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

Short running title: *Minimizing impacts of shell-boring polychaetes*

Laura H Spencer[1], Julieta C Martinelli[1], Teri L King[2], Ryan Crim[3],
Brady Blake[4], Heather M Lopes[1], Chelsea L Wood[1]

[1]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105
[2]Washington Sea Grant, University of Washington, Shelton, WA 98584
[3]Puget Sound Restoration Fund, Bainbridge Island, WA 98110
[4]Washington State Department of Fish and Wildlife, Olympia, WA 98501

Corresponding author: Laura H Spencer, lhs3@uw.edu

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: Polydora, mud worm, mudworm, mudblister, invasive species, oyster

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 1961), 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 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 on 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, Lana & Nalesso 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 mis-identified species). For the purposes of this review, we will refer to the species names as they were reported by the authors.

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 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* (Fermer & Jumars 1999), *Pseudopolydora* spp. (e.g.*,* Woodin 1984), 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 identity remains 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 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, Fewings & Garcia-Reyes 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).

IMPACTS TO AQUACULTURE PRODUCTION

By reducing the marketability of shellfish, mud worms have caused economic losses for aquaculture operations worldwide (Morse, Rawson & Kraeuter 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 flavor and presentation (Morse, Rawson & Kraeuter 2015). Burrows can also decrease shell strength, causing cracks during shipping and handling, and making shucking difficult (Bergman, Elner & Risk 1982; Bishop & Hooper 2005; Calvo, Luckenbach & Burreson 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, Handlinger & Powell 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 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 *Polydora ciliata* burden in the mussel *Mytilus edulis,* which increases 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 harboring 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, Rawson & Kraeuter 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, Neill & Rozbaczylo 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).

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 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 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 to September) and in Maine peak abundance occurs in May and June (Blake 1969a; Blake 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 persists at moderate levels through October (Omel'yanenko, Kulikova & Pogodin 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, Sugawara, & Nomura 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, Sato-Okoshi & Endo 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, Anger & Hagmeier 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, Banse &

Anderson 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.

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, 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, Luckenbach & Burreson 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 harbor 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* is more likely to be infested with mud worm; the authors suggest that the pollutants alter clam burrowing behavior, 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, Luckenbach & Burreson 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, Luckenbach & Burreson 1999). Mud worm infestation has also been associated with low-salinity environments in the Indian backwater oyster *Crassostrea madrasensis* (Stephen 1978). In Gulf of Mexico farms, *P. websteri* was reportedly least abundant in *C. virginica* where salinity was most variable (Cole 2018). 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, Kawase & MacCready 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, Kawase & MacCready 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; Feely *et al.* 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.

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, Rawson & Kraeuter 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, long-line, and elevated tray systems, such that stocks are exposed for 30 percent of each daily tidal cycle (Ogburn 2011). On the U.S. Atlantic Coast, researchers report that exposing *C. virginica* for 40 percent 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 hours (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; Nell 2007; Ogburn, White & Mcphee 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 hours), salt brine soaks (up to 5 hours), extended cool air storage (up to 3–4 weeks at 3°C), heat treatments (e.g., 40 seconds at 70°C), chemical treatments (e.g., chlorine, iodine), and various combinations thereof (Bishop & Hooper 2005; Brown 2012; Cox *et al.* 2012; Dunphy, Wells & Jeffs 2005; Gallo-García, Ulloa-Gómez & Godínez-Siordia 2004). Treatment efficacy differs among species, season, and exposure duration, but generally the most commonly used treatments are hyper-saline 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-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 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-minute hypersaline dip followed by air drying for 2 hours 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 minutes was more effective than hypersaline immersion (64 ppt) at killing *Boccardia acus* (Dunphy, Wells & Jeffs 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, Ulloa-Gómez & Godínez-Siordia 2004). However, environmental, health, and safety regulations will probably preclude chemicals other than salt from being used in Washington State (Morse, Rawson & Kraeuter 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 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 harbor 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, Rawson & Kraeuter 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, Rawson & Kraeuter 2015; Nell 2007). For instance, while *C. virginica* can survive cold-air storage for six months with ~80% survival, no *C. gigas* seed or adults survived similar cold-air conditions after 20 weeks of storage (Hidu, Chapman & Mook 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 it to large batches (Morse, Rawson & Kraeuter 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, Rawson & Kraeuter (2015) and Nell (2007).

MUD WORM INTRODUCTION VIA SHELLFISH TRANSLOCATION

Mud worms have a long history of accompanying shellfish during translocation and becoming invasive pests. In the early 1880's, 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, White & Mcphee 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 1980's, which resulted in a severe infestation and caused farmers to abandon their land-locked oyster pond (Bailey-Brock & Ringwood 1982; Eldredge 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, Lindsay & Rawson 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, Matthee & Simon 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, Neill & Rozbaczylo 2006; Rice, Lindsay & Rawson 2018; Simon & Sato-Okoshi 2015; Williams, Matthee & Simon 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 the infections were first reported from Puget Sound (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, Neill & Rozbaczylo 2006).

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 State that could be leveraged to control mud worm distribution within the state.

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 1800's, and while they are not listed as invasive species, they are considered serious pests to abalone and oyster growers (Nell 1993; Nell 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, Lleonart & Powell 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, Drinnan & Stephenson 1993; Medcof 1946). As such, Canada characterizes mud worms as a Category 4 species of "negligible regulatory significance in Canada," (Bower, McGladdery & Price 1994; Bower 2010). 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).

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 (Çinar 2013), 292 polychaete species (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 international or national governing body regulating this transport, and marine parasites are not recognized as invasive or injurious species in the United States. 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, Rawson & Kraeuter 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 spionds 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.

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 worms or eggs (WDFW, personal communication). Permits do not certify that translocated organisms are free of shell-boring spionids, as they are not currently designated as invasive or pest species.

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.

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, McGladdery & Price 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 worm. 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 move 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, Matthee & Simon 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, Luckenbach & Burreson 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 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.

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 harbored by and deleterious to cultured shellfish.

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DATA AVAILABILITY STATEMENT

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

CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to disclose.

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