



REVIEW

Polydorid polychaetes on farmed molluscs: distribution, spread and factors contributing to their success

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ABSTRACT: Species of the *Polydora*-complex (i.e. polydorids) are the most common shell-boring polychaetes found on cultured molluscs. However, which species become problematic depend on their ability to reach mollusc farms and flourish under culture conditions. We therefore hypothesise that the planktonic larval phases of pest polydorids on molluscs grown on-shore will be short (as is typical of adelphophagic larvae, which can maintain large local populations) while those of polydorids on molluscs grown off-shore will be long (as is typical of planktotrophic larvae, which can disperse long distances to farms). Principal component and discriminant analyses of information extracted from the literature partly supported this hypothesis by identifying larval developmental mode and pest species as contributing more to pest status than host species and culture mode, with differential influence on pest status in different situations and potential bias through incorrect identification of polydorid species. χ^2 analyses confirmed that pest status depended on host culture method and pest larval mode. Pest polydorids producing adelphophagic larvae in on-shore systems may reflect the development of large local populations on hosts with culture periods >2 yr. The many records of pests in off-shore and near-shore systems with pest species producing planktotrophic larvae may reflect shorter host culture periods and the higher incidence of planktotrophy among polydorid species in general. *Polydora websteri*, *P. uncinata*, *P. hoplura* and *P. haswelli* are the most frequently recorded and widespread pest species globally, although the taxonomy of these and shell-boring *P. ciliata* and *Boccardia polybranchia* need to be clarified. The positive relationships between the numbers of alien shell-borers and pests, and the number of hosts cultured per country confirm that mollusc aquaculture is an important vector and reservoir of alien pest polychaetes.

KEY WORDS: Alien species · Aquaculture · Larval developmental modes · Molluscs · Off-shore · On-shore · Polydorid pests

INTRODUCTION

Shell middens dating to as early as 12 000 BC in Europe, America, Japan, Australia and South Africa indicate that molluscs have been harvested extensively for millennia (e.g. Bailey & Milner 2002, Ogburn et al. 2007, Erlandson et al. 2008, Haupt et al. 2010, Habu et al. 2011). Oysters were highly re-

garded by the classical Romans who imported oysters from as far away as Britain, despite the proposal of a law in 115 BC to curb this practice (Andrews 1948). This demand undoubtedly prompted attempts at culturing oysters and resulted in the successful establishment of oyster beds in a lake off the greater Bay of Naples in 105 BC (Andrews 1948). At about the same time, Aboriginal Australians were

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farming oysters by catching spat on cultch (Ogburn et al. 2007). The continued demand for oysters and other molluscs has led to the overexploitation of natural stocks and consequent attempts to replenish depleted stocks with animals imported from elsewhere and the establishment of culture systems (e.g. Wolff & Reise 2002, Ruesink et al. 2005, Ogburn et al. 2007, Haydar & Wolff 2011, Castell 2012, Lucas 2012). In Japan, China and Korea the culture of molluscs began about 500 yr ago (Kusuki 1991 in Ruesink et al. 2005) while in Europe and North America it started in earnest in the 1700s and 1800s (Wolff & Reise 2002).

Modern culture of molluscs is often associated with large-scale movement of stock (Wolff & Reise 2002, Ruesink et al. 2005, McKindsey et al. 2007). At least 5 species of oysters and 2 species of clams have been imported to, and moved among, countries in western and northern Europe for aquaculture purposes since as early as 1570 (Wolff & Reise 2002). On the west coast of North America, most of the cultured species are exotic or alien (McKindsey et al. 2007) while in Chile a thriving abalone industry relies on stock originally imported from California and Japan (Moreno et al. 2006). Similarly, the South African oyster industry relies on the regular importation of spat from the Americas and Europe and the local movement of stock from nursery to grow-out facilities (Haupt et al. 2010, 2012). Up to 18 oyster species have been translocated to 73 countries or regions, with the Pacific oyster, *Crassostrea gigas*, translocated to more than 50 (Ruesink et al. 2005, Lucas 2012). Gastropods are moved less frequently and there is a tendency for indigenous species to be cultured (Castell 2012, but see Culver et al. 1997 and Moreno et al. 2006).

The cultivation of high densities of molluscs can have far-reaching ecological effects, creating habitats for other organisms, providing them with protection against predators, reducing physical and physiological stress and enhancing settlement and recruitment (e.g. Pregoner 1983, Ruesink et al. 2005, McKindsey et al. 2007, Lucas 2012). This is particularly important when the molluscs are cultured in environments where they are creating hard substrates where none existed before, such as in muddy or soft-sediment environments and suspended culture (Ruesink et al. 2005, McKindsey et al. 2007), thus providing settlement substrates for larvae that might have been otherwise lost. The arrangement of the molluscs and their shell structure may further contribute to the production of different microclimates for preferential settlement by larvae; for example, large numbers of planktonic

polydorid larvae settled in the inner, rather than outer, valve of scallops in suspended culture in Japan (Teramoto et al. 2013). Thus, cultured molluscs are often associated with infestations by disease agents and fouling organisms (e.g. Bower et al. 1994, Wolff & Reise 2002, McKindsey et al. 2007, Haydar & Wolff 2011, Castell 2012, Lucas 2012). This, together with the extensive movement of molluscs, particularly of oysters, has led to aquaculture being considered one of the main vectors of transport of exotic species. For example, Wolff & Reise (2002) estimated that more than 20 species of animals were imported to Europe with *C. gigas* alone, and they concluded that oysters are more important vectors than either hull fouling or ballast water, a conclusion supported by McKindsey et al. (2007).

There are many reviews of the diseases of cultured molluscs and of the exotic species transported with these animals, but they seldom focus on shell-boring polychaetes in any detail (Bower et al. 1994, Mortensen et al. 2000). The most common shell-borers are members of the *Polydora*-complex, often referred to as polydorids (e.g. Blake 1969b, Moreno et al. 2006, Radashevsky et al. 2006, Sato-Okoshi et al. 2008, Boonzaaier et al. 2014). While there are rare instances where high infestations by polydorids occur under natural conditions (e.g. *Polydora brevipalpa* in the scallop *Patinopecten yessoensis* and *Polydora uncinata* in the oyster *Crassostrea gigas* [Sato-Okoshi & Abe 2012], and *Dipolydora convexa*, *D. concharum* and *D. alborectalis* in the scallop *Patinopecten yessoensis* in Japan [Sato-Okoshi 1999]), high infestation by a few polydorid species is observed more frequently in mollusc culture systems where intensive commercial culture may lead to the development of ecosystems which may encourage the proliferation of pests. For example, in South Africa, Chile and Australasia, farmed molluscs were typically infested by fewer species than are present on wild molluscs occurring close to farms (e.g. Sato-Okoshi & Takatsuka 2001, Simon et al. 2006, Sato-Okoshi et al. 2008, Simon et al. 2010, Simon 2011, Boonzaaier et al. 2014, Sato-Okoshi et al. 2015). Similarly, molluscs grown in on-shore culture systems were infested by fewer species than those grown off-shore (Simon, 2015). This suggests that either only some species are prone to becoming pests in culture, or that the culture environment creates favourable conditions which only enable some species to become pests. In cases of high infestation levels, shells are damaged by the boring activity of the worms which negatively impact condition in the hosts as they

divert energy from growth to shell repair (Kojima & Imajima 1982, Lleonart et al. 2003, Simon et al. 2006). In extreme cases infestation has been implicated in causing high mortalities (for example, up to 50% of abalone stock in Tasmania, Lleonart et al. 2003) and the collapse of oyster culture concerns in Hawai'i and Australia (e.g. Bailey-Brock 1990, Ogburn et al. 2007).

