Tough, armed and omnivorous: *Hermodice carunculata* (Annelida: Amphinomidae) is prepared for ecological challenges

ANJA SCHULZE, CANDACE J. GRIMES AND TIFFANY E. RUDEK

Department of Marine Biology, Texas A&M University – Galveston Campus, 200 Seawolf Parkway, Galveston, TX 77553, USA

The bearded fireworm, Hermodice carunculata, *is a common species in the marine annelid taxon Amphinomidae. It has a widespread distribution throughout the Atlantic, Gulf of Mexico, the Caribbean, Mediterranean and Red Seas. We review its environmental tolerances, defence mechanisms and feeding habits to evaluate its potential to survive in changing ocean conditions, to increasingly emerge as a nuisance species and to invade new geographic areas.* Hermodice carunculata *tolerates a wide range of environmental conditions, including temperature, salinity, oxygen saturation and various types of pollution. It has few natural predators because it is protected by its sharp chaetae and probably by toxins.* Hermodice carunculata *is best known for consuming live cnidarians, and has been implicated in transmitting coral pathogens, but it also feeds non-selectively on detritus. In the short term, we predict that* H. carunculata *will be able to withstand many future ecological challenges and possibly contribute to coral reef decline. In the long term, ocean acidification may negatively impact its defence mechanisms and survival. Its invasive potential may be significant. We highlight the gaps in our knowledge about the reproduction and development of this species, the nature and origin of its toxins and role of microbes in their feeding behaviour and defensive strategies.*

INTRODUCTION

Marine shallow-water species currently face a multitude of ecological challenges. Coastal waters are increasingly subject to pollution, pathogens, hypoxia, overfishing, non-native species and other anthropogenic and natural disturbances. Additionally, shallow-water species are more exposed to increased UV radiation, warming temperatures and acidification than inhabitants of deeper water. We are only beginning to understand the long-term consequences of these environmental stressors, separately and in combination, on biological communities. Shallow-water coral reefs, in particular, are in decline worldwide, causing concern about the loss of biodiversity associated with hermatypic corals (e.g. Pandolfi *et al.*, 2011; De'ath *et al.*, 2012; Descombes *et al.*, 2015). Some shallow-water invertebrate species appear to be better equipped than others to cope with particular challenges. For example, calcifying species are especially vulnerable to acidification (Kroeker *et al.*, 2010, 2013).

In this contribution, we examine the potential of the bearded fireworm, *Hermodice carunculata* (Pallas, 1776) (Figure 1), to survive – and potentially thrive – in a changing ocean environment. We argue that its ability to withstand environmental extremes and fluctuations, its predator avoidance strategies and its non-selective diet will probably

Corresponding author:
A. Schulze
Email: schulzea@tamug.edu

benefit its survival and possibly lead to its widespread emergence as a nuisance species although the effects of ocean acidification could interfere with its defence mechanisms in the long term.

Hermodice carunculata is a common species of amphinomid polychaete with a distribution throughout the Atlantic Ocean, the Caribbean, Gulf of Mexico, Mediterranean and Red Seas (Yáñez-Rivera & Salazar-Vallejo, 2011; Ahrens *et al.*, 2013). The common name refers to the tufts of 'harpoon chaetae' which are flared when the worm is threatened, causing serious irritation at the site of contact.

Hermodice carunculata is primarily reported from warmer waters, but one questionable record exists from as far north as the Dogger Bank in the North Sea (Fauvel, 1923). In the south, it ranges to Rio de Janeiro in the west and to the Gulf of Guinea in the east (Ahrens *et al.*, 2013). It has also been reported from Ascension and St. Helena Islands in the South Central Atlantic (Yáñez-Rivera & Brown, 2015). *Hermodice carunculata* inhabits primarily shallow water, including the intertidal zone, but has been reported to a maximum of over 300 m depth (Ehlers, 1887). The species is common in a variety of habitats, such as coral reefs and seagrass beds, as well as artificial structures like pilings, bridge spans and shipwrecks. *Hermodice carunculata* is primarily active from dusk to dawn and often hides in crevices, under overhangs or underneath rocks throughout the day.

Ahrens *et al.* (2013) showed that *H. carunculata* is genetically homogeneous throughout its distribution range, suggesting high dispersal capabilities. Unfortunately, little is known about the larval development of the species. Based on

Fig. 1. The bearded fireworm, *Hermodice carunculata*, observed off the South Florida Atlantic coast.

chaetal characteristics, a planktotrophic larval type known as rostraria is perhaps associated with amphinomids (Bhaud, 1972), but this association has never been confirmed by direct observation of metamorphosis into a juvenile or by DNA barcoding of the larva. Even accepting that the rostraria is an amphinomid larva, assignments to particular species cannot currently be made.

