

Effects of 3DP coral-inspired shelter geometry on reef fish occupancy and shelter use

Raz Levy

razlevi97@gmail.com

Ben-Gurion University of the Negev

Asa Oren

Ben-Gurion University of the Negev

Liat Biniuri

Ben-Gurion University of the Negev

Natalie Chernihovsky

Ben-Gurion University of the Negev

Ezri Tarazi

Technion – Israel Institute of Technology

Nadav Shashar

Ben-Gurion University of the Negev

Article

Keywords: 3D printing, coral-inspired shelter geometry, coral morphology, habitat complexity, reef fish assemblages, artificial reef design, shelter use

Posted Date: August 7th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10353211/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Structural complexity shapes reef fish assemblages, yet isolating the ecological effects of individual structural characteristics under natural reef conditions remains challenging. Here, we used three-dimensional printing to experimentally manipulate coral-inspired shelter geometry while maintaining a common biological template. Twelve coral modules derived from a three-dimensional scan of a *Stylophora pistillata* skeleton were modified into four distinct designs: Original, elongated branching, enlarged (200%), and corymbose tabular. The modules were deployed on a natural reef in the Gulf of Aqaba and Eilat and monitored by scuba surveys over three months. Fish abundance, species richness, and interaction frequency were quantified, and interaction counts analyzed using a zero-truncated negative-binomial generalized linear mixed model (GLMM). Fish abundance differed among structural designs, with enlarged models supporting more individuals, whereas species richness showed a similar but non-significant trend. Structural geometry also significantly influenced interaction frequency, while time of day had no detectable effect. Because the manipulations simultaneously altered colony geometry, branch architecture, structural volume, and shelter configuration, the observed responses likely reflect the combined effects of multiple architectural features rather than colony size alone. This exploratory field experiment demonstrates the value of three-dimensional printing as a platform to investigate coral-inspired habitat architecture and inform artificial reef design.

1. Introduction

Coral reefs are diverse and productive marine environments, supporting natural biodiversity and human societies alike (Hughes et al., 2005; Kittinger et al., 2012; Hoegh-Guldberg et al., 2019). Despite their importance, reefs are increasingly affected by anthropogenic disturbances such as coastal urbanization and population growth, as well as climate-related stressors like ocean warming, marine heatwaves, and bleaching (Hughes et al., 2017; Oliver et al., 2018; van Woesik et al., 2022; Shlesinger & van Woesik, 2023). Habitat structure, particularly the structural complexity of coral colonies, is a key driver of reef fish assemblages, offering shelter, nursery habitats, and feeding grounds (Lewis, 1997; Pratchett et al., 2008; Graham & Nash, 2013; Darling et al., 2017). Structural complexity metrics such as branch spacing, surface area, and fractal dimension have been linked to higher fish biodiversity (Kerry & Bellwood, 2012; Rogers, Blanchard & Mumby, 2014). Beyond general measures of structural complexity, reef fishes may respond to specific coral morphological traits that determine the suitability of a colony as shelter, including growth form, colony size, and branching architecture (Darling et al., 2017). These traits include overall colony size and volume (Bongiorni et al., 2003), branch thickness and spacing (Helmuth et al., 1997), internal void space, surface area, and the balance between openness and concealment. Branching corals with moderate inter-branch distances often provide optimal refuges by allowing access for small and medium-sized fishes while still limiting predator entry (Hixon & Beets, 1993), whereas very dense branching can exclude larger individuals and restrict movement within the structure (Coker et al., 2014). Conversely, more open or enlarged morphologies may enhance visibility and maneuverability, facilitating social interactions, schooling behavior, and rapid escape responses. Colony architecture also

determines the diversity and availability of microhabitats, including crevices, overhangs, branch spaces, and internal cavities, which provide a range of shelter opportunities for reef fishes (Ménard et al., 2012).

Three-dimensional printing (3DP) has emerged as a promising tool for reef research, enabling the fabrication of coral-like structures with high precision, repeatability, and the potential for customizable shelter geometry (Baden et al., 2015; Gutiérrez-Heredia et al., 2016; Levy et al., 2022; Oren et al., 2023). Advances in additive manufacturing now include FDM, SLA, binder jetting, and cementitious or biopolymer materials, allowing researchers to replicate complex structures, including corals, for ecological studies (Korniejenko et al., 2025). Furthermore, sustainable materials like ceramic or terracotta have been explored, showing promise for long-term artificial reef applications (Oren et al., 2024). Beyond reproducing natural coral forms, three-dimensional printing enables the controlled manipulation of individual structural characteristics while maintaining a common biological template. This allows specific aspects of coral-inspired shelter geometry to be modified experimentally, thereby enabling researchers to investigate how different architectural features influence reef fish assemblages under natural field conditions.

