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Killing without a weapon: new morphofunctional and behavioural traits of *Hermodice carunculata* (Pallas, 1766)

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ABSTRACT

This study offers novel insights into the anatomy and predation strategy of a native invasive species in the Mediterranean Sea: the polychaete *Hermodice carunculata*, focusing on a population from Pantelleria (Sicily). By integrating direct underwater observations, optical and electron microscopy, and photographic material sourced online, we enhanced understanding of foregut anatomy, identified two feeding modalities, and suggested a relationship between the foregut structure and the species' behavioural traits. The analysis confirmed that the worm's pharynx is unarmed and revealed that the pharyngeal epithelium is adorned with bifurcated papillae whose function remains to be clarified. Considering that cnidarians are among the fireworm's preferred prey, the papillae secretions may play a role in neutralizing nematocyst toxins. During field surveys, the fireworms were detected while feeding on a small assemblage of colonies of *Eunicella singularis* transplanted during an earlier restoration initiative. *Hermodice carunculata* could ingest up to 10 cm of a gorgonian branch, corresponding to 20–30 segments of the worm's body, suggesting that *Hermodice carunculata* predation may pose a threat for restoration of temperate gorgonian forests. To conclude, this analysis provided valuable insights into the effective feeding strategy of the polychaete, which may inform targeted management approaches for controlling this invasive species.

KEY POLICY HIGHLIGHTS

- Insights into the polychaete's feeding strategy will inform targeted management approaches for controlling this native invasive species.
- *Hermodice carunculata* predation poses a threat for restoration of temperate gorgonian forests.
- Recommendations were provided to minimize predation on transplanted gorgonians.

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Pharynx; fireworm; feeding behaviour; invasive; *Eunicella*

Introduction

Hermodice carunculata (Pallas, 1766) (Polychaeta: Amphinomidae), commonly known as “bearded fireworm”, is a thermophilous and euriphagous worm distinguished by a suite of traits that contribute to its ecological success and invasiveness (De la Ballina et al. 2025), including its long-lived planktotrophic larvae (Toso et al. 2020) and its ability to regenerate even its anterior segments (Toso et al. 2024). It is a voracious predator and scavenger, feeding on a wide range of prey, such as several cnidarians including jellyfish, octopuses, starfish (Krželj et al. 2020; Cenni et al. 2025), sponges, nudibranchs, chitons, sea urchins, tunicates (Simonini et al. 2018), sea hares (Toso et al. 2022), and hooked fish (Tiralongo et al. 2023; Rescio et al. 2025). Unlike many other large-sized carnivorous polychaetes, it lacks teeth and/or jaws, while the main distinctive characteristics of its buccal apparatus are a muscular pharynx and glandular ridges (Marsden 1963a).

An exhaustive description of the feeding apparatus of *H. carunculata* is given by Marsden (1962, 1963a, 1963b, 1966). According to Marsden (1963a), the first tract of the alimentary canal (the foregut,

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Tzetlin & Purschke 2005) includes “1. the buccal cavity, which can be everted or folded forward on itself and so extruded through the mouth; 2. the pharynx, which is anchored to the body wall by anterior and posterior sets of muscles; and 3. a short esophagus” (Marsden 1963a, p. 167).

The pharynx of Amphinomida is a bulbous ventral organ, enveloped by cuticle and characterized by well-developed musculature (Rouse 2000; Tzetlin & Purschke 2005). In *H. carunculata* the pharynx “is lined with columnar epithelium folded into papillae” (Marsden 1963a, p. 168), while the epithelial cells bear cilia that protrude through the cuticle. The buccal mass comprises a glandular region (the glandular ridge) and is supported by two sets of oblique muscles that facilitate pharyngeal eversion upon contraction. The enzymes of the glandular ridge show both lipolytic and proteolytic activity, and it is likely that this region plays a role in predigesting the prey tissues (Marsden 1963b).

When prey is selected, *H. carunculata* everts its muscular pharynx and starts feeding through suction (Simonini et al. 2018). Small items (i.e. sea anemones, nudibranchs) are ingested entirely and quickly digested (taking from a few minutes to over 1 h, Lizama & Blanquet 1975), while other prey (e.g. sponges, cushion corals) are only partially consumed (Simonini et al. 2018). The bearded fireworm can prey upon branched hard-bodied corals, including the stinging fire coral *Millepora alcicornis* Linnaeus, 1758 (Pérez & Gomes 2012). After everting its pharynx, *H. carunculata* engulfs a terminal coral branch, spending from 15 to 30 min attached in this position to feed on the coral tissue, likely predigesting it through the secretion of enzymes (Pérez & Gomes 2012). Feeding on corals’ tips may last up to 130 min (Ott 1971).

Tissue disintegration in the actinarian *Stichodactyla helianthus* (Ellis, 1768) was observed during predation by *H. carunculata* (Lizama & Blanquet 1975), suggesting that prey predigestion may facilitate subsequent ingestion. However, most of the digestive activity occurs within the intestine, while the role of the abundant glandular cells in the foregut remains largely unclear (Marsden 1966).

The attention of researchers towards *H. carunculata* has intensified due to its rapid population growth and invasiveness in the Ionian and southern Tyrrhenian seas, likely driven by rising sea temperatures (Righi et al. 2020; Toso et al. 2022; Azzola et al. 2025). Its high density, coupled with predatory pressure and successful reproductive and behavioural traits, including opportunistic feeding, chemical defences and larval dispersal (Simonini et al. 2017; Toso et al. 2020; Righi et al. 2021), may pose a significant threat to several benthic species.

Understanding morphofunctional traits and trophic plasticity is essential for developing effective management plans aimed at predicting and mitigating invasions of marine invertebrates (Quell et al. 2021).

The main objective of this research is to offer novel insights into the foregut anatomy and predation strategy of the amphinomid polychaete *H. carunculata*, focusing on a population from Pantelleria (Sicily). The morphofunctional traits described herein can be useful for developing informed management plans to limit the spread of this species.

In the study area, the fireworms were observed feeding on colonies of *Eunicella singularis* (Esper 1791) transplanted during an earlier restoration initiative. In addition to documenting its behaviour, the potential effects of fireworm predation on the success of gorgonian restoration projects were discussed.

Methods

Underwater surveys and sample collection were conducted on 15 and 16 May 2025 by scientific diving operators in Secca di Campobello (Pantelleria Island, Sicily, Italy) at a depth of 24–26 m. Geographical coordinates and other sampling data are available in a spreadsheet (Supplementary File S1, following Di Camillo et al. 2018).

Morphological observation of the foregut

For the anatomical study, a total of 10 polychaete specimens were collected. Samples were fixed in 2.5% glutaraldehyde in 0.1 M buffer (pH 7.8), adjusted with 1 N NaOH, for 1 hour. All specimens were dissected to collect the foregut for examination under optical microscopy; three of these were selected for structural analysis of the bulb using scanning electron microscopy (SEM) and histological techniques. After drying the samples with a critical point dryer, two bulbs were coated with gold–palladium in a Balzer Union evaporator and examined with a TESCAN VEGA-III electron microscope (TESCAN, a.s., Brno, Czech Republic) operated with a beam of 20 kV in high vacuum (HV) mode. The third bulb was enclosed in a cold-curing resin (Technovit 8100) and then

mounted on plastic supports. Histological sections of the pharynx and the oesophagus were prepared using a Histo-Line MRS3500 microtome; 7 μm sections were collected in intervals of 10 sections. Selected slices were stained with toluidine blue and mounted with Eukitt.

