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Ecology, distribution and expansion of a Mediterranean native invader, the fireworm *Hermodice carunculata* (Annelida)

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Abstract

Global change and the overall rise in seawater temperature are causing a poleward shift in species distribution, increasing the occurrence of warm-water biota in many ecosystems worldwide. In the Mediterranean, the ongoing sea warming is promoting native subtropical species to invader status. The bearded fireworm *Hermodice carunculata* (Amphinomida) is a thermophilic generalist predator spreading in the Central Mediterranean Sea. Although it is a typical inhabitant of Ionian coasts, several sightings have occurred at more northerly localities along the Tyrrhenian and Adriatic Seas, suggesting that density increases and range expansion are underway. These distributional records are in contrast with historical literature and museum collections, which provide poor sporadic information.

The present study aimed at investigating the spatiotemporal changes that have occurred in *H. carunculata* abundances and distribution in the Mediterranean basins surrounding the Italian peninsula so far. We examined an exhaustive collection of existing information. A total of 857 reports of *H. carunculata* were collected from 368 localities. These data significantly expand knowledge on the life and feeding habits of *H. carunculata*. The integration of different data sources allowed the reconstruction of the shifts that have happened over the last 50 years, which are coherent with the consistent warming trend of Mediterranean Sea surface temperatures. Recent colonization events have occurred both along the Adriatic and Western Mediterranean coasts. The present findings provide unique insights into the expansion of *H. carunculata*, supporting future spreading throughout the Northern and Western Mediterranean. Tracking these changes is critical to assess potential impacts on coastal rocky-benthic communities, public health and commercial fisheries.

Keywords: Biogeography; Geographical distribution; Global warming; Data collection; Colonization; Amphinomida; Mediterranean Sea.

Introduction

Ongoing global changes are strongly affecting the Earth's biodiversity, causing marked alterations on several abiotic factors (Lovejoy & Hannah, 2019; Sampaio & Rosa, 2020). Climate-driven variations in environmental conditions have been reshaping the distribution of biota and threatening ecosystems and the services associated with them (Sunday *et al.*, 2012; Marzloff *et al.*, 2016; Pecl *et al.*, 2017). In the Mediterranean, seawater warming is prompting the range expansion of native species with sub-tropical affinities from the southern and eastern sub-basins towards the northern and western ones (Lejeune *et al.*, 2010; Marbà *et al.*, 2015; Bianchi *et al.*, 2018). Even though investigations of population expansions typically involve invasive alien species, considerable effects on recipient ecosystems may be owed to species that become invasive in their own native range,

which are then termed “native invaders” (Carey *et al.*, 2012; Cunningham *et al.*, 2016).

Demographic increases in native invader species often have critical repercussions on the trophic webs and the structure and function of communities (Carey *et al.*, 2012). However, the analysis of these threats requires both knowledge of population dynamics, diet and feeding behavior, and presence records, in order to compare the current distribution with historical patterns (Carey *et al.*, 2012). Unfortunately, these data are often lacking, especially for marine species. Among the marine invertebrates that will probably benefit from temperature increase is the amphinomid annelid *Hermodice carunculata* (Amphinomidae), commonly known as the “bearded fireworm” (Schulze *et al.*, 2017; Encarnação *et al.*, 2019). The native range of this amphiatlantic species includes the Caribbean and the Gulf of Mexico, the Mediterranean Sea and the Red Sea. Atlantic specimens are well known for their

corallivorous feeding behaviour, upon zoanths, anemones, gorgonians, hydrocorals and scleractinians (Schulze *et al.*, 2017; see references Simonini *et al.*, 2018). On the other hand, there are relatively few studies on the biology and distribution of *H. carunculata* colonizing the Italian coasts and the study of Mediterranean populations and their potential impacts on benthic communities has just started. A first expanding population able to prey on a sea urchin keystone species has been detected in Apulia (Simonini *et al.*, 2017; Righi *et al.*, 2019). In the lab, Mediterranean *H. carunculata* specimens turned out to be generalist predators of several benthic invertebrates, displaying powerful defensive capacities to ensure predator escape and opportunistic feeding habits (for an extensive list of prey organisms see Simonini *et al.*, 2018). Besides the ecological threats to benthic fauna, increases in abundance of this species may pose economic and health risks: *H. carunculata* consumes fish stuck in nets (Celona & Comparetto, 2010; EastMed, 2010), and its calcareous dorsal chaetae cause intense pain, inflammation and edema when they touch human skin (Schulze *et al.*, 2017; Encarnação *et al.*, 2019).

Despite the potential impacts of the bearded fireworm, its present and historical geographical occurrence are poorly understood. A preliminary investigation into the historical reports and the Mediterranean specimens conserved in the collections of the main Italian and European museums (Simonini *et al.*, 2019) suggested that *H. carunculata* has been present in the Levantine Sea, the Aegean area and eastern coast of Sicily since the first half of the 19th century (Brullé, 1832; Baird, 1870; Grube, 1837; Kinberg, 1857), and in the Dalmatian islands near Split and the Ionian Islands since the 1890s (Marenzeller, 1904). Accordingly, the checklists of polychaete fauna currently report that *H. carunculata* is present along Italian (Castelli *et al.*, 2008), Croatian (Mikac, 2015), Greek (Faulwetter *et al.*, 2017), Cyprian (Çinar, 2005) and Turkish (Çinar *et al.*, 2014) coasts. Focusing on the Central Mediterranean (i.e. the basins surrounding the Italian peninsula), museum collections and scientific literature provide information to reconstruct the fireworm's first colonization of this area up to the late 20th century (Simonini *et al.*, 2019). The most ancient records were dated back to 1835 in Sicily (Grube, 1837). Two specimens stored in the Museo della Stazione Zoologica "Anton Dohrn" (SZN Naples) were collected at the end of the 19th century in the Gulf of Naples but they remain the only records of the presence of *H. carunculata* in the area, although it has been intensively investigated since the 1820s (cf. Panceri, 1875; Gambi *et al.*, 2003; Maria Cristina Gambi, personal communication). At the beginning of the 20th century, the *H. carunculata* northern distribution limit in the Adriatic Sea was the Vis Archipelago in Croatia (Simonini *et al.*, 2019). The first sightings in the Italian peninsula are from the Ionian coasts of Calabria (late 1960s; Rullier & Amoureux, 1968). During the same period, the oceanographic cruises of the Calypso in the Mediterranean (1950s-1960s) found that the western limit of this species was in the Strait of Sicily (Rullier & Amoureux, 1968). More recent records have been col-

lected from Apulia (early 1980s; Simonini *et al.*, 2019), the Strait of Messina (Mistri & Ceccherelli, 1994), and the Strait of Sicily (Celona & Comparetto, 2010; Ahrens *et al.*, 2013).

Interestingly, this species has never been included in the list of marine annelids from continental Spain (Parapar *et al.*, 2012) but it has recently been recorded in the Southern Iberian Peninsula (Coma *et al.*, 2011), and was considered an example of poleward-distribution range expansion of a subtropical/tropical species (Encarnação *et al.*, 2019). Indeed, *H. carunculata* appears to have a large-scale dispersal pelagic larva. The duration of the planktonic stage could enable the larvae to stay in the water column for long periods of time, which may account for its high potential for dispersal, should favourable environmental conditions occur (Kudenov, 1974; Schulze *et al.*, 2017; Encarnação *et al.*, 2019; Toso *et al.*, 2020).

The lack of records in the scientific literature is in sharp contrast with the online popularity of the bearded fireworm. This showy charismatic species has frequently been photographed and "posted" on blogs and social media by marine biologists, divers and fishermen, thanks to its large size, colorful body and stinging capacity (see for instance Simonini *et al.*, 2017).

The collection of a high number of quality records is critical to investigate the current distribution and range expansion for a species in a region of interest (Ball-Damerow *et al.*, 2019). In this study, we provide a reconstruction of the past and present distribution of *H. carunculata* through an exhaustive collection of existing information on its life and feeding habits. All the data available in the scientific literature were retrieved, in addition to bibliographic searches of "grey literature" and the collection of information shared by divers and bathers through social networks, websites and personal communication. Besides, an online questionnaire was distributed to sea users, in order to rapidly assess the current fireworm distribution and improve knowledge of the substantial contribution of citizen science to data collection for scientific monitoring. Our aim was to elucidate the range expansion of *H. carunculata* and provide a first assessment of its potential as a native invader species in the Central Mediterranean basins surrounding Italy. This information is a critical requirement for any assessment of its potential repercussions for the structure and functioning of Mediterranean rocky reef ecosystems and potential public health risk especially in regions that are popular for tourism.

Materials and Methods

Selection, collection and elaboration of the reports

The research area is focused on the Mediterranean basins surrounding the Italian peninsula to include the largest latitudinal gradient in the Mediterranean and its northernmost limit.

