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Seasonal dynamics of *Polydora* infestation in eastern oysters (*Crassostrea virginica*) from a tidally restricted New England estuary

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ABSTRACT

Shell-boring polychaetes of the genus *Polydora* pose a significant threat to oyster aquaculture worldwide, yet little is known about their seasonal dynamics in tidally restricted estuaries. This study investigates the prevalence, intensity, and environmental covariates of *Polydora websteri* infestation in wild eastern oysters (*Crassostrea virginica*) over a 12-month period in the Herring River estuary (Cape Cod, Massachusetts), a system slated for tidal restoration. Oysters were collected monthly, and worms identified morphologically and by COI barcoding. Infestations were observed year-round, with prevalence and intensity lowest in late summer and peaking in fall-winter. Gravid females were only observed from April through August, indicating a seasonal reproductive window. The seasonal peak in visible infestation and pathology in colder months is therefore consistent with a lag between summer recruitment and subsequent shell damage. Using a Gaussian generalized linear model as a descriptive correlational tool, we observed a negative association between temperature and monthly mean intensity at this site and year; salinity and pH showed no detectable association. These associations are interpreted within the seasonal/lag context rather than as casual drivers. Overall, this work provides baseline data on seasonal *Polydora* dynamics in the Herring River estuary that will be essential for future, post-restoration assessments.

1. Introduction

The shellfish aquaculture industry is a cornerstone of many coastal economies, providing a sustainable seafood source and contributing over US$50 billion to global markets (Azra et al., 2021). In the United States alone, shellfish farming generates more than $250 million annually and supports tens of thousands of jobs (National Marine Fisheries Service, 2022). However, oyster production faces multiple challenges, including environmental stressors and disease outbreaks, both of which can interact synergistically to exacerbate mortality rates and reduce yields (Rowley et al., 2014; Pernet et al., 2016). In recent years, heavy infestations of shell-boring polychaete worms of the genus *Polydora* have been reported in various regions worldwide (Cole et al., 2020; Diez et al., 2022; Sato-Okoshi et al., 2023; Lezzi and Mazziotti, 2024; Davinack et al., 2024; Stadnichenko et al., 2024; Mikac et al., 2025). These worms burrow into the shells of oysters, forming unsightly blisters that reduce commercial value and increase mortality risks, largely due to the fact that oysters must divert energy from growth to shell repair (David, 2021). In the United States, three *Polydora* species are recognized as the primary borers of cultivated shellfish. *Polydora websteri*, the most widespread species, burrows into both the eastern oyster (*Crassostrea virginica*) and the Pacific oyster (*Magallana gigas*) (Rice et al., 2018; Martinelli et al., 2020; Davinack et al., 2024). *Polydora neocaeca* primarily infests bay scallops (*Argopecten irradians*) (Davinack and Hill, 2022), while *Polydora onagawaensis*, recently discovered on oyster farms in Maine, represents an emerging concern for aquaculture (Silverbrand et al., 2021).

In the northeastern United States, the Herring River Estuary in Wellfleet, Massachusetts, is home to expansive shellfish beds which have been severely impacted by tidal restriction following the construction of a dike over a century ago (Smith et al., 2020; Naseri et al., 2025). This restriction has led to poor water quality, including elevated fecal coliform levels, resulting in the closure of oyster beds for human consumption (Portnoy and Allen, 2006). The dike is currently in the process of being removed with the hope that tidal restoration will improve water quality and oyster beds reopened for harvesting and cultivation. However, even if the dike were removed and water quality improved, a recent study by Davinack et al. (2024) found 100 % prevalence of

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P. websteri in this area, with a mean intensity exceeding 20 worms per oyster. While this particular study was conducted in May and so was representative of only a single time point, concerns remain that persistent *Polydora* infestations could render these oysters commercially inviable, and that tidal restoration alone may not be sufficient to mitigate the problem.

In this study, we analyzed seasonal fluctuations in *Polydora* infestations across a 12-month period and examined associations with temperature, salinity, and pH. The primary objectives were therefore to (1) assess the seasonal persistence of *Polydora* infestation in wild oysters across an annual cycle and (2) identify the environmental factors most strongly associated with changes in infestation intensity.

