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Surface complexity enhances early invertebrate recruitment on novel substrates for coral reef restoration

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ABSTRACT

Introduction: Coral reefs are increasingly threatened by climate change and local anthropogenic stressors, prompting the development of artificial substrates for reef restoration. Although substrate material is often considered a key design variable, the relative influence of surface topography on early benthic colonization remains insufficiently resolved.

Objective: To evaluate the effects of experimental substrate material and surface topography on early benthic community assembly at Islote Zacatoso reef, Mexican Pacific.

Methods: Eighteen experimental plates (20 × 20 × 2 cm) representing three substrate materials: Net-Zero AragoReef (aragonite-enriched formulation), aragonite-enriched ceramic, and conventional Portland concrete, were manufactured with either flat or relief-added surfaces (n = 3 per material × relief combination) and deployed at 6 m depth from March to September 2023. Invertebrate abundance and morphospecies composition were analyzed using Bayesian hierarchical modeling, permutational multivariate analysis of variance, non-metric multidimensional scaling, diversity indices, and rarefaction analyses.

Results: A total of 316 morphospecies were recorded after six months of deployment. Relief-added plates supported 2.7–5.7 times higher invertebrate abundance than flat plates across all materials. Bayesian modeling confirmed a strong positive effect of surface topography on abundance, whereas substrate material showed no consistent influence. Community composition differed significantly by surface topography, with clear separation in multivariate space between flat and relief-added treatments, while material effects were not significant. Diversity indices and rarefaction curves consistently indicated higher morphospecies richness and evenness on relief-added plates. Morphospecies accumulation curve did not reach an asymptote, and Chao1 estimated 629 morphospecies (95% CI: 497–761), suggesting substantial undetected diversity.

Conclusions: Surface topography is the primary driver of early benthic colonization, exerting stronger and more consistent effects than substrate composition during initial succession. Carbonate-based substrates supported benthic communities comparable to those observed on conventional concrete, supporting their viability as sustainable alternatives for artificial reef construction. Integrating pronounced surface relief with environmentally

compatible materials may enhance early community development and promote long-term ecological integration in reef restoration contexts.

Key words: artificial reefs; carbonate-based substrates; surface topography; early colonization; Mexican Pacific.

RESUMEN

La complejidad superficial favorece el reclutamiento temprano de invertebrados en sustratos novedosos para la restauración de arrecifes coralinos.

Introducción: Los arrecifes coralinos están cada vez más amenazados por el cambio climático y diversos estresores antropogénicos locales, lo que ha impulsado el desarrollo de sustratos artificiales para la restauración arrecifal. Aunque el material del sustrato suele considerarse una variable clave de diseño, la influencia relativa de la topografía superficial en la colonización béntica temprana aún no está suficientemente resuelta.
Objetivo: Evaluar los efectos del material del sustrato y la topografía superficial en el ensamblaje temprano de comunidades bénticas en el arrecife Islote Zacatoso, en el Pacífico mexicano.
Métodos: 18 placas experimentales (20 × 20 × 2 cm) que representaron tres materiales de sustrato: Net-Zero AragoReef (formulación enriquecida con aragonita), cerámica enriquecida con carbonato de calcio, y concreto Portland convencional, fueron fabricadas con superficies planas o con relieve añadido (n = 3 por combinación material × relieve) y desplegadas a 6 m de profundidad entre marzo y septiembre de 2023. La abundancia de invertebrados y la composición de morfoespecies se analizaron mediante modelado jerárquico bayesiano, análisis de varianza multivariado permutacional, escalamiento multidimensional no métrico, índices de diversidad y análisis de rarefacción.
Resultados: Se registraron un total de 316 morfoespecies después de seis meses de despliegue. Las placas con relieve añadido presentaron abundancias de invertebrados entre 2.7 y 5.7 veces mayores que las placas planas en todos los materiales evaluados. El modelado bayesiano confirmó un efecto positivo fuerte de la topografía superficial sobre la abundancia, mientras que el material del sustrato no mostró una influencia consistente. La composición comunitaria difirió significativamente según la topografía, con una clara separación en el espacio multivariado entre tratamientos planos y con relieve añadido, mientras que los efectos del material no fueron significativos. Los índices de diversidad y las curvas de rarefacción indicaron consistentemente mayor riqueza y equidad en las placas con relieve añadido. La curva de acumulación de morfoespecies no alcanzó una asíntota y el estimador Chao1 proyectó 629 morfoespecies (IC 95%: 497–761), lo que sugiere una diversidad no detectada considerable.
Conclusiones: La topografía superficial constituye el principal impulsor de la colonización béntica temprana, ejerciendo efectos más fuertes y consistentes que la composición del sustrato durante las etapas iniciales de sucesión. Los sustratos carbonatados mostraron un desempeño ecológico comparable al del concreto convencional, lo que respalda su viabilidad como alternativas sostenibles para la construcción de arrecifes artificiales. La integración de relieve superficial pronunciado con materiales ambientalmente compatibles puede favorecer el desarrollo temprano de comunidades bénticas y promover una integración ecológica a largo plazo en contextos de restauración arrecifal.

Palabras clave: arrecifes artificiales; sustratos carbonatados; topografía superficial; colonización temprana; Pacífico mexicano.

INTRODUCTION

Coral reefs are among the most biodiverse and functionally complex ecosystems on Earth, providing habitat for nearly one-third of all marine species (Veron et al., 2016). This ecological richness depends on the three-dimensional framework built by calcifying organisms, primarily scleractinian corals (Spalding et al., 2001), along with diverse encrusting calcifiers, including crustose coralline algae, bryozoans, foraminifera, serpulids, and mollusks (Mallela & Perry, 2007; Perry & Hepburn, 2008). Despite their ecological and socioeconomic importance, coral reefs face unprecedented degradation from the combined effects of global and local stressors, including ocean warming, acidification, sea-level rise, and increasingly intense storms (Albright et al., 2023; Cornwall et al., 2023; Hughes et al., 2018). Since 1998, four global mass coral bleaching events have been documented (1998, 2010, 2014–2017, and 2023–2024; Reimer et al., 2024), with the most recent causing extreme coral mortality (>90%)

in the southern Mexican Pacific (López-Pérez et al., 2024). Projections from the latest generation of climate models indicate that severe bleaching events may occur annually by the end of this century (UNEP, 2020), underscoring the urgent need for proactive and effective reef restoration strategies (Reimer et al., 2024).

