MORPHOLOGY, ECOLOGY, AND REPRODUCTION OF A NEW POLYDORA SPECIES FROM THE EAST COAST OF NORTH AMERICA (POLYCHAETA: SPIONIDAE)

Jason D. Williams\textsuperscript{1} & Vasily I. Radashkevich\textsuperscript{2}

\textsuperscript{1}Department of Biological Sciences, 100 Flagg Road, University of Rhode Island, Kingston, RI 02881-0816, USA
\textsuperscript{2}Institute of Marine Biology, Vladivostok 690041, Russia

ABSTRACT

A new spionid polychaete species, \textit{Polydora neocalcaea}, is described from intertidal and shallow subtidal areas in Rhode Island on the east coast of North America. Adults bore into shells of living gastropods, gastropod shells occupied by hermit crabs, and bivalve shell fragments. Females deposit 13-24 egg capsules joined in a string from June-November. Each egg capsule is attached by two stalks to the inside wall of the burrow and contains 8-47 eggs, for a mean of 481 eggs per brood. The eggs have an average diameter of 116 \textmu m. Development occurs within the egg capsules until the 3-segment stage at which time planktotrophic larvae are released. A series of adult morphological characters was examined and found to vary extensively in body pigmentation but less so in palp pigmentation, prostomium shape, presence of neurosetae and notosetae of the fifth segment, and caruncle length. \textit{Polydora neocalcaea} belongs to the \textit{Polydora ciliata/websteri} species group and is characterized by palps crossed by black bars, incised prostomium, and caruncle extending up to the middle of segment 4. \textit{Polydora} species with banded palps are reviewed and systematic revision of \textit{P. agassizi} Claparède, 1869 and \textit{P. limicola} sensu Hartman (1961) is proposed.

INTRODUCTION

Spionid polychaetes of the genus \textit{Polydora} along the Atlantic coast of North America from Newfoundland to South Carolina were reviewed by Blake (1971) who recognized 12 species which he described and illustrated. Systematic and ecological studies of some \textit{Polydora} species from the east coast of North America have been provided since that time, including new records of two known species and the description of a new species (Maciolek 1984). Blake (1996) has recently resurrected and redefined the genus \textit{Dipolydora} Verrill, to which a number of former \textit{Polydora} species have been referred. Thus, only four species in the newly restricted genus \textit{Polydora} have been reported to occur along the east coast of North America: \textit{P. aggregata} Blake, 1969, \textit{P. colonia} Moore, 1907, \textit{P. cornuta} Bosc, 1802, and \textit{P. websteri} Hartman, 1943.
A Polydora species, distinct from these four species, was discovered during a survey of polydorids from Rhode Island. The species was found to match Webster’s (1879) description of Polydora caeca, a borer of oyster shells from Virginia. However, Polydora caeca Webster is the permanently invalid secondary homonym for which Hartman (1943) proposed the replacement name Polydora websteri. Rediscovery of specimens matching Webster’s description and examination of Hartman’s material inspired a taxonomic revision which ultimately led to a change in the status of Polydora websteri (Radashevsky & Williams 1998; Radashevsky 1999). In order to serve taxonomic stability a new nominal species, Polydora neocaeca, is described to replace the permanently invalid name P. caeca. Until now, only the sperm ultrastructure of Polydora neocaeca has been described (Williams 1997).

The purpose of the present report is to describe and document the adult morphology and larval development of Polydora neocaeca. Variation within a series of adult morphological characters is quantified. Data on the ecology and reproduction of the species is also presented. A comparison of Polydora neocaeca is made with closely related species of the Polydora ciliata/ websteri group.

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MATERIALS AND METHODS

Field collections were made from two sites in Rhode Island, Atlantic coast of North America. Living gastropods, living bivalves, shell fragments and gastropod shells inhabited by hermit crabs were collected intertidally and shallow sub-tidally up to 2 m depth from September 1995 to November 1996. Polydora specimens were removed from their burrows by cracking the mollusc shells with a hammer or pliers.

