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First record of non-native polychaetes *Polydora websteri* and *P. caeca* invading cultured and wild populations of mussels and oysters in the Mediterranean

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ABSTRACT

Species of *Polydora* and related genera are well known molluscs' pests transported by aquaculture activities and invading new locations worldwide. Their correct identification often requires confirmation by molecular data due to the presence of cryptic species. In the present study, using morphological and molecular data, we identified three non-native *Polydora* species associated with cultured and wild mussel *Mytilus galloprovincialis*, Pacific oyster *Magallana gigas* and European oyster *Ostrea edulis* in the Adriatic Sea (Italy). The tube-dwelling *P. cornuta* has been recorded from the Mediterranean since 1990 and is currently classified as one of the worst invaders in soft bottom communities in the region. The shell-boring *P. caeca* and *P. websteri* are here reported for the first time in the Mediterranean. This occurrence is a cause for concern, as the regular transfer of molluscs between aquaculture facilities within the Mediterranean basin and with European farms outside the basin may contribute to the further spread of the non-native *Polydora* in this region. The origin and distribution of these species in the Mediterranean should be further studied.

1. Introduction

Aquaculture, particularly that of molluscs, is one of the main vectors for the transport of non-native species in the Mediterranean Sea, with northern Adriatic Sea and Gulf of Lion being hotspots of introductions (Katsanevakis et al., 2014; Soto et al., 2024). The most important farmed molluscs in the Mediterranean are the Mediterranean mussel *Mytilus galloprovincialis*, Pacific oyster *Magallana gigas* and Manila clam *Ruditapes philippinarum*. Italy is the main producer of mussels and manila clams, while France is the main producer of oysters, followed by Italy (Graham et al., 2020; Carvalho and Guillen, 2021). Most of Italian production is in the northern Adriatic Sea, where it is relevant for the local economy. Thus, monitoring the presence of non-native species threatening aquaculture facilities in this region is of high importance. There are very few studies of fauna associated with mussels and oysters in the Mediterranean, mostly on mussel beds, especially wild ones, and in general considering only fouling species, not shell-borers (e.g. Curini Galletti and Galleni, 1981; Tsuchiya and Bellan-Santini, 1989;

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Damianidis and Chintiroglou, 2000; Chintiroglou et al., 2004; Çinar et al., 2008; Gargouri Ben Abdallah et al., 2012; Çinar et al., 2020). Studies of fauna associated with oysters are outdated and those concerning wild Pacific oysters are completely lacking (Agius et al., 1977; Igić 1984; Perera et al., 1990; Sala and Lucchetti, 2008). Therefore, introduced species could go unnoticed for a long time.

Some of the most important hitchhikers that are transported with cultured molluscs are polydorins, members of the tribe Polydorini Benham, 1896 (Polychaeta: Spionidae), well known pests of abalone, oysters and clams (Simon and Sato-Okoshi, 2015). These worms burrow in the shells of molluscs, provoking the formation of mud blisters filled with their faeces and mud. Therefore, they are commonly known as mudworms or blister worms (Blake and Evans, 1973; Zottoli and Carriker, 1974). The interior part of shells with mud blisters becomes visibly unattractive, and the organic material contained inside the blisters undergoes anaerobic decay producing hydrogen sulphide with a pungent "rotten egg" smell, which leads to a decrease in the commercial value of molluscs (Lauckner, 1983; Handley and Bergquist, 1997; Read, 2010). In oysters, heavy infestation by shell-boring polydorins can compromise their health and performance, making their shells more brittle, slowing down growth, altering physiological processes, and increasing their vulnerability to diseases, predators, and environmental stressors, which can ultimately lead to host mortality (Korringa, 1954; Owen, 1957; Wargo and Ford, 1993; Buschbaum et al., 2007; Chambon et al., 2007).

Several non-native species of mudworms have been spread with molluscs to many corners of the globe, where they become established and led to serious economic problems for the local aquaculture industry (Bailey-Brock and Ringwood, 1982; Moreno et al., 2006; Simon et al., 2006; Nell, 2007; Read, 2010; Malan et al., 2020; Martinelli et al., 2020; Rodewald et al., 2021; Martinelli et al., 2024). Translocations of adult molluscs between farms usually lead to secondary intra-regional spread of already established non-native shell-boring species (Moreno et al., 2006; Rodewald et al., 2021). They can also be transported with oyster seeds (Bailey-Brock and Ringwood, 1982; Spencer et al., 2020; Martinelli et al., 2025). Moreover, these species can further spread into natural habitat and infest wild molluscs, with negative impacts on local ecosystem and loss of ecosystem services (Moreno et al., 2006; Sato-Okoshi et al., 2008; Boonzaaier et al., 2014; Schatte Olivier et al., 2018; Martinelli et al., 2020; Puri et al., 2021).

Ultimately, polydorins that infest wild hosts in the vicinity of farms increase the risk of re-infestation of farmed molluscs (Coen and Bishop, 2015; Williams et al., 2016). Management and eradication measures should be different if non-native pests infest only farmed molluscs or they have spread also into wild habitats. If these pests infest only farmed molluscs and move within the region by translocation of stocks between farms, our knowledge on their distribution and molluscs' movements can facilitate management measures that can stop pest spreading, and eventual eradication measures can be taken. However, if non-native pests infest also wild molluscs, farmed molluscs will continuously be at a risk of re-infestation (Rodewald et al., 2021). Therefore, studies on shell-boring polydorins should include not only cultured but also wild molluscs in the vicinity of farms.

Unidentified *Polydora* sp. have often been reported as infesting farmed mussels and oysters in the Mediterranean (Fleury et al., 1998; Duault and Gillet, 2001; Gavrilović et al. 2008; Lukić 2011; Prioli, 2013). Some studies have reported two shell-boring species: *P. ciliata* (Carazzi, 1893; Parenzan, 1961, 1967; Spiga et al., 2007) and *P. hoplura* (Carazzi, 1893; Parenzan, 1961, 1967; Presečki-Labura, 1987; Labura and Hrs-Brenko, 1990; Nel et al., 1996). The taxonomy and distribution of both species in different parts of the world were recently reviewed (Radashevsky and Pankova, 2006; Radashevsky et al., 2017; Sato-Okoshi et al., 2017). As has been already shown, some of these previous Mediterranean records may belong to non-native cryptic species. In fact, the correct identification of shell-boring polydorins based only on morphology may be ambiguous because adults of different species may appear similar to each other. Thus, misidentification of worms may lead to overlooking of new invasions (Simon and Sato-Okoshi, 2015). Molecular analysis has become a helpful tool to accurately identify worms and detangle natural distribution of species and their invasion history (Sato-Okoshi and Abe, 2012; Sato-Okoshi et al., 2017; Williams et al., 2017; Rice et al., 2018; Lee et al., 2020; Malan et al., 2020; Rodewald et al., 2021; Radashevsky et al., 2023b; Martinelli et al., 2024; Radashevsky et al., 2024).

The aim of the present study was to identify polydorins associated with farmed and wild mussels and oysters in the Adriatic Sea based on their morphological and molecular characteristics.

