Harmful Shell Borers, *Polydora* Species (Polychaeta: Spionidae), from Commercially Important Mollusk Shells in East Asia and Australia

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Abstract

Shell-boring polydorids (Polychaeta: Spionidae) are economically and ecologically important species that must be monitored owing to the risk they pose to commercially important mollusk shells. Tracking polydorid species internationally requires accurate species identification, which is based on both morphological characteristics and nuclear 18S rRNA gene sequences. Four serious shell-boring *Polydora* in East

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Asian and Australian aquaculture, i.e., *Polydora brevipalpa*, *P. uncinata*, *P. haswelli*, and *P. aura*, are described here. The shell-associated polydorids that have been reported from these areas were summarized and reviewed at the same time.

1 Introduction

Spionid polychaetes are distributed in a wide variety of habitats from shallow water to deepwater depths in all oceans. They are commonly the most abundant polychaete groups in terms of biomass and number of species in the coastal benthic environment. Species of *Polydora* and related genera (Polychaeta, Spionidae) are the so-called polydorids, and they are found in a wide variety of substrata, ranging from soft mud to hard calcareous materials (Blake 1996; Sato-Okoshi 1999, 2000). Polydorids are well known for their ability to bore into various calcareous substrates, e.g., coralline algae, corals, and mollusk shells (Blake and Evans 1973; Blake 1996; Sato-Okoshi 1999). Although they excavate their burrows for use as a habitat, some species have been frequently reported as harmful invaders from the viewpoint of aquaculture, as they often damage the commercially important mollusk shells by inducing abnormal shell formation, decreasing their commercial value, reducing their growth rate and meat yield, and causing heavy mortality (Sato-Okoshi et al. 1990, 2008; Okoshi and Sato-Okoshi 1996; Handley and Bergquist 1997; Mortensen et al. 2000; Lleonart et al. 2003; Simon et al. 2006). In recent years, the heavily infested abalone shells were observed to be dead in tank-cultured system and it was forced to stop cultivating in several prefectures in Japan (personal communication). Measures of preventing or controlling polydorid infestation in commercially important mollusk shells have been suggested (Handley and Bergquist 1997; Diggles et al. 2002; Simon et al. 2010), but the problem remains unresolved.

An expansion of molluscan aquaculture has resulted in a global distribution of certain commercially important mollusk shells (Cohen and Carlton 1998). Consequently, the polydorid species that associate with these mollusk shells, such as borers and crevice inhabitants, have also spread by accompanying commercially important host shells (Bailey-Brock 2000; Radashevsky and Olivares 2005; Simon et al. 2006). Those species are not only a source of concern economically (Radashevsky and Olivares 2005; Simon et al. 2006) but also pose a threat ecologically (Cohen and Carlton 1998). Ecological disturbances caused by invasive organisms (including polychaetes) associated with these mollusks are currently seen as a major cause of diversity loss worldwide (Mack et al. 2000; Miura 2007).

The polydorids include several species groups that are morphologically indistinguishable, with an insufficient number of distinct characters to enable species level identification (Radashevsky and Pankova 2006; Sato-Okoshi and Abe 2013). At the same time, some species possess a high degree of intraspecific variation, particularly with respect to pigmentation patterns (Sato-Okoshi and Abe 2013; Teramoto et al. 2013). Recently, molecular sequence analyses were conducted in some shell-associated *Polydora* species (Sato-Okoshi and Abe 2012, 2013; Teramoto et al. 2013), and the results demonstrated that the nuclear 18S rRNA gene analysis would be an effective and useful tool to accurately discriminate between these problematic species.

The present study first summarizes the polydorid species to understand the background of the relevant species associated with commercially important mollusk shells in East Asia and Australia. Secondly, the study focuses on harmful *Polydora* species known to be responsible for heavy host shell damage and with the potential to become an invasive species as a result of accidental transport on host shells. Morphological, ecological, and molecular biological characteristics of these high-risk *Polydora* species are described here in order to better trace and monitor the threat they pose to mollusk fisheries and ocean ecologies.