Four main data sources were considered: "Scientific literature" provided by scientific journals and books, grey literature (i.e. information unavailable in commer-

cially published literature, such as papers from scientific journals of national interest, dissertations, technical reports, conference abstracts etc.) and personal communication by marine biologists; “Social networks” including the social media iNaturalist, YouTube, Flickr, Instagram and Facebook; “Online and other public sources” (hereafter “Online sources”) including magazines, newspapers, newsletters, internet forums, biodiversity databases (Global Biodiversity Information Facility - GBIF, 2020), and personal webpages of fishermen and divers; “Questionnaire” for reports from a survey we shared (see the paragraph “2.2 Questionnaire survey”). The records were cross-checked against all four data sources (e.g. scientific literature and social networks) and within each source (e.g. Facebook and Instagram) to avoid duplication.

The main search engines used were Web of Science, Scopus, Google, Google Scholar and the internal search engine of social media. Searches were carried out until December 2019, using the common names of the species in the areas where it is present (see Horton *et al.*, 2020 for the list of the countries). In particular, in addition to “*Hermodice*” and “*Hermodice carunculata*”, we looked for the keywords “vermocane” and “verme di fuoco” (Italian), “fireworm” and “bearded fireworm” (English), “Feuerwurm” and “Bart-Feuerborstenwurm” (German), “ognjeni crv” (Slovenian), “vatreni crv” and “lavljji crv” (Croatian). Whenever possible, an additional word was added to address the area of interest in the different languages (e.g. “Mediterranean”, “Adriatic”, “Tremiti”). Records provided by non-experts (e.g. from social media) were considered trustworthy only when supported with photos.

Only records with temporal and spatial references were considered informative and included in the study. In particular, at least the year and locality of the collection or sighting were considered mandatory. We use the attribute “locality” to designate any toponym of limited size (small island, promontory, cave, bay, beach or town). Time intervals and/or geographic references referring to undefined times and large areas (e.g. “before 1990”, “Sicily”) were not included. When the geographic coordinates were not specified in the record, they were derived using Google Maps.

A data set using all the information collected was created and is reported in Supplementary Table S1. All the relevant reports were recorded along with the references, investigation tool and all the available biological features. In particular, the reports were classified according to season, considering Summer (July-September), Autumn (October-December), Winter (January-March) and Spring (April-June) (Prevedelli *et al.*, 2005); substrates, grouped into rocky (including barren, infralittoral algae, caves and coralligenous assemblages; Pérès & Picard, 1964; Bellan-Santini *et al.*, 1994), sediments (sand and gravel), wreck and seagrass bed (*Posidonia oceanica* meadows); depth (beached, 0-2 m, 2-20 m, > 20 m). The records at a depth of 0-2 m and the images taken from above the sea surface were considered occasions for potential interactions between fireworms and humans.

When photos were provided, any relevant informa-

tion (i.e. habitat, feeding behaviour and size) was directly derived from the images. If fireworms were recorded eating, the prey was identified to the lowest taxonomic group possible and then assigned to a major group (e.g. sea anemone, sea urchin). Cases of fireworms feeding on dead fish or bait were also numbered. Finally, if the images had high resolution and included the whole animal, the number of chaetigers was counted to estimate fireworm body length using the morphometric relationship $y = 0.0073x^{1.7412}$ (Righi *et al.*, 2019). Then, the fireworms were classified as small (< 10 cm), medium (10-20 cm) or large (> 20 cm).

Seasonal and habitat preferences, size and prey item consumption frequency and the distribution of reports among the time intervals were compared among datasets by means of the Chi-square test (χ^2) using the statistic software Past (Hammer *et al.*, 2001). When expected counts were less than 5, data were combined from similar categories. When appropriate, the tests were also performed to compare the distribution of counts among the categories cited above in the Eastern and Western basins (see section 2.3).

Questionnaire survey

User-friendly online questionnaires were distributed to volunteer recreational divers, diving centers, members of the Italian Society of Marine Biology (SIBM) and to all the Marine Protected Areas (MPA), Marine Research Centers and the Regional Agencies for Environmental Protection along the Italian coasts. The questionnaires were distributed by email in Autumn 2018 and Summer 2019, during the optimal time for scuba diving and snorkeling to attract greater attention to the survey. The message contained a short and clear explanation of the research project and the web link to the questionnaire. A “Google Form” survey method was chosen to ensure easy distribution, accessibility and compilation even by means of tablets and smartphones.

Each questionnaire started with an initial section providing a leaflet with a description of the basic ecology of fireworms and an explanation of the research aim and images of the main distinctive features of *H. carunculata*. The second section aimed at obtaining technical information on *H. carunculata* encounters (dive place, date, depth, substrate, size range of the worms); a third concerning fireworm abundance, increase in and perception of potential ecological impact or dangerous interactions with humans. None of the questions were made compulsory and the survey could be sent even if some answers were skipped. Whenever possible, multiple answers were permitted. Answers on date, depth, size range and substrate of the reports were classified as described by scientific literature, social networks and online sources. Based on our experience and interviews, people struggle to remember the precise year of the first sighting and the passing of time increases uncertainty. Thus, the dates of the sightings were grouped into three-time intervals with different widths: before 2008 (over 10 years ago), 2009-

2014 (from 5 to 10 years ago) and 2015-2019 (during the last five years).

To test for the accuracy of *H. carunculata* presence and absence, the data collected were verified *a posteriori* using interviews (with completion of the questionnaires) or by email with representative sea users (diving centers, marine biologists, personnel of Italian MPA and researchers). The information provided in this way was included in the data source “scientific literature”. Respondents were selected based on: i) past or current interest in citizen science initiatives, as indicated by Internet searches, ii) geographical location (places closest to the current limits of fireworm distribution or where fireworms had never been seen before were carefully checked).

Distribution and areal expansion of *H. carunculata*

Based on the geographical coordinates, the records collected were attributed to one of the Mediterranean sub-basins defined by the International Hydrographic Organization (IHO 1953), to one of the nine biogeographic sectors (BS) recognized by the SIBM (Relini, 2008; Bianchi, 2007) and to an ecoregion (Spalding *et al.*, 2007).

In particular the BSs considered in this study were: BS1, Ligurian Sea; BS2, Northern Tyrrhenian Sea and Sardinia Sea; BS3, Southern Tyrrhenian Sea and Strait of Sicily; BS5, South-east of Sicily and Pelagie Islands; BS6, Ionian Sea; BS7, Southern Adriatic Sea; BS8, Central Adriatic Sea; BS9, Northern Adriatic Sea (Fig. 1). The groups BS1-3 and BS5-9 belong to the Western and Eastern Mediterranean Sea basins, respectively (Relini, 2008; Bianchi, 2007). Although BS4 (the Strait of Messina) has been considered as a stand-alone BS due to the presence of Pliocene Atlantic remnants and local endemic species, in the present study we did not consider it as a separate sector. Our study was focused on a single widespread species and BS4 is extremely small, thus we attributed the northern coasts of Capo Peloro (Sicily) and Capo Paci (Calabria) to BS3 and their southern coasts to BS6, in accordance with the IHO criteria (1953) (Fig. 1).

Considering the ecoregions, BS7, BS8 and BS9 belong to the Adriatic Sea ecoregion, while the northern part of BS5 and the southern part of BS3 are included in the Ionian ecoregion; BS1, BS2 and BS3 belong to the Western Mediterranean ecoregion (Spalding *et al.*, 2007) (Fig. 1).