2. Study site

The study was conducted in the Herring River estuary, a 1,100 acre-coastal wetland system in Wellfleet, Massachusetts, that has been tidally restricted since the early 20th century due to the installation of a dike at its mouth. This restriction has significantly altered estuarine hydrology, resulting in reduced tidal exchange, prolonged water retention, lower dissolved oxygen, and elevated fecal coliform concentrations (ENSR Corporation & Wilkinson Ecological Design, 2007; Smith et al., 2020; Naseri et al., 2025). These conditions have also contributed to changes in sediment composition, vegetation structure, and nutrient cycling – factors that may influence both oyster health and parasite recruitment dynamics. Importantly, unlike most shellfish aquaculture sites on Cape Cod, the Herring River estuary has not been used for aquaculture due to its chronically impaired water quality (Smith et al., 2020). As a result, it offers a rare opportunity to study *Polydora* infestation in a wild oyster population inhabiting a hydrologically degraded system. A previous study found that oysters from this tidally restricted site had significantly higher mean infestation intensity and prevalence than oysters from nearby active farms in more open systems, despite being less than 10 km apart (Davinack et al., 2024). Although other "trapped estuaries" exist in New England, the Herring River stands out due to the severity and presence of its tidal restriction, the absence of aquaculture, and its exceptionally high infestation levels. Moreover, the system is undergoing a large-scale restoration project that will reintroduce full tidal flow to more than 890 acres of salt marsh and estuarine habitat, making it one of the largest efforts of its kind in the region and an ideal setting for establishing ecological baselines prior to hydrologic restoration.

3. Materials and methods

3.1. Oyster sampling, worm extraction & identification

Approximately 20 to 35 eastern oysters (*Crassostrea virginica*) were hand-collected monthly from May 2024 to April 2025. (Fig. 1). These oysters were located in a permanently submerged section of the diked river, approximately 129 m downstream of the Chequessett Neck dike. To characterize environmental conditions across the sampling period, we used water quality data from the Cape Cod Cooperative Extension's remote sensor in Wellfleet Harbor (Table 1), located ~2 km from our site and hydrologically connected to the upper Herring River. These

Table 1
Summary of environmental data collected across sampling months in the present study. *CCCE Data* represent parameters recorded at high temporal resolution via a remote sensor deployed in Wellfleet Harbor by the Cape Cod Cooperative Extension. *In-situ Data* represent point measurements recorded once per week using a handheld multiparameter water quality meter during both oyster sampling and non-sampling week.

Environmental Variable	CCCE Data (Mean ± SD, Range)	In-Situ Data (Mean ± SD, Range)
Temperature (°C)	16.89 ± 8.39 (−1.67 to 27.98)	15.45 ± 9.10 (−2.0 to 25.5)
Salinity (PSU)	31.52 ± 1.06 (27.6 to 33.35)	27.75 ± 5.50 (15.5 to 36.0)
pH	8.06 ± 0.10 (7.80 to 8.33)	7.90 ± 0.68 (6.8 to 8.31)

