Ocean
and Coastal
Research

BRIEF COMMUNICATION

http://doi.org/10.1590/2675-2824071.22102mrr
ISSN 2675-2824

Abundance of the bearded fireworm *Hermodice carunculata* (Polychaeta: Amphinomidae) increases across a euphotic-mesophotic depth gradient in the remote St. Peter and St. Paul's Archipelago

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ABSTRACT

The bearded fireworm *Hermodice carunculata* is widely distributed across tropical and subtropical Atlantic and Mediterranean Oceans and was previously considered to be mostly associated with shallow reefs. We provide here data on the distribution, abundance and habitat use of *H. carunculata* across a euphotic-mesophotic gradient (0-90 m) in the Saint Peter and Saint Paul's Archipelago (SPSPA, Mid Atlantic Ridge, Brazil). Samples were obtained using SCUBA and a Remote Operated Vehicle (ROV). A total of 189 individuals were observed and a sharp increase in abundance with depth was recorded, particularly from 50 m depth onwards. In the mesophotic zone (50-90 m) individuals were closely associated with branching black-corals (*Tanacetipathes* spp.) and predation over black-corals and the scleractinian *Madracis decactis* was commonly sighted. A Boosted Regression Tree model indicated black-coral abundance as the main driver of *H. carunculata* abundance, suggesting that preference for optimal habitats to hide/forage is more important than depth *per se* on the bathymetric distribution of the fireworm. The high abundances of *H. carunculata* in the mesophotic zone, and its predation on keystone benthic cnidarians, suggests that this species play important roles in the dynamics of deep reefs.

Descriptors: Black-corals, Corallivore, *Madracis decactis*, *Tanacetipathes*, Remote Operated Vehicle.

The bearded fireworm *Hermodice carunculata* (Pallas, 1766) (Polychaeta: Amphinomidae) is commonly found in tropical and subtropical waters of the Atlantic and Mediterranean (Yáñez-Rivera and Salazar-Vallejo, 2011; Ahrens et al., 2013). It is an important predator that limits the abundance, growth and distribution of several benthic reef organisms, mainly cnidarians such as fire-corals (*Millepora* spp.), several scleractinians, octocorals, anemones and zoanthids (Lizama and Blanquet, 1975; Sebens, 1982; Witman, 1988;

Submitted: 26-Jul-2022
Approved: 30-Oct-2022

Editor: Rubens M. Lopes

Vreeland and Lasker, 1989; Pérez and Gomes, 2012). *Hermodice carunculata* also sporadically feeds on live non-cnidarian organisms, such as algae, sponges, sea cucumbers and starfish, also consuming fish feces and acting as a scavenger (Riera et al. 2014; Wolf et al., 2014; Barroso et al., 2016, 2017).

Several studies on *H. carunculata* are available for shallow reefs (e.g. Vreeland and Lasker, 1989; Lewis and Crooks, 1996), showing relatively high abundances in both, natural and artificial habitats (Riera et al. 2014; Wolf et al., 2014). Previous studies have suggested that *H. carunculata* is typical of shallow reefs, being rarely recorded in depths greater than 15 m (Ott and Lewis, 1972; Wolf et al., 2014; Schulze et al., 2017). However, there is evidence for its occurrence on deeper habitats, including a single record for *H. carunculata* at 323 m depth collected through dredging in the Caribbean (Ehlers, 1887). It was also commonly observed down to 60 m depth in the small and isolated Saint Peter and Saint Paul's Archipelago (SPSPA), Mid Atlantic Ridge, Brazil (Edwards and Lubbock, 1983). Currently, abundance comparisons across broad bathymetric gradients are still missing for *H. carunculata*, making it difficult to understand factors affecting its distribution and depth/habitat preferences. In this context, we describe here the abundance, bathymetric distribution and habitat use by *H. carunculata* in a euphotic-mesophotic depth gradient (0-90 m) in the SPSPA. We show that, contrary to previous findings, the abundance of the bearded fireworm increases with depth and that this species is prevalent in the mesophotic zone.