Impact on transplanted gorgonians

Several specimens of *H. carunculata* were observed feeding on the gorgonian *Eunicella singularis* (Esper, 1791) transplanted in the study area during an earlier restoration initiative (Project PANTHER). From 15 to 17 June 2024, a small assemblage of 159 fragments of the symbiotic gorgonian were attached on the rocky substrate using a two-component epoxy (Subcoat S, Veneziani Yachting; <https://venezianiyachting.com/>) according to Roveta et al. (2023). The coral fragments, $12.6\text{ cm} \pm 5.8\text{ cm}$ standard deviation (SD) in height and composed of two to four branches, were cut from a donor population in the site Cala Tramontana from a depth of 30 m and transplanted to Secca di Campobello at a depth of 24–26 m in an area of 110 m^2 .

Although quantitative data to estimate feeding rates or polychaete density are not available, the detrimental impact of fireworms on transplanted coral colonies was evident. Accordingly, we share our observations on the effects of worm predation on translocated gorgonians, as they may be useful for planning future restoration activities.

Feeding behaviour

The feeding activity of fireworms on benthic prey (gorgonians and echinoderms) was recorded underwater using a housed Olympus TG-6 camera.

To compare trophic strategies of the worm observed at Pantelleria with other documented predation events, photographs of *Hermodice* spp. preying on gorgonians were retrieved from online sources by leveraging Web Ecological Knowledge (WEK, Di Camillo et al. 2018). Although the images were collected outside our study area, they contribute to enhancing the robustness of our findings. The keyword “*Hermodice*” was used to retrieve images of the worm using search engines and social platforms (i.e. Instagram and iNaturalist). After excluding non-relevant images, over 40 photographs depicting fireworms feeding on octocorals were selected and critically examined. Additional images showing fireworms preying on hard-bodied corals (above all Scleractinia) were also selected to evaluate differences and gain a more comprehensive understanding of fireworm feeding strategies.

Results

Morphological observation of the foregut

In the preserved samples, the buccal apparatus is ventral, sometimes protruding $< 1\text{ cm}$ in some specimens. The foregut is a barrel-shaped structure about 1.25 cm (Figure 1(a)), referred to as the bulb, which houses the pharynx. The bulb cuticle splits into two layers: the most external sheet is thin and brownish, while the innermost lining is white and semi-transparent. The middle part of the external wall of the bulb is covered with a net of blood vessels (Figure 1(b)).

The inner walls of the pharynx exhibit pronounced folding, characterized by four series of numerous folds (the glandular ridges) encircling the alimentary canal and separated by deep horizontal grooves (Figure 1, central scheme and d). The folds, which range from 125 to $221\text{ }\mu\text{m}$ depending on their level of contraction, are characterized by epithelial cells bearing bifurcated papillae with rounded apices (Figure 1(e,f)). The papillae, whose bifurcations measure 35 – $67.5\text{ }\mu\text{m}$ ($51.1 \pm 10\text{ }\mu\text{m}$) in length and 22.5 – $50\text{ }\mu\text{m}$ ($35 \pm 7.7\text{ }\mu\text{m}$) in width, were arranged in parallel rows. Histological longitudinal sections of the glandular ridges reveal yellow, rounded bodies, likely corresponding to cross-sections of blood vessels (Figure 2(a)).

SEM revealed that the grooves surrounding the papillae are occupied by fine structures, likely corresponding to cilia or secretions (Figure 1(g,h)). However, no cilia were observed in histological sections (Figure 2(b)). The lower inner wall of the bulb (oesophagus) is likely composed of folded columnar epithelium, lacking both cilia and papillae (Figure 1(i,j)) and containing numerous secretion cells (Figure 2(c)).

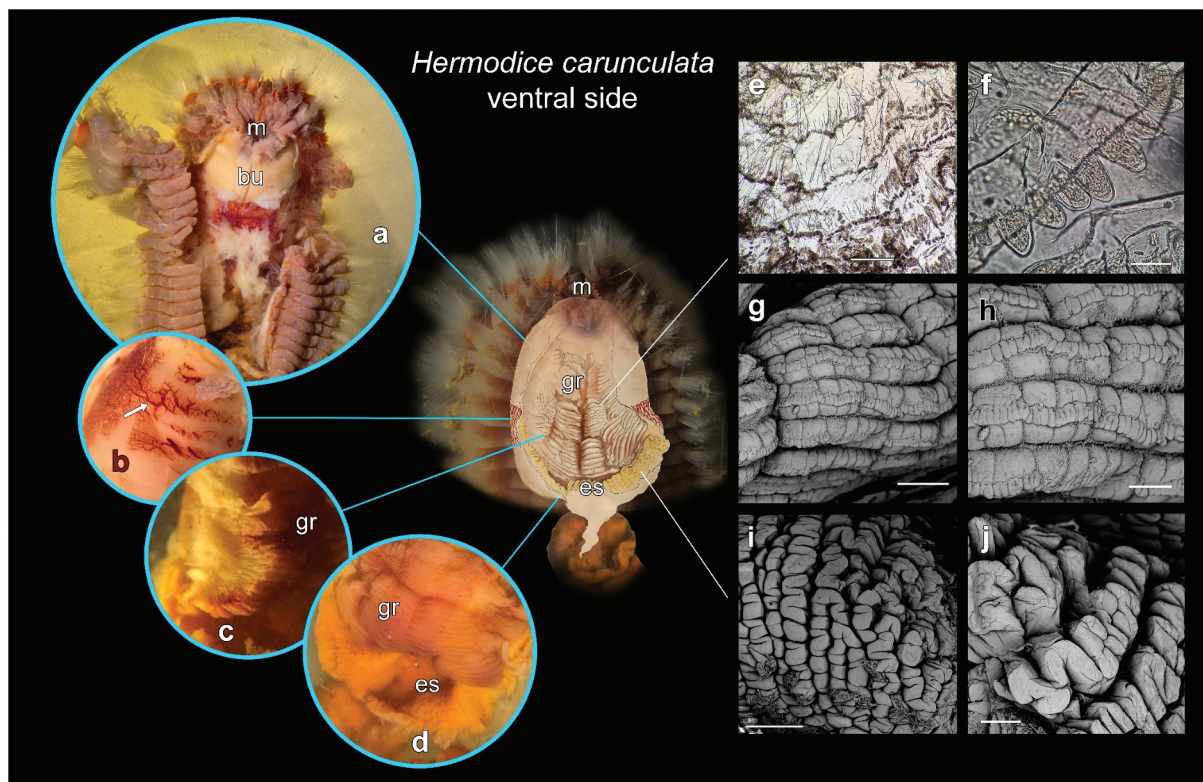


Figure 1. Buccal apparatus of *Hermodice carunculata*. (A) a dissected specimens with the inner bulb. The central scheme represents the ventral view of the anterior part of the worm. The barrel-shaped structure in the middle of the body worm is the bulb, about 1.25 cm. The pink folds are the glandular ridges of the pharynx (gr). A dense vascular net (b, arrow) is present in the central region of the bulb (chaetigers 7–8), visible in intact specimens in lateral view. In cross-section, the glandular ridges reveal a pleated structure like that of an accordion (c). The lower part of the bulb (oesophagus) shows a deeply folded yellow wall (d). The glandular ridges observed under light microscopy (e, f) and scanning electron microscopy (SEM) (g, h) exhibit parallel rows of bifurcated papillae, while the inner wall of the bulb is made of a smooth epithelium (i, j). *m* = mouth; *bu* = bulb; *gr* = glandular ridge; *es* = oesophagus. Scale bars: e, g, j: 200 μm , f: 50 μm , h: 100 μm .

