

## Rapid Communication

# New reports on *Pseudopolydora* (Annelida: Spionidae) from the East Coast of Florida, including the non-native species *P. paucibranchiata*

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## Abstract

Invasive alien species pose a threat to ecosystems and the native biodiversity they contain. Accordingly, potential or confirmed invasions require that non-native species are accurately identified and reported. Spionidae is one of the most diverse families of annelid worms, and a dominant group in terms of the number of species that have been introduced to non-native areas. *Pseudopolydora* is a genus of spionids for which most species are known from the Western Pacific. Collections around Fort Pierce, Florida resulted in identification of four *Pseudopolydora* species, including *P. floridensis*, *P. achaeta*, *P. paucibranchiata*, and *P. rosebelae*, with the last three representing new records for the Atlantic coast of North America. Specimens were identified based on morphological descriptions for this group, and the standard COI barcode region was sequenced. Introductions and subsequent invasions of marine worms such as spionids often go unrecognized and thus their ecological impacts understudied. Here, we call attention to non-native *Pseudopolydora* species so that their dispersal potentials and ecological consequences can be investigated.

**Key words:** Northwestern Atlantic Ocean, Indian River Lagoon, *Polydora* complex, polychaete, introduced species, COI

## Introduction

With around 600 species described in 39 genera (Blake et al. 2020; Blake and Ramey-Balci 2020), Spionidae Grube, 1850 is one of the most diverse families of annelid worms and a dominant group of marine invertebrates in benthic sediments. Within Spionidae, *Pseudopolydora* Czerniavsky, 1881 comprises 22 recognized species with most of them known from the Western Pacific (Radashovsky and Migotto 2009; Abe et al. 2016; Simon et al. 2019) where they inhabit muddy and sandy sediments or shells of gastropods and bivalves (Simon 2009). Many spionids are known to have a widespread distribution, particularly species associated with calcareous substrates that have been transported by humans including corals and mollusc shells (Sato-Okoshi et al. 2017). Notably, spionids have been ranked first in terms of the number of recognized introduced species among polychaetous annelids (Çınar 2013).

*Pseudopolydora* is one of nine recognized genera that comprise the “*Polydora* complex”, a group of spionids characterized by the 5<sup>th</sup> chaetiger seemingly wider than adjacent ones and showing a row of thick spines on notopodia. However, in contrast to other polydorids, the size of the 5<sup>th</sup> chaetiger in *Pseudopolydora* can look very similar to the 4<sup>th</sup> and 6<sup>th</sup> chaetigers (Radashovsky and Hsieh 2000). Only a single species of *Pseudopolydora*, *P. floridensis* Delgado-Blas, 2008 has been described from the Northwest Atlantic (Delgado-Blas 2008). However, there are more general reports of *Pseudopolydora* sp. from the coast of Florida (Santos and Simon 1980; Sheridan 1997). Even though these reports were not characterized to species, they indicate the presence of *Pseudopolydora* in this region. Further south, species have been recognized from the Caribbean Sea and Southwestern Atlantic Ocean, including *P. antennata* (Claparède, 1869) from Guadeloupe, *P. floridensis* from Venezuela, and *P. rosebelae* Radashovsky and Migotto, 2009, *P. achaeta* Radashovsky and Hsieh, 2000 and *P. diopatra* Hsieh, 1992 from Brazil (Amoureux 1980; Gillet 1986; Lana et al. 2006; Radashovsky and Migotto 2009; Díaz-Díaz et al. 2016; Radashovsky et al. 2020).

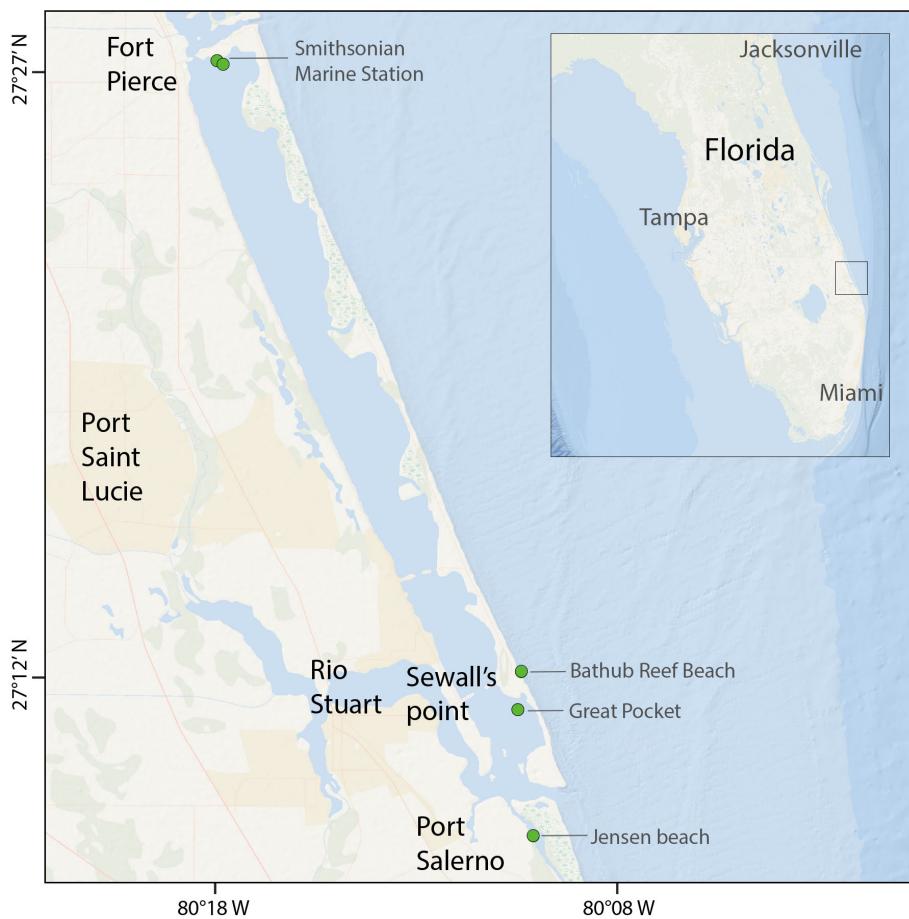
Among *Pseudopolydora*, *P. paucibranchiata* (Okuda, 1937) originally described from Japan, is now a widely distributed species with records from the Northeast Pacific, Southwest Pacific and Northeast Atlantic (Blake and Woodwick 1975; Radashovsky 1993; Dagli and Çınar 2008; Simboura et al. 2010; Çınar et al. 2011; Çınar 2013; Radashovsky et al. 2020). *Pseudopolydora paucibranchiata* is considered native for the Northwest Pacific and introduced elsewhere, including by ship fouling and ballast water (Blake and Woodwick 1975; Carlton 1979). Recent molecular data suggests that *P. paucibranchiata* may represent four species (Radashovsky et al. 2020), but population genetic studies are needed to further investigate its invasion history.