In this context, artificial reefs are a key restoration tool, designed to recreate habitat complexity, enhance species colonization, and accelerate ecosystem recovery (Hylkema et al., 2020). Beyond their applied role, artificial structures also serve as valuable experimental platforms for investigating early successional dynamics in benthic communities under controlled, replicable conditions (Mallela et al., 2017). A wide range of materials has been used in artificial reef construction, including Portland concrete, ceramics, basalt, polyvinyl chloride (PVC), and metal frameworks (Becker et al., 2018). However, their ecological performance varies substantially, reflecting differences in both physical structure and material properties. Previous studies have identified substrate composition as a key driver of larval settlement and early recruitment, with chemical cues influencing attachment, metamorphosis, and post-settlement survival (Fusetani, 2004), while structural complexity can further enhance recruitment by providing refuges and favorable settlement microhabitats (Edmunds, 2023). Unglazed ceramics and terracotta, for example, have been widely used to investigate coral recruitment and the settlement of encrusting invertebrates (Fairfull & Harriott, 1999; Hepburn et al., 2014; Kennedy et al., 2017). In the Mexican Pacific, research on benthic colonization has largely relied on PVC substrates (Alvarado-Rodríguez et al., 2022; Orrante-Alcaraz et al., 2023; Pareja-Ortega et al., 2025), providing valuable insights into community assembly under local environmental conditions.

However, growing evidence indicates that small-scale surface topography may have a stronger influence on benthic community structure than substrate material alone. Fine-scale topographic complexity shapes hydrodynamics, sediment retention, light exposure, and predator–prey interactions, thereby determining the availability and quality of microhabitats for settling organisms (Nozawa et al., 2011; Strain et al., 2021). Natural reef surfaces exhibit high microtopographic heterogeneity driven by calcifiers morphology, bioerosion, and physical forces (Bromley et al., 1990; Turicchia et al., 2022). This structural complexity enhances larval retention and survival by providing refuges from predation and environmental stress. In contrast, artificial substrates often lack comparable microtopographic variability, which can limit recruitment success and reduce early biodiversity (Evans et al., 2021).

Despite the recognized importance of surface topography, relatively few experimental studies have explicitly evaluated its influence relative to substrate material composition. This knowledge gap limits our ability to optimize artificial reef design for ecological performance and long-term functionality. Here, we assess the relative roles of substrate material and surface topography in shaping the abundance, diversity, and community composition of early-colonizing invertebrates. Experimental plates made of Net-Zero AragoReef (an aragonite-enriched formulation; Corona-Herrera & Padilla-Souza, 2024), aragonite-enriched ceramic (Corona-Herrera & Padilla-Souza, 2024) and conventional Portland concrete were deployed at the Islote Zacatoso reef in Zihuatanejo, Guerrero, Mexico. Each material was manufactured in two surface topography treatments: flat and relief-added. Net-Zero AragoReef and aragonite-enriched ceramic are high-aragonite artificial substrates engineered to approximate key physical and chemical attributes of natural reef frameworks.

By integrating morphospecies richness estimates, multivariate community analyses, and Bayesian modeling, we examine the relative contributions of surface topography and substrate material to early benthic community assembly. Our findings inform the sustainable design of artificial reefs and have direct implications for restoration efforts in regions recovering from recurrent mass bleaching events.

MATERIALS AND METHODS

Study site: This study was conducted at Islote Zacatoso (17°39'15.25" N, 101°37'19.47" W, Fig. 1A), located near the coast in Zihuatanejo, Guerrero, in the southern tropical Mexican Pacific. The region is influenced by two major currents: the southward-flowing California Current (November–April), which brings cooler, low-salinity, oxygen-rich waters, and the northward Equatorial Current (May–October), characterized by warmer, saltier, oxygen-poor waters (Fiedler & Lavín, 2017). Interannual variability in sea surface temperature (SST) is largely modulated by El Niño events, which elevate SST and deepen both the thermocline and the nutricline (Fiedler & Talley, 2006). The rainy season (June–September) increases sediment input near the coast, with adverse effects on coral communities (Nava et al., 2014). Coastal communities in the region also experience significant anthropogenic pressure, as evidenced by elevated chlorophyll concentrations and sedimentation rates linked to land-use changes (Nava et al., 2023).

Islote Zacatoso hosted a fringing coral reef spanning approximately 1.9 hectares, extending from southwest to northeast and reaching depths of up to 12 m. Historically dominated by *Pocillopora* corals, the reef supported a well-developed patch reef ecosystem (Nava et al., 2023). However, the 2023–2024 El Niño event caused extensive coral mortality, leaving the reef largely devoid of living coral. Today, only a few small, scattered colonies persist, reflecting a dramatic decline in ecological health (Nava et al., 2025).

Deployment of experimental substrates and laboratory processing: Twelve settlement plates were deployed for each of three substrate materials: Net-Zero AragoReef (hereafter AragoReef), calcium carbonate-enriched ceramic (hereafter ceramic), and conventional Portland concrete (hereafter concrete), for a total of 36

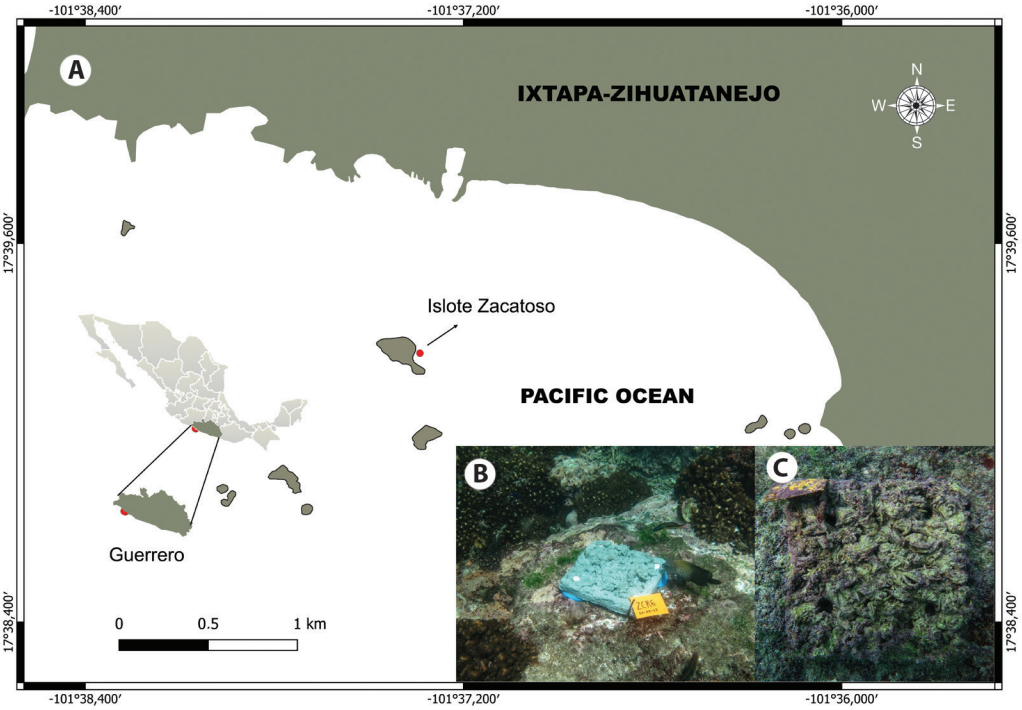


Fig. 1. A. Location of the study site in the coastal sublittoral zone in Zihuatanejo, Guerrero, Mexican Pacific. **B.** Experimental plate upon deployment and **C.** after six months of exposure.