Apart from pelagic larvae, *H. carunculata* may also disperse by rafting. Some studies have reported amphinomids rafting on marine debris (Donlan & Nelson, 2003; Thiel & Gutow, 2005; Farrapeira, 2011; Borda *et al.*, 2012), although none specifically mentions *H. carunculata*. McIntosh (1885) mentions a large specimen of *H. carunculata* swimming near the water surface.

HERMODICE CARUNCULATA IS TOUGH

Many amphinomid species occur in habitats that are commonly described as 'extreme'. A few examples are *Archinome* species which inhabit hydrothermal vents and seeps (Borda *et al.*, 2013), *Benthoscolex cubanus*, a commensal or parasite in the body cavity of sea urchins (Emson *et al.*, 1993), and *Linopherus canariensis*, a potentially invasive species in a hypersaline lagoon in Sicily (Cosentino & Giacobbe, 2011).

Hermodice carunculata is common in Caribbean coral reefs, including reef crests exposed at low tide, with significant short-term fluctuations in temperature, salinity and dissolved oxygen. During these fluctuations, the metabolic rate, as measured by oxygen consumption, only changes marginally (Sander, 1973; Ferraris, 1981). The species can be abundant in organically enriched areas where microbial activity can lead to oxygen depletion, such as the benthos underneath fish farms (Heilskov *et al.*, 2006; Riera *et al.*, 2014) or coral algae interfaces (Smith *et al.*, 2006). In the Azores, *H. carunculata* has been reported from the shallow-water hydrothermal vents at D. João de Castro Seamount (Cardigos *et al.*, 2005). Remarkably, the worms occur in very close proximity (<1.5 m) to the vents, where fluids with elevated temperatures

of up to 63.3°C, low pH and high sulphide and heavy metal concentrations are released (Cardigos *et al.*, 2005). Shiber (1981) reports that in the heavily polluted Ras Beirut, on the Mediterranean coast of Lebanon, *H. carunculata* appears to be unaffected by blasts from dynamite fishing and will feed on dead or paralysed fish sinking to the seafloor. Among benthic invertebrates in Ras Beirut, *H. carunculata* was the species with the highest concentrations of lead, cadmium, nickel, iron and zinc. *Hermodice carunculata* is also frequently reported from marine and anchialine caves in the Caribbean (Frontana-Uribe & Solís-Weiss, 2011), the Mediterranean (Gerovasileiou *et al.*, 2015; Knittweis *et al.*, 2015) and the Azores (Micael *et al.*, 2006), ranging from the cave entrance to the dark zone.

Like many annelids, amphinomids have the ability to regenerate missing body sections after injury. *Eurythoe complanata* even routinely goes through cycles of asexual reproduction during which the worms fragment into two or more parts and can regenerate both anterior and posterior body sections (Kudenov, 1974). To date, only posterior regeneration has been demonstrated in *H. carunculata* (Ahrens *et al.*, 2014). Posterior fragments without a head can survive and remain active for several weeks in an aquarium setting but no new head formation has been observed (pers. obs.).
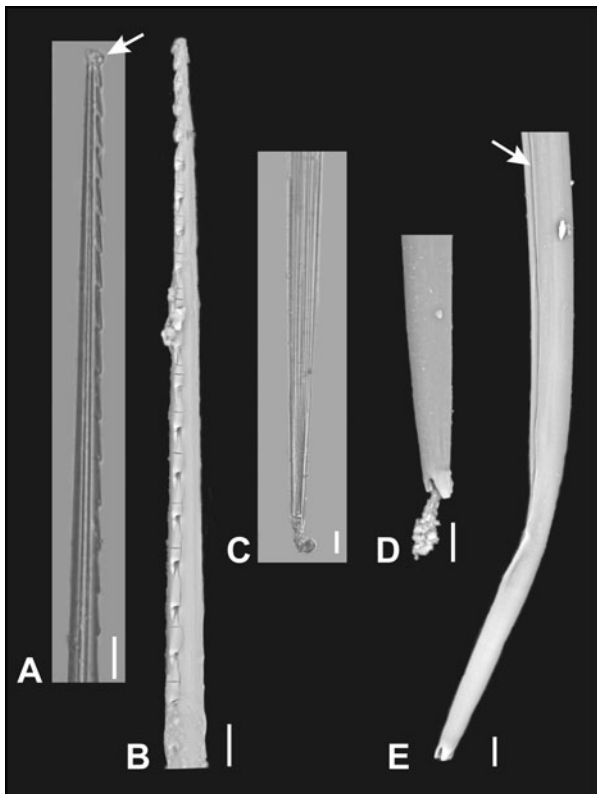
HERMODICE CARUNCULATA IS ARMED

