SUPPLEMENT

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Small-scale variability in benthic habitat shapes size structure differences in the sea urchin *Echinometra lucunter*

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ABSTRACT

Introduction: Coral reefs have undergone widespread degradation, reducing ecosystem structural complexity and altering benthic habitat conditions. These changes can affect herbivorous invertebrates such as the sea urchin *Echinometra lucunter*, a key herbivore and bioeroder that can function as a bioindicator of environmental quality.
Objectives: This study evaluated whether reef condition influences the population structure of *E. lucunter* by comparing benthic composition, rugosity, density, and test diameter between a healthy and a degraded zone at Isla de Cabra, Puerto Rico.
Methods: Two reef zones at Isla de Cabra were sampled. Benthic cover was quantified using photo quadrats analyzed with CPCe software. Rugosity was calculated using the chain-and-tape method, and urchin density and test diameter were obtained from replicated quadrats and morphometric measurements.
Results: The healthy zone showed higher coral and turf algae cover and greater rugosity, whereas the degraded zone was dominated by macroalgae. Although *E. lucunter* density did not differ significantly between zones, individuals from the healthy zone were significantly larger (4.3 ± 0.8 cm) than those from the degraded zone (3.5 ± 0.9 cm). The degraded zone exhibited a size distribution skewed toward smaller classes, suggesting growth limitation under lower habitat quality conditions.
Conclusions: Local variability in benthic habitat structure influences the size structure of *E. lucunter*, while population density remains relatively stable. Size-based metrics reflect small-scale habitat differences and complement traditional benthic descriptors when assessing local habitat condition in shallow Caribbean reefs.

Key words: *Echinometra lucunter*; benthic habitat; rugosity; size structure; coral reef degradation; Caribbean.

RESUMEN

La variabilidad a pequeña escala en el hábitat bentónico determina las diferencias en la estructura del tamaño del erizo de mar *Echinometra lucunter*

Introducción: Los arrecifes coralinos han sufrido una degradación generalizada, lo que ha reducido la complejidad estructural de los ecosistemas y alterado las condiciones del hábitat bentónico. Estos cambios pueden afectar a invertebrados herbívoros como el erizo *Echinometra lucunter*, un herbívoro clave y bioerosionador que puede funcionar como bioindicador de calidad ambiental.

Objetivos: Este estudio evaluó si la condición arrecifal influye en la estructura poblacional de *E. lucunter*, comparando la composición del bento, la rugosidad, la densidad y el diámetro de la testa entre una zona saludable y otra degradada en Isla de Cabra, Puerto Rico.
Métodos: Se muestrearon dos zonas arrecifales en isla de Cabra. Se cuantificó la cobertura bentónica mediante foto-cuadrantes analizados en el software CPCe. La rugosidad se calculó mediante el método de cadena y cinta, y la densidad y el diámetro de los erizos a partir de cuadrantes replicados y mediciones morfométricas.
Resultados: La zona saludable presentó mayor cobertura de coral y tapetes de algas y una rugosidad más elevada, mientras que la zona degradada estuvo dominada por macroalgas. Aunque la densidad de *E. lucunter* no difirió significativamente entre zonas, los individuos de la zona saludable fueron significativamente más grandes (4.3 ± 0.8 cm) que los de la zona degradada (3.5 ± 0.9 cm). La zona degradada mostró una distribución sesgada hacia clases pequeñas, lo que sugiere limitaciones en el crecimiento bajo condiciones de menor calidad del hábitat.
Conclusiones: La variabilidad local en la estructura del hábitat bentónico influye en la estructura de tallas de *E. lucunter*, mientras que la densidad poblacional se mantiene relativamente estable. Las métricas basadas en tallas reflejan diferencias del hábitat a pequeña escala y complementan los descriptores bentónicos tradicionales al evaluar la condición local del hábitat en arrecifes someros del Caribe.

Palabras clave: *Echinometra lucunter*; hábitat bentónico; rugosidad; estructura de tallas; degradación arrecifal; Caribe.

INTRODUCTION

Coral reefs are among the most biodiverse and productive ecosystems on Earth, providing food, shelter, and nursery grounds for thousands of marine species (Hughes et al., 2017; Pereira et al., 2024; Spalding et al., 2017). These ecosystems deliver crucial ecosystem services, such as coastal protection, fisheries productivity, and tourism opportunities, which collectively sustain millions of livelihoods in tropical regions (Burke et al., 2011; Moberg & Folke, 1999). Yet, despite their ecological and socioeconomic significance, coral reefs have declined sharply over the past four decades, with global coral cover decreasing by nearly half due to multiple anthropogenic stressors (Jackson et al., 2014). In the Caribbean, this decline has been particularly pronounced, driven by coastal urbanization, eutrophication, overfishing, sedimentation, and mass bleaching events linked to ocean warming (Alvarez-Filip et al., 2011b). The cumulative effect of these pressures has simplified the structural complexity of reefs, reduced coral recruitment, and altered benthic trophic interactions (Gardner et al., 2003). Habitat degradation often leads to shifts from coral-dominated to algae-dominated systems, fundamentally altering reef architecture and ecological dynamics (Hughes, 1994; Norström et al., 2009). The proliferation of macroalgae limits coral settlement, reducing substrate availability for crustose coralline algae, and modifies the microhabitats used by a variety of invertebrates and fishes (McCook, 1999; Mumby & Steneck, 2008). Furthermore, reductions in structural complexity influence refuge availability, predation pressure, and hydrodynamic conditions near the substrate (Alvarez-Filip et al., 2011a). These changes directly affect species that depend on small crevices or irregular surfaces for protection and feeding, including many echinoids that play key roles in maintaining benthic balance (Lawrence, 2013).

