Received: 23 March 2020 | Revised: 28 August 2020 | Accepted: 20 September 2020

DOI: 10.1111/are.14921

REVIEW ARTICLE

Aquaculture Research WILEY

The risks of shell-boring polychaetes to shellfish aquaculture in Washington, USA: A mini-review to inform mitigation actions

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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. Shell-boring *Polydora* spp. and related shell-boring spionid polychaetes (e.g., *Dipolydora* spp., *Boccardia* spp.), colloquially known as mud worms or mud blister worms, live in burrows within the shells of calcareous marine invertebrates, reducing the host's shell integrity, growth, survivorship and market value. Mud worms have a long history of impacting shellfish aquaculture industries worldwide by devaluing products destined for the half-shell market and requiring burdensome treatments and interventions to manage against infestation. Here, we explore the risks of mud worms to the historically unaffected aquaculture industry in Washington State. This mini-review is intended to inform shellfish stakeholders by synthesizing the information needed for immediate action in Washington State. We review the recent documentation of *Polydora* spp. in Washington State, discuss their history as pest species globally, summarize mud worm life history, and discuss effective control strategies developed in other infested regions. Finally, we review existing regulations that could be leveraged by stakeholders to avoid introduction of mud worms into uninfested areas of Washington State.

KEYWORDS

invasive species, mud blister, mud worm, oyster, Polydora

1 | INTRODUCTION

In 2017, the cosmopolitan invader *Polydora websteri* Hartman, a shell-boring polychaete worm, was positively identified in Washington State for the first time (Figure 1; Martinelli et al., 2020). These parasitic marine polychaetes in the family Spionidae bore into the shells of calcareous marine invertebrates and can pose an economic and ecological risk to cultured and native shellfish species (Lunz, 1941; Simon & Sato-Okoshi, 2015). Prior to the first report of *P. websteri* in 2017, no native or introduced shell-boring *Polydora* species had been described from Washington State (Lie, 1968; Martinelli et al., 2020).

Polydora spp. and related genera are colloquially known as mud worms, or mud blister worms, and have a long history of reducing shellfish aquaculture production and value in regions such as Australia, New Zealand, South Africa, Chile, Mexico, Hawaii, the East and Gulf coasts of the United States, and the East and West coasts of Canada (Table 1). Among the shell-boring spionids, *P. websteri* is the most notorious invader and is common to many other shellfish aquaculture regions (Simon & Sato-Okoshi, 2015), with a broad host range including seven oyster, one mussel and three scallop species (Simon & Sato-Okoshi, 2015). Despite previous observations of mud worms in nearby regions such as British Columbia (Bower et al., 1992) and California (Hartman 1941), shellfish growers have not historically identified shell-boring mud worms in Washington State. It is unclear whether the mud worms are recent invaders or have been present but were

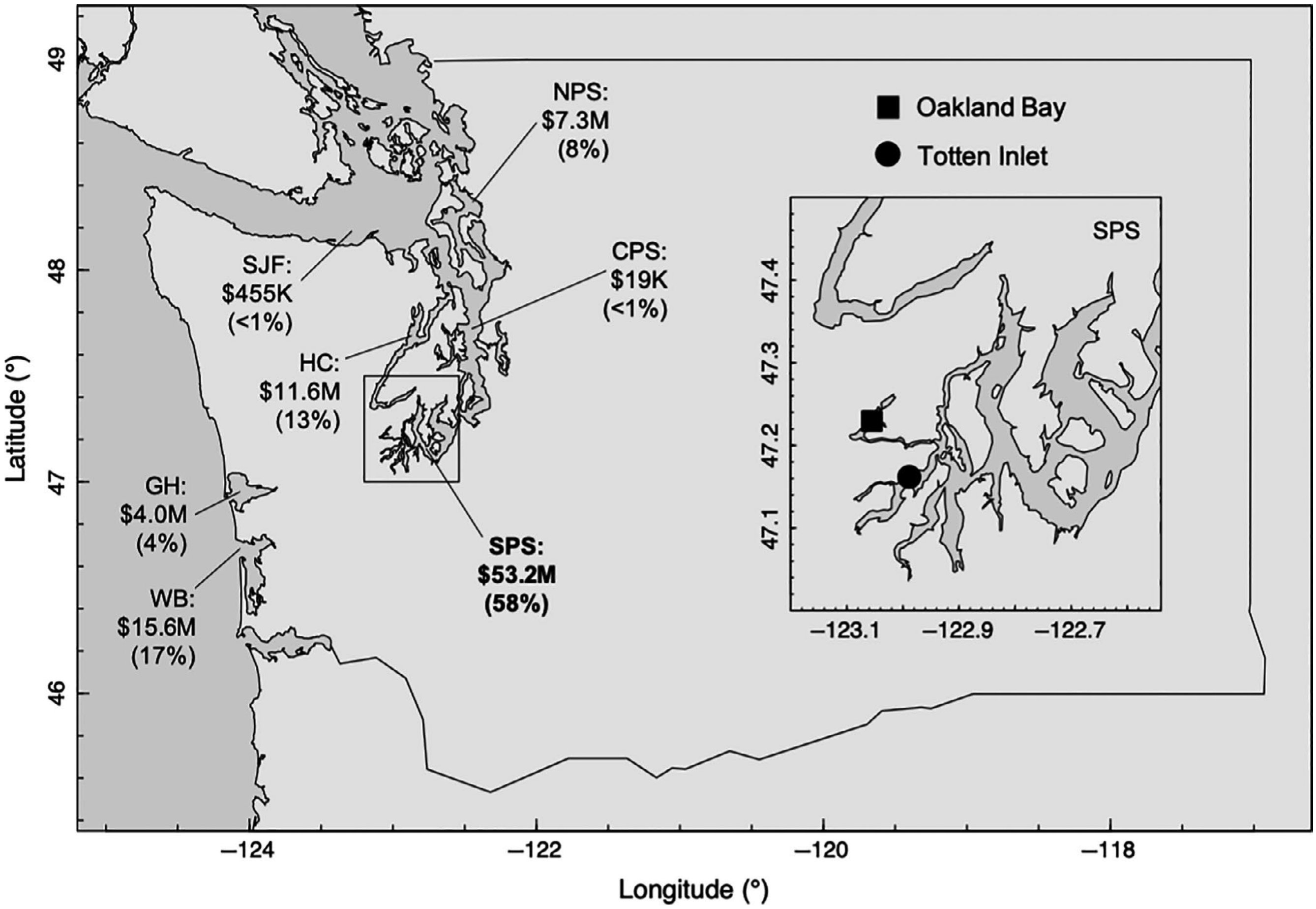

FIGURE 1 The percentage of shellfish produced by value in 2015 in each Washington State Dept. of Fish and Wildlife aquaculture area, where NPS = North Puget Sound, CPS = Central Puget Sound, SPS = South Puget Sound, HC = Hood Canal, SJF = Strait of Juan de Fuca, GH = Grays Harbor, and WB = Willapa Bay. Inlay: locations in South Puget Sound (SPS), Oakland Bay and Totten Inlet, where *Polydora* spp. were positively identified in 2017

not previously detected due to low-level infestation, sampling methods, or lack of awareness, nor is the state-wide infestation rate yet known. The 2017 study reports that mud blister prevalence in Pacific oysters (*Crassostrea gigas*) sampled from public beaches in Washington State was as high as 53% in one embayment of South Puget Sound (Martinelli et al., 2020) and suggests that infestation rates may have recently increased to levels at which observers (e.g., growers, agency personnel) take notice. Ongoing work will determine infestation rates for the Salish Sea and Willapa Bay regions.