Following removal of the worms, burrows were examined for the presence of egg capsules. Larvae were examined with video-microscopy and differential interference contrast microscopy (DIC) after relaxation in 3% magnesium chloride. Composite line-drawings of larvae were produced by a combination of camera lucida sketches and video-images. Adults, eggs, and larvae were measured using an ocular micrometer.

Adult worms were relaxed in 3% magnesium chloride prior to the production of camera lucida drawings. Variation in the following characters was quantified (mean ± SD): 1) distribution of pigmentation, 2) caruncle length, 3) number of major spines of fifth segment, 4) number of eyes, 5) prostomium
shape, and 6) presence of neurosetae and notosetae on the fifth segment. The type material was fixed in 10% formaldehyde, stored in 70% ethyl alcohol, and deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and in the Institute of Marine Biology, Vladivostok (IMBV).

Adult morphology was also examined with SEM. Specimens were fixed for 2 hr in 3% glutaraldehyde in Na-cacodylate buffer (pH 7.2) with 3% NaCl, rinsed with Na-cacodylate buffer (three 30 min changes), and dehydrated in an ascending ethanol series at 4°C. After warming to room temperature in 95% ethanol, the specimens were placed in four changes of 100% ethanol. Dehydration was achieved with Peldri II (Ted Pella, Inc.) by placing the specimens into a 1:1 mixture of 100% ethanol and Peldri II for 1 hr in a warm water bath (34°C). The specimens were transferred into 100% Peldri II for 1.5 hr and then placed into a cool water bath (15°C) and allowed to sublime overnight. Dried specimens were mounted on stubs, coated with gold-palladium mixture, and viewed in a JEOL 1200EX SEM.

RESULTS

Family Spionidae Grube, 1850
Genus Polydora Bosc, 1802 sensu Blake, 1996

Polydora neoeca sp. nov.

Figs. 1-5


type); from *I. obsoleta* and *L. littorea* inhabited by *P. longicarpus*, 30 Aug 1996 (USNM 182885: 5 paratypes); from *L. littorea* inhabited by *P. longicarpus*, 21 Oct 1996 (USNM 182886: 1 paratype).

*Diagnosis.* – A moderate-sized *Polydora* with palps crossed by black bars; prostomium incised; caruncle up to middle of segment 4. Segment 1 with small notopodia, without notosetae. Segment 5 with falcate spines having lateral flange, with dorsal and ventral tufts of winged capillaries. Neuropodial hooded hooks

**Holotype** 22.0 mm long, 0.65 mm wide at segment 7, 107 segments. Black pigment present dorsally on either side of prostomium, peristomium and first 4 segments; ventrally on peristomium and segments 2-3; palps crossed by 7 distinct bars of black pigment (Fig. 1A). Prostomium incised anteriorly with two rounded lobes; caruncle straight in life (Fig. 1A) continuing posteriorly to end of segment 3, with ciliated groove on each side (Figs. 1A, 2A, 2B). Four eyes present; occipital tentacle absent. Palps extending posteriorly for 15-16 seg-
Fig. 3. Polydora neocaeca sp. nov.: SEM micrographs of paratypes (A, B - USNM 182882; C, D - USNM 182883). - A, fifth segment in left, lateral view. - B, fifth segment in right, lateral view. - C, bidentate hooded hook; apical end in lateral view. - D, bidentate hooded hook; apical end in frontal view. Arrowheads indicate the stalk of an attached peritrichous ciliate. Scale: A, B = 15 μm; C = 2.5 μm; D = 5 μm.

ments. Laterofrontal cilia lining lateral edge of palp; frontal cilia covering the ventral median groove (Fig. 2D). Non-motile cilia extending from papillae concentrated dorsally along lateral edge of palps, above laterofrontal cilia; additional papillae in lower densities covering dorsal side of the palps (Fig. 2D).

