Minimizing the impacts of a cryptogenic aquaculture pest: protecting shellfish aquaculture from shell-boring polychaetes

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ABSTRACT

In 2017, *Polydora websteri*, a shell-boring spionid polychaete worm and cosmopolitan invader, was identified for the first time in Washington State. *P. websteri* and some of its congeners bore into the shells of calcareous marine invertebrates, reducing the host's shell integrity, growth, survivorship, and market value. Shell-boring *Polydora* spp. have a history of harming shellfish aquaculture industries worldwide by devaluing products destined for the half-shell market, and requiring burdensome treatments and interventions to manage against infection. Here, we explore the risks of *Polydora* spp. to the historically unaffected aquaculture industry in Washington State. We discuss *Polydora's* life history and pathology, its history as a pest species, and management strategies tested in other infested regions. We then propose measures that stakeholders could take to investigate and mitigate the risks of *Polydora* spp. to shellfish aquaculture, and to avoid further human-aided spread.

INTRODUCTION

In 2017, shell-boring *Polydora* spp. polychaete worms were positively identified in Washington State, including the notorious, cosmopolitan invader *Polydora websteri* (Lopes et al. in review). These parasitic marine polychaetes in the family Spionidae bore into the shells of calcareous marine invertebrates, and may pose a risk to cultured and native shellfish species (Lunz 1941; Simon and Sato-Okoshi 2015). *Polydora* spp. are colloquially known as mud worms, or mud blister worms, and have a long history of reducing shellfish aquaculture production and value in many regions, including Australia (Ogburn 2011), New Zealand (Handley and Bergquist 1997), Chile (Moreno et al 2006), British Columbia and New Brunswick (Clements et al. 2017; Shinn et al. 2015), Hawaii (Eldredge 1994; Bailey-Brock and Ringwood 1982; Bailey-Brock 1990), and the East and Gulf coasts of the United States (Lafferty and Kuris 1996; Lunz 1941; Loosanoff and Engle 1943; Brown 2012). *P. websteri* is common to many shellfish aquaculture regions (Simon and Sato-Okoshi 2015), with a broad host range, including seven oyster, one mussel, and three scallops species (Simon and Sato-Okoshi 2015). No native, shell-boring *Polydora* species have been described from Washington State. Although *P. websteri* was observed in British Columbia in 1989 (Bower et al. 1992), Puget Sound's Salish Sea neighbor, Washington State had no record in the published literature of any non-native shell-boring species until 2017 (Lopes et al, in review; Lie 1968). In the 2017 report, *Polydora* prevalence was as high as 53% in one embayment of South Puget Sound (Lopes et al. in review). The worm's invasion history and basin-wide infestation rates are unknown, but given *Polydora's* negative impacts on shellfish aquaculture in other regions, its presence in Puget Sound warrants further investigation and stakeholder awareness. Puget Sound growers produce 70% of Washington State shellfish (80% by value, over $92 million annually) (Washington Sea Grant

2015), and may soon need to address the effects of *Polydora* infestation. Here, we explore *Polydora* spp. as a potential risk to Washington State aquaculture. We discuss *Polydora's* pathology, history as a pest species, translocation in other regions, life history, and then propose measures that stakeholders could take to mitigate the risks of *Polydora* spp. to shellfish aquaculture.

HOST PATHOLOGY | Infection by boring *Polydora* spp. can reduce the host's shell integrity, growth, survivorship, and market value (Simon and Sato-Okoshi 2015). *Polydora* spp. worms bore into calcareous shells and line their tunnel with shell fragments, mucus, and detritus (Figure 1) (Wilson 1928; Zottoli and Carriker 1974). If the tunnel breaches the inner shell surface, the host responds by laying down a layer of nacre to wall itself off from the burrow and the worm (Whitelegge 1890; Lunz 1941). This produces a blister, where a thin layer of shell lies over a mass of anoxic detritus. In oysters, the blister is unsightly, its contents malodorous, and if the blister is breached during shucking the detritus can contaminate oyster meat and brine, detracting from the flavor and presentation (Morse et al. 2015). Since half-shell oysters are the most lucrative option for farmers, and *Polydora* infected oysters are often are not sellable to the half-shell market, infection significantly depreciates oyster products.

