SUPPLEMENT

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Higher bearded fireworm densities in structurally complex substrate do not increase predation on *Acropora cervicornis* (Lamarck, 1816) outplants

Arelys D. López-Pérez[1,2,4*]; https://orcid.org/0000-0002-8686-7451
Edwin A. Hernández-Delgado[1,2]; https://orcid.org/0000-0002-5504-2545
Isabela Teresa Cunio[1]; https://orcid.org/0009-0002-3365-7247
Pedro J. Alejandro Camis[1]; https://orcid.org/0009-0001-6636-9340
Samuel E. Suleimán-Ramos[1]; https://orcid.org/0000-0002-3953-964X
Alex E. Mercado-Molina[1,3,4*]; https://orcid.org/0000-0002-1162-5474

1. Sociedad Ambiente Marino, Calle 3 #1130, Urbanización Villa Nevárez, San Juan, Puerto Rico, 00927; arelys.lopez2@upr.edu (*Correspondence); edwin.hernandez13@upr.edu; cunio576@gmail.com; pedro.alejandro@upr.edu; samuel-suleiman@sampr.org; alex.mercado1@upr.edu (*Correspondence).
2. Universidad de Puerto Rico, Recinto de Rio Piedras, Facultad de Ciencias Naturales, 17 Ave Universidad, STE 1701, San Juan, Puerto Rico 00925-2537.
3. Universidad de Puerto Rico Recinto de Bayamón, 170 Carr. #174 Parque Industrial Minillas Bayamón, Puerto Rico 00959-1919
4. METAS, San Juan, Puerto Rico, 00927

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ABSTRACT

Introduction: In Puerto Rico, restoration efforts for the threatened coral *Acropora cervicornis* are increasingly affected by outbreaks of the corallivore bearded fireworm, *Hermodice carunculata.* However, limited knowledge of this polychaete's population dynamics hinders effective management.

Objectives: (1) Quantify the abundance and size distribution of *H. carunculata* across reef areas with different structural complexity; (2) Evaluate spatial and temporal variation in predation on *A. cervicornis*; (3) Examine relationships between fireworm abundance, predation, and macroalgal cover.

Methods: The abundance and size distribution of *H. carunculata* were monitored across three reef areas (lowest to highest complexity) from March to November 2023. Bearded fireworms were captured using low-cost benthic traps. Predation activity was quantified by counting bite marks on coral outplants within fixed monitoring areas and on colonies outplanted outside the study areas from December 2022 to November 2023.

Results: Bearded fireworm abundance was significantly higher in more structurally complex areas and varied over time, declining toward the end of the study period. In contrast, size distribution remained relatively stable across spatial and temporal scales. Predation rates on *A. cervicornis* outplants exhibited temporal and spatial variation; however, the number of predation marks was negatively correlated with bearded fireworm abundance. No significant relationships were detected between fireworm abundance and macroalgal cover or the presence of *Dictyota dichotoma*.

Conclusions: *H. carunculata* tended to be more abundant in structurally complex habitats, supporting the influence of habitat structure on its distribution. However, inconsistent predation patterns and the unexpected negative correlation between bearded fireworm abundance and bite marks suggest that additional factors, including prey availability and behavioral dynamics, may shape predation activity. These findings provide insights into improving monitoring, management, and site selection in *A. cervicornis* restoration programs.

Key words: coral predation; corallivore; spatial heterogeneity; coral reef restoration; population dynamics.

RESUMEN

Las mayores densidades de gusanos de fuego barbudos en sustratos estructuralmente complejos no aumentan la depredación sobre los trasplantes de *Acropora cervicornis* (Lamarck, 1816).

Introducción: En Puerto Rico, los esfuerzos de restauración del coral amenazado *Acropora cervicornis* son cada vez más afectados por brotes del poliqueto coralívoro *Hermodice carunculata*. Sin embargo, el conocimiento limitado sobre la dinámica poblacional del poliqueto dificulta su manejo efectivo.

Objetivos: (1) Cuantificar abundancia y distribución de tamaños de *H. carunculata* en áreas arrecifales con diferente complejidad estructural; (2) Evaluar la variación espacio-temporal de la depredación sobre *A. cervicornis*; (3) Examinar la relación entre abundancia de gusanos, depredación y cobertura de macroalgas.

Métodos: Se monitoreó abundancia y distribución de tamaños de *H. carunculata* en tres áreas arrecifales con diferente complejidad estructural de marzo a noviembre de 2023. *H. carunculata* fue capturado con trampas bentónicas de bajo costo. La depredación se cuantificó mediante el conteo de mordidas marcadas en trasplantes de coral en los transectos de monitoreo y fuera de las áreas de estudio entre diciembre de 2022 y noviembre de 2023.

Resultados: La abundancia de *H. carunculata* fue significativamente mayor en áreas de mayor complejidad estructural y varió temporalmente. En contraste, la distribución de tamaños se mantuvo relativamente estable espacio-temporalmente. Las tasas de depredación sobre trasplantes de *A. cervicornis,* mostraron variación espacio-temporal; sin embargo, las marcas de depredación correlacionaron negativamente con la abundancia de gusanos. No se detectaron relaciones significativas entre abundancia de gusanos y cobertura de macroalgas ni con presencia de *Dictyota dichotoma*.

Conclusiones: *H.* carunculata tendió a ser más abundante en hábitats de mayor complejidad estructural, respaldando la influencia de la estructura del hábitat sobre su distribución. Sin embargo, los patrones inconsistentes de depredación y la correlación negativa entre la abundancia de gusanos y las marcas de mordida sugieren que factores adicionales podrían influir en la actividad depredadora. Estos hallazgos aportan información para el monitoreo, el manejo y la selección de sitios en los esfuerzos de restauración de *A. cervicornis.*

Palabras clave: depredación de corales; coralívoros; heterogeneidad espacial; restauración de arrecifes de coral; dinámica poblacional.

INTRODUCTION

The bearded fireworm, *Hermodice carunculata* (Pallas, 1766), is known to be an opportunistic polychaete with high ecological plasticity (Toso et al., 2022). It demonstrates a generalist feeding behavior by consuming detritus, live or injured/dead corals, echinoderms, gorgonians, cnidarians, zoanthids, and other benthic organisms (Barroso et al., 2016; Cruz Ramos & Schizas, 2023; Pardo & Amaral, 2006; Pérez & Gomes, 2012; Schulze et al., 2017; Witman, 1988). This species has a wide distribution across the Mediterranean Sea, Red Sea, and tropical and subtropical regions of the Atlantic, including the Caribbean (Ahrens et al., 2013; Fishelson et al., 1971; Righi et al., 2020; Toso et al., 2022). Population outbreaks in these regions have raised concerns about potential impacts on marine ecosystems. In Caribbean coral reefs, *H. carunculata* preferentially prey on branching corals such as the threatened staghorn coral, *Acropora cervicornis* (Lamarck, 1816), which is also highly susceptible to environmental stressors and diseases (Bright et al., 2015; Ott & Lewis, 2011; Santiago-Padua et al., 2023; Williams & Miller, 2006; Wolf et al., 2014). By feeding on the growing tips of *A. cervicornis*, the bearded fireworm can significantly reduce colony growth and potentially compromise survival, though evidence varies among studies (Calle-Triviño et al., 2020; Knowlton et al., 1990; Santiago-Padua et al., 2023), highlighting the need for further investigation into their ecological impacts on coral reef communities (Cruz Ramos & Schizas, 2023; Schulze et al., 2017; Wolf et al., 2014)

Despite the potential negative effects of *H. carunculata* on the demographic performance of *A. cervicornis*, efforts to manage

bearded fireworm populations remain limited. This reality is due to a scarcity of information on their dynamics and behavior, particularly in restored reefs. Critical questions include: (1) What factors drive the population fluctuations of *H. carunculata* in restored reefs? (2) How frequently do bearded fireworms prey on restored *A. cervicornis* colonies over time? This knowledge gap, combined with evidence that bearded fireworm predation is common in restored *A. cervicornis* colonies (Calle-Triviño et al., 2020; Santiago-Padua et al., 2023), poses a significant risk to the long-term success of *A. cervicornis* restoration programs.

