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Spatial and Temporal Variability in Infestation of Oregon Oyster Farms by Shell-boring Polychaetes

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Highlights:

- Commercial oyster farms in Oregon are currently at risk of infestation by shell-boring polychaetes.
- Prevalence of infestation varied spatially and temporally within oyster farms and across estuaries.
- Infestation was greatest in Netarts Bay, where 72% of the Pacific oysters contained shell-boring polychaetes.
- Off-bottom culture was associated with lower infestation and offers a possible approach to mitigate loss of oyster value.
- Prevalence of infestation varied by season, but there were no associations between infestation and shell height or tissue mass.

Abstract:

Shell-boring polychaetes burrow into the shells of cultivated and wild molluscs, leading to the formation of unsightly blisters that fill with mud, detritus, and fecal material. Infestation of cultivated oysters poses economic risks for the Pacific Northwest's shellfish mariculture industry because the blisters reduce the aesthetic quality and market appeal of oysters sold on the half-shell market. To help Oregon's multimillion-dollar mariculture industry develop resilience against this emerging biosecurity threat, we quantified seasonal variability and spatial differences in the infestation of Pacific oysters (*Crassostrea gigas*) by shell-boring polychaetes, and assessed whether prevalence varied among grow-out methods, seasons, and host traits (shell height and tissue mass). In 2019–2021, we obtained 829 Pacific oysters from seven commercial shellfish farms spanning the Oregon coast (Tillamook Bay, Netarts Bay, Yaquina Bay, and Coos Bay), and observed a mean statewide infestation rate of 11–31% over four sampling seasons. We observed the highest prevalence of infestation by shell-boring polychaetes (72%) in Netarts Bay. Oysters cultivated off-bottom exhibited lower prevalence of infestation than oysters grown on-bottom. Our study also revealed a significant effect of seasonality, with higher rates of infestation during winter. Oyster shell height and tissue mass were not significantly associated with the prevalence of infestation. Our observations identify an infestation hotspot in Netarts Bay, and suggest that off-bottom culture may help reduce infestation rates, mitigating damage caused by shell-boring polychaetes in Oregon bays and estuaries.

Keywords: *Crassostrea gigas*$_1$, mud blister worm$_2$, oyster parasite$_3$, oyster aquaculture$_4$, pest$_5$

1. Introduction

Commercial mariculture of oysters is a rapidly expanding sector of the seafood industry, but shellfish parasites can pose major challenges for ongoing operations and future growth (Botta et al., 2020). Among these parasites are shell-boring polychaetes, also known as mud blister worms, which bore into the shells of oysters, clams, mussels, abalone, and other shellfish (Spencer et al., 2020). The spionid polychaete *Polydora websteri* is one of the most commonly studied blister worms due to its broad host range and global distribution, as well as the severity of its impacts on oyster production (Blake & Evans, 1973; Simon & Sato-Okoshi, 2015; Spencer et al., 2020). It is likely that *P. websteri* is indigenous to Asia (Rice et al., 2018). Lack of genetic differentiation among specimens of *P. websteri* collected across ocean basins suggests that introduction to new locations probably occurred via human-mediated transport rather than natural dispersal (Rice et al., 2018). Shell-boring *Polydora* spp. and other related shell-boring polychaetes (e.g., *Dipolydora* spp., *Boccardia* spp.) have a long history of impacts to commercial shellfish industries worldwide (Spencer et al., 2020).

Shell-boring polychaetes excavate a U-shaped burrow through the calcareous shell of their molluscan hosts (Blake & Arnofsky, 1999; Zottoli & Carriker, 1974). In response, the host secretes a layer of nacre around the irritant, creating a pocket that fills with mud, detritus, and worm fecal material, resulting in a mud blister on the inside of the shell (Blake & Arnofsky, 1999; Wargo & Ford, 1993; Zottoli & Carriker, 1974). These blisters can reduce the aesthetic quality of oysters marketed “on-the-half-shell”, which is the most lucrative and common retail product for oyster growers in the United States (Botta et al., 2020: Morse et al., 2015). While infestation by shell-boring polychaetes does not render oyster meat harmful for human consumption, it can decrease the market value of the half-shell product and has been responsible for substantial losses and, in some cases, collapse of commercial oyster industries around the world (Lunz, 1941; Bailey-Brock & Ringwood, 1982; Bower et al., 1992; Ogburn et al., 2007; Spencer et al., 2020). Further devaluation of bivalve shellfish products can also occur due to the associated reduction in host condition and body size, weakened shell, decreased oocyte size, and increased mortality rates at some locations (Chambon et al., 2007; Royer et al., 2006; Handley, 1998; Bower et al., 1992; Kent, 1981). Shell-boring polychaetes may also pose ecological risks for wild stock shellfish, as worms may spread from mariculture operations to the natural environment (Moreno et al., 2006).