plates. AragoReef (Corona-Herrera & Padilla-Souza, 2024), an aragonite-enriched composite substrate developed for reef restoration applications, and the carbonate-enriched ceramic (Corona-Herrera & Padilla-Souza, 2024) are carbonate-based substrates engineered to approximate the structural and chemical characteristics of natural reef frameworks, whereas concrete was prepared using commercially available Portland cement. For each material, plates were manufactured in two surface topography treatments: flat and relief-added, with six replicates per material-topography combination. Relief-added plates incorporated irregular topographic features, including elongated ridges and rounded protrusions, without a standardized geometric pattern, producing surface elevations of up to 1 cm. For all analyses, only the upward-facing surface of each plate was considered, representing a standardized sampling area of 400 cm^2 (20 × 20 cm) exposed to natural light, predation, and sedimentation.

The plates were uniformly distributed across a still-healthy reef area at a depth of approximately 6 m (March 2023) on hard substrates that were not colonized by corals (e.g., rocks and limestone pavement), ensuring no damage to adjacent living coral colonies (Fig. 1B). Treatments were spatially interspersed without clustering by material or topography, and plates were separated by approximately 4–5 m to minimize potential spatial autocorrelation and local environmental bias. Prior to deployment, the attachment substrate was scrubbed with a brush and knife to remove macroalgae and algal turfs, ensuring proper plate adhesion. Marine epoxy plaster (MPT-100) was used to securely attach the plates to the substrate, and each plate was labeled with site, material, topography, and replicate.

After six months of deployment, the plates were retrieved in September 2023 (Fig. 1C). A total of 14 plates were recovered: 3 AragoReef (1 relief-added and 2 flat), 4 ceramic (2 relief-added and 2 flat), and 7 concrete (4 relief-added and 3 flat). Each recovered plate was maintained underwater in individual sealed bags to preserve mobile fauna and transported to the boat in a water-filled container. On board, plates were removed from the bags, photographed, and gently rinsed with seawater to remove sediments. Mobile macrofauna, such as echinoderms and crustaceans dislodged during rinsing, were collected separately. Plates were then fixed in 4% formalin for laboratory processing.

In the laboratory, the plates were submerged separately in airtight containers with a 4% formalin solution for three days, followed by thorough rinsing and soaking in running water for an additional three days to remove fixative residues. Organisms were then carefully detached and initially sorted into major taxonomic groups. All specimens were counted and identified to the lowest possible taxonomic resolution and treated as morphospecies for all analyses. Identifications were conducted under a stereoscopic microscope (4×) based on morphological traits such as body shape, size, and color pattern, and guided by specialized references for marine invertebrates (Ramos-Morales, 2022), ophiuroids (Granja-Fernández, 2014), polychaetes (De León-González et al., 2021), bivalves (Penagos-García, 2013), gastropods (Penagos-García, 2013; Alarcón-Cháires et al., 2002; Beechey, 2025), arthropods (Fischer et al., 1995; García-Madrigal & Andréu-Sánchez, 2009; Ortiz, 2021; Cortés et al., 2010; Salgado-Barragán & Hendrickx, 2010), and sponges (Cruz-Barraza, 2008). Taxonomic names were cross-verified against the most recent records in the World Register of Marine Species (WoRMS, 2025).

Data analyses: We applied a Bayesian hierarchical modeling approach to quantify the effects of substrate material (AragoReef, ceramic, concrete) and surface topography (flat vs. relief-added) on benthic invertebrate abundance. The model assumed a negative binomial distribution with a log link function to account for overdispersion in count data:

$$\text{Abundance} \sim \text{Material} + \text{Topography} + (1 \mid \text{Code})$$

where Material and Topography were fixed effects, and Code (plate identity) was modeled as a random intercept.

Bayesian models were fitted using three Markov chain Monte Carlo (MCMC) chains, each with 10 000 iterations, including 2 000 warm-up iterations and a thinning interval of 5 to reduce within-chain autocorrelation. Weakly informative priors were specified for the dispersion parameter and the random effect variance, while default weakly informative priors were retained for fixed effects. Convergence was confirmed by Rhat values close to 1.00 and effective sample sizes (ESS > 2 000). Model fit was evaluated using Bayesian R^2 (0.77), indicating strong explanatory power. Posterior predictive checks showed a good agreement between observed and simulated data, and the Bayesian p-value (p_Bayes = 0.43) suggested no evidence of systematic model misfit. The model was implemented in Stan (Stan Development Team, 2021) via the brms package (Bürkner, 2017).

Community composition was analyzed independently using permutational multivariate analysis of variance (PERMANOVA) with Bray–Curtis dissimilarities computed from fourth-root-transformed morphospecies abundance data, which were transformed prior to distance calculation to reduce the influence of dominant taxa. An initial two-factor model including substrate material, surface topography, and their interaction was evaluated. Because the interaction term was not significant, a reduced additive model including only main effects was retained. PERMANOVA was performed with 9999 permutations using the adonis function in the vegan package (Oksanen et al., 2025). To assess whether significant PERMANOVA results reflected differences in multivariate dispersion rather than shifts in group centroids, homogeneity of dispersion was evaluated using permutational analysis of multivariate dispersions (PERMDISP) with the betadisper function in vegan. Multivariate patterns were visualized using non-metric multidimensional scaling (nMDS) based on the same fourth-root-transformed Bray–Curtis dissimilarity matrix. The resulting stress value (0.13) indicated an acceptable representation of multivariate structure. Ordinations were conducted and visualized using the vegan and ggplot2 packages (Oksanen et al., 2025; Wickham, 2016).

To evaluate morphospecies richness and standardize comparisons across treatments, we applied two complementary approaches. First, we constructed a morphospecies accumulation curve using abundance data from all settlement plates. The curve was generated with the specaccum function using random permutations to account for sampling order (Oksanen et al., 2025). Observed morphospecies richness was compared with Chao1 estimates, a non-parametric estimator that infers undetected diversity based on the frequency of rare taxa, specifically singletons and doubletons (Chao, 1984). Chao1 estimates and associated 95% confidence intervals were computed using the specpool function in the vegan package.

Second, we used rarefaction curves to compare morphospecies richness among substrate materials and surface topography treatments while accounting for differences in sampling effort. For substrate materials, morphospecies richness was rarefied to the smallest number of replicates (n = 3, corresponding to AragoReef). For surface topography treatments, which had equal replication (n = 7 plates per level), morphospecies richness was compared directly. Rarefaction curves were computed using the specaccum function with the random permutation method in the vegan package (Oksanen et al., 2025).