Echinoderms, and particularly sea urchins, are among the most important invertebrates in coral reef ecosystems due to their dual function as grazers and bioeroders (Bak, 1990; Fong et al., 2024; McClanahan, 1988). By removing epilithic algal turfs and eroding carbonate substrates, they regulate algal growth, facilitate coral recruitment, and contribute to calcium carbonate cycling (Lawrence, 2013; Sammarco, 1982). Their ecological importance became evident after the massive mortality of the long-spined sea urchin *Diadema antillarum* in the 1980s, an event that caused widespread macroalgal overgrowth and long-lasting changes in

Caribbean reef structure (Edmunds & Carpenter, 2001; Lessios, 1988). Since then, other echinoids, including *Echinometra lucunter*, have partially filled the grazing niche once dominated by *Diadema*, thereby assuming an increasingly critical role in the maintenance of reef resilience (Alvarado, 2011; McClanahan, 1995).

The red sea urchin *Echinometra lucunter* (Linnaeus, 1758) is widely distributed across shallow rocky and coral reefs in the tropical Western Atlantic and Caribbean (Alvarado, 2011; Kroh & Mooi, 2025). This species usually inhabits crevices and cavities in calcareous and basaltic substrates, where it actively grazes on algal turfs and organic films (Hendler et al., 1995; Shulman, 2020). Through its feeding activity, *E. lucunter* contributes to both bioerosion and benthic stability, making it a key determinant of reef surface composition (Perry & Harborne, 2016). Abundance and size structure of this genus tend to vary with habitat conditions, including substrate hardness, refuge availability, and algal composition (McClanahan & Shafir, 1990). Because the abundance and morphometric traits vary according to habitat characteristics, *E. lucunter* may represent a useful model to assess environmental conditions and reef habitat quality in shallow coastal systems (Belford, 2020; Rodríguez-Barreras et al., 2024). Morphometric characteristics, such as test diameter, spine length, and volume, can provide indirect information on energy allocation and environmental stress in urchin populations (Rogers-Bennett, 1994). Individuals living in optimal habitats with abundant turf algae and complex topography tend to exhibit larger sizes, while those in degraded or macroalgae-dominated areas often remain smaller, possibly due to limited food resources and increased metabolic costs (McClanahan, 1995; Perry & Harborne, 2016). Therefore, analyzing size distributions rather than simple density measures offers a more integrative approach to understanding how habitat condition affects population dynamics and growth patterns in *E. lucunter*.

In Puerto Rico, coastal degradation associated with sedimentation, eutrophication, and physical disturbance has led to the decline of many nearshore reefs, particularly along the north coast (Camargo et al., 2009; Hernández-Delgado & Ortiz-Flores, 2022). Broad-scale pressures frequently manifest through fine-scale, localized processes that generate strong spatial heterogeneity in benthic condition over distances of only a few meters. Empirical evidence from Caribbean reefs indicates that patchy sediment deposition, localized coral mortality, microtopographic variability, and spatial differences in herbivory intensity can rapidly shift benthic dominance between coral- and algae-dominated states at very small spatial scales (Hernández-Fernández et al., 2019; Simmons et al., 2022). As a result, adjacent reef patches within the same continuous reef structure may exhibit sharply contrasting benthic composition and structural complexity. Isla de Cabra, located at the entrance of San Juan Bay, represents a microcosm of these processes, where zones of contrasting coral cover, rugosity, and algal dominance coexist within short spatial scales. Prior studies have shown significant spatial heterogeneity in benthic composition and rugosity across this area (Rodríguez-Barreras et al., 2024), yet the biological consequences of habitat changes for invertebrate assemblages remain poorly understood. This study aimed to evaluate how small-scale variability in benthic habitat condition relates to the size structure and local density of the sea urchin *Echinometra lucunter* within a shallow reef at Isla de Cabra, Puerto Rico.

MATERIALS AND METHODS

Study area: This study was conducted in September 2025 at Isla de Cabra, located at the entrance of San Juan Bay in northern Puerto Rico (18°28'31" N, 66°08'09" W), ranging from 1–2 m in depth. Sampling was performed within a shallow patch reef located along the northeastern margin of the island's northwestern zone (Fig. 1A).

Within this patch reef, we defined two spatially independent microhabitat zones based on contrasting benthic conditions (Fig. 2).