The goal of this study is to identify and report several species of *Pseudopolydora* collected around Fort Pierce, Florida that were fortuitously sampled during a separate project. We discuss the implications of their presence on the Florida coast.

## Materials and methods

### Sample collection

Between July to September of 2017, spionids were collected from the Indian River Lagoon (IRL) at locations near Fort Pierce, Florida (Figure 1; Table 1) using a ponar grab with a sampling area of 225 cm<sup>2</sup> or by shovel when seawater levels were less than 1 m above sediments. Number of samples taken per site to site varied from 1 to 5. Sediment samples were processed with a 300 µm sieve in the field and materials were transported to the Smithsonian Marine Station (SMS) at Fort Pierce for further examination. Live specimens were picked from samples and anesthetized



**Figure 1.** Sampling locations for *Pseudopolydora* from the Indian River Lagoon, including sampling points around Fort Pierce, St. Lucie, Stuart, and Bathtub Reef Beach.

**Table 1.** Sampling information for all *Pseudopolydora* collected in this study.

Species	AUMNH number	Specimens examined	Date collected	Location	Latitude	Longitude	Depth (m)
<i>Pseudopolydora achaeta</i>	45693	2	25-Jul-17	St. Lucie - Great Pocket	27.1496	-80.1675	3
	45694	4	25-Jul-17	St. Lucie - Great Pocket	27.1496	-80.1675	3
	45695	3	25-Jul-17	Stuart - Jensen beach	27.1996	-80.1744	6
	45696	2	10-Jul-17	Fort Pierce - behind SMS	27.4563	-80.3087	1
	45697	3	10-Jul-17	Fort Pierce - behind SMS	27.4563	-80.3087	1
<i>Pseudopolydora floridensis</i>	45698	1	10-Aug-17	Bathtub Reef Beach	27.2146	-80.1729	1
	45699	1	10-Aug-17	Bathtub Reef Beach	27.2146	-80.1729	1
	45700	3	10-Aug-17	Bathtub Reef Beach	27.2146	-80.1729	1
	45701	2	10-Aug-17	Bathtub Reef Beach	27.2146	-80.1729	1
	45703	3	10-Jul-17	Fort Pierce - behind SMS	27.4563	-80.3087	1
<i>Pseudopolydora paucibranchiata</i>	45704	6	10-Jul-17	Fort Pierce - behind SMS	27.4563	-80.3087	1
	45705	1	25-Jul-17	Stuart - Jensen beach	27.1996	-80.1744	6
	45706	3	25-Jul-17	St. Lucie - Great Pocket	27.1496	-80.1675	3
	45707	3	25-Jul-17	Stuart - Jensen beach	27.1996	-80.1744	6
	45708	2	17-Jul-17	Fort Pierce - behind SMS	27.4548	-80.3061	1
<i>Pseudopolydora rosebelae</i>	45709	6	17-Jul-17	Fort Pierce - behind SMS	27.4548	-80.3061	1
	45702	1	17-Jul-17	Fort Pierce - behind SMS	27.4548	-80.3061	1

in 7% magnesium chloride prior to examination or fixation. Spionids were fixed in 5% formalin for voucher specimens, 95% ethanol and RNAlater for molecular studies.