Given the negative impacts of mud worms to shellfish aquaculture in other regions, their presence in Washington State warrants a region-focused review to inform further investigation and stakeholder awareness. Here, we explore mud worms as a potential risk to Washington State aquaculture. We review the recent documentation in Washington State, discuss the worms' history as pests of aquaculture, summarize mud worm life history and factors that influence larval recruitment, and finally outline measures that stakeholders can take to mitigate the risks and impacts of mud worms to Washington State shellfish aquaculture given existing regulations.

We provide information relevant to all boring spionids that infest cultured shellfish, which includes ten species of *Polydora*, eight *Boccardia* spp., and three *Dipolydora* spp. (Table 1). Where pertinent, we focus more heavily on the cosmopolitan invader *P. websteri*, due to its confirmed presence in the 2017 Puget Sound oyster survey (Martinelli et al., 2020; Table 1), and its global status as a pest to oyster aquaculture (Radashevsky et al., 2006). It is important to note that mud worm identification is difficult, and there are ongoing debates regarding spionid taxonomic classification. For instance, because *P. ciliata* is not a shell-boring species, mud worms reported from shellfish and classified as *P. ciliata* are instead likely to be *P. websteri* (Blake & Kudenov, 1978; see Simon & Sato-Okoshi, 2015 for a discussion of commonly misidentified species). For the purposes of this review, we will refer to the species names as they were reported by the authors.

2 | RECENT *POLYDORA* IDENTIFICATION IN WASHINGTON STATE

Washington State produces 45% of the molluscs cultured in the U.S. by value (USDA, 2018) and is an iconic industry that supports rural

TABLE 1 Reports of mud worm infestations in cultured shellfish. Studies include those that identified boring *Polydora*, *Dipolydora* and *Boccardia* spp. in shellfish grown on farms or in culture experiments and omit infestations documented in wild-collected shellfish

Country	Region	*Polydora* species	Cultured host species	Reference
Australia	New South Wales	spp.	*Saccostrea glomerata*	Wisely et al. (1979)
Australia	South Australia	*P. haswelli* *P. hoplura* *P. websteri* *B. chilensis* *B. polybranchia*[a]	*Mytilus edulis*	Pregenzer (1983)
Australia	New South Wales, southern Queensland	spp.	*S. glomerata*	Nell (1993)
Australia	Tasmania	*P. hoplura* *B. knoxi*	*Haliotis rubra* *Haliotis laevigata*	Lleonart et al. (2003)
Australia	Southwest	*P. uncinata (hoplura)*[b] *P. haswelli* *P. aura* *B. knoxi*	*H. laevigata* *Haliotis roei* *S. glomerata*	Sato-Okoshi et al. (2008)
Belgium	Bassin do Chasse, Ostend harbour	*P. ciliata*[a]	*Ostrea edulis*	Daro and Soroa Bofill (1972)
Brazil	Southern Brazil	spp.	*Crassostrea rhizophorae*	Nascimento (1983)
Brazil	Santa Catarina, Ribeirão da Ilha	spp.	*Crassostrea gigas*	Sabry et al. (2011)
Brazil	São Francisco River estuary, Sergipe state, northeastern Brazil	spp.	*Crassostrea gasar*	Da Silva et al. (2015)
Canada	New Brunswick	*P. websteri*	*Crassostrea virginica*	Clements et al. (2017a)
Chile	Herradura Bay	spp.	*Ostrea chilensis*	Di Salvo and Martinez (1985)
Chile	Tongoy Bay, Coquimbo	Unknown species similar to *P. ciliata*[a]	*Argopecten purpuratus*	Basilio et al. (1995)
China	Shandong Peninsula and Shanghai in eastern China	*P. onagawaensis* *P. brevipalpa*[c] *P. websteri*	*Patinopecten yessoensis* *Haliotis discus hannai* *Chlamys farreri* *C. gigas*	Sato-Okoshi et al. (2013)
Costa Rica	Chomes, Gulf of Nicoya	spp.	*C. rhizophorae* *C. gigas*	Zuniga et al. (1998)
France	Bay of Arcachon	spp.	*O. edulis*	Robert et al., 1991)
France	Bay of Brest, Brittany	spp.	*C. gigas*	Mazurie et al., 1995)
France	Brittany	*P. ciliata*[a] *P. hoplura*	*C. gigas*	Fleury et al., 2001)
France	Brittany	spp,	*C. gigas*	Fleury et al. (2003)
France	Normandy	spp.	*C. gigas*	Ropert et al. (2007)
France	Normandy	spp.	*C. gigas*	Royer et al. (2006)
France	Normandy	*P. ciliata*[a] *P. hoplura* *B. polybranchia*[a] *B. semibranchiata*	*C. gigas*	Ruellet et al. (2004)
India	Gulf of Mannar	spp.	*Pinctada fucata*	Alagarswami and Chellam (1976)
Indonesia	Padang Cermin Bay, Lampung	spp.	*Pinctada maxima*	Hadiroseyani and Djokosetiyanto dan Iswadi (2007)
Ireland	Guernsey, Kent	spp.	*C. gigas*	Steele and Mulcahy (1999)
Ireland	Dungarvan, County Waterford	spp.	*C. gigas*	Steele and Mulcahy (2001)
Italy	Adriatic Sea	*P. ciliata*[a]	*Tapes philippinarum*	Boscolo and Giovanardi (2002)
Italy	Venice Lagoon, North Adriatic Sea	*P. ciliata*[a]	*T. philippinarum*	Boscolo and Giovanardi (2003)
Japan	Abashiri Bay	*P. variegata*	*P. yessoensis*	Sato-Okoshi et al. (1990)

(Continues)

TABLE 1 (Continued)

Country	Region	*Polydora* species	Cultured host species	Reference
Japan	*Unknown, not in english*	spp.	*P. fucata*	Wada and Masuda (1997)
Japan	10 sites across Japan	*P. brevipalpa* *P. uncinata (hoplura)*[b] *P. aura*	*C. gigas* *P. yessoensis* *H. discus hannai* *Haliotis discus discus* *Haliotis gigantea* *H. laevigata* *H. roei* *Haliotis diversicolor supertexta* *P. fucata*	Sato-Okoshi and Abe (2012)
Korea	South and West coasts	*P. haswelli* *P. aura* *P. uncinata (hoplura)*[b]	*C. gigas* *P. fucata* *H. discus discus*	Sato-Okoshi et al. (2012)
Mexico	Baja California	spp.	*C. gigas*	Caceres-Martinez et al. (1998)
Mexico	Baja California	*B. proboscidea*	*Haliotis rufescens*	Caceres-Martinez et al. (2016)
New Zealand	Bay of Islands	spp.		Curtin (1982)
New Zealand	Marlborough Sound	*P. websteri* *P. hoplura* *B. knoxi* *B. acus* *B. chilensis* *B. atokouica*	*C. gigas*	Handley (1995)
New Zealand	Mahurangi Harbour	*P. websteri* *P. hoplura* *B. acus*	*C. gigas*	Handley & Bergquist (1997)
New Zealand	Marlborough Sound	*B. knoxi*	*C. gigas*	Handley (1998)
New Zealand	Houhora Harbour	spp.	*C. gigas*	Handley (2002)
New Zealand	Manukau Harbour	*B. acus*	*Tiostrea chilensis*	Dunphy et al. (2005)
New Zealand	North Island & Coromandel	*P. websteri* *P. haswelli*	*C. gigas* *Perna canaliculus*	Read (2010)
Russia	Sea of Japan	*P. brevipalpa*	*P. yessoensis*	Silina (2006)
Russia	Sea of Japan	*P. brevipalpa*	*Mizuhopecten yessoensis*	Gabaev (2013)
South Africa	Port Elizabeth	*P. hoplura*	*C. gigas*	Nel et al. (1996)
South Africa	Multiple sites	*P. hoplura* *D. capensis* *Boccardia sp.*	*Haliotis midae*	Simon et al. (2006)
South Africa	Multiple sites	*B. proboscidea* *B. pseudonatrix*	*H. midae*	Simon et al. (2010)
South Africa	Kleinzee and Saldanha Bay	*P. hoplura* *P.* cf. *websteri* *B. proboscidea* *B. pseudonatrix* *D. capensis D.* cf. *giardia* *D. keulderae* *Dipolydora spp.*	*C. gigas* *H. midae*	Simon (2015)
South Africa	Saldanha Bay, Walker Bay, and Haga Haga	*B. proboscidea*	*H. midae*	Simon et al. (2009)
South Africa	Hermanus	*B. proboscidea*	*Haliotis sp.*	Simon et al. (2010)
South Africa	Saldanha Bay	*P. hoplura*	*C. gigas*	David and Simon (2014)
South Africa	Saldanha Bay	*P. hoplura*	*C. gigas*	David et al. (2014)