Impact on transplanted gorgonians

Of the 159 colonies transplanted to Secca di Campobello in 2024, only 30% ($N = 48$) were still healthy after one year, with no predated branches. The fragments' density dropped from about 1.4 to 0.4 m^{-2} . *Hermodice carunculata* was observed actively feeding on coral colonies both one day after the transplant (about 10 individuals) and again during the May 2025 monitoring (5 individuals), while many other worms were moving within the gorgonian garden during both sampling events.

Except for a few displaced colonies, the remaining compromised gorgonian fragments remained in position, each showing at least one predated branch characterized by partial or complete loss of coenosarc (Figure 3(c–e)). Visible proteinaceous endoskeleton indicated recent fireworm feeding (Figure 3(c)), whereas branches predated long ago were overgrown by hydroids, turf algae, or Dictyotales seaweeds (Figure 3(d,e)).

Feeding behaviour

When observed on transplanted gorgonians, the worms generally started predated at the branch tips (Figure 3(a)), although central parts of the branches could be also attacked. After reaching the branch tip, the worm consumed the coral's living tissue (coenosarc), even up to the branching node, adopting an inverted U-shaped posture. The polychaete engulfed portions that extended up to 10 cm in length (Figure 3(b)).

It is likely that the worms remained in this position for at least 15 min to complete their meal, since no movement was observed during the surveys.

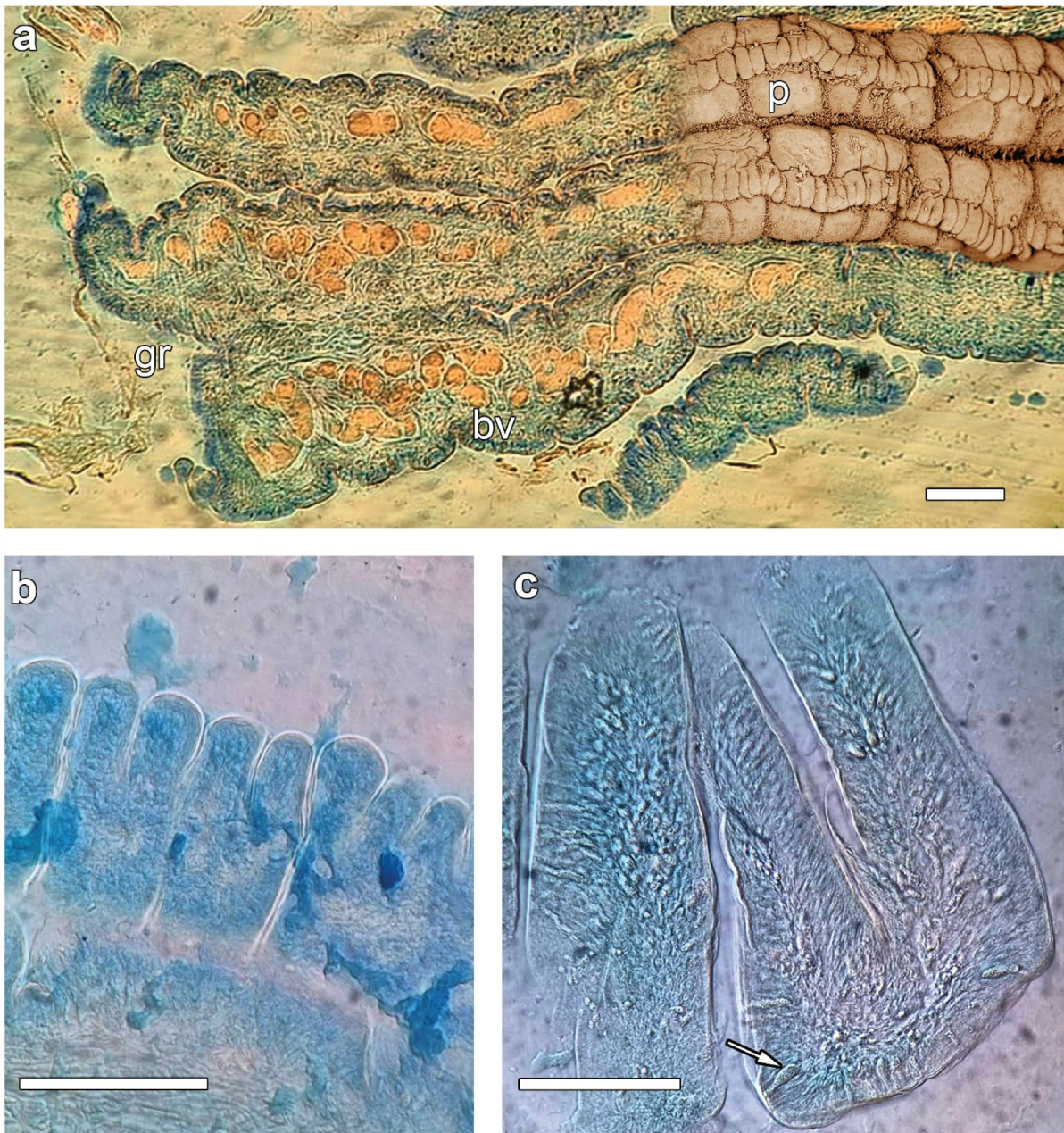


Figure 2. Histology of *Hermodice carunculata*'s foregut. (a) Longitudinal sections of the glandular ridges revealing yellow, rounded bodies, likely corresponding to cross-sections of blood vessels. A recoloured scanning electron micrograph has been partially superimposed onto the background image to highlight the position of the papillae. (b) Bifurcated papillae covered with cuticle; no cilia were present. (c) Section of the folded epithelium of the oesophagus containing numerous secretion cells (arrow). gr = glandular ridge; bv = blood vessels; p = papillae. Scale bars: 100 μ m.

Predation on other organisms was also observed, including the Ophiuroidea *Ophioderma* sp., and the Asteroidea *Coscinasterias tenuispina* (Lamarck, 1816) and *Ophidiaster ophidianus* (Lamarck, 1816). When a branch tip of *O. ophidianus* was internalized, the pharynx was not fully everted, and only a thin white lining (see details below) was visible (Figure 3(f)). When the worm was removed from the predated starfish, the white lining remained attached to the prey's arm (Figure 3(g)).

