SUPPLEMENT

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Performance of restored microfragments of *Orbicella annularis* and *Orbicella faveolata* during the 2023–2024 marine heatwave in the Mexican Caribbean

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ABSTRACT

Introduction: Coral reef ecosystems are declining worldwide due to the combined effects of climate-driven marine heatwaves and local anthropogenic stressors, leading to widespread loss of reef-building corals and degradation of carbonate frameworks. In the Caribbean, these impacts are intensified by recurrent thermal anomalies, disease outbreaks, and declining water quality, with massive corals such as *Orbicella* spp. among the most affected. Active restoration strategies, including microfragmentation, have been proposed to accelerate coral recovery, yet their performance under extreme thermal stress remains poorly understood.

Objective: We evaluated the effectiveness of *in situ* microfragment transplantation for restoring live tissue in damaged colonies of *Orbicella faveolata* and *Orbicella annularis* in the northern Mexican Caribbean.

Methods: The experiment was performed for 332 days (May 2023–April 2024) in the Arrecifes de Puerto Morelos National Park and coincided with a severe marine heatwave reaching 31.7 °C. Microfragments < 10 cm^2 were transplanted onto damaged colonies (> 50 % tissue loss) and monitored bimonthly to assess survival, growth, bleaching, and their response to environmental variables.

Results: Overall survival was 52 %, with higher survival in *O. faveolata* (60 %) than *O. annularis* (43 %), although differences were not statistically significant. Fragment size strongly influenced outcomes, with larger fragments > 4 cm^2 showing significantly higher survival (85 %). In terms of tissue growth both species experienced a substantial reduction and high bleaching prevalence during peak thermal stress event. However, *O. faveolata* exhibited partial recovery in tissue area and new polyp incorporation after the heatwave, suggesting greater physiological plasticity, whereas *O. annularis* showed persistent tissue loss and limited recovery.

Conclusions: The results indicate that microfragmentation is a promising but highly context-dependent restoration approach, with its success strongly influenced by environmental conditions. Its effectiveness was affected by thermal events, with microfragments >4 cm^2 showing higher survivorship in *Orbicella* species. These findings highlight *O. faveolata* as a more resilient and suitable candidate for assisted restoration under warming scenarios. Although microfragmentation represents an effective approach for rehabilitating damaged adult colonies, its scalability and long-term effectiveness need to be assessed before it can be established as a broadly applicable management tool.

Key words: massive corals, coral restoration, assisted intervention, Caribbean reef, micro-fragmentation, thermal stress.

RESUMEN

Desempeño de microfragmentos restaurados de *Orbicella faveolata* y *Orbicella annularis* durante la ola de calor 2023–2024 en el Caribe mexicano

Introducción: Los ecosistemas de arrecifes de coral están disminuyendo a nivel mundial debido a los efectos combinados de las olas de calor marinas inducidas por el cambio climático y los estresores antropogénicos locales, lo que ha provocado la pérdida generalizada de corales constructores de arrecife y la degradación de las estructuras carbonatadas. En el Caribe, estos impactos se intensifican por anomalías térmicas recurrentes, brotes de enfermedades y el deterioro de la calidad del agua, afectando particularmente a los corales masivos como *Orbicella* spp. Las estrategias de restauración activa, incluida la microfragmentación, se han propuesto para acelerar la recuperación coralina; sin embargo, su desempeño bajo estrés térmico extremo aún no se comprende completamente.

Objetivo: Evaluar la efectividad del trasplante in situ de microfragmentos para la restauración de tejido vivo en colonias dañadas de *Orbicella faveolata* y *Orbicella annularis* en el norte del Caribe mexicano.

Métodos: El experimento se realizó durante 332 días (mayo de 2023–abril de 2024) en el Parque Nacional Arrecifes de Puerto Morelos y coincidió con una intensa ola de calor marina que alcanzó 31.7 °C. Se trasplantaron microfragmentos < 10 cm² provenientes de colonias donadoras sanas hacia colonias dañadas (> 50 % de pérdida de tejido) y se monitorearon cada dos meses para evaluar supervivencia, crecimiento, blanqueamiento y su respuesta a variables ambientales.

Resultados: La supervivencia general fue de 52 %, siendo mayor en *O. faveolata* (60 %) que en *O. annularis* (43 %), aunque estas diferencias no fueron significativas. El tamaño del fragmento influyó fuertemente en los resultados, con fragmentos mayores a 4 cm² mostrando una supervivencia significativamente mayor (85 %). Ambas especies presentaron una reducción sustancial del crecimiento y una alta prevalencia de blanqueamiento durante el evento de estrés térmico máximo. Sin embargo, *O. faveolata* mostró una recuperación parcial del área de tejido vivo e incorporación de pólipos después de la ola de calor, lo que sugiere mayor plasticidad fisiológica, mientras que *O. annularis* presentó pérdida sostenida de tejido vivo y recuperación limitada.

Conclusiones: Los resultados indican que la microfragmentación es una estrategia de restauración prometedora pero altamente dependiente del contexto y éxito está fuertemente regulado por las condiciones ambientales. Su efectividad fue afectada por eventos térmicos, donde microfragmentos >4 cm² mostraron una mayor supervivencia para especies de *Orbicella*. Estos hallazgos destacan a *O. faveolata* como un candidato más resiliente y adecuado para la restauración asistida bajo escenarios de calentamiento. Aunque la microfragmentación representa un enfoque eficaz para la rehabilitación de colonias adultas dañadas, su escalabilidad y eficacia a largo plazo deben evaluarse antes de establecerla como una herramienta de manejo ampliamente aplicable.

Palabras clave: corales masivos, restauración de corales, intervención asistida, arrecifes del Caribe, microfragmentación, estrés térmico.