On the Caribbean Island of Puerto Rico, the non-governmental organization Sociedad Ambiente Marino (SAM) has spent over 20 years restoring degraded coral reefs by outplanting nursery-reared colonies of *A. cervicornis*. Although these efforts have increased colony numbers, the program has faced challenges from bearded fireworm (*H. carunculata*) predation. To better understand these interactions, SAM initiated studies on bearded fireworm impacts on restored coral colonies. Santiago-Padua et al. (2023), for instance, evaluated the demographic and population responses of *A. cervicornis* to bearded fireworm corallivory in restored reef areas with varying substrate structural complexity. Their study was among the first to document the demographic effects of bearded fireworm predation in Puerto Rico, showing that while overall outplant survival was not compromised, partially consumed colonies grew less than non-predated counterparts. It was also found that predation rates were higher in areas with greater reef rugosity, suggesting a link between topographic complexity and bearded fireworm activity. As an epibenthic polychaetae inhabiting crevices within complex reef structures, *H. carunculata* may preferentially forage in highly rugose areas (Cruz Ramos & Schizas, 2023; Pardo & Amaral, 2006; Santiago-Padua et al., 2023). However, these studies did not quantify bearded fireworm abundance or size, nor assessed correlations with benthic cover. For example, Wolf & Nugues (2013) reported that bearded fireworms can also use macroalgal clumps as alternative substrates, creating uncertainty about whether their population and feeding dynamics in restored reefs are driven by reef rugosity, algal cover, or both.

Our study builds on the observations of Santiago-Padua et al. (2023) by examining fine-scale spatiotemporal patterns in the abundance and size of the bearded fireworm *H. carunculata*. We also investigate how these patterns relate to reef rugosity and benthic composition in restored *A. cervicornis* reefs in Culebra, Puerto Rico. We hypothesized that bearded fireworms would be more abundant and larger in structurally complex habitats with higher algal cover, and that their abundance would increase during warmer periods when *A. cervicornis* may be physiologically stressed and more susceptible to predation (Bright et al., 2015; Morton et al., 2002; Wolf & Nugues, 2013). By quantifying these patterns and testing these relationships, our study provides insights into the ecological dynamics of *H. carunculata* in restoration settings, with implications for reef management and restoration planning.

MATERIALS AND METHODS

Study Site: The study was conducted at Punta Melones reef (PTMEL; N18°18'01.68", W65°18'43.07") in the Canal Luis Peña Natural Reserve, Culebra Island, Puerto Rico (Fig. 1). Culebra is located ~30 km east of mainland Puerto Rico (Santiago-Padua et al., 2023) and has been the focus of long-term coral restoration by SAM. Since 2003 restoration efforts have been developed to propagate and transplant *A. cervicornis* and *A. palmata* colonies. Punta Melones reef is known to be ecologically significant for its shallow fringing reefs that generally don't exceed 4m deep (Santiago-Padua et al., 2023). In December 2020, the restoration program outplanted over 3 000 colony fragments of *A. cervicornis*, and *A. palmata* (Lamarck, 1816) to the reef, coral species previously absent from the site (Santiago-Padua et al., 2023), due to the combination of stressors including, but not limited, to hurricanes and diseases (Mercado-Molina et al., 2020). As a

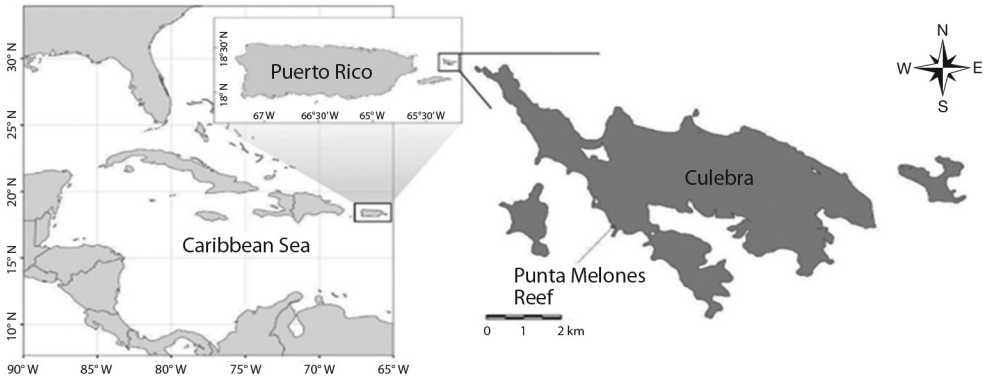

Fig. 1. The location of the study area is the Punta Melones reef, located in the Canal Luis Peña Natural Reserve on the Island Municipality of Culebra, Puerto Rico. Map reproduced from Santiago-Padua et al. (2023).

result, the reef now has restored populations of these Acroporids that support diverse reef fish communities (Hernández-Delgado & Rosado-Matías, 2017; Hernández-Delgado et al., 2006). In addition, the reef hosts abundant octocorals (*Gorgonia ventalina* (Linnaeus, 1758), *Eunicea* spp., *Plexaura* spp.), a rich assemblage of macroalgae, including *Dictyota dichotoma* (Hudson) J.V. Lamouroux, several calcareous taxa (e.g. coralline algae) and to a lesser extend other species of hard corals (*Pseudodiploria* sp., *Diploria labyrinthiformis* (Linnaeus, 1758), *Porites* spp.; Velázquez-Alvarado et al., 2025).

PTMEL is characterized by reef segments with varying structural three-dimensionality (i.e., texture and surface shape relative to the reef framework). These differences were previously evaluated by Santiago-Padua et al. (2023) using three permanent 30 × 2 m (60 m^2) transects established during the initial phase of the restoration program and separated by approximately 5 m. Substrate complexity was estimated using the chain method, where a chain was placed along the reef surface so that it conforms to the substrate contours. The rugosity index was calculated by dividing the total length of chain in a straight-line (10 m) by the length of the chain following the reef contour (Mercado-Molina et al., 2015; Nemeth & Appeldoorn, 2009; Santiago-Padua et al., 2023). Based on these measurements, Santiago-Padua et al. (2023) reported differences in substrate complexity among transects, with the southernmost transect T71 showing the lowest rugosity (r.i. = 1.17; here after T71-LR; Fig. 2), the middle transect T72 intermediate rugosity (r.i. = 1.19; here after T72-MR, Fig. 2), and the northernmost transect T73 the highest rugosity (r.i. = 1.24; hereafter T73-HR, Fig. 2), characterized by pinnacles, ridges, holes, and crevices. These categories are used here only to describe previously reported differences in structural complexity among transects. Monthly sea surface temperature (STT) data recorded during the study period (March – November 2023) were obtained from the NOAA Coral Reef Watch Database is presented in Appendix 1.