(Continues)

TABLE 1 (Continued)

Country	Region	*Polydora* species	Cultured host species	Reference
South Africa	Multiple sites	*P. hoplura* *B. proboscidea* *D. capensis*	*H. midae*	Boonzaaier et al. (2014)
South Africa	Kleinzee, Paternoster, Saldanha Bay and Port Elizabeth	*P. hoplura*	*C. gigas*	Williams et al. (2016)
Thailand	Gulf of Thailand	spp.	*Molluscs living in shrimp ponds (converted mangrove)*	Yoshimi et al. (2007)
USA	South Carolina	*P. ciliata*[a]	*C. virginica*	Lunz (1941)
USA	Connecticut	*P. websteri*	*C. virginica*	Loosanoff and Engle (1943)
USA	Delaware Bay	spp.	*C. virginica*	Littlewood et al. (1989)
USA	Hawaii	*P. nuchalis*	*C. virginica* *Penaeus vannamei*	Bailey-Brock (1990)
USA	Delaware Bay	spp.	*C. virginica*	Littlewood et al. (1992)
USA	Chesapeake Bay	spp.	*C. gigas*	Burreson et al. (1994
USA	Delaware Bay	*P. websteri*	*C. gigas* *C. virginica*	Debrosse and Allen (1996)
USA	Hawaii, shipped from Maine	*B. proboscidea*	*O. edulis*	Bailey-Brock (2000)
USA	Virginia	spp.	*C. virginica* *Crassostrea ariakensis*	Calvo et al. (2001)
USA	North Carolina	spp.	*C. ariakensis*	Bishop and Peterson (2005)
USA	North Carolina	spp.	*C. virginica* *C. ariakensis*	Bishop and Hooper (2005)
USA	North Carolina	spp.	*C. ariakensis*	Grabowski et al. (2007)
USA	Chesapeake Bay	spp.	*C. ariakensis* *C.virginica*	McLean and Abbe (2008)
USA	Maine	*P. websteri*	*C. virginica*	Brown (2012)
USA	St. Charles River near the entrance of the Richibucto Estuary	*P. websteri*	*C. virginica*	Clements et al. (2017a)

[a]There are many mud worms identified as *P. ciliata*. However, since *P. ciliata* is a non-boring species, these were likely misidentified and many should presumably be attributed to *P. websteri* (see Blake & Kudenov, 1978; Simon & Sato-Okoshi, 2015). Similarly, reports of *B. polybranchia* as an aquaculture pest may be inaccurate (see Simon & Sato-Okoshi, 2015).

[b]*P. uncinata* has been synonymized with *P. hoplura* (Radashevsky & Migotto, 2017; Sato-Okoshi et al., 2017).

[c]*P. variegata* may have been misidentified by Sato-Okoshi et al. (1990) and instead should be classified as *P. brevipalpa* (see Teramoto et al., 2013).

communities, protects water quality, and collaborates closely with research and restoration programs (FAO, 2011; Washington Sea Grant, 2015). Within Washington, Puget Sound growers produce 70% of the state's shellfish (80% by value, over $92 million annually), concentrated mostly in South Puget Sound (Figure 1) (Martinelli et al., 2020; Washington Sea Grant, 2015). Historically, Washington shellfish farmers have not reported losses from mud worms on their farms, and until 2017 no shell-boring *Polydora* species had been formally documented from the state. Related spionid polychaetes have been present, such as *Polydora cornuta* (Ferner & Jumars, 1999), *Pseudopolydora* spp. (e.g., Woodin, 1982), and *Boccardia proboscidea* (Hartman, 1940; Oyarzun et al., 2011). These are primarily benthic species, and while they can occupy mud deposits within oyster shell crevices, they do not burrow and therefore do not create blisters. Economic losses associated with *Polydora* outbreaks in this highly productive shellfish region could have nation-wide repercussions for the aquaculture industry.

In 2017, mud worm blisters were noticed in increasing abundance in cultured Pacific oysters from South Puget Sound, which triggered a preliminary survey. Martinelli et al. (2020) sampled Pacific oysters from public beaches in Totten Inlet and Oakland Bay (Figure 1). Across the two sites, 41% of oysters were infested with a shell-boring worm (53% of Oakland Bay oysters, 34% of Totten Inlet oysters) (Martinelli et al., 2020). The worm species was identified using morphology (from scanning electron microscope images), and phylogenetics (comparing 18s rRNA & mtCOI sequences against published *Polydora* sequences). Some of the worms collected from Oakland Bay were positively identified as *P. websteri*, while others did not group with any of the available sequences and their identities remain unresolved (phylogenetic trees are reported in Martinelli et al., 2020).

It is unknown whether *Polydora* spp. were historically present in Washington State at low abundance or recently introduced. If