2 Distribution and Composition of Polydorid Species Associated with Mollusk Shells

There are numerous polydorids that have been reported as being associated with commercially important mollusk shells, i.e., oysters, scallops, and abalone, in Japan, South Korea, China, and Australia (Table 1). A total of 28 species from five genera have been reported from these waters since 1970, during which time the commercial transportation of mollusk shells has increased. The percentage composition of the number of species by genus was 16 species (57 %) in *Polydora*, seven species (25 %) in *Dipolydora*, three species (11 %) in *Boccardia*, and one species (3 %) in each *Boccardiella* and *Pseudopolydora*, respectively. The results show that over half of the target species belong to the genus *Polydora*. Among these, estimates of the shell infestation condition by *Polydora brevipalpa* and *P. uncinata* from Japan (Imajima and Sato 1984; Sato-Okoshi et al. 1990; Sato-Okoshi 1994, 1998; Sato-Okoshi and Abe 2012); *P. haswelli*, *P. aura*, and *P. uncinata* from South Korea (Sato-Okoshi et al. 2012); *P. brevipalpa* from China (Sato-Okoshi et al. 2013); and *P. uncinata*, *P. hoplura*, and *Boccardia knoxi* from Australia (Lleonart et al. 2003; Sato-Okoshi et al. 2008; Sato-Okoshi and Abe 2012) revealed that these polydorid species should be considered particularly dangerous. To date, *Polydora uncinata* is the only species revealed to be harmful across all these countries, with the exception of China. This species was reported to be especially harmful in abalone shells, i.e., land-based tank-cultured abalone.

3 Morphological, Biological, and Ecological Characteristics of the Four Harmful *Polydora* Species

Detailed characteristics of the four most harmful species from the 28 polydorid species are described below. These include *Polydora brevipalpa*, *P. uncinata*, *P. haswelli*, and *P. aura*. Photographs of living specimens (Fig. 1) and the infestation condition of scallop, oyster, and abalone shells (Fig. 2) are shown.

3.1 *Polydora brevipalpa* (Fig. 1a, b)

3.1.1 Morphological Characteristics

Large-sized worms. Conspicuous black bands appear on palps. The anterior end of the prostomium is rounded, and there is no notochaetae in the 5th chaetiger. The color of the pygidium is light tan, white, black, or partially black.

3.1.2 Biological and Ecological Characteristics

The larvae showed planktotrophic development. The species is distributed in cold waters. It is very common in scallop shells particularly abundant in the left valves of wild and sown cultured scallops in the Okhotsk Sea (Fig. 2a) (Mori et al. 1985). Recently, the species was first extracted from the shells of wild and sown cultured abalone, other than scallop, in north China (Sato-Okoshi et al. 2013). They reproduce egg capsules repeatedly, except during seasons of high temperature, and showed high reproductive capacity. The larvae settle at the periphery of the left valve of the scallop during drift ice period and their life span is approximately 2.5 years (Sato-Okoshi 1994). Severe infestation by the species was observed not only in Japanese scallops but also in Chinese sown cultured scallops (Sato-Okoshi et al. 2013).

3.2 *Polydora uncinata* (Fig. 1c, d)

3.2.1 Morphological Characteristics

Large-sized worms. Conspicuous black bands appear on palps and black pigmentation presents on both dorsal and ventral sides of anterior chaetigers. Rarely no conspicuous black pigmentation is observed on the palps and body. Short occipital tentacle is present. There are special recurved notochaetae in posterior chaetigers.

Table 1 Polydorid species associated with commercially important mollusk shells in East Asia (Japan, South Korea, China) and Australia