INTRODUCTION

The stability of carbonate structures formed by coral skeletons plays a fundamental role in the construction and maintenance of coral reef frameworks, supporting biodiversity and providing essential ecosystem services to coastal human communities (Spalding et al., 2001). Despite their geo-ecological importance, the cover of reef-building coral species has declined by up to 90 % over the last three decades as a consequence of anthropogenic climate change and the increasing frequency, intensity, and duration of marine heatwaves (Hughes et al., 2018; Reimer et al., 2024). These global stressors are further exacerbated by local pressures, including coastal development and increasing sewage contamination (Rico-Esenaro et al., 2023), which degrade water quality, promote the emergence and spread of coral diseases, and contribute to coral mortality and shifts in coral community composition (Alvarez-Filip et al., 2019; Estrada-Saldívar et al., 2020).

In the Caribbean region, coral reefs have been severely affected by the synergistic effects of global disturbances, including ocean warming, thermal anomalies, hurricanes, and widespread disease outbreaks, which have escalated across up to 70% of reef locations (Bruno, 2015; Alvarez-Filip et al., 2026). These disturbances have caused substantial declines in key reef-building corals, within the genus of *Acropora*,

Pseudodiploria, and *Orbicella*, leading to major shifts in species assemblages and disruptions of critical geo-ecological processes (Weil, 2004; Alvarez-Filip et al., 2022). Among these threats, stony coral tissue loss disease (SCTLD) is considered one of the most lethal coral diseases in the Atlantic–Caribbean region, affecting at least 22 reef-building coral species (Walton et al., 2018; Papke et al., 2024). The disease progresses rapidly, often causing complete tissue loss in coral colonies within approximately 40 days, resulting in extensive mortality and substantial declines in coral cover exceeding 50 % across large areas of Mesoamerican Reefs (Alvarez-Filip et al., 2022; Papke et al., 2024; Vega-Thurber et al., 2025).

It remains uncertain whether corals will be able to acclimate naturally at a rate sufficient to cope with ongoing environmental challenges (Torda et al., 2017). Consequently, active reef restoration strategies have received increasing attention as potential tools to facilitate the recovery and rehabilitation of coral reef ecosystems worldwide (Rinkevich, 2019; Rinkevich, 2020; Boström-Einarsson et al., 2020; Tortolero-Langarica, Gutiérrez-Estrada et al., 2025, Gutiérrez-Coral et al., 2025). Among the different restoration approaches, microfragmentation has emerged as a promising technique, although it remains in relatively early stages of development and evaluation (Rinkevich, 2019). This method involves cutting coral colonies into very small fragments (< 3 cm^2) to stimulate accelerated tissue regeneration and has proven particularly effective for slow-growing massive coral species (Forsman et al., 2015; Page et al., 2018; Tortolero-Langarica, Rodríguez-Troncoso et al., 2025). The technique may be even more effective when fragments from genetically distinct individuals fuse, forming chimeras that combine functional diversity with enhanced resistance traits (Rinkevich, 2019). Furthermore, the removal of microfragments has been shown not to compromise donor colony health when the harvested tissue represents less than 10 % of the colony surface, allowing recovery within a relatively short period (Gutiérrez-Coral et al., 2025). Previous studies have demonstrated that microfragment transplantation represents a practical and highly promising restoration tool for re-skinning live coral tissue on damaged colonies and promoting the recovery of ecological functions in massive coral species (Tortolero-Langarica, Rodríguez-Troncoso et al., 2025).

Despite the promising results of coral microfragmentation, its long-term effects on tissue recovery and coral resilience under increasingly frequent and severe marine heatwave conditions remain poorly understood. *Orbicella* is an important reef-building coral genus that has demonstrated acclimatization to seasonal changes in seawater temperature, including modulation of skeletal growth under thermal stress (Carricart-Ganivet et al., 2012). Such responses may reflect an energetic trade-off in which corals prioritize the maintenance and repair of living tissue over skeletal calcification when exposed to thermal anomalies (Cabral-Tena et al., 2024). Due to the limited energy availability, investment in tissue recovery and survival may come at the expense of calcification, potentially allowing colonies to maintain physiological integrity during periods of environmental stress (Tortolero-Langarica et al., 2016). However, the magnitude and direction of this trade-off may differ between species and locations, depending on their thermal history, local environmental conditions, and inherent physiological tolerance (Cabral-Tena et al., 2024).

In this context, we investigated the use of microfragment transplants from healthy donor colonies to assess their effectiveness in promoting live tissue recovery in colonies of *Orbicella annularis and Orbicella faveolata* that had experienced substantial tissue loss due to disease. During the experimental period, an unexpected and severe 2023–2024 marine heatwave occurred, providing a unique opportunity to assess the performance and persistence of transplanted microfragments under extreme thermal stress. Specifically, we tested the hypothesis that severe thermal anomalies would be associated with reduced growth rates in *Orbicella* colonies while tissue recovery

continued, suggesting a potential trade-off between growth and recovery under stressful conditions. We further hypothesized that this pattern would differ between *O. annularis* and *O. faveolata*, reflecting differences in their life-history strategies and responses to thermal stress. This study therefore, provides new insights into the potential of assisted tissue transplantation as a restoration strategy to enhance the recovery of damaged massive corals and to support the resilience and conservation of Caribbean coral reef ecosystems.