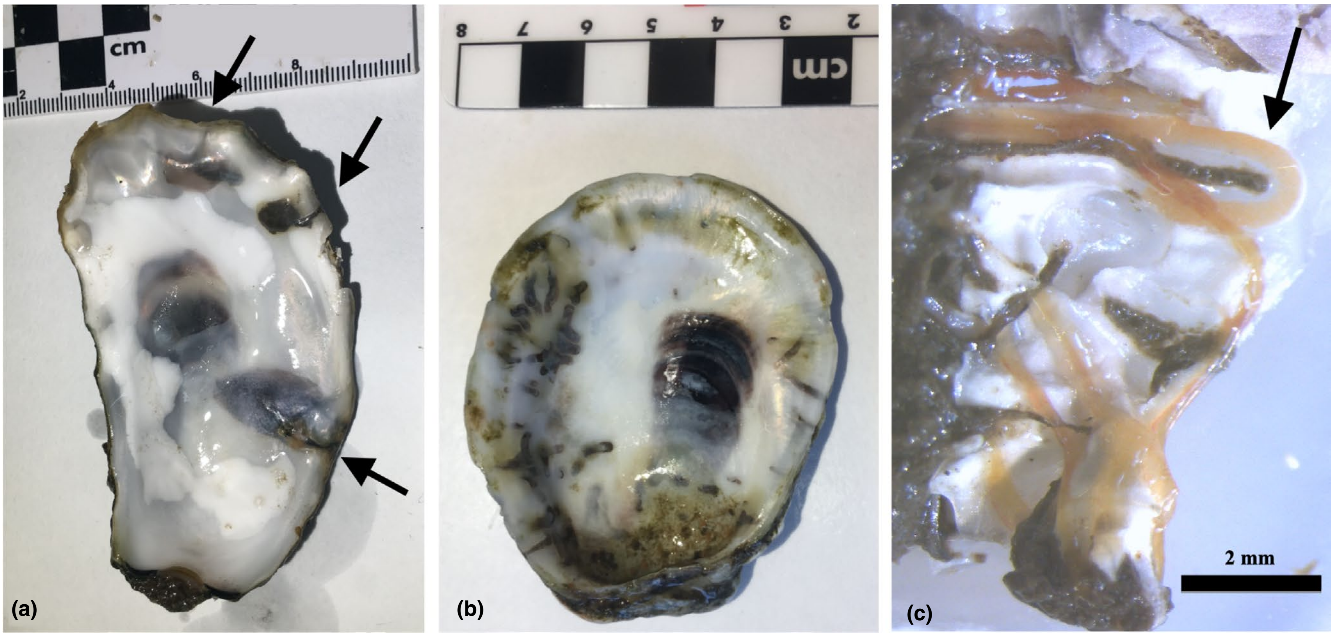

FIGURE 2 (a) *Crassostrea gigas* valve with three active *Polydora* burrows (arrows indicate entry points), (b) *Crassostrea virginica* valve with many burrows, and (c) an exposed U-shaped burrow (arrow) occupied by a shell-boring polychaete. Oysters were sampled from Puget Sound, WA in 2017 (Martinelli et al., 2020). Images courtesy of Julieta Martinelli and Heather Lopes [Colour figure can be viewed at wileyonlinelibrary.com]

the species were recently introduced, eradication might be possible (see Williams & Grosholz, 2008 for examples of successful eradication programs), or they could still be contained to a few Puget Sound basins through stakeholder awareness education, farm management, and state-wide regulation, which we discuss in more detail throughout this review (Çinar, 2013; Paladini et al., 2017). If, instead, *Polydora* spp. have been present in Washington State for a long period of time but at low levels that until recently escaped detection, the high infestation intensity reported by Martinelli et al. (2020) may be the result of a recent uptick in abundance, caused by factors such as genetic changes, relaxation of biotic pressures (e.g., predators), or environmental changes (e.g., ocean warming, siltation) (Clements et al., 2017a; Crooks, 2005). The recent marine heat waves, for instance, that resulted in anomalously elevated ocean temperatures in Washington State from 2014–2016 (Gentemann et al., 2017) may have enabled mud worm outbreaks directly, such as by increasing reproductive output (Blake & Arnofsky, 1999; Dorsett, 1961), or indirectly due to shifts in trophic ecology (e.g., altered phytoplankton community composition or phenology) (Peterson et al., 2017).

3 | IMPACTS TO AQUACULTURE PRODUCTION

By reducing the marketability of shellfish, mud worms have caused economic losses for aquaculture operations worldwide (Morse et al., 2015; Simon & Sato-Okoshi, 2015). Mud worms bore into calcareous shells and line their burrows with shell fragments, mucus, and detritus (Figure 2; Wilson, 1928; Zottoli & Carriker, 1974). If the burrow breaches the inner shell surface, the host responds by laying down a layer of nacre to protect itself from the burrow and the worm (Lunz, 1941; Whitelegge, 1890). This can produce a blister, where a thin layer of shell lies over a mass of anoxic detritus. The primary impact to oyster production is product devaluation due to negative consumer responses to unsightly blisters and burrows within the inner shell, particularly in freshly shucked oysters (Shinn et al., 2015). If a blister is breached during shucking, anoxic material can contaminate oyster meat and brine, detracting further from flavour and presentation (Morse et al., 2015). Burrows can also decrease shell strength, causing cracks during shipping and handling, and making shucking difficult (Bergman et al., 1982; Bishop & Hooper, 2005; Calvo et al., 1999; Kent, 1981). Since half-shell oysters are the most lucrative product option for oyster farmers, and mud worm-infested oysters are often not salable on the half-shell market, infestation substantially depreciates oyster products. As Washington State oysters are increasingly prized and marketed for their half-shell presentation (Washington Sea Grant, 2015), the state's oyster industry is particularly vulnerable to impacts of widespread mud worm infestations.

Mud worm infestation can also devalue shellfish products by compromising growth, survival, shell strength, and other physiological characteristics. A bivalve host's growth rate is negatively correlated with its worm burden, and while the mechanisms are not fully understood, this may be due to the energetic drain of nacre production (Ambariyanto & Seed, 1991; Boonzaaier et al., 2014; Handley, 1998; Kojima & Imajima, 1982; Lleonart et al., 2003; Royer et al., 2006; Simon, 2011; Wargo & Ford, 1993). For instance, Pacific oysters (*C. gigas*) infested with *P. websteri* grow more slowly, exhibit more frequent but shorter valve gaping, and have higher blood oxygenation, a sign of metabolic changes (Chambon et al., 2007). Infested *C. gigas* also demonstrate a threefold 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 *Polydora ciliata* burden in the mussel *Mytilus edulis*, which increases its vulnerability to predation (Kent, 1981). Oocyte size is significantly reduced in infested *C. gigas* (Handley, 1998), an indication that reproductive capacity can be altered by mud worm infestation, which could be deleterious to *C. gigas* hatchery production. While mortality directly associated with mud worm infestation is not common, these studies indicate that shellfish harbouring mud worms may be more susceptible to secondary stressors, including predation, disease, and environmental stress (Wargo & Ford, 1993).

In rare instances, large mortality events have been attributed to mud worm infestation. For instance, 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 (Bower et al., 1992; Shinn et al., 2015). In Tasmania and South Australia, *P. hoplura* killed over 50% of abalone stocks between 1995 and 2000, causing an estimated US $550,000 to $1.16 million in losses per year (Shinn et al., 2015). In the summer of 1997, one million juvenile scallops were culled in a Norwegian nursery due to a *Polydora* spp. infestation; as a result, 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).

In other regions, mud worm infestations have made certain growing practices impractical or unprofitable. In New Zealand, fattening intertidally grown oysters on longlines for a few weeks prior to sales improves oyster condition, but this practice is not recommended due to the risk it entails of mud worm infestation (Curtin, 1982). Following the collapse of native *C. virginica* in North Carolina, triploid *Crassostrea ariakensis* were assessed for culture. Feasibility was contingent on harvesting oysters prior to summer months to avoid *Polydora* spp. colonization, as revenue would be lost if infestation rate exceeded 54% (Bishop & Peterson, 2005; Grabowski et al., 2007). Many regions have experienced chronic mud worm infestation for decades (e.g., South Africa and New South Wales, Australia). Growers probably incur costs associated with cleaning or treating stocks to control mud worms, and having grow-out methods restricted to specific high tidal heights or locations (Morse et al., 2015; Nell, 2007), but these economic impacts have not yet been quantified.

In addition to becoming a pest to shellfish aquaculture, introduced shell-boring spionids can affect native shellfish species (Moreno et al., 2006). For example, the introduction and translocation of mud worm species to Australia may have contributed to the disappearance of native subtidal oyster beds (*Saccostrea glomerata*, *Ostrea angasi*), some of which never recovered (Diggles, 2013; Ogburn, 2011).