All statistical analyses were conducted in R version 4.4.2 (R Core Team, 2024). Data and annotated code are provided as supplementary material.

RESULTS

The invertebrate assemblage was dominated by Arthropoda, accounting for 41.4% of all individuals (n = 1646), followed by Mollusca (25.7%, n = 1 021) and Annelida (15.8%, n = 628). Together, these three phyla comprised over 80% of the total abundance. Secondary contributors included Echinodermata (5.9%, n = 234), Bryozoa (5%, n = 199), and Chordata (3.5%, n = 140), whereas Nematoda, Porifera,

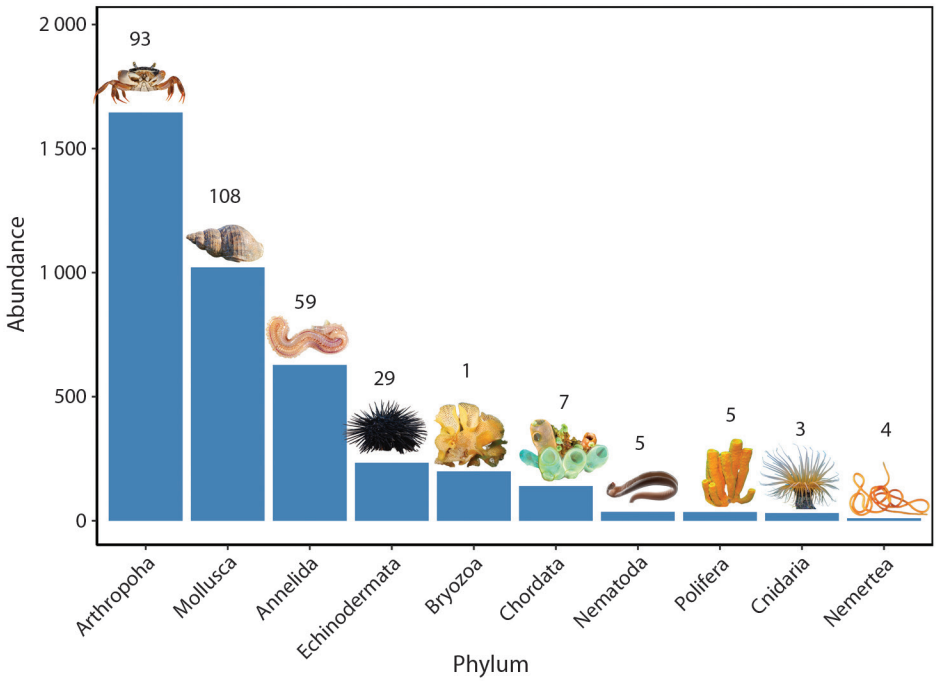


Fig. 2. Total abundance of invertebrates grouped by phylum across all experimental plates. Numbers above bars indicate the total number of morphospecies recorded within each phylum.

Cnidaria, and Nemertea collectively accounted for less than 3% (n = 117). In terms of morphospecies richness, Mollusca was the most diverse phylum, with 108 morphospecies (27.6% of the total), followed by Arthropoda (93 morphospecies, 23.8%) and Annelida (59 morphospecies, 15.1%). The remaining phyla exhibited relatively lower richness: Echinodermata (29 morphospecies), Chordata (7), Nematoda and Porifera (5 each), Nemertea (4), Cnidaria (3), and Bryozoa (1) (Fig. 2).

Although invertebrate abundance varied among treatments, it was consistently higher on relief-added plates across all substrate materials. Mean abundance increased 5.3-fold on AragoReef (400 on relief-added vs 75 ± 70 on flat plates), 5.7-fold on ceramic (583 ± 136 vs 102 ± 96), and 2.7-fold on concrete (404 ± 368 vs 151 ± 82) (Fig. 3A). Only one AragoReef relief-added plate was recovered, precluding estimation of within-treatment variability for this group. Model-predicted abundances reflected these trends, showing consistently higher expected values on relief-added plates regardless of material type (Fig. 3B). Bayesian hierarchical modeling confirmed a strong effect of surface topography on invertebrate abundance, whereas substrate material showed no consistent influence. The posterior estimate for flat plates was negative (Estimate = -1.37, 95% CI: -2.39 to -0.36), indicating lower expected abundance relative to relief-added plates. Using AragoReef as the reference material, posterior coefficients for ceramic (0.41, 95% CI: -1.00 to 1.85) and concrete (0.33, 95% CI: -1.00 to 1.60) overlapped zero, suggesting weak or negligible material effects. Posterior distributions for pairwise contrasts involving surface topography (e.g., AragoReef flat vs AragoReef relief-added) were clearly shifted below 1 on the response scale, indicating lower abundance on flat plates relative to relief-added plates. In

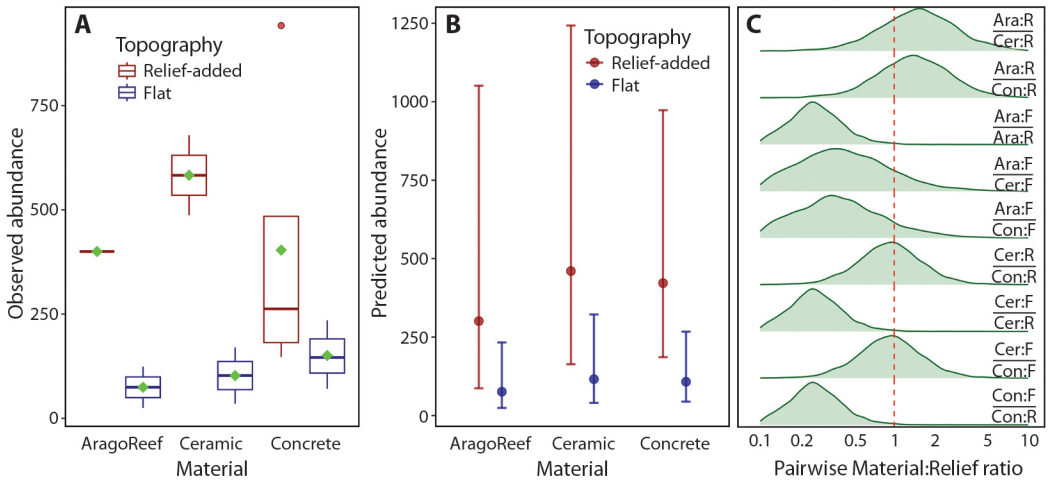


Fig. 3. Effects of surface topography and substrate material on invertebrate abundance. (A) Observed invertebrate abundances across treatments. Box plots show the interquartile range (25th to 75th percentiles), with whiskers extending to the 5th and 95th percentiles. The notch represents the confidence interval around the median (horizontal line), green diamonds indicate the mean, and red points denote extreme values. (B) Model-predicted abundances from the Bayesian hierarchical model. Points represent posterior means of expected abundance, and error bars indicate 95% credible intervals. (C) Posterior distributions of pairwise treatment contrasts expressed as response-scale ratios. Material: Ara = AragoReef, Con = Concrete, Cer = Ceramic. Topography: R = Relief-added, F = Flat. The dashed red line indicates a ratio of 1. Distributions shifted away from 1 indicate directional differences between treatments. Because contrasts were calculated as flat relative to relief-added, values below 1 indicate lower abundance on flat plates. Distributions overlapping 1 indicate weak or no evidence of differences between treatments.

contrast, pairwise comparisons among materials within the same topography level were centered around 1, with no consistent directional differences (Fig. 3C).

