Short Communication

First description of early developmental stages of the native invasive fireworm *Hermodice carunculata* (Annelida, Amphinomidae): a cue to the warming of the Mediterranean Sea

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Abstract

Observations on the reproductive behavior and larval development of the bristled fireworm *Hermodice carunculata,* a common inhabitant of shallow marine rocky bottoms in the Southern Mediterranean Sea, are reported here. In recent years, an increase in abundance and a northward expansion of the populations along the Southern Italian coast were jointly detected, presumably linked to rising water temperature in the Mediterranean Sea. After making *in situ* observations on two consecutive spawning events, live worms and fresh spawn were brought into the lab, kept at either 27ºC or 22ºC and followed through development. Complete and normal development was observed only at 27°C. By contrast, embryonic and larval development appeared to be slowed down at 22°C, stopping at the protrochophora stage. Early development of *H. carunculata* suggests the existence of a long pre-metamorphic, planktotrophic period in the water column that can explain the genetic cohesion of this species and the low genetic divergence found among populations across the Atlantic Ocean. The observed increase in abundance, invasiveness potential, and geographical northern distribution of the bearded fireworms is probably determined by a progressive northward latitudinal shift of the sea surface temperature coincident with the temperature threshold required for the developmental and reproductive success of the worm.

Keywords: Invasive species; larval development; bristleworm; meridionalization; climate change; sea surface temperature.

Introduction

The amphinomid *Hermodice carunculata* (Pallas 1766), commonly known as 'bearded fireworm', is a large-sized, venomous polychaete species characterized by the presence of dorsal tufts of white chaetae, probably filled by toxins of unknown origin and nature (Schulze *et al.*, 2017). Originally described from the West Indies (Pallas, 1766), the species is widely distributed across the warm-water coasts of the Atlantic Ocean (Gulf of Mexico and Caribbean Sea, Gulf of Guinea), the Red Sea (Fishelson, 1971; Ahrens *et al.*, 2013), and reported in the Southern Mediterranean at least since 1800 (Baird, 1868; Yanez-Riveira & Salazar-Vallejo, 2011). Although in their revision of the genus *Hermodice*, these last authors re-established the species *H. nigrolineata* Baird, 1868 for the Mediterranean form, the more recent work by Ahrens *et al.* (2013) Examining populations of *H.*

carunculata across the Atlantic Ocean and adjacent basins, suggested they belong to the same taxon, genetically cohesive across their distribution range from the Caribbean to the Mediterranean Seas. Lack of genetic structure make difficult tracing the biogeographic region of origin for *H. carunculata*, or to label it as a cryptogenic species for the Mediterranean area (Carlton, 1996), therefore we consider this species as part of Mediterranean fauna.

However, whilst in the past the finding of *H. carunculata* were restricted to the southernmost areas of the Mediterranean Sea, over the past years the species has widely expanded its known geographical distribution to northwards (Simonini *et al.*, 2019), up to the coasts of Ionian, Tyrrhenian, and Adriatic Seas, where it is now recorded as a common member of the shallow infralittoral rocky habitat communities.

The bearded fireworm is known as a voracious opportunistic consumer of a wide range of live prey items, with

the potential to change its diet according to ongoing environmental envelopes and food availability, even adopting a scavenger behavior (Simonini *et al.*, 2017, 2018). As in other amphinomid species (Cosentino & Giacobbe 2011; Arias *et al.*, 2013), a number of biological traits – adaptive dietary plasticity, high physiological tolerance, and presumed long larval dispersal – predisposes *H. carunculata* to become a highly invasive species able to take advantage of warming ocean conditions worldwide (Schultze *et al.*, 2017; Righi *et al.*, 2019).

In recent years, both fishermen and divers reported an increase in abundance of this species along the Southern Italian coast, together with a northward expansion of the populations (Righi *et al.*, in press). The increasing abundance has also been observed by several researchers, although no published data are available at present. Both the phenomena seemingly linked to the rise of water temperature in the Mediterranean Sea (Raitsos *et al.*, 2010; Pastor *et al.* 2018).