4 | BRIEF OVERVIEW OF MUD WORM LIFE HISTORY

After a planktonic larval stage, a burrowing spionid worm settles onto the prospective host's shell margin and begins to excavate a burrow. Some mud worms in the genus *Polydora* (notably *P. websteri*) create characteristic U-shaped burrows, such that two adjacent openings are created at the margin (an ‘entrance’ and an ‘exit’) (Figure 2; Blake, 1969a; Blake & Arnofsky, 1999; Haigler, 1969; Loosanoff & Engle, 1943; Wilson, 1928). The worm secretes a viscous fluid to dissolve the calcium carbonate shell material and uses a specialized segment, the 5th setiger, to stabilize the burrow as it excavates (Haigler, 1969; Zottoli & Carriker, 1974). An adult mud worm (Figure 3) dwells within the burrow, but can emerge from the burrow openings to feed on particles in the water column and materials on the shell surface (Loosanoff & Engle, 1943).

Spionid reproduction has been thoroughly reviewed (Blake, 2006; Blake & Arnofsky, 1999). Briefly, reproduction occurs when the male deposits sperm in or near a female's burrow, which females capture and hold in seminal receptacles until eggs are spawned (Blake, 2006). The female deposits egg capsules along the burrow wall, with each capsule containing multiple fertilized eggs. Many species are capable of reproducing more than once during a season, and while species vary, one fecund female can produce hundreds of larval progeny (Blake, 1969a; Blake & Arnofsky, 1999). For instance, *P. websteri* females lay strings of approximately 10 capsules, each containing 50–55 eggs (Blake, 1969a; Blake & Arnofsky, 1999). Larvae hatch from eggs and emerge from their maternal burrow at the 3-chaetiger stage and are free-swimming until they settle onto a substrate (Blake, 1969a; Orth, 1971). Growth rate in the larval stage depends on ambient water temperature; thus, the time spent in the water column differs among species and across environmental conditions, and may last as long as 85 days (Blake & Arnofsky, 1999; Blake & Woodwick, 1971). This potential for a long pelagic larval duration, particularly in cooler climates such as Washington State where spring temperatures typically average from 8–14°C, may allow for long dispersal distances (Graham & Bollens, 2010; Moore et al., 2008; Simon & Sato-Okoshi, 2015). Additionally, in some spionid species, including *P. websteri*, early hatched larvae can feed on underdeveloped eggs (‘nurse eggs’) and can remain in the burrow for a portion of their larval phase (Haigler, 1969; Simon & Sato-Okoshi, 2015). This can result in mud worm larvae being released at a much later stage. As mud worms colonize hosts during the larval phase, multiple modes of development and stages at release make it possible for larvae to be both locally sourced (e.g., autoinfection or from the same farm) or carried from distant wild or farmed shellfish.

Understanding when planktonic mud worm larvae are most abundant in Washington State will be important for shellfish growers interested in managing infestations. Generally, planktonic larval abundance tends to correlate with temperature and phytoplankton abundance, but temporal patterns vary geographically (Blake & Arnofsky, 1999; Dorsett, 1961). In Maine and New Zealand, mud worm larvae are reportedly only observed in the water column during spring and summer months (March–September), and in Maine, peak abundance occurs in May and June (Blake, 1969a, 1969b; Handley & Bergquist, 1997). In the Sea of Japan off the coast of Russia, larvae are present year-round, but abundance peaks in May then persist at moderate levels through October (Omel'yanenko et al., 2004). In the Gulf of Mexico, mud worm larvae are found in the water column year-round (Cole, 2018; Hopkins, 1958), and larval abundance peaks in May and/or November, depending on the location (Cole, 2018). The breeding season can also vary within a region. In northern Japan (Hokkaido), *P. variegata* breeding occurs during the warmest months, from August to October (Sato-Okoshi et al., 1990). In contrast, in northeastern Japan, *Polydora* larvae (species not reported) are most abundant during winter and spring months, from December through June, and loosely coincide with phytoplankton blooms (Abe et al., 2011). Although it has not been confirmed in the field, laboratory experiments indicate that diatoms may be an important larval food source for some mud worm species, as opposed to flagellates, and thus, larval abundances or recruitment could coincide with diatom blooms (Anger et al., 1986). In Washington State, phytoplankton blooms peak in late winter or spring (Horner et al., 2005), but smaller, successive blooms occur throughout the summer and into fall (Nakata & Newton, 2000; Winter et al., 1975). It is therefore likely that mud worm larvae will be most abundant in Washington State in the spring but remain present through fall. Studies are needed to identify the seasons of greatest transmission risk and the drivers of high mud worm larval abundance in Washington State. These studies should be prioritized in South Puget Sound where *Poydora* spp. have already been observed and the majority of oyster aquaculture operations are established.

5 | FACTORS THAT INFLUENCE MUD WORM RECRUITMENT

How mud worm larvae select settlement locations is not understood. Polydorin larvae are attracted to light (positively phototactic) during early stages, a trait which is commonly leveraged to isolate larvae from plankton samples (Ye et al., 2017). Mud worms readily recruit to dead oyster shells, so larvae probably do not respond to chemical cues from live hosts, but may respond to chemical or tactile signatures from shells (Clements et al., 2018). Some studies indicate that mud worm larvae may prefer to colonize certain mollusc species over others, possibly due to shell characteristics such as texture and size (Ambariyanto & Seed, 1991; Lemasson & Knights, 2019). Higher infestation rates were reported in *Ostrea edulis* compared to *C. gigas* (Lemasson & Knights, 2019). Compared to *C. virginica*, however, *C. gigas* was more susceptible to mud worm infestation, which the authors attributed to the thinness of *C. gigas* shells (Calvo et al., 1999). Larger hosts are commonly infested with more worms. In the surf clam, *Mesodesma donacium*, infestation rates increase with size and juveniles smaller than 34 mm do not harbour any mud worms, suggesting a shell size or age threshold for settlement (Riascos et al., 2008). Stressed or unhealthy hosts may be more prone to mud worm infestation. When exposed to petroleum pollutants from the Providence River system, the hard clam *Mercenaria mercenaria* was more likely to be infested with mud worm; the authors suggest that the pollutants alter clam burrowing behaviour, increasing the chances of mud worm colonization (Jeffries, 1972). In oysters, exposure to pollutants and other environmental stressors can reduce calcification rates and shell integrity (Frazier, 1976; Gazeau et al., 2007; Gifford et al., 2006), which could render them more susceptible to mud worm infestation (Calvo et al., 1999), although this mechanism has yet to be tested.

Mud worm infestation may differ among locations due to environmental conditions, particularly salinity. Evidence from Nova Scotia, Canada indicates that mud worm infestation intensity in *C. virginica* and blister size are highest at sites with lowest salinity (Medcof, 1946). A recent survey of wild *C. virginica* in two Gulf of Mexico estuaries found that *P. websteri* prevalence and abundance decrease with increasing salinity, with a marked drop in infestation at salinities exceeding 28 ppt (Hanley et al., 2019). High infestation rates were reported for *C. gigas* and *C. virginica* grown in low- and moderate-salinity locations across Virginia, but infestation rates were much lower in areas with high salinity (Calvo et al., 1999). In Gulf of Mexico farms, *P. websteri* was reportedly least abundant in *C. virginica* where salinity was most variable (Cole, 2018). Mud worm infestation has also been associated with low-salinity environments in the Indian backwater oyster *Crassostrea madrasensis* (Stephen, 1978). Whether salinity influences the current *Polydora* spp. distribution and abundance in Washington State is unknown. Salinity in Washington State estuaries typically ranges from 14–31 ppt depending on sub-basin, season, weather, and proximity to river effluent (Babson et al., 2006; Moore et al., 2008). In some parts of the Puget Sound estuary, for instance, salinity is relatively high and stable, such as in the Southern Puget Sound (26–28 ppt) and Main Puget Sound basins (28–30 ppt) (Babson et al., 2006; Moore et al., 2008). Salinity is more variable near river mouths, such as in the Skagit River estuary where it typically ranges from 18–28 ppt, but can reach as low as 0.5 ppt (Moore et al., 2008). To understand whether salinity will influence mud worm distribution or prevalence in Washington State, it will be important to document the salinity range and variability on farms with and without mud worm infestations.