Arthropoda, Mollusca, and Annelida consistently dominated across all substrate materials (Fig. 4). Relief-added plates supported higher abundances overall, particularly on concrete, which harbored the highest counts of these dominant phyla (512 Arthropoda, 407 Mollusca, and 335 Annelida individuals). Ceramic showed similarly elevated values (465 Arthropoda, 343 Mollusca), whereas AragoReef supported comparatively fewer individuals (245 Arthropoda, 56 Mollusca). In contrast, flat plates exhibited markedly lower abundances, although flat concrete retained relatively high numbers of Mollusca (n = 182) and Arthropoda (n = 156). Bryozoa and Echinodermata were recorded exclusively on relief-added ceramic and concrete, while rarer phyla such as Nemertea and Porifera occurred only sporadically and predominantly on relief-added substrates.

Both Shannon and Simpson diversity indices varied among material–topography combinations (Table 1). Relief-added plates generally supported higher diversity, with ceramic relief-added exhibiting the highest values for both Shannon (3.83 ± 0.54) and Simpson (0.95 ± 0.02) indices, accompanied by high morphospecies richness (110 ± 59.4). In contrast, ceramic flat plates showed the lowest diversity (Shannon: 1.86 ± 0.16; Simpson: 0.72 ± 0.12) and low richness (16.5 ± 6.4), reflecting strong dominance by a few taxa. Concrete maintained relatively high diversity across topography (Shannon: 3.01–3.40; Simpson: 0.88–0.93), with limited variation between flat and relief-added treatments. For AragoReef, diversity values were intermediate compared with those of other materials. Relief-added plates showed Shannon and Simpson values of 2.90 and 0.89, respectively, whereas flat plates exhibited

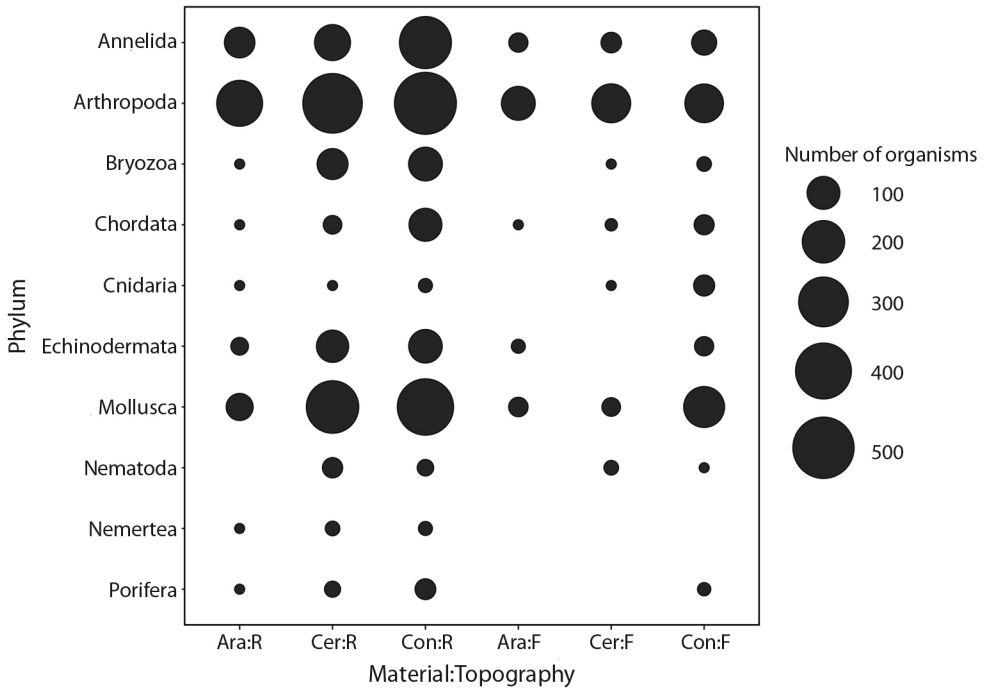


Fig. 4. Variation in invertebrate abundance across substrate materials (Ara = AragoReef, Cer = ceramic, Con = concrete) and surface topography treatments (F = flat, R= relief-added). Bubble size represents the total number of individuals recorded per material–topography combination, based on the number of plates recovered within each category.

Table 1

Mean (± SD) morphospecies richness (S), Shannon diversity (H'), and Simpson diversity (D) for invertebrate assemblages across substrate materials and surface topography treatments (flat and relief-added). N indicates the number of plates analyzed per material–topography combination. * indicates that the treatment only has one replica.

Material	Topography	S	H'	D	N
Ara	R	53.0*	2.90*	0.89*	1
Ara	F	21.0 ± 11.3	2.60 ± 0.30	0.90 ± 0.01	2
Cer	R	110.0 ± 59.4	3.83 ± 0.54	0.95 ± 0.02	2
Cer	F	16.5 ± 6.4	1.86 ± 0.16	0.72 ± 0.12	2
Con	R	66.2 ± 27.8	3.40 ± 0.47	0.93 ± 0.05	4
Con	F	41.7 ± 8.1	3.01 ± 0.51	0.88 ± 0.10	3

Material: Ara = AragoReef; Cer = ceramic; Con = concrete. Topography: R = relief-added; F = flat. For AragoReef relief-added, richness and diversity values are based on a single plate (n = 1), and standard deviations are not reported.

slightly lower Shannon diversity (2.60 ± 0.30) but comparable Simpson values (0.90 ± 0.01). Interpretation of the relief-added treatment for AragoReef is limited by the recovery of a single plate (n = 1), which precludes estimation of within-treatment variability.