Studies using natural coral colonies have demonstrated links between morphology and reef fish assemblages (Huang et al., 2024; Ferreira et al., 2025). However, it remains difficult to isolate the ecological effects of individual structural characteristics without the use of predesigned 3D-printed models (Oren et al., 2023). To address this gap, four coral-inspired structural variants were generated from a three-dimensional scan of a *Stylophora pistillata* skeleton and deployed on a natural reef. *Stylophora pistillata* was selected as the biological template because it is a common branching coral in the Gulf of Aqaba and Eilat (GOA/E) and functions as an ecologically important reef builder, forming structurally complex habitat for a wide variety of reef-associated organisms, including fishes (Loya, 1972; Shaish et al., 2006). Oren et al. (2023) demonstrated that reef fishes readily occupied 3D-printed coral structures under natural reef conditions, supporting their use as experimental analogues of natural coral habitats. As an initial proof-of-concept study, their work established the feasibility of using 3D-printed coral models as ecological research tools and suggested that structural characteristics, including colony size and geometry, may influence habitat use by reef fishes. However, the relative contribution of specific geometric modifications to reef fish assemblages remained unresolved. Building on this framework, the present study experimentally manipulated distinct aspects of coral-inspired shelter geometry to evaluate their influence on reef fish abundance, species richness, and shelter use under natural reef conditions.

Here, we tested whether controlled variation in coral-inspired shelter geometry influences reef fish assemblages by comparing four experimentally designed shelter configurations that differed in colony geometry, branch architecture, and overall colony architecture. We hypothesized that variation in shelter geometry would influence reef fish abundance, species richness, and patterns of shelter use. By experimentally isolating structural characteristics within a common biological template, this study provides new insights into how habitat architecture shapes reef fish assemblages, with implications for both coral reef ecology and the design of artificial reef structures.

2. Methods

Model creation and design were based on the four structural variants described by Oren et al. (2023). The reference model (Original) replicated the natural morphology of a *Stylophora pistillata* coral skeleton based on a three-dimensional scan.

The four experimental designs were selected to represent distinct, ecologically relevant geometric manipulations commonly associated with natural variation in coral colony architecture. Rather than modifying a single parameter in isolation, each model was designed to alter a biologically relevant combination of structural attributes, allowing the ecological consequences of different shelter configurations to be evaluated under field conditions.

The reference model (Original) had a diameter of 160.1 mm and a height of 113.3 mm, a surface area of 840.3 cm², a material volume of 214.1 cm³, and a net ecological volume of 926 cm³. From this baseline structure, three additional variants were generated. In the elongated branching model (Branching), the tips of each branch were extended along their natural growth direction by 2.5 cm, while branch thickness was increased to maintain structural stability. A second variant was produced by uniformly scaling the entire structure to 200% of its original dimensions (Large), resulting in a proportional increase in all geometric parameters. The third variant was manipulated to produce a corymbose tabular morphology (Table) with a diameter of 25 cm. Three replicas of each model type were produced, resulting in a total of twelve models. The four models represented different geometric modifications of the same reference colony, allowing comparisons among distinct shelter architectures while minimizing variation in overall colony morphology.

Models preconditioning

All models were preconditioned for two weeks in a flow-through, unfiltered seawater tank covered with shade cloth to minimize light and suppress macroalgal proliferation. This conditioning period allowed microalgae, biofilm, and other microorganisms to colonize the surfaces prior to deployment.

Experimental settings

On 31/12/2023 all models were set on the surrounding of an artificial reef, on a long metal beam, which is part of the structure of the underwater observatory (N29°30' E34°55') (Fig. 1) (Permit No. 2023 / 43439, Israeli Nature and Parks Authority). All models were set at a depth of 5m ± 20 cm with at least 1m distance between each of them. Every month the models were removed, cleared from any animals in/on them, placed on the sandy bottom (12m) for the night and set again in a different location the following morning. The models' location on the site were exchanged every month for a total of 3 different positions for each model. Identical model types were not placed adjacent to one another, and no model type occupied the same station more than once throughout the experiment.

Experimental procedure

The 3DP models were monitored between January and March, over a period of three months, by scuba surveys. In total, 33 survey dives were conducted: 24 during the daytime (08:00–17:00) and 9 at night (after sunset). During each survey, all 12 models were observed for several minutes, with the first two minutes conducted from a distance to minimize diver disturbance. After these initial observations, fish interactions with the models were recorded and filmed with an underwater camera (Nikon Coolpix). Observations were recorded onto an underwater slate at the time of each encounter. To validate the surveys, an underwater video camera was deployed on three separate occasions, each time positioned in front of a different model type (Original, Table, and Large). Each recording lasted approximately one hour, providing continuous visual documentation against which the diver-based surveys could be cross-checked.

Data analysis

Total fish counts and species richness were summarized per structure (three replicates per model type: Original, Branching, Large, and Table). Differences among model types were assessed using one-way ANOVA after verifying homogeneity of variances (Levene's test) and normality of residuals (Shapiro–Wilk test). When the overall test was significant, pairwise comparisons were performed using Tukey's HSD.

Per-interaction counts, representing the number of fish individuals observed interacting with a structure during a single observation, were analyzed using a zero-truncated negative-binomial generalized linear mixed model (GLMM). Only observations with at least one interaction (count ≥ 1) were included, making a zero-truncated distribution appropriate. Model type and time of day (day/night) were included as fixed effects, whereas month and station were included as random intercepts. Following the general GLMM framework outlined by Bolker et al. (2009), model selection was based on Akaike's Information Criterion (AIC). Model assumptions were subsequently evaluated using simulation-based residual diagnostics implemented in the DHARMA package. Exploratory associations between species and station were evaluated using Pearson's χ^2 tests, with simulated p-values when expected cell counts were low.