Morse and colleagues (2015) reviewed potential treatments to kill shell-boring polychaetes in infested oysters as well as possible management strategies for oyster farms to reduce the prevalence of boring worms in oysters cultivated in bays and estuaries. Effective treatments that could be realistically used on oyster farms in the Pacific Northwest include drying, refrigeration, and freshwater baths (Martinelli et al., 2022). Management strategies to mitigate against damage from shell-boring polychaetes often differ among farms, and may involve modifications to gear and growing methods, such as using off-bottom culture to suspend growing oysters above muddy substrate (Smith 1981; Ogburn, 2011; Morse et al., 2015; Spencer et al., 2020). In some regions, mitigating mud worm infestations may cause production to become unprofitable due to reduced oyster densities, changes in culture systems, and additional labor required to treat affected oysters (Curtin, 1982; Nell, 2007; Morse et al., 2015; Spencer et al., 2020).

The shell-boring polychaete *Polydora websteri* was positively identified on commercial oyster farms in Washington State in 2017 (Martinelli *et al.*, 2020). Considering the potential impacts of host–parasite interactions, the presence of *P. websteri* in Washington poses both economic and ecological risks for the Pacific Northwest’s multi-million-dollar oyster industry. While shell-boring polychaetes have been reported previously in Oregon (Blake & Evans, 1973), there are no records of the current distribution of shell-boring polychaetes across Oregon’s bays and estuaries.

Oregon’s oyster aquaculture industry is characterized by small-scale operations that are located primarily in Tillamook Bay, Netarts Bay, Yaquina Bay, and Coos Bay, which are some of Oregon's largest estuaries. Fewer than 20 shellfish mariculture facilities currently operate in Oregon, and most growers cultivate Pacific oysters (*C. gigas*) using both on-bottom (grown on the tidal flat with little to no equipment) and off-bottom (suspended off the bottom using various culture systems) techniques. Mariculture of oysters contributes a significant portion of total aquaculture activities in Oregon, where the economic impact is estimated at $19.6 million USD annually (USDA, 2019).

Baseline studies that document prevalence and impacts of shell-boring polychaetes to host species are an important initial step toward identifying effective mitigation strategies (Moreno et al., 2006). The research described herein was initiated to build upon earlier work by Martinelli and colleagues (2020), extending their observations of commercial mariculture operations in Washington to the bays and estuaries in Oregon. To help inform industry best practices and guide biosecurity management actions, we specifically sought to answer the following research questions: (1) What is the current spatial distribution and prevalence of shell-boring polychaetes on commercial oyster farms located in Oregon? (2) How does the prevalence of shell-boring polychaetes vary over seasons (winter and summer) and among different culture techniques (on- and off-bottom)? (3) Is the incidence of infestation by shell-boring polychaetes related to variability in oyster traits, such as shell height and tissue mass?

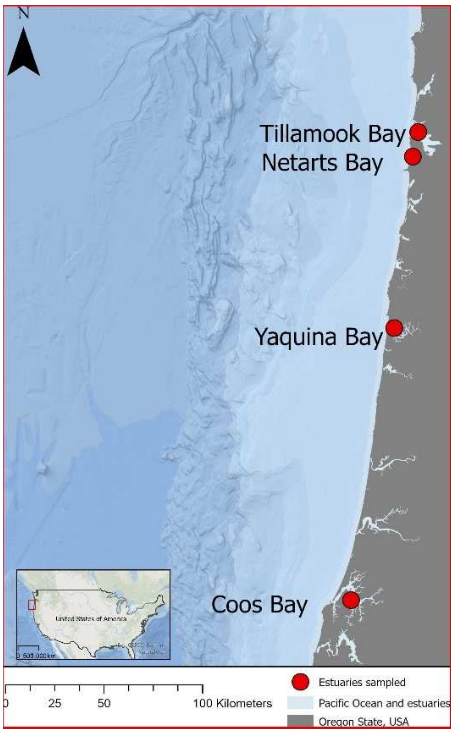
2. Materials and methods

2.1 Oyster collection

A total of 829 oysters were sampled from seven farms in four Oregon estuaries, including Tillamook Bay (Tillamook; 1 farm; 121 oysters), Netarts Bay (Netarts; 2 farms; 247 oysters),

Figure 1: Location of commercial mariculture operations in Oregon where Pacific oysters were sampled for shell-boring polychaetes.