Acropora cervicornis was found across all three transects, co-occurring with *Hermodice carunculata* and exhibiting small-scale spatial variation in susceptibility to bearded fireworm predation (Santiago-Padua et al., 2023). Although the three transects initially received the same density of outplanted colonies during the restoration program (~1 colony m^{-2}), subsequent monitoring revealed differences in colony survival among transects (Santiago-Padua et al., 2023). By the beginning of the present study, Transect 71-LR contained a higher number of live *A. cervicornis* colonies relative to the other transects (Aponte-Marcano & Mercado-Molina, unpublished data; personal

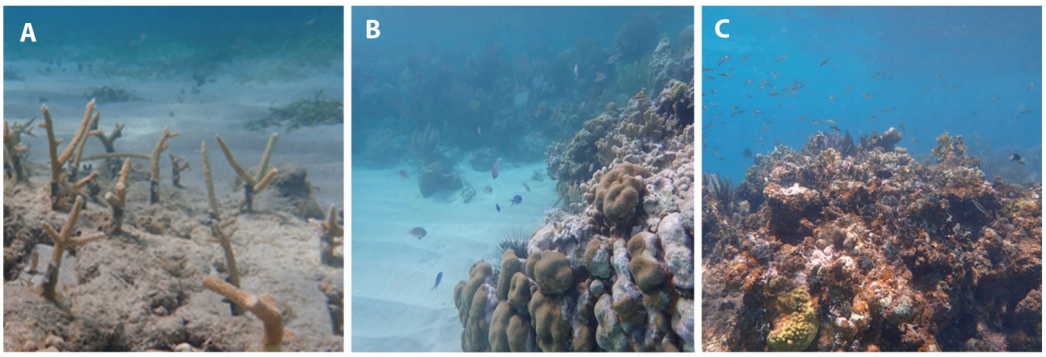

Fig. 2. Representative photographs of the three permanent transects surveyed at Punta Melones reef (PTMEL), Canal Luis Peña Natural Reserve, Culebra, Puerto Rico. Images illustrate visual differences in substrate structural complexity among transects A. T71 transect with lowest rugosity; B. T72 transect with moderate rugosity; C. T73 transect with highest rugosity; as previously characterized by Santiago-Padua et al. (2023).

observation from September 2021-April 2022). Previous monitoring by Santiago-Padua et al. (2023) also provides context for spatial variation in predation pressure across the reef. Their results showed higher predation prevalence in the northernmost transect (T73-HR), where approximately 97 % of monitored colonies showed signs of predation, compared with 79 % in T71-LR and 76 % in T72-MR (T71-LR, T72-MR, T73-HR; referred to as A, B, and C by Santiago-Padua et al., 2023), suggesting spatial differences in colony predation among transects. Notably, Santiago-Padua et al. (2023) hypothesized that spatial differences in *A. cervicornis* attack rates by *H. carunculata* may be linked to the greater abundance of bearded fireworms in more structurally complex reef areas. However, this hypothesis was not directly tested in their study, leaving open questions about the role of reef complexity in driving predation pressure.

Bearded fireworm abundance and length

Within each of the three previously established transects (T71-LR, T72-MR, T73-HR), five bearded fireworm benthic traps (Fig. 3A) were deployed in March, May, June, July, September, October, and November 2023. The 15 traps were made of PVC with a cylindrical shape (~520 cm^2). The traps were constructed from cylindrical PVC pipes measuring 30 cm in length and 5 cm in diameter (30.38 cm x 5.08 cm). Each trap was fitted with PVC caps on both ends; however, only one cap contained an opening of 1.27 cm diameter into which a smaller PVC coupling was inserted. This coupling created an inward-facing funnel like entrance, allowing bearded fireworms to enter the trap while reducing the likelihood of escape.

Traps were placed (T71-LR:#1-5, T72-MR:#6-10, T73-HR:#11-15) between 09:00 h and 12:00 h, baited with fresh fish and squid. Traps were positioned haphazardly within each transect, with the entrance (opening) facing previously transplanted *A. cervicornis* colonies in an upward and stable position (Fig. 3B). Captured bearded fireworms were counted and their size measured with a calibrated scale (cm). After processing, individuals were not returned to the transects and were removed from the study area as part of the restoration management protocol implemented by SAM, which holds the permits required to handle species affecting coral restoration sites. This procedure prevented repeated capture of the same individuals and avoided artificially inflating abundance estimates during subsequent sampling events. Data was not collected in August due to poor weather conditions.

To evaluate spatial and temporal variation in bearded fireworm abundance and size, we fitted generalized linear models (GLMs).

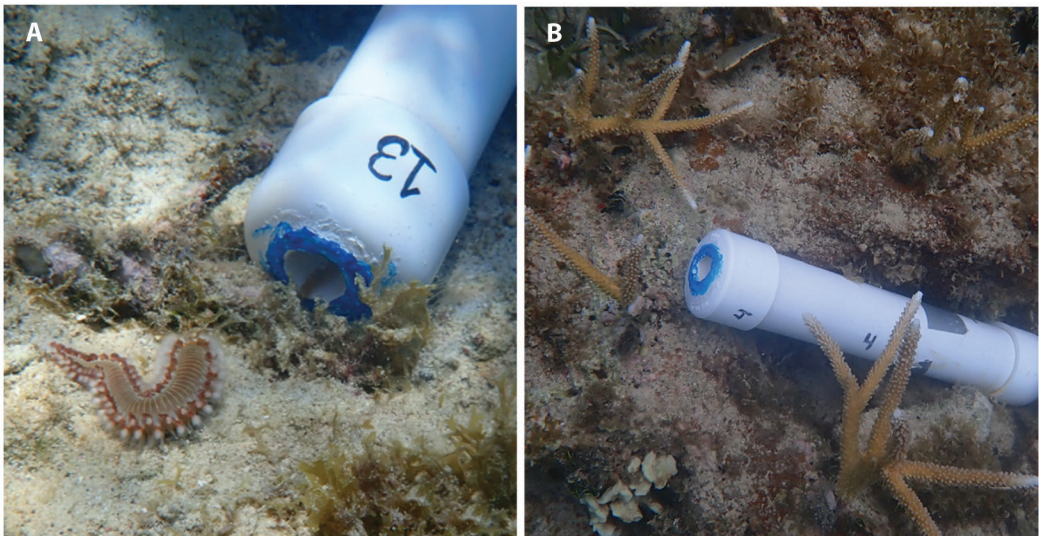

Fig. 3. A. Benthic trap placed in the study area in one of the sampling efforts; **B.** Demonstration of the position when placing the benthic trap.

Abundance and size were modeled as a function of Transect, Time, and their interaction (Transect × Time). Abundance data were analyzed using a GLM with a Poisson error distribution and log link, whereas size was analyzed using a Gaussian error distribution with an identity link. The significance of each term was evaluated using likelihood ratio tests (LRTs) comparing the full model with reduced models lacking the term of interest. Test statistics were calculated as χ^2 values based on the difference in deviance between nested models, with degrees of freedom corresponding to the number of parameters removed. Post-hoc pairwise comparisons were conducted using estimated marginal means (EMMs) with Tukey-adjusted p-values to identify significant differences among transects within each time period and among sampling periods within each transect. This approach allowed us to quantify spatial and temporal variation in bearded fireworm abundance and size while controlling for multiple comparisons. All statistical analyses were conducted in R v. 4.x (R Core Team, 2024).

Predation census, incidence and prevalence: Bearded fireworm predation was quantified along three permanent 60 m² transects (T71-LR, T72-MR, T73-HR) using a 1 m² quadrat, which was placed 30 times per transect for a total sampled area of 30 m² per transect per survey time. Sampling occurred in May, July, September, October, and November 2023. Quadrat placement was randomized during each survey to avoid spatial dependence on prior sampling locations and to ensure independent measurements of bearded fireworm predation activity. Data was not collected in June and August due to poor weather conditions. For the predation census, all *A. cervicornis* colonies within each quadrat were examined, and predation was recorded as the number of consumption injuries per colony caused by *H. carunculata*. Prevalence, defined as the percentage of colonies showing predation scars (e.g., tissue loss, white branch tips, algal colonization, or tissue regeneration; Santiago-Padua et al., 2023), was also calculated. After each census, bitten branches were trimmed as part of the restoration maintenance protocol by SAM. This procedure reduced the likelihood of carry-over marks from previous surveys, helping to treat each census as an independent measurement. This approach allowed predation pressure to be expressed consistently at the colony level across transects.