The SPSPA is a small group of five islets and rocks located in the central equatorial Atlantic Ocean, about 1000 km from the NE Brazilian coast (Figure 1). Three main benthic communities occur over rock reefs of the SPSPA in different depth zones (Magalhães et al., 2015; Rosa et al., 2016): 1) euphotic reefs (less than 30 m depth) dominated by the zoanthid *Palythoa caribaeorum*, macroalgae (*Bryopsis* spp. and *Caulerpa racemosa*) and crustose calcareous algae, 2) upper mesophotic reefs (30–50 m) dominated by *Caulerpa* spp., two scleractinians (*Madracis decactis* and *Scolymia wellsii*) and turf algae and 3) lower mesophotic zone (50–90 m) dominated mainly by sponges, branching black-corals (*Tanacetipathes* spp.) and bryozoans. Sampling occurred in seven expeditions between 2010 and 2018, using direct observations through SCUBA diving in depths lower than 30 m and footages obtained by remote-operated vehicles (ROV) in depths between 30-90 m. Each sample was composed by 5 min of continuous video recording/observations covering a circular area of ~ 4 m radius. Standardized sampling on shallow reefs was performed by adapting a stationary visual sampling technique originally delineated for estimating reef fish abundance (Minte-Vera et al., 2008) by using only the 4 m radius for counting fireworm individuals. A similar approach was used for deeper reefs, but using ROVs instead of direct observations by divers (cf. Rosa et al., 2016). A total of 124 samples were obtained across a 0–90 m depth gradient, as follows: 0-10 m (n = 17), 10-20 m (n = 27), 20-30 m (n = 22), 30–40 m (n = 17), 40–50 m (n = 17), 50–60 m (n = 16), 60–70 m (n = 5), 70–80 m (n = 2), 80–90 m (n = 1).

Relative cover of benthic organisms was quantified for the same areas in which fireworms were counted. We used photoquadrats (n= 41) in the shallow zone (depths lower than 30 m) (cf. Magalhães et al., 2015) and still frames from videos (n= 30 frames per sample) in deeper reefs (cf. Rosa et al., 2016). The Coral Point Count with Excel extensions (CPCe) software was used for image analyses (Kohler and Gill, 2006), with 300 points randomly assigned per sample unit. Organisms were classified in broad groups, as follows: ascidians, black-corals, bryozoans, crustose calcareous algae (CCA), fleshy macroalgae, scleractinian corals, sponges and turf algae (multi-specific filamentous algae less than 2 cm tall) and zoantharians. Bottom complexity was visually estimated by assigning values ranging 1 to 3 to each benthic frame, totaling 15 measurements per sample. Samples with no crevices and flat surfaces received a value of 1; samples with few crevices and/or small rocks received a value of 2; samples containing many crevices and rocks, as well as complex three-dimensional organisms (e.g., branching black-corals), received a value of