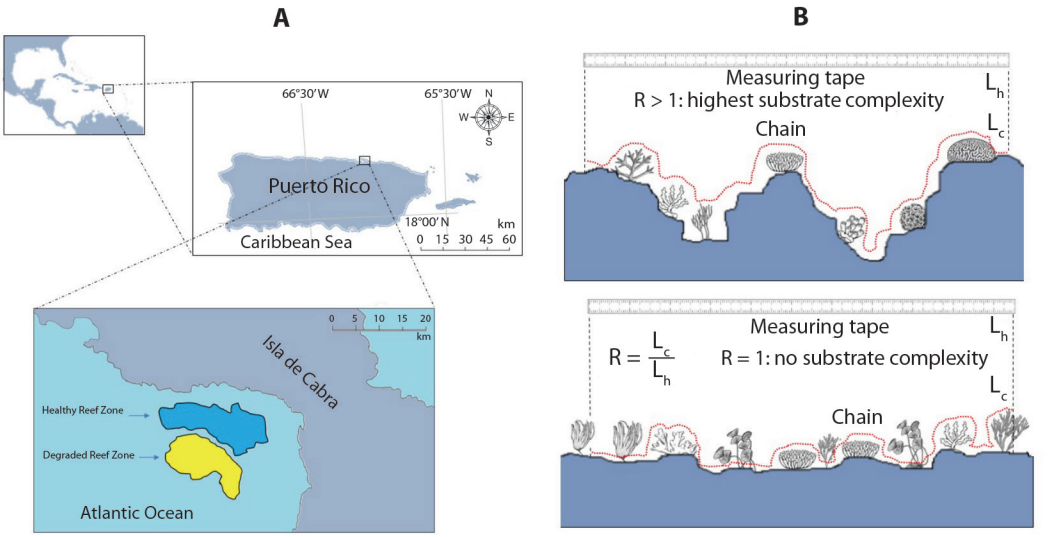
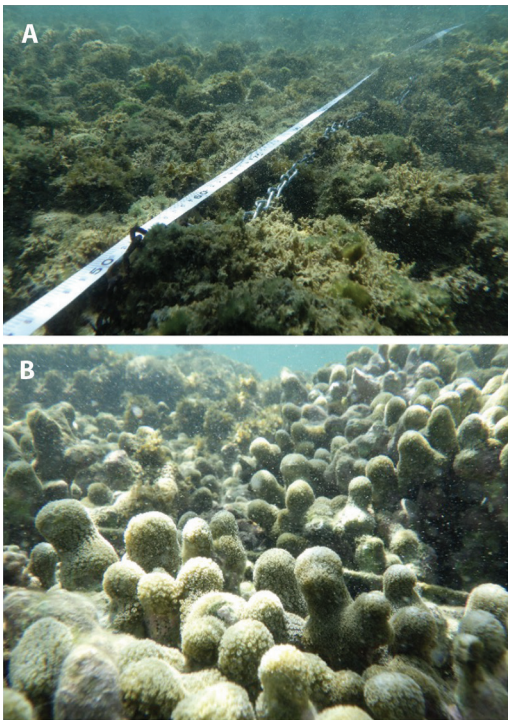


Fig. 1. Study site at Isla de Cabra and rugosity method. **A.** Location of the two zones surveyed within the reef: Healthy Reef Zone (blue) and Degraded Reef Zone (yellow). **B.** Diagram of the chain-and-tape method used to estimate rugosity (R), where *Lc* represents the contour length of the chain and *Lh* the horizontal linear distance.



Each zone was sampled using independent, non-overlapping transects, ensuring spatial independence between sampling units. The two zones were separated by a sandy channel covered by *Thalassia testudinum*, which served as a natural boundary between microhabitats and facilitated clear spatial delimitation during field sampling. Zones were operationally defined as: (1) Healthy Reef Zone (HRZ): characterized by higher live coral cover and greater structural complexity, and (2) Degraded Reef Zone (DRZ): dominated by macroalgae, turf algae, and unconsolidated substrates. These zones represent contrasting benthic conditions within the same reef structure but were treated as independent sampling areas for all analyses. The classification of both zones was carried out using criteria applied in other studies (Mujiyanto et al., 2020; Widodo et al., 2021), where a healthy reef exhibits at least 40%

Fig. 2. Representative examples of reef condition categories used in this study based on published classification criteria. **A.** (Healthy reef) illustrates a site with ≥40% live coral cover, characteristic of a healthy reef. **B.** (Degraded reef) shows a site with low live coral cover and a high abundance of macroalgae and dead coral skeletons associated with algal mats, typical of degraded reefs.

live coral cover, whereas a degraded reef is characterized not only by low coral cover but also by a high abundance of macroalgae and dead coral skeletons associated with algal mats (Gudka et al., 2023).

The HRZ was characterized by a higher relative dominance of scleractinian corals, primarily *Porites astreoides*, with additional contributions from *Siderastrea radians* and *Agaricia agaricites*, and a benthic matrix composed mainly of turf algae and calcareous macroalgae (e.g., *Halimeda* spp.). This assemblage reflects a reef state with greater structural complexity and carbonate-producing organisms (Ceccarelli et al., 2018). In contrast, DRZ was dominated by fleshy macroalgae such as *Dictyota* spp., the presence of coralline red algae such as *Amphiroa* spp., and low coral cover, indicative of a macroalgae-dominated reef and altered ecosystem functioning (Ceccarelli et al., 2018). Although the two study zones were located in close proximity (<5 m apart), this spatial juxtaposition reflects the fine-scale heterogeneity and patchy spatial patterns commonly observed in shallow Caribbean reefs, where localized disturbances, herbivory pressure, and microenvironmental conditions can generate sharply contrasting benthic states over relatively short distances (Hernández-Fernández et al., 2019).

Rugosity, benthic composition: To estimate the benthic complexity of both zones, we used the chain-and-tape method (Storlazzi et al., 2016). A 5 m stainless-steel chain was gently draped across the natural contours of the reef surface, following all depressions and crests without stretching or compressing the chain. The straight-line horizontal distance between the two chain endpoints was measured with a measuring tape (Fig. 1B). The ratio between the chain length (C) and the linear distance (L) was calculated as the Rugosity Index (RI = C / L). Five independent replicates were taken per zone, ensuring that each transect was independent and representative of the overall habitat structure. Higher RI values indicate greater surface complexity and potential availability of microhabitats for reef organisms (Fig. 1B).