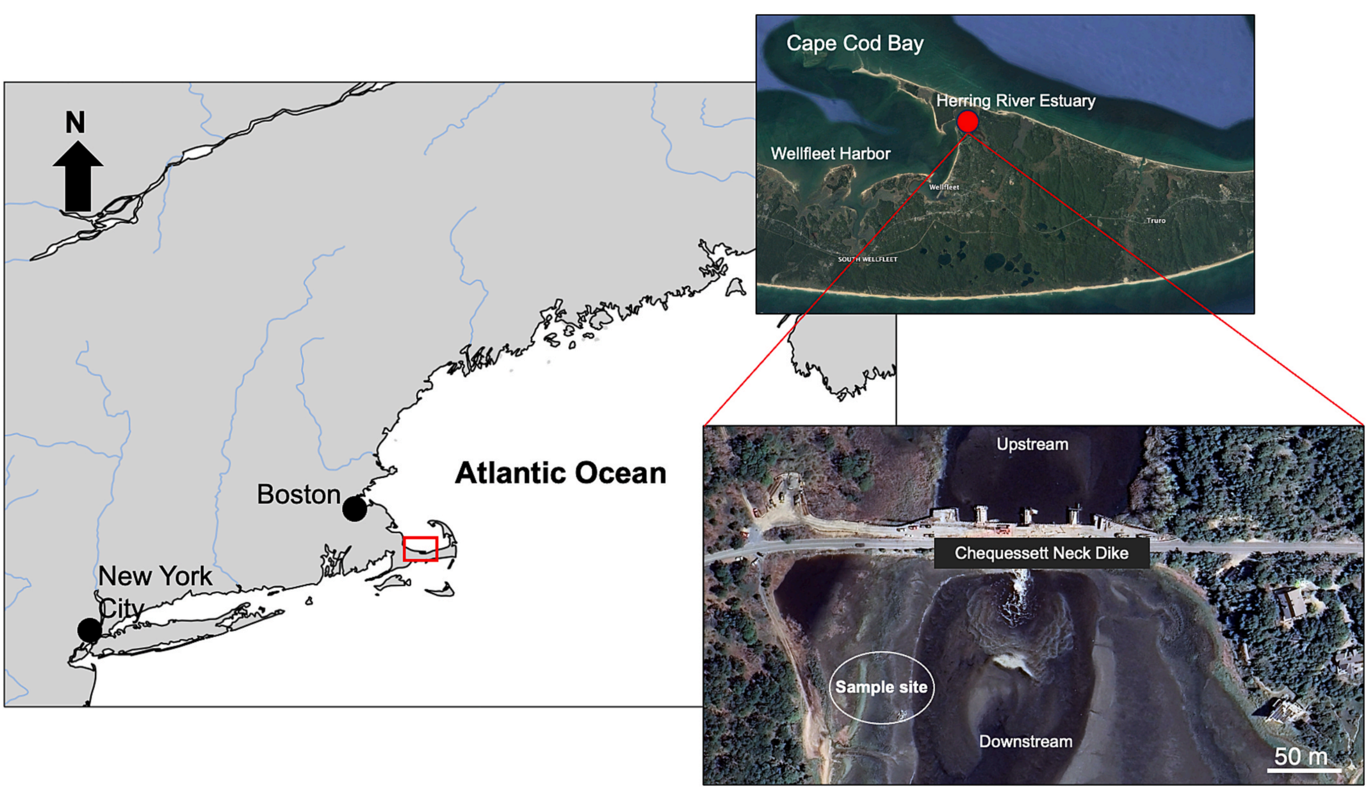

Fig. 1. Map of sampling locality for *Crassostrea virginica*.

continuous records (temperature, salinity, pH) were used in tandem with weekly *in situ* spot measurements collected using a Hanna HI 98194 multiparameter meter.

Oysters were shucked, photographed, and tagged**.** Shells were carefully cracked using pliers, and individual worms were identified to the species level using published morphological descriptions of common shell-boring polychaetes from the northeastern US (Rice et al. 2018; Davinack and Hill 2022; Davinack et al. 2024). Worms that could not be definitively identified morphologically were genetically barcoded using the cytochrome *c* oxidase I (COI) mitochondrial marker. All DNA extraction, polymerase chain reaction and Sanger sequencing protocols (including primers and conditions) are outlined in Davinack et al. (2024). Returned sequences were compared to the GenBank database using the BLASTn tool to determine the closest match via percent identity. All sequences generated in this study were submitted to the GenBank database (Accession numbers: PV472287 – PV472291).

3.2. *Assessment of parasite load and mud-blister pathology*

Parasite load was assessed using two metrics: prevalence (%) and intensity. Prevalence was calculated as a percentage by dividing the number of infected oysters by the total number of oysters sampled per month. Intensity was defined as the number of *Polydora* worms per infected oyster, and mean intensity was calculated for each sampling month using only infected individuals. To determine whether there was a significant difference in mean intensity across months sampled, a Kruskal-Wallis H test was performed followed by a Dunn's post-hoc test to determine where significance, if any, lay.

To assess the severity of *Polydora* infestation in oysters, a semi-quantitative pathology scoring system was employed, ranking individuals on a scale from 0 to 4 based on the percentage of the inner shell surface covered by mud blisters. Oysters with no visible blisters were assigned a score of 0, while those with increasing degrees of infestation were categorized into four progressive stages: 1 (1–25 % coverage), 2 (26–50 % coverage), 3 (51–75 % coverage), and 4 (76–100 % coverage). This surface-level damage scoring reflects external pathology only and does not capture overlapping or deeper burrows. However, a previous study demonstrated a statistically significant correlation between mud blister surface area and actual worm burden, providing support for the use of visible surface pathology as a reliable proxy for infestation intensity (Davinack et al. 2024). To ensure accuracy and consistency in scoring, high-resolution images of the inner shell surfaces were taken under standardized lighting conditions. Image analysis was performed using ImageJ**.** The total shell area and the portion covered by blisters were quantified through threshold-based segmentation, allowing for an objective determination of infestation severity. Each oyster's pathology score was then assigned based on the calculated proportion of blister coverage. To assess whether the severity of mud-blisters varied across months, a chi-square test of independence was conducted to determine whether the distribution of pathology scores differed significantly among months. This analysis tested the null hypothesis that pathology scores were independent of sampling month, with significant results indicating temporal variation in infestation severity.