All analyses were conducted in R version 4.4.2 (RStudio version 2025.05.1) using the packages glmmTMB, DHARMA, emmeans, car, dplyr, and ggplot2, with $\alpha = 0.05$.

Ethics statement

All observations were conducted on free-ranging wild reef fishes in their natural habitat. No animals were captured, handled, collected, euthanized, or otherwise manipulated during the study. Fish were free to approach, inspect, occupy, or avoid the experimental structures at their own discretion, and all recorded behaviors reflected voluntary, natural habitat-choice decisions without any coercion or interference by the researchers.

All fish observed during the study were naturally occurring, free-ranging wild individuals inhabiting the reef adjacent to the Underwater Observatory Marine Park in Eilat, GOA/E, Israel. No animals were obtained from a commercial supplier, breeding facility, laboratory, or research colony.

Fieldwork was conducted under scientific research permit No. 2023/43439 issued by the Israel Nature and Parks Authority (NPA), authorizing the deployment of the experimental structures and the associated scientific fieldwork within the protected marine reserve. All methods were carried out in accordance with relevant guidelines and regulations. This study consisted exclusively of non-invasive in situ observations of free-ranging wild fishes under natural field conditions.

3. Results

A total of 21 species, 231 interactions, and 313 individual fish were recorded across the 12 experimental structures. Overall, model type had a significant effect on fish interactions, whereas time of day (day/night) did not. No consistent differences were detected among stations.

Community composition and total counts varied among the experimental structures, with the largest totals generally associated with the Large models and the smallest with the Original and Table types (Fig. 2). Mean interaction counts per structure were highest in the Large models (35.7 ± 7.64) compared to Branching (15.0 ± 10.8), Table (15.0 ± 4.0), and Original models (11.3 ± 1.53). Patterns in species richness and total abundance across model types are shown in Fig. 3.

Total counts per structure

Total counts per structure differed among model types (one-way ANOVA: $F_{(3,8)} = 7.97$, $p = 0.0087$; Fig. 2). Tukey's HSD indicated a significantly higher number of interactions for the Large models compared with Original ($p = 0.0106$), Branching ($p = 0.0265$), and Table ($p = 0.0203$); other contrasts were not significant.

Note. One Branching replicate (Fig 2. Model 5; code B2) became fouled by stinging epibionts following deployment, which may have reduced interactions on that structure.

Species richness per model type

Species richness per structure was highest in the Large models and lower for Original and Table, with Branching showing greater variability (Fig. 3A). The omnibus ANOVA was not significant ($F_{(3,8)} = 1.63$, $p = 0.257$), assumption checks were satisfactory (Levene $p = 0.78$; Shapiro–Wilk $p = 0.59$), and no pairwise differences were detected. Descriptively, total abundance per structure was highest for the Large models and lower for the Original and Table models, with intermediate values observed for Branching (Fig. 3B). For descriptive comparison with Oren et al. (2023), model volume and mean monthly abundance per structure are summarized in Table 1.

Table 1. Comparison of coral model volume and mean monthly fish abundance per structure across studies

Model volume and fish abundance per structure for the four experimental coral models in Oren et al. (2023) and the present study.				
Model	Volume (cm³)	Oren et al. (2023) mean monthly abundance	Current study mean monthly abundance	SD
Original	213.53	7.50 (30 total)	4.00 (36 total)	0.88
Branching	460.55	16.00 (64 total)	6.33 (57 total)	4.18
Large	1684.38	34.25 (137 total)	18.78 (169 total)	6.95
Table	430.79	11.50 (46 total)	5.66 (51 total)	1.73

Volume values are based on Oren et al. (2023). Because Oren et al. (2023) monitored the models over four months, whereas the present study lasted three months, abundance values from both studies were normalized to mean monthly abundance per structure to allow direct comparison. Values from the present study are presented as mean monthly abundance per structure across three replicate models ($\pm$ SD among replicates). Total abundance values recorded across the full duration of each study are shown in parentheses.

Interaction Counts

Interaction counts were analyzed as the number of fish observed interacting with each model during a single observation period. Only observations in which at least one fish interaction occurred were included in this analysis, allowing us to evaluate variation in interaction intensity among model types once a structure had been selected by fish. A zero-truncated negative-binomial GLMM identified a significant effect of model type on per-interaction counts (likelihood-ratio $\chi^2 = 11.53$, $df = 3$, $p = 0.009$), while time of day was not significant ($\chi^2 = 2.95$, $df = 1$, $p = 0.086$). DHARMA diagnostics indicated good model fit without signs of overdispersion or zero inflation, and the zero-truncated model outperformed a standard negative-binomial alternative (AIC 286 vs. 657).

4. Discussion

4.1. Effects of Structural Architecture on Reef Fish Assemblages

This study shows that morphological differences among coral-like structures significantly affect reef fish assemblages. Fish abundance varied across model types, with the Large (200%) design supporting more individuals than the other morphologies, whereas species richness showed only a non-significant trend in the same direction (Table 1). These findings emphasize that the physical characteristics of shelters, such as overall size, branch spacing, and surface complexity, play a key role in determining fish occupancy.