Segment 1 with neurosetae, without notosetae, with weakly developed noto-
Fig. 4. Polydora neoeca sp. nov.: Variation in adult morphological characters. - A, percent of anterior body pigmentation. None, no anterior body pigmentation present; p, pigmentation on prostomium and/or peristomium; ps1-2, ps1-3, ps1-4, pigmentation on prostomium and/or peristomium and segments 1-2, 1-3, and 1-4, respectively (n=104). - B, plot of caruncle length versus total number of segments (n=49). - C, percent distribution of the number of eyes (n=108). - D, percent distribution of number of major spines in the fifth segment (n=90).

podial lobes. Winged capillary notosetae of segments 2-4, 6, and succeeding segments arranged in two vertical rows and superior group of longer and thinner setae (Figs. 2B, 2C); number of setae per fascicle in subsequent segments gradually diminishing, with rows of setae becoming indistinct; modified setae absent from posterior notopodia. Winged capillary neurosetae of segments 2-4, and 6 arranged in two vertical rows and inferior tuft of capillaries (Figs. 2B, 2C). Bidentate hooded hooks in neuropodia from segment 7, not accompanied by capillaries, up to 12 in series at segment 45; hooks with wide angle between teeth, with constriction on shaft; with short bristles on apical end of hood (Figs. 1C, 3C, 3D).

Segment 5 almost twice as large as segments 4 and 6, with slightly curved row of 5 exposed major spines and two developing spines alternating with pennoned companion setae; with posterioventral fascicle of 6 winged neurosetae and anteriodorsal fascicle of 4 capillary notosetae (Figs. 3A, 3B). Major spines falcate, with lateral obliquely curved flange (Figs. 1D, 3A, 3B).

Branchiae from segment 7, attaining full size by segments 8-10, gradually di-
minishing through posterior half of body, absent from the posterior 8 segments. Nototrechs from segment 7, extending onto branchiae.

Pygidium disc-like with distinct dorsal gap and shallow ventrolateral notch (Fig. 1B); non-motile cilia present along edge and dorsal side of pygidium.

Glandular pouches from segment 7, larger in segments 8-10 and diminishing in size in posterior segments. Gizzard-like structure in digestive tract absent.

Variability. – The largest specimen measured 29.5 mm long and 0.7 mm in width at segment 7 with 133 segments. The prostomium was incised in most specimens, although 3 of the individuals examined (n=66) exhibited a rounded prostomium. Black pigmentation was highly variable (Fig. 4A) but was usually present to some degree dorsally on either side of the prostomium, peristomium and first four segments; 17% of the specimens examined had pigmentation on the ventral side of at least one of the first four segments. All specimens examined had black pigment bars along the palps; a mean number of 7.5 ± 3.4 (n=86) bars was observed; Webster (1879) reported 13 bands. No pigmentation was found on the posterior segments or pygidium of any specimens examined.

Caruncle length was size-dependent, extending from the posterior margin of segment 2 to the middle of segment 4 (Fig. 4B). The number of eyes was variable from 0 to 4; 1-3 eyes were rare (Fig. 4C). The fifth segment contained between 5-10 major spines with a mean of 7.3 ± 1.0 (n=90) (Fig. 4D). Notosetae and neurosetae of the fifth segment were present in all specimens examined (n=68). Branchiae of right and left sides meet middorsally. The pygidium was disc-like with distinct dorsal gap to narrow incision; 16% of the specimens examined (n=50) were found with a ventrolateral notch.