The Venn diagrams revealed contrasting patterns of morphospecies richness associated with substrate material (Fig. 5A) and surface topography (Fig. 5B). When replicates were pooled across topography treatments, concrete supported the highest richness (208 morphospecies), with 99 (31% of the total) occurring exclusively on this material. Of the remaining taxa recorded on concrete, 51 (16%) were shared with ceramic, whereas only 13 (4%)

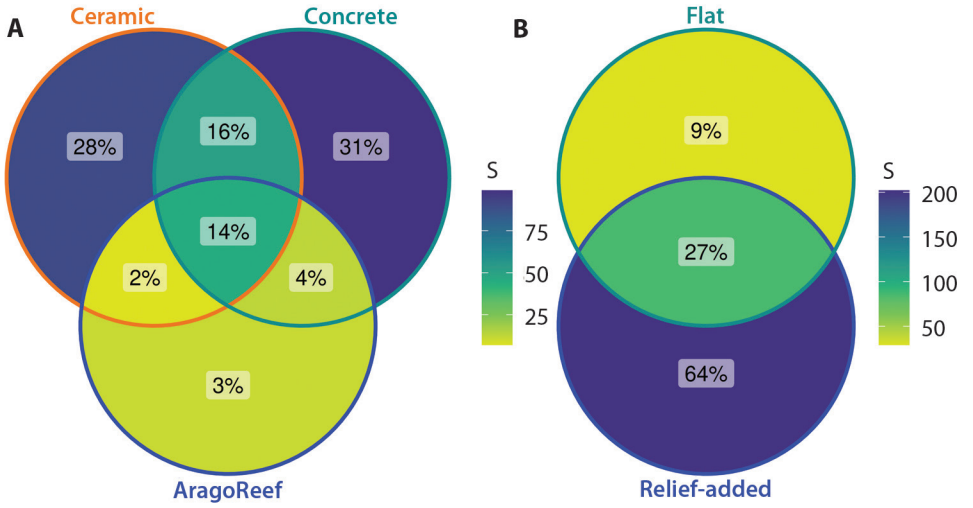


Fig. 5. Venn diagrams showing morphospecies richness pooled across replicates for (A) substrate materials and (B) surface topography. Percentages indicate the proportion of total morphospecies richness, while circle shading represents absolute morphospecies richness (S).

overlapped with AragoReef. Ceramic hosted 193 morphospecies in total, of which 90 (28%) were unique to this material and seven (2%) were shared exclusively with AragoReef. In contrast, AragoReef exhibited the lowest richness, supporting 76 morphospecies, including 11 (3%) that were exclusive to this substrate. Notably, only 45 morphospecies (14%) were common to all three materials. Patterns associated with surface topography were more pronounced. Relief-added plates supported substantially higher exclusive richness, with 202 morphospecies (64%) occurring only on relief-added substrates, compared with 29 (9%) exclusive to flat plates. An additional 85 morphospecies (27%) were shared between both topography treatments.

Community composition differed according to surface topography but not substrate material (Table 2). PERMANOVA detected no significant effect of substrate material on morphospecies composition (Pseudo-F = 1.12, R^2 = 0.155, p = 0.251), whereas surface topography had a significant effect (Pseudo-F = 2.18, R^2 = 0.151, p = 0.001). Tests for homogeneity of multivariate dispersion were not significant (PERMDISP: F = 1.33, p = 0.277), indicating no evidence of differential dispersion among topography levels.

The nMDS ordination based on Bray–Curtis dissimilarities of fourth-root transformed morphospecies abundances revealed weak differentiation in community composition among substrate materials, with substantial overlap in multivariate space across materials (Fig. 6A). In

Table 2

Results of PERMANOVA testing the effects of substrate material and surface topography on morphospecies community composition (Bray–Curtis dissimilarities based on fourth-root transformed abundance data; 9999 permutations).

Source	DF	Sum of Square	R^2	Pseudo-F	p-value
Material	2	0.552	0.155	1.116	0.251
Topography	1	0.539	0.151	2.180	0.001
Residual	10	2.474	0.694	—	—
Total	13	3.565	1.000	—	—

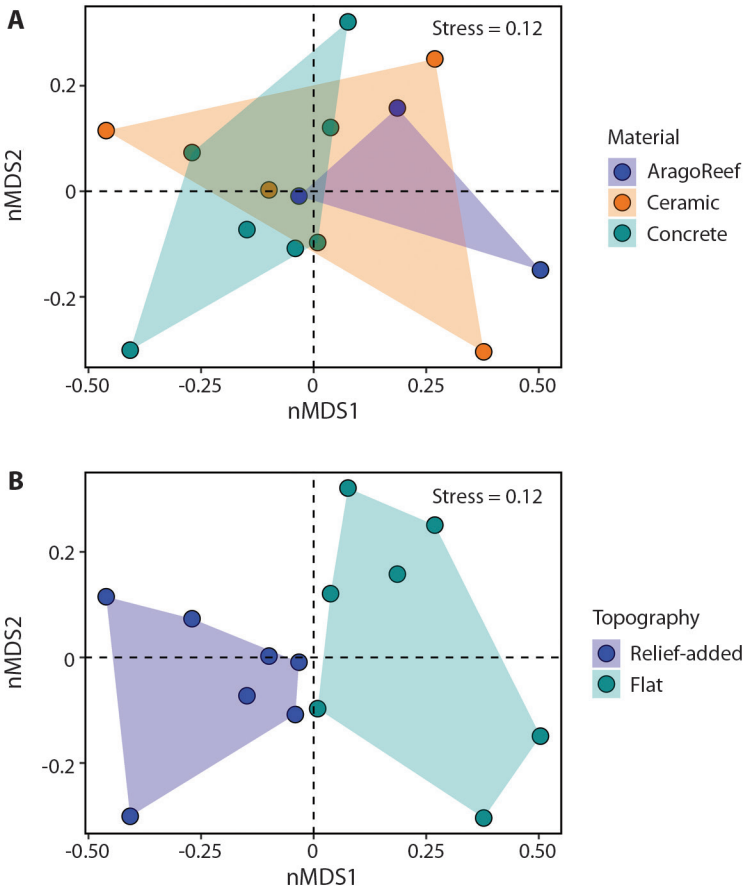


Fig. 6. Non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarities of fourth-root transformed morphospecies abundances after six months of deployment at Islote Zacatoso. (A) Community patterns among substrate materials. (B) Community patterns according to surface topography.

contrast, samples grouped according to surface topography, with relief-added and flat plates occupying distinct regions of multivariate space (Fig. 6B).

The morphospecies accumulation curve based on all 14 settlement plates showed a steep initial rise in richness with each additional sample and did not reach an asymptote at maximum sampling effort. A total of 316 morphospecies were recorded, whereas the Chao1 estimator projected 629 morphospecies (95% CI: 497–761), indicating substantial undetected diversity (Fig. 7).

Rarefaction analyses indicated modest differences in morphospecies richness among substrate materials. However, when standardized to the lowest sampling effort (e.g., two to three plates), standard deviation intervals for AragoReef, ceramic, and concrete overlapped broadly (Fig. 8A). In contrast, comparisons based on surface topography showed consistently higher morphospecies richness on relief-added plates across the entire rarefaction curve (Fig. 8B).