MATERIAL AND METHODS

Study area. This study was conducted from May 2023 to April 2024 in the Arrecifes de Puerto Morelos National Park (APMNP), located along the northern coast of the Mexican Caribbean (20°50'59.94" N & 86°49'11.20" W; Fig. 1). The APMNP consists of a 21 km long discontinuous barrier reef system, divided into two main geomorphological zones: a protected lagoon back-reef and an exposed reef-front characterized by coral terraces and spur-and-groove formations (Medina-Valmaseda et al., 2022). Oceanographic conditions in the APMNP are strongly influenced by the Yucatán Current, which flows northward along the edge of the continental shelf with an average annual temperature of approximately 27 °C, with a variability of 4°C between seasons (Rodríguez-Martínez et al., 2010). The coral assemblage is dominated by hermatypic scleractinian corals

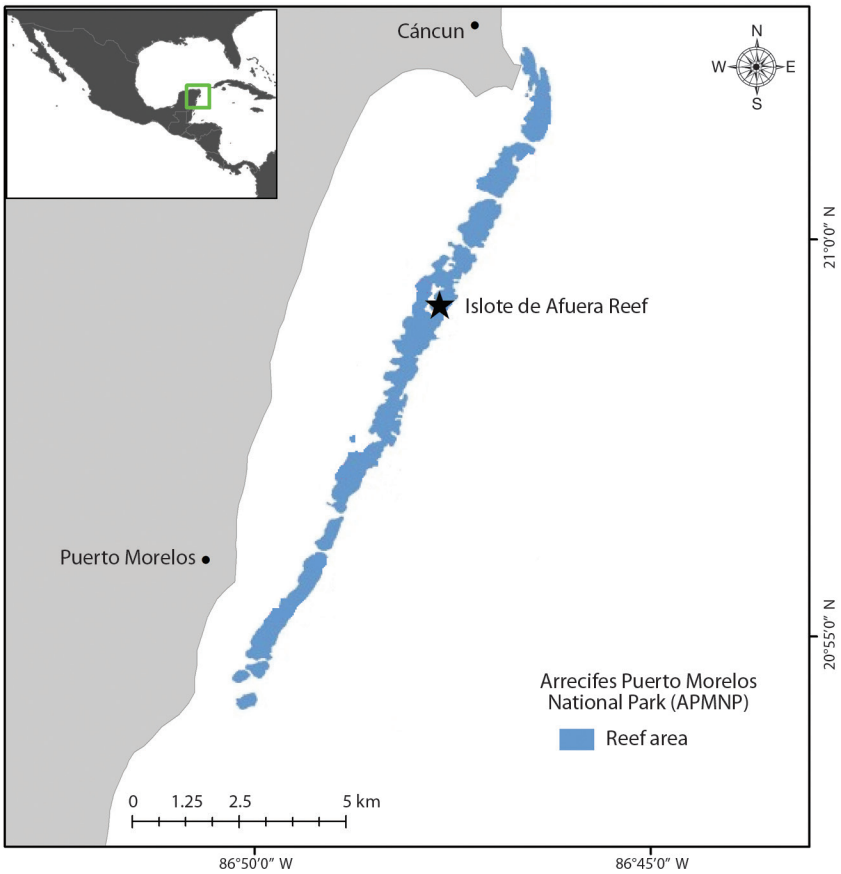


Fig. 1. Study area map in the Arrecife de Puerto Morelos National Park (APMNP), Mexican Caribbean, Mexico. Black star indicates experimental reef site.

that form the structural foundation of the reef, including *Acropora palmata*, *A. cervicornis*, *Orbicella faveolata*, *O. annularis*, *Pseudodiploria strigosa*, *Millepora complanata*, *Porites astreoides*, *Siderastrea siderea*, and *Agaricia* spp. (Alvarez-Filip et al., 2013). These taxa contribute to reef framework construction, habitat complexity, and associated biodiversity, although many populations have experienced substantial declines in recent decades (Alvarez-Filip et al., 2022).

In parallel, increasing anthropogenic pressure associated with rapid coastal development, tourism expansion, and population growth has resulted in elevated inputs of nutrients, sediments, and chemical pollutants into coastal waters, representing a persistent threat to reef ecosystem integrity (Rico-Esenaro et al., 2023). The deterioration of water quality has further promoted the emergence and spread of coral diseases, including the stony coral tissue loss disease (SCTLD), which has been widely documented throughout the Mexican Caribbean and has severely impacted key reef-building species, including *Orbicella faveolata* and *O. annularis* (Alvarez-Filip et al., 2019). In addition, the study area is repeatedly affected by increasingly frequent and intense thermal anomaly events. These anomalies are largely associated with phases of the El Niño–Southern Oscillation, including both El Niño (warm-phase) and La Niña (cold-phase) conditions in the region (Reimer et al., 2024; Eakin et al., 2026; Spady et al., 2026).

Fieldwork. The experiment was conducted *in situ* at Islote de Afuera Reef over a 332-day period. Healthy coral colonies (N = 11) showing no signs of bleaching, disease, or severe bioerosion were selected from two reef-building massive coral species, *Orbicella annularis* and *Orbicella faveolata*. Using a hammer and wood chisel, microfragments (<10 cm^2 of live tissue) were extracted from the peripheral basal margins of each selected colony, removing less than 10% of the living tissue to minimize impacts on donor colony health (Gutierrez-Coral et al., 2025). A total of 21 microfragments were obtained from *O. annularis*, whereas 25 microfragments were collected from *O. faveolata*. The microfragments were transplanted in clusters of four to five onto coral colonies exhibiting evident damage and greater than 50 % loss of living tissue, with the objective of accelerating coral tissue recovery. Each fragment was installed less than 3 cm from the remaining living tissue of the recipient damaged colony and spaced approximately 1 cm apart from adjacent transplanted microfragments. Prior to transplantation, the coral substrate was cleaned of macroalgae and algal turf using a metal brush, and all microfragments were fixed to the coral surface with epoxy putty (Klip-ton Plast, NuceQ®; sensu Tortolero-Langarica et al., 2020; Tortolero-Langarica, Rodríguez-Troncoso et al., 2025).