Other environmental factors can influence mud worm infestation rates. Higher infestation is associated with higher siltation levels (Clements et al., 2017a; Nell, 2007), more densely grown shellfish (Smith, 1981), and lower tidal height (Handley & Bergquist, 1997; Medcof, 1946). Several of these environmental factors, such as tidal height and shellfish density, can be manipulated by Washington State farmers to manage mud worm infestation (described further in the next section). Other factors may influence mud worm prevalence and intensity naturally. For instance, *P. websteri* infestation is significantly lower in oyster shells exposed to severe acidification (pH 7.0) compared to more alkaline conditions (pH 8.0) (Clements et al., 2017b). Estuaries in Washington and the broader Pacific Northwest region experience periods of low pH due to natural estuarine processes and coastal upwelling, but which are being amplified by acidifying oceans (Feely et al., 2008, 2012). It is possible that carbonate conditions in some parts of Washington State could naturally limit the spread of *P. websteri* and other mud worm species, although this hypothesis remains to be tested.

6 | FARM MANAGEMENT STRATEGIES DEVELOPED IN OTHER REGIONS

In regions infested by shell-boring spionid species, oyster producers control and prevent infestation by modifying gear and grow methods, and by treating shellfish stocks regularly. Farm management approaches focus on keeping oysters free of mud, and air drying oysters by growing them at high tidal elevations (Handley & Bergquist, 1997; Morse et al., 2015). Since the early 20th century, Australian oyster farmers in New South Wales have used off-bottom growing methods with long tidal exposures to reduce mud worm infestation rates (Diggles, 2013; Ogburn, 2011; Smith, 1981). Oysters are grown at approximately the mean low water neap height using rack-and-rail, longline, and elevated tray systems, such that stocks are exposed for 30% of each daily tidal cycle (Ogburn, 2011). On the U.S. Atlantic Coast, researchers report that exposing *C. virginica* for 40% of a tidal cycle is an effective method of avoiding substantial mud worm infestation (Littlewood et al., 1992). Growing oysters in bags that are easily raised above the water line for aerial exposures can also reduce infestation rates, particularly during the mud worm breeding season (which varies by species and location, but typically is during the warmest months) (Blake, 2006). Some growers on the U.S. Gulf Coast use floating cages and rack-and-rail systems to easily expose bags weekly for up to 24 hr (Cole, 2018; Gamble, 2016). These off-bottom methods have proven effective for avoiding high rates of infestation, but can slow oyster growth rates in some regions (Nell, 2001, 2007; Ogburn et al., 2007), and do not always prevent infestation (Clements et al., 2017a; Cole, 2018). For instance, recent mud worm outbreaks were reported in oysters suspended off-bottom in New Brunswick, Canada and may have been related to high siltation levels, which can increase infestation rates (Clements et al., 2017a). Increasing cleaning frequency to reduce siltation may therefore help to control mud worms, particularly in areas with heavy siltation. Frequent cleaning can also reduce impacts of non-boring spionids, such as *P. nuchalis* and *P. cornuta*, and other taxa such as tunicates and hydroids, which foul culture equipment with large masses of organisms, sediment, and tubes (Bailey-Brock, 1990; Fitridge et al., 2012).

A variety of treatments have been developed to kill mud worms in infested oysters. Methods include freshwater soaks (up to 72 hr), salt brine soaks (up to 5 hr), extended cool air storage (up to 3–4 weeks at 3°C), heat treatments (e.g., 40 s at 70°C), chemical treatments (e.g., chlorine, iodine), and various combinations thereof (Bishop & Hooper, 2005; Brown, 2012; Cox et al., 2012; Dunphy et al., 2005; Gallo-García et al., 2004). Treatment efficacy differs among species, season, and exposure duration, but generally the most commonly used treatments are hypersaline dips followed by air drying, and extended cold-air storage. Currently, the most effective treatment identified in other regions appears to be the 'Super Salty Slush Puppy' (SSSP), first developed by Cox et al. (2012). The protocol involves a 2-min 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 hr. The SSSP also effectively kills other fouling epibionts, such as barnacles. Petersen (2016) recently compared the SSSP method against other saltwater, freshwater, and chemical dips followed by air exposure for infested *C. gigas*, and confirmed SSSP as the best method, killing 95% of *P. websteri* while causing only minimal oyster mortality. For farms that cannot supercool saline solutions (e.g., no ice on site), longer hypersaline dips combined with aerial exposure might be effective. For *C. virginica* and *C. ariakensis* grown in North Carolina, weekly treatments using a 20-min hypersaline dip followed by air drying for 2 hr reduced mud worm infestation from 47.5% to only 5% (Bishop & Hooper, 2005). Freshwater immersion is another treatment option for Washington growers, and for some host or mud worm species may be more effective than hypersaline dips. For Chilean flat oysters (*Tiostrea chilensis*), freshwater immersion for 180–300 min was more effective than hypersaline immersion (64 ppt) at killing *Boccardia acus* (Dunphy et al., 2005). In heavily infested *C. virginica*, nearly 98% *P. websteri* mortality was achieved with a 3-day freshwater immersion followed by four days of cold-air storage (Brown, 2012). Without the cold-air storage, the freshwater immersion only killed 25%–60% of *P. websteri*, and worms occupying deep burrows were unaffected (Brown, 2012). These hypersaline and freshwater treatments may be feasible for some farms in Washington State, but precise methods will need to be developed for local conditions and species. In other regions, non-saline chemical treatments such as calcium hydroxide (lime) and mebendazone have effectively controlled mud worm infestations (Bilboa et al., 2011; Gallo-García et al., 2004). However, environmental, health, and safety regulations will probably preclude chemicals other than salt from being used in Washington State (Morse et al., 2015). Finally, no method to date has assessed whether these interventions render mud worm eggs inviable, which is an important question that needs to be answered.