Annelid bristles, or chaetae, are generally chitinous structures. Amphinomid chaetae are unique in that they contain calcium carbonate in addition to chitin (Gustafson, 1930). Each parapodium carries tufts of dorsal notochaetae and ventral neurochaetae. In *Hermodice carunculata*, the notochaetae may be smooth and hair-like or distally serrated 'harpoon chaetae' (Gustafson, 1930; Yáñez-Rivera & Salazar-Vallejo, 2011). Harpoon chaetae may be erected, or even ejected, for defence (Penner, 1970; Halstead, 1971). When touched, they will penetrate human skin and, thanks to the serration, remain stuck in it. The neuropodial tuft probably only contains a single type of chaetae (Gustafson, 1930). The texture of the chaetae may be erodible and may depend on the status of regeneration after they have been shed. Therefore they are not used as diagnostic characters. However, as they play an important role in defence and possible prey capture, chaetal structure and arrangement should be further investigated.

It is still unclear whether the irritation the chaetae cause is merely mechanical or whether they are actually venomous. Although no toxins specifically associated with the chaetae have been identified to date, there are indications that venoms are utilized. Localized reactions in the affected area include an acute, intense stinging pain, itchiness, numbness and swelling (Smith, 2002). These symptoms can last up to several weeks. More notably, however, in rare cases, systemic reactions such as nausea, cardiac and respiratory problems can occur (Ottuso, 2013). The recommended treatment is to remove the bristles with tape, to treat the area with vinegar and to apply hot water (Smith, 2002). The vinegar may dissolve the calcium carbonate in the chaetae. The heat treatment implies that a toxin is involved which can be denatured by heat.

It has long been assumed that toxins are released through a hollow core of amphinomid chaetae (e.g. Nakamura *et al.*,

2008; von Reumont *et al.*, 2014), but some studies have shed doubt on this interpretation. Under light microscopy, the clear core does appear hollow and sometimes a small amount of fluid seems to be released from the tip of the chaeta (Figure 2A). However, histological sections do not reveal any glands near the bases of the chaetae in *H. caruncu-lata* (pers. obs.) or *Eurythoe complanata* (Eckert, 1985). Gustafson (1930) found that the core is actually filled with a clear gelatinous substance consisting of individual fibrils with a hexagonal cross-section. He attributes the toxic nature of the chaetae to this substance. He described that only the outer sheath of the chaetae, including the recurved hooks, when present, are calcareous. In contrast, Tilic *et al.* (2016), based on ultrastructural observations on *Eurythoe complanata*, postulate that the central core is also filled with calcium carbonate, contributing to the brittleness of the chaetae. According to their study, the calcium carbonate is deposited after the large central microvilli of the chaetoblast retract and their canals fuse together. When exposed to acidic conditions (e.g. many fixatives), the calcium carbonate may dissolve and leave a central cavity. In some cases, we have observed pieces of tissue adhering to the base of the chaetae (Figure 2C, D) which we interpret to be the chaetoblasts. Scanning electron micrographs reveal that chaetae may also

Fig. 2. Light micrographs (LM) or scanning electron micrographs (SEM) of chaetal structure in *Hermodice carunculata*. Images were taken of chaetae released after the worms were mechanically irritated with a stream of water from a pipette. (A) LM of chaetal tip, showing the serration, a clear core and the release of a drop at the tip (arrow). (B) SEM of a chaetal tip, showing the serration. (C) LM of base of a chaeta, showing the putative chaetoblast adhering to the insertion point. (D) SEM of base of chaeta with tissue at insertion point. (E) basal portion of a chaeta with a groove (arrow). All scale bars: 10 μm.

be grooved, adding another potential conduit for toxins (Figure 2E).

While it is uncertain which, if any, toxins are associated with amphinomid chaetae, several studies have documented the presence of toxins in whole body extracts. Nakamura *et al.* (2008) isolated complanine, an inflammatory compound, from *Eurythoe complanata*. *Hermodice carunculata* sequesters palytoxin (PTX) from its zoanthid prey, *Palythoa* spp. (Gleibs *et al.*, 1995). PTX maintains its haemolytic activity on human blood when isolated from the worm tissues. Researchers observed *H. carunculata* preying on *Cassiopea* spp., the upside-down jellyfish, in the Bahamas. *Cassiopea* contains numerous toxins, indicating that *H. carunculata* may sequester their toxins from various benthic cnidarians (Radwan *et al.*, 2005; Stoner & Layman, 2015).