2. Material and methods

2.1. Material

Collections were made along the north and central Italian coast of the Adriatic Sea. The Pacific oysters *M. gigas* were collected once in May and once in October 2020 on two farms (inside and outside Sacca di Goro lagoon) and in two locations with wild oyster populations (inside Sacca di Goro lagoon, from the soft bottom at 1.5 m depth, and in Bevano River estuary from the intertidal mudflat), in the northern Adriatic Sea (Fig. 1A–C; Supplementary Table ESM1). Oysters were farmed in cylindrical multi-layered cages, lanterns. Farm outside Sacca di Goro used oyster seeds grown in the hatchery in the northern Adriatic Sea, while farm inside Sacca di Goro used seeds grown both locally and imported from north-west France (Atlantic Ocean). Fifteen oysters per site were collected in each sampling; totally 120 oysters (30–200 mm long, 23–115 mm wide) were collected and examined during the whole study. The Mediterranean mussels *M. galloprovincialis* were collected in May and October 2020 on three farms (outside Sacca di Goro lagoon, in Cervia and Cattolica) and in three sites with wild mussel beds on artificial substrates (outside Sacca di Goro lagoon from wooden pillars, in Cervia and Punta Marina from stone breakwater) in the northern Adriatic Sea (Fig. 1A–C; Supplementary Table ESM1). Mussels on farms were cultivated offshore on long-line system, using seeds grown locally as well as imported from locations in Italy and Greece. At each site and time, three clumps of mussels were collected and delivered to the laboratory in plastic containers with a capacity of 2 L each. Two individuals of the European flat oyster *O. edulis* were collected on a farm off the coast of Porto San Giorgio (central Adriatic Sea) in May 2023. This farm was conducting experimental cultivation of oysters, which were taken from their natural habitat off the coast at the age of several months.

In the laboratory, oysters were opened, the shells were fractured with pliers and carefully inspected under a stereo microscope for the presence of boring worms. Moreover, fouling on valves, as well as the water in which the oysters were transported, were inspected using a stereo microscope to collect additional *Polydora* specimens which left their burrows due to stress. To test a new method which provokes stress and drives boring polychaetes out of the shells, the two European oysters inspected, were immersed in low salinity water solution (30 g of kitchen salt per 1 L of tap water) immediately after sampling and incubated for a few hours. This method showed to be very efficient since *Polydora* specimens came out of the shells intact, while fracturing of shells with pliers caused damages of many specimens and precluded the possibility of their determination. Mussels in 2 L clump samples were too numerous to open, control inside and fracture each of them, so a subsample of 20 mussels per clump were randomly chosen to perform that procedure (720 mussels in total). In none of these mussels traces of *Polydora* burrows were noted, nor *Polydora* specimens were found after fracturing and careful inspection of content under a stereo microscope. Thus, it was decided not to repeat the procedure for each single mussel. However, all mussel clumps (divided into smaller pieces) were carefully inspected under stereo microscope and *Polydora* specimens were isolated.

For molecular analysis, worm fragments were preserved in 95 % ethanol. For morphological examination, worms were fixed in 10 % formalin solution, rinsed in fresh water, and then transferred to 70 %

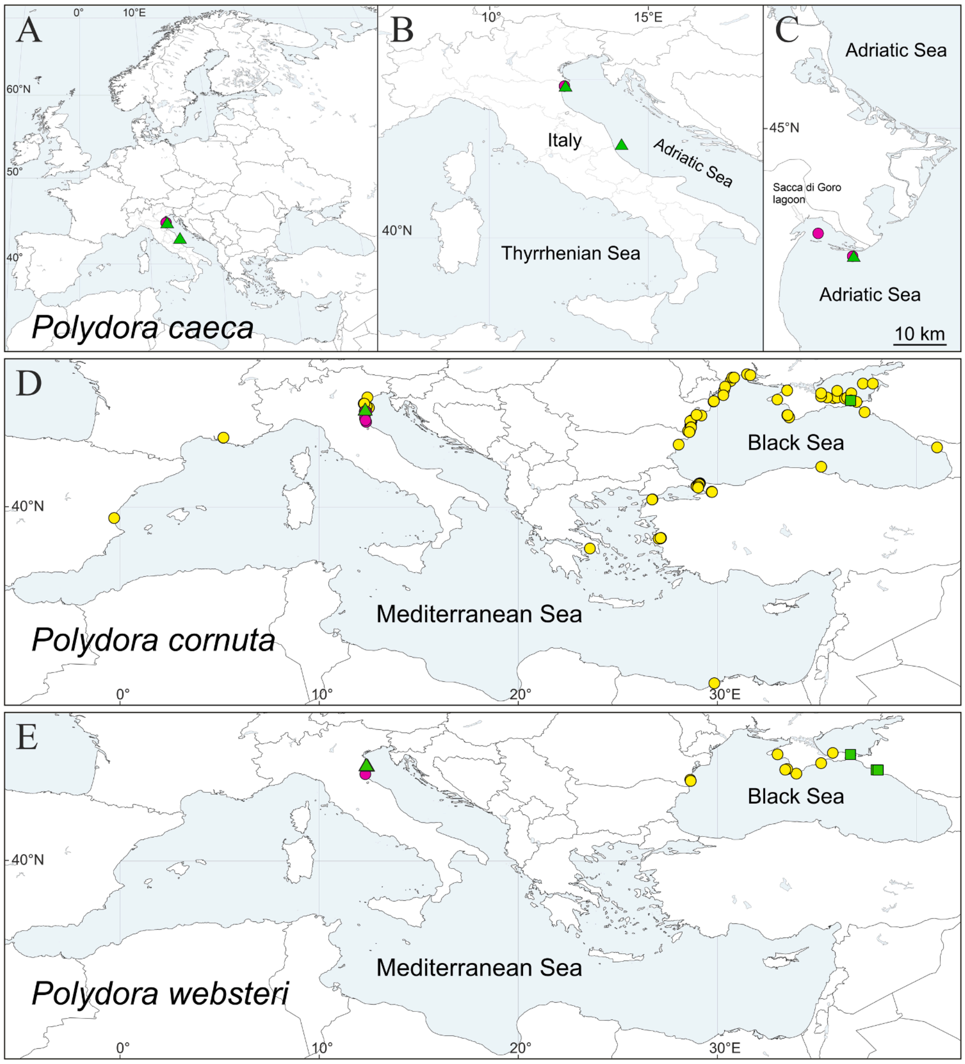

Fig. 1. Maps showing sampling sites and records of three *Polydora* species from the Mediterranean Sea and the adjacent Black Sea and the Sea of Azov. A–C – *P. caeca*. D – *P. cornuta*. E – *P. websteri*. Magenta circles – specimens identified based on the morphology in the present study (Supplementary Table ESM1); yellow circles – specimens identified based on the morphology by other authors (Supplementary Table ESM2); green triangles – specimens sequenced in the present study (Supplementary Table ESM4); green squares – specimens sequenced by other authors (Supplementary Table ESM4).

ethanol. Specimens were examined under light microscopes equipped with digital cameras. Images of multiple focal layers were stacked using Zerene Stacker 1.04 software. After morphological examination, worms were deposited in the polychaete collection of the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology (MIMB), Vladivostok, Russia. Complete information on newly collected material of three *Polydora* species is given in Supplementary Table ESM1. Information on the records of the three species from the Mediterranean and the adjacent Black Sea and the Sea of Azov by other authors is given in Supplementary Table ESM2. A list of the museums and other collections (and their acronyms) holding the samples which were reported or examined in this study is given in Supplementary Table ESM3. To link sequences used in the molecular analysis in the present study with the corresponding data, unique numbers from the second author's database (VIR) are given to samples in Supplementary Tables ESM1, 2, 4. These numbers without letters precede collecting locations names on the phylogenetic tree.