So far, evidence for predators or competitors of *H. carunculata* in the Mediterranean Sea has not been reported. Therefore, biogeographic expansion and demographic outbreak of fireworms might result in rapid and substantial changes in the structure and functioning of benthic communities. Moreover, *H. carunculata* is also known as a winter reservoir and spring/summer key vector of the pathogenic marine bacterium *Vibrio shiloi*, responsible for bleaching events in population of the scleractinian coral *Oculina patagonica* of the Eastern Mediterranean (Sussman *et al.*, 2003; Rosenberg & Falkovitz, 2004). Thus, attention needs to be paid to the "invasiveness" potential of *H. carunculata*.

In the present paper we provide the first available information on *H. carunculata* reproduction by means of field and laboratory observations on its spawning behavior, fertilization and early larval development which are critical for a better understanding of its population dynamics and geographical northward expansion across the Mediterranean Sea.

Material and Methods

The study was focused on a population of *Hermodice carunculata* located between 2- and 10-meters depth, near the Area Protected Marina of Porto Cesareo (Apulia, Italy) (40°09′ N; 17°57′ E) along the Ionian Sea (Fig. 1). Here the infralittoral rocky habitat is characterized by photophilic algae assemblages and barren grounds. Previous observations had shown that gonads of adult-sized *H. carunculata* worms were spent in early October. Thus, field observations were made by SCUBA diving in two periods, from three to ten days following the full moon in July (16/7/2019) and in August (15/8/2019), which is known to be a cue for spawning in other Indo-Pacific amphinomid worms (Bailey-Brock & Magalhães, 2015). Photographic and video recordings were made with a GoPro camera.

During the August spawning event, male and female specimens of *H. carunculata,* still releasing gametes, were jointly collected in plastic bottles and rapidly trans-

Fig. 1: Map of the study site.

ported to the Marine Biology Station of Porto Cesareo (Italy) to follow fertilization and embryonic development. In the laboratory, about 200 viable embryos were collected from the bottles used for the transportation of the spawning worms. These embryos were isolated, washed, and transferred into two jars each containing 3 liters of 0.2 µm-filtered seawater water maintained with gentle aeration.

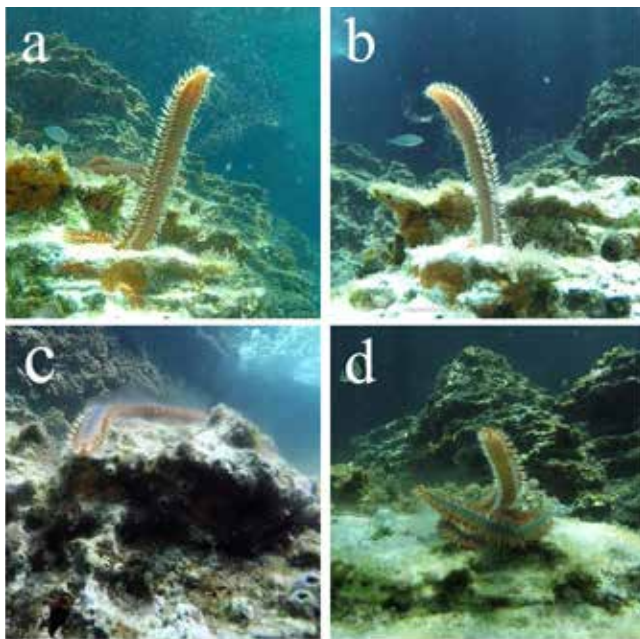At the Porto Cesareo station, mean sea surface water temperature in late July – early August, when spawning occurred is ~27 °C, whereas mean sea surface water temperature two months before (late spring) or after (early autumn) spawning event, was ~22 °C. To compare development at these two periods, one jar with ~100 embryos was kept at constant temperature of 27 °C, while the other with the remaining ~100 embryos was kept at constant temperature of 22 °C. The culturing jars were loosely covered with Parafilm to prevent evaporation and increase of salinity. Seawater was fully replaced twice a week. Larvae were fed with the Haptophyte *Isochrysis* sp. at each water change.

Embryos and larval stages growth were monitored daily using a stereomicroscope equipped with a digital camera (Carl Zeiss AxioCam ERc 5s, Zen2012, Carl Zeiss Microscopy GmbH, Jena, Germany). Some material was also fixed in a solution of 4% formaldehyde in seawater to allow further observations and measurement

Results

Spawning events were observed within each of the two periods at an average depth of 5 meters, where fireworms occurred at an approximate density of 0.6-1 ind.m^{-2}. Worms size ranged in length from 10 to 18 cm.