Country	Host shell		Associated spionid species		References
			Boring	Non-boring	
Japan	Scallop	*Patinopecten yessoensis*[S]	***Polydora brevipalpa***, *P. websteri, P. curiosa, Dipolydora alborectalis, D. concharum, D. bidentata*		Sato-Okoshi (1999) and Sato-Okoshi and Abe (2012)
		Patinopecten yessoensis[W]	***Polydora brevipalpa***, *P. websteri, Dipolydora alborectalis, D. concharum, D. bidentata*		Sato-Okoshi (1999)
		Patinopecten yessoensis[C]	***Polydora brevipalpa***, *P. onagawaensis*		Sato-Okoshi (1999) and Teramoto et al. (2013)
	Oyster	*Crassostrea gigas*[W]	*Polydora onagawaensis, P. uncinata, P. calcarea, P. websteri, P. haswelli, Dipolydora bidentata, D. concharum*	*Polydora cornuta, Boccardiella hamata, Boccardia proboscidea, B. pseudonatrix, Pseudopolydora antennata*	Sato-Okoshi (1999, 2000), Sato-Okoshi and Abe (2013), Present paper
		Crassostrea gigas[C]	*Polydora onagawaensis, P. uncinata, P. websteri, P. aura, P. haswelli, P. curiosa, Dipolydora bidentata, D. concharum, D. giardi*	*Dipolydora socialis, Boccardiella hamata*	Sato-Okoshi (1999, 2000), Sato-Okoshi and Abe (2013), Present paper
	Abalone	*Haliotis discus hannai*[W]	*Polydora calcarea, P. websteri, P.* sp., *Dipolydora armata, D. giardi*		Sato-Okoshi (1999), Present paper
		Haliotis discus hannai[S]	*Polydora* sp.		Present paper
		Haliotis discus hannai[C*]	***Polydora uncinata***		Present paper
		Haliotis discus discus[C*]	***Polydora uncinata***, *Dipolydora armata*		Present paper
		Haliotis diversicolor aquatilis[W]	*Polydora ciliata, P. flava orientalis, P. websteri, Dipolydora giardi, D. armata*		Kojima and Imajima (1982) and Sato-Okoshi (1999)
		Haliotis diversicolor aquatilis[C*]	***Polydora uncinata***, *Dipolydora armata*		Present paper
South Korea	Scallop	*Chlamys farreri*[W]	*Polydora haswelli, Dipolydora alborectalis*	*Polydora limicola*	Sato-Okoshi et al. (2012)
	Oyster	*Crassostrea gigas*[C]	*Polydora haswelli, P. aura,* ***P. uncinata***		Sato-Okoshi et al. (2012)
		Crassostrea gigas[W]		*Boccardiella hamata*	Sato-Okoshi et al. (2012)
	Abalone	*Haliotis discus discus*[W]	***Polydora haswelli, P. aura***		Sato-Okoshi et al. (2012)
		Haliotis discus discus[C]	***Polydora haswelli, P. aura***		Sato-Okoshi et al. (2012)

China	Scallop	*Patinopecten yessoensis*^{S}	***Polydora brevipalpa***, *P. onagawaensis*		Sato-Okoshi et al. (2013)
		Patinopecten yessoensis^{C}	*Polydora onagawaensis*		Sato-Okoshi et al. (2013)
		Chlamys farreri^{W}	*Polydora onagawaensis*		Sato-Okoshi et al. (2013)
		Chlamys farreri^{C}	*Polydora onagawaensis*		Sato-Okoshi et al. (2013)
	Oyster	*Crassostrea gigas*^{W}	*Polydora onagawaensis*	*Boccardiella hamata*	Sato-Okoshi et al. (2013)
		Crassostrea gigas^{C}	*Polydora onagawaensis, P. websteri*		Sato-Okoshi et al. (2013)
	Abalone	*Haliotis discus hannai*^{W}	*Polydora onagawaensis, P. brevipalpa*		Sato-Okoshi et al. (2013)
		Haliotis discus hannai^{S}	*Polydora onagawaensis, P. brevipalpa*		Sato-Okoshi et al. (2013)
Australia	Scallop	*Chlamys australis*^{W}	*Polydora uncinata*		Sato-Okoshi et al. (2008)
		Pecten alba	*Polydora latispinosa*		Blake and Kudenov (1978)
	Oyster	*Crassostrea gigas*^{W}	*Polydora calcarea*	*Boccardia proboscidea*	Sato-Okoshi and Abe (2013), Present paper
		Crassostrea gigas^{C}	*Polydora websteri, P. hoplura, Dipolydora giardi*	*Boccardia proboscidea, B. pseudonatrix*	Blake and Kudenov (1978), Present paper
		Saccostrea commercialis^{C}	*Polydora websteri* (cited as *P. haswelli*)	*Boccardia pseudonatrix* (cited as *B. knoxi*)	Blake and Kudenov (1978), Sato-Okoshi et al. (2008)
		?	*Polydora haswelli, P. latispinosa*	*Boccardia chilensis*	Blake and Kudenov (1978)
	Abalone	*Haliotis roei*^{W}	***Polydora uncinata***, *Dipolydora giardi, D. armata, D. aciculata*	*Boccardia proboscidea*	Sato-Okoshi et al. (2008)
		Haliotis roei^{C*}	***Polydora uncinata***, *Dipolydora armata* (cited as *P. armata*)		Blake and Kudenov (1978), Sato-Okoshi et al. (2008)
		Haliotis rubra^{C}	*Polydora hoplura*	***Boccardia knoxi***	Lleonart et al. (2003)
		Haliotis laevigata$^{C*, C}$	***Polydora hoplura, P. uncinata***		Lleonart et al. (2003) and Sato-Okoshi et al. (2008)
		Haliotis conicopora^{W}	*Dipolydora armata, D. aciculata*		Sato-Okoshi et al. (2008)
		Haliotis denov	*Polydora woodwicki, Dipolydora armata* (cited as *P. armata*)		Blake and Kudenov (1978)