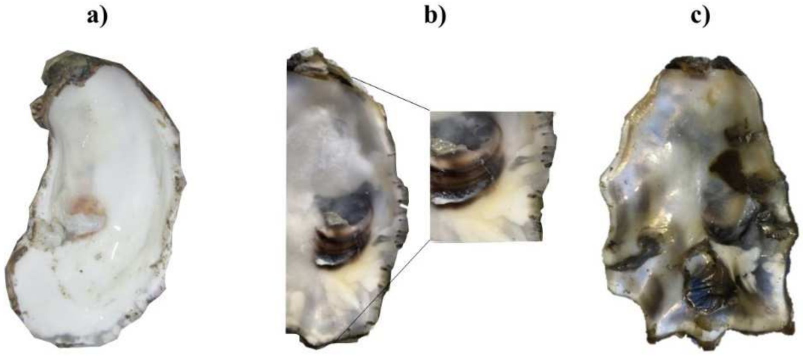
Yaquina Bay (Yaquina; 1 farm; 174 oysters), and Coos Bay (Coos; 3 farms; 287 oysters; Figure 1). Oyster collection occurred during summer months (July–September) of 2019 and 2020 and during winter months (January–April) of 2020 and 2021, for a total of four sampling seasons. For each farm, a randomly selected sample of 25 oysters was requested for on-bottom and off-bottom culture types, although not all farms were able to supply a full sample of 25 individuals or a sample from each culture type in every sampling period. The type of off-bottom culture system used was not specified by each farm.



2.2 Oyster processing

All oysters were shucked and measurements were recorded for tissue mass (g), right and left valve height (mm), length (mm), width (mm), shell mass (g), and shell thickness (mm; Galtsoff, 1964). The internal surfaces of the shells were examined with a Leica Wild M37 stereoscope to record the presence or absence of burrows (small tunnels or marks) and blisters (bubbles of nacre; Figure 2). Both the right and left valves for each oyster, regardless of infestation, were photographed for record keeping.

Figure 2: Infestation of Pacific oysters by shell-boring polychaetes: (a) non-infested oyster shell; (b) oyster shell with multiple burrows on shell margin; (c) oyster shell with multiple large blisters.



2.3 Infestation prevalence

Any oyster that had at least one burrow or blister on either the right or left valve was considered an infested individual (Figure 2). To avoid duplicating information about shell metrics (i.e. shell height, shell length, shell width, shell mass, shell thickness) by considering both right and left valves, we used correlation coefficients to determine whether the prevalence of infestation of the left (generally more deeply cupped) and right valves (generally less cupped) were significantly different. A correlation coefficient above 0.8 was deemed to have a strong positive relationship (Akoglu, 2018). Because infestation between valves was not significantly different (see Results), infestation status was evaluated by assessing whether the right valve displayed blisters or burrows.

2.4 Statistical analysis

A generalized linear model (GLM) was used to evaluate whether oyster traits, culture type, and season were significant explanatory variables for infestation by shell-boring polychaetes in Oregon estuaries. Only the oyster traits of shell height and tissue mass were used to avoid redundancy and multicollinearity. The fixed factors for the GLM were estuary (4 levels: Tillamook, Netarts, Yaquina, and Coos), culture type (2 levels: on and off-bottom), and season (2 levels: winter and summer). Shell height and tissue mass were used as continuous fixed covariates. Additionally, random factors of year (2019-2021) and farm (7 levels) were included to account for potential spatial and temporal autocorrelation among our samples. We did not nest farm within estuary due to the high degree of singularity (e.g., some estuaries had only one farm). The response variable (presence or absence of infestation) was modeled with a binomial distribution (presence = 1, absence = 0) as follows:

$$Infestation_{ijklmn} \sim ShellHeight_{ijklmn} + TissueMass_{ijklmn} + CultureType_{j} + Season_{k} + Estuary_{n} + (1|Year_{l}) + (1|Farm_{m})$$

where the response variable$_{ijklmn}$ represents the presence or absence of infestation in the ith oyster collected from the jth culture type during the kth season of the lth year in mth farm of the nth estuary.