### Morphological examination

A total of 46 *Pseudopolydora* individuals (Table 1) were examined under a Leica MDG41 stereo microscope and Nikon Alphashot-2 compound light microscope. Specimens were photographed with a Leica DFC450 digital microscope camera. Identifications at species level were based on morphological descriptions of Okuda (1937), Blake and Woodwick (1975), Blake and Kudenov (1978), Radashevsky (1993), Delgado-Blas (2008), Radashevsky and Hsieh (2000), Radashevsky and Migotto (2009), and Abe et al. (2016). Specimens were deposited at the Museum of Natural History of Auburn University (AUMNH; Table 1).

### Molecular data

Genomic DNA was extracted from specimens morphologically identified as different species with Qiagen DNeasy® Blood and Tissue Kit, following the manufacturer's protocol. DNA barcodes of a 657 base-pair fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) were amplified and sequenced with the following primers: 2F-spionid-LCO (5'-TACWCMWCYAAUCAYAAASRMATTGG-3') and 1R-spionid-HCO (5'-TAYACTTCDGGRTGTCCRAARAATCA-3') (Bogantes et al. 2018). The polymerase chain reaction (PCR) mixture for 25 µl reaction consisted of 1.5 µl of DNA template, 2.5 µl Mg(OAc)<sub>2</sub> (25 mM), 2.5 µl Taq buffer (10X), 2.5 µl dNTPs (10 mM), 1 µl of each primer (10 µM), 0.3 µl Taq DNA polymerase (25 mM) and 13.7 µl water (ddH<sub>2</sub>O). Thermal cycling protocols consisted of denaturation at 94 °C for 3 min followed by 35 cycles of 94 °C for 30 s, 54 °C for 30 s and 72 °C for 1 min, followed by a final elongation at 72 °C for 8 min. PCR products were purified using the Qiagen QIAquick PCR Purification Kit and bidirectionally Sanger sequenced by GENEWIZ Inc. Sequences were cleaned and proofread with Geneious 2020.1 <https://www.geneious.com/>.

### Results

Individuals were identified as either *Pseudopolydora floridensis*, *P. achaeta*, *P. paucibranchiata* or *P. rosebelae*. Short morphological descriptions of individuals examined for morphological differences among the four *Pseudopolydora* species from Fort Pierce (Table 2) are provided herein. COI barcodes are available for three of the species identified. The fourth species (*P. rosebelae*) was not included due to the lack of sufficient material for both molecular work and a morphological voucher.

Below, we have used a standard species description format to allow data about these Florida *Pseudopolydora* to be easily cross-referenced with each other and formal species descriptions (Okuda 1937; Radashevsky and Hsieh 2000; Delgado-Blas 2008; Radashevsky and Migotto 2009; Abe et al. 2016; Radashevsky et al. 2020).

**Table 2.** Comparison of major morphological differences of the four *Pseudopolydora* collected around Fort Pierce.

Species	Shape prostomium	Caruncle reaching chaetiger	Branchiae	Pigmentation	Shape spines 5 <sup>th</sup> chaetiger
<i>Pseudopolydora achaeta</i>	Blunt	2	7–18	Dark dorsal and ventral lines	Close to a straight line
<i>Pseudopolydora floridensis</i>	T-shaped	7	7–43	No pigmentation	U-shaped
<i>Pseudopolydora paucibranchiata</i>	Rounded	3	7–17	Live specimens with white bands in the palps	J-shaped
<i>Pseudopolydora rosebelae</i>	Incised	2	7–18	Dark and strong pigmentation covering anterior segments	J-shaped

### Systematics

Family: Spionidae Grube, 1850.

Genus: *Pseudopolydora* Czerniavsky, 1881.

#### ***Pseudopolydora achaeta* Radashevsky & Hsieh, 2000**

(Figure 2A, B)

Material examined: AUMNH-45693 (2); AUMNH-45694 (4); AUMNH-45695 (3); AUMNH-45696 (2); AUMNH-45697 (3). GenBank accession numbers: MW830148, MW830149.

Description: Prostomium blunt with four eyes, occipital antenna present. Caruncle extending until end of chaetiger 2. Branchiae from chaetigers 7–18. Notopodial lobes of 1<sup>st</sup> chaetiger reduced, and neuropodial hooded hooks present from chaetiger 8. Anterior region with dark pigmentation on the sides, which is stronger in chaetigers 1–8 and decreasing from chaetigers 9–15 (Figure 2A, B). Pigmentation is also present in the ventral side. Specimens examined have 38 to 55 segments. Spines in 5<sup>th</sup> chaetiger (Figure 2A) are almost in a straight line as described by Radashevsky and Hsieh (2000).

Habitat: specimens were found inside their tubes in muddy, silty, and sandy sediments.

