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Bearded versus thorny: the fireworm *Hermodice carunculata* preys on the sea urchin *Paracentrotus lividus*

The bearded fireworm, *Hermodice carunculata* (Polychaeta: Amphinomidae), owes its common name to the tufts of white, sharp, and venomous chaetae (Fig. 1) that, when touched, cause a painful burning sensation (Kicklighter and Hay 2006). In recent years, it has rapidly increased in abundance in Mediterranean infralittoral rocky habitats. In particular, *H. carunculata* was not common along Apulian coast (Central Mediterranean Sea) until the last decade, and it is indeed missing from lists of polychaete species found in this area published in the early 2000s (see Corriero et al. 2004). Currently, fishermen and scuba divers commonly observe tens of fireworms, 10–30 cm long, crawling on the bottom at the end of summer (approximate density 0.2–1 ind. m^{-2}, see Video S1). *H. carunculata* is a well-known generalist predator/scavenger in Western Atlantic coral reef ecosystems (Wolf et al. 2014; Barroso et al. 2015), where it is preyed upon by at least two species of fishes (Ladd and Shantz 2016). Whether these large worms can affect communities depends on their feeding behavior, prey preferences and enemies, about which there is very little information, at least for the Mediterranean. We have recently observed the bearded fireworm preying on the sea urchin *Paracentrotus lividus* (Fig. 1), which is a major determinant of algal community structure in this system (Agnetta et al. 2015). Many polychaete families such as acoetids, amphinomids, aphroditids, eunicids, glycerids and nephtyids include large, powerful, carnivorous species that consume smaller invertebrates (amphipods, isopods, other polychaetes, ophiuroids and thin-shelled bivalves). Besides, the “bobbit worm” (*Eunice aphroditois*) is able to capture also small fishes through a sit-and-wait predation strategy, while the oenonid *Halla* is a specialized predator of clams: it covers the valves with a toxic mucus that forces their opening and then consumes the disabled bivalve. The majority of amphinomid species are macrophagous carnivores or scavengers (Jumars et al. 2015). Large fireworms have previously been reported to attack injured starfishes (Barroso et al. 2015) but have not been previously reported to attack large healthy armored preys such as urchins.

Our observations were made in barren habitats (0.5–18 m depth) near the Marine Protected Area of Porto Cesareo, along the Ionian Apulian coast. During several dives between November 2015 and December

FIG. 1. Close-up of a bearded fireworm (*Hermodice carunculata*) feeding on a live sea urchin (*Paracentrotus lividus*) in coralline barrens. The remains of a sea urchin after predation by fireworms are visible in the background.

2016, we recorded large specimens of the bearded fireworm (10–30 cm long) feeding on *P. lividus*, adhering closely with their buccal mass (Fig. 1). Sometimes, two or three fireworms attacked the same urchin at the same time. In most cases, the urchins were still alive and continued to move their spines and crawl on the substrate during the attack before eventually succumbing. In other cases, the fireworms' heads were tucked inside the oral opening of a sea urchin test which lacked most of spines. The entire process required more than 20 min (the maximum duration recorded in the field). We observed a large number of nude and empty sea urchin tests in the bottom, most of which were intact with the exception of the oral area (Fig. 1). These findings suggested the cause of mortality was active, non-accidental predation by *H. caruncu-lata*, because the fishes that feed on sea urchins often break tests in small pieces to consume them (Sala 1997).

To document the full sequence of behaviors in an attack, we observed interactions between *H. carunculata* and *P. lividus* under controlled conditions in the lab. Healthy specimens of the fireworm and the urchin were collected from the field and kept separately in 90-L tanks with a recirculating system (temperature 24–25°C; salinity 32–36; photoperiod regime: 16 h light/8 h dark; total volume: 600 L). After 3 d of starvation, the fireworms regurgitated a huge number of sea urchin spines. Analysis of the shape and size of six whole, undamaged spines suggested that they belong to small-sized *P. lividus* (estimated test diameter without spines 1.8–3.2 cm; Sala and Zabala 1996).