In order to follow the temporal expansion and update

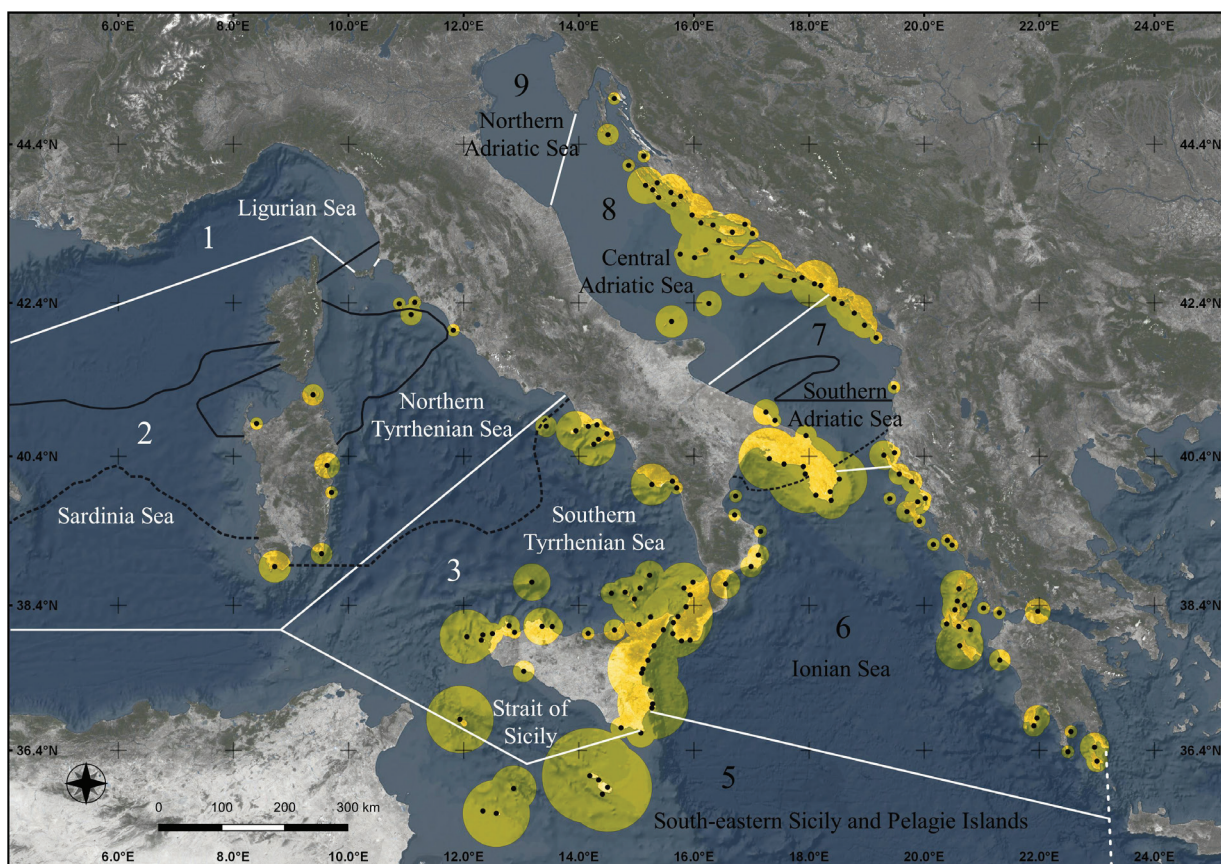


Fig. 1: Overall dataset of localities where *H. carunculata* specimens were reported in Mediterranean sub-basins surrounding the Italian coasts. Numbers refer to the biogeographic sectors (BS) and the dotted white line represents the southern limit of the Ionian Sea ecoregion (see text for further details). Western and Eastern Mediterranean basins and biogeographic sectors are shown in white and black, respectively. The northward shift of the 14°C isotherm of February is highlighted by black lines (broken lines are the one-century climatological means, solid lines the means for 1985–2006; Coll *et al.*, 2010). Circle size corresponds to number of observations and larger circles represent more observations (from the smallest observation number [n=1] to the greatest one [n=51]).

the present distribution of *H. carunculata*, point data were imported to QGIS 3.4 Madeira and geographically represented as report occurrences. To investigate potential shifts in fireworm distribution, a list of “first reports” was obtained. They were defined as the oldest locations separated by 10 km or more from the others where fireworms were recorded. They were obtained by ordering the reports by year, latitude and longitude. Then, starting from the oldest, each first report was identified by drawing a circular area with a radius of about 10 km centered in its geographical position. We assumed that *H. carunculata* had been present in the whole area since the year of the first report considered. Thus, later reports falling in the same circle were removed from the list. When multiple reports from the same site were found, the year of the first report was considered. Given the temporal distribution of the records, four time intervals were identified as references: before 1967, 1967-2008, 2009-2014 and 2015-2019. The first period included the reports collected from 1835 (first record from the Central Mediterranean; Grube, 1837) to 1966 (Rullier’s last large scale survey

along the coasts of Apulia and Calabria; Rullier & Amoureu, 1968), while the others were defined based on the time intervals categorized in the questionnaires (*i.e.* 1967-2008, 2009-2014 and 2015-2019).

Differences in the latitude of fireworm reports among periods were assessed with the non-parametric Kruskal-Wallis test, followed by pairwise Mann-Whitney tests if significant ($p < 0.05$). The procedure was repeated separately for Eastern (BS5-9, four periods) and Western (BS1-3, three periods) basins.

Results

Data sources

A total of 857 reports of *H. carunculata* were collected (Table S1). Most of the reports were derived from social networks (36.4%) and online sources (28.2%), while relatively little scientific information was available (12.8%) (Table 1). Other reliable data was obtained from

Table 1. Biological features of *H. carunculata* extrapolated from each data source (online sources, scientific literature, social networks and questionnaire). Percentage values of the biological features are reported by source (column-wise, underlined) and by the total of the counts for each category (row-wise, italic).

	Online sources		Scientific literature		Social networks		Questionnaire		Total					
	n	%	n	%	n	%	n	%	n	%				
Prey consumed														
< 1967	1	<u>0.4</u>	4.5	21	<u>19.1</u>	95.5	0	<u>0.0</u>	0.0	0	<u>0.0</u>	0.0	22	<u>2.6</u>
1967-2008	59	<u>24.4</u>	38.6	31	<u>28.2</u>	20.3	5	<u>1.6</u>	3.3	58	<u>30.1</u>	37.9	153	<u>17.9</u>
2009-2014	78	<u>41.9</u>	41.9	27	<u>24.5</u>	14.5	42	<u>13.5</u>	22.6	39	<u>20.2</u>	21.0	186	<u>21.7</u>
2015-2019	104	<u>43.0</u>	21.0	31	<u>28.2</u>	6.3	265	<u>84.9</u>	53.4	96	<u>49.7</u>	19.4	496	<u>57.9</u>
Sum	242		28.2	110		12.8	312		36.4	193		22.5	857	
Season														
Spring	37	<u>18.4</u>	24.8	21	<u>29.2</u>	14.1	57	<u>18.5</u>	38.3	34	<u>26.4</u>	22.8	149	<u>21.0</u>
Summer	129	<u>64.2</u>	30.9	39	<u>54.2</u>	9.4	172	<u>55.8</u>	41.2	77	<u>59.7</u>	18.5	417	<u>58.7</u>
Autumn	31	<u>15.4</u>	25.2	10	<u>13.9</u>	8.1	64	<u>20.8</u>	52.0	18	<u>14.0</u>	14.6	123	<u>17.3</u>
Winter	4	<u>2.0</u>	19.0	2	<u>2.8</u>	9.5	15	<u>4.9</u>	71.4	0	<u>0.0</u>	0.0	21	<u>3.0</u>
Sum	201		30.0	72		10.7	308		46.0	129		13.3	710	
Substrate														
Rocky	156	<u>82.1</u>	27.0	66	<u>84.6</u>	11.4	266	<u>92.7</u>	46.1	89	<u>69.5</u>	15.4	577	<u>84.5</u>
Sediment	20	<u>10.5</u>	33.3	5	<u>6.4</u>	8.3	14	<u>4.9</u>	23.3	21	<u>16.4</u>	35.0	60	<u>8.8</u>
Seagrass bed	4	<u>2.1</u>	13.3	6	<u>7.7</u>	20.0	2	<u>0.7</u>	6.7	18	<u>14.1</u>	60.0	30	<u>4.4</u>
Wreck	10	<u>5.3</u>	62.5	1	<u>1.3</u>	6.3	5	<u>1.7</u>	31.3	0	<u>0.0</u>	0.0	16	<u>2.3</u>
Sum	190		27.8	78		11.4	287		42.0	128		18.7	683	
Depth														
Beached	17	<u>21.0</u>	60.7	0	<u>0.0</u>	0.0	11	<u>37.9</u>	39.3	0	<u>0.0</u>	0.0	28	<u>8.8</u>
< 2 m	9	<u>11.1</u>	8.7	2	<u>4.7</u>	1.9	11	<u>37.9</u>	10.7	81	<u>49.4</u>	78.6	103	<u>32.5</u>
2-20 m	34	<u>42.0</u>	26.6	27	<u>62.8</u>	21.1	4	<u>13.8</u>	3.1	63	<u>38.4</u>	49.2	128	<u>40.4</u>
> 20 m	21	<u>25.9</u>	36.2	14	<u>32.6</u>	24.1	3	<u>10.3</u>	5.2	20	<u>12.2</u>	34.5	58	<u>18.3</u>
Sum	81		25.6	43		13.6	29		9.1	164		51.7	317	
Prey consumed														
Bait	1	<u>2.4</u>	25.0	2	<u>20.0</u>	50.0	1	<u>1.6</u>	25.0	1	<u>0.7</u>	25.0	4	<u>1.6</u>

Continued

Table 1 Continued

	Online sources		Scientific literature		Social networks		Questionnaire		Total					
	n	%	n	%	n	%	n	%	n	%				
Prey consumed														
Dead fish	10	24.4	9.2	2	20.0	1.8	12	19.0	11.0	85	61.6	78.0	109	43.4
Hydrozoan	0	0.0	0.0	0	0.0	0.0	2	3.2	100.0	0	0.0	0.0	2	0.8
Jellyfish	6	14.6	42.9	0	0.0	0.0	3	4.8	21.4	5	3.6	35.7	14	5.6
Sea anemone	0	0.0	0.0	0	0.0	0.0	1	1.6	50.0	1	0.7	50.0	2	0.8
Zoantharian	1	2.4	14.3	0	0.0	0.0	2	3.2	28.6	4	2.9	57.1	7	2.8
Gorgonian	7	17.1	19.4	2	20.0	5.6	22	34.9	61.1	5	3.6	13.9	36	14.3
Scleractinian	1	2.4	33.3	1	10.0	33.3	1	1.6	33.3	0	0.0	0.0	3	1.2
Tube worm	1	2.4	12.5	0	0.0	0.0	1	1.6	12.5	6	4.3	75.0	8	3.2
Chiton	0	0.0	0.0	1	10.0	100.0	0	0.0	0.0	0	0.0	0.0	1	0.4
Sea slug	0	0.0	0.0	0	0.0	0.0	2	3.2	66.7	1	0.7	33.3	3	1.2
Octopus	0	0.0	0.0	0	0.0	0.0	1	1.6	50.0	1	0.7	50.0	2	0.8
Sea cucumber	1	2.4	16.7	0	0.0	0.0	2	3.2	33.3	3	2.2	50.0	6	2.4
Sea urchin	8	19.5	33.3	2	20.0	8.3	6	9.5	25.0	8	5.8	33.3	24	9.6
Starfish	5	12.2	26.3	0	0.0	0.0	5	7.9	26.3	9	6.5	47.4	19	7.6
Bryozoan	0	0.0	0.0	0	0.0	0.0	1	1.6	33.3	2	1.4	66.7	3	1.2
Thaliacean	0	0.0	0.0	0	0.0	0.0	1	1.6	100.0	0	0.0	0.0	1	0.4
Sponge	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	1	0.7	100.0	1	0.4
Bivalve	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	6	4.3	100.0	6	2.4
Sum	41		16.3	10		4.0	63		25.1	138		55.0	251	

the questionnaires (22.5%).