Bolds show harmful species for the host shells
W wild, *C* culture, *C** Land-based tank culture, *S* sown culture

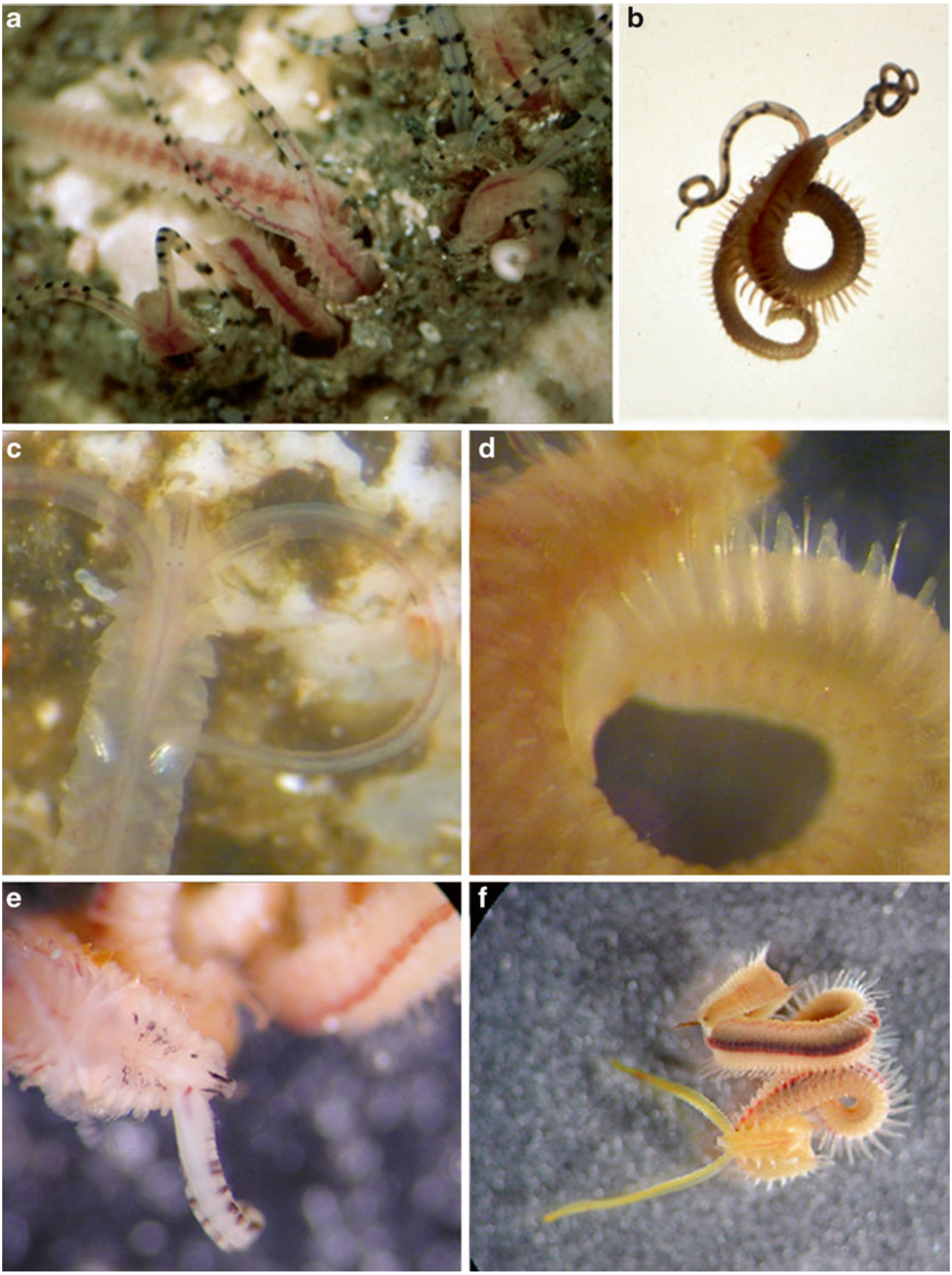

Fig. 1 Pictures of live individuals extracted from the shells. *Polydora brevipalpa* (**a**), anterior chaetigers with palps with black bars and a white pygidium, both protruding from their burrows in scallop shell (From Sato-Okoshi and Abe 2012). (**b**) A complete individual extracted from its burrow (From Sato-Okoshi and Abe 2012). *Polydora uncinata* (**c**), anterior chaetigers with palps with inconspicuous black bars (From Sato-Okoshi and Abe 2012). (**d**) Posterior chaetigers with special hooks on the notopodia (From Sato-Okoshi and Abe 2012). *Polydora haswelli* (**e**), distinct black pigmentation along the prostomium, on peristomium, and on anterior chaetigers and palp with black bars (From Sato-Okoshi et al. 2012). *Polydora aura* (**f**), a complete individual with orange in color (From Sato-Okoshi and Abe 2012)

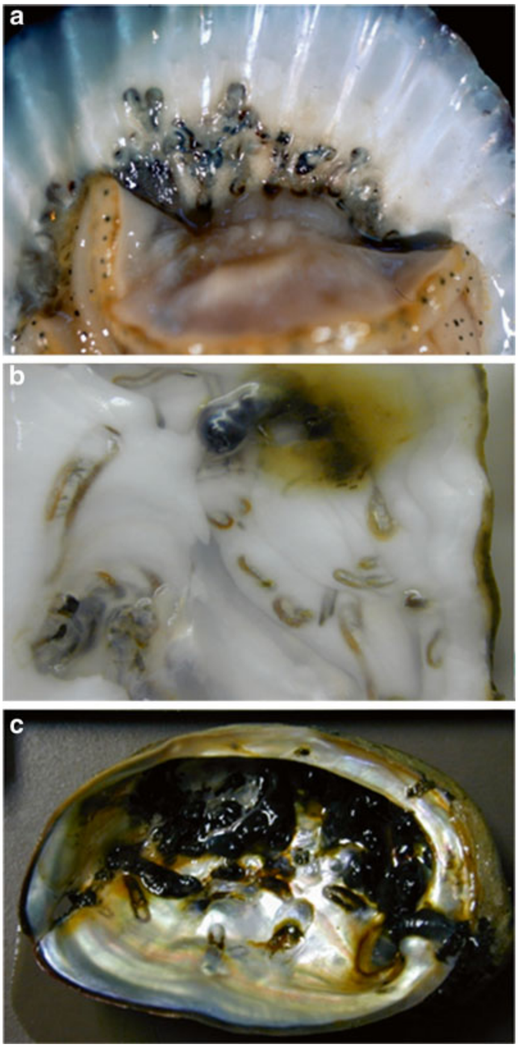

Fig. 2 Pictures of shells infested by *Polydora* species. (**a**) Inner surface of the left valve of scallop shell showing heavy infestation by *P. brevipalpa* after removing the mantle (From Sato-Okoshi and Abe 2012). (**b**) Inner surface of the oyster shell showing heavy infestation by *P. uncinata* and *P. haswelli* (From Sato-Okoshi and Okoshi 2014). (**c**) Inner surface of the abalone shell showing heavy infestation by *P. uncinata* (From Sato-Okoshi et al. 2012)

3.2.2 Biological and Ecological Characteristics

Larvae showed direct development and adelphophagy with many nurse eggs within egg capsules. Their hatched-out stage was ca 17-chaetiger larvae and showed no or very short planktonic larval stage. One female seemed to reproduce egg capsules repeatedly and reproduction capacity was suggested to be very high. Life span was predicted to be more than 2 years in the tank-cultured environment. The species was distributed widely in Asian and Australian waters, and it was extracted commonly from both wild and cultured mollusk shells. It is noteworthy to cite that a high number of these species have been suddenly observed in suspended cultured oyster shells in South Korea (Fig. 2b), which is speculated to be the result of host oysters being introduced from different waters (Sekino et al. 2003; Sato-Okoshi et al. 2012). In addition to Japan and Australia, heavy infestation of this species has been reported on land-based tank-cultured abalone in Chile. It is also speculated that this infestation was the result of host abalone being transported from Japan to Chile accompanying the *P. uncinata* population (Radashevsky and Olivares 2005). This species is regarded as one of the most dangerous polydorids, especially in the case of enclosed aquaculture systems such as abalone land-based tank culture (Fig. 2c).

