

Effect of benthic organisms on *Acropora palmata* (Lamarck, 1816) fragment survival and growth

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Abstract

Interactions between reef organisms such as overgrowth or release of allelopathic substances, constitute key elements to consider when planning and conducting restoration efforts. We investigated the impact of interactions with benthic organisms on the survival and growth of *Acropora palmata* fragments outplanted in three reef crests in Cuba. We established a field-based experiment with controls and treatments in each crest that consisted of placing a fragment of *A. palmata* in proximity to: (1) *Porites astreoides*, (2) *Millepora complanata*, (3) *Cladophora* sp., (4) *Sargassum polyceratum*, (5) *Dictyota* sp., (6) *Stypopodium zonale* or (7) *Palythoa caribaeorum*. Survival and growth of *A. palmata* fragments varied significantly among treatments. The fragments in proximity to *P. astreoides* showed high survival relative to the controls and overgrew the *Porites* colonies, suggesting asymmetric competition. In contrast, *M. complanata* overgrew the fragments, resulting in low fragment survival. A significant interaction between the La Puntica crest and fragments paired with *P. astreoides* and *M. complanata* suggests the influence of local environmental conditions on survival and growth of the fragments on this crest. Algal interactions had limited effects. Overall, fragments increased in mean area of live tissue over time, although the growth rates were lower than reported in the literature for *A. palmata*. These results highlight that *A. palmata* fragment survival and growth are affected by biotic interactions and site-specific conditions, underscoring the importance of understanding these processes to inform effective restoration strategies.

Introduction

The coral species *Acropora palmata* (Lamarck 1816) plays a critical role in reef accretion and coastal protection due to its branching morphology and rapid growth, which generate complex three-dimensional habitats. It also provides shelter, feeding, and nursery areas for invertebrates and fishes, thereby enhancing biodiversity on reef crests (Larson et al. 2014; Cramer et al. 2021). The decline of this species over the last 75 years has resulted in reduced reef structure and functioning (Cramer et al. 2020; Manzello et al. 2025) and this species has been listed as Critically Endangered by the International Union for Conservation of Nature (IUCN) since 2008 (Aronson et al. 2008). Currently, *A. palmata* populations are considered unable to recover naturally due to the impact of various anthropogenic and natural factors such as water pollution, coral diseases and increased ocean temperatures (Jackson et al. 2014; Dutra et al. 2021; Manzello et al. 2025). Consequently, restoration programs have been implemented as a strategy to recover *Acropora* spp. populations throughout the Caribbean via the outplanting of fragments of opportunity, or those that have been pruned from mother colonies (Ladd et al. 2018; Boström-Einarsson et al. 2020). Additionally, land-based and in-water coral nurseries have been established to produce a sustainable source of corals for restoration, thereby reducing the need for translocation or repeated harvesting from wild populations (Steinberg 2021). Outplanted *A. palmata* fragments, used in restoration programs in general, have high survival (63–95%) and growth (21 cm/yr), but these projects have been mostly of short duration (1–2 years) (Bayraktarov et al. 2020). Fragment mortality has been associated with damage from storms, high temperatures, predation and poor water quality (Meesters et

al. 2015). However, little is known about how ecological processes such as competition, influence early-stage establishment of fragments (Ladd et al. 2019).

Interactions among reef organisms can be a key element to consider in coral restoration efforts (Ladd et al. 2019). Benthic organisms compete with corals, inhibiting the settlement and establishment of coral larvae and decreasing the survival of settled recruits and juveniles (Birrell et al. 2005; Mumby 2006). Macroalgae, in particular, outcompete corals by physical abrasion, producing allelopathic substances, promoting sediment accumulation, causing overgrowth, and shading (Box and Mumby 2007; Inagaki and Longo 2024). Other strong competitors include the hydrozoans of the genus *Millepora* capable of rapid colonization and overgrowth (Lewis 2006; Wegener et al. 2018; Ladd et al. 2019) and the zoanthid *Palythoa caribaeorum* (Duchassaing and Michelotti 1860), which can overgrow corals due to its faster growth rate (Guppy et al. 2019; Lonzetti et al. 2022; Grillo et al. 2024) and release palytoxin, a potent biotoxin that can be harmful to corals (Patocka et al. 2015). In contrast, the weedy coral *Porites astreoides* (Lamarck 1816) is a weaker competitor, but has increased cover on coral reefs since the early 1960s and 1980s (Cramer et al. 2021).

Macroalgae, *Millepora* and *Porites* are benthic organisms that dominate the reef crests and can occupy space that could serve as substrate for other species (Connell 1976; Hastings 1980; Chadwick and Morrow 2011), thus jeopardizing the success of restoration efforts through direct competition with outplanted coral species. In this context, this study addresses the question: To what extent do benthic competitors influence the survival and growth of *A. palmata* fragments? We hypothesize that benthic competitors differentially influence the performance of outplanted *A. palmata* fragments: macroalgae, *Millepora complanata* (Lamarck 1816) and *P. caribaeorum* will negatively affect survival and growth through space competition, overgrowth or allelopathic inhibition, whereas interactions with the weedy coral *P. astreoides* will result an asymmetric interspecific competition through resource use, as it is a weak competitor. Therefore, we investigated the impact of different benthic organisms on the survival and growth of *A. palmata* fragments outplanted in three reef crests with different physical and ecological characteristics, differentially impacted by multiple natural and anthropogenic stressors, and varying levels of management (Pina-Amagós et al. 2014; Rey-Villiers et al. 2021; Ramos et al. 2024). By clarifying the impacts of benthic competitors on outplanted coral fragments, we seek to provide insights for improving the effectiveness of coral restoration strategies.

Methods

Study Area

The study was conducted in three shallow (1–3 m) reef crests in Cuba. Two sites are located in the northwest region, in Playa Baracoa, Artemisa Province (23°03'20"N, 82°33'10"W) and Rincón de Guanabo, La Habana Province (23° 10'23.63"N, 82°05'57.46"W) and the third site, La Puntica (20°49'52.69"N, 78°58'44.62"W) lies to the south of central Cuba, in the Jardines de la Reina National Park (Fig. 1). These reefs differ in distance from the coast, coral cover, abundance and diversity of reef

species such as fish and sea urchins, anthropogenic stressors, as well as management and protection (Duran et al. 2023; Ramos et al. 2024).