Seventy-one percent of the questionnaire respondents observed *H. carunculata* during SCUBA diving, snorkeling, apnea and fishing (48%, 29%, 19% and 6% of questionnaire sightings, respectively). Among all the volunteers, 58% were professional divers (divemaster or instructor), 33% were recreational divers (7% open water divers, 26% advanced open water divers) and 9% were apneists. The detailed information provided by the survey are shown in Supplementary Figure S1.

The distribution of the reports provided by the data sources differed among the time intervals considered (Chi-square test, $\chi^2_{df=3} = 131, p < 0.001$, counts grouped into “before 2008” and “2009-2019”). The oldest reports, dating back to before 1967, were largely derived from the scientific literature (21 out of 22, 95.5%), while the most recent, belonging to the 2015-2019 period, were mainly provided by online sources (104 out of 491, 43.0%) and social networks (265 out of 491, 53.4%) (Table 1).

Life habit of *H. carunculata*

All four data sources considered reported the majority (58.7%) of fireworm sightings during the summer, followed by spring (21.0%) and autumn (17%). Sightings reported during the winter were rare (3%) (Chi-square test for sources, $\chi^2_{df=6} = 8.49, p = 0.18$, counts grouped in “Summer”, “Winter-Spring” and “Autumn”). However, this finding could have been biased by the habits of recreational divers and holiday periods (Table 1).

Body size measurements were provided by the questionnaires ($n = 89$; Fig. S1), the literature and the images available on social networks ($n = 67$ in total for the literature and social networks; Table S2). In the questionnaires, sightings of small fireworms (< 10 cm in length) were more common ($n = 51, 57%$) than those of middle and large-sized specimens (10-20 cm and > 20 cm in length, $n = 20, 23%$ and $n = 18, 20%$ respectively). The opposite trend was found in the scientific literature and social networks, in which records referring to small-sized fireworms were rare ($n = 9, 13%$). The biggest specimens were photographed in the Tyrrhenian Sea at Sapri (Gulf of Policastro), Cala di Puolo (Gulf of Naples) and Salina (Aeolian Islands). They showed 205, 162 and 160 chaetigers respectively, corresponding to estimated body lengths of about 77 cm, 51 cm and 50 cm, respectively, according to the relationship calculated between the number of chaetigers and body length (Righi *et al.*, 2019; see Table S2 for the links to the web pages).

The majority of the data sources examined (84.5%) reported *H. carunculata* from rocky substrates (bare or covered by infralittoral algae or coralligenous assemblages and in caves), confirming that hard substrates are preferred (Chi-square test, $\chi^2_{df=3} = 37.4, p < 0.001$, counts grouped into “rocky” and “other”). Fireworms were also occasionally observed on sediments, seagrass beds and wrecks (8.8%, 4.4% and 2.3%, respectively; Table 1). As was the case with seasonality, this finding could have been biased by the habits of sea users that usually prefer rocky shores for their activities.

Even fireworm depth distribution differed between

the data sources (Chi-square test, $\chi^2_{df=3} = 45.4, p < 0.001$, counts were grouped into “beached and < 2 m depth” and “> 2 m depth”). The maximum depth for a report was 100 m, however fireworms were mostly recorded at shallow depths (< 2 m, 32.5%; between 2-20 m, 40.4%). A low percentage was observed deeper (> 20 m, 18.3%), while 8.8% concerned beached specimens (Table 1). The abundance of records at 10-20 m could have been affected by the most common dive depth of recreational divers, whereas the shallow sightings (< 2 m) are strictly related to fireworm presence, even near the sea surface and on emerging rocks. Indeed, 114 volunteers who filled in the questionnaires reported contact with *H. carunculata* both in the water (n = 99, 87%) and out of the water (n = 17, 13%). Thirty-two percent of the respondents reported cases of intentional contact with fireworms, while 68% reported accidental contact (Fig. S1), as claimed by several online newspapers during the summer. Indeed, most of the scientific and grey literature considered here highlighted the danger of fireworm stings and panic among sea users, who struggle with the presence of fireworms on beaches, rocks and in fishing nets (see Table S2 for references). Cases of people needing medical care after accidental contact were also found (e.g. Pauk, 2019. <https://sibenskiportal.rtl.hr/aktualno/foto-opasni-vatreni-crvi-potjerali-kupace-iz-rogoznicke-uvale-peles-nekoliko-ih-je-zavrсило-na-hitnoj/> Accessed 1st October 2019).

Feeding habits of *H. carunculata*

There were 251 reports of *H. carunculata* feeding, and the type of food item recorded differed among the data sources (Chi-square test, $\chi^2_{df=3} = 37.4, p < 0.001$,

counts grouped into “dead fish and bait” and “live macrofauna”). The majority of the reports were derived from the questionnaires (n = 138, 55.0%), additional data was derived from online sources (n = 41, 16.3%) and from pictures published on social networks (n = 63, 25.1%). The most frequently consumed food items were dead fish (n = 109, 43.4%), gorgonians (n = 36, 14.3%), sea urchins (n = 24, 9.6%) and starfish (n = 19, 7.6%). More uncommon prey included other cnidarians (hydrozoans, jellyfishes, sea anemones, zoantharians, scleractinians), annelids (tube worms), mollusks (chitons, sea slugs, an octopus, bivalves), other echinoderms (sea cucumbers), bryozoans, sponges and planktonic tunicates (thaliaceans) (Table 1).

Central Mediterranean distribution

H. carunculata specimens were reported from 368 locations corresponding with 150 first reports (Tables S1, S3). Most of the reports were collected from the Eastern basins (BS5-8: n = 651, 76.0%), while a lower number concerned the Western basins (BS2,3: n = 206, 24.0%; Fig. 1A, Table 2). However, the distribution of both the overall dataset (*i.e.* the 857 reports) and the first reports in the Eastern and Western basins did not change over the four time intervals (Chi-square test, $\chi^2_{df=3} = 2.82, p = 0.42$, for the overall dataset; $\chi^2_{df=3} = 1.90, p = 0.59$, for the first reports). Only 2.5% of the reports (n = 22) were dated back to before 1967 (Fig. 2A), while 17.9% (n = 153) and 21.7% (n = 186) were collected in 1967-2008 and 2009-2014, respectively (Fig. 2B,C). The majority (n = 496, 57.9%) referred to the last five years (2015-2019) (Fig. 2D; Table 2). In all four time intervals, most reports were recorded in BS6 (n = 312, 36.4%; Table 2). Here,

Table 2. Summary of the overall dataset of the reports collected in each biogeographic sector (BS) and Western or Eastern basin per time interval. Percentage values of the BSs and basins are reported by time-interval (column-wise, underlined) and by the total of the counts for each category (row-wise, italic).

	<u>< 1967</u>		<u>1967-2008</u>		<u>2009-2014</u>		<u>2015-2019</u>		<u>Total</u>	
	n	%	n	%	n	%	n	%	n	%
Biogeographic Sector (BS)										
2	0	<u>0.0</u>	0	<u>0.0</u>	3	<u>1.6</u>	18	<u>3.6</u>	21	<u>2.5</u>
3	3	<u>13.6</u>	43	<u>28.1</u>	41	<u>22.0</u>	98	<u>19.8</u>	185	<u>21.6</u>
5	2	<u>9.1</u>	29	<u>19.0</u>	39	<u>21.0</u>	90	<u>18.1</u>	160	<u>18.7</u>
6	13	<u>59.1</u>	59	<u>38.6</u>	68	<u>36.6</u>	172	<u>34.7</u>	312	<u>36.4</u>
7	0	<u>0.0</u>	6	<u>3.9</u>	13	<u>7.0</u>	24	<u>4.8</u>	43	<u>5.0</u>
8	4	<u>18.2</u>	16	<u>10.5</u>	22	<u>11.8</u>	94	<u>19</u>	136	<u>15.9</u>
Western basins (BS2,3)	3	<u>13.6</u>	43.0	<u>28.1</u>	44.0	<u>23.7</u>	116	<u>23.4</u>	206	<u>24.0</u>
Eastern basins (BS5-8)	19	<u>86.4</u>	110.0	<u>71.9</u>	142.0	<u>76.3</u>	380	<u>76.6</u>	651	<u>76.0</u>
Sum	22	2.6	153	17.9	186	21.7	496	57.9	857	