The main aim of this review was 2-fold. In the first instance, the literature was explored to determine whether pest species, larval developmental mode, host species and culture method influence the pest status of polydorids on cultured molluscs. The second aim was to provide the first review of polydorid pests on cultured molluscs on a global scale. Such a review will help to (1) highlight which species are most problematic globally, (2) alert importers of molluscs to the species that are problematic in the countries from which their molluscs originate, (3) trace the possible source of new alien pest species, (4) determine if any species show host specificity and (5) highlight problems in species identification.

MATERIALS AND METHODS

Reviewing the literature

A review of the literature reporting shell-infesting polydorids in cultured or commercially harvested molluscs was conducted and the following information extracted: location, the polydorid and host species, culture method (classified as on-shore, intertidal, near-shore [bottom and subtidal] and off-shore suspended), pest status (rare, common and pest) and larval developmental mode (planktotrophic, adelphophagic, lecithotrophic and poecilogonous). A species was classified as 'pest', when it was called as such by the author, when the author demonstrated a significant negative impact on the host or when infestation exceeded 10 worms per individual (see Kojima & Imajima 1982). It was classified as 'common' if many of the hosts were infested, but the author did not consider it a pest or had not demonstrated a negative impact on the host (this usually applied to small species which were often present in high densities without negatively affecting the host, or if the boring activity of the worm was not destructive), or if the infestation level was <10 worms ind.⁻¹. 'Rare' was used when a species infested few individuals per sample). The larval developmental mode was only considered in the analysis when it was included in the study reporting the pest. Every

record was considered separately as a single species might not always be a pest, may behave differently in different circumstances or may have been misidentified.

Statistical analysis

A principal component analysis (PCA, conducted in SPSS 22), run on a correlation matrix with varimax rotation to reduce the number of describing variables, was used to determine which of the traits (worm species, host species, culture system and larval developmental mode) contributed most to the pest status (discriminating variable) of the polydorids recorded in the literature (Pallant 2007). The pest and host species were coded 1–23 and 1–19, respectively, arranged in alphabetical order. Pest status was coded 1–3 in increasing order of severity as rare, common and pest. Culture method was coded 1–4, in order of increasing distance from the shoreline for hosts cultured 'in the sea'; intertidal, near-shore and off-shore, and finally those cultured on-shore. Larval mode was coded 1–4 as adelphophagic, lecithotrophic, planktotrophic and poecilogonous, respectively. Two components explaining 62.45% of the variance were extracted when the eigenvalue was set >0.9 . These were run through a descriptive discriminant analysis (DA) to detect differences in pest status depending on host, culture method, pest species and larval developmental mode.

A χ^2 analysis was used to test the hypothesis that the larval development of pests depends on the culture system in which the molluscs are reared, using only those records from the literature which indicated both the pest status and larval developmental mode of the polydorids in question, and previously unpublished data collected by the authors.

Simple linear regressions were used to determine whether there was a relationship between the number of hosts cultured and the number of shell-infesting, non-indigenous polydorids and non-indigenous pest polydorids recorded per country, and between the number of shell-boring, non-indigenous polydorid species and the number of shell-boring, non-indigenous pest polydorids recorded on commercially reared hosts, per country. For the latter analysis, cryptogenic species, species which had only been identified to genus level and references to *P. ciliata* (this species is not a shell-borer and will be discussed in more detail in 'Problems with taxonomy' below) were omitted as their alien statuses could not be confirmed.

WHY DO ONLY SOME POLYDORID SPECIES BECOME PESTS?

Culture methods

Molluscs are cultured in a variety of ways which differ in terms of location, production costs, feeding and exposure of the molluscs to water movement and air (Appleford et al. 2012, Castell 2012, Lucas 2012). In on-shore systems, animals may be grown in baskets, cages or bags suspended in outdoor raceways, ponds or dams, or indoor tanks; water is usually pumped in from the sea, through the farm and back to sea, while the molluscs are usually constantly submerged (Appleford et al. 2012). Alternatively, animals may be grown in on-bottom culture where spat or hatchery-reared seed are sowed directly onto the seabed or suspended off long-lines or floating rafts in cages or bags subtidally or in the off-shore (Nell 2001, Appleford et al. 2012, Castell 2012, Lucas 2012). These will also be submerged permanently, but are subject to prevailing water currents which will depend on depth and distance from the shore. These systems can be utilised for most molluscs. Certain bivalves may also be grown in the intertidal; spat are 'captured' on sticks, nets or in bags which are set on frames or trestles or they may be sowed directly onto the rocks (Nell 2001, Appleford et al. 2012, Lucas 2012). These animals are exposed during low tide. Animals in near- and off-shore and intertidal culture are seldom fed. Thus, depending on the culture method, molluscs will experience different levels of water movement and exposure during tidal cycles which could, in turn, influence their exposure to larvae of fouling organisms. Additionally, the degree of feeding of the molluscs may influence the amount of food available to shell-boring worms, which could further affect their populations.

Larval developmental modes

The success of shell-boring pest polychaetes can probably be attributed to favourable conditions on farms relative to the natural environment. Simon et al. (2005) suggested that the enhanced reproductive output and recruitment of the pest sabellid polychaete *Terebrasabella heterouncinata* could probably be attributed to the high availability of potential hosts and suspended organic matter derived from degraded abalone food and faeces, which may have been further influenced by the nature of the abalone feed (Simon et al. 2002). Similarly, the high volumes

of faeces and pseudofaeces produced by cultured bivalves (Lucas 2012) may also contribute to the success of pest polychaetes. Furthermore, the success of pests may be related to their life history strategies; polydorids usually have high fecundity, with some species producing >5000 planktotrophic larvae per brood, and an average of approx. 2574 (Blake 1969a, Sato-Okoshi et al. 1990, Blake & Arnofsky 1999) which may result in high propagule pressure. However, not all worms that become established on farms become pests (e.g. *Dipolydora capensis* on farmed abalone in South Africa) (Simon et al. 2006, Simon & Booth 2007, Boonzaaier et al. 2014, Simon 2015). The discrepancies between the shell-boring polydorid worms that could be imported onto mollusc farms and those that do become established, and between the degrees to which the different species flourish, may be related to differences in the larval developmental modes among polydorids (Simon 2015).

Polydorids lay their eggs in capsules brooded in the maternal burrows, but species differ with respect to the size, number and feeding mode of larvae produced; females may produce many planktotrophic larvae, few adelphophagic larvae which feed on unfertilised nurse eggs in the brood capsules, or few lecithotrophic larvae which are nourished by endogenous yolk (Gibson 1997, Blake & Arnofsky 1999, Blake 2006). Planktotrophic larvae usually emerge from the maternal burrow when 3 to 8 chaetigers long, while adelphophagic and lecithotrophic larvae emerge when 5 to 19 chaetigers long (Blake 1969a, Blake & Arnofsky 1999). Some species are poecilogonous, thus producing different types of larvae as described above, either by the same individual, or different individuals within the same population (Gibson 1997, Blake & Arnofsky 1999, Blake 2006, David et al. 2014). However, irrespective of the size at emergence from the maternal burrow, the larvae of most species metamorphose when they are 15 to 20 chaetigers and 900 to 1600 µm long (Blake & Arnofsky 1999, David & Simon 2014). This also coincides with the size at which larvae usually become too heavy to swim actively and sink in preparation for settlement (Hansen et al. 2010). Thus, the time spent in the water column depends on the difference between the size at emergence and the size at metamorphosis; depending on water temperature, planktotrophic larvae can spend up to 85 d in the water column before settling, while larger adelphophagic or lecithotrophic larvae can settle within a day of emergence (Blake & Arnofsky 1999). Thus the larval developmental modes of species will ultimately affect the ability of their larvae to reach molluscs in culture.