The reefs in the northwestern region are impacted due to their proximity to the capital city and to coastal development (González-Díaz et al. 2018; Ramos et al. 2024). Pollution by heavy metals and fertilizers, from street runoff, the Almendares and Quibú rivers, and Havana Bay, are the main anthropogenic factors that affect reefs (Rey-Villiers et al. 2020, 2021; Ramos et al. 2024). The crest in Playa Baracoa is 764 m long, between 20 and 60 m wide, and located roughly 230 m from Baracoa, a small fishing village. The study site is 2 km east of Santa Ana River, where untreated wastewater from a local educational institution (Latin American School of Medicine with an average annual enrollment of 10,000 students) is released. There is no official information on pollution rate, type, or impact, but anecdotal information and personal experience indicates that an unpleasant smell emanates from the waters of the Santa Ana River (Ramos et al. 2024). Rincón de Guanabo is a marine protected area (Protected Natural Landscape/seascape similar to category V IUCN) located 800 m from the coastline, with an approximate extension of 950 m. The crest is nearly 3 km west of an oil drilling and extraction area (Boca de Jaruco thermoelectric power station), but data on nutrient load or pollutants (e.g., hydrocarbons) are either absent or unavailable. Both northwestern region crests are influenced by subsistence overfishing pressure, and there are no effective management plans for these areas (Pina-Amargós et al. 2023). Overall, coral cover is low, at approximately 9% in Playa Baracoa and 17% in Rincón de Guanabo. The density of *Diadema antillarum* in Playa Baracoa is 1.7 ± 1.1 ind. m², compared to 0.1 ± 0.2 ind. m² in Rincón de Guanabo (Ramos et al. 2024). Fish biomass is also low, averaging about 12 g m² (Duran et al. 2018).

On the other hand, Jardines de la Reina National Park is located approximately 50 miles from the main island of Cuba and presents low human impact (Beyer et al. 2018). It is a protected area with effective strategies for the management and conservation of fisheries, as outlined in the Ministerial Resolution 562/92 of the Fishing Industry. It has been classified as an oligotrophic system, where nutrient input is by organic matter from mangroves, muddy sediments, and from open waters such as the Gulf of Ana María and the Caribbean Sea (Pina-Amargós et al. 2021). La Puntica crest, prior to the summer of 2023, was primarily formed by *A. palmata* covering 44% of the area. The density of *D. antillarum* is 3.8 ind/m² (Hernández-Fernández et al. 2016). The crest and slope reef habitats in Jardines de la Reina exhibit high herbivorous fish biomass, approximately 60 g m⁻² (Duran et al. 2023). According to Pina-Amargós et al. (2014), the crests has high abundances of commercially important fish species, including *Epinephelus striatus* (0.2 ± 0.02 ind /1,000 m²), *Lutjanus cyanopterus* (0.2 ± 0.03 ind/ 1,000 m²), and *L. apodus* (53.2 ± 2.2 ind/ 1,000 m²).

Experimental Design

To test the effect of competition with benthic organisms on survival and growth of *A. palmata* fragments, we established a field experiment with control fragments and three to five treatments of a locally

abundant competitor species paired with a fragment of *A. palmata* at each study site. Before placing the control fragments, we cleared an area of approximately 20 cm in diameter to prevent contact with other benthic organisms. The number of treatments depended on the availability of the most abundant organisms at each of the crests. In Playa Baracoa, four treatments were established, and consisted of placing fragments in proximity to: (1) *P. astreoides*, (2) *M. complanata*, (3) *Cladophora* sp., and (4) *Sargassum polyceratum* Montagne 1837. In Rincón de Guanabo, five treatments were implemented: (1) *P. astreoides*, (2) *M. complanata*, (3) *Cladophora* sp., (4) *Dictyota* sp. and (5) *Styopodium zonale* (J. V. Lamouroux) Papenfuss 1940. In La Puntica, three treatments were established with: (1) *P. astreoides*, (2) *M. complanata*, and (3) *P. caribaeorum*. At each of the three study crests, each control and treatment consisted of seven replicates (Fig. 2, Online Resource 1).

The *A. palmata* fragments were randomly collected from multiple colonies at each crest and outplanted on the same day at the same crest where they were collected. They were cut with forceps from the apical portions of different branches of several colonies, with a roughly rectangular shape and lacking secondary branching and were in good health. These fragments were subsequently outplanted onto the same reef crest as the parental colonies, rather than in a common garden. Within an approximate area of 100 m², fragments were attached to the substrate with epoxy (KLIPTON ACUAPLAST) and each was labeled and monitored over time. *A. palmata* fragments were placed less than 1 cm to coral, zoanthid and hydrocoral competitors to ensure an interaction (Ladd et al. 2019) and to take advantage of their natural location at each crest. Due to flexibility and wave-induced movement of algal species, coral fragments were outplanted so at least one side of the fragment was in direct contact with algal species. Potential confounding factors such as shading, water flow, and sedimentation from benthic organisms were not explicitly measured in the experimental design.

In Playa Baracoa, the experiment was carried out in February 2021 and fragments were monitored at 0, 90, 180 and 370 days. In Rincón de Guanabo, the experiment began in March 2021 and the fragments were monitored at 0, 80, 170 and 320 days. In La Puntica, the experiment started in February 2022 and fragments were measured at 0, 50, 170, 292 and 423 days. The duration of the experimental monitoring was determined by logistical constraints. Fragments were measured for maximum width and height with a Vernier caliper. The same attachment technique was used for all treatments by the same team.

Data analysis

Statistical analyses were conducted using the R program, created by the R Core Team (2016, version 4.0.5). Data were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Levene’s test) prior to selecting the appropriate test. When assumptions of normality and homoscedasticity were met, differences in the initial size of fragments among the controls and the treatments for each crest and among crests were analyzed using analysis of variance (ANOVA). Otherwise, the non-parametric Kruskal–Wallis test was applied. To assess whether the initial size of fragments influenced their survival, a Cox regression model [coxph (Surv(survival time, Survival) ~ height + width, data = data)] was conducted using the survival package (Therneau and Grambsch 2000).

The probability of fragment survival (p_s) of controls and treatments over time was estimated using the non-parametric Kaplan-Meier estimator. This estimator models survival probability over time by accounting for the exact timing of mortality events by partitioning the follow-up period into intervals defined by the occurrence of events (e.g., fragment mortality) and estimating the conditional survival probability for each interval. These conditional probabilities were then multiplied sequentially to obtain the cumulative survival function. The function *survfit* was used to generate survival curves and censored data (i.e., fragments that remained alive at the end of the monitoring period) were included in the estimation. The differences between survival distributions among the controls and treatments were analyzed using the Log-Rank test (non-parametric), which compares the cumulative hazard functions between groups. The survival (Therneau and Grambsch 2000) and survminer (Kassambara et al. 2021) packages were used for statistical analysis. A p-value < 0.05 was considered statistically significant.

A Cox regression model was used to estimate the influence of explanatory variables (e.g., crest, treatment) on survival probability. Model outputs included hazard ratios (HR) with 95% confidence intervals to quantify the relative mortality risk among treatments. In this model, the reference levels were Playa Baracoa for crest and control for treatment, with values set to 0 for the coefficient and 1 for the hazard ratio (relative risk).