Polydora infection can also devalue other oyster products by compromising growth and survival. *Polydora* worm burden is negatively correlated with growth rate, and while the mechanisms are not fully understood, this may be due to the energetic drain of nacre production (Simon 2011; Boonzaaier et al. 2014; Lleonart et al. 2003; Kojima and Imajima 1982; Wargo and Ford 1993; Royer et al. 2006). *C. gigas* infected with *P. websteri* grows more slowly, exhibits more frequent but shorter valve gaping, and has higher blood oxygenation (Chambon et al. 2007). Infected *C. gigas* also demonstrate a three-fold increase in abundance of Cytochrome P450, a protein involved in the oyster's stress response, which could increase susceptibility to secondary stressors (Chambon et al. 2007). Shell strength is negatively correlated with *P. ciliata* burden in *Mytilus edulis,* which increases vulnerability to predation (Kent 1981). Interestingly, fecundity increases in *P. websteri*-infected *Striostrea margaritacea*, a rock oyster (Schleyer 1991). These oysters could be exhibiting a response to stress from infection by reproducing while resources allow it. Similar phenomena have been documented in nematode-parasitized mice, which produce larger litters than uninfected mice (Kristan 2004; Schleyer 1991) and plants that prematurely reproduce ("bolt") during periods of drought (Barnabás et al 2008).

***POLYDORA* LIFE HISTORY** | *Polydora's* impact on shellfish aquaculture arises from its life history as a shell-borer. After a planktonic larval stage, a burrowing *Polydora* worm settles onto the prospective host's shell and begins building a tunnel (Wilson 1928; Loosanoff and Engle 1943; Blake 1969; Blake and Arnofsky 1999). The worm enters along the margin of the shell and excavates its burrow toward the shell center, using its specialized segment, the 5th setiger, to stabilize its tunnel during burrowing and secreting a viscous fluid to dissolve the calcium carbonate shell material, (Haigler 1969; Zottoli and Carriker 1974). The *Polydora* adult dwells within the tunnel, but can emerge from openings on the outer surface of the host's shell to feed on particles in the water column and on materials on the shell surface (Figure 2) (Loosanoff and Engle 1943).

Reproduction occurs when the male deposits sperm in a female's burrow, and the female deposits egg cases along the burrow wall, with each case containing dozens of eggs. While species vary, one fecund female can produce hundreds of larval progeny (Blake 1969). It should be noted that some hermaphroditic species have been observed (e.g. *Polydora commensalis*) (Hatfield 1965). Larvae hatch from eggs and emerge from their maternal burrow and are free-swimming until they settle onto a substrate (Orth 1971; Blake 1969). Growth rate in the larval stage depends on ambient water temperature, thus the time spent in the water column differs between species and with environmental conditions, and may last as long as 85 days (Blake and Woodwick 1971; Blake and Arnofsky 1999). This potential for a long larval stage, particularly in colder climates, may allow for long dispersal distances (Simon and Sato-Okoshi 2015). Additionally, in some instances, early hatched larvae can feed on underdeveloped eggs ("nurse eggs"), and complete development in the burrow (Haigler 1969). This could result in an individual host's parasitic burden compounding over time due to high rates of autoinfection.

IMPACT ON AQUACULTURE PRODUCTION AND MANAGEMENT STRATEGIES IN OTHER REGIONS | *Polydora* infection has caused economic losses for aquaculture operations worldwide. The primary impact occurs due to negative consumer responses to worms, blisters, and anoxic material in products, particularly in freshly shucked oysters (Shinn et al. 2015). No estimates exist of the revenue lost due to the effects of *Polydora* infection on shellfish growth and survival, but large mortality events suggest that *Polydora* can impact an industry via this mechanism as well. For example, in British Columbia, *P. websteri* caused up to 84% mortality in scallop grow-out sites from 1989 to 1990, resulting in up to US $449,660 in lost revenue that year (Shinn et al. 2015; Bower et al. 1992). In Tasmania and South Australia, *P. hoplura* killed over 50% of abalone stocks between 1995 and 2000, causing an estimated $0.55 to $1.16 million in losses per year (Shinn et al. 2015). Other large-scale mortality events include infection in a Norwegian scallop nursery in the summer of 1997, when one million juvenile scallops were culled due to a