To visualize associations between environmental covariates and monthly mean intensity, we fit a generalized linear model (Gaussian, identity link). Analyses are correlational (single site/year) and are interpreted as such rather than as a causal inference. Because the response variable—mean intensity per oyster per month—is continuous rather than discrete counts, the Gaussian distribution was deemed more appropriate than a Poisson model. Predictor variables included salinity, temperature, pH, and mean oyster size, and an intercept term was included in the model. Prior to model fitting, multicollinearity among predictor variables was assessed using Variance Inflation Factors (VIFs), with a threshold of VIF > 5 indicating potential collinearity issues. Model performance and goodness-of-fit were evaluated using residual deviance, log-likelihood, and visual inspection of residual plots. To assess the potential influence of sampling bias, we also ran a secondary GLM excluding August data, as oysters collected during that month were notably smaller due to tidal access limitations. All statistical tests were performed using the statsmodels package (Seabold and Perktold, 2010) in Python ver. 3.

4. Results

Morphological and molecular characterization of extracted worms confirmed that *Polydora websteri* was the only shell-boring polychaete infecting oysters in the Herring River estuary. All barcoded specimens had 99.37 – 100 % identity matches to *P. websteri*. Oysters were infected throughout the 12-month study period; however, clear seasonal differences in prevalence were observed, with the highest prevalence recorded in the fall and winter months, and the lowest during late spring and summer (Fig. 2). The highest prevalence (100 % infection) was recorded in September, October, December and January while the lowest prevalence (17 %) was recorded in August. Mean intensity followed a similar seasonal trend, with significantly higher infestation levels in fall and winter (Kruskal-Wallis $H = 106.98$, $p < 0.05$; Fig. 3). Peak mean worm intensities occurred in November (26.3 ± 13.5), December (22.2 ± 10.9), and January (28.9 ± 11.7), whereas the lowest intensity was recorded in August (0.8 ± 2.1).

A chi-square test of independence revealed that the distribution of mud-blister pathology scores differed significantly across months ($\chi^2 = 80.26$, $df = 33$, $p < 0.05$), indicating seasonal variation in infestation severity. Higher proportions of severe pathology scores (3–4) were observed during the fall and winter months, suggesting a temporal shift toward more intense infestations during cooler periods (Fig. 4).

A Gaussian Generalized Linear Model (GLM) found that temperature was a significant negative predictor of infestation intensity ($\beta = -0.934$, $p = 0.040$) (Table 2). To test whether this relationship was influenced by the sampling bias in August – when only small oysters were collected – we re-ran the model excluding the August data. The temperature-intensity relationship remained significant ($\beta = -0.381$, $p = 0.048$), indicating the trend is robust to this sampling artifact (Table S1). Oyster size showed a positive but non-significant effect ($\beta = 0.724$, $p = 0.461$), suggesting a trend toward larger oysters harboring more worms. Neither salinity nor pH were significant predictors ($p > 0.2$). Model predictions reflected this inverse relationship between temperature and infestation intensity (Fig. 5).

During field observations, gravid female worms first appeared in April, with egg capsules and larval emergence occurring through the spring and summer months. Egg capsules were not connected to each other in a continuous string within the worm's burrows. The primary developmental mode observed in *P. websteri* was adelphophagy, with individuals producing 40–80 nurse eggs per capsule. No gravid females, larvae, or egg capsules were observed after August.

5. Discussion

This study provides new insights into the seasonal dynamics of *Polydora websteri* infestation in wild eastern oysters from the northeastern United States. A key feature of this work is its focus on a tidally restricted estuary in the Herring River system of Cape Cod, where limited tidal exchange creates stable, localized water quality conditions that offer a unique opportunity to examine infestation patterns over time. The findings serve as critical baseline data on the seasonal prevalence and intensity of *P. websteri* infestation under current, restricted conditions. This data will be essential for assessing ecological change following the planned removal of the Herring River dike in Wellfleet, and will directly inform future management decisions regarding the restoration and commercial viability of local oyster beds**.**