We tested whether the number of bearded fireworm bite marks varied among sampling times and transects using a generalized linear model (GLM) with a Poisson error distribution and log link function. The model included Time (five sampling months) and Transect (T71-LR, T72-MR, T73-HR) as fixed factors, as well as their interaction (Time × Transect). Although transects were surveyed repeatedly through time, 1 m² quadrats were placed haphazardly during each survey, such that the same spatial units were not resampled. Observations were therefore considered independent across sampling times, and repeated measures or mixed-effects structure were not required. The overall significance of each factor and their interaction was assessed using likelihood ratio tests (LRTs) comparing the full model with reduced models lacking the term of interest. Test statistics were calculated as χ^2 values based on the difference in deviance between nested models, with degrees of freedom equal to the number of parameters removed. Pairwise comparisons among transects and sampling times were conducted using estimated marginal means (EMMs) from the Poisson GLM, with Tukey-adjusted p-values to control for multiple comparisons. This approach allowed us to determine how the number of bearded fireworm bite marks varied spatially across transects, temporally across months, and according to their interaction.

Prevalence (percentage of colonies showing predation scars) was analyzed using a generalized linear model (GLM) with a Gaussian error distribution. The model included Transect and Time as fixed factors. The interaction between Transect and Time was not included because preliminary exploration of the data indicated limited replication within each transect–time combination, which could lead to overfitting and reduce model reliability. Observations were considered independent because 1 m² quadrats were placed haphazardly during each survey and the same spatial units were not resampled. The overall significance of each factor was assessed using likelihood ratio tests, comparing the deviance of the full model to a reduced model with the factor removed. The resulting χ^2 values quantify the contribution of each term to explaining variation in prevalence, with degrees of freedom equal to the number of parameters removed. Post-hoc pairwise comparisons among sampling times within each transect were performed using estimated marginal means (EMMs) with Tukey-adjusted p-values to control for multiple comparisons. Comparisons among transects at individual time points could not be reliably estimated due to limited replication. All statistical analyses were performed in R v. 4.x (R Core Team, 2024).

To complement the transect-based census, a cohort of 30 *A. cervicornis* colonies was transplanted at the end of the most structurally complex transect (T73-HR). This design allowed us to evaluate whether newly outplanted colonies were more susceptible to bearded fireworm predation than older, previously established colonies. New outplants could not be introduced directly into the established transects, as this would have interfered with other ongoing studies in the area. The transplanted cohort was monitored in December 2022 and in February, March, May, July, September, October, and November 2023 to assess incidence of predation, providing insights into how establishment history influences vulnerability to *H. carunculata*. Because predation was observed in these newly established colonies only once during the study period, no statistical analyses were conducted.

To evaluate the relationship between bearded fireworm abundance and predation activity, Pearson correlation analyses were conducted between mean predation prevalence and mean *H. carunculata* abundance across sampling periods. Mean prevalence values were calculated as the percentage of *A. cervicornis* colonies showing predation scars within each survey period and mean bearded fireworm abundance was calculated as the average number of individuals captured per trap during the corresponding sampling month. Correlation coefficients (r) and associated p-values were calculated using Pearson's product–moment correlation.

All analyses were performed in R v. 4.x (R Core Team, 2024).

Benthic cover: To examine the relationship between algal cover and bearded fireworm abundance, fifteen 0.0625 m^2 (0.25m x 0.25m) quadrats were haphazardly established within each transect (n = 45), with at least 1 m spacing between them. Each quadrat was permanently tagged with a unique number to facilitate relocation during surveys. At each quadrat, a photo was taken to estimate benthic cover. Images were analyzed using Coral Point Count with Excel (CPCe; Kohler & Gill, 2006) software, applying the point count method with 25 randomly superimposed points per image. The number of points falling on each algal species was divided by the total number of points to estimate percent cover.

We analyzed temporal and spatial variation in macroalgal cover and *Dictyota dichotoma* cover using generalized linear mixed-effects models (GLMMs) implemented in the glmmTMB package in R (v. 4.x) (R Core Team, 2024). Because the data included a high frequency of zeros and were right-skewed, models were fit using a Tweedie distribution with a log link, which accommodates zero-inflated continuous responses. To account for excess zeros beyond those expected under the Tweedie distribution, we included a zero-inflation component. For each response variable, Time (month), Transect, and their interaction (Time × Transect) were specified as fixed effects. Quadrat was included as a random intercept to account for repeated measures through time within sampling units.

Post-hoc pairwise comparisons among transects and time points were conducted using estimated marginal means (EMMs) with Tukey adjustment for multiple comparisons, implemented with the emmeans package. Significance of fixed effects and interactions was evaluated using z-tests from the model output, and effect sizes were reported as model estimates (β coefficients) on the log scale. All statistical analyses were performed in R v. 4.x (R Core Team, 2024). To evaluate the relationship between algal cover and bearded fireworm abundance, we calculated Pearson correlation coefficients between the mean macroalgal cover per quadrat and the mean bearded fireworm abundance per transect. This approach allowed us to test both the effect of environmental and spatial factors on algal cover and the potential association between algal abundance and bearded fireworm densities.

RESULTS

Bearded fireworm abundance: Results of the GLM revealed significant main effects of Time ($\chi^2 = 45.554$, df = 6, $p < 0.001$) and Transect ($\chi^2 = 34.087$, df = 2, $p < 0.001$) on bearded fireworm abundance (Fig. 4). However, the Time × Transect interaction was not significant ($\chi^2 = 9.072$, df = 12, $p = 0.697$), indicating that temporal patterns in abundance were broadly consistent across transects.

Post-hoc pairwise comparisons using estimated marginal means (EMMs; Tukey-adjusted) showed no significant temporal differences within Transect 71-LR (all $p \geq 0.70$). In contrast, limited temporal differences were detected at the other transects. At Transect 72-MR, abundance in March was significantly higher than in November (estimate = 1.846, $p = 0.047$). Similarly, at Transect 73-HR, abundance in June and November was significantly lower than in March (June: estimate = 1.482, $p = 0.044$; November: estimate = 1.705, $p = 0.029$). No other within-transect temporal contrasts were significant after adjustment ($p > 0.05$).

Comparisons among transects within each time period indicated that Transect 71-LR consistently exhibited lower abundance early in the study. Specifically, in March and May, abundance at Transect 71-LR was significantly lower than at both Transect 72-MR and Transect 73-HR (all $p < 0.05$). In October, abundance at Transect 71-LR was also lower than at Transect 73-HR ($p = 0.037$). No significant differences among transects were detected in June, July, September, or November (all $p > 0.05$).

Overall, these results indicate that bearded fireworm abundance varies significantly

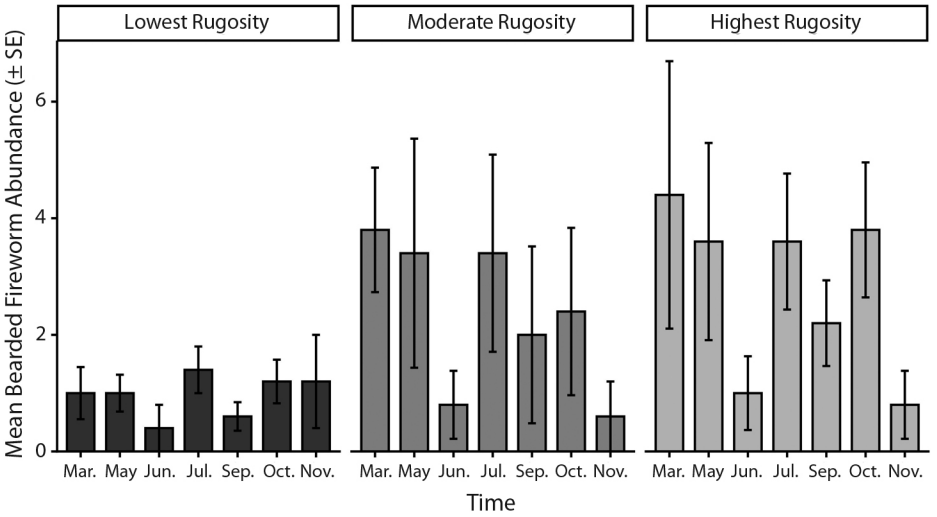

Fig. 4. Spatiotemporal variation in the abundance of *H. carunculata* at Punta Melones reef, Culebra. Bars represent mean abundance expressed as the number of individuals per trap across survey times (March – November 2023) and transects with different rugosities (Lowest Rugosity = 71-LR, Moderate Rugosity = 72-MR, Highest Rugosity = 73-HR). Error bars = standard error.

among transects, with generally higher densities at Transects 72-MR and 73-HR relative to Transect 71-LR. Although a significant main effect of time was detected, temporal variation was modest and not consistent across all comparisons.