Polydora spp. infestation; in total, one-third of Norway's 1997 scallop cohort was lost (Mortensen et al. 2000). In 1998, intense infestations (up to 100 worms per oyster) of *P. ciliata* in *C. gigas* oysters in Normandy, France correlated with considerable reduction in growth and meat weight, which may have contributed to unusually high summer mortality rates of up to 51% (Royer et al. 2006). Of the shell borers, *P. websteri, P. ciliata,* and *P. hoplura* are the most widely distributed and notorious for invading and infecting shellfish farms (Radashevsky et al. 2006) (see Table 1). Non-boring species, such as *P. nuchalis* and *P. cornuta,* can also impact growers by fouling culture equipment with large masses of sediment and tubes (Bailey-Brock 1990).

In regions with noxious *Polydora* spp., producers are burdened with costs of infection avoidance and control. Farm management approaches include modifying gear for off-bottom culture to keep products free of mud (Ogburn et al. 2007; Morse et al. 2015), increasing cleaning frequency to reduce siltation (Clements et al. 2017), increasing tidal exposure time (Morse et al. 2015), and regular stock treatments. For example, Australian oyster farmers have largely adopted off-bottom growing methods with long tidal exposures to reduce mud worm infestation rates. Off-bottom methods have proven effective for avoiding infection, but this method does slow oyster growth rates (Ogburn et al. 2007; Nell 2007; Nell 2001).

A variety of treatments have been developed to kill worms once stocks are infected. Currently, the most effective method is the "Super Salty Slush Puppy" (SSSP), first developed by Cox et al. (2012). The protocol involves a 2-minute full submersion of oysters in brine (250 g/L) between -10°C and -30°C (i.e., ice-water), followed by air drying for 3 hours. The SSSP also effectively kills other nuisance epibionts, such as barnacles. Petersen (2016) recently compared the SSSP method against other saltwater, freshwater, and chemical dips followed by air exposure, and confirmed SSSP as the best method, killing 95% of *P. websteri* while causing only minimal mortality in *C. gigas.* Other methods investigated include freshwater and salt brine soaks, heat treatments, and chemical treatments (Nel et al. 1996; Dunphy et al. 2005; Hooper and Kirby-Smith 2001; Gallo-García et al. 2004).

No method to date has reliably killed 100% of worms, nor recorded the rate at which these interventions render *Polydora* eggs inviable, which is an important question that needs to be answered. Treatments and exposures have primarily been developed for species not commonly grown in Washington State (e.g., *C. virginica, Saccostrea glomerata, C. ariakensis, Tiostrea chilensis*), and none of this work has been conducted in the Pacific Northwest because, until recently, there had been no need for it.

***POLYDORA* INVASION VIA SHELLFISH TRANSLOCATION |** *Polydora* spp. have a long history of accompanying shellfish during translocation and becoming invasive pests. In the early 1880's, oysters believed to have been infected with *P. ciliata* were imported from New Zealand into the George's River in Southeast Australia. Before being sold in Australian markets, they were routinely refreshed or fattened in bays adjacent to native shellfish beds (Roughley 1922; Edgar 2001; Ogburn 2007). By 1889, mud worm outbreaks had infected thirteen separate estuaries in the region, and oyster growers abandoned leases that were below the low-water mark (Roughley 1922). The introduction and translocation of mud worm spp. to Australia may have contributed to the disappearance of native subtidal oyster beds, some of which never recovered (Ogburn 2011). More recently, *Polydora* spp. were introduced into Hawaii, probably from stock shipped from mainland United States or Mexico (Eldredge 1994). In one case, *P. websteri* brought to

Oahu via California oyster seed resulted in a severe infestation, and caused farmers to abandon their land-locked oyster pond (Bailey-Brock and Ringwood 1982).