As an interesting ethnographic side note, Davis (1983) reports that *H. carunculata* is one of many ingredients in a potent concoction used in Haitian voodoo rituals during which victims are turned into 'zombies'. During the preparation of the poison, the worms are combined with a toad in a closed container, stimulating the toad to increase its own toxin secretions. It is unclear, however, whether *H. caruncu-lata* actually contributes any toxins to the final potion in which tetrodotoxin is probably a key ingredient (Davis, 1983).

Even though *H. carunculata* is powerfully armed with chaetae and toxins, it does have some natural predators. Most notably, it provides a primary source of nutrition for at least three species of cone snails in the Caribbean (Kohn *et al.*, 1972; Vink, 1974; Vink & von Cosel, 1985). Recently Ladd & Shantz (2016) published the first observations of two fish species, the white grunt (*Haemulon plumierii*) and the sand tilefish (*Malacanthus plumieri*) feeding on *H. carun-culata* in Florida. Whitebone porgies (*Calamus leucosteus*) also seem to have an appetite for amphinomids, although the species of amphinomid prey has not been identified (Sedberry, 1989). D. Meyer, pers. comm. in Sebens (1982), noted the predatory anemone *Phyllactis flosculifera* consum-ing *H. carunculata* when the worms were trapped in eddies in sand depressions. Specimens of *H. carunculata* have also been fatally injured by snapping shrimp (*Alpheus armatus*) living as symbionts with the anemone *Bartholomea annulata*. The snapping shrimp thus successfully defend their host ane-mones from fireworm predation (McCammon & Brooks, 2014). In aquarium settings, the coral-banded shrimp (*Stenopus* spp.), the six-lined wrasse (*Pseudocheilinus hexatae-nia*) and cleaner shrimp (*Lysmata* spp.) have been observed preying on bristle worm species. Whether this also occurs in natural settings remains to be determined.

HERMODICE CARUNCULATA IS OMNIVOROUS

Most reports of feeding activity of *H. carunculata* are on live cnidarians, such as hermatypic corals (Ott & Lewis, 1972; Miller & Williams, 2007; Wolf & Nugues, 2013; Miller *et al.*, 2014), gorgonians (Vreeland & Lasker, 1989), fire corals (Whitman, 1988; Lewis & Crooks, 1996), zoanthids (Sebens, 1982; Francini-Filho & Moura, 2010), anemones (Lizama & Blanquet, 1975) and upside-down jellyfish (Stoner & Layman, 2015). Barroso *et al.* (2016) recently reported feeding on several species of sea stars. Due to its relatively slow movements, *H. carunculata* is limited in its feeding

activity to slow moving, sedentary or sessile prey. When feeding on cnidarians, it apparently remains unaffected by their stings or toxins. It feeds by everting its buccal cavity over a portion of its prey and drawing soft tissue into its complex, muscularized pharynx. The digestive tract was described by Marsden (1963) and consists of five regions: (1) the buccal cavity, (2) the pharynx, (3) a short oesophagus, (4) a long intestine and (5) a short rectum which terminates in the anus. Using micro-computed tomography, Faulwetter et al. (2013) demonstrated the presence of a rasping organ in the buccal cavity, which would explain how the worms remove soft tissues from the hard skeleton of corals or gorgonians.

Apart from feeding on a variety of live prey, H. carunculata is also an opportunistic scavenger which will feed on virtually any dead animal or animal parts on the seafloor (pers. obs., Wolf et al., 2014). It actually seems to prefer decaying corals, corals overgrown with algae or dead fish to live cnidarians (Wolf et al., 2014). In captivity, H. carunculata will even devour injured members of its own species (pers. obs.).

In the coral conservation community, H. carunculata has a bad reputation, not only because it feeds on live corals, especially new recruits (Miller & Williams, 2007; Miller et al., 2014), but also because it can act as a vector and reservoir for coral pathogens. This has been demonstrated so far only for the Oculina patagonica/Vibrio shiloi system in the Mediterranean Sea (Sussman et al., 2003) but there is concern that the phenomenon is more widespread.

CONCLUSIONS

We have reviewed the ability of amphinomids in general, and Hermodice carunculata in particular, to withstand environmental extremes, including a wide range of and fluctuations in temperatures, salinities, oxygen levels, heavy metals and other disturbances. Thanks to its arsenal of chaetae and toxins, whether produced endogenously or sequestered from prey, H. carunculata has few natural predators and its own diet is highly flexible.