Sampling locations of three *Polydora* species identified in the present study and records of these species from the Mediterranean and adjacent Black Sea and the Sea of Azov by other authors are plotted on maps using QGIS 3.28.11 software and the geodata provided by the OpenStreetMap Project (https://osmdata.openstreetmap.de) (Fig. 1). Final maps and plates were prepared using CorelDRAW®2022 software.

2.2. DNA extraction, amplification, and sequencing

Ten *Polydora* specimens were chosen for molecular analysis. We used the cetyl trimethylammonium bromide (CTAB)-based protocol for the extraction of DNA. Partial sequences of nuclear *18S* and *28S* rRNA and mitochondrial *16S* rRNA and *COI* genes were amplified by PCR using the primer pairs 18Sa2/9 R, 28SC1/28SC2, 16Sar/16Sbr and Dorid COI.3 F/Dorid COI.1 R (Radashevsky and Pankova, 2013; Radashevsky et al., 2014; Sato-Okoshi et al., 2023; Martinelli et al., 2024). We performed the PCR in a 24 µL reaction mixture containing 2.5 µL of template DNA, 14.3 µL of sterilized water, 2.5 µL of 1 × buffer, 1.5 µL of 2.5 µM MgCl2, 1 µL of 200 µM dNTPs mix, 1 µL of 0.5 µM of each primer and 0.2 µL of 5 U Taq polymerase. Cycling parameters were as follows: denaturation at 94°C for 5 min, 35 cycles at 94°C (*16S*, *18S* and 28S) and 95°C (*COI*) for 15 s, 49°C (*18S*), 52°C (*28S* and *COI*) and 57°C (*16S*) for 30 s and 72°C for 60 s, with a final extension at 72°C for 7 min for Taq polymerase. PCR products were purified using ExoSAP-IT (Affymetrix, Cleveland, OH) and sequenced by MACROGEN EUROPE (Milan, Italy). Forward and reverse complementary sequences and contigs were assembled using MEGA 11. GenBank accession numbers of the obtained sequences are given in Supplementary Table ESM4.

2.3. Molecular analysis

In the analysis, we also included sequences of *Polydora* spp. obtained in our previous studies (Radashevsky et al., 2023a; 2023b) and provided by other authors (Rice et al., 2008; Sato-Okoshi and Abe, 2013; Ye et al., 2015; 2017; 2019a,b; Abe and Sato-Okoshi, 2020; Malan et al., 2020; Martinelli et al., 2020; Waser et al., 2020; Abe and Sato-Okoshi, 2021; Rodewald et al., 2021; Silverbrand et al., 2021; Sato-Okoshi et al., 2023). The phylogenetic tree was rooted using the sequences of *Dipolydora giardi* (Mesnil, 1893) according to the phylogenetic analysis of molecular data for spionid polychaetes, where *Polydora* appeared sister to the *Dipolydora* clade (Abe and Sato-Okoshi, 2021: fig. 2; Radashevsky et al. unpublished).

We aligned DNA sequences using the ClustalW method implemented in the MEGA 11 software (Tamura et al., 2021). The sequences were not trimmed to match the shortest one in the alignment. Ambiguous positions and internal gaps were excluded from subsequent analysis using GBlocks (Castresana, 2000) with settings for a less stringent selection. We concatenated DNA data partitions using SequenceMatrix (Vaidya et al., 2011). The terminal gaps as well as the lack of some data for individual concatenated sequences were coded as 'missing data'. The number of variable and parsimony informative sites in the datasets, and uncorrected values of sequence divergence (pairwise distances, *p*) both within and between groups, were calculated in MEGA 11 (Tamura et al., 2021). The best-fitting nucleotide substitution models for Bayesian analysis (TIM+I+G for *COI*, TVM+I+G for *16S*, GTR+I+G for *18S*, GTR+I for *28S*) were selected in MrModeltest version 3.7 (Posada and Crandall, 1998) using Akaike Information Criterion (AIC).

Phylogenetic analysis was conducted with MrBayes 3.2.7 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) via the CIPRES web portal (Miller et al., 2010). The Bayesian analysis was run with 20,000,000 generations, four parallel chains and sample frequencies set to 500, in two separate runs. Based on the convergence of likelihood scores, 25 % of sampled trees were discarded as burn-in.

3. Results

3.1. Molecular analysis

The combined aligned sequences, with gaps excluded, comprised in total 4129 bp, including 1134 bp for *COI* (100 % of original aligned sequences), 447 bp (93.1 %) for *16S* rDNA, 1781 bp (99.4 %) for *18S* rDNA and 767 bp (98.8 %) for *28S* rDNA. The combined concatenated dataset contained 691 variable sites, 668 of which were parsimony informative. The frequency of variable sites in the datasets was 36.6 % for *COI*, 19.2 % for *16S* rDNA, 5.5 % for *18S* rDNA, and 12 % for *28S* rDNA. The average *p*-distances for the individual gene fragments between the groups of samples are given in Supplementary Table ESM5. The Bayesian analysis of the combined dataset resulted in a fully resolved consensus tree with high support of all branches and indicated the presence of three species from our samples, *Polydora caeca* Webster, 1879a, *P. cornuta* Bosc, 1802 and *P. websteri* Hartman in Loosanoff and Engle, 1943 (Fig. 2).

The *18S* rDNA sequences of *P. caeca* from Italy were identical ($p = 0.00$ %) to the sequences of *P. caeca* from USA (New York and Rhode Island), China, Japan, and South Korea. The *16S* rDNA and *COI* sequences from Italy were invariable. The *16S* rDNA and *COI* haplotypes from Italy were common to those of one specimen from South Korea. The same *COI* haplotype was detected in one specimen from Japan (Tokyo). The maximum uncorrected *p*-distance values between Italian individuals and *P. caeca* from other localities were 0.35 % for *28S*, 0.9 % for *16S*, and 4.57 % for *COI* gene fragments. The *18S* and *28S* rDNA sequences of *P. websteri* from Italy and other locations were invariable, except *18S* sequence of one Italian specimen, which differed from the others by one substitution ($p = 0.17$–0.19 %). For *P. cornuta* from Italy, we have sequenced only *28S* rDNA gene fragments of two individuals. The obtained sequences were identical ($p = 0.00$ %) to those of *P. cornuta* from Japan (Honshu Is.), Russia (Sea of Azov), and USA (California, Maine). Our analysis of a small set of available sequences revealed a large genetic distance between *P. cornuta* and specimens from Florida studied by Rice et al. (2008), as well as high genetic variability of *P. cornuta* populations (Supplementary Table ESM5).

3.2. Morphology and biology

Spionidae Grube, 1850
Polydora Bosc, 1802

3.2.1. Polydora caeca Webster, 1879

Fig. 3

Polydora caeca Webster (1879b): 252–253, pl. IX: figs. 119–122. Radashevsky (2025): 3–6. Not *Leucodorum coecum* Örsted, 1843.