DISCUSSION

Our study indicates that surface topography was the dominant driver of early benthic community assembly, whereas substrate

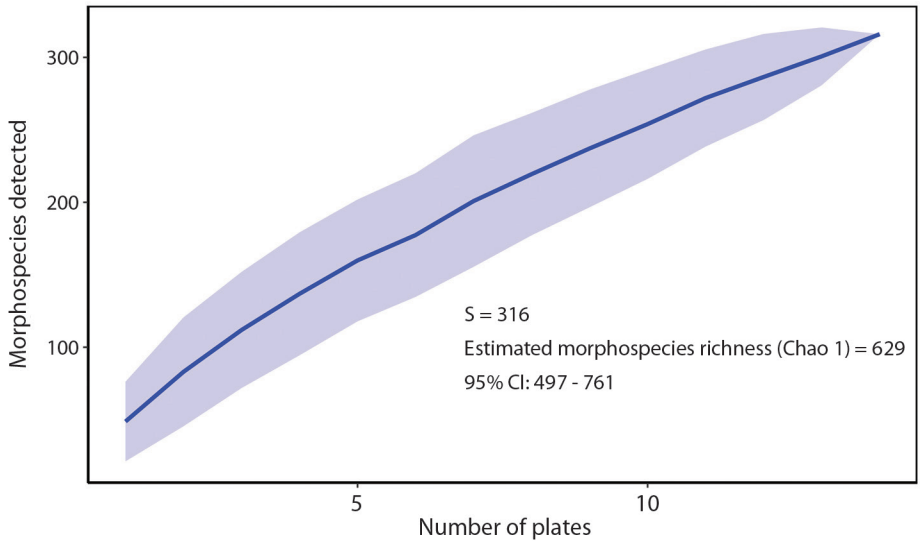


Fig. 7. Morphospecies accumulation curve based on all 14 settlement plates. The solid blue line represents mean observed morphospecies richness as a function of sampling effort (number of plates), with shaded ribbons indicating standard deviation among random permutations. Observed morphospecies richness (S = 316) is shown together with the Chao1 estimated morphospecies richness (S = 629; 95% CI: 497–761).

material exerted comparatively minor effects once structural complexity was statistically accounted for. Relief-added plates consistently supported higher invertebrate abundance and morphospecies richness across all materials, with increases of up to 5.7-fold relative to flat plates. This cross-phyletic response underscores the ecological importance of small-scale structural heterogeneity in enhancing larval settlement, refuge availability, and post-settlement survival (Nozawa et al., 2011; Skinner & Coutinho, 2005; Strain et al., 2021; Tourneux & Bourget, 1988; Walters & Wethey, 1991; Whalan et al., 2015; Witte, 2025). The consistency of this pattern across abundance metrics, diversity indices, multivariate analyses, and rarefaction curves indicates that microhabitat heterogeneity functions as a strong ecological filter during early successional stages. Notably, relief-added plates harbored more than six times the number of exclusive morphospecies recorded on flat plates and were generally associated with higher Shannon and Simpson diversity values. Structural complexity likely modifies local hydrodynamics, sediment retention, and predator-prey interactions, generating microhabitats that promote niche differentiation and sustain broader taxonomic representation (Edmunds et al., 2014; Nozawa et al., 2011; El Hedeny et al., 2021; Randall et al., 2021; Bauer et al., 2024). Recent modeling work further suggests that topographic features can alter benthic boundary-layer flow and create recirculatory structures that enhance passive larval transport and settlement, potentially explaining the strong effects of surface relief observed across substrate materials in the present study (Gysbers et al., 2025).

Contrary to previous reports of material-specific recruitment and settlement preferences (Anderson & Underwood, 1994; Glasby, 2000; Kennedy et al., 2017; Siddik et al., 2018; Yus et al., 2024), our Bayesian models detected no consistent differences among carbonate-based substrates and conventional concrete once surface topography was incorporated. PERMANOVA similarly indicated that only surface topography exerted a statistically detectable influence on community composition, accounting for approximately 15% of the

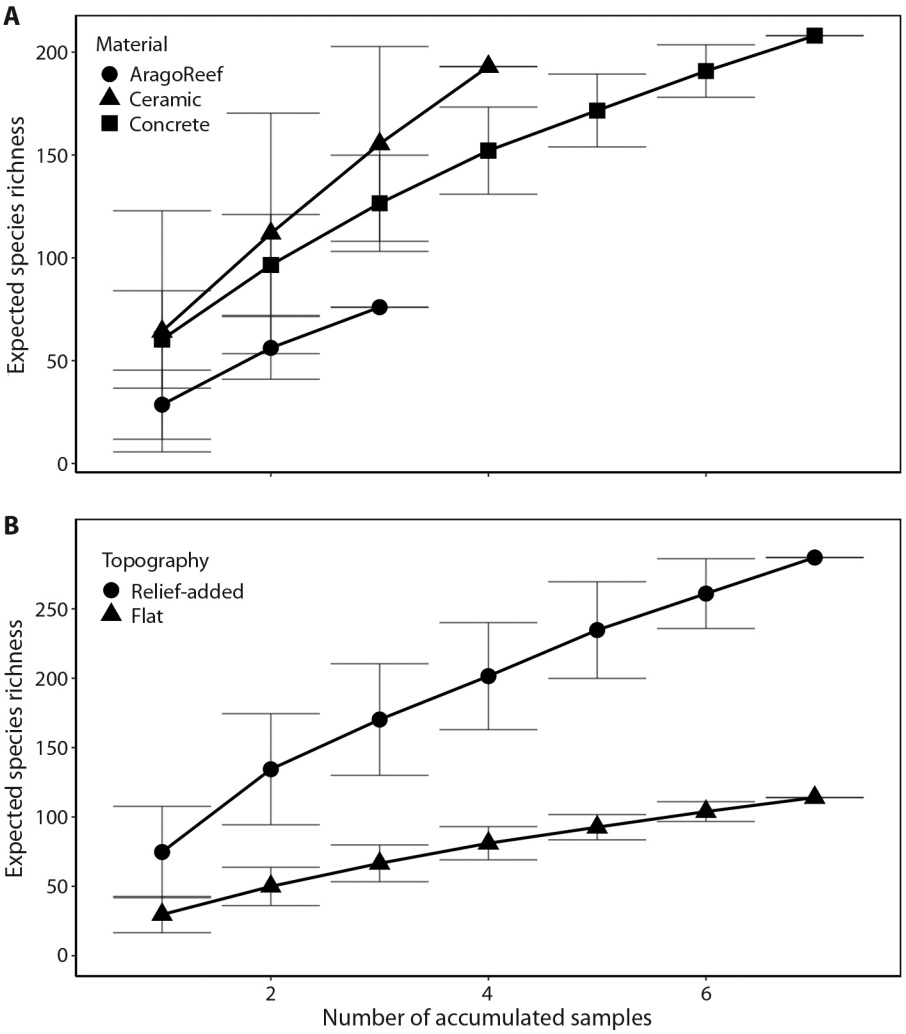


Fig. 8. Rarefaction curves showing expected morphospecies richness as a function of sampling effort (number of accumulated plates) for (A) substrate materials and (B) surface topography treatments. Vertical bars represent standard deviation among random permutations.

observed variation, whereas substrate material did not produce significant compositional divergence. Importantly, this outcome indicates that carbonate-based substrates performed comparably to conventional concrete during early colonization. Abundances and multivariate community structure overlapped substantially among ceramic, AragoReef, and concrete, suggesting functional equivalence at initial successional stages and reinforcing the viability of carbonate-based alternatives in restoration contexts (Burt et al., 2009; Encomendero & Dupré, 2003; Field et al., 2007).