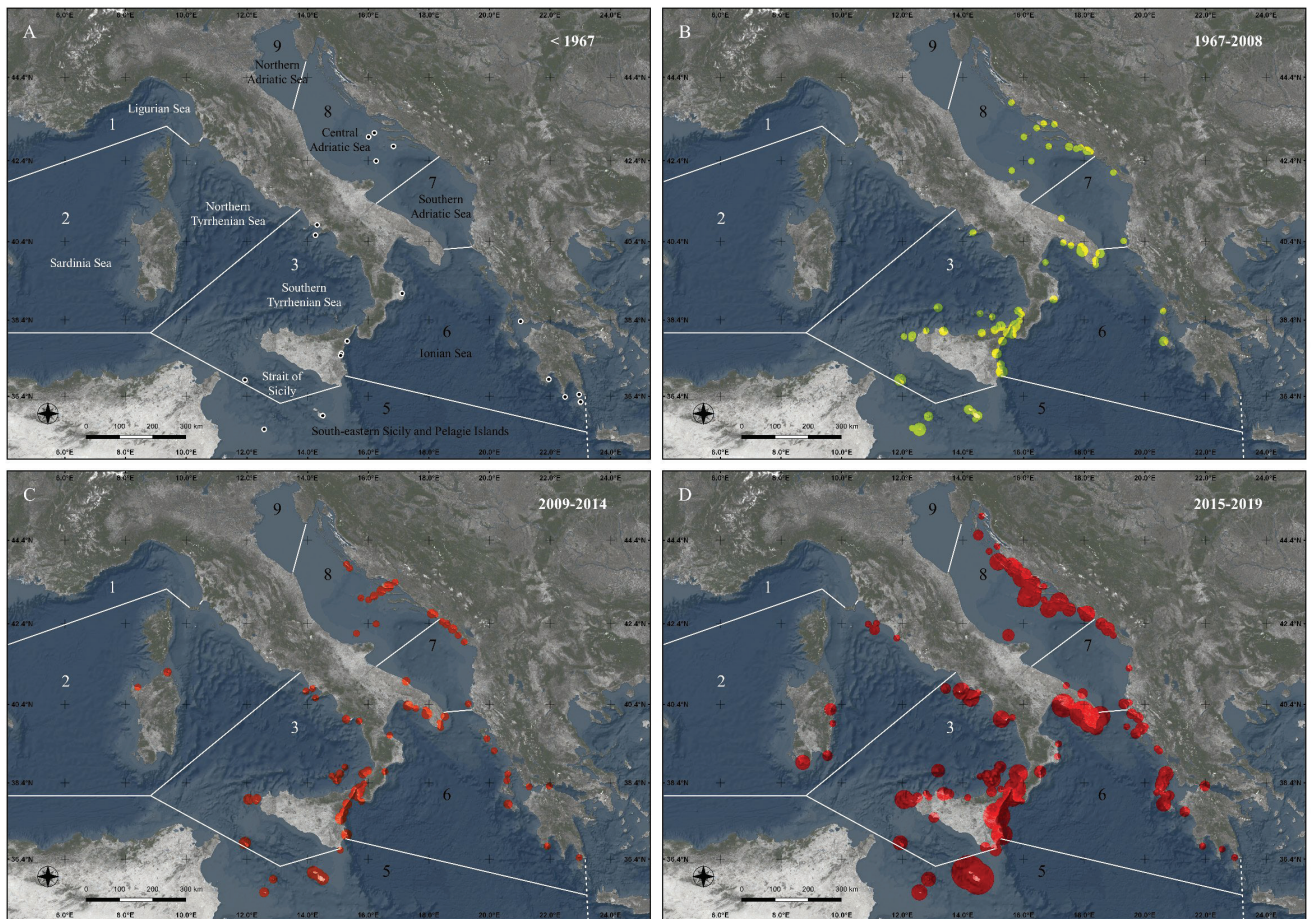


Fig. 2 (A-D): Overall number of reports collected *per* time interval. The numbers refer to the biogeographic sectors (BS) and the dotted line represents the southern limit of the Ionian Sea ecoregion (see text for further details). (A) The first reports dated back to before 1967, the Western and Eastern Mediterranean basins and biogeographic sectors are shown in white and black, respectively. The first reports belonging to the periods 1967-2008 (B), 2009-2014 (C) and 2015-2019 (D). Circle size corresponds to number of observations and larger circles represent more observations (from the smallest observation number [$n=1$] to the greatest one [$n=35$]). The latitudinal shift is mainly associated with the recent sightings in the BS2 and in the northern portion of the BS8.

the reports were concentrated along the Ionian coast of Apulia (the localities of Nardò, Maruggio and Porto Pirrone account for a total of $n = 53$ records), in the Strait of Messina (Scilla and Gallico-Messina, $n = 36$) and along the Eastern coast of Sicily (Catania and Siracusa, $n = 43$). In BS5, the large majority of the sightings were reported from a small number of localities on islands (e.g. Malta and Gozo, $n = 87$) (Fig. 1; Table 2; Table S1). These data are coherent with the perception of increasing and/or expanding populations reported by sea users in the questionnaire in the Ionian Sea (53%) (Fig. S1).

The Kruskal-Wallis test revealed significant differences between the median latitudes of the first reports among the periods considered, both for the Western ($H = 8.90$, $p = 0.011$) and the Eastern basins ($H = 9.65$, $p = 0.022$). In particular, the median latitudes of the first reports dated back to before 2008 and to 2009-2014 differed significantly between the Western basins ($U = 18.5$, $p = 0.001$), while in the case of the Eastern basins, the first reports before 1967 had median latitudes different from those of the 2009-2014 and 2015-2019 periods ($U = 82$, $p = 0.037$ and $U = 126$, $p = 0.002$, respectively).

Before 1967, most of the first reports were placed in the BS6 ($n = 9$, 50.0%; Fig. 3A, Table 3). The north-

ernmost sightings of *H. carunculata* from the Western (BS2,3) and Eastern (BS5-8) basins were from the Gulf of Naples (BS3, about 40.80N) and Lastovo Island (Central Dalmatia, Croatia, BS8, about 42.75° N), respectively (Fig. 3A-D; Table 3; Table S3).

From 1967 to 2008, 50 first reports were collected (33.3%) and they were mainly distributed in BS3 ($n = 16$, 32.0%), BS6 ($n = 14$, 28.0%) and BS8 ($n = 10$, 20.0%) (Fig. 3B; Table 3; Table S3). In BS8, the northernmost report was Murter (Northern Dalmatia, Croatia, about 43.80° N), while in the Western basins the new first reports remained along the southern coast of BS3 (Fig. 3B; Fig. 4A,B; Table S3).

From 2009 to 2014, 29 additional first reports were recorded (19.3% of the total), but the northernmost limit of *H. carunculata* did not change in either the Western or Eastern basins. The Gulf of Naples remained the northernmost reach in the Tyrrhenian Sea, as confirmed by reports from the questionnaires (Ischia and Nisida, about 40.8° N) (Fig. 4C; Table S3). Similarly, the northernmost sightings in BS8 were almost at the same latitude as in the 1967-2008 period (Kornat and Kasela, Northern Dalmatia, Croatia, 43.83° N and 43.74° N respectively) (Fig. 3C; Table S3). Noteworthy, in the 2009-2014 time