Benthic composition was assessed using photo quadrats and the random point count technique in Coral Point Count (CPCe) version 4.1 (Kohler & Gill, 2006). A total of ten 50 x 50 cm PVC quadrats were randomly placed in each zone, and each quadrat was photographed using a Pentax WG-8 waterproof camera (20 MP). All images were uploaded and analyzed to determine the percentage of points of the benthic community. Fifteen randomly distributed points per image were used to classify substrate cover into seven benthic categories: C = Coral, CJ = Coral juvenile, MA = Macroalgae, TF = Turf algae, CA = Coralline algae, SPR = Sand, pavement, and rubble, and U = Unknown. Benthic composition was expressed as the percentage of points assigned to each benthic category relative to the total number of points per image, ((points per category × 100)/total points), and reported as mean ± SD.

Urchin density and size structure: Within each zone, ten 50 x 50 cm PVC quadrats were randomly placed to count all visible *E. lucunter* individuals. For morphometric measurements, a total of 50 individuals of *E. lucunter* were manually collected from crevices and cavities within each reef zone. Individuals were carefully handled and measured in situ using a Vernier caliper (± 0.05 mm precision). The diameter test was recorded as the maximum horizontal axis across the peristome. After the measurement, all sea urchins were immediately returned to their original location to minimize disturbance.

Statistical analysis: Normality of data distributions was evaluated using the Shapiro–Wilk test, and Levene's test was applied to assess homogeneity of variances. Student's t-tests was used to compare rugosity and urchin density between the Healthy Reef Zone (HRZ) and Degraded Reef Zone (DRZ). Sea urchin density and rugosity data met the assumptions of normality and homogeneity of variances and were analyzed without transformation. Test diameter data were $\log_{10}$-transformed to meet normality assumptions and to allow comparisons

of size structure between reef zones. Benthic cover data were not normalized or transformed because no inferential statistical tests were conducted. All statistical analyses were performed in R v4.5.0 (R Core Team, 2025), using a significance threshold of $\alpha = 0.05$.

RESULTS

Spatial community structure: Benthic composition (frequency of points) differed between the Healthy Reef Zone (HRZ) and the Degraded Reef Zone (DRZ) at Isla de Cabra (Fig. 3). In the HRZ, the substrate was dominated by live coral (C) and juvenile coral colonies (CJ), which together accounted for approximately one third of the total points recorded (Fig. 3A). Turf algae (TF) and coralline algae (CA) were also present but in moderate proportions, while macroalgae (MA) and sand, pavement, and rubble (SPR) contributed minimally. This composition reflects a structurally more complex reef surface. In contrast, the DRZ was characterized by a strong dominance of turf and macroalgae, with the combined categories (MA + TF) representing over 70 % of the frequency of points (Fig. 3B). Coral and juvenile colonies were scarce (< 10 %), and the substrate consisted largely of sand and rubble.

When the main benthic categories were grouped, the contrast between reef zones became even more evident. The combined macroalgal cover (MA + TF) was markedly higher in the Degraded Reef Zone (DRZ), exceeding two-thirds of total substrate coverage and reflecting a benthic surface dominated by filamentous and fleshy algae (Fig. 3C). In contrast, the Healthy Reef Zone (HRZ) displayed substancially greater coral cover (C + CJ), averaging close to 40–45 % of total substrate (Fig. 3D).