3.3 *Polydora haswelli* (Fig. 1e)

3.3.1 Morphological Characteristics

Medium- to large-sized worms. Conspicuous black bands appear on palps and black pigmentation presents on both dorsal and ventral sides of anterior chaetigers.

3.3.2 Biological and Ecological Characteristics

Larvae revealed planktotrophic development. Little is currently known about other characteristics, e.g., life history or reproductive characteristics. Although the species exhibits medium sizes in Japan, it reaches larger sizes and is very common in South Korean mollusk shells (Fig. 2b) (Sato-Okoshi et al. 2012). The species causes harmful infestations in many commercially important shells, but appears limited to South Korea (Sato-Okoshi et al. 2012).

3.4 *Polydora aura* (Fig. 1f)

3.4.1 Morphological Characteristics

Medium- to large-sized worms. The body and palps are light orange but some worms without conspicuous color. A short inconspicuous occipital tentacle is present. Special notochaetae are present in the posterior chaetigers which exhibit tight cylindrical bundles of short needles.

3.4.2 Biological and Ecological Characteristics

All the larvae in the capsule developed simultaneously and revealed planktotrophic development. Little is currently known about other characteristics, i.e., life history or reproductive characteristics. As for *P. haswelli*, this species was very large in size and common in South Korean mollusk shells (Sato-Okoshi et al. 2012). The species caused severe infestations in many commercially important shells, but again appears limited to South Korea (Sato-Okoshi et al. 2012).

4 Phylogenetic Analysis of 18S rRNA Gene Sequences

Misidentification and taxonomic confusion of *Polydora* species often arise because of a lack of efficient morphological key characteristics and a high degree of intraspecific variation. In recent years, an increasing number of taxonomic studies are relying on molecular methods for accurate species identification. 18S rRNA gene sequences of seven *Polydora* species (*P. onagawaensis*, *P. calcarea*, *P. brevipalpa*, *P. websteri*, *P. haswelli*, *P. aura*, and *P. uncinata*) have been analyzed (Sato-Okoshi and Abe 2012, 2013; Teramoto et al. 2013). The results of these studies showed that the nucleotide sequence of the 18S rRNA gene was completely identical within a species even between separate populations and distinct between different species (Fig. 3). Therefore, 18S rRNA gene analysis is an effective tool for the identification of these *Polydora* species, including the four species described above.

5 Discussion and Conclusion

As little data exists on the species characteristics of *Boccardia knoxi*, a species reported to be a severe shell-boring parasite of abalone shells by Lleonart et al. (2003), it should be considered as the focus of future studies. Additionally, discriminating between the morphologically identical species *P. hoplura* and *P. uncinata*, for which only *P. uncinata* has undergone molecular analysis (Sato-Okoshi and Abe 2012), remains problematic. As such, only data from *P. uncinata* will be presented here. The key morphologically identifying characteristics of these four species are summarized in Table 2.

The *Polydora* species differed according to locality and in their host shells. The species considered to be the most damaging to East Asian and Australian aquaculture were *P. brevipalpa*, *P. uncinata*, *P. haswelli*, and *P. aura*. It is now possible to speculate that some of these species have been transported all over the world with commercially important host shells over a prolonged period of time, making it difficult or impossible to trace their origins. It has been demonstrated that once invasive nonindigenous species successfully are introduced to an area, it is very hard and costly to eradicate them (Miura 2007). Although it is difficult to prevent polydorid infestation after they succeed in boring into the shells, one of the most effective ways to avoid their influences may be preventing their early settlement on shells applying their life history traits. However, the harmful species tended to be continuous breeders and have high reproductive ability and possess long life span, so as a result, they show long settling periods. Moreover, once *P. uncinata* is introduced to the land-based tank-cultured system, the species has the capacity to increase its population rapidly according to its direct development.