Because this experiment relied exclusively on artificial 3D-printed modules, it effectively isolated the physical structural component of habitat use while excluding biological and chemical cues present in

living corals (Pratchett et al., 2008). This approach provides valuable mechanistic insight into how morphology alone can shape fish assemblages, but it also highlights the need for future comparisons with natural coral colonies to evaluate ecological realism.

The higher abundance observed on the Large models is likely linked to their greater internal volume and larger inter-branch spaces (Table 1), which provide both refuge and maneuverability for small and medium-sized reef fishes. Previous studies have shown that habitat complexity enhances fish abundance and diversity by increasing the availability of microhabitats and reducing predation risk (Lewis, 1997; Kerry & Bellwood, 2012; Rogers et al., 2014; Darling et al., 2017). When considered alongside the results of Oren et al. (2023), a consistent pattern emerges in which fish abundance per structure increases with model volume across both studies (Table 1; Fig. 3), while the broader structural comparison is summarized in Table 2. In both datasets, the 200% scaled models supported the highest number of individuals, whereas smaller models consistently showed lower abundance. Although the Branching model displayed greater structural heterogeneity, its narrow branch spacing may have restricted access for larger individuals, explaining the lower total counts recorded, with Large models consistently showing the highest total abundance and species richness (Table 1). These findings suggest that while fine-scale morphology may influence habitat accessibility, overall structural volume is a key factor determining the carrying capacity of artificial coral habitats for reef fishes.

Beyond fish assemblages, the experimental models also supported a diverse range of invertebrates, including shrimps (Fig. 4A), Trapeziidae crabs (Fig. 4A), nudibranchs (Fig. 4D), polychaeta worms, and echinoderms, suggesting that these structures function as habitat for multiple taxa. Notably, several egg masses were observed on some models (Fig. 4B), likely deposited by nudibranchs (presumably *Hexabranhus sanguineus*), and a crab exuvia was recorded on one of the structures (Fig. 4C), indicating potential use for reproduction and shelter. Although these observations were not systematically quantified and fall outside the primary scope of this study, they highlight the broader ecological role of structural complexity in supporting reef associated communities.

(A) A shrimp and two crabs occupying structural crevices (red circles). (B) Egg mass deposited on a model surface. (C) Crab exuvia observed on a model (red circle). (D) Nudibranch observed on the structure (red circle).

4.2 Species Richness and Habitat Suitability

Species richness did not differ significantly among model types, indicating no detectable effect of structural variation within the scope of this study. Although mean richness values were higher in the Large models, this difference was not statistically supported and should be interpreted with caution.

It is possible that the relationship between structural complexity and species richness is non-linear, potentially reflecting a threshold beyond which additional niches become available. Similar relationships have been proposed in previous studies, where fish habitat selection reflects a balance between protection and mobility (Ferreira et al., 2025).

However, because this experiment did not include natural coral references, such as live colonies or dead skeletons, it remains uncertain to what extent these patterns reflect natural reef conditions. Including such references in future work would help clarify whether 3D-printed modules can fully replicate the ecological functions of natural corals or serve only as partial substitutes.

4.3 Behavioral Patterns and Diel Activity

Interestingly, time of day had no significant influence on fish interactions, indicating that diel patterns in this system are likely less pronounced than the structural effects. This contrasts with other reef settings where nocturnal reef fishes maintain daytime resting areas on the reef and move away from these sites during twilight or at night (Collins et al., 2024). The lack of a strong diel signal here might stem from the artificial setting, the limited spatial scale of the experiment, or the predominance of species that remain active throughout daylight transitions, such as *Chromis viridis*.

Despite the absence of a significant diel effect in the statistical models, qualitative observations may suggest a subtle "daytime playground - nighttime quarters" dynamic. During the day, many individuals were seen actively swimming around the modules or briefly hovering within their outer cavities, whereas at night some fishes were repeatedly observed sheltering deeper inside the structures. Such dual-use behavior is consistent with well-documented patterns in reef fishes, which typically forage above the substrate during the day but rely on crevice-rich shelters for nocturnal protection (Holbrook & Schmitt, 2002; Collins et al., 2024). These nighttime observations may indicate that, even if overall interaction rates did not differ significantly between day and night, certain species could nonetheless perceive the modules as safe or suitable refuges for resting.

Behavioral aspects may also have contributed to the observed distribution patterns. Many reef fishes exhibit strong preferences for shelter types that balance concealment with visibility, facilitating both predator avoidance and social interactions (Kerry & Bellwood, 2012). The open geometry of the enlarged models may have promoted such balanced conditions, attracting species that form loose aggregations around coral heads.

4.4 Comparison with Previous Findings

Our results are consistent with those of Oren et al. (2023), together indicating that structural scale is a key determinant of fish abundance. In both studies, the large (200%) models supported the highest abundance, suggesting that increased internal volume and inter-branch spacing enhance carrying capacity for reef fishes. A similar pattern was observed for species richness, where larger structures tended to support more species in both studies, although this relationship was statistically significant only in Oren et al. (2023) and not in the present study. Taken together, these findings suggest that geometric enlargement consistently increases the number of individuals, while its effect on species richness may be more context-dependent, potentially influenced by factors such as temporal scale, community composition, or local environmental conditions. Overall, structural size appears to act as a robust driver of abundance, with a more variable influence on biodiversity across studies. A broader

comparison of structural characteristics and assemblage responses across studies is summarized in Table 2.