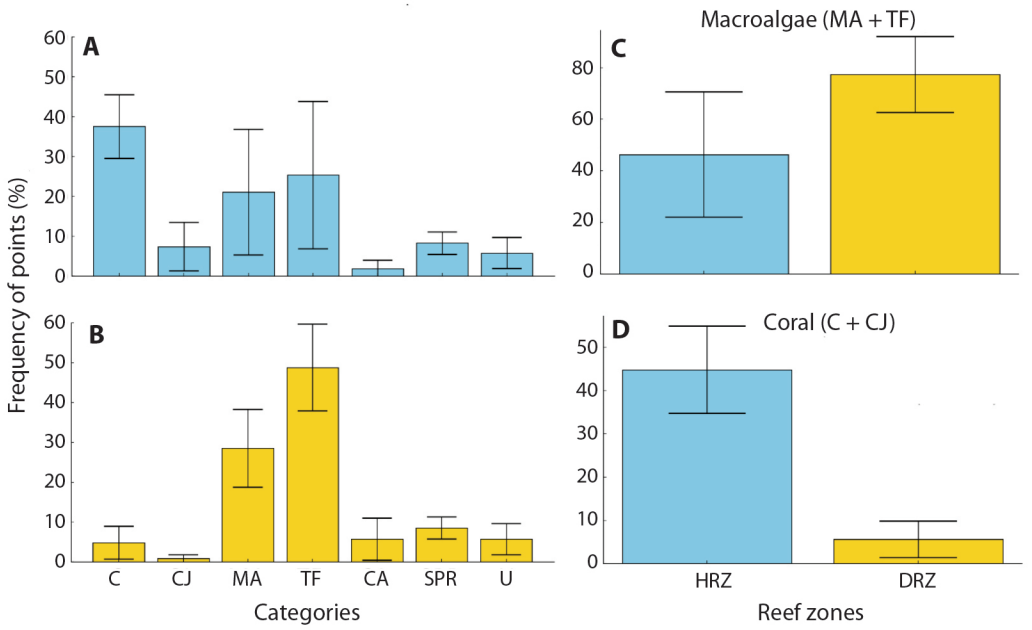


Fig. 3. Frequency of point (%) by benthic category and reef zones at Isla de Cabra, Puerto Rico. **A.** Healthy Reef Zone (HRZ). **B.** Degraded Reef Zone (DRZ). Categories: C = Coral; CJ = Coral juvenile; MA = Macroalgae; TF = Turf algae; CA = Coralline algae; SPR = Sand, pavement, and rubble; U = Unknowns. **C.** Combined macroalgal cover (MA + TF) showing higher values in DRZ. **D.** Combined coral cover (C + CJ) showing higher values in HRZ. Error bars represent standard deviations. Colors denote reef condition: blue = HRZ, yellow = DRZ.

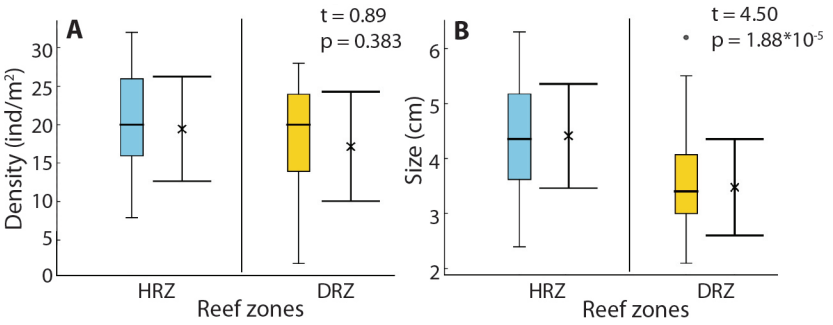


Fig. 4. Density and test diameter of the sea urchin *Echinometra lucunter* in two reef zones at Isla de Cabra, Puerto Rico. **A.** Mean density (individuals m^{-2}) of *E. lucunter* showing no significant difference between the Healthy Reef Zone (HRZ) and Degraded Reef Zone (DRZ). **B.** Test diameter (cm) illustrating significantly larger individuals in the HRZ ($t = 4.50$, $p = 1.88 \times 10^{-5}$). Boxes represent interquartile ranges, horizontal lines the medians, whiskers the minimum and maximum values, and crosses the means. Colors denote reef condition: blue = HRZ, yellow = DRZ.

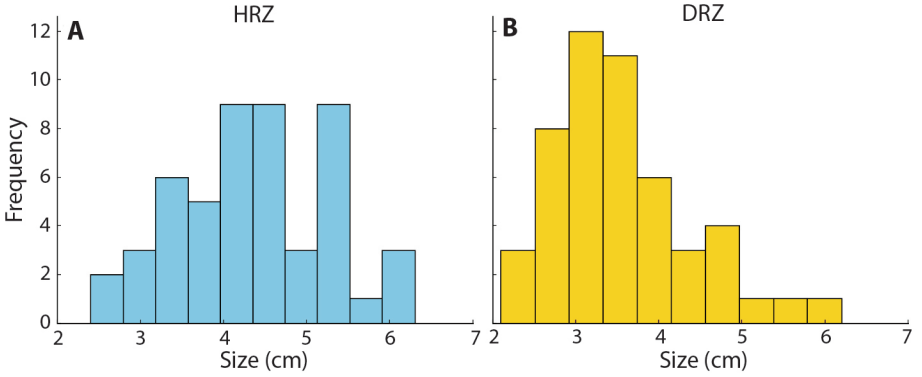


Fig. 5. Size–frequency distribution of the sea urchin *Echinometra lucunter* by reef zone at Isla de Cabra, Puerto Rico. **A.** Healthy Reef Zone (HRZ); **B.** Degraded Reef Zone (DRZ). Bars represent the frequency of individuals per 0.5 cm test diameter class. Colors denote reef condition: blue = HRZ, yellow = DRZ.

Sea urchin abundance and size structure: The density and body size of *Echinometra lucunter* exhibited contrasting patterns between the two reef zones at Isla de Cabra (Fig. 4A). The HRZ exhibited a mean density of 20.27 ± 7.25 ind. m^{-2}, while the DRZ showed a slightly lower value of 17.87 ± 7.58 ind. m^{-2}. Mean density did not differ significantly between zones ($t = 0.89$, $p = 0.383$; Fig. 4A). Regarding mean size, individuals from the HRZ had a larger mean test diameter (mean = 4.3 ± 0.8 cm), whereas those from the DRZ were significantly smaller (mean = 3.5 ± 0.9 cm). Average size showed significant differences between the two zones ($t = 4.50$, $p = 1.88 \times 10^{-5}$; Fig. 4B).

Size-frequency distribution of *E. lucunter* varied between reef zones (Fig. 5). Diameters ranged from 2.5 to 6.2 cm, with a modal class around 4.5–5.0 cm in the HRZ (Fig. 5A). The distribution was relatively symmetrical, with frequent representation of medium and large size classes. Larger individuals (> 5 cm) were frequent in this zone. Conversely, the distribution was skewed toward smaller size classes in the DRZ, with most individuals measuring between 2.5 and 4.0 cm and few exceeding 5 cm (Fig. 5B).