Hermodice carunculata is clearly an opportunistic species with broad environmental tolerances. One factor that could potentially affect it negatively is ocean acidification, as a diminished pH could interfere with the formation or structural integrity of the calcified chaetae, a key feature for its survival. On the other hand, the occurrence of H. carunculata in very close vicinity to acidic vent sites (Cardigos et al., 2005) suggests that a minor decrease in pH leaves adult H. carunculata relatively unaffected. Larvae generally tend to be more strongly impacted by acidification than adults (Kurihara, 2008; Dupont & Thorndike, 2009; Byrne & Przeslawski, 2013), presenting another reason to investigate the complete life cycle of H. carunculata. In the short term, H. carunculata will probably increasingly become a nuisance species. In particular, it may interfere with coral reef restoration efforts due to its feeding behaviour (Bruckner & Bruckner, 2001; Wolf & Nugues, 2013; Miller et al., 2014). This would be even more troubling if new evidence emerges that it is involved in transmission of other coral pathogens, in addition to the reported Oculina patagonica/Vibrio shiloi system (Sussman et al., 2003).

It is also noteworthy that H. carunculata probably has significant invasive potential, as is the case with other amphinomids (Cosentino & Giacobbe, 2011; Arias et al., 2013). Its genetic homogeneity throughout the Atlantic and its adjacent basins (Ahrens et al., 2013) suggests that it has remarkable capabilities for long-distance dispersal. The existence of a long-lived planktotrophic larva is likely and its potential to colonize new habitats may be increased by anthropogenic vectors such as ships' ballast water. Additionally, juveniles and adults may be transported on ship hulls, natural and anthropogenic marine debris, or 'live rock' in the aquarium trade. 'Live rock' is a common hiding place for amphinomids which can become aquarium pests (Calado et al., 2007). To date, there are no reports of H. carunculata in the Pacific or Indian Oceans, except for the Red Sea. Oddly, it has been referred to as a Lessepsian species which invaded the Eastern Mediterranean through the Suez canal from the Red Sea, not vice versa (Fishelson, 2001). Considering that the Red Sea is the only location not originally connected to the Atlantic Ocean, it does appear that it was introduced there at some point, but whether this happened through the Suez Canal or by other means cannot be confirmed.

Hermodice carunculata is widespread, common and easy to maintain in captivity. It therefore lends itself to experimental studies of physiology, toxicology and behaviour. In the future, it will be important to fill some gaping holes in our understanding of its biology. The most important of these are its reproduction and development and the origin and nature of its toxins. Microbiome studies could additionally shed some light on toxin synthesis as well as their potential to transmit coral and other pathogens. Future studies should also consider the effects of ocean acidification on this calcifying annelid.

REFERENCES

Ahrens J.B., Borda E., Barroso R., Paiva P.C., Campbell A.M., Wolf A., Nugues M.M., Rouse G.W. and Schulze A. (2013) The curious case of *Hermodice carunculata* (Annelida: Amphinomidae): evidence for genetic homogeneity throughout the Atlantic Ocean and adjacent basins. *Molecular Ecology* 22, 2280–2291.

Ahrens J.B., Kudenov J.D., Marshall C.D. and Schulze A. (2014) Regeneration of posterior segments and terminal structures in the bearded fireworm, *Hermodice carunculata* (Annelida: Amphinomidae). *Journal of Morphology* 275, 1103–1112.

Arias A., Barroso R., Anadón N. and Paiva P.C. (2013) On the occurrence of the fireworm *Eurythoe complanata* complex (Annelida, Amphinomidae) in the Mediterranean Sea with an updated revision of the alien Mediterranean amphinomids. *ZooKeys* 337, 19–33.

Barroso R., Almeida D., Contins M., Filgueiras D. and Dias R. (2016) *Hermodice carunculata* (Pallas, 1766) (Polychaeta: Amphinomidae) preying on starfishes. *Marine Biodiversity* 46, 333–334.

Bhaud M. (1972) Identification des larves d'Amphinomidae (annélides polychètes) recueillies près de Nosy-Bé (Madagascar) et problèmes biologiques connexes. *Cahiers ORSTOM. Série Océanographie* 10, 203–216.

Borda E., Kudenov J.D., Bienhold C. and Rouse G.W. (2012) Towards a revised Amphinomidae (Annelida, Amphinomida): description and affinities of a new genus and species from the Nile Deep-sea Fan, Mediterranean Sea. *Zoologica Scripta* 41, 307–325.

Borda E., Kudenov J.D., Chevaldonne P., Blake J.A., Desbruyeres D., Fabri M.C., Hourdez S., Pleijel F., Shank T.M., Wilson N.G., Schulze A. and Rouse G.W. (2013) Cryptic species of *Archinome* (Annelida: Amphinomida) from vents and seeps. *Proceedings of the Royal Society of London Series B* 280, 20131876.