Table 2

Structural characteristics of coral models and associated fish assemblage responses across studies

Structural characteristics and descriptive fish assemblage responses for the four experimental coral models, including comparison with Oren et al. (2023).						
Model	Structural characteristic	Oren et al. (2023) total abundance	Current study total abundance	Oren et al. (2023) species richness	Current study species richness	Notable observation
Original	Natural <i>Stylophora pistillata</i> morphology reconstructed from a 3D scan of coral skeleton (100%; diameter 16.0 cm, height 11.3 cm).	30	36	9	15	Lowest total abundance; exclusive species: <i>Gobiodon citrinus</i>
Branching	Branch tips extended by 2.5 cm along their growth direction and thickened to maintain structural stability.	64	57	13	15	Intermediate abundance; one replicate showed particularly high species richness
Large	All structural parameters scaled proportionally to 200% of the original model.	137	169	20	19	Highest total abundance and highest species richness
Table	Branches manipulated to form a corymbose tabular canopy with a diameter of 25 cm.	46	51	15	15	Dominated by <i>Thalassoma rueppellii</i> ; exclusive species: <i>Ecsenius frontalis</i>
Abundance and species richness values from Oren et al. (2023) represent observations from a single structure, whereas values from the present study represent cumulative observations across three replicate structures per model type. These values are presented for descriptive purposes only and should not be interpreted as direct quantitative comparisons between studies.						

4.5 Implications for Conservation and Artificial Reef Design

From a conservation perspective, these findings reinforce the importance of structural design in artificial reef applications. The ability to fine-tune coral-inspired shelter geometry through additive manufacturing provides a powerful platform for experimentally testing habitat use and optimizing artificial modules not only to mimic coral form, but also to deliver ecological functions such as refuge provision, microhabitat creation, and support for reef-associated organisms (Levy et al., 2022; Oren et al., 2023; Tarazi & Levy, 2026). While this study focused on short-term fish responses, the observed effects suggest that relatively small modifications in structural geometry can influence reef fish community structure under natural reef conditions. These manipulations simultaneously altered multiple structural attributes, including colony geometry, branch architecture, refuge configuration, and the spatial arrangement of internal shelter spaces, indicating that the observed fish responses likely reflect the combined effects of shelter architecture rather than colony size alone.

To fully evaluate the ecological relevance of such artificial structures, future experiments should include direct comparisons with live corals and natural dead skeletons. Such comparisons would help determine whether 3D-printed modules can fully replicate the ecological functions of natural corals or provide only partial habitat substitution. They would also clarify how biological characteristics, including living tissue, surface microtopography, and chemical cues, interact with structural geometry to influence reef fish assemblages.

Future research incorporating longer deployment periods, expanded spatial replication, additional structural metrics (e.g., rugosity and fractal dimension), and different material compositions could further elucidate how individual design parameters shape ecological outcomes. As with many controlled field experiments, treatment replication ($n = 3$ per structural design) and the three-month monitoring period warrant caution when extrapolating these findings across broader spatial and temporal scales. Nevertheless, the experimental design provided a controlled framework for isolating how geometric modifications influence reef fish assemblages under natural reef conditions. Despite these limitations, this work highlights the strong interplay between structural morphology and fish behavior, demonstrating that artificial structures can serve not merely as physical substrates but as active determinants of ecological interactions. Together, these findings underscore the importance of structural design in shaping reef-associated communities and provide a framework for the development of next-generation artificial reefs and habitat-based restoration strategies.

Declarations

Funding

This research received no external funding.

Author Contribution

R.L. and A.O. contributed equally to this work. R.L. conducted field surveys, analyzed the data, prepared the figures, and co-wrote the manuscript. A.O. contributed to study conception, experimental design, data interpretation, and co-wrote the manuscript. L.B. and N.C. assisted with fieldwork, data collection, statistical review, and manuscript preparation. E.T. designed and developed the 3D-printed coral models. N.S. conceived and supervised the study, contributed to experimental design, data interpretation, and manuscript preparation. All authors reviewed and approved the final manuscript.

Acknowledgement

We thank Mr. Aviv Levy and the Underwater Observatory Marine Park, Eilat, for technical support. We also thank the Interuniversity Institute for Marine Sciences in Eilat (IUI), the students who assisted with diving activities, and especially the diving club staff, Nahumi Sela and Genadi Zalzman, for their assistance and support throughout the project. We are grateful for the friendship and support of Malinda Goldrich, Peter Schechter, Rosa Puech and Ted Goldberg.

Data Availability

The datasets generated and analyzed during the current study are not publicly available because they form part of ongoing research activities. The data are available from the corresponding author upon request.