Five experiments, in which three healthy urchins were placed for 6 h into an aquarium containing 25 *H. carunculata* (20–30 cm long, starved for 1 week before the trial), revealed an interesting feeding strategy (Appendix S2, Video S2). The bearded fireworms moved haphazardly around the tank without turning towards the sea urchins for 1–2 h. Yet, upon a fortuitous contact (Appendix S2: Fig. S1A), a fireworm rapidly initiated an attack on the urchin, everting its pharynx over it and starting to suck and ingest the spines. The attack forced the detachment of the urchin from the substrate and the exposure of its oral side (Appendix S2: Fig. S1B). Then, the fireworm moved toward the urchin mouth, placed its buccal mass over the Aristotle's lantern (the large powerful urchin "jaw"), removed it with a suction generated by the pharyngeal musculature and entered the test (Appendix S2: Fig. S1B, C). A few minutes after the initial contact, other fireworms became more active. They converged from different directions to the urchin on which the former was already feeding and adhered to it (Appendix S2: Fig. S1C–G). This coordinated behavior may arise from the well-developed chemoreceptive ability of *H. carunculata* for detecting carrion and injured organisms (Stoner and Layman 2015). The fireworms consumed the urchin spines, external and internal tissues in the next 2–4 h (Appendix S2: Fig. S1C–H, Video S2). The day after, pieces of the Aristotle's lantern were found in a small area on the tank bottom. These fragments permitted us to reconstruct an almost complete Aristotle's lantern, suggesting that the whole urchin jaw had been consumed and regurgitated by a single fireworm, perhaps the first which entered the test (Fig. 2). At the end of the laboratory experiments, only empty

Fig. 2. Pieces of the Aristotle's lantern, collected from the tank bottom the day after the predation event, were arranged to reconstruct an almost complete "exploded" urchin "jaw" (the coin diameter measures 18.75 mm).

tests lacking of spines were recovered (diameters from 2.59 to 2.80 cm), intact but with a single large hole in correspondence of the oral opening. These remains were very similar to those found in the field (Fig. 1) and differed from ones commonly left by the other sea urchin predators (see Gianguzza et al. 2009). Therefore, our records provided evidences that *H. carunculata* can effectively prey upon healthy urchins.

Fishes (in particular *Diplodus* spp.) are currently considered the main consumers of *P. lividus,* even if most of them act as scavengers since only a few species are able to break open the tests of healthy sea urchins (Sala 1997). In particular, small urchins (<3 cm; Sala 1997), with less robust tests and shorter spines than the large ones, are preyed upon at higher rate. They usually shelter in crevices and beneath boulders to escape fish predation (Guidetti 2004; Guidetti and Mori 2005): however, these refuges cannot protect urchins from *H. carunculata* because the fireworms readily navigate small spaces inside crevices.

Paracentrotus lividus is one of the most important invertebrate herbivores in Northeastern Atlantic shallow rocky habitats, where it can induce the transition from macroalgal beds to barren grounds, i.e. bare rocks dominated by encrusting corallines (Guidetti and Mori 2005; Agnetta et al. 2015). The diet of *P. lividus* is mainly based on erect fleshy macrophytes, such as canopy-forming seaweed of the genus *Cystoseira,* which provide hundreds of algae and invertebrate species with shelter, food and settlement opportunities. When the density of *P. lividus* is high, the massive removal of *Cystoseira* canopy reduces the local biodiversity and prepares naked substrates for the colonization by encrusting algae, which can be maintained by the scraping activity of another urchin, *Arbacia lixula* (Agnetta et al. 2015). When an increase in *P. lividus* mortality caused by predation occurs, a top–down control of communities may take place, triggering different habitat formation (algal forest vs. barren) (Bonaviri et al. 2009). Further research on the effects of the predation of the bearded fireworm on urchin populations is required to assess their potential repercussions for the structure and functioning of Mediterranean rocky reef ecosystem.

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