The surface area of live tissue of fragments was estimated as: $2 \text{ (width} \times \text{height)} \times \% \text{ live tissue}$, considering the fragments roughly rectangular shape and two exposed surfaces, at the initial establishment of the fragments and during each study period.

The growth rate of the fragments was determined for both width and height during each study period, using the formula of Mercado-Molina et al. (2014):

$$\text{Growth rate} = \frac{(\text{initial size} - \text{final size})}{\text{time}}$$

Initial size is the height and/or width (cm) of fragment at the beginning of each period, final size is the height and/or width (cm) reached by fragments at the end of each period, and

time is the number of days included in each study period.

A linear mixed-effects model was used to evaluate the effect of (1) crest, (2) treatments, and (3) time on the area of live tissue of fragments ($\text{growth} \sim \text{crest} * \text{treatments} + \text{Period} + (1 | \text{Fragment})$, data =Data), using the lmerTest (Kuznetsova et al. 2017) package. In this model, the reference levels were Playa Baracoa for crest and control for treatment.

Results

Initial size of the fragments

Initial fragment sizes for controls and treatments were analyzed within (Online Resource 2) and between crest sites (Online Resource 3). The initial size of *A. palmata* fragments was similar between controls and treatments for each crest (Online Resource 2). However, significant differences (ANOVA, $p = 0.02$) were detected in the width of the control fragments, being greater in the northwestern region (PB: 3.3 ± 0.7 cm, RG: 3.2 ± 0.7 cm) than in La Puntica (2.3 ± 0.8 cm) (Online Resource 2). The cox regression model did not show an effect on the initial size of the fragments on the survival of fragments for the three crests.

Survival

In Playa Baracoa, the model indicated that survival probability varied significantly among the control and treatments (Likelihood ratio test = 10.3, $p = 0.04$). The survival of control fragments decreased to 0.7 at 135 days and remained constant thereafter until the end of the experiment. The fragments paired with *P. astreoides* exhibited similar survival (0.7 at 135 days) to the control, with a slight reduction to 0.6 at 275 days (Table 1). In contrast, fragments associated with *M. complanata* showed lower survival than the control (HR = 5.7, 95% CI: 1.1–29.1, $p = 0.04$) (Table 2), decreasing from 0.5 at 135 days to complete loss ($p_s = 0$) by 275 days. The fragments paired with *Cladophora* sp. showed a marked decrease from 0.8 to 0.2 during the monitoring period, whereas those paired with *S. polyceratium* maintained consistently high survival ($p_s = 0.8$) through 275 days (Table 1; Fig. 3a).

Table 1

The survival probability (p_s) of *Apalmata* fragments for controls and treatments during the study period in the crests at Playa Baracoa (PB), Rincón de Guanabo (RG), and La Puntica (LP).

Crests	Treatment	Time (day)	p_s
	Control	135	0.7
	<i>Porites astreoides</i>	135	0.7
		275	0.6
PB		45	0.8
	<i>Millepora complanata</i>	135	0.5
		275	0
	<i>Cladophora</i> sp.	135	0.8
		275	0.2
	<i>Sargassum polyceratum</i>	275	0.8
	Control	125	0.8
	<i>Porites astreoides</i>	245	0.4
	<i>Millepora complanata</i>	125	0.6
		245	0
RG	<i>Cladophora</i> sp.	125	0.4
		245	0.1
	<i>Dictyota</i> sp.	125	0.9
	<i>Stypopodium zonale</i>	125	0.9
		245	0.6
	Control	25	0.5
		110	0.4
		358	0.3
LP	<i>Porites astreoides</i>	358	0.9
		110	0.8
	<i>Millepora complanata</i>	231	0.7
		358	0.5

Crests	Treatment	Time (day)	p _s
	Control	135	0.7
	<i>Palythoa caribaeorum</i>	231	0.8

In Rincón de Guanabo, survival varied slightly among treatments (Likelihood ratio = 10.8, $p = 0.05$). The survival of control fragments remained high ($p_s = 0.8$) for up to 125 days. After this time, the fragments were not found, probably because they detached from the substrate. The survival of fragments paired with *P. astreoides* declined to 0.4 at 245 days. The survival of fragments paired with *M. complanata* decreased from 0.6 at 125 days to zero at 245 days. The survival of fragments paired with *Cladophora* sp. decreased over time, reaching 0.1 by the last monitoring period. Fragments paired with *Dictyota* sp. maintained high survival ($p_s = 0.9$) for 125 days. After this time, the fragments were not found. The survival of fragments paired with *S. zonale* was 0.6 at 245 days (Tables 1 and 2; Fig. 3b). In La Puntica, survival varied significantly among treatments (Likelihood ratio = 9.9, $p = 0.02$). Control fragments showed 0.5 survival over 25 days. The *P. astreoides* treatment maintained highest survival of 0.9 at 358 days relative to the control (HR = 0.08, 95% CI: 0.01–0.7, $p = 0.02$). Fragments paired with *M. complanata* showed a survival of 0.5 for 358 days. Finally, fragments paired with *P. caribaeorum* exhibited a survival of 0.8 for 231 days (Table 1; Fig. 3c). Significant interactions were recorded between the La Puntica crest and *M. complanata* (HR = 0.07, 95% CI: 0.008–0.6, $p = 0.01$) and *P. astreoides* (HR = 0.05, 95% CI: 0.003–0.8, $p = 0.04$) treatments (Table 2).

The Cox regression model indicated that both crest and treatments significantly affected coral fragment survival. Fragments at Rincón de Guanabo, including the control and those paired with *P. astreoides* and *M. complanata* exhibited a 6.2-fold lower survival compared to Playa Baracoa (HR = 6.2, 95% CI: 1.1–33.3, $p = 0.03$), while La Puntica showed a similar trend (HR = 4.3, 95% CI: 0.9–21.1, $p = 0.08$) to Playa Baracoa (Table 2). The number of fragments measured varied in each period due to mortality, attachment failure, or the inability to locate them during each monitoring period.

Table 2

Results of the Cox regression model estimating the influence of explanatory variables (crests and treatments) on coral fragment survival probability. The table shows the direction of effects (coefficients), effect sizes (hazard ratios, HR), measures of dispersion (95% confidence intervals, CI), and significance levels ($p < 0.05$) indicated in bold. Reference levels were Playa Baracoa for reef and control for treatment.