DISCUSSION

Small-scale habitat variability and sea urchin size structure: Our results demonstrate that small-scale benthic heterogeneity within a single reef system influences the size structure of the sea urchin *Echinometra lucunter*, even when population densities remain stable between zones. Zones defined as "healthy" and "degraded" are used here in an operational sense, reflecting local differences in structural complexity and benthic composition, rather than broad reef-scale condition. Greater rugosity and coral cover in the Healthy Reef Zone created a more heterogeneous habitat, offering microrefuges and substrates better suited for the foraging activity of *E. lucunter*. A previous study demonstrated the importance of structural complexity as a key determinant of population density and size structure in this species (Rodríguez-Barreras et al., 2024). The predominance of large individuals in the Healthy Reef Zone aligns with observations from other Echinometra populations, where complex habitats promote higher epilithic turf availability and lower environmental stress (McClanahan & Shafir, 1990).

In contrast, the Degraded Reef Zone exhibited a significantly higher dominance of macroalgae (e.g., *Dictyota* spp., *Sargassum* spp.) and lower structural complexity (rugosity), as documented by our benthic surveys. Because macroalgae are not the primary food resource of *Echinometra lucunter*, which mainly feeds on epilithic turf algae, this shift in benthic composition likely reduces the availability of preferred food resources. In combination with reduced habitat complexity, these conditions may increase intraspecific competition for suitable feeding and refuge microhabitats, potentially generating bioenergetic constraints that limit individual growth. This interpretation is supported by a recent study in Puerto Rico showing that substrate characteristics (artificial basaltic vs. natural) directly influence body size in *E. lucunter* (Rodríguez-Barreras et al., 2024), as well as by previous studies highlighting the role of habitat structure in regulating sea urchin performance (McClanahan & Shafir, 1990; Perry & Harborne, 2016). Consequently, the reduced sizes observed in the Degraded Reef Zone reflect are consistent with the documented differences in benthic composition and habitat complexity.

Stable population dynamics despite degradation: The absence of significant differences in *Echinometra lucunter* density between the healthy and degraded zones suggests that the species can maintain relatively stable populations even under altered or low-complexity environmental conditions (Rodríguez-Barreras et al., 2024). This pattern is consistent with observations from other sea urchin species that exhibit ecological flexibility across contrasting habitats. For example, the temperate sea urchin *Paracentrotus lividus* maintains comparable densities across a range of habitat types—including rocky substrates, seagrass meadows, and mixed sand–rock environments—and shows marked trophic plasticity that allows it to adjust to variable resource availability (Camps-Castellà et al., 2020; Hereu et al., 2012). Similarly, *Centrostephanus rodgersii* is known to persist at high densities in depauperate "urchin barren" habitats, where structural complexity and algal cover are greatly reduced, demonstrating its capacity to thrive in ecologically degraded conditions (Przeslawski et al., 2025). These examples highlight that tolerance of habitat modification is not unique to *Echinometra* but rather a trait shared with other echinoids that can tolerate and exploit marginal environments.

However, stable density does not necessarily indicate a favorable population condition. The dominance of small individuals in the degraded zone suggests sustained recruitment but limited growth. This combination—high proportions of juveniles and small adults—has been documented in sea urchins subjected to nutritional stress or limited availability of microrefuges in degraded reefs (Perry & Harborne, 2016). Moreover, the higher proportion of macroalgae in the degraded area may slow the transition of juveniles into larger size classes by reducing access to epilithic turfs,

an important food resource for *E. lucunter* (Sammarco, 1982). Functionally, a population dominated by small individuals may exert insufficient grazing pressure to counteract algal expansion, thereby perpetuating the reef's degradation state (Mumby & Steneck, 2008). This negative feedback dynamic is common in Caribbean reefs that have undergone structural simplification (Alvarez-Filip et al., 2011b).

Functional implications: Our results have important implications for understanding the functional resilience of coastal shallow-water reefs. Although *Echinometra lucunter* maintained similar densities between zones, the marked reduction in size in the degraded reef suggests a decline in its potential for bioerosion and grazing—key processes in benthic reef dynamics. Previous studies have shown that larger urchins are responsible for greater algal removal and substrate bioerosion, contributing to the maintenance of suitable surfaces for coral settlement (Bak, 1990; Sammarco, 1982). Therefore, communities dominated by small individuals, such as those observed in the degraded zone, may lose part of their functional capacity, facilitating algal expansion and perpetuating reef degradation.

Likewise, the predominance of macroalgae in the Degraded Reef Zone reinforces a well-documented ecological pattern in the Caribbean, in which coral loss and structural simplification reduce habitat complexity and create conditions favorable to algal proliferation (Alvarez-Filip et al., 2011b; Hughes et al., 2007). This shift in the coral–algal balance alters energy flows, reduces coral productivity, and modifies trophic interactions. In systems where *Diadema antillarum* remains reduced or absent—as is the case across much of the Caribbean—secondary herbivores such as *E. lucunter* play an even more critical role in algal control (Lessios, 2016). However, if these populations are functionally limited by adverse environmental conditions, their capacity to compensate for the loss of primary herbivory is also diminished.