Dozens of photos of *H. carunculata* feeding on gorgonians from both tropical and temperate reefs were found using WEK (Figure 4). Among these images, over 40 showed the fireworm engulfing octocorals' branches or the bare skeleton left after predation. The worm's body adopts an inverted U-shaped posture, with the head positioned near the proximal section of the branch, the central segments curved around the

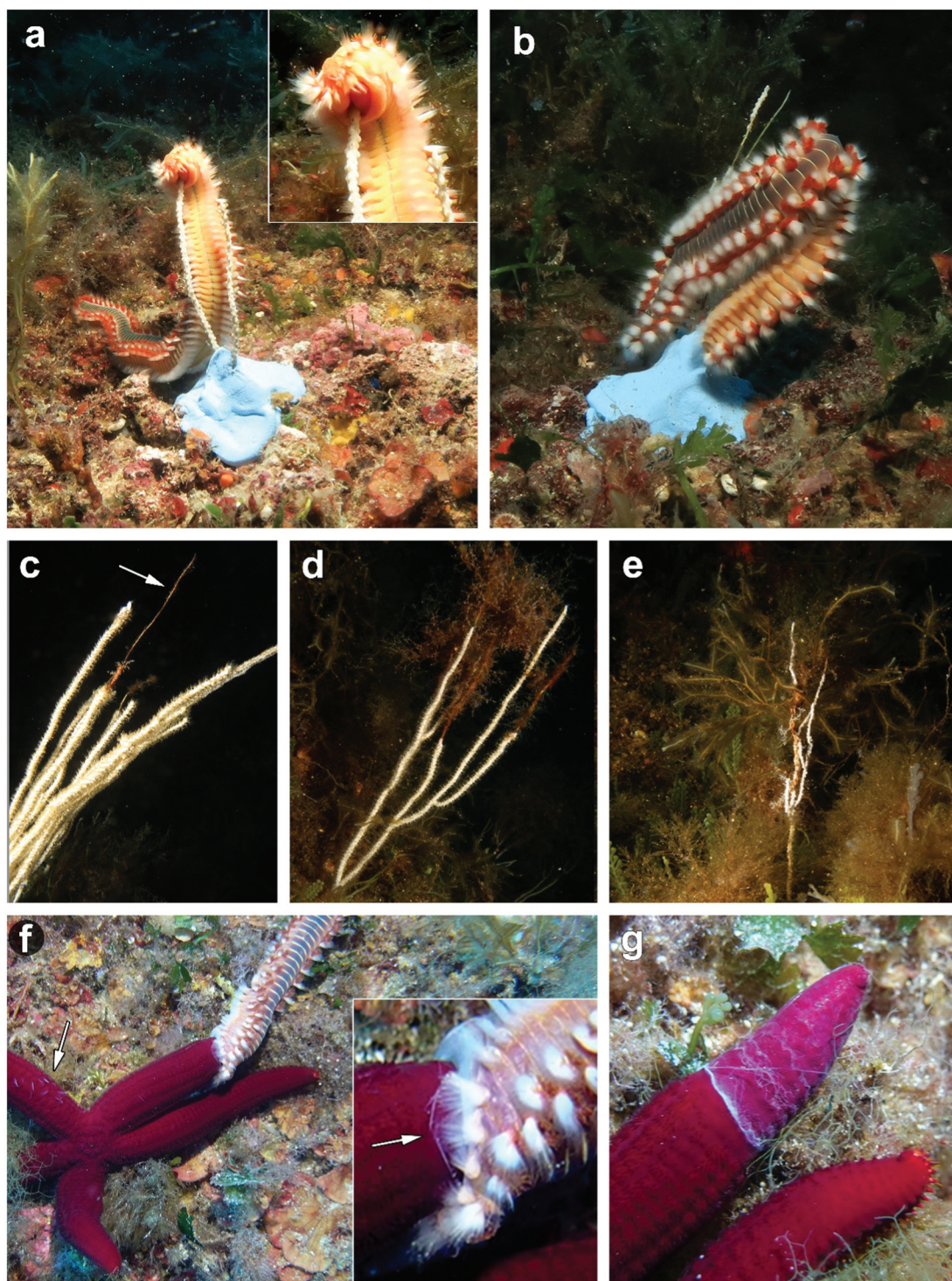


Figure 3. Predation of *Hermodice carunculata*. (a,b) Polychaete specimens feeding on transplanted fragments of the gorgonian *Eunicella singularis*. The blue area is the resin used to attach the gorgonians to the substrate. Predation begins at the tips of the gorgonian branches (a), after which several centimetres of the branch are engulfed (b). (c–e) Predated colonies of *Eunicella singularis*. Recently predated branches (a) display exposed skeletons (arrow), which are subsequently colonized by turf algae, hydroids (d), or large seaweed (e). (f,g) Predation on *Ophidiaster ophidianus*. The arrow indicates a few chaetae on one arm. When a branch tip of *O. ophidianus* was internalized (f), the pharynx was not fully everted, and only a thin white lining was visible (inset, arrow). When the worm was removed from the predated starfish, the white lining remained attached to the prey's arm (g).