Bruckner A. and Bruckner R. (2001) Condition of restored *Acropora palmata* fragments off Mona Island, Puerto Rico, 2 years after the Fortuna Reefer ship grounding. *Coral Reefs* 20, 235–243.

Byrne M. and Przeslawski R. (2013) Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology* 53, 582–596.

Calado R., Vitorino A., Dionísio G. and Dinis M.T. (2007) A recirculated maturation system for marine ornamental decapods. *Aquaculture* 263, 68–74.

Cardigos F., Colaço A., Dando P.R., Ávila S.P., Sarradin P.M., Tempera F., Conceição P., Pascoal A. and Serrão Santos R. (2005) Shallow water hydrothermal vent field fluids and communities of the D. João de Castro Seamount (Azores). *Chemical Geology* 224, 153–168.

Cosentino A. and Giacobbe S. (2011) The new potential invader *Linopherus canariensis* (Polychaeta: Amphinomidae) in a Mediterranean coastal lake: colonization dynamics and morphological remarks. *Marine Pollution Bulletin* 62, 236–245.

Davis E.W. (1983) Preparation of the Haitian zombi poison. *Botanical Museum Leaflets* 29, 139–149.

De'ath G., Fabricius K.E., Sweatman H. and Puotinen M. (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences USA* 109, 17995–17999.

Descombes P., Wisz M.S., Leprieur F., Parravicini V., Heine C., Olsen S.M., Swingedouw D., Kulbicki M., Mouillot D. and Pellissier L. (2015) Forecasted coral reef decline in marine biodiversity hotspots under climate change. *Global Change Biology* 21, 2479–2487.

Donlan C.J. and Nelson P.A. (2003) Observations of invertebrate colonized flotsam in the eastern tropical Pacific, with a discussion of rafting. *Bulletin of Marine Science* 72, 231–240.

Dupont S. and Thorndike M.C. (2009) Impact of CO_2-driven ocean acidification on invertebrates early life-history – What we know, what we need to know and what we can do. *Biogeosciences Discussions* 6, 3109–3131.

Eckert G.J. (1985) Absence of toxin-producing parapodial glands in amphinomid polychaetes (fireworms). *Toxicon* 23, 350–353.

Ehlers E. (1887) Reports on the results of dredging under the direction of L. F. Pourtalès during the years 1868–1870 and of Alexander Agassiz, in the Gulf of Mexico (1877–1978) and in the Caribbean Sea (1878–1879), in the US Coast Survey Steamer "Blake", Lieut.-Com. C. D. Sigsbee, U. S. N., and Commander J. R. Barlett, U. S. N., commanding. XXXI. Report on the Annelids. *Memoirs of the Museum of Comparative Zoology* Volume XV, 1–335.

Emson R.H., Young C.M. and Paterson G.L.J. (1993) A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea-urchin *Archeopneustes hystrix* (A. Agassiz, 1880). *Journal of Natural History* 27, 1013–1028.

Farrapeira C.M.R. (2011) Invertebrados macrobentônicos detectados na costa brasileira transportados por resíduos flutuantes sólidos abiogênicos. *Associacao Portuguesa dos Recursos Hidricos* 11, 85–96.

Faulwetter S., Vasileiadou A., Kouratoras M., Dailianis T. and Arvanitidis C. (2013) Micro-computed tomography: introducing new dimensions to taxonomy. *ZooKeys* 263, 1–45.

Fauvel P. (1923) *Polychètes errantes.* Faune de France Volume 5. Paris: Paul Lechevalier.

Ferraris J.D. (1981) Oxygen uptake with acute variation in temperature and salinity in two coral reef polychaetes. *Marine Ecology* 2, 159–168.

Fishelson L. (2001) Community structure and fish and invertebrate biodiversity in marine ecosystems: the consequences of our actions. *Boletim do Museu Municipal do Funchal* 6, 331–348.

Francini-Filho R.B. and Moura R.L.d. (2010) Predation on the toxic zoanthid *Palythoa caribaeorum* by reef fishes in the Abrolhos Bank, eastern Brazil. *Brazilian Journal of Oceanography* 58, 77–79.

Frontana-Uribe S.C. and Solís-Weiss V. (2011) First records of polychaetous annelids from Cenote Aerolito (sinkhole and anchialine cave) in Cozumel Island, Mexico. *Journal of Cave and Karst Studies* 73, 1–10.

Gerovasileiou V., Chintiroglou C., Vafidis D., Koutsoubas D., Sini M., Dailianis T., Issaris Y., Akritopoulou E., Dimarchopoulou D. and Voutsiadou E. (2015) Census of biodiversity in marine caves of the eastern Mediterranean Sea. *Mediterranean Marine Science* 16, 245–265.