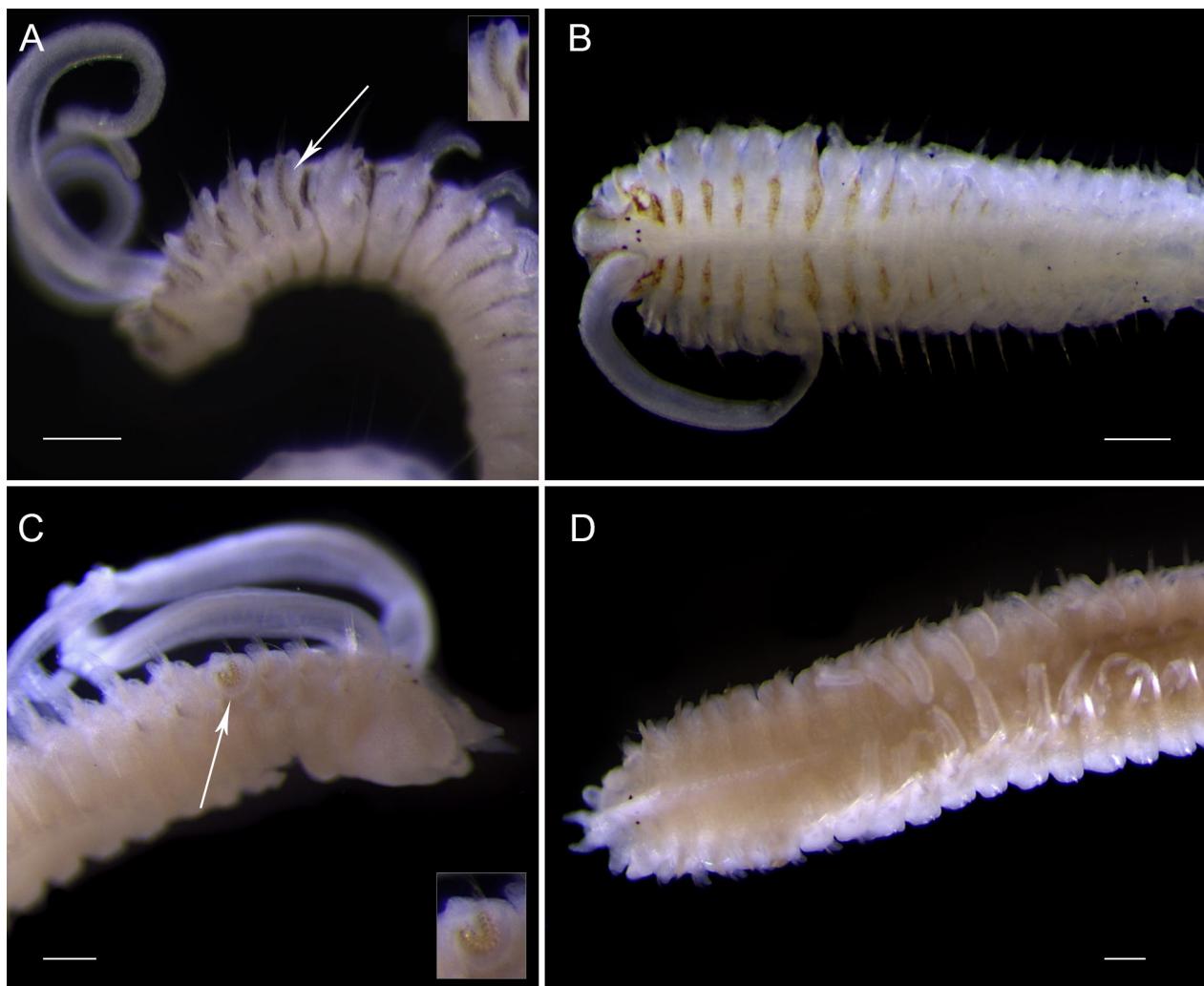
Remarks: *P. achaeta* can be distinguished from other *Pseudopolydora* that have dark pigmentation in the anterior region, in that *P. achaeta* has the spines in the 5<sup>th</sup> chaetiger almost in a straight line (Figure 2A).

#### ***Pseudopolydora floridensis* Delgado-Blas, 2008**

(Figure 2C, D)

Material examined: AUMNH-45698 (1); AUMNH-45699 (1); AUMNH-45700 (3); AUMNH-45701 (2). GenBank accession number: MW830143.

Description: prostomium T-shaped (Figure 2C, D) with four eyes in a trapezoid arrangement, occipital antenna present. Caruncle extending until chaetiger 7. Branchiae present from chaetiger 7 to 43. First chaetiger with neuropodial chaetae only. Neuropodial hooks from chaetiger 8 to 22 in most of the specimens. Chaetiger 5 with modified chaetae and 2 types of spines in a double row with a U-shaped arrangement (Figure 2C), outer row



**Figure 2.** A–B. *Pseudopolydora achaeta*; A. Lateral view and arrangement of spines in 5<sup>th</sup> chaetiger in almost a straight line (arrow); B. Dorsal view of anterior end showing pattern of pigmentation, palp from right side is missing, occipital antenna also missing. C–D. *Pseudopolydora floridensis*; C. Lateral view with U-shaped arrangement of spines in 5<sup>th</sup> chaetiger (arrow); D. dorsal view of anterior end, both palps missing. All scale bars = 0.2 mm. Photo by V.E. Bogantes.

with pennoned spines and inner row with falcate spines as describe by Delgado-Blas (2008).

Habitat: specimens were found inside their tubes from muddy and sandy sediments.

Remarks: *P. floridensis* is similar to *P. corniculata* Radashevsky & Hsieh, 2000, but they can be distinguished in that the later has spines in the 5<sup>th</sup> chaetiger arranged in a J-shaped, while *P. floridensis* has spines in the 5<sup>th</sup> chaetiger in a U-shaped (Figure 2C). Specimens examined in this study show variation in the number of segments with branchiae extending until chaetigers 38 to 43.