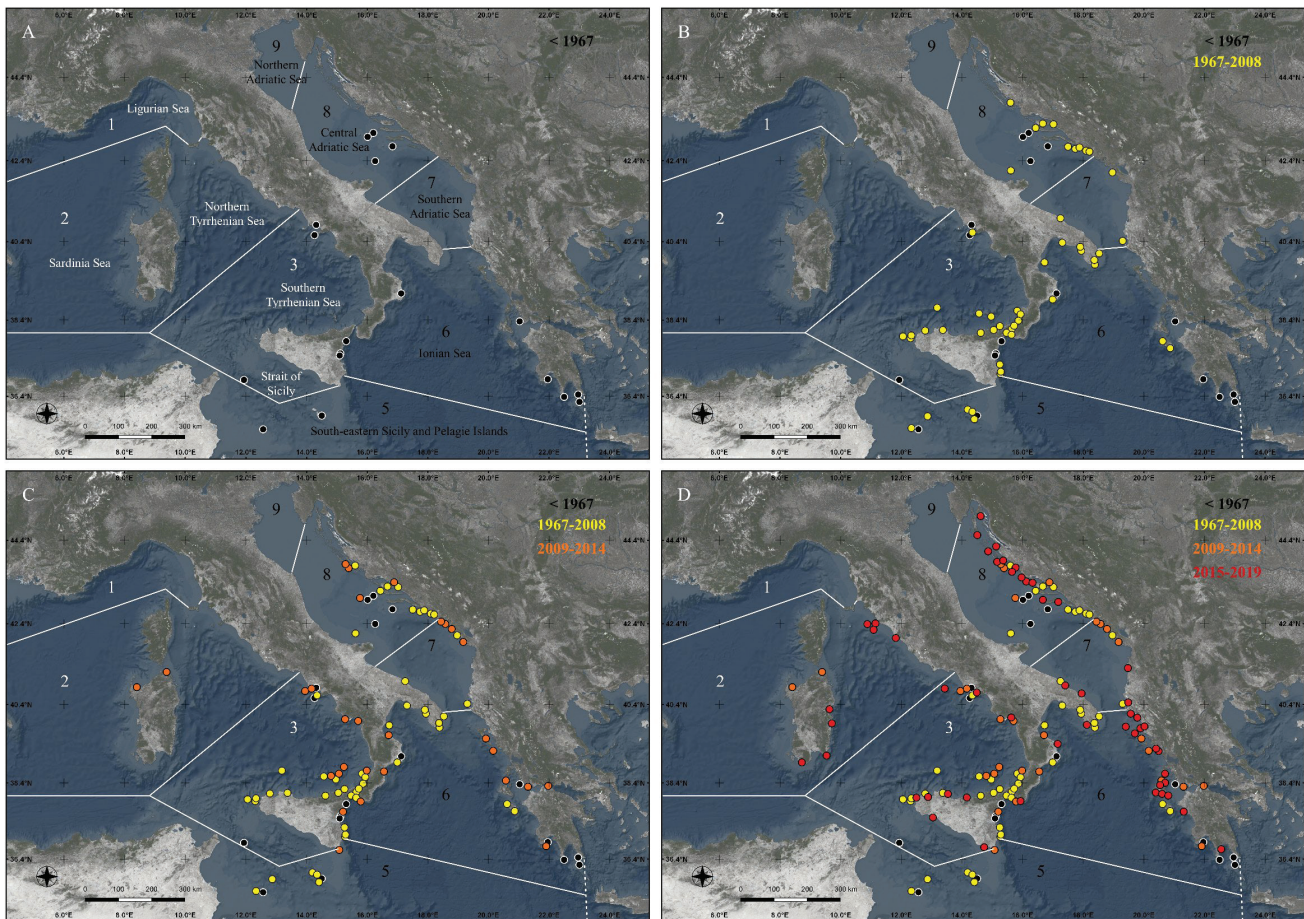


Fig. 3 (A-D): First reports collected *per* time interval. The numbers refer to the biogeographic sectors and the dotted line represents the southern limit of the Ionian Sea ecoregion (see text for further details). (A) The first reports dated back to before 1967 (first-time interval), the Western and Eastern Mediterranean basins and biogeographic sectors are shown in white and black, respectively; (B) The first reports belonging to the first and the second time intervals (before 1967 and 1967-2008, respectively); (C) the first reports up to 2014 (including the time interval 2009-2014) and up to 2019 (including all the four time intervals) (D). The latitudinal shift is mainly associated with the recent sightings in the BS2 and in the northern portion of the BS8.

Table 3. Number of first reports collected in each biogeographic sector (BS) and Western or Eastern basin per time interval. Percentage values of the biological features are reported by source (column-wise, underlined) and by the total of the counts for each category (row-wise, italic).

	< 1967		1967-2008		2009-2014		2015-2019		Total	
	n	%	n	%	n	%	n	%	n	%
Biogeographic Sector (BS)										
2	0	<u>0.0</u> <i>0.0</i>	0	<u>0.0</u> <i>0.0</i>	2	<u>6.9</u> <i>18.2</i>	9	<u>17.0</u> <i>81.1</i>	11	<u>7.3</u>
3	3	<u>16.7</u> <i>8.8</i>	16	<u>32.0</u> <i>47.1</i>	8	<u>27.6</u> <i>23.5</i>	7	<u>13.2</u> <i>20.6</i>	34	<u>22.7</u>
5	2	<u>11.1</u> <i>20.0</i>	6	<u>12.0</u> <i>60.0</i>	1	<u>3.4</u> <i>10.0</i>	1	<u>1.9</u> <i>10.0</i>	10	<u>6.7</u>
6	9	<u>50.0</u> <i>18.0</i>	14	<u>28.0</u> <i>28.0</i>	10	<u>34.5</u> <i>20.0</i>	17	<u>32.1</u> <i>34.0</i>	50	<u>33.3</u>
7	0	<u>0.0</u> <i>0.0</i>	4	<u>8.0</u> <i>28.6</i>	4	<u>13.8</u> <i>28.6</i>	6	<u>11.3</u> <i>42.9</i>	14	<u>9.3</u>
8	4	<u>22.2</u> <i>12.9</i>	10	<u>20.0</u> <i>32.3</i>	4	<u>13.8</u> <i>12.9</i>	13	<u>24.5</u> <i>41.9</i>	31	<u>20.7</u>
Western basins (BS2,3)	3	<u>16.7</u> <i>6.7</i>	16	<u>32.0</u> <i>35.6</i>	10	<u>34.5</u> <i>22.2</i>	16	<u>30.2</u> <i>35.6</i>	45	<u>30.0</u>
Eastern basins (BS5-8)	15	<u>83.3</u> <i>14.3</i>	34	<u>68.0</u> <i>32.4</i>	19	<u>65.5</u> <i>18.1</i>	37	<u>69.8</u> <i>35.2</i>	105	<u>70.0</u>
Sum	18	<u>12.0</u>	50	<u>33.3</u>	29	<u>19.3</u>	53	<u>35.3</u>	150	

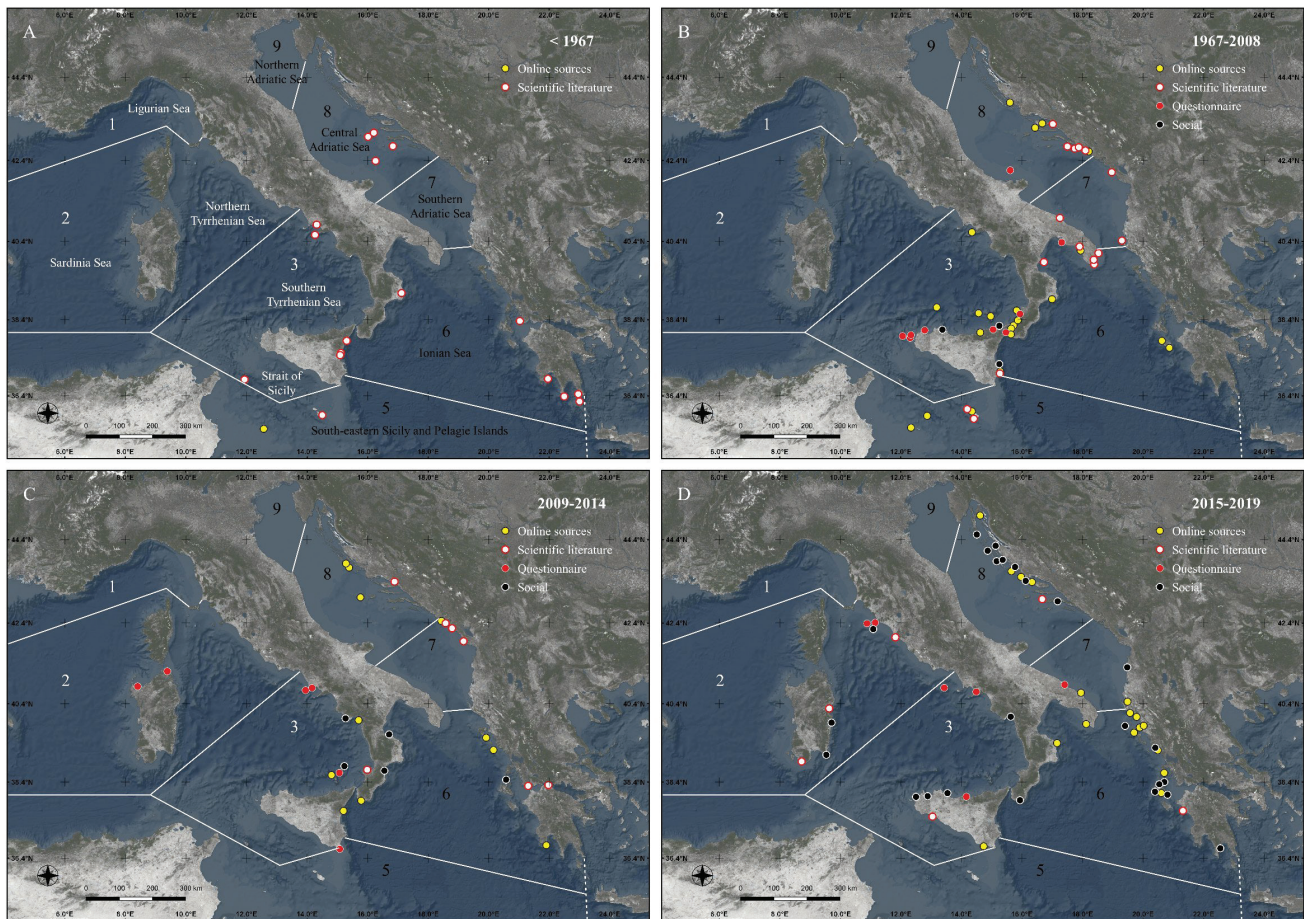


Fig. 4 (A-D): First reports collected *per* time interval and subdivided according to the source of the datum. (A) The first reports dated back to before 1967, the Western and Eastern Mediterranean basins and biogeographic sectors are shown in white and black, respectively; (B) the first reports belonging to the time intervals 1967-2008, 2009-2014 (C) and 2015-2019 (D).

interval the questionnaires provided the first two reports in BS2 along Northern Sardinia at latitudes 40.83° N (Porto Torres, 2012) and 41.21° N (La Maddalena, 2012) (Fig. 3C; Fig. 4C; Table S3).