References

1. Baden, T., Chagas, A. M., Gage, G., Marzullo, T., Prieto-Godino, L. L., & Euler, T. (2015). Open Labware: 3-D printing your own lab equipment. *PLoS Biology*, 13(3), e1002086. <https://doi.org/10.1371/journal.pbio.1002086>
2. Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, 24(3), 127-135. <https://doi.org/10.1016/j.tree.2008.10.008>.
3. Bongiorni, L., Shafir, S., Angel, D., & Rinkevich, B. (2003). Survival, growth and gonad development of two hermatypic corals subjected to in situ fish-farm nutrient enrichment. *Marine Ecology Progress Series*, 253, 137-144. <https://doi.org/10.3354/meps253137>
4. Coker, D. J., Wilson, S. K., & Pratchett, M. S. (2014). Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries*, 24(1), 89-126. <https://doi.org/10.1007/s11160-013-9319-5>
5. Collins, W. P., Bellwood, D. R., Morais, R. A., Waltham, N. J., & Siqueira, A. C. (2024). Diel movement patterns in nominally nocturnal coral reef fishes (Haemulidae and Lutjanidae): Intra vs. Interspecific variation. *Coral Reefs*, 43(6), 1749-1760. <https://doi.org/10.1007/s00338-024-02573-x>

6. Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, 36(2), 561-575. <https://doi.org/10.1007/s00338-017-1539-z>
7. Ferreira, S. B., Burns, J. H. R., Fukunaga, A., Tuttle Raz, L. J., McKenna, S. A., Annandale, K., & Monello, R. J. (2025). 3D Habitat Complexity and Coral Morphology Modulate Reef Fish Functional Structure in a Marine National Park. *Ecology and Evolution*, 15(9), e71992. <https://doi.org/10.1002/ece3.71992>
8. Graham, N. A. J., & Nash, K. L. (2013). The Importance of Structural Complexity in Coral Reef Ecosystems. *Coral Reefs*, 32(2), 315-326. <https://doi.org/10.1007/s00338-012-0984-y>
9. Gutierrez-Heredia, L., Keogh, C., Keaveney, S., & Reynaud, E. G. (2016). 3D printing solutions for coral studies, education and monitoring. *Reef Encounter*, 31, 39-44.
10. Helmuth, B. S. T., Sebens, K. P., & Daniel, T. L. (1997). Morphological variation in coral aggregations: branch spacing and mass flux to coral tissues. *Journal of Experimental Marine Biology and Ecology*, 209(1-2), 233-259. [https://doi.org/10.1016/S0022-0981\(96\)02687-1](https://doi.org/10.1016/S0022-0981(96)02687-1)
11. Hixon, M. A., & Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101. <https://doi.org/10.2307/2937124>
12. Hoegh-Guldberg, O., Pendleton, L., & Kaup, A. (2019). People and the changing nature of coral reefs. *Regional Studies in Marine Science*, 30, 100699. <https://doi.org/10.1016/j.rsma.2019.100699>
13. Holbrook, S. J., & Schmitt, R. J. (2002). Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology*, 83(10), 2855-2868. [https://doi.org/10.1890/0012-9658\(2002\)083\[2855:CFSSCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2855:CFSSCD]2.0.CO;2)
14. Huang, L., McWilliam, M., Liu, C., Yu, X., Jiang, L., Zhang, C., Luo, Y., Yang, J., Yuan, X., Lian, J., & Huang, H. (2024). Loss of coral trait diversity and impacts on reef fish assemblages on recovering reefs. *Ecology and Evolution*, 14(11), e70510. <https://doi.org/10.1002/ece3.70510>
15. Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., & Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, 20(7), 380-386. <https://doi.org/10.1016/j.tree.2005.03.022>
16. Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., Babcock, R. C., Beger, M., Bellwood, D. R., Berkelmans, R., Bridge, T. C., Butler, I. R., Byrne, M., Cantin, N. E., Comeau, S., Connolly, S. R., Cumming, G. S., Dalton, S. J., Diaz-Pulido, G., Eakin, C. M., Figueira, W. F., Gilmour, J. P., Harrison, H. B., Heron, S. F., Hoey, A. S., Hobbs, J.-P. A., Hoogenboom, M. O., Kennedy, E. V., Kuo, C.-Y., Lough, J. M., Lowe, R. J., Liu, G., McCulloch, M. T., Malcolm, H. A., McWilliam, M. J., Pandolfi, J. M., Pears, R. J., Pratchett, M. S., Schoepf, V., Simpson, T., Skirving, W. J., Sommer, B., Torda, G., Wachenfeld, D. R., Willis, B. L., & Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, 543(7645), 373-377. <https://doi.org/10.1038/nature21707>
17. Kerry, J. T., & Bellwood, D. R. (2012). The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs*, 31(2), 415-424. <https://doi.org/10.1007/s00338-011-0859-7>