Predictions

We hypothesised that species which become pests depend on their larval developmental modes and the culture methods applied to the hosts for 3 reasons: (1) molluscs farmed in off-shore and on-shore conditions are exposed to different levels of seawater movement, (2) the duration of the planktonic phases of different polydorid species differ and (3) competent larvae are of a similar size. In on-shore culture systems, larvae produced in wild source populations may enter farms with water pumped onto the farm, but, irrespective of the duration of their planktonic phases, only competent larvae can infest the molluscs and remain in the system. If the adult worms then produce larvae with an obligate protracted planktonic phase, these will be lost from the system via the outflow. Thus resident worms will probably not contribute to the establishment of large local populations on farms and we can predict that worms with this life history strategy will not become very abundant in on-shore systems. By contrast, if the larval planktonic phase is short or absent, resident worms would contribute to the establishment of a large local population as the larvae remain on the farm, infesting the same or nearby hosts (David et al. 2014, see also Simon 2005 concerning *T. heterouncinata*). We can therefore predict that species producing larvae that emerge at a very late stage of development will dominate in on-shore culture systems.

In near-shore or off-shore culture systems, molluscs will be exposed to the prevailing currents and plankton which can include high densities of spionid (including polydorid) larvae (e.g. Omel'yanenko & Kulikova 2002, Abe et al. 2014). The plankton will presumably include larvae that may have long or short planktonic phases, but probably more of the former; of the larvae captured off-shore in Onagawa Bay by Abe et al. (2014), 3 of the 5 spionids identified to species level are known to produce planktotrophic larvae (Blake & Arnofsky 1999, Teramoto et al. 2013), while *Polydora uncinata*, a species known to produce larvae with short planktonic phases and found wild in this bay (Sato-Okoshi & Abe 2012) were absent. Thus we can predict that in off-shore and near-shore cultures molluscs will be infested primarily by species producing larvae with long planktonic phases. However, if species which produce lecithotrophic or adelphophagic larvae are introduced to off-shore culture systems by way of infested molluscs, then we can expect these worms to remain on these farms and flourish (for example, it has been suggested that the sudden appearance of *P. uncinata* in oysters in sus-

pending culture in South Korea was a consequence of the introduction of new oyster stocks from a different source population [Sekino et al. 2003, Sato-Okoshi et al. 2012]).

Results and discussion

Influence of pest species and larval developmental mode, and host species and culture method on pest status

Eighty instances of infestation (from the literature and unpublished data collected by the authors of the present study) included information of the larval developmental modes of the pest and the culture method of the hosts (the pest and host species included in this analysis are in bold in Table 1). These records included 23 species of polydorids infesting 19 host species (Table 1). Approximately half of the records were from off-shore culture systems, a third from on-shore systems, a quarter from near-shore systems and only 5% from intertidal culture systems (Table 2). Furthermore, when all the records are considered (i.e. not just those included in the PCA analysis), we found that most species (14) were in off-shore culture systems, 9 in on-shore, 8 in near-shore and 3 in the intertidal.

The PCA extracted 4 components but only 2 had eigenvalues >0.9 which explained a total of 62.45% of the variation in the sample. Discriminant analyses of these components showed that the model was valid (Box's M = 6.65, $p > 0.05$) and that component 1 (larval developmental mode and polychaete species) explained 92.6% of the variance in pest status. With the exception of *P. hoplura* and *P. websteri*, the polydorid species considered here only ever produced one type of larva in all records (different developmental modes were also recorded for *Boccardia chilensis*, which was not included in the analysis, Table 1). Thus larval developmental mode and polydorid species may to a large extent be surrogates of each other. Furthermore, 22% of the species (*P. onagawaensis*, *P. uncinata*, *P. haswelli*, *P. websteri* and *P. hoplura*) accounted for 58% of the records. However, this analysis cannot account for species which may have been misidentified; consequently the importance of pest species may have been overestimated. Component 2 (host and culture method) contributed <8% to the variability. Certain mollusc species dominated the records and were usually cultured in a particular manner. Nearly half of the records related to just 2 species; *Crassostrea gigas* contributed 22 records and *Patinopecten yessoensis* 16. Fourteen of

Table 1. Global distribution of shell-infesting and pest species that are associated with cultured or commercially harvested molluscs. Excludes species identified just to genus level. Pest status in native and invasive range given as pest (p), common (c), or rare (r). Larval developmental mode: adelphophagy (ad), lecithotrophy (le), planktotrophy (pl), poecilogony (po). Culture environment:

Species name	Type region	Country where present on cultured molluscs	Host infested
<i>Boccardia</i>			
<i>B. acus</i>	New Zealand	New Zealand	<i>Crassostrea gigas</i>, <i>Tiostrea chilensis</i>
<i>B. atokouica</i>	New Zealand	New Zealand	<i>C. gigas</i>
<i>B. chilensis</i>	Chile	Australia, New Zealand	<i>C. gigas</i> , <i>Mytilus edulis</i> , <i>Saccostrea cucullata</i> , <i>T. chilensis</i>
<i>B. knoxi</i>	New Zealand	Australia, New Zealand	<i>C. gigas</i> , <i>Haliotis rubra</i>
<i>B. polybranchia</i>	Australia	Australia, France	<i>C. gigas</i> , <i>M. edulis</i>
<i>B. proboscidea</i>	West coast of USA	Australia, Japan, South Africa, USA (Hawaii)	<i>C. gigas</i> , <i>Haliotis midae</i>
<i>B. pseudonatrix</i>	South Africa	Australia, South Africa	<i>C. gigas</i> , <i>Saccostrea commercialis</i> , <i>H. midae</i>
<i>B. semibranchiata</i>	France (Mediterranean)	France, Spain	<i>C. gigas</i>
<i>Boccardiella</i>			
<i>B. hamata</i>	East coast of USA	China, Japan	<i>C. gigas</i> , pearl mussels
<i>Dipolydora</i>			
<i>D. alborectalis</i>	Sea of Japan, Vostock Bay	Japan	<i>Patinopecten yessoensis</i>
<i>D. armata</i>	Atlantic Ocean, Madeira	Japan, South Africa	<i>Haliotis discus hannai</i>, <i>Haliotis diversicolor</i>, <i>H. midae</i>
<i>D. bidentata</i>	Sea of Japan, Peter the Great Bay	Japan	<i>C. gigas</i> , <i>P. yessoensis</i>
<i>D. capensis</i>	South Africa	South Africa	<i>H. midae</i>
<i>D. cf. giardi</i>	South Africa	South Africa	<i>H. midae</i>
<i>D. concharum</i>	New England to Newfoundland	Japan	<i>P. yessoensis</i>
<i>D. giardi</i>	Spain	Chile, Japan	<i>Argopecten purpuratus</i> , <i>C. gigas</i> , <i>Ostrea chilensis</i>
<i>D. huelma</i>	Chile	Chile	<i>Haliotis rufescens</i>
<i>D. keulderae</i>	South Africa	South Africa	<i>C. gigas</i> , <i>H. midae</i>
<i>D. normalis</i>	South Africa	South Africa	<i>H. midae</i>
<i>D. socialis</i>	Pacific Ocean, Chile	Chile	<i>O. chilensis</i>
<i>Polydora</i>			
<i>P. aura</i>	Japan	Japan, Korea	<i>C. gigas</i> , <i>H. discus discus</i> , <i>Pinctada fucata</i>

intertidal (int), near-shore bottom and subtidal (nr), off-shore suspended (off-s), on-shore pond or tank (on-p). Pest status columns: pest status is only in relation to the infestation of cultured or harvested molluscs; blank spaces indicate that pest status is not known. ?: unknown. Species names in **bold** were included in the principal component analysis