Bearded fireworm size: Results of the Gaussian GLM revealed a significant main effect of Time on bearded fireworm size (χ^2 = 22.776, df = 6, $p < 0.001$), whereas the effect of Transect was marginally non-significant (χ^2 = 5.214, df = 2, p = 0.074). The Time × Transect interaction was not significant (χ^2 = 9.507, df = 12, p = 0.659) (Fig. 5), indicating that temporal patterns in size were broadly consistent across transects.

Post-hoc pairwise comparisons using estimated marginal means (EMMs; Tukey-adjusted) showed no significant temporal differences within Transects 71-LR and 72-MR (all $p > 0.40$). However, at Transect 73-HR, size in June was significantly greater than March (estimate = 6.86, p = 0.005), May (estimate = 7.14, p = 0.004), July (estimate = 7.85, p = 0.001), September (estimate = 7.72, p = 0.003), October (estimate = 8.00, $p < 0.001$), and November (estimate = 9.00, p = 0.008). No other within-transect temporal contrasts were significant.

Comparisons among transects within each time period indicated very limited spatial differences. A significant difference was detected only in June, where size at Transect 72-MR was lower than at Transect 73-HR (estimate = −6.25, p = 0.036). No significant differences among transects were observed in the remaining months (all $p > 0.12$).

Overall, these results indicate that bearded fireworm size varies significantly over time but shows weak and inconsistent spatial differences among transects. Temporal variation was primarily driven by a marked increase in size during June at Transect 73-HR, while size remained relatively stable across other transects and months.

Predation census, prevalence, and incidence:

Bites: The generalized linear model (GLM) revealed a significant effect of Transect (χ^2 = 6.99, df = 2, p = 0.030) and a significant Time × Transect interaction (χ^2 = 21.51, df = 8,

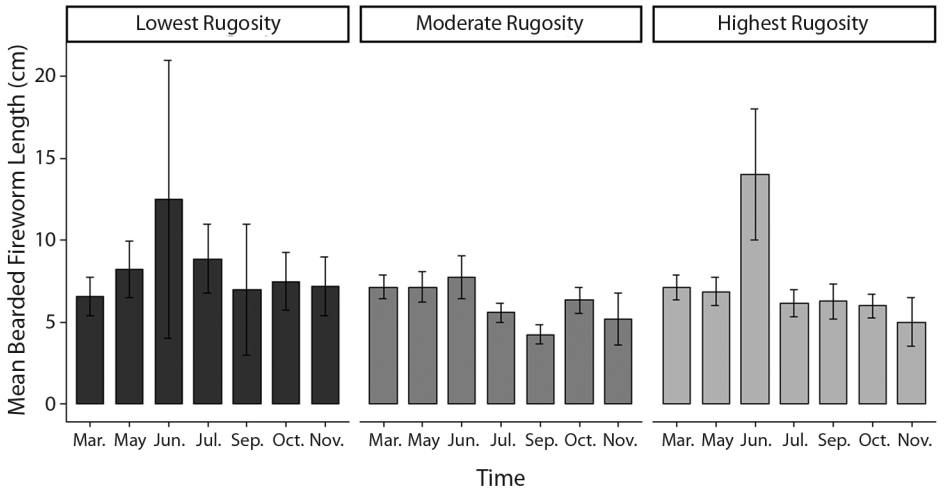

Fig. 5. Spatiotemporal variation in the size-frequency distribution of *H. carunculata* at Punta Melones reef, Culebra. Bars represent mean bearded fireworm length expressed in cm across survey times (March – November 2023) and transects with different rugosities (Lowest Rugosity = 71-LR, Moderate Rugosity = 72-MR, Highest Rugosity = 73-HR). Error bars = standard error.

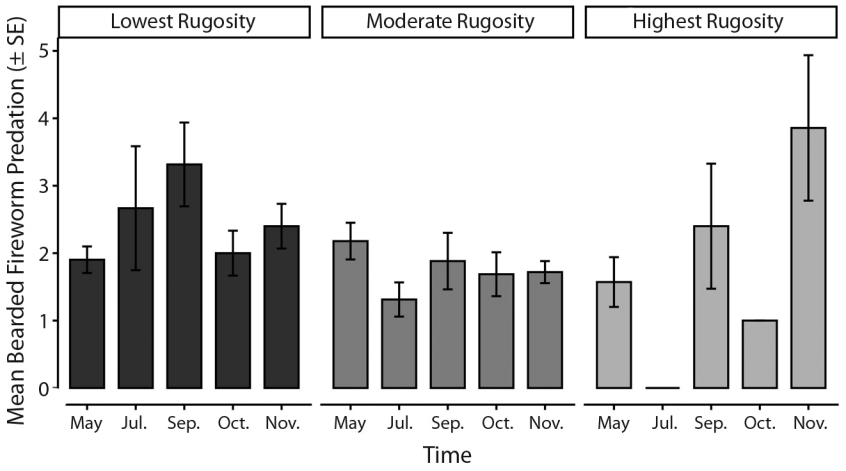

Fig. 6. Spatiotemporal variation in the *H. carunculata* predation bites in *Acropora cervicornis* colonies at Punta Melones reef, Culebra. Bars represent mean predation, expressed as the number of bite marks per colony, across survey times (May, July, September, October and November 2023) and transects with different rugosities (Lowest Rugosity= 71-LR, Moderate Rugosity = 72-MR, Highest Rugosity = 73-HR). Error bars = standard error.

p = 0.006), whereas the main effect of Time was marginally non-significant ($\chi^2 = 8.84$, df = 4, p = 0.065). This indicates that temporal patterns in bite frequency differed among transects (Fig. 6). Post-hoc comparisons using estimated marginal means (Tukey-adjusted) showed that within Transect 71-LR, bite rates were significantly higher in September than in May (estimate = −0.556, p = 0.009), corresponding to approximately a 1.7× increase on the response scale. No other temporal comparisons were significant within this transect (all p ≥ 0.28).

Within Transect 72-MR, none of the pairwise comparisons among sampling times were significant (all $p \geq 0.26$).

Within Transect 73-HR, several contrasts involving July produced extremely large standard errors (SE ≈ 1280), indicating sparse or zero observations for that time period. As a result, comparisons involving July could not be reliably interpreted. All other temporal contrasts within this transect were non-significant (all $p \geq 0.088$).

Comparisons among transects within each sampling time revealed that at September, bite rates were significantly higher in Transect 71-LR than in Transect 72-MR (estimate = 0.566, $p = 0.025$), corresponding to roughly a 1.8× difference on the response scale. At November, bite rates were significantly lower in Transect 72-MR than in Transect 73-HR (estimate = −0.808, $p = 0.002$). No other pairwise comparisons among transects were statistically significant (all $p \geq 0.082$).

Prevalence along transects: The generalized linear model (GLM) revealed a significant effect of Time ($\chi^2 = 43.70$, df = 4, $p < 0.001$) and a significant effect of Transect ($\chi^2 = 9.27$, df = 1, $p = 0.0023$) on Prevalence (Fig. 7). The Time × Transect interaction was not included in this model, as initial tests indicated it was not significant.

Post-hoc pairwise comparisons among Times within Transect 72 (Tukey-adjusted) showed that Prevalence in July was significantly lower than in May (estimate = 22.08, $p = 0.0092$) and November (estimate = −29.05, $p = 0.0014$). The difference between October and November was also significant (estimate = −20.34, $p = 0.0151$). Other pairwise comparisons among time points were not statistically significant.