Throughout the experimental period, digital photographs (20 MP) of each intervened colony were obtained every two months using a GoPro HERO10 Black camera configured with a linear field of view. A plastic Vernier caliper (precision: 0.05 mm) was included in each image as a reference scale. The resulting images of each microfragment cluster were analyzed using ImageJ version 1.52s to quantify the relative monthly growth rate, defined as the difference between the initial and final measurements for each monitoring period across four coral morphometric variables. Maximum diameter (Dmax) was defined as the longest linear distance (cm) measured with the virtual straight-line tool, whereas minimum diameter (Dmin) corresponded to the perpendicular distance (cm) adjacent to Dmax. All growth measurements were standardized to an initial value of 0 cm, and subsequent measurements represented the cumulative growth of each fragment over the experimental period. Additionally, the number of newly incorporated polyps per coral fragment during each bimonthly interval was quantified using the virtual multi-point counting tool. To quantify area growth (cm^2 and %) and the annual rate of live tissue regeneration ($cm^2\ yr^{-1}$), the perimeter of each microfragment was delineated to calculate its surface area

using the "Freehand" tool by tracing the temporal progression of the live tissue over the time.

Survival rate (%) over the experiment was determined based on the initial number of fragments and the number of fragments surviving at the end of each monitoring period. For this study, a microfragment was considered surviving if it preserves >50 % live tissue and showed no evidence of overgrowth or competition from macroalgae, sponges, or cyanobacteria. To assess bleaching prevalence, a bimonthly visual comparison was conducted using the images collected during each sampling event, with reference to *The Coral Health Charts* proposed by Siebeck et al. (2006) CoralWatch (https://coralwatch.org). For this study, corals were evaluated using the CoralWatch scale (D1–D6), which reflects the density of symbiotic algae within coral tissue (Siebeck et al., 2006). Categories D5–D6 were considered healthy/recovered, D3–D4 as pale or recovering, and D1–D2 as bleached, with D1 indicating severe bleaching. Assuming all deployed microfragments initially presented D5–D6 coloration, bleaching prevalence was quantified during subsequent monitoring events. Fragments were also classified into five health categories (recovered, pale, dead, bleached, and overgrown), and the proportion of fragments (%) within each category was calculated.

Monthly seawater temperature (SWT) and photosynthetically active radiation (PAR) were considered environmental variables and were derived from daily records provided by the Academic Monitoring and Meteorological Oceanographic Service (SAMMO) of the Academic Unit of Reef Systems, ICML, Universidad Nacional Autónoma de México, throughout the study period (https://sammo.icmyl.unam.mx/).

Data analysis. Means (± standard deviation, SD) for coral morphometrics of *Orbicella faveolata* and *Orbicella annularis* and environmental variables were computed, and for each growth variable, normality (Shapiro–Wilk, $P < 0.05$) and homoscedasticity (Levene, $P < 0.05$) tests were conducted prior to comparative growth analyses. Survival comparisons between the two species throughout the experimental period (332 days) were performed using the non-parametric Kaplan–Meier test. For comparative purposes, fragments were additionally classified into two categories according to their initial surface area size (< 4 cm^2 and ≥ 4 cm^2) in order to evaluate the influence of initial fragment size on growth and survival. Growth differences were evaluated using two-way repeated measures Analysis of Variance (ANOVA) under a generalized linear model (GLM), with species and time as fixed factors. Simple linear regression models (R^2) were applied using SWT and PAR as explanatory environmental variables to assess their relationship with microfragment growth variables. All statistical analyses were performed in SigmaPlot ver. 11 and Rstudio software with 95 % of confidence interval ($\alpha = 0.05$).

RESULTS

Survival. At the end of the study period, the overall survival rate combining both species was 52.17 %, with a total of 24 surviving coral microfragments (N = 9 for *Orbicella annularis,* and N = 15 for *Orbicella faveolata*). Survival analysis revealed that *O. annularis* exhibited an estimated mean survival time of 259 days, with survival probabilities 42.9 % at the end of the experimental period (Fig. 2A). In contrast, *O. faveolata* presented a mean survival time of 271 days, with a survival probability of 60 % at 288 days, with no additional losses recorded thereafter. Comparison of survival curves between species using the Log-rank test showed no significant differences ($\chi^2 = 0.837$, $P = 0.360$), indicating that mortality rates between both groups were statistically similar. For both species, mortality occurred primarily during the summer of 2023 (June–November), coinciding with a prolonged marine heatwave that persisted for more than 60 days (Fig. 2). In terms of fragment size at the end of the monitoring period, microfragments larger than 4 cm^2 exhibited significant ($\chi^2 = 16.015$, $P = 0.001$) a higher survival rate (85 %) compared with those smaller than 4 cm^2 (26.9 %; Fig. 2B).