Ecology. – Polydora neocaeca bores into calcareous substrata. It has been found intertidally and shallow subtidally in shells of the gastropods Busycotypus canaliculatus, Ilyanassa obsoleta, Littorina littorea, Lunatia heros, and Urosalpinx cinerea occupied by Pagurus longicarpus; no worms were found to be associated with Pagurus pollicaris Say which was also collected in the field. The species has been found in shells of living gastropods, Crepidula fornicata and Littorina littorea, and in shell fragments of the bivalves Mya arenaria and Mercenaria mercenaria. Webster (1879) found his specimen boring into the upper valve of Anomia simplex d’Orbigny (= Anomia glabra Verrill). As many as 12 worms have been found boring in one shell. The worms reside in unbranched U-shaped burrows within the shell. The walls of the burrow are lined with detritus, forming a detrital tube within the burrow. The ends of the burrow are extended by a smooth silty tube, typically < 5 mm in length. Polydora neocaeca was found associated in the same shells with P. websteri.

A stalked peritrichous ciliate (Ciliophora: Oligohymenophorea) was found attached to 12.7% of the specimens examined (n=126). The peritrich attaches to the bidentate hooded hooks of the worms, usually 2-3 individuals per fascicle of hooks. The holdfast of the peritrich is attached to the hood of the bidentate
hooks on or below the main fang (Figs. 3C, 3D). In life the stalks of the peritrichs extend dorsally such that the main body and oral region are positioned near the branchiae of the worm.

Reproduction. — Polydora neocaeca is a gonochoric species; 42 females and 30 males have been recognized within the specimens examined. The smallest female and male specimens with gametes in the coelom had 59 and 60 segments, respectively. Gametogenic segments were present in the middle portion of the body, in males from segments 18-45 to 40-83; in females from segments 19-46 to 40-92. The average number of segments containing developing gametes was 38.1 ± 14.9 (n=11) in males and 31.6 ± 10.2 (n=26) in females. The number of the first gametogenic segment and the total number of gametogenic segments per worm were slightly positively correlated with the total number of segments, \( r^2 = 0.38 \) and \( r^2 = 0.51 \) (n=36, P<0.01), respectively.

Spermatozoa have an elongate cylindrical nucleus and a bullet-shaped acrosome. The middlepiece of the sperm contains mitochondria closely aligned with the axoneme which is inserted into the nucleus in a short centriolar fossa. The spermatozoa have the following measurements: acrosome 0.9 ± 0.1 μm (n=10), nucleus 4.8 ± 0.4 μm (n=11), middlepiece 4.2 ± 0.4 μm (n=7).

Females deposit eggs in 13-24 capsules (mean = 19.4 ± 3.2; n=7) joined in a string on the inside of the burrow (Fig. 5A). Each egg capsule is attached to the burrow wall by two thin stalks and contain 8-47 eggs (mean = 24.8 ± 1.3, n=21), the mean number of eggs per brood is approximately 481. Eggs deposited within capsules had a mean diameter of 116.2 ± 10.0 μm (n=50).

Larval development. — All eggs in capsules develop into larvae; no unfertilized or nurse eggs were found. The protrochophore measured 130 μm (Fig. 5B). The larvae have a blunt anterior end, a small ciliated vestibule, paired ventro-lateral ciliary patches and contain yolk macromeres in the center. Later in development the larvae exhibit the cilia of the telotroch and prototroch, 2 small lateral eyespots anterior to the prototroch and setae in the first segment (Fig.5C). Larvae with 2 setigers containing observable setae are approximately 200 μm in length. The larvae have 3 sets of eyespots, a round median pair and a cup-shaped configuration of 2 pairs of lateral eyespots. The yolk has been partially depleted and the gut is beginning to form at this stage.

The early 3-segment larva (Figs. 5D, 5E, 5F) is 240 μm long. Large branched or ramified chromatophores are present between the lateral and median eyespots which are arranged in a row. The prototroch is developed and extends from the mouth vestibule almost to the median eyespots. The telotroch is composed of ciliary cells interrupted by a dorsal gap. Tactile cilia are present anteriorly on the head and posteriorly on the pygidium in number 4 and 2, respectively. The setae in segments 1, 2, and 3 are present in fascicles of approximately 9, 6, and 3 spines, respectively; those of segment 1 are the longest. A nototroch and grasping cilia are present on segment 3. A transverse band of black
pigment is present on the dorsal side of segment 3 in some larvae. Slight black pigment has developed on the pygidium.