When invasive *Polydora* spp. are introduced to new regions, they can disperse during their planktonic larval stage to infect other shellfish within a basin (Simon and Sato-Okoshi 2015; Blake and Arnofsky 1999; David et al.2014; Hansen et al. 2010). As shellfish farmers grow oysters in high-density bags, racks, or lines, a *Polydora* infestation can spread readily within a farm, and the subsequent movement of stock is considered the primary pathway for *Polydora* introduction into new regions (Simon and Sato-Okoshi 2015; Moreno et al. 2006). *Polydora* spp. worms do not usually kill the host, nor do they inhabit living host tissue, so infections can go undetected via traditional disease screening and may not be recognized until an area is fully infested (Korringa 1976). The infection mechanism might explain why *Polydora* spp. were found to be very prevalent in the year in which the infections were first reported from Puget Sound (up to 53% of *C. gigas* infected in Oakland Bay) (Lopes et al. in review). Many *Polydora* species have broad host ranges, making it possible for the species to persist in non-cultured reservoir hosts, regardless of growers' control treatments (Moreno et al. 2006). Once introduced, aquatic invasive species are rarely eradicated, and the most feasible option is often to limit further geographic spread of the invader (Çinar 2013; Paladini et al. 2017; Bower et al. 1994).

STATUS OF *POLYDORA* MONITORING AND REGULATIONS IN THE USA | Shell-boring *Polydora* spp. are not monitored or regulated in the the United States. Their ubiquity and long history as a pest species in infected regions of the Atlantic and Gulf Coasts may be the reason for this lack of federal regulation (Lunz 1941; Lafferty and Kuris 1996). However, researchers and government agencies continue to help Atlantic and Gulf farmers control infection. For example, in the past five years the Maine Sea Grant (Morse et al. 2015), Alabama Cooperative Extension System (Walton et al. 2012; Gamble 2016), New Jersey Sea Grant (Calvo et al. 2014.), and the USDA Sustainable Agriculture Research & Education (USDA Grant FNE13-780) invested in communication tools and methods for farmers to mitigate the effects of mud worm on their shellfish products.

In Australia, *Polydora* spp. have been common since they were introduced in the late 1800's, and are not identified as invasive species, but are considered pests to abalone and oyster growers. In 2005, Tasmania developed a comprehensive management program for mud worm control in cultured abalone in response to outbreaks (Handlinger et al. 2004). In Victoria, Australia, the Abalone Aquaculture Translocation Protocol categorizes mud worms as a "significant risk", and regulates that movement of heavily infected stock to uninfected areas (Victorian Fisheries Authority 2015). In New South Wales, the Department of Primary Industries researchers developed and tested control measures for shellfish farmers (Nell 2007). While Canada characterizes *Polydora* spp. as a Category 4 species of "negligible regulatory significance in Canada," the Canadian Aquaculture Collaborative Research and Development Program (ACRDP) recently funded a project in New Brunswick to identify increasing, sporadic *P. websteri* outbreaks in off-bottom oyster sites, which raises questions about the potential for *Polydora* spp. intensity to shift over time, particularly in response to changing climate conditions (Government of Canada and Services 2017).

LIVE SHELLFISH REGULATIONS IN WASHINGTON STATE | In Washington State, shellfish movement is regulated to avoid introducing species identified by the Washington Administrative