Polydora neocaeca Williams and Radashevsky, 1999: 117–127, figs. 1–5 (adult and larval morphology). Williams 2000: 123–129, figs. 1–3 (sperm ultrastructure). Malan et al. (2020): 9–12, figs. 2–4. Davinack and Hill (2022): 123–128. *Fide* Radashevsky (2025).

Polydora haswelli: Read and Handley (2004): 30–31, text figs. Read (2010): 83–100, figs. 1A–G, 2A, C, E, 3A, B, 4A–C. Sato-Okoshi et al. (2012): 85, figs. 2F, 3D, 4C, 5A. Sato-Okoshi and Abe (2013): 1282, fig. 4A–F. Not Blake and Kudenov (1978). *Fide* Radashevsky (2025).

Material examined: Italy, Adriatic Sea, Emilia-Romagna Region: outside of Sacca di Goro lagoon, from shells of cultured Pacific oysters *M. gigas*, May 2020, MIMB 47671 (5); Oct 2020, MIMB 47672 (1). Inside of Sacca di Goro lagoon, from shells of wild oysters *M. gigas*, May 2020, MIMB 47670 (3). Marche Region: Porto San Giorgio, from shells of cultured European flat oyster *O. edulis*, taken for cultivation from their natural habitat off the coast at the age of several months, May 2023, VIR 26060 (2). Complete information on the examined specimens is given in Supplementary Table ESM1.

Diagnostic features: Adults up to 18 mm long, 1.2 mm wide for 100 chaetigers. Palps with up to 15 paired black bands on sides of frontal longitudinal groove (Fig. 3D); narrow black stripes present on anterior lateral sides of prostomium (in front of eyes); paired black spots present on dorsal side of peristomium and 2−4 anterior chaetigers (Fig. 3A, C); median black spots present on ventral side of chaetigers 2 and 3 (Fig. 3B) or chaetigers 2−4 (some spots absent in some individuals). Prostomium incised anteriorly. Caruncle to middle of chaetiger 4 (shorter in small individuals). Occipital antenna absent. Chaetiger 5 twice as large as chaetiger 4 or 6, with dorsal superior and ventral capillaries, up to seven dorsal heavy falcate spines alternating with pennoned companion chaetae (Fig. 3E). Falcate spines with a subterminal lateral longitudinal flange; upper part of flange partly broken in old worn spines in anterior part of row; outer part of flange thick, resembling narrow tooth connected to main fang by thin sheath in young spines in posterior part of row. Bidentate hooded hooks in neuropodia from chaetiger 7 onwards. Branchiae from chaetiger 7, absent on 1/3−1/4 of body. Posterior notopodia with only capillary chaetae.

Habitat: *Polydora caeca* is an opportunistic borer of various calcareous biogenic substrata. It occurs worldwide (see *Remarks* below) in the intertidal and shallow water, burrowing in shells of various live bivalves and gastropods, empty gastropod shells inhabited by hermit crabs, and in corals (Radashevsky, 2025). In this study, worms were found in U-shaped burrows in shells of the cultured and wild Pacific oysters *M. gigas* and cultured European flat oyster *O. edulis*.

Remarks: *Polydora caeca* was originally described boring in a mollusc shell from Virginia, USA, by Webster (1879b). Hartman in Loosanoff and Engle (1943) considered it as a homonym of *Polydora coeca* (Örsted, 1843) from Denmark and described *P. websteri* Hartman in Loosanoff and Engle, 1943 from Milford, Connecticut, USA, which was long considered a replacement name for *P. caeca* Webster. Radashevsky and

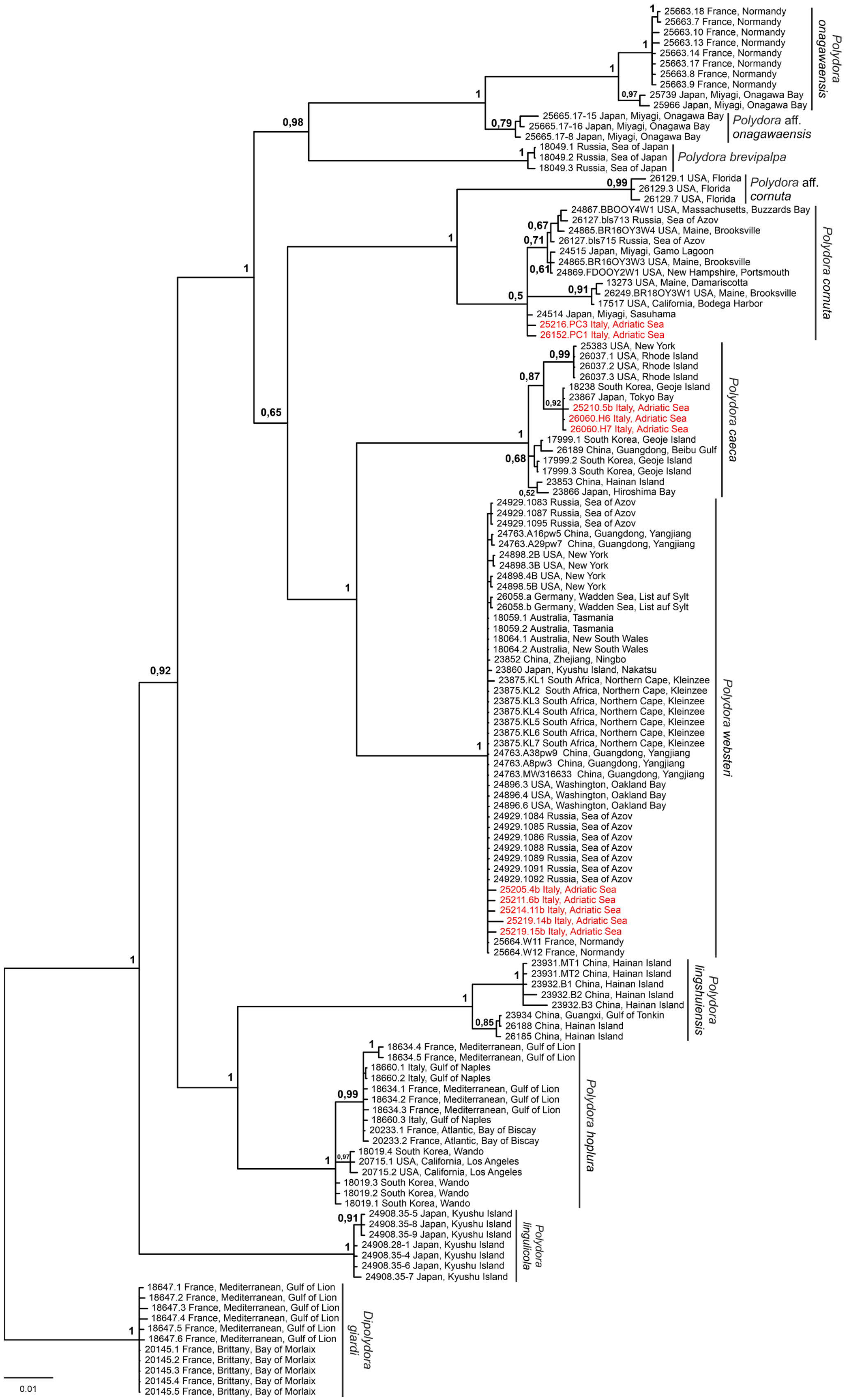

Fig. 2. Majority rule consensus tree of the Bayesian inference analysis of the combined *COI*, *16S*, *18S* and *28S* gene sequences of *Polydora* spp. rooted with sequences of *Dipolydora giardi*. Posterior probabilities are shown on the branches. The numbers preceding collecting locations are unique numbers from the VIR database linking the individuals on the tree with the sampling data in Supplementary Tables ESM1, 2, 4; isolate numbers are separated from sample numbers by dots.