Comparisons among transects at individual time points could not be estimated due to limited replication within each Time × Transect combination. Visual inpection, however, indicate that prevalence varied considerably spatially within sampling time.

Surprisingly, there was a significant negative correlation between the number of predation marks and the abundance of *H. carunculata* ($r = -0.691$, $p = 0.0043$; Fig. 8). Across sampling periods, mean predation prevalence was negatively correlated with the mean abundance of H. carunculata (in italic) among transects (Pearson correlation, r= -0.6842, $p = 0.0048$; Fig. 9), indicating that higher prevalence of predation bites occurred during periods of lower observed fireworm abundance.

Predation prevalence by *Hermodice carunculata* on the outplanted cohort of 30 *Acropora cervicornis* colonies peaked approximately five months post-outplant, a pattern similar to

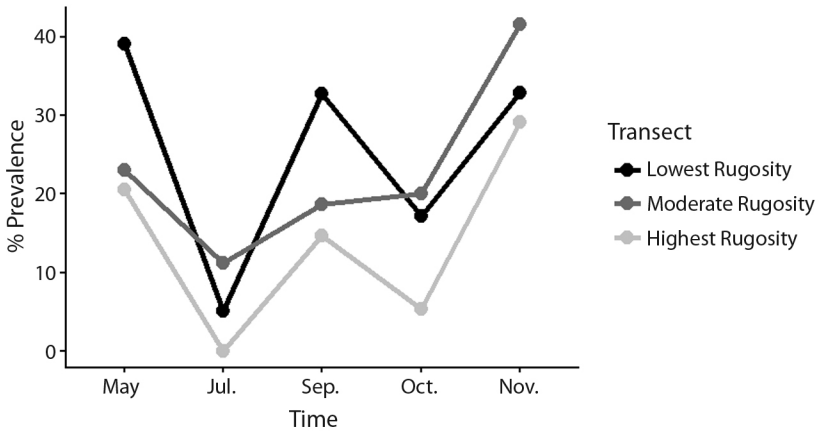

Fig. 7. Prevalence of bearded fireworm predation over time (May, July, September, October and November) in staghorn coral colonies within the study transects. Lowest Rugosity = 71-LR; Moderate Rugosity = 72-MR; Highest Rugosity = 73-HR.

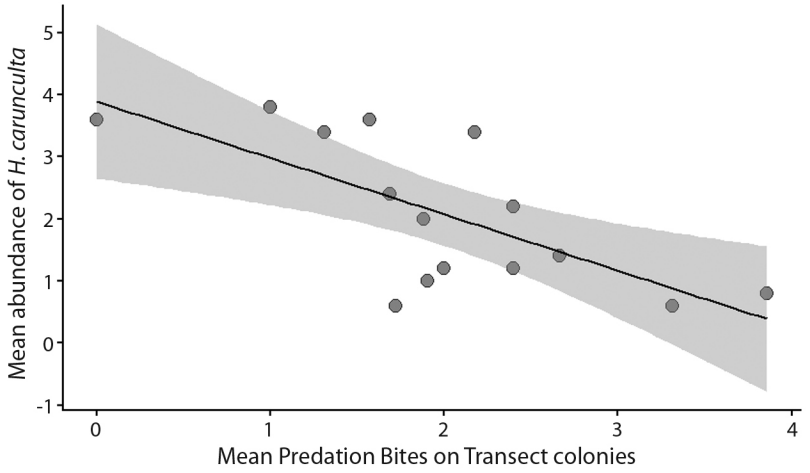

Fig. 8. Relationship between Predation Scars (mean number of predation scars per colony) and mean abundance of *H. carunculata* (individuals per trap) abundance across survey times (May, July, September, October & November). Pearson Correlation; (r= -0.691, p= 0.0043).

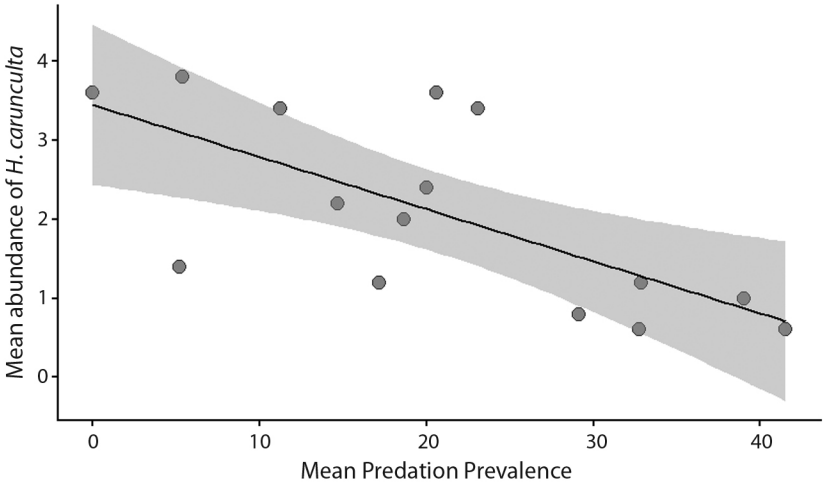

Fig. 9. Relation with mean prevalence (% colonies with predation scars) of bearded fireworm and mean abundance of H. carunculata (individuals per trap) across the three transects and sampling periods (May, July, September, October & November). Pearson Correlation; (r = -0.6842, p = 0.0048).

that observed by Santiago-Padua et al. (2023) (Fig. 10). Prevalence remained at 0 % from December through May, increased to 4.8 % in July, peaked at 26.3 % in September, and slightly decreased to 25 % in October. Incidence, the percentage of new predation events at each monitoring period was 0 % from December to May, increased to 14.3 % in July, increased to 17.6% in September, and returned to 0% in October (Fig. 11).

Benthic cover: Results of the GLMM revealed no significant main effect of Transect (χ^2 = 3.52, p = 0.17) and a marginally significant main effect of Time (χ^2 = 7.98, p = 0.045) on macroalgal cover. The interaction

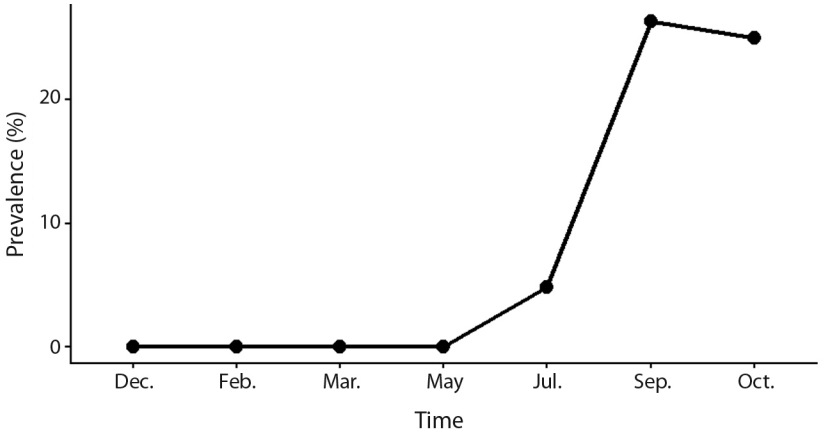

Fig. 10. Prevalence of bearded fireworm predation in staghorn coral colonies outplanted and monitored at the end of Transect 73-HR, the area with highest reef rugosity.