Pest status in native range	Pest status outside of native range	No. of pest records (total records)	Larval developmental mode	Culture environment	Reference
p		1(3)	po	int, off-s, nr	Handley (1995), Handley & Bergquist (1997), Dunphy et al. (2005)
c		0(1)	?	off-s	Handley (1995)
	p & c	1(6)	ad, pl	int, off-s, nr	Skeel (1979), Pregonzer (1983), Handley (1995), Handley & Bergquist (1997), Nell (2001), Dunphy et al. (2005)
p	p	4(4)	pl	off-s, nr	Handley (1995), (2000), Lleonart (2001), Nell (2001), Lleonart et al. (2003)
c	p	1(2)	?	int, off-s	Pregonzer (1983), Ruellet (2004), Royer et al. (2006)
	p, c, r	5(8)	po	int, on-p	Bailey-Brock (2000), Sato-Okoshi (2000), Simon et al. (2006), Simon & Booth (2007), Simon et al. (2010), Walker (2014)
c, p	r?	1(6)	ad	off-s, on-p	Sato-Okoshi et al. (2008) (as <i>Boccardia knoxi</i>), Simon et al. (2010), Sato-Okoshi & Abe (2012), Walker (2014), Simon (2015), S. De Lange, C.A. Simon & L.G. Williams unpubl. data
r		0(2)	?	int	Ruellet (2004), Martinez et al. (2006), Royer et al. (2006)
	c	0(2)	pl	off-s	Sato-Okoshi (2000), Zhou et al. (2010)
p		2(2)	pl	off-s	Mori et al. (1985), Sato-Okoshi (1999)
	p	1(2)	?	on-p	Simon (2011), W. Sato-Okoshi unpubl. data
p	c	1(2)	pl	off-s, nr	Sato-Okoshi (1999), W. Sato-Okoshi unpubl. data
c		0(1)	pl	on-p	Simon et al. (2006), Boonzaaier et al. (2014)
r		0(1)	?	on-p	Boonzaaier et al. (2014)
	c	2(2)	pl	nr	Mori et al. (1985), Sato-Okoshi (1999)
	c	0(4)	pl	off-s	Sato-Okoshi (1999), Sato-Okoshi & Takatsuka (2001)
p		1(1)	?	nr	Vargas et al. (2005)
r		0(2)	?	off-s, on-p	Simon (2011), Boonzaaier et al. (2014)
r		0(1)	?	on-p	Simon (2011)
r		0(1)	?	off-s	Sato-Okoshi & Takatsuka (2001)
p		4(4)	pl	off-s, on-p	Sato-Okoshi & Abe (2012), Sato-Okoshi et al. (2012)

(continued on next page)

Table 1 (continued)

Species name	Type region	Country where present on cultured molluscs	Host infested
<i>P. biocipitalis</i>	California	Chile	<i>Mesodesma donacium</i>
<i>P. brevipalpa</i>	Sea of Japan, Vostock Bay	China, Japan	<i>H. discus hannai</i> , <i>P. yessoensis</i>
	Brazil	Brazil	<i>C. gigas</i> , <i>Crassostrea rhizophorae</i>
<i>P. ciliata</i>	England	India, France, Germany, Italy, UK	<i>C. gigas</i> , <i>M. edulis</i> , <i>Ostrea madrasensis</i> , <i>P. fucata</i> , <i>Tapes philippinarum</i>
<i>P. cornuta</i>	East coast of USA	USA	<i>Crassostrea virginica</i>
<i>P. curiosa</i>	Pacific Ocean, Kurile Islands	Japan	<i>P. yessoensis</i>
<i>P. ecuadoriana</i>	Ecuador	Brazil	<i>C. gigas</i> , <i>C. rhizophorae</i>
<i>P. cf. haswelli</i>	Australia?	Brazil	<i>C. gigas</i> , <i>C. rhizophorae</i>
<i>P. haswelli</i>	Australia	Australia, Korea, Japan, New Zealand	<i>C. gigas</i> , <i>M. edulis</i> , <i>O. chilensis</i> , <i>Pecten novaezelandiae</i> , <i>Perna canaliculus</i> , <i>P. fucata</i> , <i>S. cucullata</i> , <i>H. discus discus</i>
<i>P. hoplura</i>	Bay of Naples	Australia, Belgium, France, Holland, New Zealand, South Africa, Spain (Canary Islands)	<i>C. gigas</i> , <i>M. edulis</i> , <i>H. midae</i> , <i>Haliotis tuberculata coccinea</i> , <i>H. rubra</i> , <i>Haliotis laevigata</i>
<i>P. onagawaensis</i>	Japan	China, Japan	<i>C. gigas</i> , <i>Chlamys farreri</i> , <i>P. yessoensis</i> , <i>H. discus hannai</i>
<i>P. rickettsi</i>	Southern California	Argentina, Brazil, Chile	<i>Aequipecten tehuelchus</i> , <i>A. purpuratus</i> , <i>Nodipecten nodosus</i> , <i>C. gigas</i> , <i>H. rufescens</i>
<i>P. uncinata</i>	Japan	Australia, Chile, Japan, Korea	<i>C. gigas</i> , <i>H. discus discus</i> , <i>H. discus hannai</i> , <i>H. diversicolor</i> , <i>Haliotis diversicolor supertexta</i> , <i>Haliotis gigantea</i> , <i>Haliotis roei</i> , <i>H. laevigata</i>
<i>P. websteri</i> ^a	East coast of USA	Australia, Brazil, Canada, China, Japan, Namibia, Mexico, New Zealand, South Africa, USA, Ukraine, Venezuela	<i>C. gigas</i> , <i>C. rhizophorae</i> , <i>C. virginica</i> , <i>M. edulis</i> , <i>P. yessoensis</i> , <i>Placopecten magellanicus</i> , <i>P. fucata</i> , <i>Pinctada imbricata</i> , <i>S. commercialis</i> , <i>S. cucullata</i> , <i>Saccostrea glomerata</i> ?
<i>Pseudopolydora</i> <i>Ps. dayii</i>	South Africa	South Africa	<i>H. midae</i>

^aPreliminary data from Williams (2015) suggest that specimens identified as *Polydora websteri* in southern Africa, Japan and Australia are molecularly distinct from specimens from the east coast of America, and he consequently referred to them as

Table 1 (continued)

Pest status in native range	Pest status outside of native range	No. of pest records (total records)	Larval developmental mode	Culture environment	Reference
	p	1(1)	?	nr	Riascos et al. (2008)
p		7(7)	pl	nr, off-s	Imajima & Sato (1984), Sato-Okoshi (1999), Sato-Okoshi & Abe (2012), Sato-Okoshi et al. (2013), Teramoto et al. (2013)
r		0(2)	le	int	Radashevsky et al. (2006)
p, r	p	5(7)	?	int, off-s	Kent (1979), Velayudhan (1983), Ghode & Kripa (2001), Boscolo (2002), Ruellet (2004), Buck et al. (2005), Royer et al. (2006), Brenner et al. (2009)
p		1(2)	?	int	Gaine (2012) (as <i>P. ligni</i>)
r		0(1)	le	off-s	Sato-Okoshi (1999)
	p	1(2)	pl	int	Radashevsky et al. (2006)
?	?	?(2)	pl	?, int	Radashevsky et al. (2006)
c	p, c, ?	8(13)	pl, ?	off-s, int, nr, on-p	Skeel (1979), Pregonzer (1983), Read & Handley (2004), Read (2010), Sato-Okoshi et al. (2012), Walker (2014), Sato-Okoshi & Abe (2013)
p	p, c, r, ?	11(20)	ad, ad & pl	int, off-s, on-p	Korringa (1951) in Wolff & Reise (2002), Skeel (1979), Pregonzer (1983), Handley (1995), Lleonart (2001), Nell (2001), Lleonart et al. (2003), Ruellet (2004), Royer et al. (2006), Simon et al. (2006), Kerckhof et al. (2007), Simon & Booth (2007), Bilbao et al. (2011), Boonzaaier et al. (2014), Walker (2014), Simon (2015), S. De Lange, C.A. Simon & L.G. Williams unpubl. data
p		6(6)	pl	off-s	Sato-Okoshi et al. (2013), Teramoto et al. (2013), Williams (2015)
	p	6(7)	pl	nr, off-s	Sato-Okoshi & Takatsuka (2001), Radashevsky & Cáderas (2004), Vargas et al. (2005), Diez et al. (2013)
p	p	16(15)	ad	off-s	Sato-Okoshi (1999), Radashevsky & Olivares (2005), Sato-Okoshi et al. (2008, 2012), Sato-Okoshi & Abe (2012), W. Sato-Okoshi unpubl. data
c, p	c, p, r	12(26)	ad, po, pl, ?	int	Loosanoff & Engle (1943), Hartman (1954), Skeel (1979), Bailey-Brock & Ringwood (1982), Bergman et al. (1982), Pregonzer (1983), Sato-Okoshi & Nomura (1990), Bower et al. (1992), Handley (1995), Handley & Bergquist (1997), Sato-Okoshi (1999), Nell (2001), Diaz & Liñero Arana (2003), Sabry & Magalhães (2005), Sato-Okoshi et al. (2008, 2013), Litisitskaya et al. (2010) in Surugiu (2012), Read (2010), Simon (2011) (as <i>P. ciliata</i>), Sato-Okoshi & Abe (2013), Simon (2015), Williams (2015), De Lange et al. (2011), authors' unpubl. data
r		0(1)	pl	on-p	Simon et al. (2009)