Code (WAC) as invasive. Under WAC 220-340-050 and WAC 220-370-200, import permits are mandatory for any entity importing live shellfish from outside Washington State for any purpose, such as aquaculture, research, or display, but this regulation excludes animals that are market-ready that are not expected to contact Washington waters. These permits are regulated by the Washington State Department of Fish and Wildlife (WDFW), and require a “clean bill of health” certifying that the origin is disease-free, and free of green crab (*Carcinus maenas*) and oyster drills (*Urosalpinx cinerea* and *Ocinebrellus inornatus*). Transfer permits are also required under WAC 220-340-150 when moving adult shellfish and seed between and within basins. These regulations do not certify that organisms are free of *Polydora*. WDFW import permits do require all live oyster seed and stock that will enter Washington State waters to be dipped in a dilute chlorine solution, but this treatment is a requirement only where there is potential exposure to the invasive Green crab (i.e. natural or unfiltered/untreated waters), and it has not been evaluated for use against *Polydora*. In instances where the chlorine dip is lethal (e.g. any form of mussel and geoduck), imports are only allowed from locations isolated from European green crab infested waters, and thus the treatment is not required. Oyster shell (cultch), which is moved throughout the state for oyster bed enrichment and hatchery seeding for farming and restoration purposes, is required to be "aged” out of the water for a minimum of 90 days, so it is unlikely to harbor viable *Polydora* worms or eggs (WDFW, personal communication).

Under WAC 220-370-200 and WAC 220-370-180 aquaculture groups must immediately report any disease outbreak to the WDFW. Consequently, hatchery staff and farmers monitor for large mortality events that indicate disease. Widespread mortalities due to infectious pathogens are common to shellfish aquaculture, however, aided by diligent stakeholders, Washington has so far avoided several of the most notorious diseases infecting other regions, such as the oyster herpes virus variants (e.g. OsHV-1 found in Tomales Bay, CA), the highly lethal OsHV-1 microvariant (OsHV-1 µVar, recently found in San Diego, CA, likely transferred from Europe or Oceania), the abalone withering syndrome (present in California), Dermo (*Perkinsus marinus,* Gulf and Atlantic Coasts of USA), Pacific oyster nocardiosis (Atlantic and Gulf Coast), MSX disease (*Haplosporidium nelsoni*, detected in British Columbia), and Bonamiasis (it was once identified in WA in oyster stock sourced from California) (Elston et al.1986; Alfjorden, et al. 2017; Meyer 1991). No regulations require stakeholders to monitor for or report *Polydora.* Mortality directly associated with *Polydora* infection is rare, but the worm's impact on aquaculture in other regions due to product devaluation and increased susceptibility to secondary stressors (including diseases) highlights the need to take a closer look at this threat.

RECOMMENDED RESEARCH & REGULATORY ACTIONS | To minimize the impact of *Polydora* spp. on Washington State shellfish aquaculture, current distribution needs to be mapped, stakeholders should be informed of the risks of infection and treatment options, and if warranted, regulations updated to avoid translocation, via the following recommendations:

Polydora presence and baseline infestation rates need to be fully established to best control further human-aided spread into uninfected areas. A quantitative survey of live shellfish should be conducted in Puget Sound, Willapa Bay and Grays Harbor, three estuaries where shellfish aquaculture and stock transport occurs. To understand why *Polydora* infestation rates are higher in certain areas, sampling site details should be collected alongside the distribution survey including sediment type, culture gear type and tidal elevation, and environmental data such as temperature, salinity, and aragonite saturation or pH. Environmental data will help to characterize *Polydora* spp. potential impact on shellfish aquaculture under projected climate conditions. Species distributions will also inform potential regulatory and control actions. It is possible that *Polydora* spp. have been present in Washington State at low levels for many years, perhaps controlled by environmental conditions, local ecology, or culture techniques.

Washington State shellfish growers and direct-to-consumer purveyors (e.g., oyster shuckers) should be equipped to recognize *Polydora*-infected product, and to understand the impact *Polydora* could have on their businesses. Shellfish growers and aquaculture facilities with *Polydora* may need to start implementing treatment measures to control *Polydora* spp. in their products. While prior work in other regions provides some hints as to which treatments might work for eliminating *Polydora*, growers require information on the relative efficacy and practicality of these treatments in local conditions, on locally cultured species, and whether existing handling practices (e.g., air exposure during transport, chemical dips) can be effective against the worm. For example, WDFW import permits require that clam, oyster, and mussel seed or stock intended to touch Washington waters to be treated for the invasive green grab using a dilute chlorine dip (WDFW, n.d.); this treatment may be effective against epibionts such as *Polydora* spp., but has yet to be tested.