18. Kittinger, J. N., Finkbeiner, E. M., Glazier, E. W., & Crowder, L. B. (2012). Human dimensions of coral reef social-ecological systems. *Ecology and Society*, 17(4), 17. <https://doi.org/10.5751/ES-05115-170417>
19. Korniejenko, K., Oliwa, K., Gądek, S., Dynowski, P., Żróbek, A., & Lin, W. T. (2025). A Review of Additive Manufacturing Techniques in Artificial Reef Construction: Materials, Processes, and Ecological Impact. *Applied Sciences*, 15(8), 4216. <https://doi.org/10.3390/app15084216>
20. 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>
21. Lewis, A. R. (1997). Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Marine Ecology Progress Series*, 161, 37-50. <https://doi.org/10.3354/meps161037>
22. Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine biology*, 13(2), 100-123. <https://doi.org/10.1007/BF00366561>
23. Ménard, A., Turgeon, K., Roche, D. G., Binning, S. A., & Kramer, D. L. (2012). Shelters and their use by fishes on fringing coral reefs. *PloS one*, 7(6), e38450. <https://doi.org/10.1371/journal.pone.0038450>
24. Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuisen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, 9(1), 1324. <https://doi.org/10.1038/s41467-018-03732-9>
25. Oren, A., Berman, O., Neri, R., Edery-Lutri, M., Chernihovsky, N., Tarazi, E., & Shashar, N. (2024). Ecological succession on 3D printed ceramic artificial reefs. *Science of the Total Environment*, 954, 176371. <https://doi.org/10.1016/j.scitotenv.2024.176371>
26. Oren, A., Berman, O., Neri, R., Tarazi, E., Parnas, H., Lotan, O., Zoabi, M., Josef, N., & Shashar, N. (2023). Three-dimensional-printed coral-like structures as a habitat for reef fish. *Journal of Marine Science and Engineering*, 11(4), 882. <https://doi.org/10.3390/jmse11040882>
27. Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinner, J. E., Bellwood, D. R., Jones, G. P., Polunin, N. V. C., & McClanahan, T. R. (2008). Effects of climate-induced coral bleaching on coral-reef fishes: Ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review*, 46, 251-296. 10.1201/9781420065756.ch6
28. Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, 24(9), 1000-1005. <https://doi.org/10.1016/j.cub.2014.03.026>
29. Shaish, L., Abelson, A., & Rinkevich, B. (2006). Branch to colony trajectory in a modular organism: Pattern formation in the Indo-Pacific coral *Stylophora pistillata*. *Developmental Dynamics*, 235(8), 2111-2121. <https://doi.org/10.1002/dvdy.20861>
30. Shlesinger, T., & van Woesik, R. (2023). Oceanic differences in coral-bleaching responses to marine heatwaves. *Science of the Total Environment*, 871, 162113.

<https://doi.org/10.1016/j.scitotenv.2023.162113>

31. Tarazi, E., & Levy, O. (2026). Ecosystemism: harnessing biological and 3D new design technologies to regenerate reef functions. *npj Ocean Sustainability*. <https://doi.org/10.1038/s44183-026-00211-3>
32. van Woesik, R., Shlesinger, T., Grottoli, A. G., Toonen, R. J., Vega Thurber, R., Warner, M. E., Marie Hulver, A., Chapron, L., McLachlan, R. H., Albright, R., Crandall, E., DeCarlo, T. M., Donovan, M. K., Eirin-Lopez, J., Harrison, H. B., Heron, S. F., Huang, D., Humanes, A., Krueger, T., Madin, J. S., Manzello, D., McManus, L. C., Matz, M., Muller, E. M., Rodriguez-Lanetty, M., Vega-Rodriguez, M., Voolstra, C. R., & Zaneveld, J. (2022). Coral-bleaching responses to climate change across biological scales. *Global Change Biology*, 28(14), 4229-4250. <https://doi.org/10.1111/gcb.16192>

Figures



Figure 1

Metal frame at the study site with four yellow coral models. Each representing a different structural design, placed alongside naturally growing coral colonies. The setup enabled monitoring of fish interactions with the models under natural reef conditions.