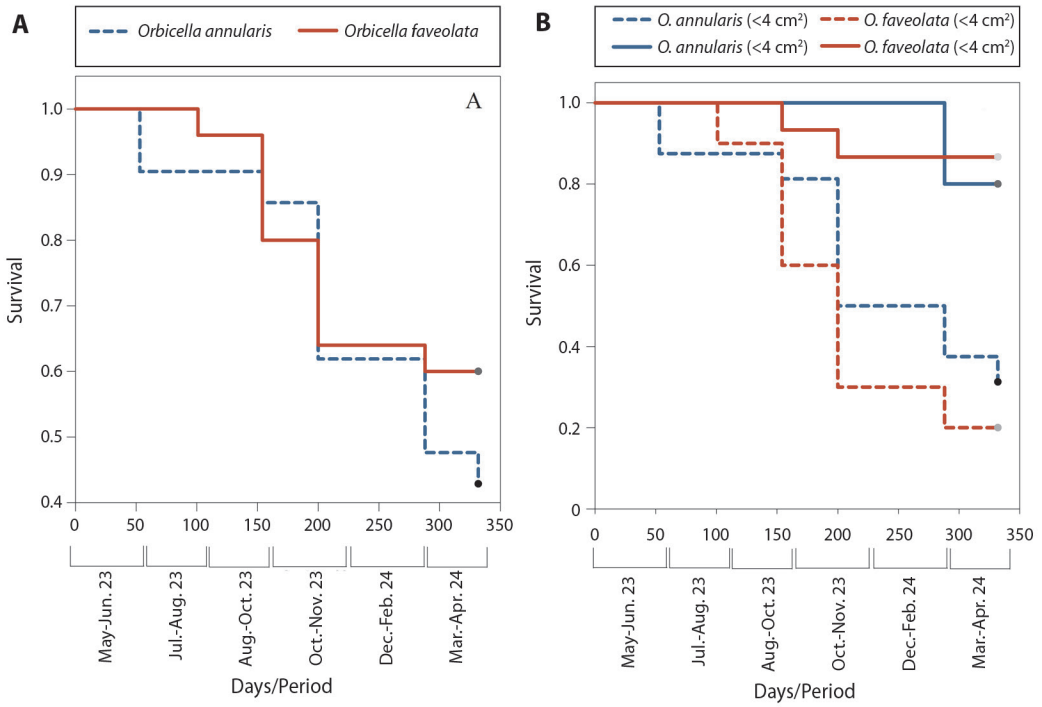


Fig. 2. Survival (%) of *Orbicella faveolata* (red lines) and *Orbicella annularis* (blue lines) microfragments during the study period (May 2023–April 2024). A) Survival patterns between species, and B) survival patterns among microfragment size classes within each species.

Coral growth performance. Overall, the growth metrics of microfragments showed a similar trend toward reduced dimensions in both species. At the end of the study period, the Dmax of *O. annularis* decreased by 0.73 cm, whereas Dmin decreased by 0.45 cm compared with the initial diameters. Surface area of live tissue also exhibited a total reduction of 1.05 ± 1.32 cm², accompanied by a loss of ~7 polyps (Table 1, Fig. 3), with no signs of physiological recovery after the bleaching event (Fig. 3, Fig. 4). For *O. faveolata*, both diameters also decreased: the Dmax by 0.47 cm and the Dmin by 0.15 cm. However, the reduction in live tissue area was minimal (0.39 ± 1.83 cm²). However, recovery signs were present at after bleaching at the end heatwave events, with an increase on diameters and live tissue area (Fig. 3A, Fig. 3B, Fig. 3C, Fig. 4).

The GLM results showed no differences between growth species, indicating that the factor time had a significant effect on tissue area (P= 0.002) (Table 2). The *O. annularis* microfragments exhibited negative values across all measurements. From the first sampling event May–June, it showed an average decrease of 0.02 cm. This trend persisted in subsequent sampling periods from June–August to October–November, from this point onward, microfragment diameters, tissue area and density of polys showed a more pronounced decrease (0.12 cm, 0.32 cm², and ~4 polyps, respectively) at the end of sampling period (Fig. 3, Fig. 4). For *Orbicella faveolata*, negative values were also observed in most sampling periods, yet during the initial phase, microfragments of this species showed slight growth of 0.15 cm. It was not until the June–August period that tissue loss became evident, likely associated with the thermal stress event. This trend continued in the following sampling period until the end of the experiment period, where a slight recovery

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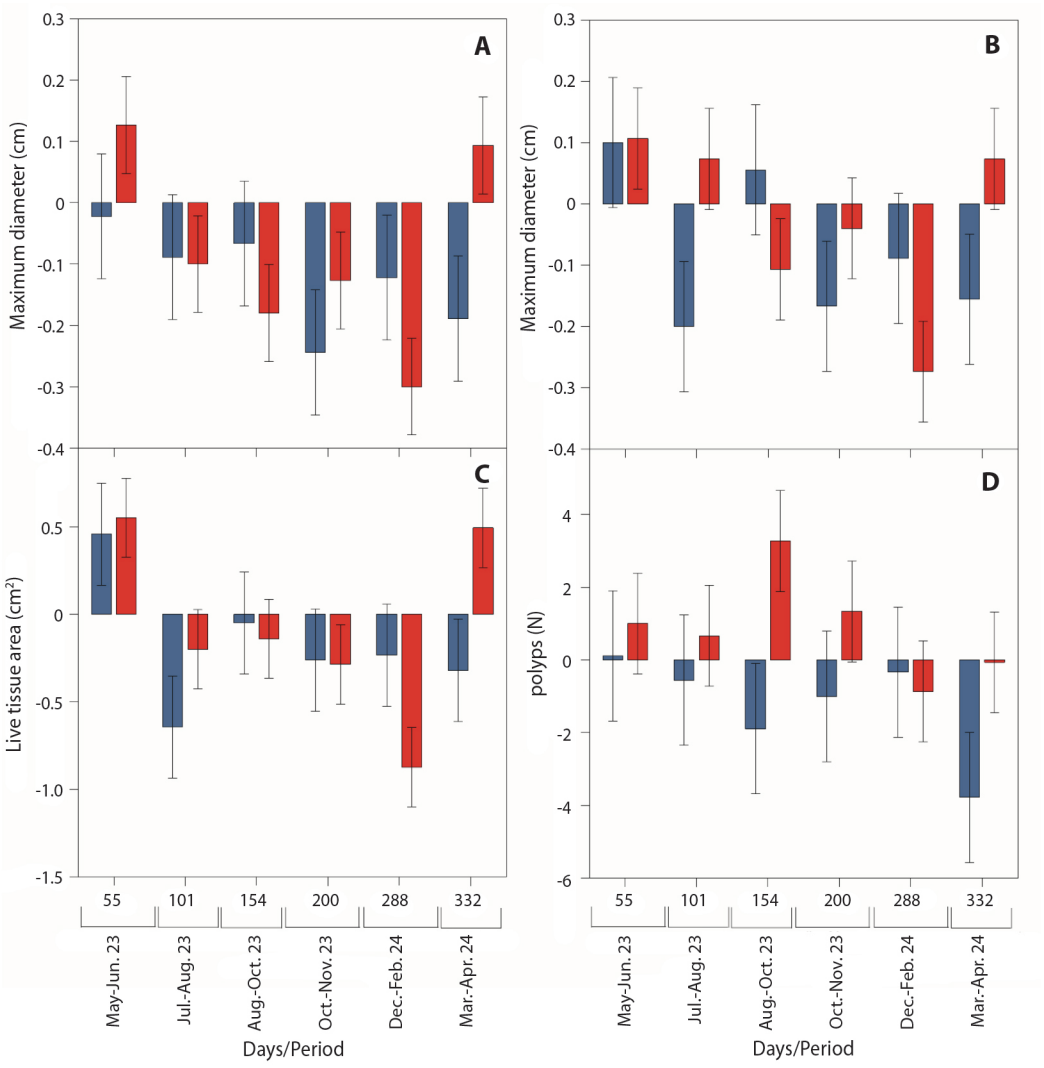