P. cf. websteri. However, since this separation has not been clarified, we here refer to all as *P. websteri*

Table 2. Number of records of polydorids with different larval developmental modes in different mollusc culture systems. Pest statuses are pest (p), common (c) and rare (r); see 'Materials and methods' for definitions. Blank cells: no data available

Developmental mode	Host culture method				Total (pest only)
	Off-shore suspended	On-shore	Near-shore (bottom or suspended)	Intertidal (bottom or racks)	
Adelphophagy	3p	8p, 2c			13 (11)
Lecithotrophy	1r			1r	2
Planktotrophy	25p, 3c, 4r	3p, 2r	14p	2p, 2c	54 (44)
Poecilogony	2p, 1c	6p, 1c	1c		11 (8)
Grand total (pest only)	39 (30)	22 (17)	15 (14)	4 (2)	80 (63)

the records of *C. gigas* were from off-shore culture systems, 6 were on-shore, and 2 were from the intertidal. For *Patinopecten yessoensis*, 8 records each were from near-shore and off-shore culture systems. Furthermore, *Haliotis discus discus* and *H. midae* were cultured in the same way in 4 out of 5 and 5 out of 6 records, respectively. Seven species were recorded 2 or more times and were always cultured in the same way. The importance of host species and culture method is also highlighted when the incidence of pests were considered for the most frequently recorded species. In all of the records of *Patinopecten yessoensis* in the near-shore and 71% of the records in the off-shore, the polydorids were considered pests. Similarly, 71, 67 and 50% of the records of polydorids infesting *C. gigas* in the off-shore, on-shore and intertidal, respectively, were of pests.

Although the PCA and discriminant analyses identified 2 components which described the variability, the Wilks lambda values were not statistically significant (Wald = 0.951, $\chi^2_{(4)} = 3.84$, $p = 0.428$; Fig. 1). This indicates that polydorid species, culture system, larval developmental mode and host species all contribute to pest status, irrespective of the actual pest status but that different variables were important for determining the pest status under different conditions. This was further explored using only the records of pests (which made up 79% of the records), with χ^2 analyses showing that the frequency of the instances of pests depended on mollusc culture system and the larval development of the worms ($\chi^2_{(6,55)} = 30.12$, $p < 0.001$; Table 2). Most of these were in off-shore culture systems (48%), followed by those in on-shore, near-shore and intertidal culture (27, 22 and 3% of the records, respectively) (Table 2). The comparatively few records of pests in intertidal culture compared to other culture systems is not surprising — intertidal culture has long been implemented as a way to minimise polydorid infestation, with exposure to air for 30% of the tidal cycle considered sufficient to limit infestation (Ogburn et al. 2007).

Furthermore, oysters in near-shore culture are usually infested more frequently than those in the intertidal (Schleyer 1991, Ogburn et al. 2007). In on-shore culture systems 82% had adelphophagic larvae or were poecilogonous. By contrast 83% and 100% of the records of pests in the off-shore and near-shore, respectively, were of species producing planktotrophic larvae.

Adelphophagy

The accumulation in on-shore systems of species producing larvae which emerge at a late stage of development may be a consequence of local recruitment of larvae settling soon after emergence from

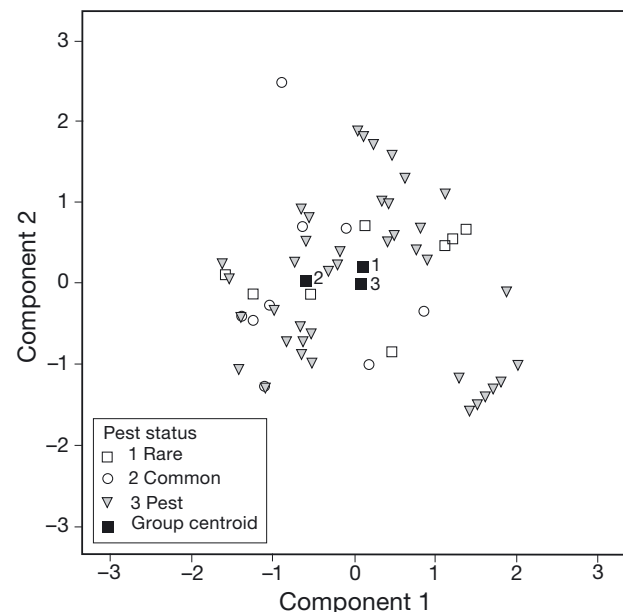


Fig. 1. Canonical discriminant functions plot showing the distribution of instances of shell-boring polydorids with different pest status as they are separated according to component 1 (larval mode and worm species) and component 2 (host species and culture system). See 'Materials and methods' for details on categories

maternal burrows coupled with their high survival, even if the number of larvae per brood is low (Simon 2005, David & Simon 2014). Since relatively few adelphophagic larvae are produced per brood and since they usually emerge just before they settle (e.g. Blake & Kudenov 1981, Gibson 1997, Blake & Arnofsky 1999, Blake 2006) at a size when their swimming or dispersal ability is reduced (Hansen et al. 2010), their ability to reach off-shore culture systems in appreciable numbers would probably be hampered. In spite of this, *P. hoplura* and *P. uncinata*, for which only adelphophagy has been widely recorded (e.g. Wilson 1928, Read 1975, Lleonart 2001, Sato-Okoshi 1998, 1999, Sato-Okoshi et al. 2008), were identified as important pests in 5 off-shore systems. In at least 3 of these instances the hosts did not develop from natural spatfall and had been transported from nursery systems (Lleonart et al. 2003, Simon 2015). It is therefore possible that the worms had reached the culture systems artificially, and, once established, a large local population could develop in the same way as proposed for on-shore culture systems. It is, however, still possible that the hosts had been infected by free-swimming larvae (Williams 2015). The absence of pests with adelphophagic or lecithotrophic larvae in the near-shore and intertidal is unexpected; if the source population is inter- or subtidal, the relative proximity to the cultured subtidal molluscs should enable infestations by such larvae.

Planktotrophy

Planktotrophic larvae are particularly well suited to infest molluscs in the off-shore for 3 reasons. Firstly, they are produced by the thousands per brood and should therefore be common components of the plankton. For example, Abe et al. (2014) recorded up to 5000 larvae m^{-3} of *P. onagawaensis* at up to 5 m depth in Onagawa Bay. Secondly, these larvae usually spend 3 to 4 wk in the water column (e.g. Blake & Arnofsky 1999, David & Simon 2014, David et al. 2014) which would increase their opportunities for reaching off-shore systems. Finally, planktotrophic larvae are usually active swimmers until they become too heavy and are ready to settle (Hansen et al. 2010). Together with movement by water currents, these characteristics should enable planktotrophic larvae to reach molluscs in off-shore culture in high enough numbers to become problematic even though larval mortality may be high. Intensive culture in near-shore and off-shore systems may further

enhance the successful recruitment of planktotrophic larvae by providing substrates which would otherwise not be available in the area.