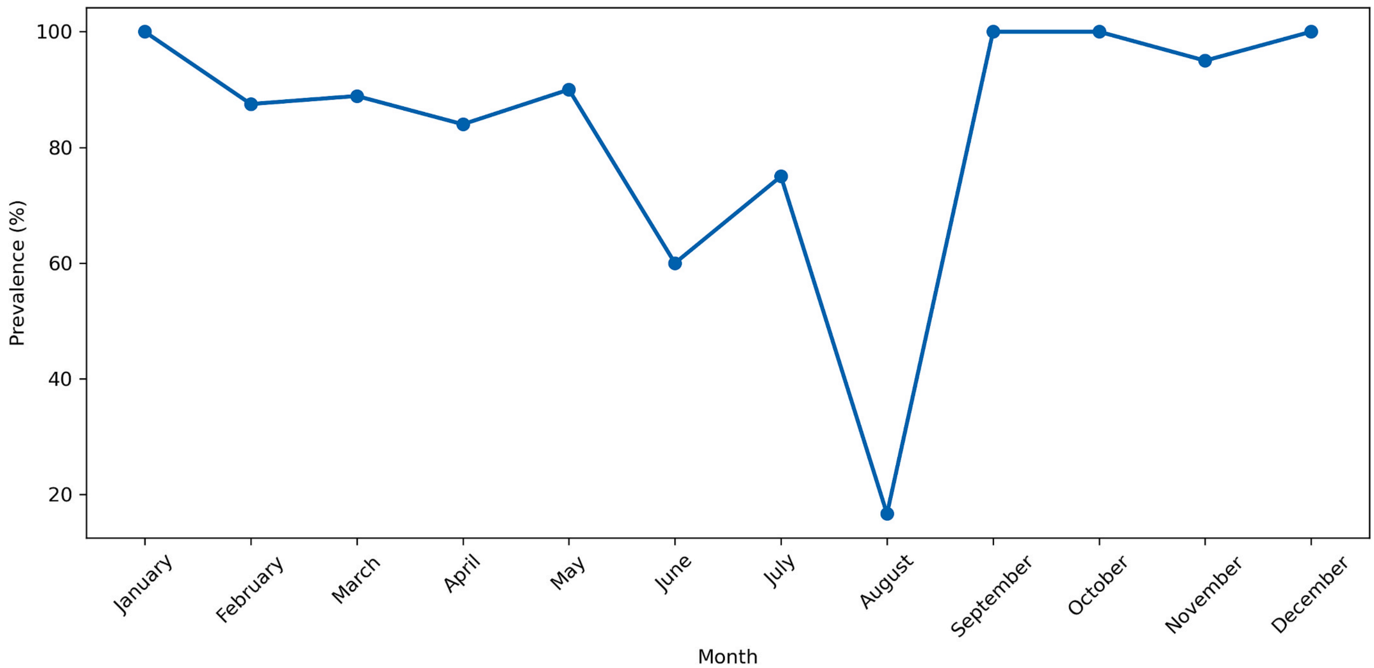

Fig. 2. Monthly prevalence of *Polydora websteri* infestation in eastern oysters collected from the Herring River Estuary between May 2024 and April 2025.

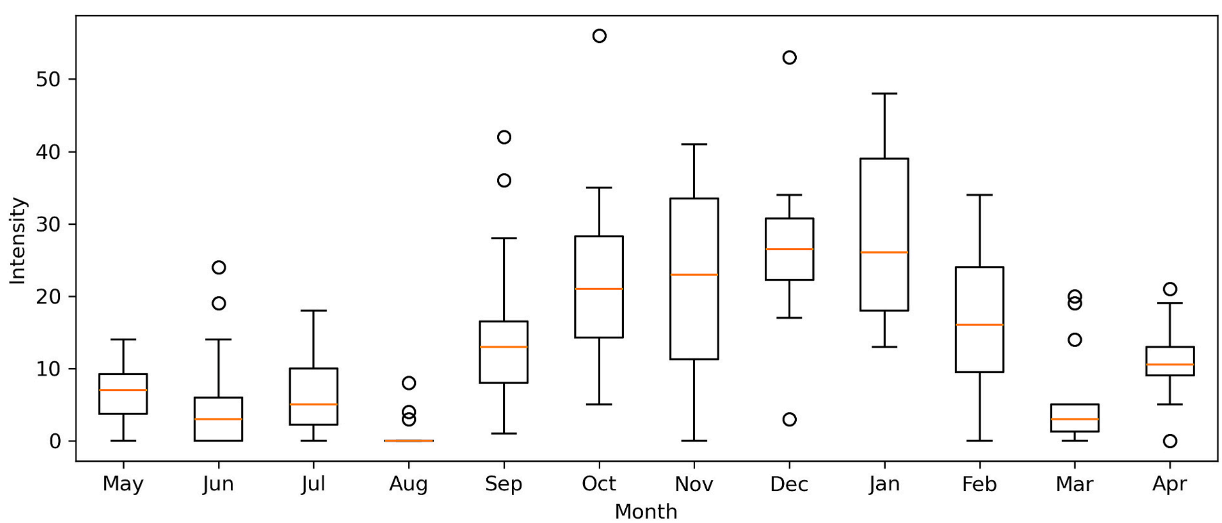

Fig. 3. Boxplot showing intensity of *Polydora websteri* infestation in eastern oysters collected from the Herring River Estuary between May 2024 and April 2025.