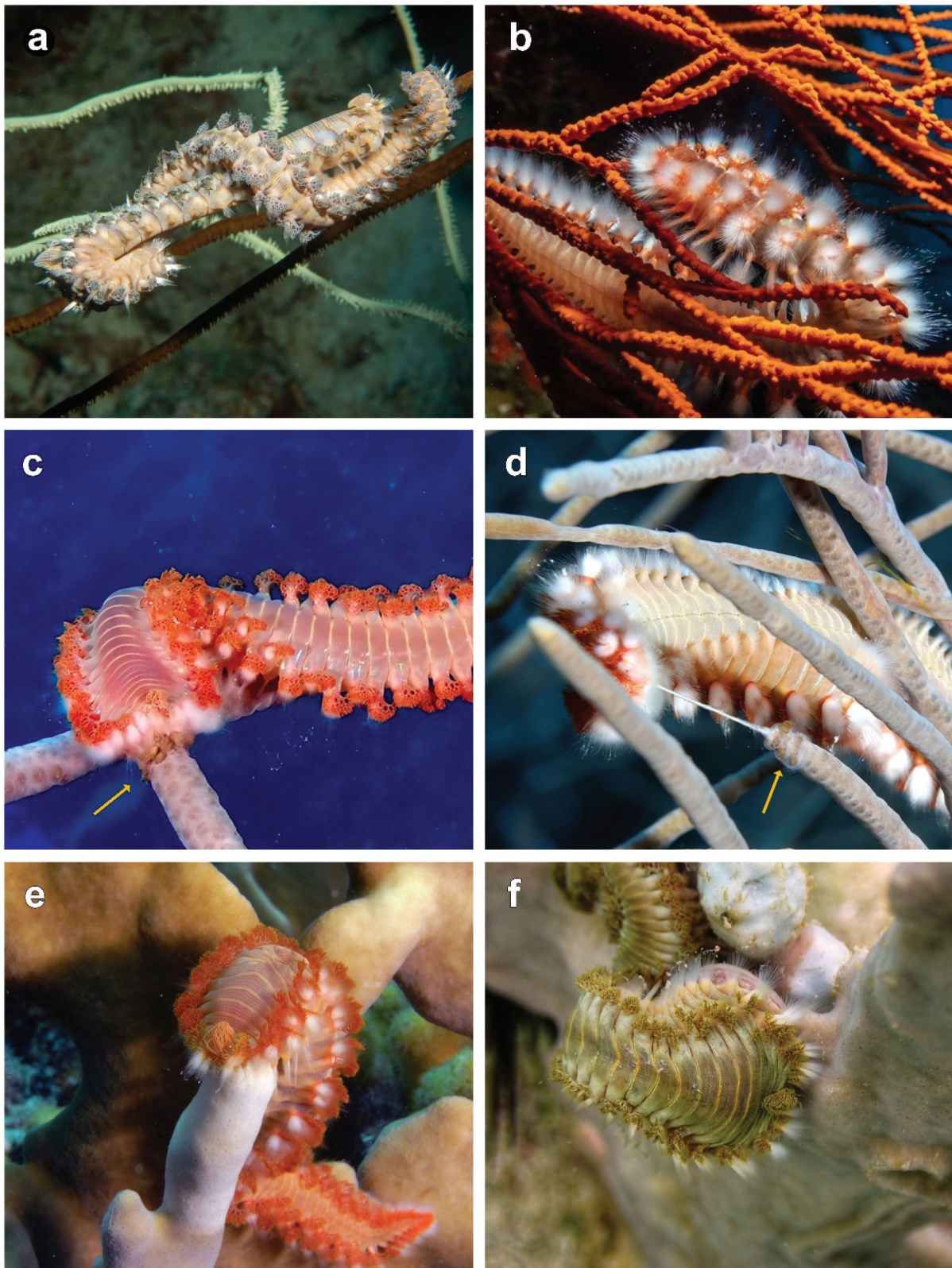


Figure 4. (a–c) Photographs from iNaturalist of *Hermodice* preying on corals with proteinaceous or chitinous (a–d) and carbonatic (e–f) skeletons. (a) Photo 224706902 CC BY-NC 4.0 Scott Johnson, Petrie’s pillars, Bonaire, Caribbean Netherlands; (b) Photo 51511519 CC BY-NC 4.0 nacho Amatt, Mar Caribe, San Andrés y providencia, Colombia; (c) photo 288805593 CC0 1.0 Universal Chris Spain, Bapor Kibrá, Willemstad, Curaçao; (d) photo 458059844 CC-BY-NC 4.0 Craig Howe modified (enlarged), Curaçao 2024; (e) photo 20047133 BY-NC 4.0 Terence Zahner, Bonaire, Caribbean Netherlands; (f) photo 104549528 CC BY-NC 4.0, Sheldon Logan, Columbus Cove Drax Hall, Jamaica. Arrows indicate decaying coral tissue.

flexible branch tip, and with the posterior portion hanging below it. The engulfed part can correspond to 20–30 segments of the body.

The mouth generally was not everted when thin octocorals or antipatharians were engulfed (Figure 4(a,d)). When visible, the area just outside the worm's mouth between healthy and predated coral tissue appeared discoloured and degraded, exhibiting signs of tissue decay (Figure 4(c,d)). All these features were also observed at the Sicilian coral garden.

A similar posture was observed in fireworms photographed during predation on *Acropora* spp., even if in this case the body assumed an inverted V-shaped posture, with the rigid coral tip positioned at the vertex of the configuration. In contrast, fireworms browsing on large branches or unbranched hard-bodied corals exhibited pharyngeal eversion during feeding (Figure 4(f)).

Few or no chaetae remained on the predated branches, both in photos obtained from the sampled coral forest and in the online images.

Discussion

Morphological observation of the foregut

We confirmed that the foregut of *Hermodice carunculata* is unarmed. The rasping organ hypothesized by Faulwetter et al. (2013) most likely corresponds to the glandular ridges in transverse section, as they exhibit comparable morphology and a pitch of approximately 200 µm.

The observations of the pharynx in *Hermodice carunculata* provided novel insights into the morphology of its feeding apparatus and the behavioural traits of this voracious, invasive species. For the first time, images revealed that the pharyngeal epithelium is adorned with bifurcated papillae and probable secretions whose function should be still clarified.

Both the pharynx and oesophagus present a multi-folded epithelium and a dense network of muscular fibres, whose contractions likely facilitate (1) suction, (2) food movement, and (3) the release of substances. However, the distinct architecture of the folds in the pharynx and of the oesophagus of *H. carunculata* suggests an anatomical and functional separation between these two foregut regions that needs future investigation.

According to Marsden (1963a, 1963b) and Simonini et al. (2018), the buccal mass is everted during feeding due to the contraction of oblique muscles of the pharynx and to the pressure of coelomic fluid, which generate suction. It is likely that enzymes produced by glandular ridges start a preliminary digestion of the prey (Marsden 1962, 1963a, 1963b, 1966). The contraction of the muscular pharynx could exert pressure, promoting the expulsion of the content of the glandular cells.

After feeding, “the animal withdraws the buccal region into the body and the food particles appear to be held by the contracted muscular ridge [...] and coated with secretions” (Marsden 1963b, p. 160); food may remain in the buccal apparatus for several hours while defaecation takes place after 16 to 30 h (Marsden 1963b). This suggests that the foregut plays a minor role in digestion and that the functions of the glandular ridges are far from being totally understood.

Marsden (1966) identified two distinct types of secretory cells within the pharyngeal wall. The first type produces mucopolysaccharides, likely serving a lubricating function. The second type, which appears only following prey capture, is presumed to secrete digestive enzymes.

Polychaetes produce feeding mucus and offensive/defensive compounds released through the alternating contraction and relaxation phases of the foregut (Ferri et al. 2024).

Coral nematocysts – both unidentified empty capsules and undischarged holotrichous isorhizas – were observed by Marsden (1962) in the worm's feeding apparatus and faeces, suggesting that fireworms are immune to cnidarian toxins.

Given that cnidarians are the preferred prey of *Hermodice carunculata*, we speculate that the extensive glandular set in the foregut contributes to neutralizing nematocysts toxins.

Impact on transplanted gorgonians

Among the many cnidarian prey items (Fauchald & Peter 1979; Jumars et al. 2015), the worm feeds on the coenosarc of the branch tips of the Ellisellidae *Ellisella paraplexauroides* Stiasny, 1936 in the Chafarinas Islands

(Western Mediterranean). However, this predation typically results in minor injuries at the coral tips, which tend to recover rapidly (Maldonado et al. 2013). In contrast, the fireworm threatened the implementation of a restoration project of the staghorn coral *Acropora cervicornis* (Lamarck, 1816) in the Dominican Republic (Calle-Triviño et al. 2017) by preying upon transplanted coral fragments. In general, a rapid algal colonization of the exposed skeleton is observed, thus hindering recovery of lesions (Lewis & Crooks 1996 and references therein).