Treating infested oysters has mitigated the effects of severe infestation in other regions, but this may not be possible for some Washington growers. First, costs can be prohibitive. Growers can incur expenses associated with handling and specialized equipment, such as increasing staff hours to perform treatments, and purchasing refrigerated containers for cold-air storage (Nell, 2007). Modifying grow methods to accommodate frequent mud worm treatments, or to minimize secondary stressors following treatments, may also be necessary. Treatment costs also depend on re-infection rates, which occur more readily on farms that harbour mud worm reservoirs such as dead oyster shell, and nearby wild and cultured shellfish that cannot themselves be treated (Clements et al., 2018; Lemasson & Knights, 2019). Second, many of the existing treatments have been developed for species not commonly grown in Washington State. A common treatment for *C. virginica* is long-term cold-air storage. Maine growers have found that after 3–4 weeks at ~3°C, 100% of adult mud worms are killed, with minimal *C. virginica* mortality (Morse et al., 2015). Prolonged air exposure is also commonly used for the Australian oyster *S. glomerata* (7–10 days, in the shade; Nell, 2007). These oyster species have different physiological tolerances than *C. gigas*, the dominant aquaculture species in Washington, and therefore the same treatments may not be feasible for many of the state's oyster growers (Morse et al., 2015; Nell, 2007). For instance, while *C. virginica* can survive cold-air storage for several months (up to 6) with ~80% survival, no *C. gigas* seed or adults survived similar cold-air conditions after 20 weeks of storage (Hidu et al., 1988). Irrigating stored *C. gigas* continuously with seawater can increase survival in cold-air storage (52% adults and 80% juveniles at 7°C), but whether irrigation also increases mud worm survival is not known (Seaman, 1991). Finally, oyster mortality can be an issue following mud worm treatments regardless of the oyster species (Nell, 2007), therefore Washington growers are highly encouraged to test treatments on a small number of oysters before applying them to large batches (Morse et al., 2015). Making adjustments to grow methods might be necessary to improve oyster survival following treatments. For instance, increasing flow rates in a nursery upweller system can increase *C. ariakensis* and *C. virginica* survival following hypersaline and drying treatments (Bishop & Hooper, 2005). More details and recommendations for treatment options are available in Morse et al. (2015) and Nell (2007).

7 | MUD WORM INTRODUCTION VIA SHELLFISH TRANSLOCATION

Mud worms have a long history of accompanying shellfish during translocation and becoming invasive pests. In the early 1880s, oysters believed to be 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 (Edgar, 2001; Ogburn et al., 2007; Roughley, 1922). 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). More recently, mud worms have been introduced to Hawaii via translocated shellfish. *P. websteri* was probably brought to Oahu via California oyster seed in the 1980s, which resulted in a severe infestation and caused farmers to abandon their land-locked oyster pond (Bailey-Brock & Ringwood, 1982; Eldredge & Humphries, 1994). The non-boring *Polydora* species *P. nuchalis* was probably introduced to Hawaii in a shipment of shrimp from Mexico, fouling oyster culture ponds with masses of mud tubes (Bailey-Brock, 1990). South Africa recently detected *P. websteri* for the first time in cultured oysters (*C. gigas*); the invader was probably introduced when juvenile oysters were translocated from Namibia (Simon, 2011, 2015; Williams, 2015). *B. proboscidea* has become a pest to abalone farms in South Africa since 2004 when it was first observed burrowing into cultured abalone (Simon et al., 2009). The introduced *B. proboscidea* presumably originated from the North American Pacific Coast where it is found in the wild benthos (Hartman, 1940, 1941; Jaubet et al., 2018; Simon et al., 2009), although the species is now widely distributed throughout the world (Canada, Australia, New Zealand, Argentina, South Africa, Asia, and Europe) (Radashevsky et al., 2019). The presumed origins of introduced mud worms are, however, often based on circumstantial evidence such as documented movement of shellfish stock and the first described locations of mud worm infestations. Researchers are increasingly using molecular markers to compare the genetic structure of introduced mud worms to those in other regions (e.g., comparing mtDNA sequences) (Rice et al., 2018; Simon et al., 2009; Williams, 2015). These genetic tools, which Martinelli et al. (2020) leveraged to identify the Washington State *Polydora* spp. in 2017, will be essential to establish the possible origin(s) of the newly identified Washington mud worms.

When invasive mud worms are introduced to new regions, they can disperse during their planktonic larval stage to infect other shellfish within a basin (Blake & Arnofsky, 1999; David et al., 2014; Hansen et al., 2010; Simon & Sato-Okoshi, 2015). As shellfish farmers grow oysters in high-density bags, racks, or lines, a mud worm infestation can spread readily within a farm, and the subsequent movement of stock is considered the primary pathway for mud worm introductions both within and between regions (Moreno et al., 2006; Rice et al., 2018; Simon & Sato-Okoshi, 2015; Williams et al., 2016). Mud 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). This infection mechanism might explain why *Polydora* spp. were found to be very prevalent in the year in which they were first reported in Puget Sound oysters (up to 53% of *C. gigas* infected in Oakland Bay) (Martinelli et al., 2020). Many mud worm species have broad host ranges, making it possible for all cultured shellfish species in Washington State to be infested, including the native Olympia oyster (*Ostrea lurida*) and introduced *C. gigas*, *C. virginica*, and *C. sikamea*. Furthermore, mud worms can persist in non-cultured reservoir hosts, regardless of growers' control treatments, making it difficult to eradicate from a farm (Moreno et al., 2006).

8 | STATUS OF MUD WORM MONITORING AND REGULATIONS

Few countries formally regulate mud worm translocation or monitor outbreaks to mitigate infestations in regions with naturalized populations. The following is a brief discussion of regulatory approaches (or lack thereof) that this review identified at the global and national scales, followed by a more comprehensive survey of existing regulations in Washington that could be leveraged to control mud worm distribution within the state.

8.1 | Examples of mitigation strategies globally

Australia and Canada represent two countries at very different stages of mud worm management. In Australia, mud worms have been common since the early 1800s, and while they are not listed as invasive species, they are considered serious pests to abalone and oyster growers (Nell, 1993, 2001). Australia manages mud worms at the state level. In New South Wales, the Department of Primary Industries continues to develop and test control measures for shellfish farmers (Nell, 2007). Tasmania developed a comprehensive management program for mud worm control in cultured abalone in response to outbreaks in 2005 (Handlinger et al., 2004). In Victoria, Australia, the Abalone Aquaculture Translocation Protocol categorizes mud worms as a 'significant risk', and now regulates the movement of infected stock to uninfected areas within the state (Victorian Fisheries Authority, 2015). In contrast, mud worms have been present since at least 1938 in Canada, but have not historically posed a significant threat to oyster aquaculture (McGladdery et al., 1993; Medcof, 1946). As such, Canada characterizes mud worms as a Category 4 species of 'negligible regulatory significance in Canada', (Bower, 2010; Bower et al., 1994). Recently, however, the Canadian Aquaculture Collaborative Research and Development Program (ACRDP) funded a project to identify potential causes of increasing, sporadic *P. websteri* outbreaks in off-bottom oyster sites in New Brunswick. The recent outbreaks raise questions about the potential for mud worm intensity to shift geographically and over time, particularly in response to changing climate conditions (Government of Canada, 2017).

8.2 | Mud worm status in the United States

Marine polychaete species, including shell-boring polydorins, are not monitored or regulated in the United States. According to a 2013 review of global polychaete species (Çinar, 2013), 292 polychaetes (15% of all described polychaetes) have been relocated to new marine regions via human transport. Of these, 180 are now established, 16 are in the genus *Polydora*, 9 in *Boccardia*, and 4 in *Dipolydora* (Çinar, 2013). Despite this, there is no national governing body regulating transport into or within the United States, and marine parasites are not recognized as invasive or injurious species. For example, the U.S. Geological Services list of Nonindigenous Aquatic Species includes only two annelids, both freshwater species (USDI n.d.). While the United States Department of Agriculture's 2019 reportable disease list does include seven molluscan parasites, it does not include shell-boring polychaetes (USDA, 2019).

The ubiquity of mud worms and their long history as pests in the Atlantic and Gulf Coasts may be the reason for this lack of federal regulation (Lafferty & Kuris, 1996; Lunz, 1941). Nevertheless, researchers and government agencies continue to help Atlantic and Gulf farmers control infection. In the past twenty years, the Maine Sea Grant (Morse et al., 2015), Alabama Cooperative Extension System (Gamble, 2016; Walton et al., 2012), New Jersey Sea Grant (Calvo et al., 2014), Virginia Fishery Resource Grant Program (Gryder, 2002), and the USDA Sustainable Agriculture Research & Education (USDA Grant no. FNE13-780) invested in communication tools and methods for farmers to mitigate the effects of mud worm on their shellfish products. These investments highlight that shell-boring spionids are an ongoing, high-priority issue for farmers in infested regions, and that Washington growers may need to respond if mud worm prevalence continues to increase in the state.