Buck et al. (2005) and Brenner et al. (2009) concluded that the dilution of polydorid larvae due to distance from near-shore source populations significantly reduced the susceptibility of mussels, *Mytilus edulis*, in off-shore suspended culture to infestation. These distances (11 to 27 km) were, however, considerably greater than, for example, in South Africa and Japan (1 km, Williams 2015; W. Sato-Okoshi pers. obs.), and probably other countries too, and could account for the different findings. Buck et al. (2005) also suggested that the short planktonic phase of the polydorid, which they identified as *P. ciliata* (2 wk planktonic phase, as described by Daro & Polk 1973; but see also 'Problems with taxonomy' below), also played a role. Undoubtedly, here the effects of a short planktonic phase and the great distance off-shore were further exacerbated by a small source population where only 1.7 to 2.7% of the samples were infested by a mean of up to 6 worms per infested shell (Buck et al. 2005, Brenner et al. 2009). Larger source populations that are closer to the culture systems and composed of species with longer planktonic phases would pose a greater risk (e.g. *P. brevipalpa* infesting wild and cultured *Patinopecten yessoensis* in Abashiri Bay [Sato-Okoshi & Abe 2012], and *P. onagawaensis* found on farmed scallop and wild abalone in the same localities [Sato-Okoshi & Abe 2013]).

Poecilogony

Poecilogony is a rare reproductive dimorphism (Chia et al. 1996, David et al. 2014). A perceived advantage to poecilogony for pest polydorids is that they may benefit from dispersal by the planktotrophic larvae to the off-shore systems, and the later development and maintenance of local populations by the adelphophagic larvae (Chia et al. 1996, David & Simon 2014, David et al. 2014). However, the type of poecilogony could affect the ability of a species to become established in off-shore systems as a consequence of the final number of larvae that metamorphose. Poecilogony was recently described for *P. hoplura* from South Africa, with females producing either planktotrophic or adelphophagic larvae (David et al. 2014). Purely planktotrophic broods of *P. hoplura* contain more than a thousand larvae while purely adelphophagic broods contain a mean of 20 (David et al. 2014). In Simon (2015), all the develop-

ing broods observed in the off-shore contained planktotrophic larvae, while all those from the on-shore populations contained adelphophagic larvae. The larval type of females not brooding at the time of sampling was not determined, so it is possible that they produced different types of larvae, since mixed populations have been found (David 2015). This suggests that in South Africa at least, off-shore populations may have been established by planktotrophic larvae and then maintained by later generations of females producing adelphophagic larvae. By contrast, poecilogonous species producing both larval types simultaneously appear not to capitalise on the dual advantages of different larval types, as evidenced by the low number of records of poecilogonous pests in off-shore culture systems. This might be a consequence of inter-sibling competition. In mixed broods of *Boccardia proboscidea*, planktotrophic larvae are often cannibalised by their adelphophagic siblings, reducing the number of dispersive larvae entering the water column (David & Simon 2014). Furthermore, planktotrophic larvae in mixed broods lack swimming chaetae which may inhibit their swimming abilities compared to that of larvae from pure broods (Gibson 1997). This might also apply to other species which produce mixed broods.

The high incidence of pests with planktotrophic larvae may be because the larvae are produced in such high numbers that they out-compete species with adelphophagic larvae. Alternatively, or additionally, it may reflect the fact that many polydorid species produce planktotrophic larvae. Of the species included in this review for which the larval developmental modes are known, 62.5% produce planktotrophic larvae, 8.3% each produce adelphophagic or lecithotrophic larvae or are poecilogonous, with a further 12.5% having different modes in different records (Table 1). These proportions are very similar to those found among the *Boccardia*, *Boccardiella*, *Dipolydora* and *Polydora* species; 59, 21 and 3% produced planktotrophic, adelphophagic and lecithotrophic larvae, respectively, while 16% were poecilogonous (Blake & Arnofsky 1999). These proportions are also similar to that of individual records of polydorids in different culture systems (Table 2): planktotrophy (68%), adelphophagy (16%), lecithotrophy (2%) and poecilogony (14%). Thus the high incidence of pest species producing planktotrophic larvae in the intertidal, near-shore and off-shore may be a proportionate representation of species with planktotrophic larvae among the polydorids. However,

the disproportionately high number of records for adelphophagic and poecilogonous development among species recorded as pests in on-shore facilities supports the hypothesis that some selection does occur there (e.g. *P. hoplura*, *B. proboscidea* and *Boccardia pseudonatrix* in South Africa [Simon 2015], *P. uncinata* and *B. pseudonatrix* [as *B. knoxi*, Sato-Okoshi et al. 2008] in Australia and *P. uncinata* in Japan [Sato-Okoshi et al. 2015]).

Host and culture system

The link between larval development and pest status of worms in different culture systems may be further enhanced by the culture period of the hosts in the different systems. Thus the dominance of species with larvae that emerge at a late stage of development in on-shore culture systems may also be related to the fact that 16 of the 22 records in on-shore facilities included in this study were of slow-growing abalone which remain in culture for >4 yr (Castell 2012). This would facilitate the accumulation of many polydorids (Pregenzer 1983) and over many generations; e.g. *B. proboscidea* start reproducing within about 1 mo of settling and live for approx. 1 yr, during which time they produce many successive broods, leading to almost constant recruitment on farmed abalone (Simon & Booth 2007; see also Sato-Okoshi et al. 2015, for more examples). Thus, when hosts remain in culture for several years, exponential growth of the worm population can be expected if conditions remain the same or effective remedial measures are not taken. Conversely, 18 of the 39 records of off-shore cultures were of oysters and mussels that remain in culture for <2 yr (Lucas 2012), suggesting that for these species at least, the duration of the grow-out period is not long enough to allow species with adelphophagic larvae to form large local populations. Thus care should be taken with farming molluscs with different grow-out periods in close proximity to each other. In Simon (2015), the abalone and oysters examined in off-shore culture systems were grown close to each other and the oysters were infested by a higher diversity of worms than those in on-shore systems (see also Haupt et al. 2012). Thus the abalone probably served as a reservoir of infestation for the oysters which remain in culture for less than a year. This would also apply to the fouling on old or infrequently cleaned support structures of off-shore culture systems (Buck et al. 2005).

GLOBAL SPECIES DIVERSITY, DISTRIBUTION, HOST SPECIFICITY AND TAXONOMY

Movement of pests with molluscs in aquaculture

Reviews that consider polydorids in general, and shell-infestors associated with cultured molluscs in particular, usually have a regional focus: Chile (Sato-Okoshi & Takatsuka 2001, Moreno et al. 2006), South Africa (Simon et al. 2006, Boonzaaier et al. 2014, Simon 2015), Japan (Sato-Okoshi 1999, Sato-Okoshi & Abe 2013), Korea (Sato-Okoshi et al. 2012), China (Zhou et al. 2010, Sato-Okoshi et al. 2013), Australia (Blake & Kudenov 1978, Sato-Okoshi et al. 2008, Walker 2011, Walker 2014), New Zealand (Read 2004) and the United States of America (e.g. Blake 1969b). These often indicate the presence of species that are outside of their natural distribution ranges, but there is no comprehensive global review of the shell-boring polydorid pests of cultured molluscs.