#### *Pseudopolydora paucibranchiata* (Okuda, 1937) (Figure 3C)

Material examined: AUMNH-45703 (3); AUMNH-45704 (6); AUMNH-45705 (1); AUMNH-45706 (3); AUMNH-45707 (3); AUMNH-45708 (2); AUMNH-45709 (6). GenBank accession numbers: MW830144–MW830147.



**Figure 3.** A–B. *Pseudopolydora rosebelae*; A. Lateral view with J-shaped arrangement of spines in 5<sup>th</sup> chaetiger (arrow); B. Dorsal view of anterior end showing pigmentation and fold in 3<sup>rd</sup> chaetiger (arrow); palp from right side is missing. C. *Pseudopolydora paucibranchiata* in lateral view with J-shaped arrangement of spines in 5<sup>th</sup> chaetiger. All scale bars = 0.2 mm. Photo by V.E. Bogantes.

**Description:** Prostomium rounded (Figure 3C) with four eyes, occipital antennae present. Caruncle extending to chaetiger 3. Branchiae from chaetiger 7 until 17. Without notopodial capillary chaetae in the 1<sup>st</sup> chaetiger. Spines in 5<sup>th</sup> chaetiger follow a J-shaped arrangement. Neuropodial hooded hooks from chaetiger 8, reaching up to 7 per fascicle in posterior chaetigers. Most of the specimens with 50–55 segments. Live specimens with white fine lines present in the palps.

**Habitat:** worms were found inside of their tubes in soft sediments, and *Thalassia* beds.

**Remarks:** *P. paucibranchiata* looks very similar to *P. vexillosa* and, morphologically, these two species can only be separated by extremely fine characters (Radashevsky et al. 2020); the most clear is represented by the length of the caruncle (to 3<sup>rd</sup> chaetiger in *P. paucibranchiata*, to 4<sup>th</sup> chaetiger

in *P. vexillosa*). All specimens examined for this study had caruncle length extending until chaetiger 3, thus fitting *P. paucibranchiata* and not *P. vexillosa*.

### ***Pseudopolydora rosebelae* Radashevsky & Migotto, 2009**

(Figure 3A, B)

Material examined: AUMNH-45702 (1).

Description: prostomium incised with four eyes, occipital antenna missing but probably present in complete individuals. Caruncle reaching the end of the 2<sup>nd</sup> chaetiger. With a fold in the 3<sup>rd</sup> chaetiger. Branchiae from chaetigers 7–18. First chaetiger without notochaetae. Chaetiger 5 with modified chaetae in a J-shaped arrangement (Figure 3A). Specimen with dark pigmentation around the prostomium and the anterior region, being stronger in the first segments (Figure 3B).

Habitat: specimen was collected on soft bottoms within *Thalassia* beds.

Remarks: among *Pseudopolydora*, strong pigmentation in the anterior region is characteristic for *P. achaeta*, *P. glandulosa*, *P. pulchra*, and *P. rosebelae*. However, the examined individual has spines in the 5<sup>th</sup> chaetiger in a J-shaped arrangement (Figure 3B), and a fold in the 3<sup>rd</sup> chaetiger that are considered diagnostic of *P. rosebelae*. Only one specimen was collected, and it corroborates findings from Radashevsky and Migotto (2009) who indicated that this species is usually present in very low abundances.

### *COI barcodes for Pseudopolydora*

COI barcodes were generated for *Pseudopolydora achaeta*, *P. floridensis* and *P. paucibranchiata*, with an aligned length of 668 nucleotides, data is deposited in GenBank (GenBank accession numbers MW830143–MW830149). We downloaded all COI sequences of *Pseudopolydora* from GenBank to attempt comparison with known sequences. However, in GenBank, only two species of *Pseudopolydora* are identified to species level. Additionally, sequences from this study and GenBank used different regions of the mtDNA COI gene, yielding an alignment with too small of an overlap region (approximately 133 base pairs) to be useful.

### **Discussion**

*Pseudopolydora paucibranchiata*, *P. achaeta*, and *P. rosebelae* were discovered along the Atlantic coast of North America constituting new records for these three species. Reports of *Pseudopolydora* species for the North Atlantic have been rare with only one recognized species known for the region (Delgado-Blas 2008) prior to this record. Of the *Pseudopolydora* species previously unreported from this region: *P. paucibranchiata* is a species previously documented from many regions including Japan, West Coast of the US, Australia, and others (Okuda 1937; Blake and Woodwick 1975; Blake and Kudenov 1978; Radashevsky et al. 2020); *P. achaeta* is

previously known from Taiwan, Japan, Russia and Brazil (Radachevsky and Hsieh 2000; Lana et al. 2006; Buzhinskaja 2013; Abe et al. 2016); and *P. rosebelae* is only known from Brazil (Radachevsky and Migotto 2009). The presence of *P. achaeta* and *P. rosebelae* in Florida represents a significant extension on the previous known distribution records of these species. Radachevsky et al. (2020) reported on our unpublished findings (Bogantes et al. 2019) of *P. paucibranchiata* occurring in Florida, but, without justification, incorrectly assumed this to be *P. vexillosa*.