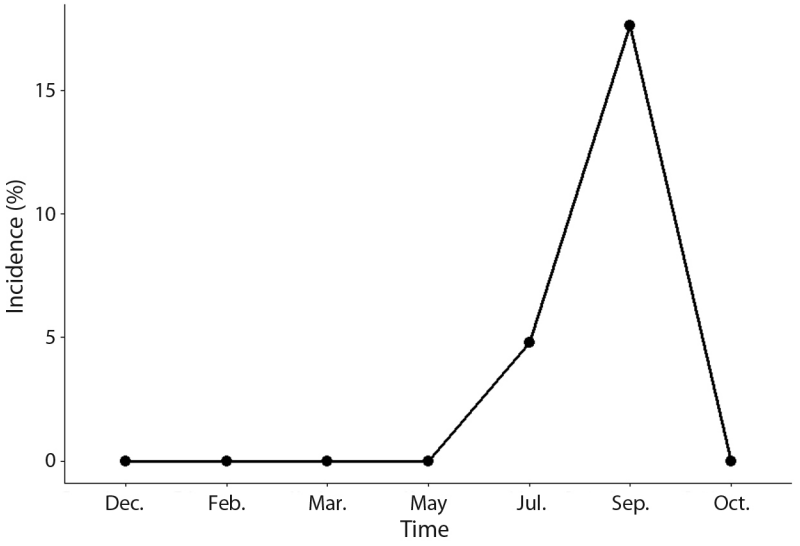

Fig. 11. Incidence of bearded fireworm predation in staghorn coral colonies outplanted and monitored at the end of Transect 73-HR, the area with highest reef rugosity. Error bars = standard error.

between Time and Transect was not significant (χ^2 = 2.31, p = 0.64), indicating that temporal changes in macroalgal cover were generally consistent among transects. Parameter estimates indicated that, relative to Transect 71-LR, mean cover was slightly lower at Transect 72-MR (estimate = –0.074, p = 0.090) and slightly higher at Transect 73-HR (estimate = 0.032, p = 0.445). Temporal effects showed that macroalgal cover in September was marginally lower than the baseline month (July, estimate = –0.059, p = 0.045), whereas March and October did not differ significantly from July (p > 0.15).

Post-hoc pairwise comparisons using estimated marginal means (EMMs, Tukey-adjusted) confirmed these patterns. Within transects, no pairwise differences among months were statistically significant (p > 0.05). Comparisons among transects within each month also revealed no significant differences (p > 0.05). Overall, macroalgal cover showed minor temporal variation, with a modest decline in September,

but no strong spatial differences among transects. It should be noted that the model produced a convergence warning, indicating potential uncertainty in parameter estimates; therefore, these results should be interpreted cautiously.

Results of the GLMM using a Tweedie distribution (log link) revealed a significant main effect of Time (χ^2 = 8.21, p = 0.008) but no significant main effect of Transect (χ^2 = 2.44, p = 0.30) on *Dictyota dichotoma*. The interaction between Time and Transect was not significant (χ^2 = 4.17, p = 0.52), indicating that temporal changes in *Dictyota dichotoma* were consistent among transects. Parameter estimates indicated that, relative to the baseline month (May), mean *log_Dd* was significantly higher in March (estimate = 0.389, p = 0.008) and marginally higher in October (estimate = 0.283, p = 0.054). Interaction terms were not significant (p > 0.39 for all), indicating that temporal patterns did not differ among transects.

Post-hoc pairwise comparisons using estimated marginal means (EMMs, Tukey-adjusted) confirmed these patterns. Within each transect, *D. dichotoma* in November was significantly lower than in July (Transect 71-LR: estimate = –29.05, p = 0.002; Transect 72-MR: estimate = –29.05, p = 0.002; Transect 73-HR: estimate = –29.05, p = 0.002) and lower than in October (Transect 71-LR: estimate = –20.34, p = 0.019; Transect 72-MR: estimate = –20.34, p = 0.019; Transect 73-HR: estimate = –20.34, p = 0.019). No other within-transect temporal differences were statistically significant (p > 0.05).

Comparisons among transects within each month revealed that in May, *D. dichotoma* was significantly lower at Transect 71-LR than at Transect 73-HR (estimate = 11.44, p = 0.038), whereas differences between Transects 7-LR1 and 72-MR were not significant (estimate = 2.50, p = 0.79). No significant transect differences were detected in the remaining months (p > 0.10). Overall, *D. dichotoma* varied significantly among months, with elevated values during March and October and a marked decline by November. Spatial differences among transects were minor but showed consistently higher *D. dichotoma* at Transect 73-HR relative to Transect 71-LR. These results suggest moderate temporal variation in *D. dichotoma* with limited spatial heterogeneity among transects.

Correlation analyses: Surprisingly, there was a significant negative correlation between the number of predation marks and the abundance of *H. carunculata* (r = –0.691, p = 0.0043; Fig. 12). In contrast, Pearson correlation analyses revealed no significant relationships between

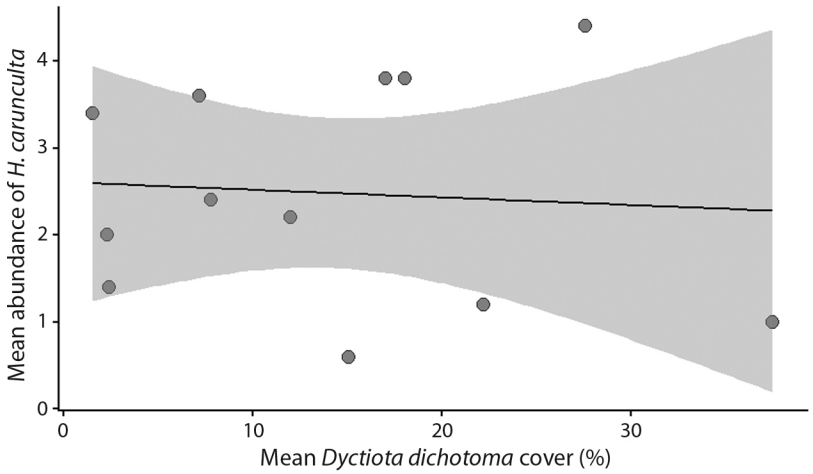

Fig. 12. Relation with mean abundance of *Dictyota dichotoma* cover (%) and mean abundance of *H. carunculata* abundance (individuals per trap). Pearson Correlation; (r = -0.0754, p = 0.8158).

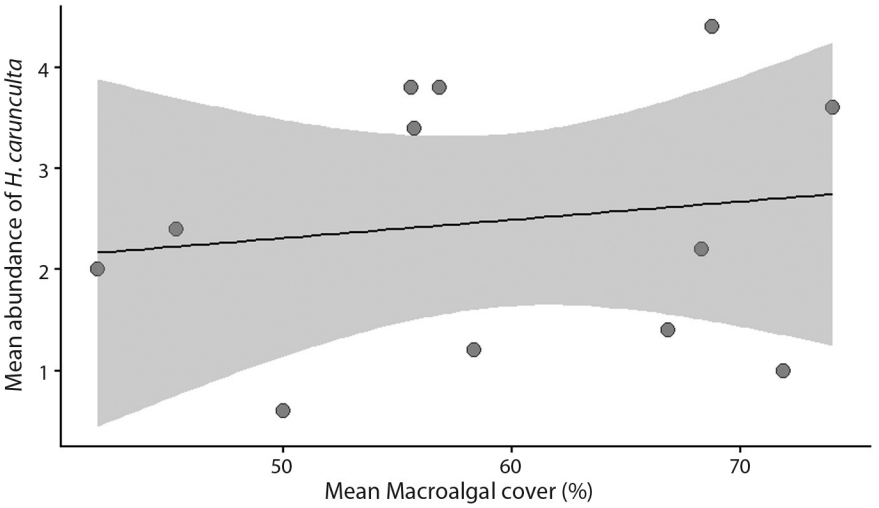

Fig. 13. Relation with mean abundance of Macroalgal cover (%) and mean abundance of *H. carunculata* abundance (individuals per trap). Pearson Correlation; (r = 0.149, p = 0.6451).

mean bearded fireworm abundance and overall macroalgal cover (r = 0.149, p = 0.6451; Fig. 13), nor with the cover of *Dictyota dichotoma* specifically (r = –0.0754, p = 0.8158; Fig. 13).