Fig. 3. Mean coral growth rate (± SD) of *Orbicella faveolata* (red bars) and *Orbicella annularis* (blue bars) transplants during the experimental period (2023–2024). (A–B) Changes in maximum and minimum colony diameters. (C–D) Live tissue area and polyp density of coral microfragments.

in diameter, live tissue area was observed with 0.09 cm, 0.49 cm^2 respectively, suggesting a potential recovery process (Fig. 3, Fig. 4).

During the study period, significant thermal variability was recorded in the Arrecife de Puerto Morelos National Park, with an average sea surface temperature (SST) of 29.3°C. The highest SWT were recorded between June and August (31.70 ± 0.77°C) associated with the heatwave event of 2023 (Table 2). Photosynthetically active radiation showed an average value of 28,142 μmol·quanta m^{-2} throughout the study period. The highest values were observed between May and June (32,672 ± 4,821 μmol·quanta m^{-2}), when solar radiation was most intense, coinciding with the peak of the thermal anomaly during the heatwave (Table 2). Linear regression analysis showed

Table 1

Bimonthly mean growth rate of *Orbicella* microfragments (±SD) in maximum (Dmax) and minimum diameter (Dmin), live tissue area, number of polyps, and environmental variables of the study site over the experimental period.

	Period	May-Jun	Jun-Aug	Aug-Oct	Oct-Nov	Dec-Feb	Mar-Apr	
	Days	53	101	154	200	288	332	mean
Orbicella annularis	Dmax (cm)	-0.02 ± 0.21	-0.09 ± 0.22	-0.07 ± 0.22	-0.24 ± 0.32	-0.12 ± 0.24	-0.19 ± 0.18	-0.73 ± 0.49
	Dmin (cm)	0.10 ± 0.34	-0.20 ± 0.37	0.06 ± 0.17	-0.17 ± 0.19	-0.09 ± 0.16	-0.16 ± 0.31	-0.46 ± 0.56
	Area (cm^2)	0.46 ± 0.39	-0.64 ± 0.72	-0.05 ± 0.79	-0.26 ± 0.76	-0.23 ± 0.32	-0.32 ± 0.40	-1.05 ± 1.33
	Polyps (N)	0.11 ± 4.04	-0.55 ± 4.19	-1.89 ± 3.02	-1.00 ± 2.96	-0.33 ± 5.68	-3.78 ± 2.91	-7.44 ± 14.3
Orbicella faveolata	Dmax (cm)	0.15 ± 0.38	-0.10 ± 0.27	-0.18 ± 0.40	-0.13 ± 0.19	-0.30 ± 0.28	0.09 ± 0.45	-0.47 ± 0.65
	Dmin (cm)	0.12 ± 0.24	0.07 ± 0.54	-0.11 ± 0.38	-0.04 ± 0.20	-0.27 ± 0.28	0.07 ± 0.30	-0.15 ± 0.78
	Area (cm^2)	0.61 ± 0.85	-0.20 ± 1.18	-0.14 ± 1.24	-0.29 ± 0.60	-0.87 ± 0.79	0.49 ±1.14	-0.39 ±1.83
	Polyps (N)	1.00 ± 3.12	0.67 ± 7.27	3.27 ± 9.42	1.33 ± 4.73	-0.87 ± 5.36	-0.07 ± 4.20	5.33 ± 20.57
Eviromental factors	SWT (°C)	30.23 ± 0.57	31.70 ± 0.77	31.05 ± 0.77	28.67 ± 1.21	26.60 ± 1.20	27.44 ± 1.12	29.02 ± 2.18
	PAR (µmol·q)	32,672 ± 4,821	32,584 ± 4,405	28,313 ± 6,003	22,760 ± 5,980	20,848 ± 5,557	31,677 ± 3,905	27285 ± 7258

Table 2

General Linear Model, RM ANOVA results of coral growth comparisons *Orbicella faveolata* and *Orbicella annularis* microfragments over the experiment period.

	Source	DF	MS	F	P
Dmax (cm)	Species	1	0.0570	0.895	0.355
	Time	5	0.208	2.087	0.072
	Species x Time	5	0.169	1.698	0.141
	Residual	132	0.0879		
Dmin (cm)	Species	1	0.0782	0.914	0.349
	Time	5	0.200	1.905	0.099
	Species x Time	5	0.213	2.035	0.079
	Residual	132	0.0873		
Area (cm^2)	Species	1	0.335	0.674	0.420
	Time	5	3.306	4.028	**0.002**
	Species x Time	5	1.382	1.684	0.144
	Residual	132	0.671		
Polyps (N)	Species	1	153.067	2.673	0.116
	Time	5	21.075	0.905	0.480
	Species x Time	5	23.797	1.022	0.408
	Residual	132	29.589		

that both diameter measurements (R^2 = 0.668, P= 0.047; R^2 = 0.795, P= 0.017) of *O. faveolata* were significantly related with PAR.