Introduction of *P. paucibranchiata* to various localities has been well documented (see above), but consequences of its effects on native communities have not been well studied. This species might represent an aggressive worm with the ability to outcompete or displace other species with similar feeding habits and ecological needs (Çinar et al. 2012). Previous work (Levin 1982) has found that interactions between *Pseudopolydora* and other tube-building annelids, including the spionids *P. paucibranchiata*, *Streblospio benedicti* Webster, 1879, and the sabellid *Fabricia limnicola* Hartman, 1951, often ended in the loss of the other species. Similarly, *Boccardia proboscidea* Hartman, 1940, also a spionid in the *Polydora*-complex group, is a worm native to California and introduced to different regions including the Southwestern Atlantic Ocean, that has been shown to cause an exclusion of the mussel *Brachidontes rodriguezii* (d'Orbigny, 1842) considered the dominant ecosystem engineer and resulting in a reduction in diversity and species richness (Elías et al. 2015; Jaubet et al. 2018).

Spionids show a wide variety of reproductive and feeding strategies facilitating establishment of introduced species from one region to another. For example, *Pseudopolydora* has been shown to steal food from other surface deposit feeders (Levin 1982). Of concern for Florida, *P. paucibranchiata*, once established, can reach high abundances and may even become the dominant spionid worm in sandy beaches (Blake and Woodwick 1975). Moreover, reports of *P. paucibranchiata* from many regions indicate that this species seems to be able to tolerate different climate ranges favoring its establishment in new locations. Similarly, this thermal adaptability has been observed in other invasive species like the isopod *Paranthura japonica* Richardson, 1909 native to the Northwest Pacific (Russia to Hong Kong) but also reported off the coast of California, Italy, and France (Lavesque et al. 2013; Lorenti et al. 2016). Even though no abundance data was recorded for this study, *P. paucibranchiata* was the most common spionid collected around Fort Pierce, and importantly, this species was observed in other regions of the East coast of Florida (Blake pers. comm.).

Bioinvasions are one of the primary threats to biodiversity loss, and risks associated with introductions of non-native species are higher in regions with international shipping ports (Katsanevakis et al. 2014). Florida is no exception, as it contains more records of introduced aquatic species when compared with any other state within the United States (USGS-NAS 2020). However, introductions of marine worms, including spionids, typically

remain undetected and therefore understudied, making assessment of their dispersal potentials and ecological consequences difficult. Further studies are needed to assess the status of *Pseudopolydora* species around Florida and to evaluate their impacts on existing native communities, and among other introduced competitors.

## Conclusions

Of four *Pseudopolydora* species found on the East coast of Florida, only *P. floridensis* was previously known from the Atlantic coast of North America. *Pseudopolydora rosebelae* reported in this study constitutes the second record of this species increasing its known range extension from Brazil to South Florida, suggesting a contiguous distribution along the Western coast of the American continent. Although, *P. paucibranchiata* and *P. achaeta* originally from Japan and Taiwan respectively represent two new introductions. Among annelids, spionids include several invasive species, that are known to be harmful to the environment and promote faunal change. Recording these previously unknown distributions is essential, so that the spread and effects of these non-native taxa can be evaluated.

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## Authors contribution

VEB conceptualized and designed the research, collected, and analyzed the data, prepared figures, and tables, wrote the manuscript, and approved the final draft. MJB conceptualized and designed the methodology, collected the data, reviewed drafts and approved the final draft. KMH conceptualized and designed the methodology, wrote the manuscript, reviewed drafts and approved the final draft.

## Ethics and permits

Marine worms belonging to *Pseudopolydora* are not listed as a species at risk of extinction. Field collection methods were approved by the supervisorial staff at the Smithsonian Marine Station, which included the SMS Director, Dr. Valerie Paul, and the graduate fellowship advisor of VEB, Dr. Michael J. Boyle. The collection permit for this project was a saltwater fishing license issued by Florida's FFWCC (Customer ID: 1002479572).

## References

- Abe H, Kondoh T, Sato-Okoshi W (2016) First report of the morphology and rDNA sequences of two *Pseudopolydora* species (Annelida: Spionidae) from Japan. *Zoological Science* 33: 650–658, <https://doi.org/10.2108/zs160082>