DISCUSSION

Coral reefs have been experiencing rapid declines, with little evidence of successful natural recovery for many of them, thus making continuous human intervention (restoration efforts) increasingly necessary (Suggett et al., 2024). Outplanting nursery-grown corals has become a common restoration strategy, but its long-term success remains debated (Suggett et al., 2024). This uncertainty reflects the ecological complexity of reefs, where multiple interacting processes and spatiotemporal variables influence outcomes. Understanding what drives the survival and growth of outplanted corals requires examining key processes that can affect demographic stability, including predation, which can locally extirpate populations (Wolf & Nugues, 2013). Despite its importance, few restoration studies have investigated or accounted for the population dynamics of corallivores. Here, we focus on one of the Caribbean's most common coral predators, the bearded fireworm *Hermodice carunculata*. Our results indicate that its spatial dynamics (i.e., abundance and size), particularly in relation to reef benthic composition and complexity, are more intricate than previously assumed.

Building on the hypothesis proposed by Santiago-Padua et al. (2023), our study examined whether higher levels of bearded fireworm predation on *A. cervicornis* outplants in areas of greater reef complexity could be explained by increased bearded fireworm abundance, as more complex habitats might provide additional hiding spaces. If this hypothesis were correct, we would expect consistently higher bearded fireworm abundance over time in the most structurally complex transects. In this sense, our results support the proposed hypothesis, as the transect with the lowest complexity generally exhibited the lowest bearded fireworm abundance. However, the most complex transect did not consistently show the highest abundance over time. Similarly, Wolf et al. (2014) found that the highest bearded fireworm abundance did not necessarily occur in areas of high complexity. This indicates that reef structural complexity alone does not fully

determine the small-scale distribution and predation dynamics of bearded fireworms.

Wolf et al. (2014) suggested that *Hermodice carunculata* often uses algal mats and turf algae as shelter. Therefore, spatiotemporal variation in algal cover could potentially influence its abundance. However, our results did not reveal a strong positive relationship between algal cover and *H. carunculata* abundance; in fact, the trend appeared negative. This suggests that the relationship between algal cover and *H. carunculata* abundance may be context-dependent and that, at our study site, algae does not appear to play a major role.

Previous studies have reported increases in *H. carunculata* abundance associated with ocean warming, suggesting that higher temperatures may enhance larval recruitment and metamorphosis (e.g. Toso et al., 2020; Toso et al., 2022). Based on this, we might expect bearded fireworm populations at Punta Melones to peak during the warmest months (June–September). Yet, our results did not reveal consistently higher abundance during these periods, even though they coincided with seasonal temperature maxima and bleaching events in 2023. Interestingly, after June, most individuals observed were smaller than 15 cm, suggesting a recruitment pulse (Toso et al., 2022). However, this apparent recruitment was not reflected in clear abundance peaks, suggesting that early-stage individuals may experience high post-settlement mortality or that their detection is limited to smaller sizes. Such contention, however, should be tested directly in the field.

An alternative explanation for the lack of consistency between substrate complexity and bearded fireworm abundance could be variation in food availability, particularly the distribution of coral prey. For instance, Wolf et al. (2014) suggested that the presence of live coral may strongly influence bearded fireworm aggregation. This suggests that prey availability may play an important role in shaping local predation pressure. Although the three transects initially received the same number of *A. cervicornis* colonies during restoration efforts (one colony per m^2), subsequent monitoring revealed differences in colony survival among transects (Santiago-Padua et al., 2023). By the time our study began, *A. cervicornis* colonies were more abundant at Transect 71-LR (Aponte-Marcano and Mercado-Molina, unpublished data; personal observation), likely due to small-scale variation in survival. Higher coral availability at this transect may therefore have increased feeding opportunities for *H. carunculata*, which is consistent with our observation that predation rates on colonies were highest at the least complex Transect 71-LR.

However, this argument alone does not explain why, at certain times, abundances peaked at Transect 73-HR or Transect 72-MR instead of Transect 71-LR. This spatiotemporal variability may reflect behavioral aspects of *H. carunculata*, such as opportunistic foraging movements across patches of available prey or short-term aggregations driven by localized mortality events. Bearded fireworms are known to exhibit high mobility and can rapidly exploit ephemeral food sources (Toso et al., 2022), which could result in shifting patterns of local abundance over small spatial scales. Additionally, stochastic processes (e.g., small-scale recruitment, predation pressure from higher trophic levels) and unmeasured environmental variables (e.g., microhabitat refugia, hydrodynamic conditions) could further contribute to this variability.

Taking together, our findings suggest that prey availability may be an important driver of bearded fireworm distribution, but its effect is likely not straightforward. As mentioned, above, bearded fireworm abundance may also be influenced by behavioral factors, such as opportunistic foraging and short-term aggregations around localized mortality events, as well as stochastic processes like small-scale recruitment or predation from higher trophic levels. These factors may contribute to the spatiotemporal variability we observed and may help explain the surprising negative correlation between the number of predation marks and the abundance of coral outplants. Overall, bearded fireworm abundance may result from a combination of bottom-up effects (prey availability)

and local ecological conditions, rather than from any single factor. Our arguments, however, need to be tested experimentally in field studies to better understand the mechanisms driving bearded fireworm distribution.

Additionally, consistent with findings from Santiago-Padua et al. (2023), we observed that predation on newly outplanted *A. cervicornis* colonies did not occur immediately but became apparent only several months after transplantation. In contrast, older, established colonies within the fixed transects were subject to predation throughout the study period. This suggests that colony age and establishment history may influence vulnerability to *H. carunculata* predation. Testing this hypothesis experimentally or through focused field studies could help clarify the mechanisms underlying these temporal patterns.

Several factors may contribute to this pattern. Older colonies may produce stronger chemical or structural cues that attract bearded fireworms, similar to how *Coralliophila abbreviata* preferentially feeds on damaged or stressed *Acropora* tissue (Bright et al., 2015), indicating that prey condition can influence predator foraging behavior. Additionally, older colonies tend to be larger and more branched (Santiago-Padua et al., 2023), providing both more food and shelter for predators, which may further increase outplants predation risk. Finally, bearded fireworms may engage in opportunistic foraging, aggregating around patches with higher prey availability, conditions more likely found in well-established colonies (Toso et al., 2022). Together, these observations suggest that the probability of coral outplants being consumed may increase as they grow and integrate into the reef, highlighting the importance of considering colony age, size, and tissue condition in restoration planning.

From a restoration perspective, our results underscore the challenges of mitigating corallivore impacts on outplanted corals (Suggett et al., 2024). Building on Santiago-Padua et al. (2023), we show that both substrate relief and prey availability may influence bearded fireworm dynamics, but high predation risk can still occur across a range of reef conditions. Our findings suggest that local prey availability may influence predation pressure independently of fireworm abundance, as areas with greater coral availability may experience higher feeding intensity per colony. This suggests that simply targeting areas of high structural complexity may not be sufficient to reduce predation pressure on outplants. Instead, restoration programs could benefit from incorporating predator monitoring into site selection and considering strategies to limit corallivore access to newly transplanted colonies. Continued research on both biotic factors (e.g., reef community structure, live coral cover) and abiotic factors (e.g., sedimentation, temperature anomalies) is needed to better predict bearded fireworm population dynamics and improve restoration outcomes. Experimental studies and long-term monitoring may help refine these strategies and enhance the success of coral restoration efforts.

Finally, it is important to note that the spatial interpretation of our results may be constrained by the limited number of study sites (n = 3). This reduced spatial replication may limit statistical power to detect potential site-level differences and may restrict the extent to which spatial patterns observed here could be generalized beyond the studied reef system. As a result, the spatial trends identified in this study should be interpreted cautiously, as additional replicated sites may be necessary to determine whether similar patterns occur across broader reef contexts.

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

See supplementary material
a17v74s1-suppl. 1

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