During the spawning event, both male and female specimens were observed vertically elevating the anterior and mid-body parts of their body while remaining anchored to the substrate with the posterior end (Fig 2). Simultaneously, the specimens started an oscillating movement to facilitate the emission of gametes in the water column seemingly from the nephridiopores (go-
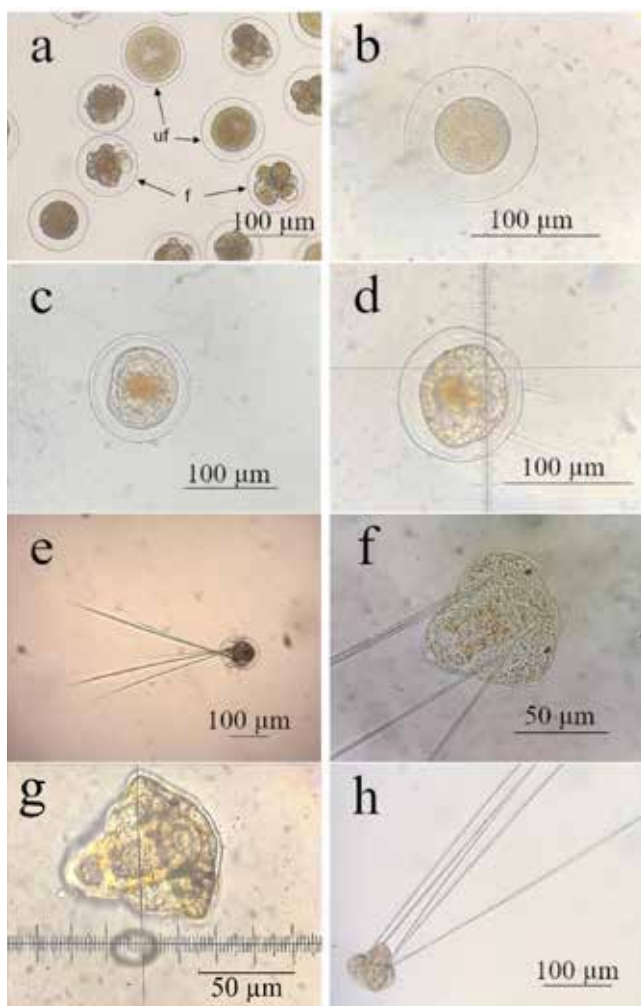
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Fig. 2: Spawning of *H.carunculata*. a, b female, c, d male.

Fig. 3: Development of *H. carunculata* from the fertilization event to 216h p.f.: a) Fertilized eggs at different stages of cleavage 2h p.f., unfertilized eggs can be identified by their reduced perivitelline space and visible nucleolus; b) zygote 24h p.f., c) pro-trochophora stage 32h p.f.; d) trochophora stage 48h p.f.; e) trochophora stage 72h p.f.; f) trochophora stage 96h p.f.; g) trochophora stage 144h p.f.; h) trochophora stage 216h p.f.

nopores) of gametogenic segments, over about two/thirds of the body length, i.e. the erect part of the worm. Apparently, females oscillate more intensively than males (Video S1). Throughout our observations, no fish was attracted by the remarkable cloud of eggs released by female worms.

Most of the eggs collected during the natural spawning in the field and transported to the laboratory appeared to be fertilized and started the embryonic development. Zygotes measured approximately 100 μm in diameter and were recognizable by the occurrence of fertilization membrane (Fig 3a). Many fertilized eggs sank to the bottom, whereas a minority remaining floating in the water column. To avoid contamination of organic debris from the bottom, we separated floating embryos, up to a total number of 200, for further laboratory rearing at two different temperatures: 27°C and 22°C.

At both temperatures, zygote first cleavage started about 12 hours post fertilization (p.f). All embryos remained protected by their fertilization membrane until 96h p.f. (Fig 3b).