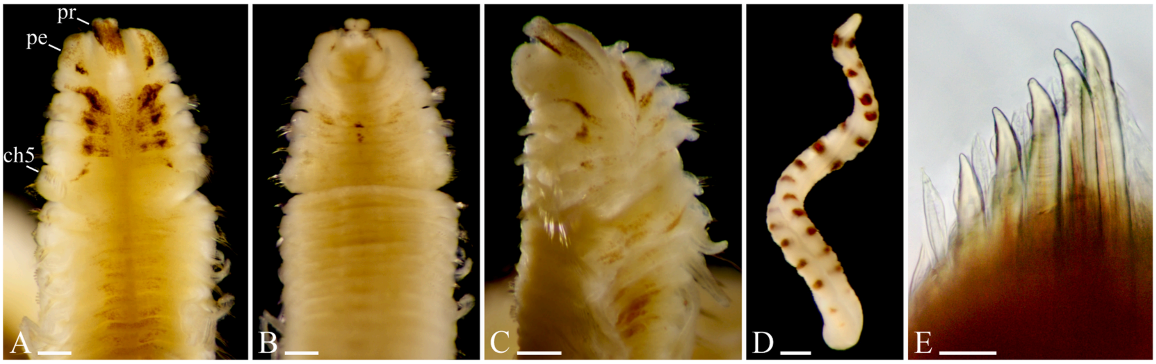

Fig. 3. Adult morphology of *Polydora caeca* boring into shell of the cultured Pacific oyster *Magallana gigas* collected outside of Sacca di Goro lagoon, Adriatic Sea (MIMB 47671): A – anterior end, dorsal view, palps missing, showing typical pigmentation on prostomium, peristomium and anterior chaetigers; B – anterior end, ventral view, showing typical median pigmentation on chaetigers 2 and 3; C – anterior end, palps missing, left dorso-lateral view. D – palp, showing typical black bands on sides of frontal longitudinal groove; E – chaetiger 5 dorsal falcate spines alternating with pennoned companion chaetae. Abbreviations: *ch5* – chaetiger 5; *pe* – peristomium; *pr* – prostomium. Scale bars: A–C – 200 µm; E – 30 µm.

Williams (1998) realized that Webster (1879b) and Hartman in Loosanoff and Engle (1943) dealt with two different species, and Williams and Radashevsky (1999) described shell-boring worms from Rhode Island as a new species, *Polydora neocaeca* Williams and Radashevsky, (1999). Although Radashevsky and Williams (2000: 111) noted that "*P. neocaeca* represents the same taxon as Webster described", they established *P. neocaeca* as a new nominal, not replacement, species, which "has its own holotype, description and type locality". Establishing *P. neocaeca*, Williams and Radashevsky (1999) overlooked *Polydora haswelli* Blake and Kudenov, 1978 described from Sydney Harbour, Australia. The type specimens of the latter species were all from sandy bottom, but three non-type specimens were from oyster mud blisters in Camden Haven, Australia. This gave the impression that *P. haswelli* is capable of boring in mollusc shells, and soon the species was reported as boring in oysters, mussels and scallops in Australia and New Zealand (Skeel, 1979; Pregenzer, 1983; Handley, 2003; Read and Handley, 2004; Read, 2010). Outside of Australia and New Zealand, shell-boring *P.* cf. *haswelli* was reported from Brazil (Radashevsky et al., 2006) and then "suggested to be distributed widely and commonly in mollusk shells at least in Australia, New Zealand, Korea, and possibly Japan and Canada" (Sato-Okoshi et al., 2012: 89), and then reported from Japan (Sato-Okoshi and Abe, 2013), China (Ye et al., 2015; 2019b) and South Korea (Lee et al., 2020). Gradually, it was suspected that the tube-building type specimens of *P. haswelli* may not be conspecific with shell-boring worms in Australia and other countries (Walker, 2013). Malan et al. (2020: 1) reexamined the types and supported the hypothesis that "sand tube-dwelling … and shell-boring species identified as *P. haswelli* are different species." They recommended that "shell-boring species previously identified as *P. haswelli* be referred to *P. neocaeca*."

Radashevsky (2025) once again reviewed the taxonomic history of *P. caeca*, *P. haswelli* and *P. neocaeca*, previous descriptions of these species and specimens from different localities. He showed that the original description of *P. caeca* was detailed and correct in all essential respects and Webster (1879b: 52–53) unambiguously distinguished this species from other *Polydora* on the Atlantic coast of North America. To resolve the uncertainty of the names, Radashevsky (2025) treated *P. neocaeca* Williams and Radashevsky, 1999 as a junior subjective synonym of *P. caeca* Webster, 1879. This treatment also resolved uncertainty of the taxonomy of shell-boring worms with morphological features of *P. haswelli-neocaeca*. No matter if they are conspecific or not with the tube-dwelling worms from Sydney Harbour, they belong to *P. caeca* Webster. The molecular analysis performed in the present study confirmed their conspecificity. The only uncertainty remains regarding the tube-dwelling worms from Sydney Harbour. If future molecular analysis confirms that they are different from shell-boring worms, *P. haswelli* should be considered as a valid tube-dwelling species. If not, *P. haswelli* should be treated as a junior synonym of *P. caeca*.

In our first brief report of *Polydora* associated with mussel and oyster aggregations in the Mediterranean, we used the name *P. haswelli* for worms boring into oyster shells in Italy (Mikac et al., 2023a, 2023b). However, after the taxonomic revision provided by Radashevsky (2025), we follow his suggestion and apply the name *P. caeca* for these worms. *Polydora caeca* is an oyster pest that can cause serious problems for molluscs aquaculture worldwide (Malan et al., 2020).

Distribution: As *P. haswelli* or *P. neocaeca*, shell-boring *P. caeca* Webster was reported from North and South America, Asia, Australia, and New Zealand (see Radashevsky, 2025). None of these species have been reported from European waters. We report this species from the northern and central parts of the Adriatic Sea (Fig. 1A–C), hereby revealing its first finding for the Europe and the Mediterranean.