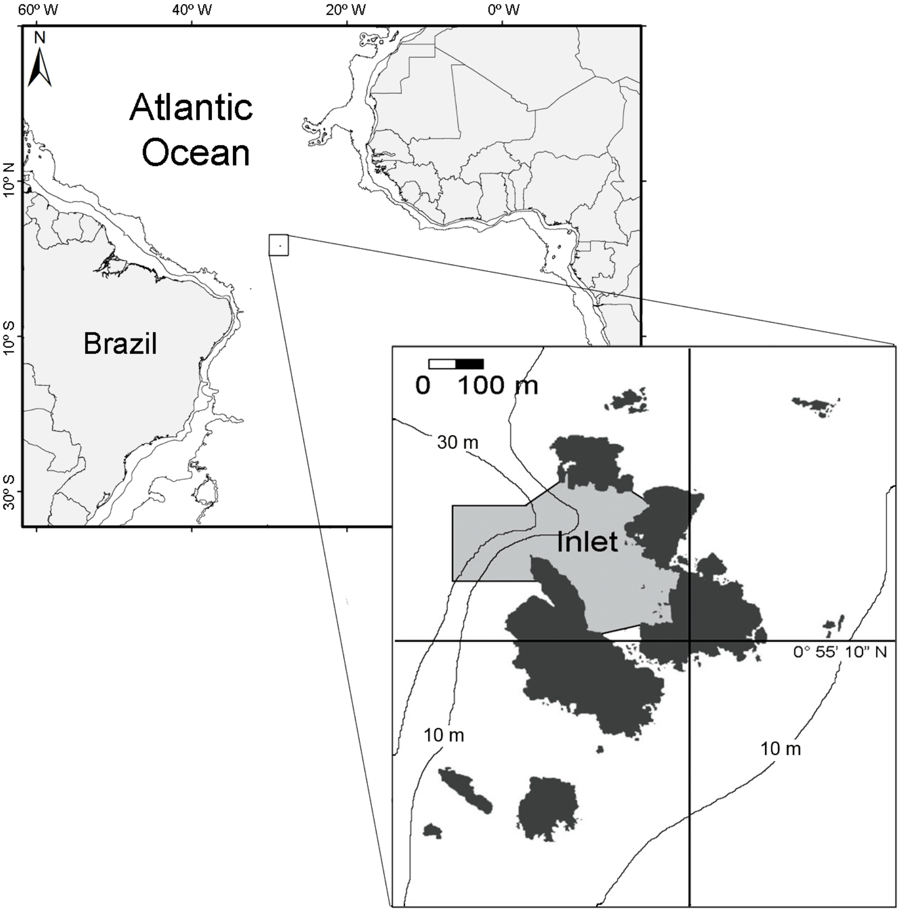

Figure 1. Location of the St. Peter and St. Paul's Archipelago (SPSPA) in the central equatorial Atlantic and detail of the SPSPA (insert) showing the islands (black) and the study area that includes the cove and adjacent drop-offs in the NW side of the island (light gray).

3. Results obtained may be considered as a reliable metric considering the gross resolution applied (Wilson et al., 2007; Rosa et al., 2016).

The relationship between depth and abundance of *H. carunculata* was explored using locally weighted regression (LOESS), a non-parametric tool widely used for visually investigating the relationship between variables (Cleveland, and Devlin, 1988; Jacoby, 2000). Boosted Regression Trees (BRT) were used to evaluate the relative influence of environmental (depth) and biotic (benthic cover) drivers of *H. carunculata* abundance. The BRT models were built following the procedures of Elith et al. (2008). The basic BRT approach consists on the combination of a large number of simple regression trees (in which predictions are based on recursive binary splits) using the technique of boosting in order to improve model accuracy. The most important attributes of BRT models are bag-fraction (proportion of data selected at random to fit a tree at each step), learning rate (contribution of each tree to the overall model explanation) and tree complexity (number of nodes (splits) of each tree). Optimal BRT models (i.e. the ones with lowest values of cross-validation deviance and standard error) were selected by examining all possible combinations of values for bag-fraction (0.5 and 0.75), learning rate (0.001, 0.005, 0.01 and 0.05) and tree complexity (1 to 5) (Elith et al., 2008). All analyses were carried out in R (R Core Development Team 2021).

A total of 189 individuals of *H. carunculata* were recorded. The fireworm abundance sharply increased with depth, particularly from 50 m downwards (Figure 2). The BRT analysis showed that the four most important variables affecting *H.*

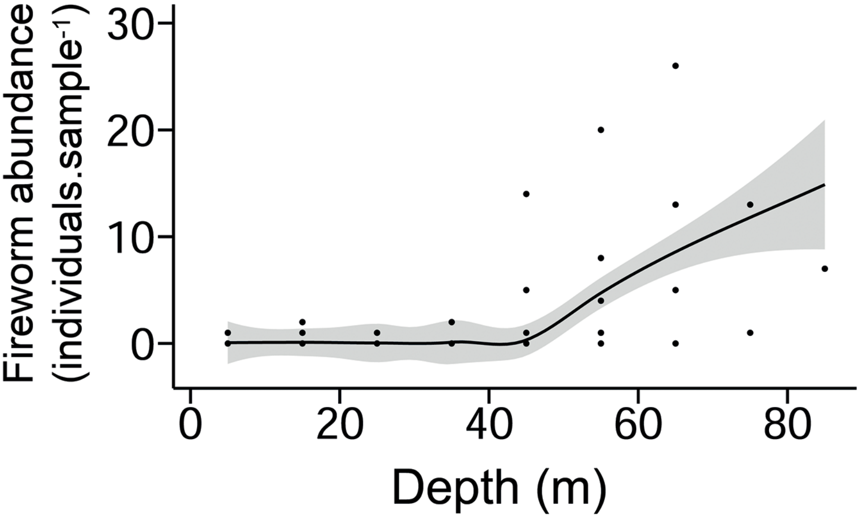

Figure 2. Relationship between *Hermodice carunculata* abundance and depth as illustrated by a locally weighted regression (LOESS).

carunculata abundance were black-coral cover (47.8% of variation explained), turf algae (17.4%), sponge (8.3%) and depth (6.2%) (Figure 3). The bearded fireworm was most abundant in areas dominated by black-corals (relative cover between 10-40%), nearly devoid of turf algae (less than 5% of cover), with sponge cover greater than 20% and in depths greater than 50 m (Figure 3).