Variables	Effect direction	Effect size	CI (95%)	p-value
Crests effect				
Rincón de Guanabo	1.8	6.2	1.1–33.3	0.03
La Puntica	1.4	4.2	0.9–21.1	0.08
Interactions (crest x treatments)				
Rincón de Guanabo x <i>M. complanata</i>	-1.4	0.2	0.03–1.7	0.2
La Puntica x <i>M. complanata</i>	-2.7	0.07	0.008–0.6	0.01
Rincón de Guanabo x <i>P. astreoides</i>	-1.2	0.3	0.03–3	0.3
La Puntica x <i>P. astreoides</i>	-3	0.05	0.003–0.8	0.04
Treatment effect in Playa Baracoa				
<i>M. complanata</i>	1.7	5.7	1.1–29	0.04
<i>P. astreoides</i>	0.3	1.3	0.2–7.8	0.8
<i>S. polyceratum</i>	-0.8	0.5	0.04–5.2	0.5
<i>Cladophora</i> sp.	1.1	2.9	0.6–15.3	0.2
Treatment effect in Rincón de Guanabo				
<i>M. complanata</i>	0.3	1.3	0.4–4.1	0.7
<i>P. astreoides</i>	-1.1	0.3	0.08–1.4	0.1
<i>Cladophora</i> sp.	0.03	1	0.3–3.4	0.9
<i>Dictyota</i> sp.	-0.05	0.9	0.3–3	0.9
<i>S. zonale</i>	-1.4	0.2	0.05–1	0.04
Treatment effect in La Puntica				
<i>M. complanata</i>	-0.9	0.4	0.1–1.6	0.2
<i>P. astreoides</i>	-2.5	0.08	0.01–0.7	0.02
<i>P. caribaeorum</i>	-2.1	0.1	0.01–1.03	0.05

Mean live tissue area of fragments

Growth is presented in terms of area of live tissue (Table 3) and changes in width and height of the coral fragments (Online Resource 4). In the three crests, we observed tissue growth of *A. palmata* fragments over the epoxy base starting at 80 to 170 days post-transplantation in both control and treatments, except for fragments paired with *M. complanata*. In addition, we observed overgrowth of *A. palmata* fragments on *P. astreoides* colonies, as well as overgrowth of *M. complanata* on *A. palmata* fragments, beginning between 90 to 180 days.

In Playa Baracoa, the mean area of live tissue of control fragments increased 2.8-fold, from 18.3 to 50.4 cm² ($p = 0.04$), during the monitoring period. Fragments paired with *P. astreoides* maintained a similar live tissue area throughout the study period, measuring 19.9 cm² initially and 22.6 cm² by the end of the experiment. Fragments paired with *M. complanata* increased 2-fold in live tissue area (range: 10.6 to 22.3 cm²) and showed a significantly lower area (estimate = - 24.4, $p = 0.016$) compared to the control (Table 4). The fragments paired with *Cladophora* sp. and *S. polyceratum* increased 2.4-fold ($p = 0.003$) and 2.1-fold ($p = 0.04$), respectively (Table 3; Fig. 4). The area of live tissue of fragments paired with *P. astreoides*, *Cladophora* sp. and *S. polyceratum* did not significantly varied relative to control. Overall, a significant increase in area of live tissue was observed over time (estimate = 5.1, $p = 0.01$).

In Rincón de Guanabo, the live tissue area of control fragments ranged from 15.1 to 33.2 cm² during the monitoring period. The area of live tissue of fragments paired with *P. astreoides* increased 4-fold, from 12.9 cm² to 49.9 cm² ($p = 0.007$). Fragments paired with *M. complanata* showed the lowest growth, reaching a final size of 6.1 cm². The live tissue area increased 2.4-fold for *Cladophora* sp. ($p = 0.004$), 2-fold for *Dictyota* sp., and 2.6-fold for *S. zonale* ($p = 0.03$) (Table 3; Fig. 4). The area of live tissue in all treatments was similar to the control. In addition, no significant temporal changes were detected.

In La Puntica, the area of live tissue of control fragments ranged from 13.4 to 32.2 cm². The area of live tissue of fragments paired with *P. astreoides* increased 2-fold, from 13.3 cm² to 26.7 cm² ($p = 0.005$), during the monitoring period. Fragments paired with *M. complanata* also increased 2-fold (from 13.5 to 21.0 cm²), as long as they survived. The highest growth was recorded in fragments paired with *P. caribaeorum*, which increased 3.6-fold, from 10.1 cm² to 36.7 cm² ($p = 0.002$) (Table 3; Fig. 4). The area of live tissue in all treatments was similar to the control. A significant increase in area of live tissue was recorded over time (estimate = 3.4, $p < 0.001$). Significant interactions were recorded between La Puntica crest and *M. complanata* (estimate = 27.3, $p = 0.009$) and *P. astreoides* (estimate = 19.6, $p = 0.04$) treatments (Table 4).

Table 3
Mean initial and final sizes (surface area of live tissue) of the controls and treatments fragments on the crests at Playa Baracoa (PB), Rincón de Guanabo (RG) and La Puntica (LP). The p-value < 0.05 indicates a significant difference over time, indicated in bold.

Crests	Treatments	Size (cm ²)		
		Initial	Final	p-value
PB	Control	18.3	50.4	0.04
	<i>P. astreoides</i>	19.9	22.6	0.4
	<i>M. complanata</i>	10.6	22.3	0.5
	<i>Cladophora</i> sp.	17.7	42.2	0.003
	<i>S. polyceratium</i>	18.1	38.4	0.04
RG	Control	15.1	33.2	0.09
	<i>P. astreoides</i>	12.9	49.9	0.007
	<i>M. complanata</i>	7.6	6.1	0.8
	<i>Cladophora</i> sp.	8.8	21.6	0.004
	<i>Dictyota</i> sp.	19.5	32.8	0.2
LP	<i>S. zonale</i>	16	41	0.03
	Control	13.4	32.2	0.2
	<i>P. astreoides</i>	13.3	26.7	0.005
	<i>M. complanata</i>	13.5	21	0.2
	<i>P. caribaeorum</i>	10.1	36.7	0.002

The lineal mixed-effects model indicated that fragments at Rincón de Guanabo (estimate = -22, p = 0.003) and La Puntica (estimate = -20.9, p = 0.004), including the control and those paired with *P. astreoides* and *M. complanata* exhibited lower area of live tissue compared to Playa Baracoa (Table 4).

Table 4

Results of the linear mixed model estimating the influence of explanatory variables (crests and treatments) area of live tissue on the coral fragments, showing the direction and size of effects (estimates), measures of dispersion (standard error), and significance levels ($p < 0.05$), indicated in bold. Reference levels were Playa Baracoa for crest and control for treatment.