More recently (2015-2019), the number of first reports increased in all the sectors ($n=53$, 35.3%; Table 3; Table S3). They were concentrated in BS6 ($n = 17$, 32.1%), BS8 ($n = 13$, 24.5%) and BS2 ($n = 9$, 17.0%) (Fig. 3D; Table 2). The additional first reports in the Eastern basins were mainly provided by social networks and the online sources and were focused along the coasts of Southern Albania and Greece in BS6, and towards the Croatian coasts in BS8 (Fig. 4D). In BS8, fireworms showed a great northward spread up to the Quarnero islands (Losinj and Krk, about 44.58° N and 44.97° N, respectively) (Fig. 3D; Table S3). In BS2, several reports from the Southern and Eastern coasts of Sardinia were provided by social networks and personal communication (Capo Spartivento and Villasimius for the South; Tortoli and Osala in the Eastern coast) (Fig. 4D). In the Western basins, the fireworm northward limit reached Southern Tuscany (Gianutri Island and Argentario, about 42.25° N and 42.40° N, respectively) (Fig. 3D; Table S3).

None of the sources reported sightings of *H. carunculata* in BS1 or BS9. Indeed, all the questionnaire respondents that had never observed fireworms (29%) dived

in the northernmost sub-basins (Ligurian Sea, Northern Tyrrhenian Sea and Northern Adriatic Sea). Besides, fireworm absence in the Ligurian Sea and in the Northern Adriatic Sea was cross-checked by personal communication via telephone or email provided by representative sea users of these areas.

Discussion

Our study significantly expands knowledge on the life and feeding habits of *H. carunculata* colonizing the Mediterranean basins surrounding the Italian peninsula. This species is clearly a common component of the infralittoral fauna in many areas of both the Western and Eastern basins, particularly where hard substrates are available. The distribution of observations *per* season suggests the hypothesis that, besides substrate, water temperature could be an important environmental factor involved in the bathymetric distribution and seasonal activity of fireworms. *H. carunculata* is a thermophilic species and its frequent observation in shallow waters during summer months may be coherent with fireworm occurrence in subtropical and tropical regions (Schulze *et al.*, 2017; Encarnação *et al.*, 2019) (Table 1).

Most of the data was obtained from social networks

and online sources (Table 1). The scarcity of reports from the scientific literature could be explained by sampling methodologies that did not reveal fireworm presence even where they were known to dwell. Studies on the Central Mediterranean hard bottom benthic biocoenoses were often carried out by focusing on large sessile organisms and the small-sized fauna living on rocky surfaces or in the interstices, while large mobile species like *H. carunculata* were not collected. For instance, surveys on benthic polychaetes of the Apulian coasts have usually been carried out by sampling with the use of dredges, visual estimation of the sessile fauna in quadrats, or by scraping surfaces of 100 or 400 cm² (e.g. Frascchetti *et al.*, 2002; Giangrande *et al.*, 2003 Corriero *et al.*, 2004; Mastrototaro *et al.*, 2010). These studies did not account for *H. carunculata*, but some of the authors confirmed that they have commonly observed fireworms along Ionian Apulia over the last 20 years (e.g. Adriana Giangrande, personal communication).

Although *H. carunculata* has generally been reported as a corallivorous and scavenger species, recent laboratory experiments on the feeding behaviour of Mediterranean specimens highlighted their ability to consume a wide range of marine invertebrates, exploiting dorsal stinging chaetae and their eversible pharynx to harm even large, defended prey (Simonini *et al.*, 2017, 2018). In the present study, evidence of predation activity on live organisms was mainly provided by online sources and social networks, supporting the flexibility of *H. carunculata* in feeding (Table 1). In addition to anthozoans, which represent a well-known food source for Atlantic specimens in reef habitats (Wolf & Nugues, 2013), Mediterranean fireworms were recorded preying on an octopus, bryozoans, thaliaceans, bivalves, sponges and tube worms. These events have never been reported so far and emphasize opportunistic feeding ability (see Table S2 for links to photos).

The ability of *H. carunculata* to feed on jellyfish, starfish and sea cucumber, already observed in Atlantic populations, was also confirmed for the Mediterranean ones (Stoner & Layman, 2015; Barroso *et al.*, 2016, 2017). This opportunistic feeding behaviour could lead to specialization in trophic habits among populations colonizing different geographical areas.

Noteworthy, while reports confirmed that predation on sea urchins occurs widely along the Ionian Apulian coast (Simonini *et al.*, 2017), it seems that *H. carunculata* specimens from the Tyrrhenian coast of Calabria do not consume urchins and are often observed eating gorgonians and starfish (Fabrizio Fabroni, personal communication). Thus, real time data provided by sea users represent critical information to investigate fireworm feeding habits in different locations, particularly if data reliability can be checked using public digital content. Indeed, posts on social networks have provided images of some of the largest specimens of *H. carunculata* observed so far. On the basis of the relationship between the number of chaetigers and body length (Righi *et al.*, 2019), fireworms photographed at Sapri (Gulf of Policastro, Tyrrhenian Sea), Cala di Puolo (Gulf of Naples) and Salina

(Aeolian Islands) had body lengths of about 77 cm, 51 cm and 50 cm. Previous studies reported maximum length of 30-60 cm (estimated by divers, Chafarinas Islands, Western Mediterranean Sea; Maldonado *et al.*, 2013), 30 cm (Righi *et al.*, 2019) and 25 cm in length (Yáñez-Rivera & Salazar-Vallejo, 2011).

The broad extent of social media information has already been recognized as an innovative data source for research, biodiversity monitoring and conservation sciences (Lopez *et al.*, 2019; Toivonen *et al.*, 2019). Noteworthy, social networking sites (Kaplan & Haenlein, 2010) provide a great amount of fine resolution data, which can be obtained directly from posts. Nowadays, social media sites have a great potential to become efficient sources for the collection of relevant information that is not constrained by the economical and logistic limits of field monitoring campaigns. Platforms such as Facebook, Instagram and Flickr have millions of users and are the foremost suppliers of the images, videos and comments that are available online (Lopez *et al.*, 2019). Some of these contents can be geotagged or geographic references can be provided directly by users or derived from the post itself.

On the other hand, social media data are created spontaneously and not generated within a well-defined citizen science program, thus they could be biased by what people consider worth posting. Hence the importance of comparing and integrating this information with more traditional sources, such as scientific literature and citizen science surveys, which have proven to be an effective tool for the monitoring of biological invasions and could even be helpful in the study of native invader species (Azzurro *et al.*, 2017; Giovos *et al.*, 2019; Toivonen *et al.*, 2019).

The foremost strength in the integration of the data sources considered was highlighted by the overall reports collected on fireworm distribution (Fig. 1,4). The findings of *H. carunculata* in the Central Mediterranean Sea have significantly updated the information available to date (Simonini *et al.*, 2019), allowing the reconstruction of the shifts that have occurred over the last 50 years. Given the first reports from before 1967 (Fig. 3A), fireworms have progressively increased their distribution range spreading towards the whole of Sicily and Ionian Apulia (Fig. 3B). During the following six years, the northernmost latitude of the reports rose in both the Western and Eastern basins (Fig. 3C), reaching the northernmost limit of BS2 and BS8 during the last five years (Fig. 3D). Noteworthy, while the oldest reports were provided by the scientific literature (e.g. museum collections and first research cruises in the Mediterranean, see Table S1 for references), information from the following periods were mainly obtained from online sources (e.g. news websites and divers' blogs), social networks and questionnaires (Fig. 4A-D). Indeed, the support of these "digital sources" has become critical in assessing the spread of *H. carunculata* that has occurred during the last fifteen years. The number of sightings increased greatly during the 2015-2019 interval, with the highest concentrations along the Adriatic coast of Croatia, Ionian Apulia, the Strait of Messina,

the North-Eastern coast of Sicily and the Strait of Sicily (Fig. 2A-D). Since there was no published record of this species in the North Tyrrhenian and Sardinian Seas (BS2) before 2009, the sightings reported during the last decade may be indicative of a northerly shift in fireworm distribution. The only reports above the Gulf of Naples are represented by hotspots of the species recorded at Civitavecchia and the Tuscan islands (Giglio Island and Argentario; Table 1; Fig. 1-4). The limited and fragmented occurrence of *H. carunculata* in the BS2 suggests a recent colonization event in this area and indicates that these rocky shores may present favourable conditions for further colonization and expansion. This northward spread seems to match with an increase in population densities in the native range of *H. carunculata* (Righi *et al.*, 2019) and it is possibly attributable to the seawater warming that is occurring in the Mediterranean Sea (Coll *et al.*, 2010; Bianchi *et al.*, 2013, 2018). Indeed, the available scientific literature suggests that the species was not present along the Mediterranean Spanish coast before 2010, since *H. carunculata* was not reported among the marine annelids of the “Iberian Fauna” (Parapar *et al.*, 2012). However, it seems to be currently under rapid northward expansion along the coasts of Andalusia and Murcia (Coma *et al.*, 2011; Murcia Enclave Ambiental, 2012. <http://www.murciaenclaveambiental.es/cuarto-trimestre-2012.html?idRe=174&iw4re=36> Accessed on 4th November 2019).