We accounted for potential collinearity by checking the generalized variance inflation factors (GVIFs), which can accommodate combinations of categorical and continuous predictor variables. A VIF above 5 was considered to indicate multicollinearity among our samples (Mason and Perreault, 1991; Becker et al., 2015). The GLM model was performed in R Studio using the 'glm' function, and GVIFs were calculated for the final model using the 'vif' function in the 'car' package (Fox and Weisberg 2018). Data management, correlation coefficients, and data visualization were also carried out in R Studio (Version 4.0.5, R citation).

3. Results

Right and left valves of the oyster shell were equally infested by shell-boring polychaetes (Wilcoxon test, V = 810, p-value = 0.3389), so we chose right valves for all further analyses to avoid duplication of measurements for a given oyster. The average prevalence of infestation by shell-boring polychaetes on commercial Pacific oysters was 2% for Tillamook Bay, 72% for Netarts Bay, 3% for Yaquina Bay, and 1% for Coos Bay (ordered north to south; Figure 1).

All GVIF values were below 5 indicating low multicollinearity (Table 1). The GLM indicated a significant difference for the effect of estuary ($p < 0.0001$; Figure 4), due to the elevated prevalence of infestation in Netarts Bay in comparison with other estuaries. The GLM also indicated that on-bottom culture had 34% higher prevalence of infestation than off-bottom culture ($p < 0.0001$; Figure 3), and that there was a significant effect of season with winter having a higher rate of infestation ($p = 0.0048$; Figure 3). The GLM analysis did not reveal significant differences in shell-boring polychaete infestation for shell height or tissue mass (Table 2).

Coefficients	GVIF	Df	GVIF^(1/(2*Df))
Height	2.307	1	1.519
Tissue Mass	2.440	1	1.562
Culture Type	1.153	1	1.074
Season	1.174	1	1.083
Estuary	2.409	3	1.158

Table 1: Generalized variance inflation factors showing low multicollinearity values among coefficients for oyster traits (shell height, tissue mass) and fixed sampling factors (culture type, season, estuary).

Coefficients	Estimate	Standard Error	*z*-value	*p*-value
Intercept	-8.028	1.171	-6.856	7.10e-12 ***
Height	0.1375	0.3336	0.412	0.6802
Tissue Mass	0.08252	0.3301	0.250	0.8026
Culture Type	1.885	0.4465	4.221	2.43e-05 ***
Season	1.185	0.4205	2.819	0.00482 **
Netarts	6.964	0.8703	8.002	1.23e-15 ***
Tillamook	1.228	0.9306	1.320	0.1869
Yaquina	1.574	0.8669	1.816	0.06943

Table 2: Output from Generalized Linear Model indicates differences in mud blister worm infestation of Pacific oysters among coefficients for oyster traits (shell height, tissue mass) and fixed sampling factors (culture type, season, estuary).

Figure 3: Effect of (a) tissue mass (in grams), (b) shell height (in mm), (c) season (i.e., summer or winter), and (d) culture type (i.e., on or off bottom) on the prevalence of shell-boring polychaete infestation (1 = infested, 0 = not infested), where data represent predicted (fitted) values for the response of infestation, computed while keeping all other factors (including random effects) in the model constant using the ggpredict() function in the ggeffects package in R (Ludecke, 2018). All error bars and bands represent 95% confidence intervals. Significance is based on a generalized linear model, see Table 2. For a plot of the raw data used to calculate these predictions, please see Supplementary Figure S.1.