Variables	Effect direction and size	Standard Error	p-value
Crests effect			
Rincón de Guanabo	-22	7.1	0.003
La Puntica	-20.9	7	0.004
Interactions (crest x treatments)			
Rincón de Guanabo x <i>M. complanata</i>	18.4	10.1	0.07
La Puntica x <i>M. complanata</i>	27.3	10.1	0.009
Rincón de Guanabo x <i>P. astreoides</i>	15.6	9.9	0.1
La Puntica x <i>P. astreoides</i>	19.6	9.7	0.04
Treatment effect in Playa Baracoa			
<i>M. complanata</i>	-24.4	9.7	0.02
<i>P. astreoides</i>	-15.6	9.2	0.1
<i>S. polyceratum</i>	-4.1	9.3	0.7
<i>Cladophora</i> sp.	-11.5	9.1	0.2
Treatment effect in Rincón de Guanabo			
<i>M. complanata</i>	-7.5	5.8	0.2
<i>P. astreoides</i>	0.1	5.9	0.9
<i>Cladophora</i> sp.	-2.4	5.9	0.7
<i>Dictyota</i> sp.	7.6	5.8	0.2
<i>S. zonale</i>	6.9	5.8	0.2
Treatment effect in La Puntica			
<i>M. complanata</i>	1.1	4.4	0.8
<i>P. astreoides</i>	3.6	4.1	0.4
<i>P. caribaeorum</i>	-1.4	0.8	0.7

Growth rates of the fragments

The growth rates of the fragments were consistently low and fluctuated during the study period. In Playa Baracoa, control fragments showed limited growth (0.003 cm/day in width and 0.007 cm/day in height, in the last monitoring period). Growth in fragments paired with *M. complanata* was only observed in the first period, showing minimal vertical growth (0.002 cm/day) and slight tissue loss in width (-0.001 cm/day). Fragments paired with *P. astreoides* (range: 0.01 to -0.0005 cm/day in width and range: 0.005 to 0.001 cm/day in height), *Cladophora* sp. (range: 0.01 to 0.007 cm/day in width and height) and *S. polyceratum* (range: 0.02 to 0.0005 cm/day in width and range: 0.02 to -0.003 cm/day in height) exhibited decreasing growth trends over time (Online Resource 4).

In Rincón de Guanabo, fragments exhibited higher growth rates than on the other crests, particularly in the control fragments (0.02 cm/day in width and 0.03 cm/day in height, in the second period). Growth of fragments paired with *P. astreoides* (range: -0.02 to 0.008 cm/day in width and range: 0.0006 to 0.02 cm/day in height), *M. complanata* (range: -0.01 to 0.008 cm/day in width and range: -0.004 to 0.006 cm/day in height), *Cladophora* sp. (range: -0.005 to 0.008 cm/day in width and -0.01 to 0.01 cm/day in height), *Dictyota* sp. (range: 0.001 to 0.03 cm/day in width and range: 0.009 to 0.02 cm/day in height) and *S. zonale* (range: -0.01 to 0.006 cm/day in height) increased over time, with initially negative or low values becoming positive by later periods (Online Resource 4).

In La Puntica, the growth rates of control fragments were negative for width (-0.001 cm/day) in the last monitoring period and increased slightly in height over time from 0.002 to 0.003 cm/day. Fragments paired with *P. astreoides* showed a significant increase ($p = 0.001$) in both width (range: 0.002 to 0.005 cm/day) and height (range: 0.002 to 0.003 cm/day) over time. Fragments paired with *M. complanata* (range: 0.002 to 0.004 cm/day in height) and *P. caribaeorum* (range: 0.001 to 0.005 cm/day in width and range: -0.002 to 0.009 cm/day in height) also exhibited small but increasing growth rates toward the final monitoring period. Overall, coral fragments in La Puntica tended to recover or maintain low but positive growth rates over time (Online Resource 4).

Discussion

In this study we identified that both survival and growth of *A. palmata* fragments were influenced by biological interactions and possibly local reef location. Fragments at Playa Baracoa exhibited the highest growth, whereas those at Rincón de Guanabo and La Puntica showed more variable responses. The significant interactions between site and treatment in La Puntica crest suggest that the survival and growth of *A. palmata* fragments are influenced potentially by site location. Differences observed among control fragments among sites could be attributed to genotypic variability of *A. palmata* fragments or to site-local conditions. The fragments in proximity to *P. astreoides* showed high survival compared to the control and other treatments, with some fragments overgrowing the *Porites* colonies suggesting asymmetric competition. On the other hand, *M. complanata* significantly reduced survival of the fragments through overgrowth. In Rincón de Guanabo, the control and *Dictyota* treatment fragments detached after 125 days which may have been caused by wave action, fishing impacts, epoxy failure, or human error during outplanting.

The fragments paired with *P. astreoides* showed similar survival to the control in Playa Baracoa, and higher survival in the La Puntica crest, indicating that this interaction probably did not negatively affect the performance of *A. palmata*. The significant interaction between La Puntica crest and *P. astreoides* treatment suggests that localized environmental conditions can modulate fragment survival and mitigate possible negative effects of competition. Notably, the fragments of *A. palmata* grew over the living tissue of *P. astreoides* colonies. Skeletal overgrowth is one of the main mechanisms of competition used during interference competition among reef cnidarians (Álvarez-Noriega et al. 2018). This finding aligns with Ladd et al. (2019), who identified *Porites* as one of the least aggressive coral species on the reef. Although this interaction scenario was experimentally induced rather than naturally occurring, it provides insights into the potential outcomes of space competition in areas of high density of *P. astreoides* or in multi-species restoration settings. In such contexts, understanding interspecific tolerance and competitive hierarchies can inform strategies for mixed coral assemblages. From a restoration perspective, where the goal is to increase coral cover and the diversity of restored species, competition between corals that negatively impacts at least one species is undesirable.

The fragments paired with *M. complanata* showed lower survival compared to the control, with no survivors by the end of the monitoring period, in Playa Baracoa and Rincón de Guanabo crests, except in La Puntica crest. This hydrozoan caused high mortality and competed successfully with *A. palmata* fragments by overgrowing them, as was also observed by Ladd et al. (2019). Although this study did not provide direct evidence, species of the genus *Millepora* can compete by producing toxins stored and delivered through nematocysts, which are used for defense and predation (Hernández-Elizarraga and López 2025). Despite the low survival of *A. palmata* fragments, identifying detrimental interactions, such as competition with *M. complanata* provides insights into the biotic conditions that modulate early survival in restoration contexts. The purpose of this experiment was not to promote outplanting in unsuitable competitive environments, but to identify potential biotic stressors that could limit restoration success. In natural reef crests, *Millepora* spp. are common and may represent frequent competitors for available substrate (Dubé et al. 2019; Cramer et al. 2021). Therefore, understanding their interaction dynamics with *A. palmata* helps refine site-selection criteria and spatial planning during restoration activities.