The reports collected suggest that the locality of Polignano (Northern Adriatic coasts of Apulia, 40.98° N) has been a fireworm distribution limit along the Italian Adriatic coasts since the 1967-2008 period (Fig. 1, Fig. 2B). Indeed, *H. carunculata* spreading above the Strait of Otranto could follow the same pattern as other invasive species, which from Ionian Apulia tend to colonize firstly the Montenegrin and Albanian, and subsequently the Apulian coasts on the Adriatic side (e.g. *Percnon gibbesi*; Ungaro & Pastorelli, 2015). Otherwise, for many species, a common way of introduction into the Adriatic is from the Greek Ionian coastline to Albania and Montenegro via gradual expansion (Katsanevakis *et al.*, 2011a,b).

Temperature is a major driver for species range shifts, since it may facilitate settlement and spreading processes (Stachowicz *et al.*, 2002; Samperio-Ramos *et al.*, 2015). Among marine annelids, range shifts driven by temperature increase have been documented in the distribution of the burrower bioturbator *Arenicola marina* (Arenicolidae) and the tube-dwelling sediment-stabilizer *Diopatra* spp. (Onuphidae). As global warming intensifies, these species are expected to continue expanding along the European coasts of the Atlantic Ocean, causing alterations in sedimentary habitats, community composition and abundances of the other infauna (Berke *et al.*, 2010; Pires *et al.*, 2015).

A consistent warming trend has been found for Mediterranean Sea surface temperatures (SST) in the 1982–2016 period, with a clear increase in the annual mean SST after 1993 especially in the eastern basins (Pastor *et al.*, 2018; Pisano *et al.*, 2020). The nearly continuous warming trend of the Mediterranean Sea accounts for a

total SST increase of about 1.5°C from 1982 to 2018. However, decadal and spatial analyses of SST variations highlighted that the warming rate is not uniform. Short local cooling trends were observed until 2005, but since then no pausing phases occurred in the overwhelming warming tendency (Pisano *et al.*, 2020). At sub-basin level, the Western Mediterranean and the Ionian Seas show lower warming trends, while the most intense values are observed in the Adriatic Sea and in the Gulf of Taranto, which seem to reflect the greater increases in temperature in the Levantine-Aegean Sea (Pisano *et al.*, 2020; Sakalli, 2017).

This general warming tendency has been supported by a northward shift of sea surface isotherms. From the 1980s to the first decade of the 2000s, the 14°C and 15°C isotherms of February (the coldest month of the year) have moved in recent times, favouring the expansion of many native and invasive warm-water species from the southern sectors to the Western basins (Coll *et al.*, 2010). Notably, the geographical distribution of *H. carunculata* in the Central Mediterranean presently seems to coincide with the maximum summer temperatures of 26-27°C (Georgiou *et al.*, 2016) and especially with the northward displacement of February 14°C isotherm in the Western basins (Coll *et al.*, 2010) (Fig. 1). Recent occasional occurrences of the species north of the Gulf of Naples suggested that this area, where the lower minimum temperature in winter is about 13°C (Georgiou *et al.*, 2016), is probably still too cold for the establishment of large populations of this thermophilic species (Fig. 1).

Although the Adriatic Sea is warming fast (Pisano *et al.*, 2020), fireworm presence in BS8 only concerned the Croatian coasts. This may be due to the general surface circulation in the Adriatic basin, which brings Levantine and Ionian warm-waters northwards along the Croatian eastern coast, up to the Northern Adriatic where they are affected by the cold Bora wind effect before moving southward along the Italian west coast (Bergamasco & Malanotte-Rizzoli, 2010; Millot & Taupier-Letage, 2015). Besides, the geomorphologies of the Adriatic coasts of Italy and Croatia are in sharp contrast. The Italian (western) coast is relatively smooth, with few islands, and is characterized mostly by soft sediments, due to the large amounts of material transported by the Po and other rivers. Croatia presents an insular rocky shore coastline, with several islands and islets, the optimal substrate for *H. carunculata*. In the Adriatic, maximum water temperature can reach 29°C in summer, while in winter it can drop to a minimum of 9-4°C in the Northern sector, especially when the cold Bora wind blows (Mikac, 2015). Together with the Gulf of Lion (Ligurian Sea), this area is the coldest sector of the Mediterranean, showing ecological and biogeographical similarities with the North Atlantic and hosting species with cold-temperate water affinities (Bianchi *et al.*, 2004; Mikac, 2015). Given that increasing scarcity or disappearance of cold-water species from the Gulf of Lion (Ligurian Sea) and the Northern Adriatic has already been recorded, sea water warming could lead to biotic homogenization of Mediterranean basins (Bianchi *et al.*, 2012), favouring the range expan-

sion of warm-water species as in the case of *H. carunculata*. Currently, the fireworm's northernmost reports have already reached the Northern Adriatic at the Quarnero islands (Losinj and Krk; present study) and further spreads may be forthcoming. Future sightings of the species in BS1 and BS9 could be considered as new colonization events, since these areas are intensively studied by marine biologists and research institutes, who so far have never observed *H. carunculata* (Federico Betti, Valentina Pitacco and Saul Ciriaco, personal communication).

Several examples of northward range expansion of plant and animal species in the Mediterranean Sea are available, like the bluefish *Pomatomus saltatrix* and the yellow barracuda *Sphyraena viridensis* (Coll *et al.*, 2010; Francour *et al.*, 2010; Lejeusne *et al.*, 2010; Katsanevakis *et al.*, 2011b; Ordóñez *et al.*, 2015; Sbragaglia *et al.*, 2020). Besides, the ornate wrasse *Thalassoma pavo* and the orange coral *Astroides calycularis* were very common in the Eastern and Southern shores and have recently shifted their distribution northwestwards into the Ligurian and Adriatic Seas (Lejeusne *et al.*, 2010). Accordingly, the northward displacement of species range attributable to the warming of the Tyrrhenian Sea was supported by recent findings of autochthonous (Psomadakis *et al.*, 2006, 2008a, 2008b) and allochthonous (Psomadakis *et al.*, 2009) thermophilic fish species, such as the native blue runner *Caranx crysos* (Psomadakis *et al.*, 2011). In the Western Mediterranean, southern subtropical non-indigenous species and warm-water natives are establishing, with their northernmost reach in the Gulf of Genoa (Ligurian Sea; Bianchi *et al.*, 2018).

Simulations of Mediterranean SST increases up to 2100 are coherent with a drastic continuous rise in the future towards the west (Collins *et al.*, 2013; Sakalli, 2017). Within this framework, critical changes in warm-water species populations and their interactions with local communities are envisaged for the future. The present findings suggest that *H. carunculata* could keep expanding rapidly, reaching higher densities in its native range. Invasive species that move across biogeographical barriers are usually exposed to severe environmental changes and may adapt rapidly to new environments under the pressure of novel selective forces (Chown *et al.*, 2015; Dlugosch *et al.*, 2015). Environmental change, absence of predators and availability of food supplies are common drivers of marine biological invasions, including native invaders (Carey *et al.*, 2012; Giakoumi *et al.*, 2019). Widespread fireworm distribution has great potential to promote this species to invader status in its native range in the Central Mediterranean. Once this transition has occurred, quantifying the impacts on coastal rocky-reef benthic communities and possible trophic cascade effects is a forthcoming challenge. The impacts of native invaders are not well documented, since they require knowledge of population size and dynamics and impacts of the native invader on prey populations and communities (Carey *et al.*, 2012).

Furthermore, given that *H. carunculata* has expanded geographically beyond its native range in the Northern Tyrrhenian Sea and in the northernmost limit of the Central Adriatic Sea, it could also be considered a neonative

(Essl *et al.*, 2019), which is a range-expanding species responding to anthropogenic environmental change, such as the ongoing sea water warming.

Ad hoc monitoring is needed to assess the distribution of *H. carunculata* on a finer scale. Fireworm presence could be assessed through catching by trap rather than SCUBA diving, as, if population density is too low, they may not be detectable by *visual census*. Further investigation is especially needed in the Northernmost sectors of BS2 and BS9, where occasional colonization events could be already ongoing. The data collected can be used to model habitat suitability and future expansion scenarios, in order to assess the invasive potential of *H. carunculata* and its potential impacts.

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Supplementary data

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

Fig. S1: Questions related to the underwater experiences of sea users, life habitat and feeding behaviour of *H. carunculata*. The answers are reported as percentages.

Table S1. Overall dataset of finding localities of *H. carunculata*. “N” indicates the order of the reports.

Table S2. Overall dataset of references and web pages which provided reports of *H. carunculata*. “N” indicates the order of the reports and it corresponds to the order of Table S1.

Table S3. First reports of *H. carunculata* in Mediterranean sub-basins surrounding the Italian coasts. “N” indicates the order of the reports.