Bleaching prevalence. A coral bleaching event was recorded during the study, associated with thermal anomalies from June to November 2023. In *O. annularis*, bleaching was detected early (May–June), affecting more than 60 % of fragments. The most severe impact occurred between June and August, coinciding with peak sea surface temperature (31.7 °C), reaching 71.4 % bleaching prevalence and associated tissue loss. Although some partial recovery was observed later, cumulative mortality reached 57.1 %, and 42.9 % of fragments remained bleached at the end of the experiment. In contrast, *O. faveolata* showed lower initial impact, with mostly healthy or slightly pale fragments, bleaching also peaked between June and August (68 %), followed by a clearer recovery trend and reduction in bleaching prevalence. However,

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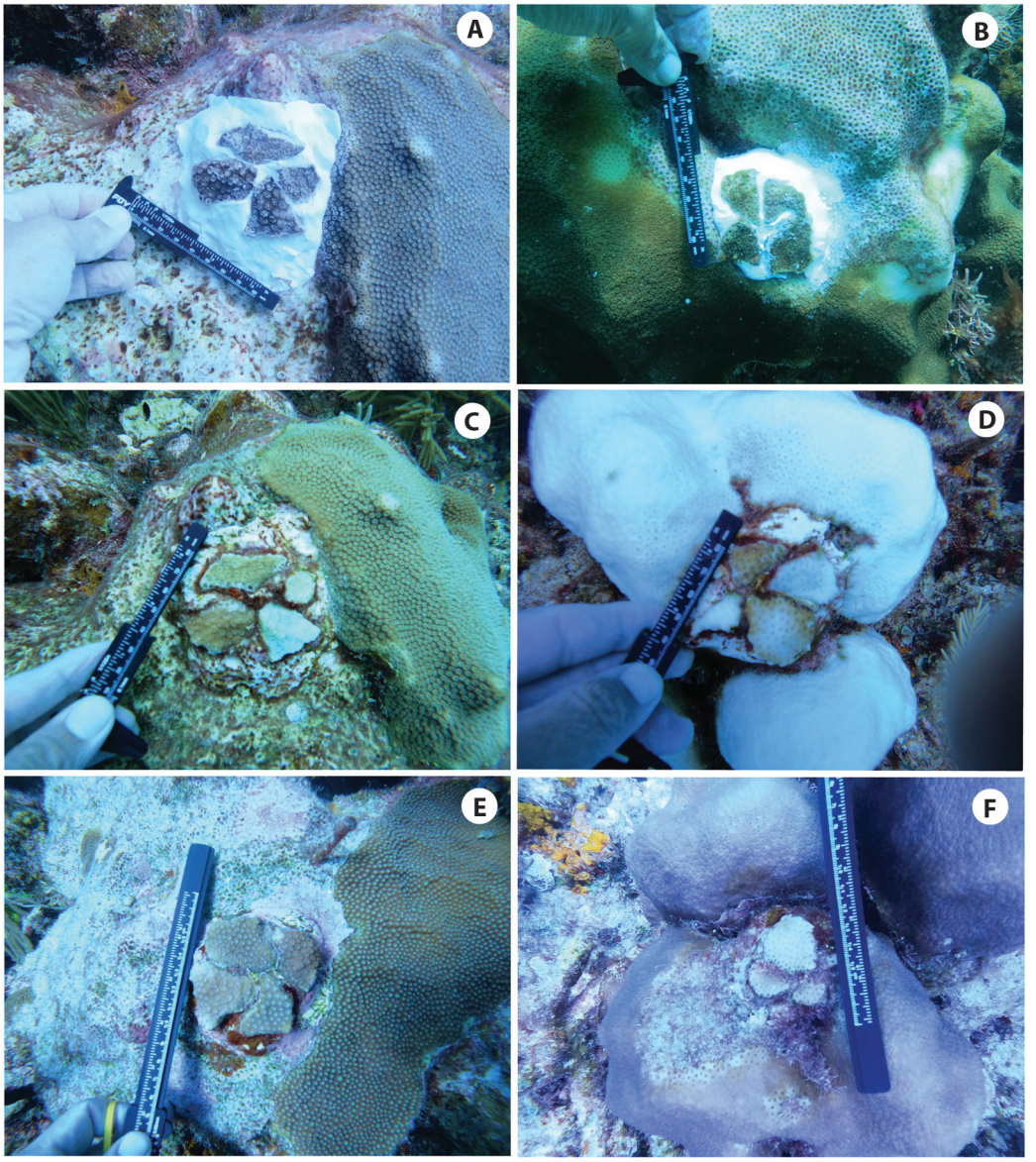


Fig. 4. Coral microfragment clusters transplanted onto damaged colonies. (A–B) Representative microfragment sizes at the start of the experiment. (C–D) Bleaching responses observed in microfragments during the 2023 marine heatwave (E–F). Microfragment sizes at the end of the experimental period after 332 days of growth.