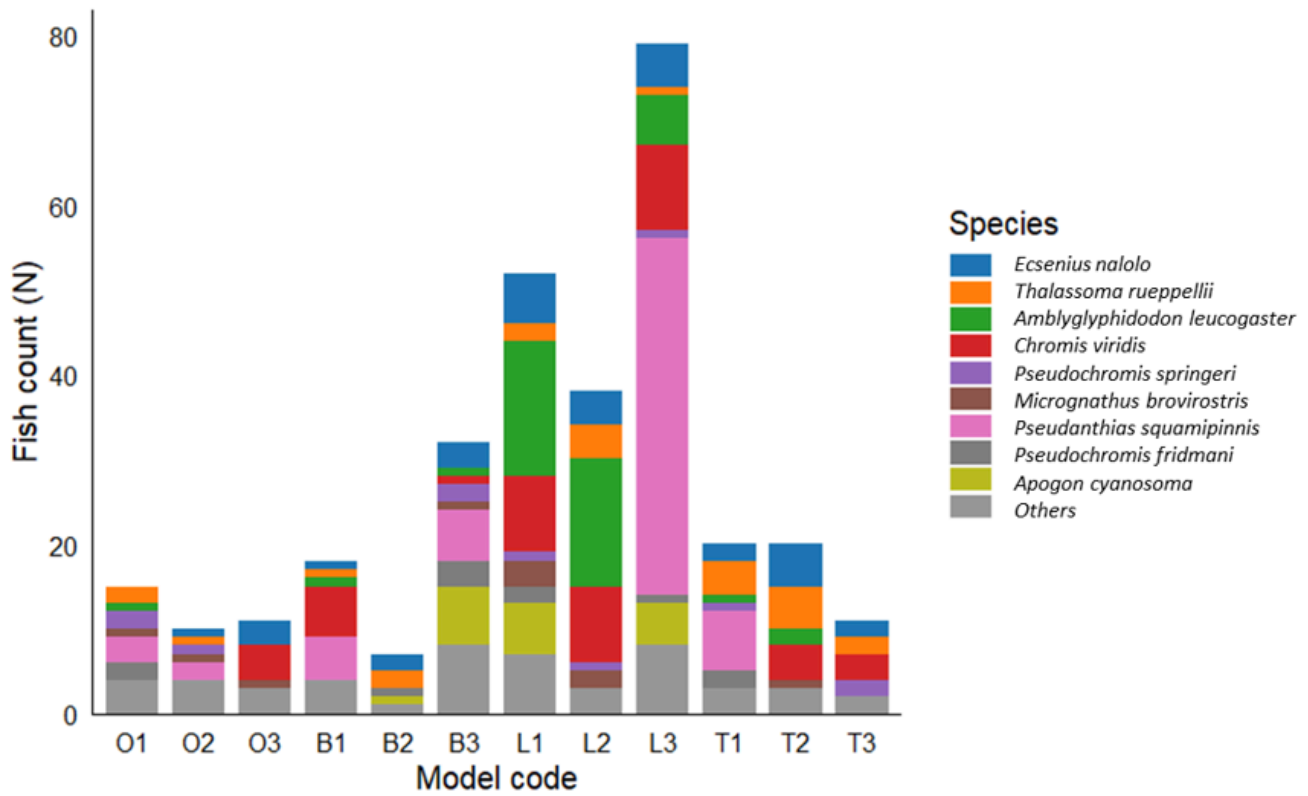


Figure 2

Species richness and abundance of fish observed per coral model. Model codes represent Original (O1–O3), Branching (B1–B3), Large (L1–L3), and Table (T1–T3). The category Others includes species with fewer than ten interactions across all models.

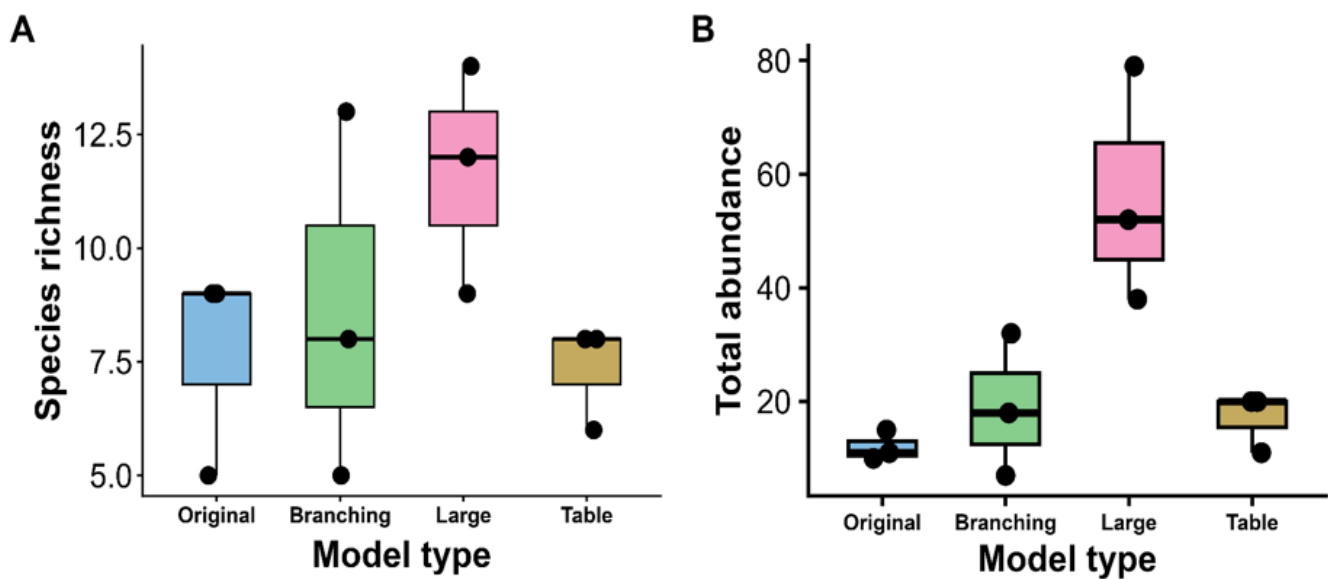


Figure 3

Fish assemblage responses across experimental coral models.

(A) Species richness and (B) total abundance observed for the four coral model types (Original, Branching, Large, and Table). Boxplots represent the distribution among replicates; the central line indicates the median, boxes show the interquartile range, whiskers indicate the range, and black points denote mean values.



Figure 4

Invertebrate interactions associated with experimental coral models.

(A) A shrimp and two crabs occupying structural crevices (red circles). (B) Egg mass deposited on a model surface. (C) Crab exuvia observed on a model (red circle). (D) Nudibranch observed on the structure (red circle).