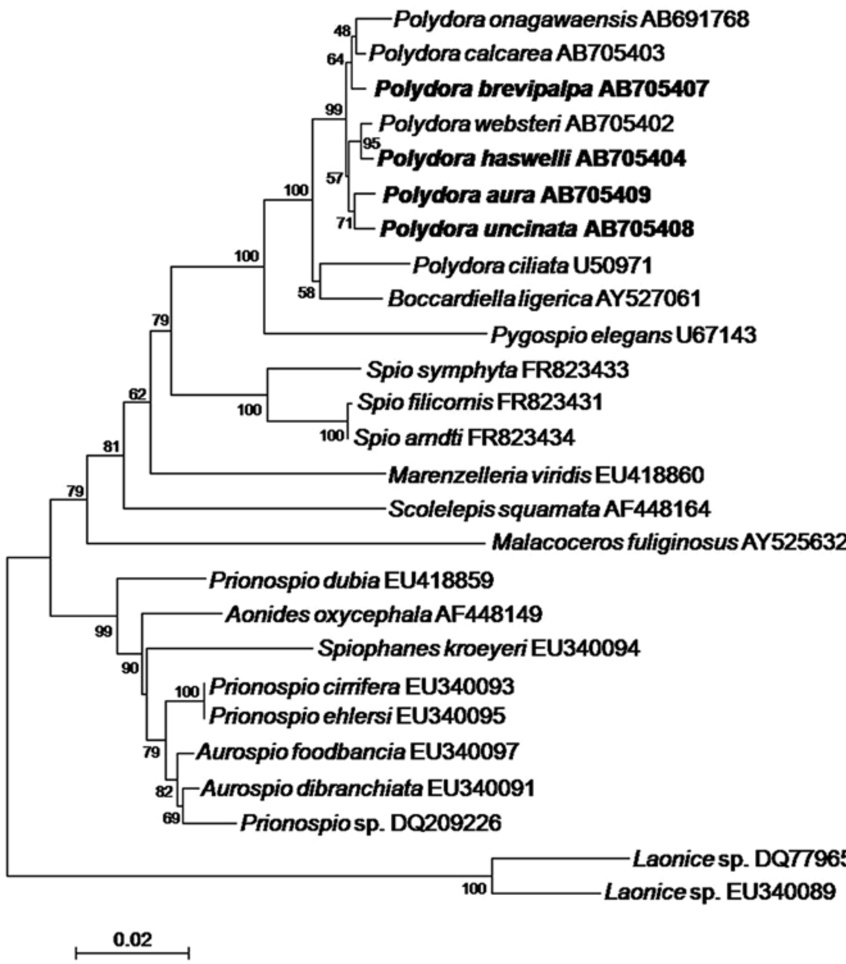

Fig. 3 A neighbor-joining tree inferred from the nuclear 18S rRNA gene sequences of spionid polychaetes. The 18S rRNA gene sequences of the four harmful *Polydora* species are highlighted in *boldface type*. Bootstrap values of >50 % as a percentage of 1,000 bootstrap replicates are given at the respective nodes. The *scale bar* represents the number of substitutions per site

The transportation of live animals therefore requires great care and suitable precautions to maintain sustainable aquaculture and biological diversity. Monitoring studies are indeed necessary to avoid the further dispersal of species already known to be harmful in existing cultured and natural environments. It is needless to say that not only these polydorid polychaetes but other as yet unrecognized and potentially invasive animals and plants may have been unintentionally transported as a result of the international trade in economically important mollusk species.

Table 2 Comparison of morphological characteristics among four harmful shell borers, *Polydora brevipalpa*, *P. uncinata*, *P. haswelli*, and *P. aura* from Japan, South Korea, northeast China, and Australia

		Pigmentation						
Polydora species	Body color	Palps	Prostomium	Chaetigers 1–4	Pygidium	Occipital tentacle	Notochaetae on chaetiger 5	Special notochaetae in posterior chaetigers
Polydora brevipalpa	Tan	**Black bars**	Absent	**Absent**	Absent or white or black	Absent	**Absent**	Absent
Polydora uncinata	Tan	**Black bars or absent**	Black or absent	Black or absent	Absent or black	**Present**	Present	**Recurved hook accompanying capillaries**
Polydora haswelli	Tan	**Black bars**	Black or absent	Black or absent	Absent	Absent	Present	Absent
Polydora aura	**Orange or tan**	Absent	Absent	Absent	Absent	**Present**	**Absent**	**Tight cylindrical bundles of short needles accompanying capillaries**

Bold entries show distinguishable characters of the species

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