While *H. carunculata* individuals were observed foraging over a wide range of substrata in the euphotic zone, such as algae, sand and zoanthids, they were generally associated with the scleractinian *Madracis decactis* and branching black-corals in the mesophotic zone, where several instances of coral predation were witnessed. Fireworm predation was concentrated on the tips of the branches of black-coral colonies and also focused on an epibiont zoantharian commonly found over black-corals (Figure 4). The same feeding behavior on terminal branches was described for colonies of fire-corals *Millepora alcicornis* by Pérez and Gomes (2012).

Despite a record from the last century of *H. carunculata* at 323 m depth (Ehlers, 1887) and the previous observation of this species down to 60 m depth in the SPSPA (Edwards and Lubbock, 1983), most subsequent studies suggested that this species occurs preferentially in warm waters of shallow reefs above 15 m depth (Wolf et al., 2014; Schulze et al., 2017). Inversely, we show here that *H. carunculata* abundance actually increases with depth, leading to higher abundances in the mesophotic than the euphotic zone of the SPSPA. Although size measurements were difficult to obtain from footages, there was an apparent trend of declining size with depth, suggesting an ontogenetic shift in habitat use across the euphotic-mesophotic depth gradient and/or selective predation over smaller individuals on shallow reefs. In fact, Yáñez-Rivera and Salazar-Vallejo (2011) stated in their revision of the genus *Hermodice* that “The report of Ehlers (1887) from 323 m deep probably belongs to a juvenile specimen”. These authors were probably referring to the small size of the collected specimen, instead of the life stage, as juveniles of this species were never observed (R. Barroso, pers. comm.). The notion that *H. carunculata* is restricted to shallow reefs is possibly due to the poor sampling at mesophotic depths and future studies are warranted.

Explanations for the relatively high abundances of *H. carunculata* at mesophotic depths in the SPSPA include three non-mutually exclusive hypotheses: 1) the preference for optimal habitats to hide/forage on deeper reefs, 2) preference for low light levels and 3) lower predation risk. Our BRT model corroborates the first hypothesis, as the abundance of black-corals was more important

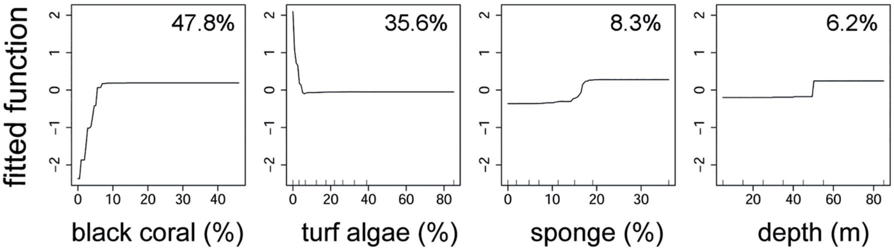

Figure 3. Partial dependence plots obtained with Boosted Regression Trees showing most important predictors (> 5% of explanatory power) of *Hermodice carunculata* abundance at the St. Peter and St. Paul's Archipelago. Relative contributions (%) of each explanatory variable are given in the top right of each panel. Y axes are centered to have zero mean over the data distribution.