5.1. Seasonal fluctuation in Polydora websteri infestation

Worms were present throughout the year, with the highest prevalence and intensities recorded in the fall and winter months when temperatures ranged from −2.1 °C to 14.4 °C. Parasite load in August was notably low. This likely reflects a sampling artifact, as the oysters collected in August were considerably smaller (mean shell length: 4.4 cm) compared to other months. Given that smaller oysters tend to host fewer *Polydora* worms, the lower observed intensity during this period may be due to size-related differences in infestation risk rather than a true seasonal decline. Other studies have reported contrasting seasonal patterns in *P. websteri* infestation, though these cannot be directly compared due to differences in site conditions, sampling design, and environmental regimes. For instance, Cole et al. (2020) found that infestations in farmed eastern oysters in the northern Gulf of Mexico peaked during summer, with larvae present year-round. In contrast, Martinelli et al. (2024) observed peak infestation in Pacific oysters on the U.S. West Coast during winter months, aligning more closely with the seasonal pattern observed in our study. While these patterns may reflect regional environmental differences, such as temperature regimes or hydrology, our data are limited to a single site and year, and cannot resolve these broader drivers. Instead, our findings support the interpretation that infestation intensity can remain high during fall and winter in the absence of active reproduction, possibly due to a lag between larval recruitment and the development of visible infestation. This is consistent with previous work suggesting that several months may pass between larval settlement and the appearance of mud blisters (Zottoli and Carriker, 1974; David and Simon, 2014). Future studies incorporating multi-site or multi-year comparisons will be essential for evaluating the role of regional environmental drivers in shaping parasite population dynamics.

Patterns of pathology followed a similar seasonal trend, with more severe mud-blisters appearing in the fall and winter months. Our chi-square analysis confirmed that the distribution of pathology scores