The survival rate of the transplanted fragments of *Eunicella singularis* in Pantelleria was only 30% and, although some coral fragments were dislodged due to inadequate adhesion, the majority presented signs of fireworm predation. Even the overgrowing organisms were restricted to the coral tips, further supporting the hypothesis that fireworm predation was the primary driver of coral mortality.

The higher abundance of fireworms at Secca di Campobello may be attributed to the site's shallower depth range (24–26 m), compared to the donor area (30 m), where fireworms were not observed. *Eunicella singularis* may be particularly susceptible to predation by this worm because its long branches with few nodes can be easily engulfed and released after feeding. The presence of symbiotic algae could also increase the cnidarian's palatability.

These findings suggest that restoration planning should account for the abundance of fireworms at the intended translocation site. *Eunicella singularis* is a relatively fast-growing gorgonian, with annual height increments reaching nearly 8 cm (Viladrich et al. 2018). This trait could facilitate restoration efforts and potentially limit fireworm control measures to just a few years, helping to balance predation pressure with coral growth rates.

Therefore, the following measures were suggested to improve the survival of transplanted gorgonians:

- Although fireworm corallivory on *Acropora cervicornis* (Lamarck, 1816) increases with branching complexity (Santiago-Padua et al. 2023), transplanting larger and more branched coral colonies could enhance the likelihood of success in the restoration programme of the fast-growing *E. singularis*;
- some experiments should be carried out in aquaria to test deterrent devices such as rings or inverted cones placed at the base of the transplanted gorgonians or different types of predator exclusion cages (Raker et al. 2023);
- baited traps represent a cost-effective tool for the targeted removal or relocation of fireworms (Simonini et al. 2021), offering a practical approach to reducing predation risk and supporting animal forests conservation efforts;
- citizen science projects (Coppari et al. 2024; De la Ballina et al. 2025) involving local stakeholders and recreational scuba divers could support long-term monitoring of the coral forest and inform more coordinated removal/relocation interventions.

Feeding behaviour

Two distinct feeding modalities emerged from the analysis of photographs collected in the study area and from photos sourced online. In the first modality, fireworms engulf finger-like coral branches – both those of gorgonians and those of hard-bodied corals – for several centimetres along their length. This strategy was also documented by studies on gorgonians (Marsden 1962), hydrocorals (Witman 1988; Lewis & Crooks 1996; Pérez & Gomes 2012), and scleractinians (Ott 1971; Ott & Lewis 1972; Calle-Triviño et al. 2017; Santiago-Padua et al. 2023). The first strategy is similar to that observed when the worm feeds on arms of starfish (Krželj et al. 2020 and present work). The white lining observed on the arm of *Ophidiaster ophidianus* corresponds to the glandular ridge with papillae, which remained attached to the starfish's arm due to strong adhesion. The powerful suction created by the pharynx primarily causes the digestion of the echinoderm's epidermis, revealing the underlying dermaskeleton (Simonini et al. 2018). Injuries in large starfish predated by fireworms such as *Hacelia attenuata* Gray, 1840 ranged from simple white wounds scattered on the arms to totally devoured epidermis (Krželj et al. 2020). Predated starfish may exhibit the loss of one or more arms, as arm autotomy is likely a response to sustained predation, as confirmed by experiments carried out in aquaria (Simonini et al. 2018).

In the second feeding modality, fireworms attack large, unbranched hard-bodied cnidarians by everting the pharynx, likely to maximize contact surface area with the prey.

In both strategies, given that bare coral skeletons or decaying tissue are occasionally observed just below the mouth, this suggests that the worm first internalizes the coral tip, then reaches the farthest point along the branch, and subsequently moves backward as it feeds by sucking up the pre-digested coral tissue, unveiling the denudated skeleton in its wake.

Hermodice specimens have been documented consuming both healthy and diseased – or even deceased – organisms, including both sessile and vagile species. The only constraint on fireworm predation seems to be the prey's ability to evade capture.

The defensive function of notochaetae in fireworms is well known (Simonini et al. 2021). The chaetae are made of chitin, crystalline CaCO₃ and clusters of amorphous apatite (Righi et al. 2021), and are fanned out to threaten potential enemies; their harpoon-like tips can penetrate the predator's tissue and break on contact. Although the mechanisms for injecting toxic compounds, known as carunculines, have not yet been clarified (Tilic et al. 2017; Righi et al. 2022), the chaetal design and the potency of these toxins contribute to the success of *H. carunculata* (Simonini et al. 2021). Mobile prey can be stung by the notochaetae if they react to the polychaete's attack (Simonini et al. 2021). The analysed pictures obtained by WEK show that there were no or few free chaetae on poorly mobile prey such as gorgonians or scleractinians, suggesting that chaetae are mainly used for defence or to immobilize prey trying to escape.

Conclusions

This study offers novel insights into the foregut anatomy and predation strategy of *Hermodice carunculata*, a native invasive species in the Mediterranean Sea and a voracious predator of gorgonians and other benthic organisms. We contribute to the understanding of the morphology and function of the polychaete's buccal apparatus, revealing that the pharyngeal epithelium is adorned with bifurcated papillae and highlighting two distinct feeding strategies that vary according to prey shape and size. Further investigation into the ultrastructure of the pharynx and oesophagus may clarify the nature of the secretory cells and the biochemical properties of the secreted compounds.

Our results indicate that *Hermodice carunculata* predation may pose a threat for restoration of temperate gorgonian forests. The low survival rate of transplanted gorgonians highlights the need for deeper knowledge of *H. carunculata*'s predation on living benthic organisms.

Climate change has already driven significant declines in Mediterranean gorgonian populations due to recurrent marine heatwaves (Cerrano et al. 2010; Garrabou et al. 2022; Gómez-Gras et al. 2022); the spread and increasing abundance of *H. carunculata* could further intensify these declines through direct predation (Mistri & Ceccherelli 1994; Krželj et al. 2020; Righi et al. 2020; Cenni et al. 2025).

Integrating morphofunctional and behavioural traits will guide the development of targeted management approaches aimed to mitigate the impact of this native invasive species. Quantitative data on worm and gorgonian densities, coral growth and predation rates will be essential for calibrating coral transplantation and enhancing the likelihood of successful restoration.