However, higher resistance of the *A. palmata* fragments was observed when interacting with *M. complanata* in La Puntica and the interaction between crest and the *M. complanata* treatment was significant, indicating that localized environmental conditions within crest modulate fragment survival. The differences in survival response of the fragments in competition with *M. complanata* across crests could be associated with (1) abiotic characteristics of the crest, (2) a more resistant genotype of *A. palmata* or (3) a more susceptible genotype of *M. complanata* in La Puntica. The potential genetic differences in the survival of *A. palmata* when exposed to competition with *M. complanata* could be assessed by identifying the genotypes of the pruned colonies. However, genotyping is costly and was not evaluated during this study. According to Chadwick and Morrow (2011) and Ladd et al. (2019), the interaction mechanisms between organisms, even of the same species, can vary at different intensities of light, waves, nutrients, temperature, sedimentation; depending on the genotype, age, size, morphology,

interaction time and stresses to which the reef is subjected. Such variability in survival among crests highlights the importance of considering site-specific and genetic factors when planning restoration efforts.

In our experiment, the survival of fragments paired with algae treatments was similar to that of the control in Playa Baracoa. In the case of *Styopodium* at Rincón de Guanabo, survival was highest compared to the other treatments with fragments being monitored until the end of the experiment.. This species of algae has been reported to exhibit chemical activity, primarily tested in relation to herbivorous fish and sea urchins (Gerwick and Fenical, 1981), but further testing is required to assess its effects on corals.

In La Puntica, the survival of *A. palmata* fragments paired with *P. caribaeorum* was high and no overgrowth was observed in either of these two species. Lonzetti et al. (2022) demonstrated negative effects of *P. caribaeorum* on *M. alcicornis* when both species were in direct contact. In contrast, in our experiment the organisms were placed adjacent rather than overlapping, which may explain the absence of a negative effect. Nevertheless, such interactions could become evident over longer observation periods, as zoanthid overgrowth and direct contact may develop gradually. Most studies suggest that together with macroalgae, *Palythoa* is one of most successful competitors of reef (Chadwick and Morrow 2011; Cruz et al. 2016; Ladd et al. 2019). However, different coral species can be more resistant to competition with the zoanthid (Lustic et al. 2020). Species of the *Acropora* genus (Suchanek and Green 1981) and other coral species (Chornesky 1983; Chadwick and Morrow, 2011; Pineda-Munive and Garcia-Uruena, 2022) present defensive strategies, such as sweeper tentacles, mesenteric filaments, secondary metabolites and/or nematocyst discharge that guarantee their survival in the face of such interactions. In this study, we have no evidence of a defensive strategy used by *A. palmata* fragments against *Palythoa*, but competitive interactions possibly occurred as indicated by survival of *A. palmata*.

Coral size is a key indicator of growth, reproduction, survival and success or failure in interactions with other organisms (Mumby and Harborne 2010; Ferrari et al. 2012). However, in this study, the survival of the *A. palmata* fragments was not affected by their initial size (average range: two to 3.5 cm). Over time, the surface area of live tissue increased significantly in fragments from Playa Baracoa and La Puntica crests, indicating active growth and establishment. The area of live tissue of fragments in treatments over time was similar to the control in La Puntica crest, while in Playa Baracoa, the fragments paired with *M. complanata* showed a significantly lower area compared to the control. In Playa Baracoa crest, the fragments showed the highest live tissue area values compared to the other two crests, suggesting (1) a potential adaptation to environmental conditions, despite the impact of local anthropogenic stressors or (2) differences in genotype that may influence growth; however, these factors were not measured in this study. Significant interactions between the La Puntica crest and the area of live tissue of fragments in *M. complanata* and *P. astreoides* treatments suggest that the response of *A. palmata* fragments may be influenced not only by the treatment itself, but also by local environmental conditions. These patterns indicate that site-specific factors could modulate fragment performance. However, environmental

variables such as sedimentation rates, light intensity, and wave energy were not quantified in this experiment and therefore their potential influence cannot be directly assessed.

The growth rates of the fragments in this study were slower than that recorded for *A. palmata* in the wild (Gladfelter et al. 1978; Lirman 2000; Bak et al. 2009) and similar to storm-generated fragments (Lirman 2000). The stress caused by hurricanes could be similar to the trauma induced by the transplanting process, also known as initial transplantation shock (Forrester et al. 2012) in addition to the stress caused by interactions with competing species. Growth rates were negative during some periods of the experiment, possibly due to corallivory or bites from herbivorous fish, as some fragments displayed bite marks on their apical portions.

These results underscore that *A. palmata* fragments survival and growth are determined by the combined influence of biotic interactions and site-location. The significant interactions observed between treatments and the La Puntica crest suggest that restoration outcomes could be context-dependent and cannot be predicted solely based on species interactions in isolation. La Puntica crest exhibits higher coral cover, greater herbivorous fish biomass, and lower human impact compared to northwestern Cuban crests, where multiple anthropogenic stressors may constrain fragment performance. These contrasting conditions likely facilitate different competitive dynamics, ultimately influencing fragment performance. This highlights the importance of integrating ecological studies and localized monitoring into coral restoration planning.

In our study, the control involved the removal of all sessile organisms that could potentially interact with the coral fragments. Substrate cleaning and maintenance prior to transplantation have been proposed as useful interventions to enhance coral restoration success by reducing space competition and shading (Smith et al. 2022). However, in this study, control fragments did not consistently exhibit higher survival or growth compared to treatments involving biological interactions, suggesting that the removal of potential competitors alone may not be sufficient to maximize *A. palmata* performance and that other biotic and site-specific factors may play an important role. Furthermore, due to logistical constraints, site maintenance was conducted only at the time of monitoring, which may have further limited the effectiveness of competitor removal. Some of these interactions may not be evident at the time of outplanting but can become significant over longer periods, thereby influencing fragment performance and overall reef recovery. The purpose of this experiment was not to simulate restoration practices by outplanting corals directly beside benthic competitors, but rather to experimentally evaluate the potential influence of these common reef organisms on *A. palmata* performance.

In natural reef crests, species such as *P. astreoides*, *M. complanata*, *P. caribaeorum*, and macroalgae often occur in high abundances competing for space (Cramer et al. 2021). Small-scale experimental outplanting, as implemented here, remains an essential step for identifying potential biotic stressors and environmental constraints before scaling up restoration efforts. Understanding how *A. palmata* fragments respond to such interactions, even if not immediately visible during early outplanting, provides valuable information that ultimately helps reduce failure risk within restored coral assemblages.

Therefore, minimizing competition and overgrowth interactions between benthic organisms is crucial for enhancing outplant survival and growth and thus the success of restoration efforts.

Incorporating these context-dependent dynamics into restoration planning can ultimately improve the effectiveness and resilience of restored coral assemblages.

Declarations

Statements and Declarations

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Author Contribution

All authors conceived and designed the experiments performed the experiments, analyzed the data, prepared figures and/or tables. The first draft of the manuscript was written A. R. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

The datasets generated and/or analyzed during the current study are not publicly available at this stage. However, if the manuscript is accepted for publication, all raw data supporting the findings will be made available as Supplementary Information associated with the article. In the meantime, data are available from the corresponding author .