The movement of molluscs for aquaculture has been implicated in the inadvertent spread of many alien species, including polychaetes (e.g. Wolff & Reise 2002, McKindsey et al. 2007, Ruesink et al. 2005, Haupt et al. 2012, Çinar 2013). In particular, Haupt et al. (2012) demonstrated that even after cleaning, oysters still harboured polydorid shell-borers after translocation. Yet the records which confirm oysters and abalone as the vectors of transportation are limited; *Polydora websteri* and *Boccardia proboscidea* were transported from mainland USA to Hawai'i (Bailey-Brock & Ringwood 1982, Bailey-Brock 2000), *P. uncinata* from Japan to Chile (Radaševsky & Olivares 2005), and probably *P. websteri* from Namibia to South Africa (Simon 2015, Williams 2015), while the sabellid *Terebrasabella heterouncinata* was transported from South Africa to California and further (Culver et al. 1997, Moreno et al. 2006). In some instances aquaculture may not have been the vector of introduction of a pest to a new region, but is responsible for its spread within its introduced range (e.g. Simon et al. 2009, Haupt et al. 2012, Williams 2015). Despite this close association between polydorid polychaetes and cultured molluscs, reviews of the contribution which aquaculture makes to the movement of aliens pay little or no attention to polydorids (e.g. Wolff & Reise 2002, Ruesink et al. 2005, McKindsey et al. 2007).

This neglect might be because molluscs would be treated against polydorids in general rather than any specific species (Royer et al. 2006), rendering the identification of individual pest species meaningless to many farmers. The neglect would be further exac-

erbated by the many taxonomic problems associated with polydorids (Sato-Okoshi et al. 2015). However, the failure to identify species means that their spread beyond their natural distribution ranges is often only noticed after they have become established and are then almost impossible to eradicate (Bailey-Brock 1990).

Results and discussion

A total of 178 records from the literature and authors' unpublished data identified 38 polydorid species (8 *Boccardia* spp., 1 *Boccardiella* sp., 11 *Dipolydora* spp., 17 *Polydora* spp., 1 *Pseudopolydora* sp., excluding those that had only been identified to genus level), infesting 36 cultivated or commercially harvested mollusc species in 25 countries on all continents except Antarctica (Table 1). Half the species considered in this review are, or have the potential to be, problematic alien species. The most virulent of these are undoubtedly *P. websteri*, *P. uncinata*, *P. haswelli* and *P. hoplura*, which collectively infest 21 hosts in 17 countries. Among these species, *P. uncinata* was always considered a pest (in 15 records) while *P. hoplura*, *P. websteri* and *P. haswelli* were considered pests in approximately half of the instances where they were reported with cultured molluscs (Table 1). Twelve species were recorded in 2 countries and 21 in only one. Eighteen species were associated with commercially important molluscs only within the native range of the polychaete, 8 were recorded within and outside of their native ranges, and 9 were recorded only outside of their native ranges. From among these species, where the proportion of records as pests exceeded 50%, the maximum total number of records was 8. Thirteen species were never recorded as pests (Table 1). Among the species infesting only 1 host, only *Boccardia semibranchiata*, infesting *Crassostrea gigas*, was recorded in more than one country (France and Spain). Of the species that infested more than 2 hosts, 11 were restricted to either one country, or one region (e.g. *P. onagawaensis* has only been found in China and Japan, and *P. aura* has only been found in Japan and Korea, while *P. rickettsi* which, although restricted to South America, was recorded in Chile, Argentina and Brazil).

Çinar (2013) suggested that 36 of the 292 alien polychaete species that he reviewed were probably moved by aquaculture, including 1 sabellid and 15 polydorid shell-borers. However, he undoubtedly underestimated the full extent of the distribution of

these pests as he only considered records where worms were specifically identified as alien; for example, he did not list *P. hoplura* as an alien in Australia, although it had already been recorded there several times (Blake & Kudenov 1978, Hutchings & Turvey 1984, Leonart et al. 2003). Our tally has increased the number of known alien shell-infesting polydorids to 17, with the addition of *Boccardia chilensis* and *Dipolydora concharum*. Furthermore, the alien ranges of 9 species have been extended (*Boccardiella hamata*, *Boccardia polybranchia*, *Boccardia pseudonatrix*, *D. armata*, *D. concharum*, *P. ciliata*, *P. haswelli*, *P. hoplura*, *P. rickettsi* and *P. websteri*) while *Boccardia semibranchiata* and *P. hoplura* should be considered cryptogenic, rather than alien, on the Atlantic coast of Europe (cf. Çinar 2013 and Haydar & Wolff 2011).

Relationship between aquaculture and the spread of alien species

Although there are few instances where the movement of molluscs for aquaculture was the confirmed vector for the transport of polydorids, this review confirms the conclusions of previous authors that aquaculture is an important vector and reservoir of exotic species, including polychaetes (e.g. Wolff & Reise 2002, Çinar 2013). Linear regressions showed significant positive relationships between the number of hosts cultured in a country and the number of (1) shell-infesting, (2) non-indigenous polydorids and (3) non-indigenous pest polydorids recorded per country (Table 3). Furthermore, a positive significant relationship was found between the number of non-indigenous shell-boring polydorid species and the number of shell-boring non-indigenous pests recorded on commercially reared hosts, per country (Table 3). For the latter analysis, cryptogenic species (such as *P. hoplura* in France and Belgium) were omitted, as were species identified only to genus level and references to *P. ciliata* because their alien status could not be confirmed. In spite of a small sam-

ple size, these analyses provide a telling indictment on the role which aquaculture plays in the spread and flourishing of alien pest polydorid species. This conclusion is further reinforced by the fact that the most non-indigenous pests were recorded in Japan, which also cultivated the most hosts (e.g. Sato-Okoshi & Nomura 1990, Sato-Okoshi 1999, Sato-Okoshi & Abe 2012, 2013). Additionally, all of the pest polydorids associated with cultured oysters in Australia (Walker 2014), 5 of the 6 species in Chile (Moreno et al. 2006) and 3 of the most important pests in South Africa (Boonzaaier et al. 2014, Simon 2015, Williams 2015) are alien.

Host specificity

Although host species was identified as a factor in determining pest species, shell-infesting polydorids are usually not host-specific (Moreno et al. 2006, Sato-Okoshi et al. 2008, Simon 2011, 2015). This is supported by this review. Eight of the 37 species infested more than 4 hosts, with *P. websteri*, *P. haswelli*, *P. uncinata* and *P. hoplura* recorded on 6 or more hosts (Table 1). Eleven and 13 species were recorded on 2 hosts or one host, respectively, when unidentified species are excluded. The species which were recorded on only one host may in fact represent a restricted distribution range of the worm since some of these species were recorded only in one country or region each (e.g. *B. semibranchiata*, *D. alborectalis*), while others have been recorded on other hosts which are not commercially important (e.g. *D. socialis*, *D. concharum*, Blake 1971). Similarly, 10 species infested only bivalves but this might reflect the situation on farms rather than host specificity (Table 1); for example, *P. websteri* has only been recorded on bivalves in culture, but also on gastropods in the wild (Blake 1971) while, *D. armata* has only been found on farmed abalone, but is not restricted to gastropods in the wild (e.g. Sato-Okoshi 1999). One exception is *D. capensis*, which has been recorded widely on wild and farmed

gastropods in South Africa but never on oysters, even when present on abalone close by (Simon 2011, 2015). The physical structure of the host may, however, affect its susceptibility to infestation. For example, the rugose nature of the shell of *C. gigas* is believed to contribute to its effectiveness at creating habitats for other organisms (Haydar &

Table 3. Relationships between the number of mollusc hosts cultured per country and the number of non-indigenous polydorids and non-indigenous polydorid pest species recorded in those countries. Relationships were significant at $p < 0.05$

	Equation (n)	R ²	p
Polydorids vs. hosts	$y = 0.24 + 1.24x$ (25)	0.651	<0.0001
Alien polydorids vs. hosts	$y = 0.54 + 0.64x$ (25)	0.610	<0.001
Alien pest polydorids vs. hosts	$y = 0.92 + 0.29x$ (25)	0.560	<0.003
Alien polydorids vs. alien pest polydorids	$y = 0.84 + 0.4x$ (17)	0.710	<0.001

Wolff 2011). Similarly *Haliotis midae* is infested by more species (Boonzaaier et al. 2014) than any other haliotid included in the present study and this may be a consequence of the rugose nature of its shell compared to that of other haliotids (Fig. 2).