A series of confusing records (without any details of worm morphology) was provided in ecological studies from Turkey. Çinar et al. (2006) first reported *P. coeca* Örsted, 1843 from a 9-meter-deep station in Izmir Bay, Aegean Sea, and then from the Sea of Marmara (Çinar et al., 2011). Dağli et al. (2007) and Çinar et al. (2008) reported *P. coeca* Webster, 1879 from the faunal assemblages of the mussel *M. galloprovincialis* in Izmir Bay. In the *Checklist of Annelida from the coasts of Turkey*, Çinar et al. (2014) included only *Dipolydora coeca* (Örsted); *P. coeca* Webster has not been mentioned in their publications since. In the study on bioeroding (boring) polychaetes from the Aegean Sea, Çinar and Dagli (2021) reported *Dipolydora coeca* (Örsted) as one of the dominant species with the highest frequency scores (>50 %) in the 0–5 m depth interval, despite *D. coeca* is an exclusively tube-dwelling species, common in the Northwest Atlantic and Arctic waters (Radashevsky unpublished).

3.2.2. *Polydora cornuta* Bosc, 1802

Polydora cornuta Bosc, 1802: 151–153, pl. 12, figs. 7–8. Blake and Maciolek (1987): 12 –14, fig. 1. Blake 1996: 171, fig. 4.28 H. Çinar et al. (2005): 824 –826, figs. 3–4. Radashevsky (2005): 3 –19, figs. 1–4 (adult and larval morphology, references); 2025: 6 –7. Surugiu (2005): 66 –67; 2012: 47 –50, Fig. 2. Boltachova and Lisitskaya (2007): 33 –35, fig. 1. Radashevsky and Selifonova (2013): 263 –264. Bertasi (2016): 79 –85, fig. 2–5. Kurt-Sahin et al. (2019): 160 –161, fig. 7. Boltachova et al. (2021): 14 –15.

Polydora ligni Webster 1879a: 119; 1886: 148–149, pl. 8, figs. 45–47. *Fide* Blake and Maciolek (1987).

Material examined: Italy, Adriatic Sea, Emilia-Romagna Region: outside of Sacca di Goro lagoon, on shells of cultured Pacific oysters *M. gigas*, May 2020, MIMB 47686 (3). Inside of Sacca di Goro lagoon, on shells of wild oysters *M. gigas*, May 2020, MIMB 47683 (1), Oct 2020, MIMB 47684 (2); on shells of wild Mediterranean mussels *M. galloprovincialis*, May 2020, MIMB 47682 (9); on shells of cultured oysters *M. gigas*, Oct 2020, VIR 26152 (1). Bevano river estuary, on shells of wild Pacific oysters *M. gigas*, Oct 2020, MIMB 47685 (6). Punta Marina, on shells of wild mussel *M. galloprovincialis*, May 2020, MIMB 47681 (2). Complete information on the examined specimens is given in Supplementary Table ESM1.

Diagnostic features: Adults up to 20 mm long, 1 mm wide for 80 chaetigers. Prostomium bifurcated anteriorly. Caruncle to end of chaetiger 3 (shorter in small individuals). Cirriform occipital antenna present. Chaetiger 5 twice as large as chaetiger 4 or 6, with up to seven dorsal heavy falcate spines alternating with companion chaetae; falcate spines with a small lateral tooth and a small subdistal longitudinal flange above it; companion chaetae with feathery, disheveled tips, tightly adhered to convex side of falcate spines; dorsal superior and ventral capillaries absent (present in newly settled juveniles only). Bidentate hooded hooks in neuropodia from chaetiger 7 onwards. Branchiae from chaetiger 7 through most of body. Posterior notopodia with only capillary chaetae.

Habitat: *Polydora cornuta* is an opportunistic tube-dweller, occurring worldwide in intertidal and shallow waters. Adults build silty tubes in soft sediments and on the surface of hard substrata, including mollusc shells. In the Adriatic Sea, worms were first found in silty tubes in soft-bottom sediments (Bertasi, 2016). In 2023, we found this species on the surface of wild and cultured oysters *M. gigas* and wild mussels *M. galloprovincialis* (Mikac et al., 2023a, 2023b).

Remarks: Transportations in ballast waters and ship fouling, as well as on the surface of commercial molluscs, have been proposed as the main vectors of distribution of *P. cornuta* across the globe (Radashevsky, 2005; Radashevsky and Selifonova, 2013). The native distribution, as well as the age and routes of anthropogenic transportation of this species have never been studied and may no longer be possible to determine due to their roots in the darkness of the ancient past. *Polydora cornuta* is an opportunistic species, tolerant to a wide range of salinity and temperature fluctuations and able to colonize disturbed and organically rich environment and to establish high density populations in a short time (Grassle and Grassle, 1974; Rice and Simon, 1980; Dauer et al., 1981; Zajac 1991a, b; Radashevsky, 2005; Boltachova et al., 2021). It is considered a pollution indicator species in the eastern Mediterranean (Çinar et al., 2012). Adults of this species can be unambiguously distinguished by the presence of occipital antenna, specific shape of the companion chaetae alternating with falcate spines in notopodia of chaetiger 5, and absence of dorsal superior and ventral capillaries in chaetiger 5.

Genetic studies on *P. cornuta* are quite few and mainly focused on local populations (Rice et al., 2008; Takata et al., 2011; David and Krick, 2019; Abe and Sato-Okoshi, 2021). Rice et al. (2008) suggested that *P. cornuta* populations in North America represent a cryptic species complex of at least three distinct lineages but did not study or permit further study of these. Four gene fragments were sequenced in two individuals of *P. cornuta* from the Strait of Kerch, which connects the Black Sea with the Sea of Azov (Ptushkin and Moskalenko GenBank; Supplementary Table ESM4). In Italy, we have sequenced only *28S* rDNA gene fragments from two individuals. These are the only available sequences of *P. cornuta* from the whole Mediterranean.

Distribution: *Polydora cornuta* was originally described from South Carolina, but in European waters it was mainly known by its junior synonym *Polydora ligni* Webster, 1879. The species has been widely reported from temperate and subtropical waters throughout the world. In 1962, adult worms were first recorded from the north-western part of the Black Sea (Losovskaya and Nesterova, 1964; Losovskaya, 1969). They were widely reported from the Black Sea and the Sea of Azov but misidentified as *P. ciliata* (Johnston, 1838), *P. ciliata limicola* and *P. limicola* Annenkova, 1934 until Radashevsky and Selifonova (2013) clarified their identity. In the Mediterranean, *P. cornuta* was first recorded from Valencia (Spain) outer harbour in 1990 (Tena et al., 1991) and then identified in Turkey, Greece, Italy, and France. In Italy, the species was reported from lagoons in the northwestern Adriatic Sea (Bertasi, 2016; Mikac et al., 2023a). Complete information on earlier records of *P. cornuta* from the Mediterranean and the adjacent Black Sea and the Sea of Azov is given in Supplementary Table ESM2 (mapped in Fig. 1D).

3.2.3. *Polydora websteri* Hartman in Loosanoff and Engle, (1943) Fig. 4

Polydora websteri Hartman in Loosanoff and Engle, 1943: 70 –72, fig. 1. Blake (1969): 10 –16, figs 5 –10 (larval morphology); 1971 (Part.): 6 –8, fig. 3. Radashevsky (1999): 110 –112, fig. 1. Surugiu (2005): 67; 2006: 54; 2012: 50 –53, fig. 3. Lisitskaya et al. (2010): 74 –78, fig. 1. Read (2010): 91 –93, fig. 1H–J, 2B, 2D, 2 F, 4D–G. Sato-Okoshi and Abe (2013): 1280 –1281, fig. 2. Ye et al. (2017): 702 –705, figs. 1, 2 (adult and larval morphology). Lisitskaya and Shchurov (2020): 77. Boltachova et al. (2021): 15. Syomin et al. (2021): 95 –100, fig. 2–4. Sato-Okoshi et al. (2023): 213, fig. 5A, B. Davinack et al. (2024): 4–8, fig. 5.