Our findings show that *Echinometra lucunter* exhibits changes in size structure across locally contrasting benthic habitats within a shallow reef, while population density remains relatively stable. Rather than reflecting broad reef-scale degradation states, the observed differences emphasize the ecological relevance of within-reef spatial variability in shaping population size structure and potential grazing and bioerosion capacity of *E. lucunter*. Accordingly, size-based metrics derived from this species may provide valuable information for detecting localized habitat heterogeneity and assessing ecological condition at the scale at which key organisms–habitat interactions occur. By complementing traditional benthic descriptors such as coral cover and structural complexity, this small-scale perspective provides a clearer framework for interpreting reef functioning in shallow, urban-influenced environments.

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.

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REFERENCES

Alvarado, J. J. (2011). Echinoderm diversity in the Caribbean Sea. *Marine Biodiversity*, *41*(2), 261–285. https://doi.org/10.1007/s12526-010-0053-0

Alvarez-Filip, L., Dulvy, N. K., Côté, I. M., Watkinson, A. R., & Gill, J. A. (2011a). Coral identity underpins

architectural complexity on Caribbean reefs. *Ecological Applications*, *21*(6), 2223–2231. https://doi.org/10.1890/10-1563.1

Alvarez-Filip, L., Gill, J. A., Dulvy, N. K., Perry, A. L., Watkinson, A. R., & Côté, I. M. (2011b). Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*, *30*(4), 1051–1060. https://doi.org/10.1007/s00338-011-0795-6

Bak, R. P. M. (1990). Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Marine Ecology Progress Series*, *66*(3), 267–272.

Belford, S. G. (2020). Spatial abundance and colour morphotype densities of the rock-boring sea urchin (*Echinometra lucunter*) at two different habitats. *Thalassas*, *36*, 157–164. https://doi.org/10.1007/s41208-019-00170-2

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). *Reefs at risk revisited.* World Resources Institute.

Camargo, C., Maldonado, J. H., Alvarado, E., Moreno-Sánchez, R., Mendoza, S., Manrique, N., Mogollón, A., Osorio, J. D., Grajales, A., & Sánchez, J. A. (2009). Community involvement in management for maintaining coral reef resilience and biodiversity in southern Caribbean marine protected areas. *Biodiversity and Conservation*, *18*(4), 935–956. https://doi.org/10.1007/s10531-008-9555-5

Camps-Castellà, J., Romero, J., & Prado, P. (2020). Trophic plasticity in the sea urchin *Paracentrotus lividus*, as a function of resource availability and habitat features. *Marine Ecology Progress Series*, *637*, 71–85. https://doi.org/10.3354/meps13235

Ceccarelli, D. M., Loffler, Z., Bourne, D. G., Al Moajil-Cole, G. S., Boström-Einarsson, L., Evans-Illidge, E., Fabricius, K., Glasl, B., Marshal, P., McLeod, I., Read., M., Schaffelke, B., Smith, A. K., Jorda, G. T., Williamson, D. H., & Bay, L. (2018). Rehabilitation of coral reefs through removal of macroalgae: state of knowledge and considerations for management and implementation. *Restoration Ecology*, *26*(5), 827–838. https://doi.org/10.1111/rec.12852

Edmunds, P. J., & Carpenter, R. C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences*, *98*(9), 5067–5071. https://doi.org/10.1073/pnas.071524598

Fong, C. R., Smith, N., Catalan, E., Caraveo, B. A., Barber, P. H., & Fong, P. (2024). Herbivorous sea urchins (*Echinometra mathaei*) support resilience on overfished and sedimented tropical reefs. *Scientific Reports*, *14*, 3829. https://doi.org/10.1038/s41598-024-52222-0

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science, 301*(5635), 958–960. https://doi.org/10.1126/science.1086050

Gudka, M., Aboud, S., & Obura, D. (2023). Establishing historical benthic cover levels for coral reefs of the Western Indian Ocean. *Western Indian Ocean Journal of Marine Science*, *22*(1),103–115. https://doi.org/10.4314/wiojms.v22i1.11

Hendler, G., Miller, J. E., Pawson, D. L., & Kier, P. M. (1995). *Sea stars, sea urchins, and allies: Echinoderms of Florida and the Caribbean*. Smithsonian Institution Press.

Hereu, B., Linares, C., Sala, E., Garrabou, J., Garcia-Rubies, A., Diaz, D., & Zabala, M. (2012). Multiple processes regulate long-term population dynamics of sea urchins on Mediterranean rocky reefs. *PloS One*, *7*(5), e36901. https://doi.org/10.1371/journal.pone.0036901

Hernández-Delgado, E. A., & Ortiz-Flores, M. F. (2022). The long and winding road of coral reef recovery in the anthropocene: a case study from Puerto Rico. *Diversity*, *14*(10), 804. https://doi.org/10.3390/d14100804

Hernández-Fernández, L., González de Zayas, R., Weber, L., Apprill, A., & Armenteros, M. (2019). Small-scale variability dominates benthic coverage and diversity across the Jardines de La Reina, Cuba coral reef system. *Frontiers in Marine Science*, *6*, 747. https://doi.org/10.3389/fmars.2019.00747

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90. https://doi.org/10.1038/nature22901

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*(4), 360–365. https://doi.org/10.1016/j.cub.2006.12.049

Jackson, J. B. C., Donovan, M. K., Cramer, K. L., & Lam, V. V. (2014). *Status and trends of Caribbean coral reefs: 1970–2012* (Ed). Global Coral Reef Monitoring Network, International Union for Conservation of Nature and Natural Resources.

