures.

### 4.2 Design robustness across materials

The helix design was the main driver of recruitment success. Material influenced initial settlement, with slightly higher densities on concrete, but this difference disappeared over time. Coral larvae are known to settle on a wide range of materials, including coral skeletons, terracotta, cement, glass, and PVC (Babcock and Mundy, 1996; Hunte and Wittenberg, 1992; Soong et al., 2003; Wilson and Harrison, 1998). While some studies report preferences for ceramic tiles or coral skeletons, site-specific environmental conditions usually have a stronger influence on recruitment patterns (Burt et al., 2009). The higher initial settlement on concrete in our study likely reflected small differences in recess geometry or surface properties (Figure 1). Trapezoidal recesses in concrete rods appear less favorable for long-term persistence than the rounder recesses in clay structures. This may be due to differences in hydrodynamics or shading, as coral larvae prefer microscale recesses (Nozawa, 2008; Petersen et al., 2005) and porous surfaces (Hoog Antink et al., 2018). Although surface textures varied slightly due to production methods, this likely did not drive the observed pattern. The concrete superdome, cast from a clay-printed template, shared the same layered surface. More likely, chemical or nanoscale surface differences such as porosity

or potential leachates from the concrete affected recruit survival (Natanzi et al., 2021). Weaker long-term attachment of larvae to smoother concrete surfaces may also have contributed (Carl et al., 2012).

In summary, these findings demonstrate that helix designs robustly enhance coral settlement and survival across different materials, such as clay and concrete. Concrete offers advantages in terms of cost, durability, and scalability (Spieler et al., 2001; Knoester et al., 2024). Since no differences in long-term survival were observed, concrete appears to be a suitable material for producing coral settlement modules for reef restoration.

### 4.3 Trade-offs between settlement and survival based on recess size

The large clay rods had wider, rounded recesses because of printing limitations. Despite lower initial settlement, they maintained the highest recruit densities between 2 and 6 months. This suggests that larger recesses can enhance post-settlement survival. This result complements our earlier finding that narrow recesses promote early settlement (Reichert et al., 2024), but suggests that wider recesses improve persistence under field conditions. Likely explanations include higher light availability, lower competition with sessile invertebrates, and improved water circulation for gas exchange and feeding (Chadwick and Morrow, 2011; Mass et al., 2010; Sebens et al., 1997). These results underline the need to consider multiple life stages when refining microhabitat features. Future work should test a wider range of recess dimensions to identify designs that balance settlement and survival.

### 4.4 Recess functionality and module size effects

Coral larvae were consistently found inside the recesses, confirming that recesses function as key microhabitats, also on cylindrical substrates. This preference was strongest after one week, indicating an early selection for protected areas. Recruitment did not differ between small and large rod diameters, suggesting similar larval behavior and hydrodynamics across the tested centimeter scales. Reasons for the reduced settlement and survival on the outsides might be increased grazing pressure and competition from benthic algae on these surfaces (Doropoulos et al., 2016). These results underline the functional value of helix recesses as a protective habitat for coral recruits.

### 4.5 Implications for coastal engineering and reef restoration

This study demonstrates that helix-shaped recesses enhance coral recruitment on cylindrical structures. The design was effective across both concrete and clay, allowing material choice to depend on durability, cost, or environmental footprint. Helix recesses can therefore be integrated into cylindrical and pylon-like elements, such as pilings, tetrapods, seawalls, or groin foundations, commonly used in coastal engineering and shore protection. With that, coastal structures could be adapted to provide ecological function as coral settlement habitat and serve as part of nature-based solutions and hybrid infrastructure, where shoreline protection and reef restoration are achieved simultaneously. This dual function improves the cost-effectiveness of restoration by building on established engineering practice.

Over longer periods, this method could also improve the stability and lifespan of coastal infrastructure. Corals can rapidly grow out of the recesses (Reichert et al., 2025, Schiettekatte et al., in prep) and extend across exposed surfaces, creating a biological reinforcement layer that could further stabilize the base structures.

An important next step is to evaluate how recesses perform over extended periods, including whether they can support repeated settlement events that build self-sustaining coral populations. Furthermore, this study emphasizes that recess design must strike a balance between features that support initial settlement and those that promote survival. Varying recess size across modules may improve performance across coral life stages. Future research should therefore systematically investigate larger recess geometries, as well as a broader range of coral species and reef environments, to establish general design rules for restoration-oriented engineering.

In summary, cylindrical elements with helix recesses are scalable and low-cost. They can be mass-produced in concrete and incorporated into coastal engineering projects to combine shoreline protection with reef restoration.

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## Author contributions

Conceptualization: JR, HJ, and JSM
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Data curation: JR, ADN, LHR
Formal analysis: JR
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Visualization: JR
Writing—original draft: JR
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## Use of generative AI

During the preparation of this work, Gemini (Google AI) and ChatGPT (OpenAI) were used to improve the clarity and language of the manuscript. The authors thoroughly reviewed all content and take full responsibility for the published article.

## Data and materials availability

Data and scripts will be made available from GitHub.

## Declaration of interest statement

Joshua S. Madin, Jessica Reichert, and Hendrikje Jorissen have patent #PCT/US2024/051295 pending to University of Hawai'i.

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