Material examined: Italy, Adriatic Sea, Emilia-Romagna Region: outside of Sacca di Goro lagoon, from shells of cultured oysters *M. gigas*, May 2020, MIMB 47676 (5). Inside of Sacca di Goro lagoon, from shells of wild oysters *M. gigas*, May 2020, MIMB 47673 (11); Oct 2020, MIMB 47674 (8); from shells of wild mussel *M. galloprovincialis*, May 2020, MIMB 47675 (10). Bevano river estuary, from shell of wild oysters *M. gigas*, Oct 2020, MIMB 47687 (1). Complete information on the examined specimens is given in Supplementary Table ESM1.

Diagnostic features: Adults up to 25 mm long, 0.8 mm wide for 90 chaetigers. Palps with narrow continuous (occasionally partially discontinuous) black line on sides of frontal longitudinal groove (Fig. 4A); black pigment absent on body segments. Prostomium incised anteriorly. Caruncle to end of chaetiger 2 (occasionally to middle of chaetiger 3). Occipital antenna absent. Chaetiger 5 twice as large as chaetiger 4 or 6, with dorsal superior and ventral capillaries, up to seven dorsal heavy falcate spines alternating with pennoned companion chaetae (Fig. 4B); falcate spines with a wide lateral flange; upper part of flange partly broken in old worn spines in anterior part of row. Bidentate hooded hooks in neuropodia from chaetiger 7 onwards. Branchiae from chaetiger 7 through most of body. Posterior notopodia with only capillary chaetae.

Habitat: *Polydora websteri* is an opportunistic borer of various calcareous biogenic substrata, occurring worldwide in intertidal and shallow water. It burrows in shells of various live gastropods and bivalves, including abalone, oysters, mussels and clams, as well as empty gastropod shells inhabited by hermit crabs (Radashevsky, 2025). In this study, worms were found in U-shaped burrows in shells of the wild and cultured Pacific oysters *M. gigas* and wild Mediterranean mussel *M. galloprovincialis*.

Remarks: The name *Polydora websteri* Hartman in Loosanoff and Engle, 1943 was proposed as a replacement for *Polydora caeca* Webster, 1879a, a junior secondary homonym of *P. coeca* (Örsted, 1843) (see the above Remarks on *P. caeca*). However, Radashevsky and Williams (1998) showed that Webster and Hartman were dealing with two different species. Accordingly, the specific name *P. websteri* Hartman was conserved (ICZN 2001), and a lectotype from Milford, Connecticut, USA, was designated for *P. websteri* by Radashevsky (1999). Rice et al. (2018) compared sequence divergence at the *COI* gene for *P. websteri* from oysters and scallops from molluscs farms along the US Atlantic and Gulf coasts, Hawaii, and Guangdong Province, China. They observed little genetic variation, overall, and a striking lack of genetic differentiation among populations, even for populations from separate ocean basins. Based on these data, they suggested that the high levels of connectivity among populations of *P. websteri* have been produced by human-mediated transport of commercial mollusc products or by shipping. Moreover, they found that the greatest sequence diversity was among the Chinese sequences, the most common haplotype, H3, was

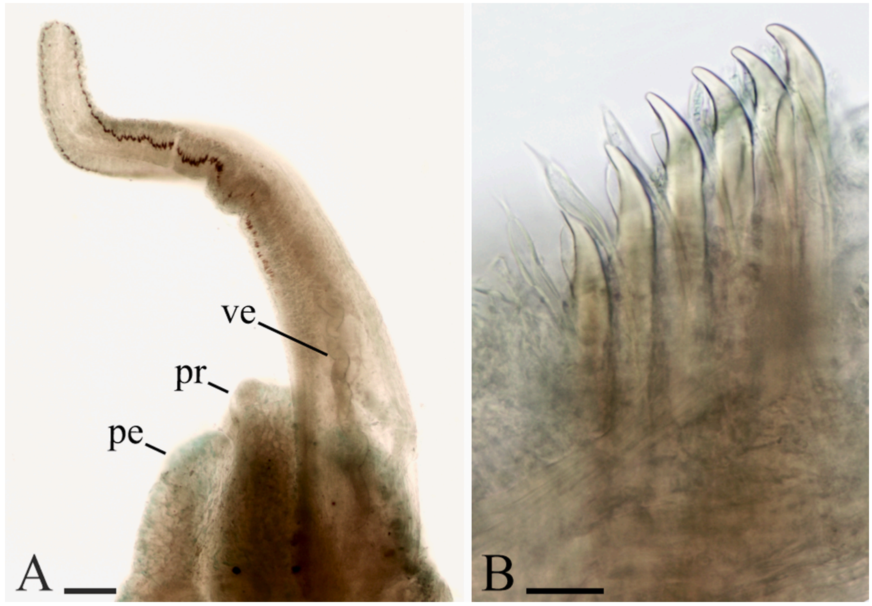

Fig. 4. Adult morphology of *Polydora websteri* boring into shell of the wild Pacific oyster *Magallana gigas* collected inside of Sacca di Goro lagoon, Adriatic Sea (MIMB 47673): A – anterior end, dorsal view, showing typical pigmentation on right palp, left palp missing; B – chaetiger 5 dorsal falcate spines alternating with pennoned companion chaetae. Abbreviations: *pe* – peristomium; *pr* – prostomium; *ve* – single blood vessel inside palp. Scale bars: A – 100 μm; B – 30 μm.

also in China, and therefore suggested that *P. websteri* may be of Asian origin. *Polydora websteri* is an oyster pest that can cause serious problems for mollusc aquaculture (Bailey-Brock and Ringwood, 1982; Nell, 2007; Read, 2010; Rodewald et al., 2021).

Distribution: Originally described from Connecticut, *P. websteri* has been widely reported from temperate and subtropical waters throughout the world. In the Black Sea, it was first found in the western part (Romania; Surugiu, 2005, 2006), then in the northern part (Crimea; Gaevskaya and Lebedovskaya, 2010; Lisitskaya et al., 2010; Boltachova et al., 2021), subsequently in Kerch Strait and the Sea of Azov (Syomin et al., 2021) and recently in the north-western part (Ukraine; Stadnichenko et al., 2024). For the Mediterranean, it was first preliminary reported boring into shells of wild and cultured oysters in the northern Adriatic Sea, Italy (Mikac et al., 2023a, 2023b). Present study confirms its first finding for the Mediterranean. Complete information on records of *P. websteri* from the Mediterranean and the adjacent Black Sea and the Sea of Azov is given in Supplementary Table ESM2 (mapped in Fig. 1E).