Nevertheless, patterns of exclusive morphospecies indicate some degree of substrate-associated partitioning. After rarefaction was standardized by replicate number, ceramic plates exhibited the highest exclusive morphospecies richness. Although these differences were not supported by formal statistical

tests and should therefore be interpreted cautiously, particularly given the recovery of only a single relief-added AragoReef plate, they suggest that substrate identity may contribute to subtle niche differentiation. Such effects could arise from differences in biofilm development and microscale chemical cues influencing early settlement processes (Tran & Hadfield, 2011; Webster et al., 2004). The low proportion of morphospecies shared across all materials further indicates that only a subset of generalist taxa colonized all substrates, whereas most displayed substrate-associated affinities. Although concrete also supported a relatively high number of exclusive morphospecies, these descriptive patterns were not statistically supported and therefore should not be interpreted as evidence of superior substrate performance. Similarly, environmental filtering as well as interespecific competition, grazing and predation during early community assembly has been documented in studies showing that substrate type and associated biofilms alter settlement patterns in artificial substrates (Fong et al., 2024; Rippen et al., 2025; Salta et al., 2013; van der Steeg et al., 2025).

We recorded 316 morphospecies, whereas the Chao1 estimator projected 629, indicating that a substantial proportion of the local species pool remained undetected. Such discrepancies are characteristic of early successional assemblages, which are typically structured by high frequencies of rare taxa and episodic recruitment events (Chase, 2003). In our case, the six-month deployment period likely captured only the initial stages of colonization, when diversity and abundance are still developing and many species remain undetected. Studies following longer immersion periods have shown that species richness and community complexity tend to increase progressively through successive stages of colonization, often accompanied by shifts in species composition as early colonizers are supplemented or replaced by later-arriving taxa (e.g., Antoniadou et al., 2010). Under these conditions, stochastic settlement dynamics and priority effects can strongly influence community trajectories, reducing the statistical detectability of subtle treatment effects (Sloots et al., 2025; Valdivia et al., 2021). Such stochasticity likely also contributed to the substantial unexplained variation in community composition, as reflected by the relatively low proportion of variance accounted for by the PERMANOVA model. This context is particularly relevant when interpreting the modest material-associated differences observed here. Additionally, because specimens were classified as morphospecies based on external morphology, some taxa with cryptic diversity or limited diagnostic characters at early life stages may have been under- or overrepresented, potentially influencing richness estimates.

The absence of coral recruits across treatments likely reflects the severe global thermal stress in 2023 (Reimer et al., 2024) and the documented decline in local coral populations (López-Pérez et al., 2024; Nava et al., 2025). Although successful coral recruitment is reportedly low in the Mexican Pacific, particularly for *Pocillopora* sp. (Alvarado-Rodríguez et al., 2023), low recruitment rates have been widely documented throughout the Eastern Tropical Pacific and are consistent with broader global declines in coral recruitment over recent decades (Price et al., 2019; Edmunds, 2023). Another explanation is that the experimental design did not include cryptic undersurfaces, which frequently serve as preferred settlement microhabitats for coral spat (Harper et al., 2021; Price, 2010). In disturbed reef systems, early colonization is often dominated by opportunistic invertebrates, whereas reef-building taxa may require specific biological or physicochemical cues and longer stabilization periods before successful recruitment occurs (Airoldi & Bulleri, 2011; Hughes et al., 2007; Leonard et al., 2022). Our results therefore characterize colonization under post-disturbance conditions, an important consideration when evaluating short-term substrate performance in restoration contexts.

Several limitations should be considered when interpreting these findings. The loss of experimental plates during deployment reduced replication and resulted in an

unbalanced design, particularly for the relief-added AragoReef treatment, which may have limited the statistical power to detect subtle material-specific effects. Additionally, the six-month deployment period captured only the earliest stages of benthic colonization and may not fully represent longer-term successional trajectories (Antoniadou et al., 2010). Recruitment dynamics are also influenced by temporal variability in reproductive output, larval supply, and post-settlement survival (Edmunds, 2023; Price, 2010), factors that were beyond the temporal scope of the present study. Future research incorporating greater replication, longer deployment periods, and repeated assessments across multiple recruitment seasons would help evaluate the consistency and generality of the patterns observed here.

From a restoration design perspective, our results suggest that material selection may benefit from considering not only short-term ecological performance but also sustainability and long-term integration. Although enriched ceramic and AragoReef were more susceptible to fragmentation during handling, both remained structurally stable under field conditions throughout the deployment period, and progressive encrustation by calcareous organisms is likely to enhance consolidation over time (Sempere-Valverde et al., 2024). Over longer timescales, carbonate mineralogy may facilitate the recruitment, settlement, and calcification of reef-building taxa (Temmink et al., 2021; Yus et al., 2024), though this potential advantage requires validation through extended monitoring. These observations highlight an important design consideration in artificial reef construction: balancing handling durability with ecological integration and reduced long-term environmental persistence (Medeiros et al., 2025; Mohammadi Ghahsareh et al., 2025).

Collectively, our findings provide evidence that microtopographic complexity plays an important role in structuring early benthic assemblages and identify surface relief as a practical design variable in artificial reef construction. Carbonate-based substrates exhibited ecological performance comparable to conventional concrete during initial colonization, supporting their viability as sustainable alternatives in restoration initiatives. Artificial substrates that integrate pronounced relief with carbonate-based composition may enhance early community development while maintaining long-term ecological compatibility. In regions recovering from recurrent bleaching events, where coral recruitment is episodic and constrained by recent thermal history, such approaches may help rebuild habitat structure and facilitate the recovery of reef-associated communities. Rather than converging on a single optimal material, restoration strategies should prioritize adaptable design principles that integrate structural complexity with environmentally compatible materials tailored to local conditions.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

See supplementary material
a02v74s4-SUPPL 1

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