Problems with taxonomy

An important outcome of this review is that it has highlighted the species for which identifications are (probably) problematic. Since its initial identification as a pest of oysters by Haswell (1885), *B. polybranchia* has been recorded as a pest of *C. gigas* in France (Ruellet 2004, Royer et al. 2006) and *Mytilus edulis* in Australia (Pregenzer 1983). There is, however, much confusion in the literature around this species (Blake & Kudenov 1978, Simon et al. 2010) and it probably includes several morphologically similar species. Additionally, it has not been recorded with oysters in Australia since 1983 (Pregenzer 1983, Walker 2014), while the photograph provided in Ruellet (2004, their Fig. 50), though not very clear, more closely resembles *B. proboscidea*, which has also been recorded on the Atlantic coast of Spain (Martinez et al. 2006), in Roscoff, France (T. Struck & C. A. Simon unpubl. data) and Belgium (Kerckhof & Faasse 2014). It is therefore possible that the identifications of this species as a pest are incorrect. Similarly, *P. ciliata* was originally described in sediment (Johnston 1838) and its identification as a shell-borer is therefore very controversial. Blake (1971) and Blake & Kudenov (1978) suggested that *P. ciliata* infesting cultured molluscs on the east coast of North America and in Australia were probably *P. websteri*. Later, Mustaquim (1988) demonstrated that shell-boring *P. ciliata* in Europe were molecularly distinct from non-boring forms; yet *P. ciliata* has been identified as a shell-borer several times since 1988, in

Europe, India and China (our Table 1, Gao et al. 2014), thus perpetuating earlier errors.

Recent morphological and molecular analyses suggest that extensive revision to 3 important pest species is necessary. Here we identified *P. websteri* as the most wide-spread shell-boring polydorid. However, recent molecular analysis suggested that *P. websteri* from near the type locality is molecularly distinct from conspecifics in southern Africa, Japan and Australia, suggesting that at least these latter records represent a different species which Williams (2015) referred to *P. cf. websteri*. Additionally, it is uncertain whether *P. websteri* in Brazil (Sabry & Magalhães 2005) should be referred to *P. haswelli* (see Radashevsky et al. 2006). Thus the records considered here of *P. websteri* may actually represent several species. To further complicate matters, preliminary molecular investigations also suggest that *P. onagawaensis* may be synonymous with *P. websteri* (Williams 2015). Additionally, studies by Read (2010), Walker (2014) and Williams (2015) provide compelling arguments for synonymising shell-boring *P. haswelli* with *P. neocaeca* and *P. uncinata* with *P. hoplura*. If they are right, the known distribution of these species will change considerably, and *P. hoplura* will be the most widespread pest in the world.

The literature reviewed here also included 7 *Polydora*, 2 *Boccardia* and 3 *Dipolydora* species identified only to genus level. Given the frequency with which polydorids may be moved with aquaculture and shipping (Çinar 2013), it is imperative that pest polydorid worms be identified properly. This will increase our understanding of the actual movement and distribution of shell-infesting polydorids and help identify new alien species in time to enable eradication before the worms become established. It is clear that polydorids can be difficult to identify, especially for many aquaculturists who lack taxonomic training and access to the literature. For example, South Afri-



Fig. 2. (A) *Haliotis midae*, (B) *H. gigantea* and (C) *H. discus hannai* showing the difference in the rugosity of the abalone shells (scale bars = 2 cm), which can influence the species' susceptibility to infestation by polydorid species

can farmers initially assumed that locally cultured abalone were infested by a '*Polydora*' species, when they were, in fact, infested by *P. hoplura*, *B. proboscidea* and *D. capensis* (Simon et al. 2006, Simon et al. 2010). It is therefore imperative that an alternative means to identify worms is developed, and that a molecular database of polydorids, using common DNA markers such as 18S rRNA, 28S rRNA and COI, be generated. Such a database will facilitate the rapid identification of pests, even when regional taxonomic expertise is lacking.

CONCLUSIONS

Observations of the larval developmental modes of polydorid pests of cultured molluscs in South Africa (Simon 2015) suggested that molluscs grown in on-shore culture systems are more likely to be infested by species producing larvae which leave the maternal burrow at a late stage of development while those in off-shore culture systems would be infested by species producing larvae with a longer planktonic phase. Our review of the literature reporting the pest statuses and larval developmental modes of polydorids infesting cultured (or commercially harvested, wild) molluscs suggest that these observations are valid on a more global scale. However, a more complete analysis is hampered by several confounding factors. (1) Polydorids are usually investigated only when they become problematic, and many countries are therefore presumably not experiencing problems with infestations. For example, *Crassostrea gigas* is cultured in more than 50 countries (Ruesink et al. 2005, Castell 2012), but we found records of infestation for just a third of that. This does not necessarily mean that oysters in the remaining countries are free of polydorids, just that they have not been investigated. Thus the rare and common polydorid species would probably have been under-represented in the analysis. (2) Polydorids are sometimes investigated during targeted research by taxonomists, but the pest status of the worms may not always be indicated (e.g. Blake 1971, Walker 2014). Furthermore, the positive relationship between the numbers of shell-boring polydorid species and cultured hosts examined per country may be influenced by the level and number of taxonomic studies conducted in different countries. For example, since the 1990s, one of the authors (W. Sato-Okoshi) has recorded 15 polydorid species associated with 9 cultured mollusc species in Japan (e.g. Sato-Okoshi & Nomura 1990, Sato-Okoshi 1999, Sato-Okoshi & Abe 2012, 2013). Similarly, many polydorid

species (including non-indigenous and pest species) have been recorded in South Africa (14; e.g. Boonzaaier et al. 2014, Williams 2015), Australia (9; Blake & Kudenov 1978, Skeel 1979, Sato-Okoshi et al. 2008, Walker 2014), New Zealand (7; Handley & Bergquist 1997, Read & Handley 2004, Read 2010), Chile (6; Sato-Okoshi & Takatsuka 2001, Moreno et al. 2006) and Brazil (5; Radashevsky et al. 2006). In contrast, only 4 polydorid species have been recorded in China, on 5 hosts (Zhou et al. 2010, Sato-Okoshi et al. 2013). Since China is the leading producer of molluscs globally, culturing at least 11 species (Castell 2012, Lucas 2012), this is undoubtedly an underestimate of the shell-boring polydorids in that country. (3) Certain culture methods have been used more frequently than others. Among the records considered here, off-shore suspended culture was the most frequently used (for 14 species in 24 countries), followed by near-shore culture (13 species in 13 countries), on-shore (11 species in 13 countries) and intertidal culture (5 species in 12 countries). The apparent preference for off-shore suspended culture may have biased the analyses.

To fully understand regional polydorid species diversity and the risk of species becoming pests or being moved along with their hosts, polydorid infestations must be surveyed under cultured and natural conditions. Species which are benign in their native ranges may become pests when translocated to a new region or exposed to novel hosts, as did *B. proboscidea* in South Africa. While we provide strong evidence suggesting that larval developmental mode determines which species will become pests (particularly in on-shore systems), other life history characteristics may also play a role, such as the life span and the timing and duration of the reproductive and settlement periods (i.e. the longer the more severe the infestation). Such information will enable aquaculturists to predict which species could become problematic while knowledge of the timing of the settlement of juveniles will allow the timely implementation of control measures.

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