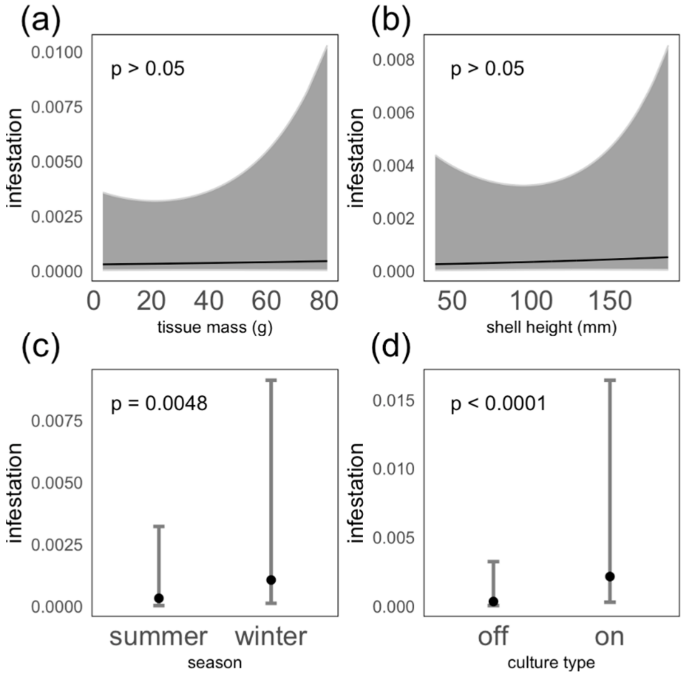


Figure 4: Differences in prevalence of infestation for estuary presented as boxplots indicating the median, quartiles with whiskers, and mean with diamond. Significance is based on a generalized linear model, see Table 2.

Prevalence

4. Discussion

While shell-boring polychaetes were present in all the estuaries sampled, Netarts Bay consistently exhibited the highest prevalence of infestation. We postulate that the elevated prevalence of shell-boring worms observed in Netarts Bay could be due to differences in the estuarine environment and growing conditions (Ruesink et al., 2005; Spencer et al., 2020). Interestingly, Netarts Bay is a bar-built estuary that experiences a considerably lower tidal prism, less freshwater influence, and lower hydrodynamic residence time than the other estuaries sampled, making the higher prevalence by shell-boring polychaetes unexpected (Glanzman, 1971; McCallum, 1977). Investigations conducted in other locations in North America found that infestation decreased with increasing salinity (Loosanoff & Engle, 1943; Calvo et al., 1999; Hanley et al., 2019) and one study documented lower prevalence where salinity was more variable (Cole, 2018). Additionally, larval transport studies indicate that the dispersal of meroplankton largely depends on the length of planktonic development and the hydrodynamic regime (Roegner, 2000). Larval transport becomes more complex in an estuarine setting where organisms may be exported out to sea with regular tidal flushing, such as Netarts Bay (Weinstein, 1988; Roegner, 2000). Larval development of shell-boring polychaetes varies depending upon the species, with some entering the water column after hatching and remaining for up to 85 days prior to settlement while others live in the burrow for an extended period (Blake, 1969; Orth, 1971; Blake & Woodwick, 1971; Haigler, 1969; Blake & Arnofsky, 1999; Simon & Sato-Okoshi, 2015). While the reasons for a higher prevalence of shell-boring polychaetes in the marine-dominated waters of Netarts Bay remain unknown, the small bar-built estuary is identified as a troublesome hotspot with a pressing need for industry and resource management actions.

Our study did identify significant effects of seasonality, in alignment with investigations in other regions, which indicate that seasonal changes in temperature or salinity may contribute to prevalence of infestation by shell-boring polychaetes. For example, mud worm larval development, growth, and settlement have been shown to be temperature dependent, and seasonal patterns vary geographically (Blake & Arnofsky, 1999; Blake & Woodwick, 1971). In Oregon, during spring and summer months coastal upwelling influences estuarine temperatures as cold bottom water moves in during the tidal cycle (Brown & Power, 2011; Coogan et al., 2019). Additionally, increased salinity is generally associated with a lower prevalence of infestation by the shell-boring worms, and in Oregon, freshwater influences increase during winter months (McCallum, 1977). Spencer and colleagues (2021) hypothesize that changes in carbonate chemistry, which occurs seasonally in Oregon due to coastal upwelling, could impact mud worm infestation, although this proposition remains untested. Higher infestation during winter months agrees with findings from other west coast states (Martinelli et al., *in revision*). Understanding the influence of seasons on infestation may help inform management strategies such as the timing of treatments to control or eradicate worms.

Our study did not find differences in prevalence of infestation among oysters of different sizes, which is not consistent with earlier studies on the impacts of shell-boring polychaete to host fitness (Bower et al., 1992; Royer et al., 2006; Chambon et al., 2007*).* Reduced oyster condition, especially tissue mass, can further devalue oyster products. For this study, the causality and significance of this relationship could not be fully established. Future research is needed to improve our understanding about the impacts to physiological characteristics and the mechanisms behind these observations.