Gleibs S., Mebs D. and Werding B. (1995) Studies on the origin and distribution of palytoxin in a Caribbean coral reef. *Toxicon* 33, 1531–1537.

Gustafson G. (1930) Anatomische studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. *Zoologiska Bidrag, Uppsala* 12, 301–471.

Halstead B.W. (1971) Venomous echinoderms and annelids: starfishes, sea urchins, sea cucumbers, and segmented worms. In Bücherl W. and Buckley E.E. (eds) *Venomous animals and their venoms.* Waltham, MA: Academic Press, pp. 419–441.

Heilskov A.C., Alperin M. and Holmer M. (2006) Benthic fauna bio-irrigation effects on nutrient regeneration in fish farm sediments. *Journal of Experimental Marine Biology and Ecology* 339, 204–225.

Knittweis L., Chevaldonné P., Ereskovsky A., Schembri P.A. and Borg J.A. (2015) A preliminary survey of marine cave habitats in the Maltese Islands. *Xjenza Online – Journal of the Malta Chamber of Scientists* 3, 153–164.

Kohn A.J., Nybakken J.W. and Van Mol J.-J. (1972) Radula tooth structure of the gastropod *Conus imperialis* elucidated by scanning electron microscopy. *Science* 176, 49.

Kroeker K.J., Kordas R.L., Crim R., Hendriks I.E., Ramajo L., Singh G.S., Duarte C.M. and Gattuso J.-P. (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* 19, 1884–1896.

Kroeker K.J., Kordas R.L., Crim R.N. and Singh G.G. (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* 13, 1419–1434.

Kudenov J.D. (1974) *The reproductive biology of* Eurythoe complanata *(Pallas, 1766), (Polychaeta: Amphinomidae).* Dissertation, University of Arizona, Tucson, USA.

Kurihara H. (2008) Effects of CO2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373, 275–284.

Ladd M.C. and Shantz A.A. (2016) Novel enemies – previously unknown predators of the bearded fireworm. *Frontiers in Ecology and the Environment* 14, 342–343.

Lewis J. and Crooks R. (1996) Foraging cycles of the amphinomid polychaete *Hermodice carunculata* preying on the calcareous hydrozoan *Millepora complanata. Bulletin of Marine Science* 58, 853–856.

Lizama J. and Blanquet R.S. (1975) Predation on sea anemones by the amphinomid polychaete, *Hermodice carunculata. Bulletin of Marine Science* 25, 442–443.

Marsden J.R. (1963) The digestive tract of *Hermodice carunculata* (Pallas). Polychaeta: Amphinomidae. *Canadian Journal of Zoology* 41, 165–184.

McCammon A.M. and Brooks W.R. (2014) Protection of host anemones by snapping shrimp: a case for symbiotic mutualism? *Symbiosis* 63, 71–78.

McIntosh W.C. (1885) Report on the Annelida Polychaeta collected by the H.M.S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of the H.M.S. Challenger during the years 1873–1876 under the command of the Captain George S. Nares, R. N., F. R. S. and the Late Captain Fran Tourle Thomson, R. N., Challenger Report, Volume 12, 1–554.

Micael J., Azevedo J.M.N. and Costa A.C. (2006) Biological characterisation of a subtidal tunnel in São Miguel island (Azores). *Biodiversity and Conservation* 15, 3675–3684.

Miller M.W., Lohr K.E., Cameron C.M., Williams D.E. and Peters E.C. (2014) Disease dynamics and potential mitigation among restored and wild staghorn coral, *Acropora cervicornis. PeerJ* 2, e541.

Miller M.W. and Williams D.E. (2007) Coral disease outbreak at Navassa, a remote Caribbean island. *Coral Reefs* 26, 97–101.

Nakamura K., Tachikawa Y., Kitamura M., Ohno O., Suganuma M. and Uemura D. (2008) Complanine, an inflammation-inducing substance isolated from the marine fireworm *Eurythoe complanata. Organic and Biomolecular Chemistry* 6, 2058–2060.

Ott B. and Lewis J.B. (1972) The importance of the gastropod *Coralliophila abbreviata* (Lamarck) and the polychaete *Hermodice carunculata* (Pallas) as coral reef predators. *Canadian Journal of Zoology* 50, 1651–1656.

Ottuso P. (2013) Aquatic dermatology: encounters with the denizens of the deep (and not so deep) a review. Part I: the invertebrates. *International Journal of Dermatology* 52, 136–152.

Pandolfi J.M., Connolly S.R., Marshall D.J. and Cohen A.L. (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418.