Embryos reared at 27°C were followed for up to 9 days (216 hours post fertilization, hpf). At 32 hpf, embryos reached pro-trochophore stage (Fig 3c), characterized by a completely ciliated surface. Gastrulation was evidenced by formation of an inner archenteron composed by orange yolky cells from the blastopore towards the anus openings. At 48 hpf, the trochophore stage was reached (Fig 3d) through a gradual change in shape, restriction of cilia to the equatorial prototrochal and metatrochal ciliary bands, the appearance of larval eyes and two pairs of long chaetae. No other significant morphological changes were detectable until 72 hpf (Fig 3e), when both mouth and anus opened and the larvae started feeding on microalgae. At 96 hpf, larvae reached the elongated metatrochophore stage still having evident eyes, anus, mouth and ciliated bands (Fig 3f). The hyposphere became enlarged at 114 hpf (Fig 3g). From 6 to 9 days post fertilization, all larvae elongated (Fig 3g, h), developing up to 6 (3 pairs) very long chaetae from the first chaetigerous segment. At this stage, the larval guts were clearly full of *Isochrysis* sp. cells after feeding, and larvae swam around using the long chaetae as an additional propulsory, oar-like device (Video S1). Larval mortality was high throughout all 9 days: survivors were nearly halved every day, and death rate was higher especially after the anus developmentally opened. The last developing larval stage died at 9 days after the start of the rearing process.

Embryos reared at 22°C exhibited a significant delay in development compared to those reared at 27°C. They reached the protrochophora stage (Fig 3c) at about 52 hpf and further development stalled; they progressively died over the following days and were all dead by day 8.

Discussion

Due to its omnivorous diet, high densities of the fireworm *Hermodice carunculata* can exerts powerful predatory impacts on key sessile and sedentary taxa of benthic communities, including cnidarians, molluscs, echinoderms, and tunicates (Simonini et al, 2017, 2018). Nonetheless, its geographical distribution and abundance has recently become the focus of attention (Simonini *et al.*, 2019), a critical lack of ecological and biological information, still remais especially concerning its life cycle.

The increasing abundance of *H. carunculata* along the coasts of the northern Ionian Sea allowed for direct field observations on its reproductive behavior and two spawning events of a shallow-water population. While documentation of specific details, e.g., how gametes were discharged, was not possible during underwater observations, we noticed that spawning gamete clouds occurred along most part of the erect body length of the worm (i.e., the anterior and central chaetigers), which would correspond gametes being released through gonopores, and almost certainly not via the anus or tears in the rectal epithelium (so-called pygidial "pseudopores" described in *Eurythoe complanata* see Kudenov, 1974). Body lining ruptures were never observed also in any of the spawning individuals of different size collected and transported to the laboratory. After spawning, worms did not die. Therefore, even in the absence of direct microscopic evidence, we can reasonably assume that spawning occurred through gonopores and that *H. carunculata* can likely be considered iteroparous.

This study also achieved rearing of newly fertilized embryos of *H. carunculata* in laboratory cultures for up to 9 days, making possible a description of early stages of its larval development for the first time. Present observations indicated as developmental program is conservative in the family Amphinomida, showing a high similarity of the development, and the presence of similar long chaetae recorded also in the larval stages of *Eurythoe complanata*, and of *Eurythoe* sp., the only other amphinomid species whose early development was investigated so far (Kudenov, 1974, Yáñez Rivera, 2015). The morphology of *H. carunculata* metatrochophore larvae with very long chaetae may be interpreted as an adaptation to a long pelagic duration.

Polychaete larvae are generally known to have relatively short pelagic life spans, from hours to a few days, although exceptions are known (e.g. up to one month in *Owenia* spp., *Sabellaria* spp; see Giangrande, 1997 for a review). Long larval duration is also reported for the Amphinomidae, although late larval stages attributed to this family are known only from plankton samples (Bhaud, 1972). The relatively short observation period of the present paper do not allows further speculations, there is still a morphological/developmental gap of knowledge between the metatrochophore stage at 9d p.f. described here and the supposed amphinomid 'rostraria' larval stages described from plankton. However, taking into consideration the duration of the first stages here observed, we can assume a long duration of post-embryonic life stages for *H. carunculata*.

Prolonged planktonic stages can also explain the genetic cohesion of this species and the basis of its low genetic divergence among populations across the Atlantic Ocean (Arhens *et al.*, 2013). Investigated at temperature ranging 27-30 °C, the early development of *Eurythoe complanata* displays a comparable duration, even if its metatrocophore stage was reached earlier (72-88h p.f.) than in *H. carunculata* (96h p.f.).