- Amoureaux L (1980) Annélides benthiques récoltées à l'entrée de la lagune de la Manche-à-Eau, Guadeloupe (Antilles). *Bulletin du Muséum d'Histoire Naturelle, Paris* 7: 93–107
- Blake JA, Kudenov JD (1978) The Spionidae (Polychaeta) from southeastern Australia with a revision of the genera of the family. *Memoirs of the National Museum of Victoria* 39: 171–280, <https://doi.org/10.24199/j.mmv.1978.39.11>
- Blake JA, Ramey-Balci PA (2020) A new genus and species of spionid polychaete (Annelida, Spionidae) from a deep-water cold seep site in the Eastern Mediterranean Sea off Turkey. *Zoosymposia* 19: 121–134, <https://doi.org/10.11646/zoosymposia.19.1.14>
- Blake JA, Woodwick KH (1975) Reproduction and larval development of *Pseudopolydora paucibranchiata* (Okuda) and *Pseudopolydora kempfi* (Southern) (Polychaeta: Spionidae). *Biological Bulletin* 49: 109–127, <https://doi.org/10.2307/1540483>
- Blake JA, Maciolek NJ, Meißner K (2020) Spionidae Grube, 1850. In: Purschke G, Schmidt-Rhaesa A, Böggemann M, Westheide W (eds), *Handbook of Zoology. Annelida. Volume 2: Pleistoannelida, Sedentaria II*. DeGruyter, Berlin, pp 1–103
- Bogantes VE, Halanych KM, Meißner K (2018) Diversity and phylogenetic relationships of North Atlantic *Laonice* Malmgren, 1867 (Spionidae, Annelida) including the description of a novel species. *Marine Biodiversity* 48: 737–749, <https://doi.org/10.1007/s12526-018-0859-8>
- Bogantes VE, Halanych KM, Boyle MJ (2019) Larval development of *Pseudopolydora paucibranchiata* (Spionidae, Annelida) from Florida. In: Pernet B, Fitzhugh K, Harris L, Lovell L, Whiteraff C (eds), 13<sup>th</sup> International Polychaete Conference, Los Angeles, USA, August 4–9, 2019, pp 24, [https://nhm.org/sites/default/files/2019-07/IPC13\\_program\\_final\\_26Jul19.pdf](https://nhm.org/sites/default/files/2019-07/IPC13_program_final_26Jul19.pdf)
- Buzhinskaja GN (2013) Polychaetes of the Far East Seas of Russia and adjacent waters of the Pacific Ocean: annotated checklist and bibliography. KMK Scientific Press, Moscow, Russia, 131 pp
- Carlton JT (1979) Introduced invertebrates of San Francisco Bay. In: Conomos TJ (ed), *San Francisco Bay: The Urbanized Estuary*. California Academy of Sciences, San Francisco, pp 427–444
- Çinar ME (2013) Alien polychaete species worldwide: Current status and their impacts. *Journal of the Marine Biological Association of the United Kingdom* 93: 1257–1278, <https://doi.org/10.1017/S0025315412001646>
- Çinar ME, Dagli E, Açık S (2011) Annelids (Polychaeta and Oligochaeta) from the Sea of Marmara, with descriptions of five new species. *Journal of Natural History* 45: 2105–2143, <https://doi.org/10.1080/00222933.2011.582966>
- Çinar ME, Katagan T, ÖzTÜRK B, Bakır K, Dagli E, Açık S, Dogan A, Bitlis B (2012) Spatio-temporal distributions of zoobenthos in soft substratum of Izmir Bay (Aegean Sea, eastern Mediterranean), with special emphasis on alien species and ecological quality status. *Journal of Marine Biological Association of the United Kingdom* 92: 1457–1477, <https://doi.org/10.1017/S0025315412000264>
- Claparède E (1869) Les annélides chétopodes du Golfe de Naples. Seconde partie. Annélides sédentaires. *Mémoires de la Société de physique et d'histoire naturelle de Genève* 20: 1–225, <https://doi.org/10.5962/bhl.title.2142>
- Czerniavsky V (1881) Materialia ad zoographiam ponticam comparatam. *Bulletin de la Société impériale des naturalistes de Moscou* 56: 338–420
- Dagli E, Çinar ME (2008) Invasion of polluted soft substratum of Izmir Bay (Aegean Sea, eastern Mediterranean) by the spionid polychaete worm, *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae). *Cahiers de Biologie Marine* 47: 87–96
- Delgado-Blas VH (2008) *Polydora* and related genera (Polychaeta: Spionidae) from the Grand Caribbean region. *Journal of Natural History* 42: 1–19, <https://doi.org/10.1080/00222930701831240>
- Díaz-Díaz OF, Bone D, López-Ordaz A (2016) Polychaetes associated to calcareous sediments, Venezuela: Canalipalpata. *Panamerican Journal of Aquatic Sciences* 11: 26–38
- d'Orbigny A (1842) Mollusques. Voyage dans l'Amérique Méridionale 5, Paris: P. Bertrand, 758 pp
- Elías R, Jaubet ML, Llanos EN, Sanchez MA, Rivero MS, Garaffo GV, Sandrini-Neto L (2015) Effect of the invader *Boccardia proboscidea* (Polychaeta: Spionidae) on richness, diversity and structure of SW Atlantic epilithic intertidal community. *Marine Pollution Bulletin* 91: 530–536, <https://doi.org/10.1016/j.marpolbul.2014.10.007>
- Gillet P (1986) Contribution à l'étude des Annélides Polychètes des lagunes de la Manche-à-Eau et de Belle-Plaine (Guadeloupe) Description d'un nouveau Capitellidae: *Scyphoproctus guadalupensis* n. sp. *Bulletin du Muséum d'Histoire Naturelle, Paris* 8: 803–817
- Grube AE (1850) Die Familien der Anneliden. *Archiv für Naturgeschichte* 16: 249–364
- Hartman O (1940) *Boccardia proboscidea*, a new species of spionid worm from California. *Journal of the Washington Academy of Sciences* 30(9): 382–387
- Hartman O (1951) Fabricinae (feather-duster polychaetous annelids) in the Pacific. *Pacific Science* 5(4): 379–391
- Hsieh HL (1992) *Pseudopolydora diopatra*, a new species (Polychaeta: Spionidae) from Taiwan. *Proceedings of the Biological Society of Washington* 105(3): 630–635