Penner L.R. (1970) Bristleworm stinging in a natural environment. *University of Connecticut Occasional Papers (Biological Sciences Series)* 1, 275–280.

Radwan F.F.Y., Román L.G., Baksi K. and Burnett J.W. (2005) Toxicity and mAChRs binding activity of *Cassiopea xamachana* venom from Puerto Rican coasts. *Toxicon* 45, 107–112.

Riera R., Pérez O., Rodríguez M., Ramos E. and Monterroso Ó. (2014) Are assemblages of the fireworm *Hermodice carunculata* enhanced in sediments beneath offshore fish cages? *Acta Oceanologica Sinica* 33, 108–111.

Sander F. (1973) A comparative study of respiration in two tropical marine polychaetes. *Comparative Biochemistry and Physiology Part A: Physiology* 46, 311–323.

Sebens K.P. (1982) Intertidal distribution of zoanthids on the Caribbean coast of Panama: effects of predation and desiccation. *Bulletin of Marine Science* 32, 316–335.

Sedberry J.R. (1989) Feeding habits of whitebone porgy, *Calamus leucosteus* (Teleostei: Sparidae), associated with hard bottom reefs off the southeastern United States. *Fishery Bulletin* 87, 935–944.

Shiber J.G. (1981) Metal concentrations in certain coastal organisms from Beirut. *Hydrobiologia* 83, 181–195.

Smith J.E., Shaw M., Edwards R.A., Obura D., Pantos O., Sala E., Sandin S.A., Smriga S., Hatay M. and Rohwer F.L. (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters* 9, 835–845.

Smith M.L. (2002) Cutaneous problems related to coastal and marine worms. *Dermatologic Therapy* 15, 34–37.

Stoner E.W. and Layman C.A. (2015) Bristle worms attack: benthic jellyfish are not trophic dead ends. *Frontiers in Ecology and the Environment* 13, 226–227.

Sussman M., Loya Y., Fine M. and Rosenberg E. (2003) The marine fireworm *Hermodice carunculata* is a winter reservoir and spring-summer vector for the coral-bleaching pathogen *Vibrio shiloi. Environmental Microbiology* 5, 250–255.

Thiel M. and Gutow L. (2005) The ecology of rafting in the marine environmnet. I. The floating substrata. *Oceanography and Marine Biology: An Annual Review* 42, 181–264.

Tilic E., Pauli B. and Bartolomaeus T. (2016) Chaetal arrangement of the fireworm *Eurythoe complanata* (Pallas, 1766) (Amphinomida). 12th International Polychaete Conference (poster and abstract).

Vink D.L.N. (1974) A strange food preference of *Conus aurantius. Hawaiian Shell News* 12, 8.

Vink D.L.N. and von Cosel R. (1985) The *Conus cedonulli* complex: historical review, taxonomy and biological observations. *Revue Suisse de Zoologie* 92, 525–603.

von Reumont B.M., Campbell L.I., Richter S., Hering L., Sykes D., Hetmank J., Jenner R.A. and Bleidorn C. (2014) A polychaete's powerful punch: venom gland transcriptomics of *Glycera* reveals a complex cocktail of toxin homologs. *Genome Biology and Evolution* 6, 2406–2423.

Vreeland H.V. and Lasker H.R. (1989) Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. *Journal of Experimental Marine Biology and Ecology* 129, 265–277.

Whitman J.D. (1988) Effects of predation by the fireworm *Hermodice carunculata* on milleporid hydrocorals. *Bulletin of Marine Science* 42, 446–458.

Wolf A.T. and Nugues M.M. (2013) Predation on coral settlers by the corallivorous fireworm *Hermodice carunculata. Coral Reefs* 32, 227–231.

Wolf A.T., Nugues M.M. and Wild C. (2014) Distribution, food preference, and trophic position of the corallivorous fireworm *Hermodice carunculata* in a Caribbean coral reef. *Coral Reefs* 33, 1153–1163.

Yáñez-Rivera B. and Brown J. (2015) Fireworms (Amphinomidae: Annelida) from Ascension and Saint Helena Island, Central South Atlantic Ocean. *Marine Biodiversity Records* 8, e149.

and

Yáñez-Rivera B. and Salazar-Vallejo S.I. (2011) Revision of *Hermodice* Kinberg, 1857 (Polychaeta: Amphinomidae). *Scientia Marina* 75, 251–262.

Correspondence should be addressed to:
A. Schulze
Department of Marine Biology, Texas A&M University – Galveston Campus, 200 Seawolf Parkway, Galveston, TX 77553, USA
email: schulzea@tamug.edu