Our findings suggest that off-bottom culture could be used to mitigate against infestation by shell-boring polychaetes in Oregon oyster farms. The significant difference in prevalence between on and off-bottom culture may be due to differences in aerial exposure or siltation levels, although our correlational study cannot tease out the mechanism underlying this pattern or draw conclusions about causation. Studies in other locations have shown prevalence of infestation to be higher with higher siltation levels and lower tidal height, and growers have previously reported higher infestation for on-bottom culture (Littlewood et al., 1992; Handley & Berguist, 1997; Nell, 2007; Morse et al., 2015; Clements et al., 2017). Additionally, in the state of Oregon, permit approval for off-bottom culture systems is site-dependent and not all growers are able to implement this strategy (Oregon Department of Agriculture, n.d.). The permitting process involves a commenting period where input is received from multiple sources including federal and state agencies, tribal governments, local jurisdictions, private businesses, NGOs, the public, and other interested parties (Oregon Department of Agriculture, n.d.). Proposed changes to oyster mariculture operations sometimes receive social opposition due to the visual impacts from farm infrastructure (Knapp et al., 2016; Krause & Mikkelsen, 2017; Botta et al., 2020), and off-bottom methods can increase visibility of structures during low tides, making it difficult to obtain permit approval. While the mechanisms underlying the lower prevalence of infestation by shell-boring polychaetes are unclear for off-bottom culture operations, our findings suggest this culture method may offer a potential mitigation strategy for growers that are able to acquire permit approval.

Signs of shell-boring polychaete infestation have also been found in several species of wild-stock native clams, including native littleneck clams (*Leukoma staminea*) and butter clams (*Saxidomus giganteus),* collected from Netarts Bay and Tillamook Bay, respectively (Considine & Rumrill, *unpublished data*). The infestation of native molluscan hosts may create a reservoir that promotes further dispersal of shell-boring polychaetes, making eradication difficult. The potential to spread pests from mariculture facilities to the natural environment also has implications for resource management, commercial harvest of wild stocks, and recreational fisheries (Moreno et al., 2006; Spencer et al., 2020). For example, the introduction of shell boring polychaetes through mariculture activities in Australia has been identified as a primary causative factor for the loss of subtidal native oyster reefs and consequent impacts on wild harvest industries (Ogburn, 2007; Diggles, 2013).

Spatial transport of cultivated oysters for mariculture purposes has been identified as a major pathway for introduction of aquatic invasive species in the Pacific Northwest (Molnar et al., 2008; Ruesink et al., 2005). The history of oyster transfers in this area began in the late 1800s with introduction of the eastern oyster (*Crassostrea virginica*) from the U.S. East Coast and Pacific oyster (*C. gigas*) from Asia to replace the overharvested and depleted native Olympia oyster, *Ostrea lurida* (Ruesink et al., 2005). The shell-boring polychaetes observed in Oregon may be recent invaders or they may be long-term residents that were not previously detected due to low infestation level or lack of awareness (Spencer et al., 2020).

Regulatory and management options may include limiting the transfer of oysters from areas of high prevalence such as Netarts Bay, inspecting oysters for diseases and pests prior to transfer approval, and implementing treatments prior to movement to reduce the abundance or kill living worms (Ruesink et al., 2005; Moreno et al., 2006; Morse et al., 2015). Outreach and engagement with the commercial oyster mariculture industry is also an important management action for reducing market and shellfish resource impacts. Local industry–researcher partnerships have made this research possible and should be continued to inform successful mitigation strategies.

5. Conclusion

Infestation of commercial shellfish mariculture areas by shell-boring polychaetes is an emerging issue in the state of Oregon. This research provides a baseline reference to describe the presence and absence of shell-boring polychaetes on Oregon commercial oyster farms. Of the four estuaries sampled, Netarts Bay consistently exhibited the highest prevalence of infestation, and off-bottom culture was identified as a potential mitigation strategy. These findings provide initial information for resource management and industry best practices. Future research is needed to better understand the effects of environmental conditions as well as impacts to native shellfish and host fitness.

6. Author Contributions

Megan E Considine: Investigation, Formal Analysis, Data Curation, Visualization, Writing – Original Draft. **Julieta C Martinelli**: Conceptualization, Methodology, Validation, Supervision, Writing – Review & Editing. **Teri L King**: Conceptualization, Methodology, Writing – Review & Editing. **Steve S. Rumrill**: Conceptualization, Methodology, Validation, Resources, Supervision, Writing – Review & Editing. **Chelsea L Wood**: Conceptualization, Methodology, Validation, Project Administration, Writing – Review & Editing.

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9. Data Statement

Data files are provided in Dryad.

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