Hatcheries and nurseries in Washington produce shellfish seed that is sold to growers. These facilities are particularly important in pest management, since they are the nodes from which a significant portion of shellfish move about the region. Broodstock are frequently held in one location, brought to the hatchery for spawning, and returned. Larvae are reared in the hatchery, sent to nurseries to grow to seeding size, and then distributed to shellfish growers. As a result, hatchery-production involves moving oysters multiple times throughout their lifetimes. Shellfish seed are also imported into Washington from hatcheries in Canada, Hawaii, California, and Oregon. Hatchery and nursery biosecurity protocols should include inspecting and treating translocated stock for *Polydora* infection. How infestation rate and abundance change as a function of shellfish seed size and age, and whether viable *Polydora* spp. eggs can be transferred alongside translocated shellfish larvae, will be important considerations. These areas requires additional research.

Once distribution is understood, stakeholders should consider including *Polydora* and other shell-boring polychaetes as a pest to be screened for and managed against as part of the import and transfer permit conditions. The best method to screen for *Polydora* in oysters is to shuck and inspect the inside of the valves for evidence of burrowing and blisters. If screening is required, governing agencies that require sampling should coordinate, so as to minimize producers' burden and product loss.

BROADER ISSUE: NO NATIONAL REGULATION FOR MARINE POLYCHAETES | According to a 2013 review, 292 polychaete species (15% of all described polychaetes) have been relocated to new marine regions via human transport. Of these, 180 are now established and 16 are in the genus *Polydora (Çinar 2013)*. Despite this, there is no international or national governing body regulating this transport.

This oversight is evident in United States wildlife regulations. The United States Lacey Act of 1900 bans trafficking of illegal wildlife, particularly injurious species, but no annelids are listed as injurious (USFWS 2019) and overall invasive species regulations are limited. The United States National Invasive Species Council, formed in 1999, stated in their 2016–2018 management plan, "the United States currently lacks a comprehensive authority to effectively prevent, eradicate, and control invasive species that cause or transmit wildlife disease" (National Invasive Species Council 2016). While the United States Department of Agriculture's 2017 reportable disease list does include seven molluscan parasites, it do not include shell-boring polychaetes (USDA 2017). Aquatic parasites are not recognized on any United States list of invasive or injurious species. For example, the United States Geological Services list of Nonindigenous Aquatic Species includes only two annelids, both freshwater species (USDI n.d.).

CONCLUSION **|** *Polydora* spp. have a long history of invasion via oyster translocation and becoming a pest to shellfish farmers, however the movement of shell-boring polychaetes is not regulated in the United States, including into and within Washington State. Devaluation of shellfish farms across the globe due to *Polydora* infections suggest that this could be a costly oversight, and pose a threat to uninfected shellfish industries. *P. websteri*, the most notorious and cosmopolitan *Polydora* spp., was confirmed to be present in Washington State in 2017. To minimize the threat of *P. websteri* to the Washington State shellfish industry, early signs of infection should be addressed by mapping current distribution, alerting the shellfish industry of the risk, and if warranted, augmenting regulations to control further spread and introduction of other shell-boring polychaetes. More broadly, United States regulatory gaps should be addressed for better monitoring of parasitic species harbored and introduced by shellfish translocation.

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Tables

Table 1: Shell-boring *Polydora* species of concern in shellfish aquaculture, adapted and expanded from *Simon & Sato-Okoshi, 2015. Polydora websteri* is the species recently identified in Washington State (Lopes et al. *in review*). Host species in bold are currently approved for import to Washington State for culture (approval is dependent on source location, see WDFW, 2019), and countries in bold are the suggested *Polydora* spp. origins.