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Figures

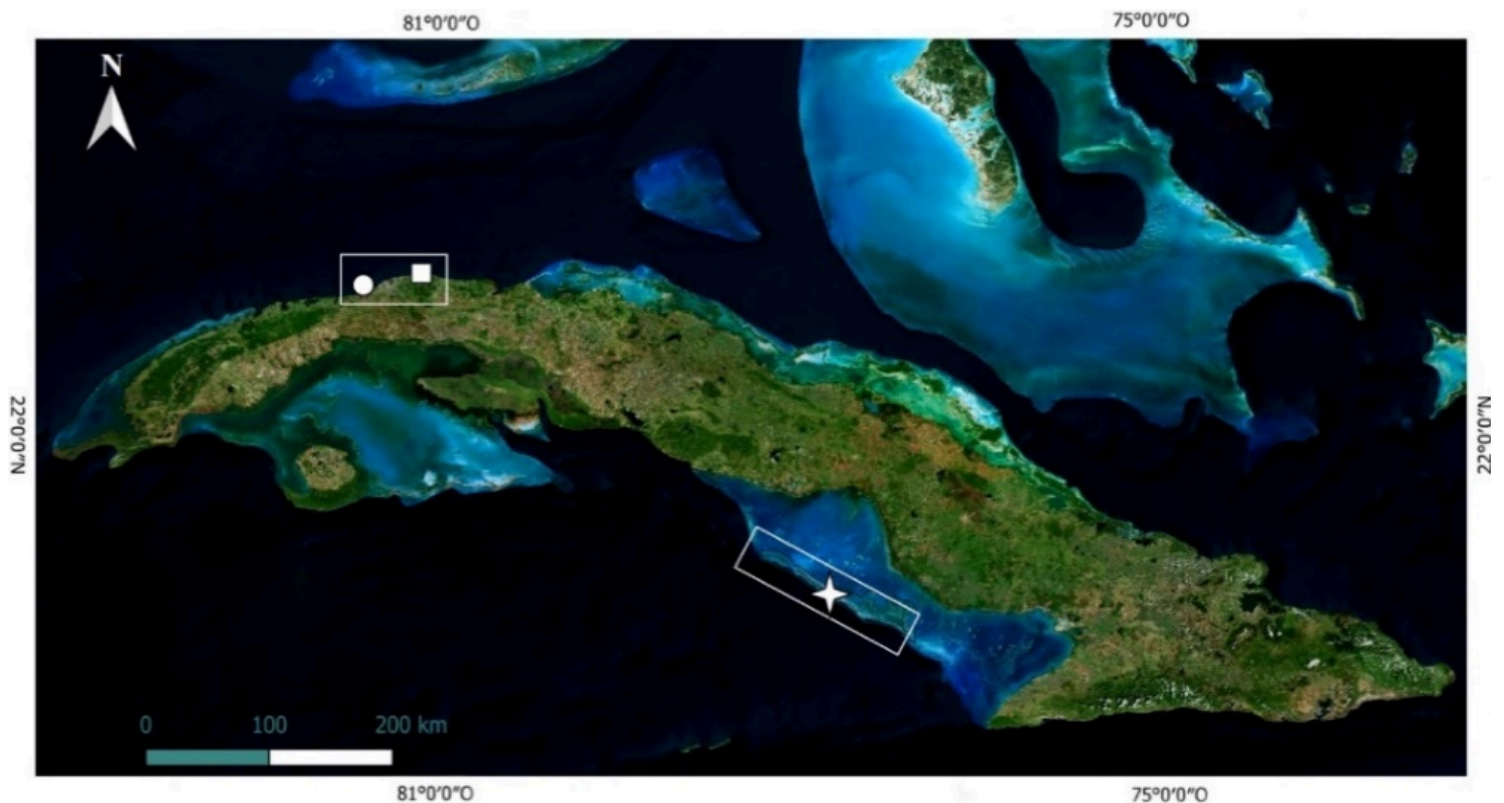


Figure 1

Location of reef crests where the experiments were conducted. The map of Cuba shows Playa Baracoa (circle), Rincón de Guanabo (square) and La Puntica (star) crests. Map data©2024 Google Earth, Image Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image©2024 Airbus; Image©2024 Maxar Technologies



Figure 2

Outplanted *Acropora palmata* fragments. (A) shows the control, where the fragment is not in contact with any benthic organism, and some of the treatments, where fragments are in contact with: (B) *Millepora complanata*, (C) *Stypopodium zonale*, (D) *Cladophora* sp., (E) *Sargassum polyceratum*, and (F) *Porites astreoides*. The red circle in photo C indicates the *A. palmata* fragment