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Disclosure statement

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References

- Azzola A, Montefalcone M, Righi S, Cenni E, Robello C, Atzori F, Simonini R. 2025. Cascading effects of global warming: Evidence for the impact of range-expanding thermophilic species invasion on resident species. *Biological Invasions* 27 (1):37. DOI: [10.1007/s10530-024-03483-3](https://doi.org/10.1007/s10530-024-03483-3).
- Calle-Triviño J, Cortés-Useche C, Sellares R, González JEA. 2017. First record of the fireworm *Hermodice carunculata* preying on colonies of the threatened staghorn coral *Acropora cervicornis* in the southeastern outplanting sites of the Dominican Republic. *Novitates Caribaea* 11:97–98. DOI: [10.33800/nc.v0i11.17](https://doi.org/10.33800/nc.v0i11.17).
- Cenni E, Di Camillo CG, Righi S, Fermo R, Bozzoli C, Prevedelli D, Simonini R. 2025. Winning in the era of global change: New findings on the invasive fireworm *Hermodice carunculata* (Annelida) along the Italian coasts obtained using citizen science. *Mediterranean Marine Science* 26(4):860–876. DOI: [10.12681/mms.41723](https://doi.org/10.12681/mms.41723).
- Cerrano C, Danovaro R, Gambi C, Pusceddu A, Riva A, Schiaparelli S. 2010. Gold coral (*savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodiversity and Conservation* 19(1):153–167. DOI: [10.1007/s10531-009-9712-5](https://doi.org/10.1007/s10531-009-9712-5).
- Coppari M, Roveta C, Di Camillo C, Garrabou J, Lucrezi S, Pulido Mantas T, Cerrano C. 2024. The pillars of the sea: strategies to achieve successful marine citizen science programs in the Mediterranean area. *BMC Ecology and Evolution* 24 (1):100. DOI: [10.1186/s12862-024-02289-0](https://doi.org/10.1186/s12862-024-02289-0).
- De la Ballina NR, Maresca F, Real E, Baena-Vega I, Diez S, Martin-Arjona A, Diaz D. 2025. Signs of northward expansion of the fireworm *Hermodice carunculata* in the Spanish western Mediterranean Sea. *Mediterranean Marine Science* 26 (3):515–532.
- Di Camillo CG, Gravili C, De Vito D, Pica D, Piraino S, Puce S, Cerrano C. 2018. The importance of applying Standardised Integrative Taxonomy when describing marine benthic organisms and collecting ecological data. *Invertebrate Systematics* 32(4):794–802. DOI: [10.1071/IS17067](https://doi.org/10.1071/IS17067).
- Di Camillo CG, Ponti M, Bavestrello G, Krzelj M, Cerrano C. 2018. Building a baseline for habitat-forming corals by a multi-source approach, including web ecological knowledge. *Biodiversity and Conservation* 27(5):1257–1276. DOI: [10.1007/s10531-017-1492-8](https://doi.org/10.1007/s10531-017-1492-8).
- Fauchald OK, Peter AJ. 1979. The diet of worms: a study of polychaete feeding guilds. Vol. 17. Aberdeen, Scotland: Aberdeen University Press. pp. 193–284.
- Faulwetter S, Vasileiadou A, Kouratoras M, Dailianis T, Arvanitidis C. 2013. Micro-computed tomography: introducing new dimensions to taxonomy. *ZooKeys* 263:1. DOI: [10.3897/zookeys.263.4261](https://doi.org/10.3897/zookeys.263.4261).
- Ferri A, Simonini R, Sabia C, Iseppi R. 2024. Exploring the antimicrobial potential of Hallachrome, a defensive anthraquinone from the Marine worm halla parthenopeia (Polychaeta). *Marine Drugs* 22(9):380. DOI: [10.3390/md22090380](https://doi.org/10.3390/md22090380).
- Garrabou J, Gómez-Gras D, Medrano A, Cerrano C, Ponti M, Schlegel R, Harmelin JG. 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology* 28(19):5708–5725.
- Gómez-Gras D, Bensoussan N, Ledoux JB, López-Sendino P, Cerrano C, Ferretti E, Garrabou J. 2022. Exploring the response of a key Mediterranean gorgonian to heat stress across biological and spatial scales. *Scientific Reports* 12 (1):21064.
- Jumars PA, Dorgan KM, Lindsay SM. 2015. Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7(1):497–520. DOI: [10.1146/annurev-marine-010814-020007](https://doi.org/10.1146/annurev-marine-010814-020007).
- Krželj M, Cerrano C, Di Camillo CG. 2020. Enhancing diversity knowledge through marine citizen science and social platforms: The case of *Hermodice carunculata* (Annelida, Polychaeta). *Diversity* 12(8):311. DOI: [10.3390/d12080311](https://doi.org/10.3390/d12080311).
- Lewis JB, Crooks RE. 1996. Foraging cycles of the amphinomid polychaete *Hermodice carunculata* preying on the calcareous hydrozoan *Millepora complanata*. *Bulletin of Marine Science* 58(3):853–856.
- Lizama J, Blanquet RS. 1975. Predation on sea anemones by the amphinomid polychaete, *Hermodice carunculata*. *Bulletin of Marine Science* 25(3):442–443.
- Maldonado M, López-Acosta M, Sánchez-Tocino L, Sitjà C. 2013. The rare, giant gorgonian *ellisella paraplexauroides*: Demographics and conservation concerns. *Marine Ecology Progress Series* 479:127–141. DOI: [10.3354/meps10172](https://doi.org/10.3354/meps10172).
- Marsden JR. 1962. A coral-eating polychaete. *Nature* 193(4815):598–598. DOI: [10.1038/193598a0](https://doi.org/10.1038/193598a0).
- Marsden JR. 1963a. The digestive tract of *Hermodice carunculata* (Pallas). *Polychaeta: Amphinomidae*. *Canadian Journal of Zoology* 41(2):165–184. DOI: [10.1139/z63-020](https://doi.org/10.1139/z63-020).
- Marsden JR. 1963b. A preliminary report on digestive enzymes of *Hermodice carunculata*. *Canadian Journal of Zoology* 41 (2):159–164. DOI: [10.1139/z63-019](https://doi.org/10.1139/z63-019).
- Marsden JR. 1966. The coelomocytes of *Hermodice carunculata* (Polychaeta: Amphinomidae) in relation to digestion and excretion. *Canadian Journal of Zoology* 44(3):377–389. DOI: [10.1139/z66-041](https://doi.org/10.1139/z66-041).
- Mistri M, Ceccherelli VU. 1994. Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series* 103:291–296. DOI: [10.3354/meps103291](https://doi.org/10.3354/meps103291).
- Ott B, Lewis JB. 1972. The importance of the gastropod *Coralliophila abbreviata* (Lamarck) and the polychaete *Hermodice carunculata* (Pallas) as coral reef predators. *Canadian Journal of Zoology* 50(12):1651–1656. DOI: [10.1139/z72-217](https://doi.org/10.1139/z72-217).
- Ott BS. 1971. Hermatypic coral predation at Barbados, West Indies, by *Coralliophila abbreviata* (Gastropoda, Prosobranchia) and *Hermodice carunculata*. *Veterinary medicine, small animal clinician : VM, SAC* 66(10):993–996. Polychaeta, Errantia.