The late 3-segment larvae grow to about 340 μm. The 2 lateral eyespots are slightly anterior to the median eyespots. The larvae contain little or no yolk at this stage and are capable of feeding and swimming. Attempts at culturing larvae beyond the 3-segment stage were unsuccessful.

*Etymology.* – The species name refers to *Polydora caeca* described by Webster (1879).

*Distribution.* – Atlantic coast of North America.

**DISCUSSION**

*Polydora neocaeca* belongs to the *Polydora ciliata*/*websteri* group as defined by
Blake (1996). It closely resembles Polydora aggregata, P. ciliata Johnston, 1838, P. curiosa Radashevsky, 1994, P. limicola Annenkova, 1934, and P. websteri in adult morphology. It differs from all these species in having palps crossed by black bars and in longer caruncle continuing to the middle of segment 4 rather than colorless or diffusely pigmented palps and caruncle typically extending to anterior border or end of segment 2. Polydora neocaeca resembles P. agassizi Claparède, 1869, P. brevipalpa Zachs, 1933, and Polydora sp. Blake (1996: 176-177) in pigmentation of the palps and caruncle length. Polydora neocaeca differs from the last two mentioned species in having an incised prostomium instead of entire, rounded prostomium; it also differs from P. brevipalpa in having, rather than lacking, dorsal capillaries on segment 5, and from P. agassizi and Polydora sp. by Blake (1996) in possessing a curved flange on the major spines instead of a large accessory tooth. Additionally, Polydora neocaeca differs from P. agassizi based on habitat. Morphological characters of these eight species of the Polydora ciliata/websteri group and Polydora neocaeca are compared in Table 1.

Several Polydora species have been reported to possess palps clearly pigmented with distinct bars or blotches of black pigment including P. agassizi, P. alloporis Light, 1970, P. brevipalpa, P. limicola by Hartman (1961) (not Annenkova, 1934), P. maculata Day, 1963, P. narica Light, 1969, P. wobberi Light, 1970, and Polydora sp. by Blake (1996). All of these species are from the North Pacific except Polydora agassizi from the Gulf of Naples and P. maculata from South Africa. Polydora agassizi was originally described by Claparède (1869) and was re-described by Carazzi (1893) who provided the characters given in Table 1. Carazzi (1893) erroneously referred Polydora agassizi to synonymy with P. ciliata and this was accepted until the present (see Hartman 1959; Blake 1996) although P. ciliata has never been described as having banded palps.

Polydora limicola was originally poorly described by Annenkova (1934) as an intertidal and shallow subtidal tube-dweller in the Commander Islands and Kamchatka. Hartman (1961) provided a description based on her own material from California and greatly emended the diagnosis of the species. One of us (Radashevsky, unpublished) examined Polydora specimens from Kamchatka matching Annenkova's description and found that although Annenkova's and Hartman's specimens are close in some respects (e.g., tube-building) they clearly differ in other characters including palp pigmentation (see Table 1). Sato-Okoshi & Okoshi (1997) reported Polydora limicola from Vancouver Island as boring into mollusc shells and barnacles, in spite of the fact that they concluded boring activity to be a species specific trait. Information regarding deposited materials was not provided but a brief description of the specimens by the authors matches the diagnosis of Polydora neocaeca. Their report has therefore been included into questionable synonymy with Polydora neocaeca.

It is noteworthy that while diffuse body and palp pigmentation is variable within the genus Polydora, species with banded palps are invariably found with this unique pattern. Therefore, the palp banding pattern of Polydora neocaeca, in
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combination with other taxonomic characters, can be used to distinguish this species. Additional investigations are required to elucidate the systematics of both Polydora agassizi and P. limicola sensu Hartman. With the exception of Polydora neoaecea, no other Polydora species with banded palps have been described from the east coast of North America.

REFERENCES