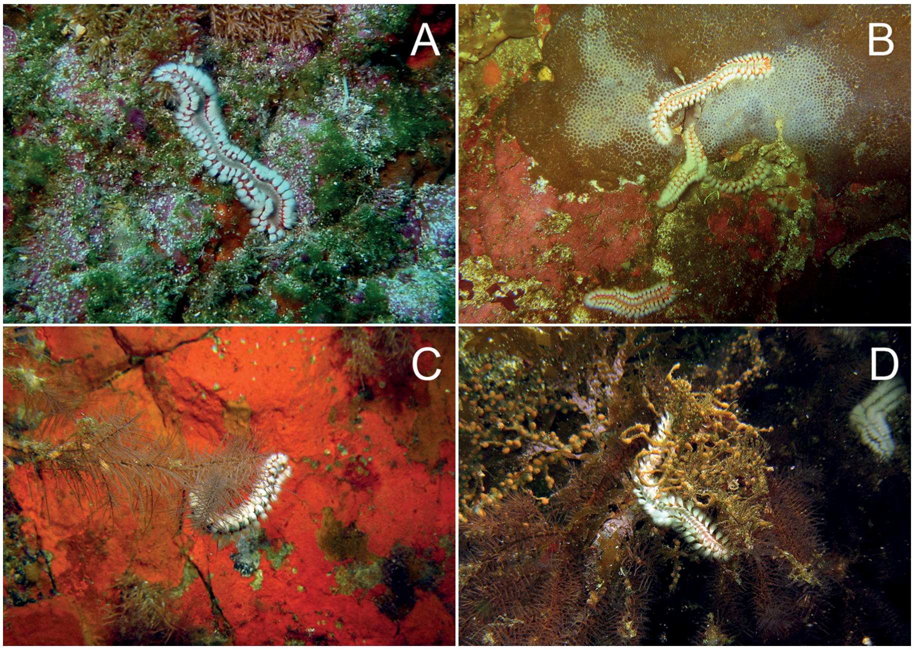

Figure 4. The bearded fireworm *Hermodice carunculata* at the St. Peter and St. Paul's Archipelago (SPSPA). **A)** A relatively large individual (> 10 cm length) at shallow reefs (8 m depth). **B)** Small *H. carunculata* individuals (6-8 cm) preying upon the scleractinian *Madracis decactis*, **C)** a small *H. carunculata* individual foraging on the tip of the branch of a black-coral colony (*Tanacetipathes* sp.) and **D)** *H. carunculata* preying upon a common black-coral epibiont (zoantharian) at mesophotic reefs of the SPSPA. All images by R.B. Francini-Filho.

than depth *per se* in explaining the bathymetric distribution of the fireworm. *Hermodice carunculata* individuals are known to aggregate around their preferential prey, which include several coral species (Wolf et al., 2014). Black-corals are important foraging grounds for fireworms in the SPSPA, with predation over black-corals and the scleractinian *Madracis decactis* commonly sighted in the mesophotic zone. Thus, the higher abundances of the bearded fireworm in deeper reefs of the SPSPA could plausibly reflect their preferential associations with such coral-dominated habitats. Interestingly, Wolf et al. (2014) recorded higher preference for coral preys and coral predation rates by smaller *H. carunculata* individuals, which may explain the concentration of relatively small *H. carunculata* individuals in mesophotic reefs of the SPSPA. The potential preference for low light levels by the fireworm is corroborated by laboratory and *in situ* observations. For example, in Barbados higher *H. carunculata* activity and frequency of coral predation events were recorded during crepuscular and night periods, with fewer observations at midday (Marsden, 1962). Similarly, Ott and Lewis (1972) recorded most coral predation by *H. carunculata* during late afternoon, while Genovese and Witman (2004) showed that foraging activity and abundances of *H. carunculata* were higher during crepuscular periods. Finally, higher mortality rates due to predation at shallow reefs could also explain increased abundances of *H. carunculata* at mesophotic depths of the SPSPA, although this hypothesis is less likely due to the rarity of *H. carunculata* predators on reef systems (Ladd and Shantz, 2016).

The present study raises several insights on the possible roles played by *H. carunculata* on the ecology of mesophotic reefs. Because this species may exert intense top-down control of their coral prey (Wolf and Nugues, 2013; Miller et al. 2014), as well as work as a vector for coral diseases (Sussman et al., 2003; Miller and Williams 2007; Moreira et al., 2014), additional studies on the roles of *H. carunculata* in controlling coral population dynamics at mesophotic depths are warranted.

ACKNOWLEDGMENTS

We thank R. Barroso and one anonymous reviewer for their insightful comments and suggestions. ICMBio for providing research permits. The crew of Transmar I and Transmar III, as well as Secretaria de Comissão Interministerial para os Recursos do Mar (SECIRM) for logistical support. Financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico — CNPq (Grant #557185/09-2 to RBFF). RBFF and PYS are grateful to research productivity scholarships provided by CNPq (#309651/2021-2 and #301554/2019-6, respectively). We are indebtedly grateful to Gilberto Menezes Amado-Filho (In memoriam) for his friendship and assistance in the field. This is a contribution of the NP-BioMar USP.

AUTHOR CONTRIBUTIONS

M.R.R.: Data collection, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review and editing;

E.F.C.S., G.M.F.: Formal analysis, Writing - review and editing;

P.Y.G.S.: Resources, Methodology, Funding acquisition, Supervision, Writing - review and editing;

R.B.F.F.: Conceptualization, Data collection, Data curation, Resources, Methodology, Formal analysis, Funding acquisition, Supervision, Writing - original draft, Writing - review and editing.

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