8.3 | Live shellfish regulations in Washington State

In Washington State, regulations are in place to avoid introducing diseases and invasive species, which are identified in the Washington Administrative Code (WAC). Here, we review existing Washington State code to highlight regulations that control the spread of invasive species throughout the state, which may be leveraged to limit movement of shellfish heavily infested with mud worms to uninfested regions, if warranted.

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 excluding animals that are market-ready and not expected to contact Washington waters. Import permits require a 'clean bill of health' certifying that the origin is disease-free, and free of the invasive green crab (*Carcinus maenas*) and oyster drills (*Urosalpinx cinerea* and *Ocinebrellus inornatus*). The Washington State Department of Fish and Wildlife (WDFW) import permits can require that clam, oyster, and mussel seed or stock intended to touch Washington waters be treated for the invasive green crab using a dilute chlorine dip (WDFW & n.d., 2019). In instances where the chlorine dip is lethal (e.g., mussels and geoduck), imports are only allowed from locations isolated from European green crab-infested waters, and thus the treatment is not required. The chlorine dip has not been evaluated for use against mud worms. If effective, it could be adopted as a treatment required by WDFW when translocating stocks from areas with heavy mud worm infections. Transfer permits are also required under WAC 220-340-150 when moving adult shellfish and seed between and within Washington State basins. These permits are regulated by the WDFW. 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 and is inspected by WDFW prior to placement into state waters, so it is unlikely to translocate viable mud worms or eggs (WDFW, personal communication). Permits do not certify that translocated organisms are free of shell-boring spionids, as no mud worms are currently designated as invasive or pest species.

FIGURE 3 *Polydora websteri* found in *Crassostrea gigas* valve in Southern Puget Sound, WA, in 2017 (Martinelli et al., 2020). Adult *P. websteri* can grow up to ~20mm long and are 1–2 mm in diameter (Morse et al., 2015). For higher resolution images of *P. websteri* from Washington State, see the scanning electron microscope images published in Martinelli et al. (2020). Image courtesy of Julieta Martinelli [Colour figure can be viewed at wileyonlinelibrary.com]

Under WAC 220-370-200 and WAC 220-370-180, aquaculture groups must report any disease outbreak to the WDFW. Consequently, hatchery staff and farmers monitor for large mortality events that might indicate disease. Widespread mortalities due to infectious pathogens are common to shellfish aquaculture. However, aided by diligent stakeholders, Washington has so far avoided some of the most notorious diseases infecting other regions, such as 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, probably transferred from Europe or Oceania), and dermo (*Perkinsus marinus*, present in the Gulf and Atlantic Coasts of USA) (Alfjorden et al., 2017; Meyer, 1991; USDA, 2013). These regulations do not currently require mud worm infestation to be reported, as it is not a designated disease.

9 | STAKEHOLDER COMMUNICATION AND RESEARCH NEEDS IN WASHINGTON STATE

To minimize the impact of mud worms on Washington State shellfish aquaculture, stakeholders need to be informed of the risks of infestation and treatment options. Shellfish growers should be equipped to recognize mud worm-infected products, and to understand the impact mud worms could have on their businesses. Growers in uninfested regions may wish to inspect for mud worms before translocating shellfish to their properties. The best method to screen for mud worms in oysters is to shuck and inspect the inside of the valves for evidence of burrowing and blisters (Figure 2; Bower et al., 1994). If mud worms are found on their properties, shellfish growers and aquaculture facilities will probably need to implement treatment measures to control infestations in their products, and to avoid further spread. While prior work in other regions provides some hints as to which treatments might work for eliminating mud worms, growers require information on the relative efficacy and practicality of these treatments in local conditions, on locally cultured species, and on whether existing handling practices can be effective against the worms. For example, air drying during long tidal exposures, or environmental conditions such as high salinity, could mitigate or inhibit mud worm infestation in some areas (e.g., coastal estuaries such as Willapa Bay).

Hatcheries and nurseries produce shellfish seed that is sold to growers in Washington State. These facilities are particularly important in pest management, since they are nodes from which a substantial portion of shellfish moves about the region. Oyster larvae are reared in the hatchery, sent to nurseries to grow to seeding size, and then are distributed to shellfish farms and gardens (USDA, 2013). Broodstock are frequently held in one location, brought to the hatchery for spawning, and returned. As a result, hatchery production involves moving oysters multiple times throughout their lifespans (Breese & Malouf, 1975; Toba, 2002). Shellfish seed are also imported into Washington from hatcheries in Canada, Hawaii, California, and Oregon. To mitigate intraregional and interregional mud worm spread, hatcheries and nurseries may need to update biosecurity protocols to inspect and treat translocated stocks (Williams, 2015; Williams et al., 2016). How infestation rate and abundance change as a function of shellfish seed size and age, and whether viable mud worm eggs can be transferred alongside translocated shellfish larvae, will be important considerations and require additional research.

To better inform Washington State stakeholders and to control further human-aided spread into uninfected areas, mud worm presence and baseline infestation rates need to be fully established with a quantitative survey of live oysters. To understand why mud worm infestation rates are higher in certain areas, site characteristics should be documented alongside the mud worm distribution survey, including sediment type, culture gear type and tidal elevation, and environmental data such as salinity and pH (Calvo et al., 1999; Clements et al., 2017b; Cole, 2018). Species distributions will inform potential regulatory and control actions. It is possible that *Polydora* spp. have been present in Washington State at low levels of abundance for many years, perhaps controlled by environmental conditions, local ecology, or culture techniques. Environmental data will also help to characterize potential impacts of mud worms on shellfish aquaculture under projected climate conditions. Finally, phytoplankton abundance and community composition should be monitored in areas where mud worms have been positively identified to understand factors predicting mud worm larval abundance. Predicting when and where mud worm larvae are most likely to colonize shellfish may allow growers to relocate products temporarily (e.g., higher tidal height) to avoid infestation.

10 | CONCLUSION

Mud worms have a long history of invasion via oyster translocation, of devaluing shellfish products, and of necessitating treatments or changes to growing methods. Historically, Washington State has been one of the few oyster-growing regions unaffected by shell-boring spionids, but that time has unfortunately passed with the recent confirmation of *P. websteri* in southern Puget Sound. To minimize the risk of *P. websteri* and other shell-boring spionids to the Washington State shellfish industry, early signs of infestation should be addressed by mapping current distribution, alerting the shellfish industry of the risk, and, if warranted, leveraging or augmenting regulations to control further spread and introduction of other shell-boring polychaetes. More broadly, federal regulatory gaps should be addressed for better monitoring of pest species harboured by and deleterious to cultured shellfish.

CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to disclose.

ACKNOWLEDGEMENTS

The authors thank Ralph Elston, Brent Vadopalas, Sandy Shumway, Jeff Clements and an anonymous reviewer for providing comments and guidance during the research and development of this manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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How to cite this article: Spencer LH, Martinelli JC, King TL, et al. The risks of shell-boring polychaetes to shellfish aquaculture in Washington, USA: A mini-review to inform mitigation actions. *Aquac Res* 2021;52:438–455. https://doi.org/10.1111/are.14921