4. Discussion

The molecular analysis performed in the present study confirmed our preliminary identification of the Adriatic *Polydora* associated with mussels and oysters based on their morphology. Three species have been identified: *P. caeca*, *P. cornuta* and *P. websteri*, all non-native for the Mediterranean. Adults of these species can be unambiguously distinguished and identified according to their habitat and diagnostic morphological features as described above, when these features are fully developed. However, juveniles and even adults of shell-boring *P. caeca* and *P. websteri* can be confused with each other when the specific pigmentation is not developed. Moreover, they can be misidentified and assigned to other similar, commonly reported species (e.g. *P. ciliata* or *P. hoplura*), since the taxonomic revision of the Mediterranean *Polydora* has not yet been completed. In fact, the presence of *P. caeca* and *P. websteri* in the Mediterranean Sea might have been overlooked for a long time, due to these misidentifications. In this regard, all previous records of shell-boring *P. ciliata* in the basin require further study and verification, since some of these records might likely belong to *P. websteri*, or even *P. caeca* (Manchenko and Radashevsky, 1998; Boonzaaier et al., 2014). *Polydora ciliata* was originally described from the North Sea, Northumberland, UK, and its habitat preferences and taxonomy remain uncertain to date (Radashevsky and Pankova, 2006).

Polydora websteri and *P. caeca* are spreading worldwide, apparently mainly by transporting infested molluscs for aquaculture purposes (Simon and Sato-Okoshi, 2015; Rice et al., 2018; Malan et al., 2020; Radashevsky, 2025). Our findings of these species in the Mediterranean Sea support that they are extending their distribution range. Shell-boring *P. caeca*, originally described from the northwest Atlantic (Virginia, USA), has never been recorded from the European waters or Mediterranean until now (see Radashevsky, 2025). On the other hand, *P. websteri*, likely native to the Asian Pacific, was already reported in Europe, firstly in 1997 as boring in the limestone rock in the Black Sea (Romania) (Surugiu, 2005). Different findings along the Romanian and northern coasts of the Black Sea followed, from the limestone rocks and shells of the cultured oysters and mussels (Surugiu, 2006; Gaevskaya and Lebedovskaya, 2010; Lisitskaya et al., 2010; Surugiu, 2012; Lisitskaya and Shchurov, 2020; Boltachova et al., 2021). In 2020 the species was also reported boring into shells of the bivalve *Anadara kagoshimensis* (Tokunaga, 1906) in the Sea of Azov, Russia (Syomin et al., 2021), while in 2023 and 2024 it was found in the shells of wild mussel *M. galloprovincialis* in the Sea of Azov, Russia and along the north-western coast of the Black Sea, Ukraine (Lisitskaya et al., 2024; Stadnichenko et al., 2024). Recently, the species was found in the North European Atlantic waters, invading cultured Pacific oysters in the Wadden Sea (Netherlands and Germany, Waser et al., 2020) and English channel (Normandy, France, Sato-Okoshi et al., 2023), and wild Pacific oysters on the western coast of Sweden (Obst, 2020). Considering frequent recent findings of infested oysters along European coasts, our Mediterranean records are not surprising. After detection of *P. websteri* in Swedish waters, the Native Oyster Restoration Alliance (NORA) expressed the concern for its expansion and potential infection of the native European oyster *O. edulis*, and launched the call to report eventual findings of this species in European oysters or other native bivalves, apart from *M. gigas* (Wrange, 2021). In this context our results are particularly important for the ongoing initiatives to restore the European oyster in the North Atlantic and the Mediterranean. New polydorins could be introduced into restoration sites by transplanted oysters or infest them later, jeopardizing successful reef restoration. Therefore, managers should be informed, and regular monitoring of oyster pests should be carried out as part of the restoration projects.

Import and export of mussel and oyster seeds and adults are regularly performed by the aquaculture companies in the northern Adriatic Sea (Fossi et al. unpublished). Commerce and translocations are carried out between Italian farms, and hatcheries and farms in Greece, France and Spain, placed both in the Mediterranean and along the Atlantic coast. Thus, if new polydorins have been introduced in the Adriatic Sea by transportation of molluscs, it can be suspected that there are more aquaculture sites in Europe, including the Mediterranean, where these species might have been already established but remained unnoticed to date. Translocation activities could contribute to the further spread of *P. websteri* and *P. caeca* in the Adriatic Sea and the Mediterranean. Thus, it is important to strengthen collaboration between scientists, mollusc farmers and management authorities to develop successful monitoring and regulatory measures to prevent their introduction and spread.

The tube-dwelling *P. cornuta* was in this research reported for the first time on the surface of wild and cultured oysters in the Mediterranean (Mikac et al., 2023a, 2023b). Although this species does not bore into shells, it can become a significant pest in molluscs aquaculture. Excessive growth of this worm on the surface of molluscs shells may result in accumulation of sediment, feces, and rejected material which decomposes, and provoke death of molluscs (Galtsoff, 1964). Moreover, dense aggregations of mud tubes may eventually encumber aquaculture equipment. Thus, new findings of this opportunistic species on oysters in our research, especially in estuary and lagoon area, call for additional attention and monitoring in these environments. Despite the fact that this species is distributed all over the world, including the Mediterranean, it was discovered in the Adriatic Sea quite recently, on the soft bottom in the lagoons of the northwestern Adriatic, relatively close to the sites of our study (Bertasi, 2016). However, its presence in Italian waters probably dates back at least to early 1990s when it was reported as *P. ligni* (Casellato and Ragazzo, 1997; Tagliapietra et al., 1998; Bertasi, 2016). Also, some previous findings of *P. ciliata* in the Adriatic likely belong to *P. cornuta*, as already confirmed in the Black Sea and the Sea of Azov (Radashevsky and Selifonova, 2013). High genetic variability between *P. cornuta* populations revealed by our analyses, suggests a need for further study of their relationships.

In the aquaculture facilities where our samples were taken, farmers usually do not consider the identities of polydorin pests (Mikac pers. obs.) and treat oysters against shell-borers in general, not individual species, as also has been noticed by researchers in other places (Royer et al., 2006; Rodewald et al., 2021). However, timely detection and correct identification of polydorins in farmed molluscs is important for effective control measures. Correct identification of species would provide information regarding the probability of a species becoming a pest, which depends on its reproductive strategy and the system in which the molluscs are cultured (Simon and Sato-Okoshi, 2015). The detection of *P. caeca* and *P. websteri* pests on several farms, as well as on wild mussels and oysters, in our research requires the development of effective control measures for these species. Such measures have never been applied before in the Adriatic and the Mediterranean aquaculture, making it necessary to draw on established protocols used in other molluscs farming areas where infestations by the same species have been observed, such as the Pacific Northwest of the United States (Martinelli et al., 2022). However, eradication measures may reveal to be impossible because farmed molluscs could be at risk of re-infestation from wild habitats.

Our findings call for further extensive research based on both morphological and molecular analyses to elucidate the distribution of *P. caeca*, *P. cornuta* and *P. websteri* in cultivated and wild mussels and oysters in the Adriatic Sea and the Mediterranean as a whole.

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CRediT authorship contribution statement

Barbara Mikac: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Vasily I. Radashevsky:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Eugenio Fossi:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Victoria V. Pankova:** Writing – review & editing, Data curation. **Marina Antonia Colangelo:** Writing – review & editing, Formal analysis, Data curation. **Giuseppe Prioli:** Writing – review & editing, Funding acquisition. **Marco Abbiati:** Writing – review & editing, Funding acquisition, Conceptualization. **Federica Costantini:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2025.102713.

Data availability

Data will be made available on request.

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