Kohler, K. E., & Gill, S. M. (2006). Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences*, *32*(9), 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009

Kroh, A., & Mooi, R. (2025). *World Echinoidea Database. Echinometra lucunter* (Linnaeus, 1758) [Web data base]. World Register of Marine Species. https://www.marinespecies.org/aphia.php?p=taxdetails&id=213380

Lawrence, J. M. (2013). *Sea urchins: Biology and ecology* (3rd ed.). Academic Press.

Lessios, H. A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics*, *19*, 371–393. https://doi.org/10.1146/annurev.es.19.110188.002103

Lessios, H. A. (2016). The great *Diadema antillarum* die-off: 30 years later. *Annual Review of Marine Science*, *8*, 267–283. https://doi.org/10.1146/annurev-marine-122414-033857

McClanahan, T. R. (1995). Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. *Environmental Biology of Fishes*, *43*(2), 187-193. https://doi.org/10.1007/BF00002490

McClanahan, T. R. (1988). Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. *Oecologia*, *77*(2), 210–218. https://doi.org/10.1007/BF00379188

McClanahan, T. R., & Shafir, S. H. (1990). Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia, 83*(3), 362–370. https://doi.org/10.1007/BF00317561

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs, 18*(4), 357–367. https://doi.org/10.1007/s003380050213

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Mujiyanto, M., García, M., Haryadi, J., Rahayu, R., & Budikusuma, R. (2020). Health status of coral reef in Tunda Island, Banten Province, Indonesia. *Indonesian Journal of Marine Sciences*, *25*(2), 66–74. https://doi.org/10.14710/ik.ijms.25.2.66-74

Mumby, P. J., & Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology & Evolution*, *23*(10), 555–563. https://doi.org/10.1016/j.tree.2008.06.011

Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series*, *376*, 295–306. https://doi.org/10.3354/meps07815

Pereira, P. H. C., de Lima, G. V., da Silva, E. G., de Farias-Pontes, A. V., Côrtes, L. G. F., Sampaio, C. L., Kramer-Pinto, T., Pinto-Bellucci, M. d. S., Cunha-Cardoso, A. T., & Normande, I. C. (2024). Spatial distribution, management zoning and depth effects on reef biodiversity and productivity at the largest Brazilian coastal marine protected area. *Coral Reefs*, *43*(5), 1271–1283. https://doi.org/10.1007/s00338-024-02536-2

Perry, C. T., & Harborne, A. R. (2016). Bioerosion on modern reefs: impacts and responses under changing ecological and environmental conditions. In D. Hubbard, C. Rogers, J. Lipps, & G. Jr. Stanley (Eds.), *Coral reefs at the crossroads.* (Vol. 6, pp. 69–101) Springer. https://doi.org/10.1007/978-94-017-7567-0_4

Przeslawski, R., Chick, R. C., Davis, T., Day, J. K., Glasby, T. M., Knott, N., & Byrne, M. (2025). A review of urchin barrens and the longspined sea urchin (*Centrostephanus rodgersii*) in New South Wales, Australia. *Marine and Freshwater Research*, *76*(5), MF24149. https://doi.org/10.1071/MF24149

R Core Team. (2025). *R: A language and environment for statistical computing* (Version 4.5.0) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rodríguez-Barreras, R., Rodríguez-Aponte, A., & Solano-González, S. (2024). Assessing the suitability of an artificial basaltic substrate for the rock-boring urchin *Echinometra lucunter*. *Caribbean Journal of Science*, *54*(2), 534–546. https://doi.org/10.18475/cjos.v54i2.a28

Rogers-Bennett, L. (1994). *Spatial patterns in the life history characteristics of red sea urchins, Strongylocentrotus franciscanus: implications for recruitment and the California fishery* [Doctorate dissertation]. University of California, United States of America.

Storlazzi, C. D., Dartnell, P., Hatcher, G., & Gibbs, A. E. (2016). End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology. *Coral Reefs*, *35*(3), 889–894. https://doi.org/10.1007/s00338-016-1462-8

Sammarco, P. W. (1982). Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. *Journal of Experimental Marine Biology and Ecology*, *61*(1), 31–55. https://doi.org/10.1016/0022-0981(82)90020-X

Simmons, K. R., Bohnenstiehl, D. R., & Eggleston, D. B. (2022). Spatiotemporal variation in coral assemblages and reef habitat complexity among shallow fore-reef sites in the Florida Keys National Marine Sanctuary.

Diversity, *14*(3), 153. https://doi.org/10.3390/d14030153

Spalding, M., Burke, L., Wood, S. A., Ashpole, J., Hutchison, J., & Zu Ermgassen, P. (2017). Mapping the global value and distribution of coral reef tourism. *Marine Policy*, *82*, 104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Shulman, M. J. (2020). *Echinometra* sea urchins on Caribbean coral reefs: diel and lunar cycles of movement and feeding, densities, and morphology. *Journal of Experimental Marine Biology and Ecology*, *530–531*, 151430. https://doi.org/10.1016/j.jembe.2020.151430

Widodo, E., Katili, A., & Ibrahim, M. (2021). Coral reef ecosystem health status of Paladan Islands, Indonesia: An assessment criteria using coral cover percentage. *Indo Pacific Journal of Ocean Life*, *5*(1), 8–13. https://doi.org/10.13057/oceanlife/o050102