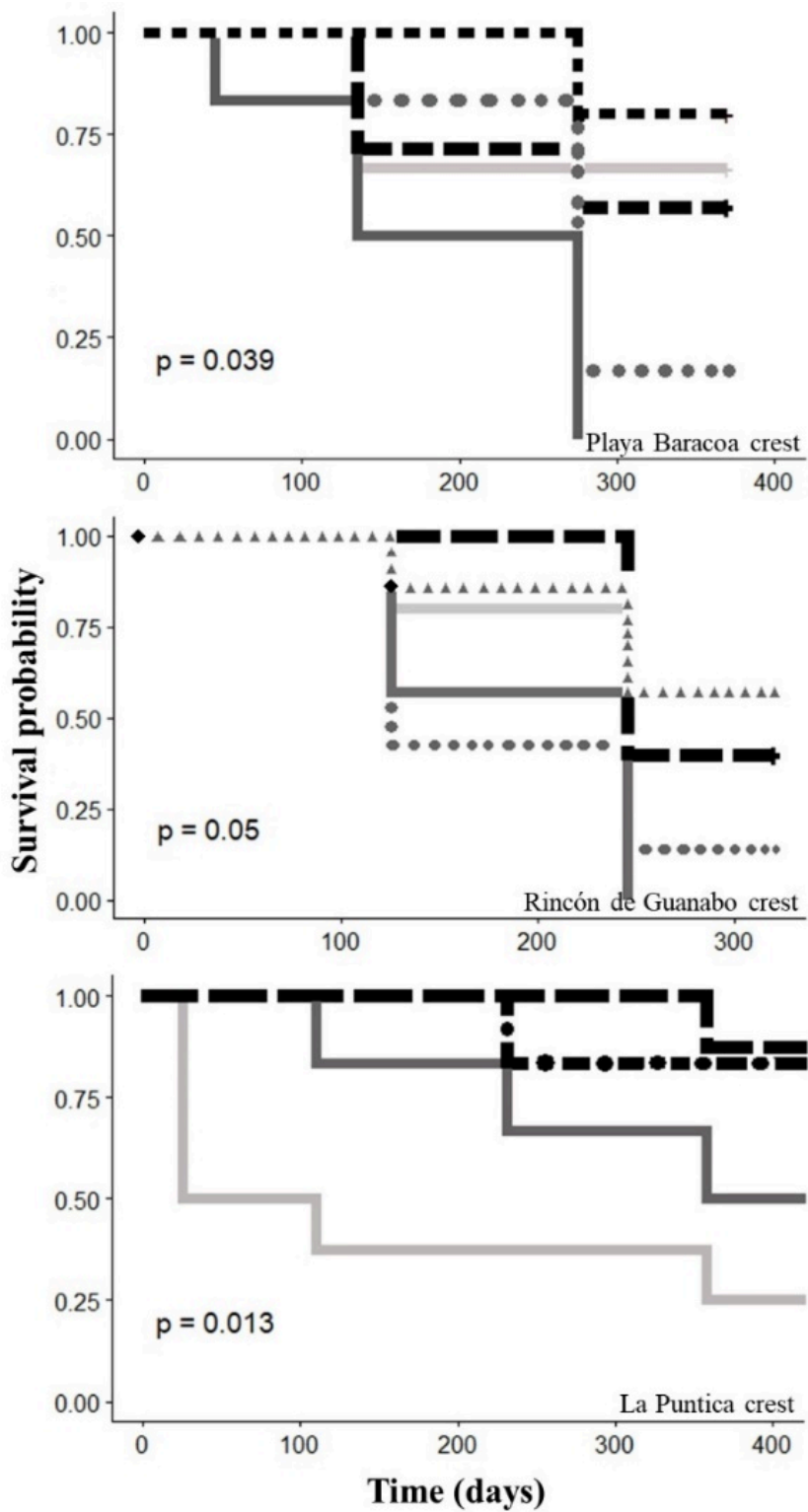


Figure 3

Kaplan–Meier estimated survival probabilities for control fragments (light gray solid line), and fragments paired with *Porites astreoides* (long-dashed line), and *Millepora complanata* (dark gray solid line, *Cladophorasp.* (dotted line), *Sargassum polyceratum* (short-dashed line), *Dictyota sp.* (diamond pattern), *Stypopodium zonale* (triangle-patterned line) and *Palythoa caribaeorum* (dash and dot line), in Playa

Baracoa, Rincón de Guanabo and La Puntica crests. The p-value < 0.05 indicates significant differences between control and treatments for each crest

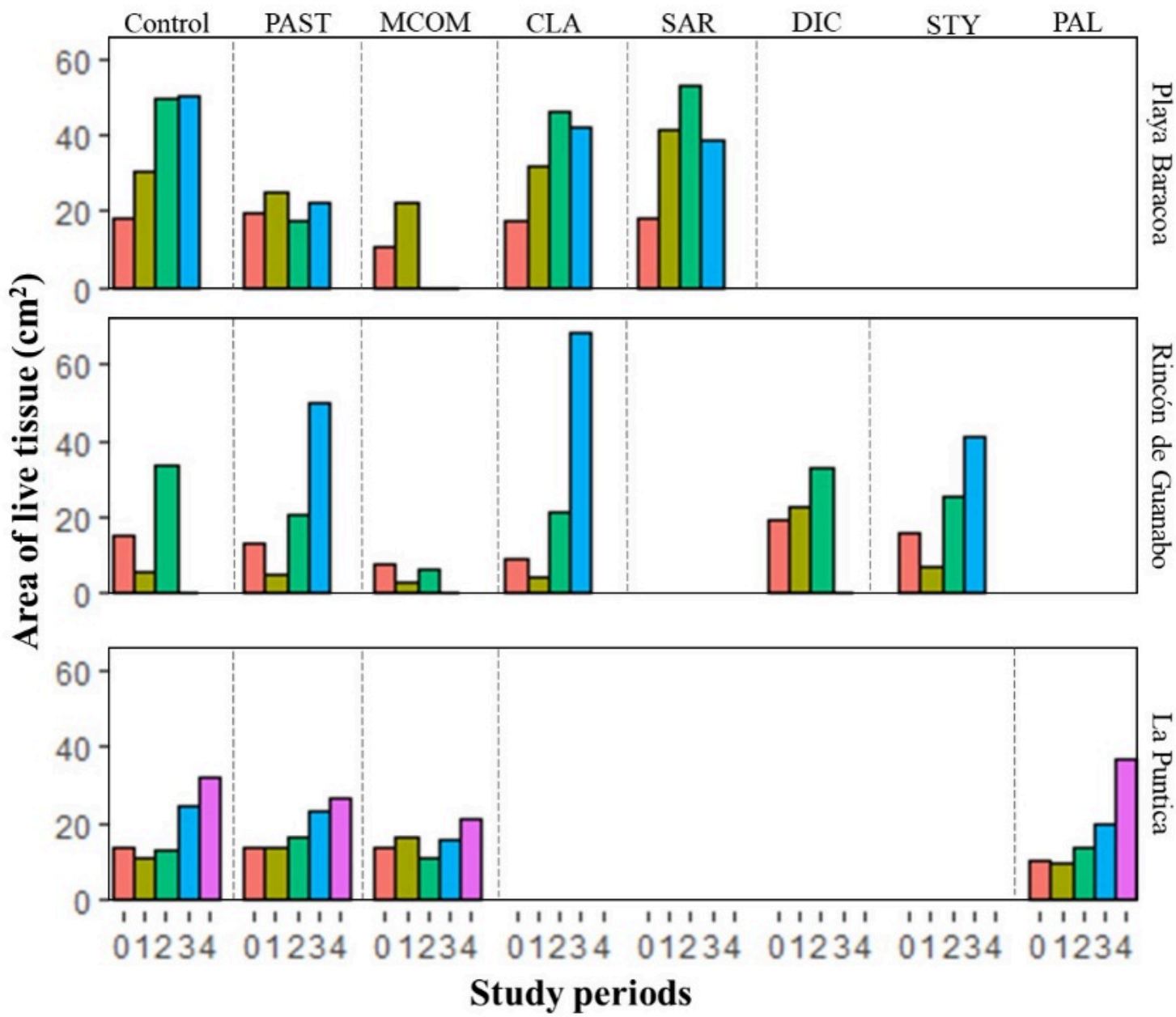


Figure 4

Changes in surface area of live tissue of *Acropora palmata* fragments measured during each monitoring period under control conditions and in association with different benthic organisms: *Porites astreoides* (PAST), *Millepora complanata*(MCOM), *Cladophora* sp. (CLA), *Sargassum polyceratium* (SAR), *Dictyota* sp. (DIC), *Stypopodium zonale* (STY), and *Palythoa caribaeorum* (PAL). Bars represent mean values (cm²) recorded at each study period for the three reef crests: Playa Baracoa, Rincón de Guanabo, and La Puntica. Crest names are indicated on the right side of each panel

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