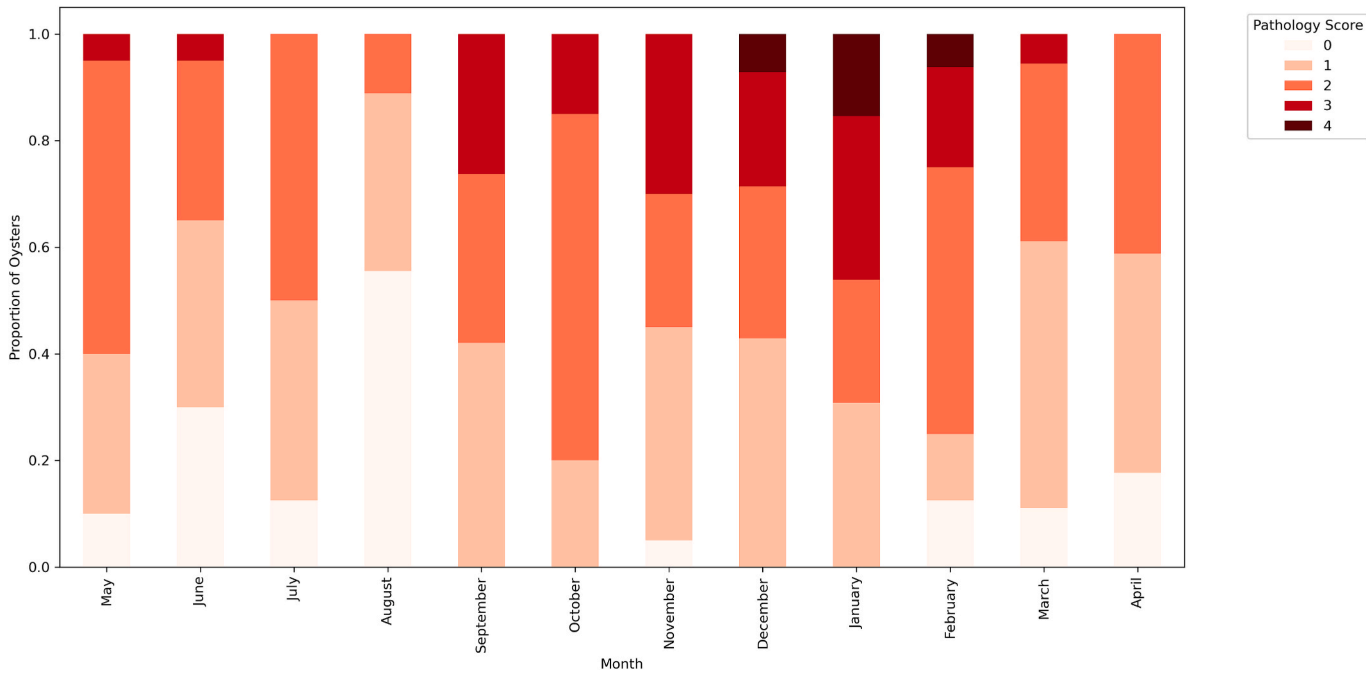

Fig. 4. Seasonal distribution of *Polydora websteri* pathology scores in wild eastern oysters collected from the Herring River Estuary, from May 2024 to April 2025. Each bar represents the monthly proportion of oysters assigned to a pathology score category, based on the percentage of the inner shell surface covered by mud blisters.

Table 2
Gaussian Generalized Linear Model (GLM) results assessing the effect of temperature, salinity, pH, and oyster size on *Polydora websteri* infestation intensity.

Predictor	Coefficient (β)	Std. Error	z-value	p-value	95 % CI (Lower)	95 % CI (Upper)
Intercept	20.5941	17.839	1.155	0.291	−20.112	61.300
Salinity	0.125	0.162	0.774	0.465	−0.264	0.515
Temperature	**−0.934**	**0.382**	**−2.448**	**0.040**	**−1.822**	**−0.045**
pH	−2.633	1.566	−1.681	0.129	−6.231	0.965
Oyster size	0.724	0.927	0.781	0.461	−1.060	2.509

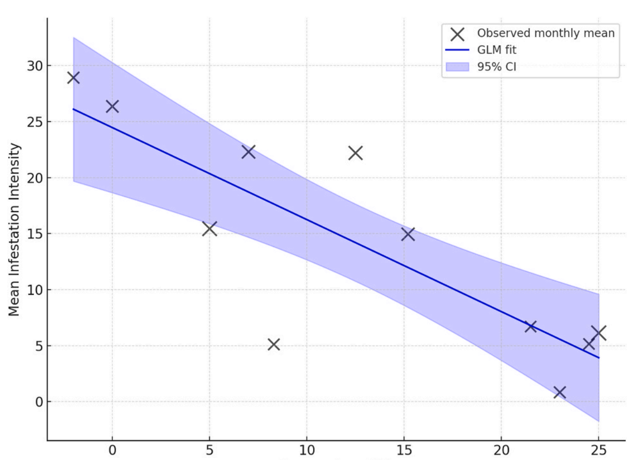

Fig. 5. Observed monthly mean intensity of *Polydora websteri* infestations in *Crassostrea virginica* (black points; point size scaled by monthly sample size) plotted against mean monthly temperature, with fitted generalized linear model (line) and 95% confidence interval (shaded area).

varied significantly by month, with a greater proportion of oysters exhibiting high-severity scores (3–4) during colder periods. This supports the interpretation that visible infestation reflects a biological lag between earlier larval recruitment and later shell colonization. Although both worm intensity and pathology scores peaked during fall and winter, this pattern may result from larvae settling in the warmer months and only becoming visibly established weeks or months later, as has been found in other studies (Zottoli and Carriker, 1974; David and Simon, 2014). Our findings support the notion that *Polydora* infestations reflect a continuum of interaction intensity, ranging from minimally damaging to overtly parasitic. While lower-grade infestations (Grades 1–2) may appear low-grade and inflict little overt harm, the boring activity itself incurs energetic costs to the host by triggering shell repair and maintenance responses (David 2021). Even in the absence of gross pathology, this diversion of resources establishes a fundamentally antagonistic interaction. Higher pathology grades (3–4), on the other hand, are more likely to compromise shell integrity and reduce host condition and marketability. As reviewed by David (2021), such infestations have been linked to increased metabolic demands, reduced growth, and impaired reproduction in bivalves. Our application of a semi-quantitative pathology scale allows for a more nuanced evaluation of when *Polydora* crosses from a low-cost association into a clearly parasitic relationship. While our surface-level damage scale does not account for deeper or overlapping burrows, prior work has shown that visible pathology can serve as a meaningful proxy for worm intensity. In a related study, Davinack et al. (2024) demonstrated a significant positive correlation between the percent shell area covered by mud blisters and actual worm burden in *Crassostrea virginica*. This supports the biological relevance of our approach, even if it underestimates hidden damage. However, given that structural impacts such as shell weakening or adductor muscle detachment may occur beneath the nacreous layer, future work incorporating histological or 3D imaging would provide a more complete picture of infestation severity and its consequences.