Polydora species	**Identified host species**	**Positively identified countries**	**References**
P. aura	***Crassostrea gigas**, Haliotis discus discus, Pinctada fucata*	**Japan**, Korea	Simon & Sato-Okoshi 2015; Sato-Okoshi and Abe 2012
P. bioccipitalis	*Mesodesma donacium*	**USA (California)**, Chile	Simon & Sato-Okoshi 2015; Riascos et al. 2009
P. brevipalpa	*H. discus hannai, Patinopecten yessoensis, **C. gigas**, Crassostrea rhizophorae*	China, **Japan**, Brazil	Simon & Sato-Okoshi 2015
P. calcarea	*Gastropod and bivalve molluscs*	Arctic, **Ireland, Japan**	Simon & Sato-Okoshi 2015; Radashevsky and Pankova 2006
P. carinhosa	***C. gigas**, C. rhizophorae*	Brazil	Simon & Sato-Okoshi 2015; Radashevsky et al. 2006
P. ciliata	***C. gigas,** Mytilus edulis, Ostrea madrasensis, P. fucata, **Venerupis (=Tapes) philippinarum**, Saccostrea glomerata*	**England**, India, France, Germany, Italy, UK	Simon & Sato-Okoshi 2015
P. convexa	***Panopea generosa***	**USA** (**California**), Canada (BC), **Japan``**	Simon & Sato-Okoshi 2015; Sato-Okoshi and Okoshi 1997
P. ecuadoriana	***C. gigas**, C. rhizophorae, Crassostrea braziliana*	**Ecuador**, Brazil	Simon & Sato-Okoshi 2015; Radashevsky et al. 2006
P. giardi	***P. generosa***	Canada	Simon & Sato-Okoshi 2015; Sato-Okoshi and Okoshi 1997
P. haswelli	***C. gigas,** M. edulis, S.*	**Australia**, Korea,	Simon & Sato-Okoshi 2015;

	glomerata, Ostrea chilensis, Pecten novaezelandiae, Perna canaliculus, P. fucata, Saccostrea cucullata, H. discus discus, C. braziliana	Japan, New Zealand	Sato-Okoshi et al. 2012
P. hoplura	***C. gigas**, M. edulis, S. glomerata, Haliotis midae, Haliotis tuberculata coccinea, Haliotis rubra, Haliotis laevigata*	**Italy (Bay of Naples),** Australia, Belgium, France, Holland,New Zealand, South Africa, Spain (Canary Islands)	Simon & Sato-Okoshi 2015
P. onagawaensis	*Aequipecten tehuelchus, Argopecten purpuratus, Nodipecten nodosus, **C. gigas**, Haliotis rufescens*	China, **Japan**	Simon & Sato-Okoshi 2015; Teramoto et al. 2013
P. limicola	***P. generosa***	Canada, Korea	Simon & Sato-Okoshi 2015; Sato-Okoshi and Okoshi 1997
P. pygidialis	***P. generosa,** Ostrea lurida,*	Canada	Simon & Sato-Okoshi 2015; Sato-Okoshi and Okoshi 1997
P. rickettsi	*Aequipecten tehuelchus, A. purpuratus, Nodipecten nodosus, **C. gigas**, O. chilensis, H. rufescens*	**USA (California)**, Argentina, Brazil, Chile, Mexico	Simon & Sato-Okoshi 2015
P. uncinata	***C. gigas**, H. discus discus, H. discus hannai, Haliotis diversicolor, Haliotis diversicolor supertexta, Haliotis gigantea, Haliotis roei, H. laevigata*	Australia, Chile, **Japan**, Korea	Simon & Sato-Okoshi 2015
P. websteri	***C. gigas**, C. rhizophorae, **Crassostrea virginica**, O. lurida, M. edulis, Mercenaria mercenaria, P. yessoensis, Placopecten magellanicus, P. fucata, Pinctada imbricata, Saccostrea commercialis, S. cucullata, S. glomerata, Argopecten irradians*	Australia, Brazil, Canada, China, Japan, Namibia, Mexico, New Zealand, South Africa, USA, Ukraine, Venezuela	Simon & Sato-Okoshi 2015; Lopes et al. *in review*