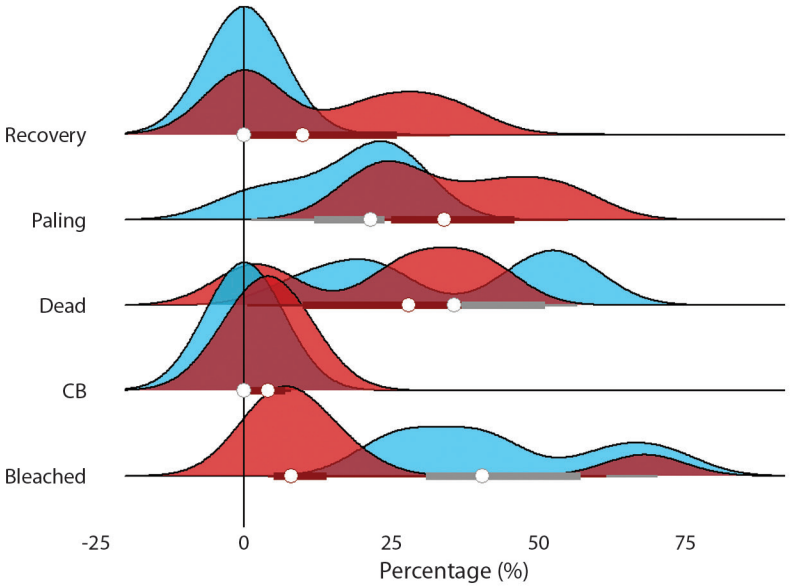


Fig. 5. Ridgeline density plot showing the distribution of coral colony condition categories for *Orbicella faveolata* (red curves) and *Orbicella annularis* (blue curves) microfragments, and their proportional response to bleaching, recovery, paling, mortality, and cyanobacterial overgrowth. White dots indicate median values, while horizontal red and gray bars represent the interquartile range (25th–75th percentiles). The vertical black line at 0% serves as a reference point.

final mortality still reached 40 % (Fig. 5). Overall, both species were strongly affected by the thermal anomaly, but *O. faveolata* exhibited greater resistance and recovery capacity compared to *O. annularis* (Fig. 5).

DISCUSSION

Coral reef ecosystems are undergoing accelerated degradation due to the combined effects of climate change and anthropogenic pressures (Hughes et al., 2018; Tortolero-Langarica et al., 2020). In this context, improving and evaluating restoration tools is critical, particularly for massive corals in the Caribbean, a region severely affected by environmental stress (Rinkevich, 2019; Alvarez-Filip et al., 2022). This study provides one of the first evaluations of microfragmentation for restoring live tissue in Caribbean *Orbicella* corals under thermal stress conditions (Gutiérrez-Coral et al., 2025). Despite adverse environmental conditions, including significant thermal anomalies during 2023–2024, this study showed relatively high survival rates, particularly for *O. faveolata*, as well as signs of recovery in growth and polyp number at the end of the experiment. These results provide evidence on species-specific susceptibility and the feasibility of tissue transplantation for the restoration of massive corals, which have traditionally been excluded from restoration programs due to their slow growth rates (Page et al., 2018; Tortolero-Langarica, Rodríguez-Troncoso et al., 2025).

Despite El Niño 2023–2024 thermal anomalies, overall survival was relatively high (52.17 %), with *O. faveolata* showing higher survival (60 %) than *O. annularis* (42.9 %), consistent with previous reports of higher thermal tolerance in *O. faveolata* (Röthig et al., 2016; Galindo-Martínez et al., 2022). Although the differences were not statistically significant, likely due to shared thermal stress, species-specific patterns of resilience were evident; however, further evaluation at the community level is recommended. Fragment size was a key

determinant of success, with larger microfragments (> 4 cm²) achieving 85 % survival, supporting previous findings that larger microfragments retain greater energetic reserves and recovery capacity (Lirman et al., 2010; Forsman et al., 2015).

Thermal conditions (26.6–31.7 °C) exceeded regional bleaching thresholds and coincided with mass bleaching and reduced coral performance (Grottoli et al., 2014; Eakin et al., 2026). Elevated temperatures may disrupt coral-symbiont relationships, reduce energy availability, and potentially contribute to declines in growth and survival observed herein (Hoegh-Guldberg, 1999), particularly in O. annularis, consistent with its reported vulnerability (Bruckner & Bruckner, 2006). Both species exhibited reduced growth, consistent with an energetic trade-off in which resources may be prioritized toward tissue maintenance and repair rather than skeletal growth under stress (Anthony et al., 2002). However, *O. faveolata* showed partial recovery and an increase in polyp numbers, suggesting potential compensatory responses associated with greater physiological plasticity and/or heterotrophic energy acquisition (Allemand et al., 2011; Houlbrèque & Ferrier-Pagès, 2009). Similar patterns have been reported in the region (Tortolero-Langarica, Rodríguez-Troncoso et al., 2025) and are consistent with evidence of resilience in some *O. faveolata* populations (Page et al., 2018).

Post-bleaching recovery was possible associated with environmental stabilization of SWT and light availability (PAR), which showed positive relations with growth. This relationship supports the role of light in regulating energy transfer between symbionts and hosts (Allemand et al., 2011) and agrees with evidence of physiological plasticity in this species (Lorenzo-Jiménez et al., 2024). Ecologically, these results align with the "winners and losers" framework under climate change, highlighting species-specific thermal tolerance as an important factor influencing restoration success (Grottoli et al., 2014; Boström-Einarsson et al., 2020). Cold-period fluctuations (November–February) may have further constrained recovery, suggesting that both prolonged warming and rapid cooling can impose physiological stress and impair calcification (Jokiel & Coles, 1977), consistent with previous observations of unsuccessful bleaching recovery (Baird & Marshall, 2002; Grottoli et al., 2014; Manzello, 2015).

Microfragmentation of massive species proved viable but highly dependent on environmental conditions and post-transplant management (Tortolero-Langarica et al., 2020; Knapp et al., 2022). Success could also be influenced by substrate, depth, competition, and timing (Page et al., 2018), emphasizing the need for environmental synchronization before outplanting stage and continuous monitoring. Therefore, microfragmentation represents a promising but context-dependent restoration strategy for massive corals (Tortolero-Langarica, Rodríguez-Troncoso et al., 2025). Under extreme thermal stress, restoration performance appears to be strongly modulated by species identity, and environmental conditions, which are important determinants of restoration success, particularly for slow-growing species. *O. faveolata* emerges as a potentially more resilient candidate for assisted restoration, whereas *O. annularis* showed lower survival and less evidence of functional recovery under the conditions evaluated here. Overall, restoration success in the Caribbean will depend not only on the restoration technique but also on integrating climate resilience, environmental management, and species-specific selection criteria to support long-term reef recovery under ongoing climate change.

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