- Jaubet ML, Bottero MAS, Hines E, Elías R, Garaffo GV (2018) *Boccardia proboscidea* (Polychaete: Spionidae) in the SW Atlantic: How far has the invasion spread? *Aquatic Invasions* 13: 351–363, <https://doi.org/10.3391/ai.2018.13.3.04>
- Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çınar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. *Aquatic Invasions* 9: 391–423, <https://doi.org/10.3391/ai.2014.9.4.01>
- Lana PC, Santos CSG, Garraffoni ARS, Oliveira VM, Oliveira VM, Radashevsky VI (2006) Checklist of polychaete species from Paraná state (Southern Brazil). *Check List* 2: 30, <https://doi.org/10.15560/2.3.30>
- Lavesque N, Sorbe JC, Bachelet G, Gouillieux B, de Montaudouin X, Bonifacio P, Blanchet H, Dubois S (2013) Recent discovery of *Paranthura japonica* Richardson, 1909 (Crustacea: Isopoda: Paranthuridae) in European marine waters (Arcachon Bay, Bay of Biscay). *BioInvasions Records* 2: 215–219, <https://doi.org/10.3391/bir.2013.2.3>
- Levin LA (1982) Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. *Journal of Experimental Marine Biology and Ecology* 65: 107–119, [https://doi.org/10.1016/0022-0981\(82\)90039-9](https://doi.org/10.1016/0022-0981(82)90039-9)
- Lorenti M, Keppel E, Petrocelli A, Sigovini M, Tagliapietra D (2016) The non-indigenous *Paranthura japonica* Richardson, 1909 (Isopoda: Anthroidea: Paranthuridae) from the Mar Piccolo lagoon, Taranto (Italy, Mediterranean Sea). *Environmental Science and Pollution Research* 23: 12791–12796, <https://doi.org/10.1007/s11356-015-4994-5>
- Okuda S (1937) Spioniform polychaetes from Japan. *Journal of the Faculty of Science* 5: 217–254
- Radashevsky VI (1993) Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta: Spionidae). *Publications of the Seto Marine Biological Laboratory* 36: 1–60, <https://doi.org/10.5134/176224>
- Radashevsky VI, Hsieh HL (2000) *Pseudopolydora* (Polychaeta: Spionidae) species from Taiwan. *Zoological Studies* 39: 218–235, <https://doi.org/10.1007/s10661-010-1847-z>
- Radashevsky VI, Migotto AE (2009) Morphology and biology of a new *Pseudopolydora* (Annelida: Spionidae) species from Brazil. *Journal of the Marine Biological Association of the United Kingdom* 89: 461–468, <https://doi.org/10.1017/S002531540800177X>
- Radashevsky VI, Malyar VV, Pankova VV, Gambi MC, Giangrande A, Keppel E, Nygren A, Al-Kandari M, Carlton JT (2020) Disentangling invasions in the sea: molecular analysis of a global polychaete species complex (Annelida: Spionidae: *Pseudopolydora paucibranchiata*). *Biological Invasions* 22: 3621–3644, <https://doi.org/10.1007/s10530-020-02346-x>
- Richardson H (1909) Isopods collected in the northwest Pacific by the U.S. Bureau of Fisheries steamer "Albatross" in 1906. *Proceedings of the United States National Museum* 37: 75–129, <https://doi.org/10.5479/si.00963801.37-1701.75>
- Santos S, Simon J (1980) Response of Soft-Bottom Benthos to Annual Catastrophic Disturbance in a South Florida Estuary. *Marine Ecology Progress Series* 3: 347–355, <https://doi.org/10.3354/meps003347>
- Sato-Okoshi W, Abe H, Nishitani G, Simon CA (2017) And then there was one: *Polydora uncinata* and *Polydora hoplura* (Annelida: Spionidae), the problematic polydorid pest species represent a single species. *Journal of the Marine Biological Association of the United Kingdom* 97: 1675–1684, <https://doi.org/10.1017/S002531541600093X>
- Sheridan P (1997) Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, U.S.A. *Estuarine, Coastal and Shelf Science* 44: 455–469, <https://doi.org/10.1006/ecss.1996.0125>
- Simboura N, Kurt Sahin G, Panagoulia A, Katsiaras N (2010) Four new alien species on the coasts of Greece (Eastern Mediterranean). *Mediterranean Marine Science* 11: 341–352, <https://doi.org/10.12681/mms.81>
- Simon CA (2009) *Pseudopolydora* species associated with mollusc shells on the south coast of South Africa, with the description of *Ps. dayii*, sp. nov. *Journal of the Marine Biological Association of the United Kingdom* 89: 681–687, <https://doi.org/10.1017/S0025315409000034>
- Simon CA, Sato-Okoshi W, Abe H (2019) Hidden diversity within the cosmopolitan species *Pseudopolydora antennata* (Claparède, 1869) (Spionidae: Annelida). *Marine Biodiversity* 49: 25–42, <https://doi.org/10.1007/s12526-017-0751-y>
- USGS-NAS (2020) US Geological Survey Nonindigenous Aquatic Species online database (USGS-NAS). <https://nas.er.usgs.gov/> (accessed 29 February 2020)
- Webster HE (1879) The Annelida Chaetopoda of New Jersey. *Annual Report of the New York State Museum of Natural History* 32: 101–128