Figures

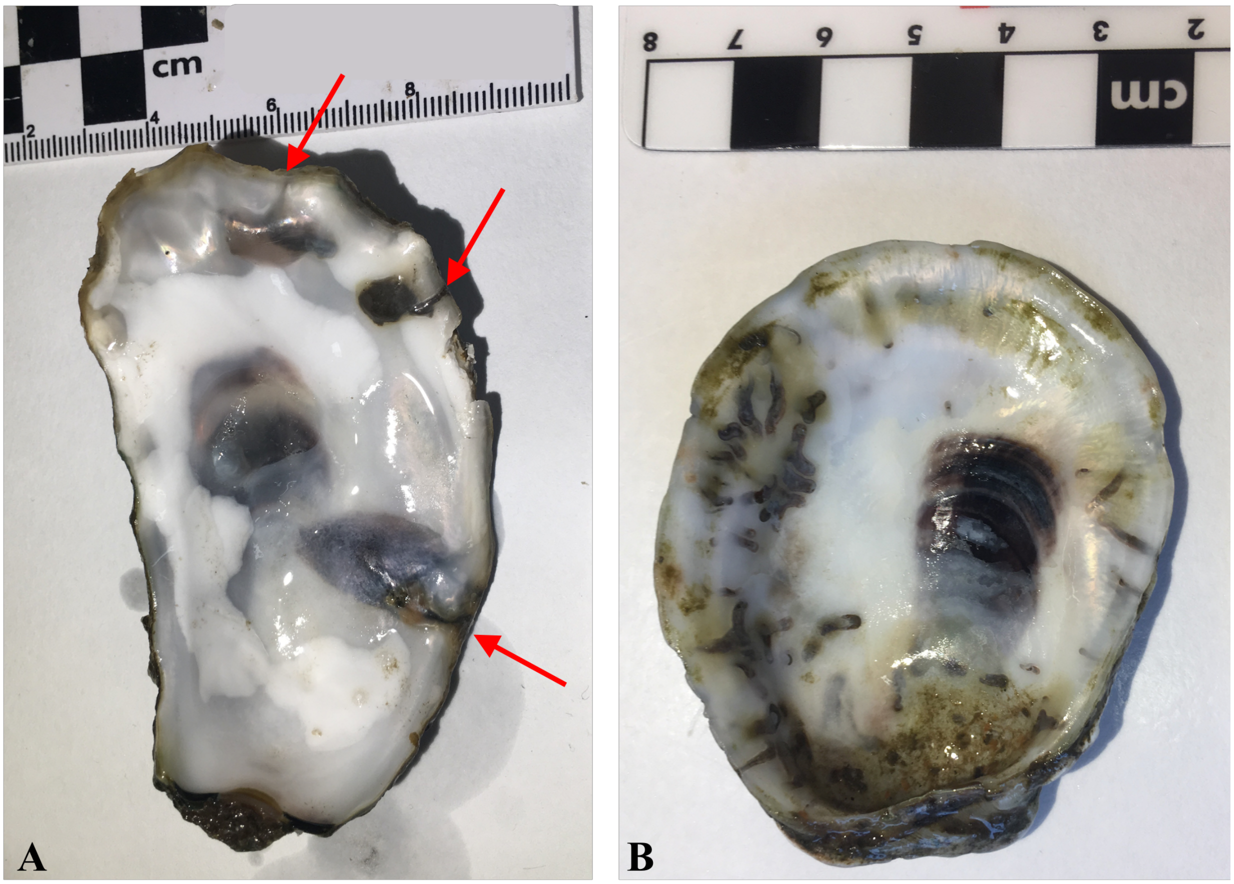

Figure 1. A. *Crassostrea gigas* valve with three active *Polydora* burrows (red arrows indicate entry points) and B. *Crassostrea virginica* valve with many burrows. Both were sampled from Puget Sound, WA in 2017 (Lopes et al. in review). Images courtesy of Heather Lopes and Julieta Martinelli.

Figure 2. *Polydora websteri* found in *Crassostrea gigas* valve in Puget Sound, WA in 2017 (Lopes et al. in review). Image courtesy of Heather Lopes and Julieta Martinelli.