The metatrochophore larvae of *H. carunculata* use their long chaetae as a oar-like propulsive tools which produce faster movements compared to any other types of polychaete larvae, that move through the beating of their ciliary bands. At first, the angle between each chaetal bundle and body is slowly opened relative to the larvae's main body axis. Secondly, the angle between the chaetae and body gently closes the angle so that chaetae are parallel to the main body axis. In effect, larvae appear to move most abruptly in a way that recalls the whipping action of a swimmer's frog-style stroke (Video S1). This behavior in amphinomid metatrochophorae, not recorded in *E. complanata* by Kudenov (1974), was also observed for *Eurythoe* sp. (Yáñez Rivera, 2015). The ability to adjust the orientation of these long chaetae would also make it possible to regulate the larval buoyancy in the water column. These structures could be interpreted as defensive chaetae, as occurs in other polychaetes with long planktotrophic development such as spionids and sabellariids (Bhaud, 1972), but the present observations suggest they could be better labeled as defensive and swimming chaetae.

Amphinomidae are reported to remain in the water for long time also after their larval metamorphoses (Bhaud, 1972). However, amphinomid larvae have been described only at advanced stages from plankton collections and indicated with the name of 'rostraria' larvae, showing two long feeding tentacles, but no swimming chaetae (Bhaud, 1972). These "larvae" are, however, already metamorphosed and characterized by at least 10 chaetigers, therefore they can be defined as "planktonic juveniles".

The long chaetae observed in the early stages of *H. carunculata,* as well as in *E. complanata,* may therefore occur as a transient feature, such as the feeding tentacles in rostraria larvae. Notably, these tentacles were not observed in the early larval stages neither in *Eurythoe* genus or in *H. carunculata* here described. This reinforces the fact that current knowledge on amphinomid larvae is very limited: indeed, complete embryonic and larval development from fertilization to metamorphosis is still unknown for any amphinomid species and further investigations are urgently needed.

A better knowledge of amphinomid larval development can have important implications both from phylogenetic and ecological point of views. Concerning Annelida Phylogeny, Amphinomida have been shown to be a likely early branching lineage (Struck *et al.*, 2007, 2011; Weigert & Bleidorn, 2016): closely related to the Oweniidae and Magelonidae, they are hypothesized to be the sister group of Pleistoannelida, the large clade comprising most other extant annelids. Indeed, early development of amphinomid larvae presents a high similarity to

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that of Magelonidae (Wilson, 1982), leading to reconsider whether planktotrophy, instead of lecitotrophy, could represent the most probable ancestral condition for polychaetes (Rouse, 2000).

Furthermore, observations on *H. carunculata* development suggest that rising sea temperature could be one of the most important factors explaining its invasive behavior. As thermophilic organisms, fireworm adults and juveniles do not tolerate low temperatures: at 19 °C they stop most activities (Sala *et al.*, in press), although they do not die. Instead, our observations show that uninterrupted embryonic and larval development of the *H. carunculata* does not take place at 22°C. Thus, recruitment and establishment of the fireworms, and consequently their potential for spreading into new areas might be constrained by a developmental, temperature-dependent bottleneck.

The present 30 year warming trend in the Mediterranean Sea has led to a concomitant northward latitudinal shift of sea surface temperatures (Pastor *et al.*, 2018). Such elevated temperature changes tend to enhance ecological opportunities for invasive species, especially if temperature thresholds promote the developmental and reproductive success of such populations. As a working hypothesis it will be interesting to verify whether the observed increase in abundance, invasiveness potential, and geographical northern distribution of the bearded fireworms in the Mediterranean Sea is paralleled by the progressive northward latitudinal shift of the sea surface temperature coincident with the temperature threshold required for the developmental and reproductive success of *H. carunculata*.

Further investigations on *H. carunculata* biology and ecology are urgently required for understanding of its massive proliferation and rapidly increasing geographical distribution. For instance, raising larvae at additional experimental temperatures between 22 and 27 °C would offer a better resolution of the developmental, temperature-dependent bottleneck. Gathering new experimental evidence with models of sea warming may support predictions of future expansions in the Mediterranean Sea of this "ecologically cumbersome" amphinomid predator.

As a corollary, validation of such developmental temperature-driven bottleneck hypothesis may also lead us to consider the bearded fireworm as a flag species, a biological marker of the 'meridionalization' of a warming Mediterranean Sea. In turn, this would support implementation of mitigation measures to avoid the spread of *H. carunculata* and the dramatic ecological impact it may cause on a number of native shallow benthic communities.

Acknowledgements

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Supplementary data

The following supplementary information is available on line for the article:

Video: Spawning of *Hermodice carunculata* and first developmental stages