- Pérez CD, & Gomes PB. 2012. First record of the fireworm *Hermodice carunculata* (Annelida, Polychaeta) preying on colonies of the fire coral *millepora alvicornis* (Cnidaria, Hydrozoa). *Biota Neotropica* 12:217–219. DOI: [10.1590/S1676-06032012000200022](https://doi.org/10.1590/S1676-06032012000200022).
- Quell F, Schratzberger M, Beauchard O, Bruggeman J, Webb T. 2021. Biological trait profiles discriminate between native and non-indigenous marine invertebrates. *Aquatic Invasions* 16(4):571–600. DOI: [10.3391/ai.2021.16.4.01](https://doi.org/10.3391/ai.2021.16.4.01).
- Raker C, Olmeda-Saldaña M, Williams SM, Weil E, Prada C. 2023. Use of predator exclusion cages to enhance *Orbicella faveolata* micro-fragment survivorship and growth during restoration. *Frontiers in Marine Science* 10:1122369. DOI: [10.3389/fmars.2023.1122369](https://doi.org/10.3389/fmars.2023.1122369).
- Rescio F, Scianna C, Di Franco A, Milisenda G, Bava S, Grasso G, Calò A. 2025. Increasing occurrence of the bearded fireworm (*Hermodice carunculata*) poses a threat for small-scale fisheries in the central Mediterranean sea. *Journal of Environmental Management* 395:127773.
- Righi S, Forti L, Simonini R, Ferrari V, Prevedelli D, Mucci A. 2022. Novel natural compounds and their anatomical distribution in the stinging fireworm *Hermodice carunculata* (Annelida). *Marine Drugs* 20(9):585. DOI: [10.3390/md20090585](https://doi.org/10.3390/md20090585).
- Righi S, Prevedelli D, Simonini R. 2020. Ecology, distribution and expansion of a Mediterranean native invader, the fireworm *Hermodice carunculata* (Annelida). *Mediterranean Marine Science* 21(3):558–574. DOI: [10.12681/mms.23117](https://doi.org/10.12681/mms.23117).
- Righi S, Savioli M, Prevedelli D, Simonini R, Malferrari D. 2021. Unravelling the ultrastructure and mineralogical composition of fireworm stinging bristles. *Zoology* 144:125851. DOI: [10.1016/j.zool.2020.125851](https://doi.org/10.1016/j.zool.2020.125851).
- Rouse GW. 2000. Morphology and physiology. In: Beesly PL, Ross GJB, Glasby CJ, editors. *Polychaetes allies: The southern synthesis. Fauna of Australia. Vol. 4A. Melbourne: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula.* CSIRO. pp. 9–32.
- Roveta C, Coppari M, Calcinai B, Di Camillo CG, Marrocco T, Pulido Mantas T, Cerrano C. 2023. What's the key for success? Translocation, growth and thermal stress mitigation in the Mediterranean coral *Cladocora caespitosa* (Linnaeus, 1767). *Frontiers in Marine Science* 10:1199048.
- Santiago-Padua P, Velázquez-Alvarado J, López-Pérez ADM, Nevárez-Mélendez J, Díaz-Druet LE, Suleimán-Ramos SE, Mercado-Molina AE. 2023. Demographic and population response of the threatened coral *Acropora cervicornis* (Scleractinia, Acroporidae) to fireworm corallivory. *Revista de Biología Tropical* 71. DOI: [10.15517/rev.biol.trop.v71i1.54912](https://doi.org/10.15517/rev.biol.trop.v71i1.54912).
- Simonini R, Maggioni F, Zanetti F, Fai S, Forti L, Prevedelli D, Righi S. 2021. Synergy between mechanical injury and toxins triggers the urticating system of marine fireworms. *Journal of Experimental Marine Biology and Ecology* 534:151487. DOI: [10.1016/j.jembe.2020.151487](https://doi.org/10.1016/j.jembe.2020.151487).
- Simonini R, Maletti I, Righi S, Fai S, Prevedelli D. 2018. Laboratory observations on predator–prey interactions between the bearded fireworm (*Hermodice carunculata*) and Mediterranean benthic invertebrates. *Marine and Freshwater Behaviour and Physiology* 51(3):145–158. DOI: [10.1080/10236244.2018.1502031](https://doi.org/10.1080/10236244.2018.1502031).
- Simonini R, Righi S, Maletti I, Fai S, Prevedelli D. 2017. Bearded versus thorny: The fireworm *Hermodice carunculata* prey on the sea urchin *Paracentrotus lividus*. *Ecology* 98(10):2730–2732. DOI: [10.1002/ecy.1919](https://doi.org/10.1002/ecy.1919).
- Simonini R, Righi S, Zanetti F, Fai S, Prevedelli D. 2021. Development and catch efficiency of an attracting device to collect and monitor the invasive fireworm *Hermodice carunculata* in the Mediterranean Sea. *Mediterranean Marine Science* 22(3):706–714. DOI: [10.12681/mms.26916](https://doi.org/10.12681/mms.26916).
- Tilic E, Pauli B, Bartolomaeus T. 2017. Getting to the root of fireworms' stinging chaetae—chaetal arrangement and ultrastructure of *Eurythoe complanata* (Pallas, 1766)(Amphinomida). *Journal of Morphology* 278(6):865–876. DOI: [10.1002/jmor.20680](https://doi.org/10.1002/jmor.20680).
- Tiralongo F, Marino S, Ignato S, Martellucci R, Lombardo BM, Mancini E, Scacco U. 2023. Impact of *Hermodice carunculata* (Pallas, 1766) (Polychaeta: Amphinomidae) on artisanal fishery: A case study from the Mediterranean sea. *Marine Environmental Research* 192:106227. DOI: [10.1016/j.marenvres.2023.106227](https://doi.org/10.1016/j.marenvres.2023.106227).
- Toso A, Boulamail S, Lago N, Pierri C, Piraino S, Giangrande A, Cinar M. 2020. First description of early developmental stages of the native invasive fireworm *Hermodice carunculata* (Annelida, Amphinomidae): A cue to the warming of the Mediterranean Sea. *Mediterranean Marine Science* 21(2):442–447. DOI: [10.12681/mms.22043](https://doi.org/10.12681/mms.22043).
- Toso A, Furfaro G, Fai S, Giangrande A, Piraino S. 2022. A sea of fireworms? New insights on ecology and seasonal density of *Hermodice carunculata* (Pallas, 1766) (Annelida) in the Ionian sea (SE Italy). *European Zoological Journal* 89(1):1104–1114. DOI: [10.1080/24750263.2022.2113156](https://doi.org/10.1080/24750263.2022.2113156).
- Toso A, Mammone M, Rossi S, Piraino S, Giangrande A. 2024. Effect of temperature and body size on anterior and posterior regeneration in *Hermodice carunculata* (Polychaeta, Amphinomidae). *Marine Biology* 171(8):152. DOI: [10.1007/s00227-024-04468-5](https://doi.org/10.1007/s00227-024-04468-5).
- Tzetlin A, Purschke G. 2005. Pharynx and intestine. *Hydrobiologia* 535(1):199–225. DOI: [10.1007/s10750-004-1431-z](https://doi.org/10.1007/s10750-004-1431-z).
- Viladrich N, Gori A, Gili JM. 2018. Fast growth rate in a young colony of the Mediterranean gorgonian *Eunicella singularis*. *Marine Biodiversity* 48(2):951–952. DOI: [10.1007/s12526-016-0554-6](https://doi.org/10.1007/s12526-016-0554-6).
- Witman JD. 1988. Effects of predation by the fireworm *Hermodice carunculata* on milleporid hydrocorals. *Bulletin of Marine Science* 42(3):446–458.