The Generalized Linear Model (GLM) in our study identified temperature as the strongest environmental correlate of infestation intensity. This contrasts with Cole et al. (2020), who found that salinity fluctuations and dissolved oxygen levels played a more prominent role in infestation patterns in the Gulf of America, where estuarine conditions are warmer and more variable. Similarly, Martinelli et al. (2024) reported a significant association between low-salinity conditions and higher infestation levels in Pacific oysters cultured on-bottom, likely due to increased sediment exposure and organic loading. In contrast, our study site—a tidally restricted estuary with relatively stable salinity and pH—temperature emerged as the strongest negative correlate of intensity; however, we interpret this as a consequence of the seasonal reproductive window and a lag to visible pathology, not necessarily as evidence that temperature is a direct driver. Additional sampling across multiple years will be needed to support more robust predictive modeling.

These seasonal trends likely reflect a combination of parasite reproductive timing, host growth, and cumulative oyster mortality. Smaller oysters collected in the summer may not have been suitable hosts during the prior infestation window, or they may have supported early-stage burrows that were not detectable using our surface-level assessment. While our pathology scale provides a practical proxy for damage, it cannot account for newly recruited or deeply embedded worms. Future work incorporating metrics such as worm developmental stage or burrow depth, using techniques like histology or 3D imaging, will be essential to fully capture the dynamics of prevalence and intensity over time and ensure early infestations are not overlooked.

5.2. Reproduction in Polydora websteri in the Herring River estuary

Throughout the reproductive period, *P. websteri* females produced primarily adelphophagic larvae from individual egg capsules that were connected via a discontinuous chain. In adelphophagic development, females deposit egg capsules in which only a subset of eggs develop into larvae, while the remaining eggs serve as nurse eggs (Rice and Rice, 2009). This often leads to sibling competition, resulting in hatchlings of varying sizes (David and Simon, 2014). These differences can significantly influence larval ecology: larger adelphophagic larvae typically spend less time in the plankton and have reduced dispersal potential compared to their smaller, planktotrophic counterparts, although oceanographic conditions may also influence final settlement patterns (David et al., 2014; David, 2021). A previous study by Davinack et al. (2024) confirmed the presence of planktotrophic broods from the same site, and genetic barcoding ruled out the presence of cryptic species. Thus, the *P. websteri* population in Cape Cod is poecilogonous, exhibiting multiple larval developmental modes. This contrasts with populations from China and Brazil, where *P. websteri* is known to produce only planktotrophic larvae (Ye et al., 2017; Barros et al., 2017). Interestingly, populations producing both planktotrophic and adelphophagic larvae have also been found in Maine, USA (Tomasetti, 2024), Virginia, USA (Haigler, 1969) and South Africa (Simon, 2015).

5.3. Implications for oyster harvesting and management

Polydora websteri infestations were present year-round, with peak intensities and pathology in colder months. This seasonal pattern is important to consider as tidal restoration of the Herring River proceeds and oyster beds may reopen. Tidal restriction has likely favored *P. websteri* through organic accumulation and reduced flushing. Reintroducing tidal flow may alleviate some of these conditions, yet our findings suggest that parasite pressure will persist, particularly given this species' winter activity when other estuarine parasites typically decline. If harvesting resumes, mitigation strategies may help reduce impacts. Off-bottom culture systems can lower exposure to sediments (Clements et al., 2017; Martinelli et al., 2024), although complete control remains elusive (Morse et al., 2015). Harvesting during spring and early summer, when intensities are lower, may also help avoid the peak damage of overwintering infestations. Routine monitoring of larval activity and settlement after restoration will be essential to track changes and inform adaptive management.

Overall, the success of oyster restoration in the Herring River will depend not only on improved water quality following tidal restoration, but also on a proactive approach to parasite management that incorporates local biological dynamics. These observations generate testable hypotheses for future work, but management implications await multi-year, post-restoration data.

CRediT authorship contribution statement

Ava Sheedy: Visualization, Methodology, Formal analysis, Data curation. **Andrew A. Davinack:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: [Andrew A. Davinack reports financial support was provided by Wellfleet Oyster Alliance. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.].

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jip.2025.108472.

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