Relationship between infaunal invertebrates and abiotic factors in intertidal mudflats on the Northwest Fundy shore, Bay of Fundy

by

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Abstract

Intertidal mudflats are unique ecosystems supporting diverse biotic communities, including infaunal organisms that live buried in sediments. Infaunal invertebrates have adapted to burrow, move, respire, and process sediment particles for food. This study explores how sediment organic content, carbonate content, grain size, pH and alkalinity influence abundance of four infaunal species (*Tubificoides benedii*, *Corophium volutator*, *Macoma balthica* and *Hediste diversicolor*) along the Northwest Bay of Fundy shore, based on Fall 2023 sampling at 10 sites. Results indicate that site had a significant effect on species abundance. The environmental variables that had the most influence on *Tubificoides benedii*, *Corophium volutator*, *Macoma balthica*, and *Hediste diversicolor* in generalized linear mixed models were sediment organic content, alkalinity and carbonate content. *Hediste diversicolor* appeared to also be influenced by sediment pH. Further investigation into the effects of sediment pH and alkalinity is needed to enhance understanding of ecology of mudflat invertebrates and provide a foundation for future species or environment specific studies.

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Introduction

Intertidal mudflats are distinct ecosystems characterized by unique environmental features, including alternating aerial exposure and submersion in seawater, that support abundant biotic communities (Dissanayake et al., 2018; Paterson et al., 2009). Mudflats serve as a transition area between marine and terrestrial environments (Foster et al., 2013) and consist of a mixture of sand and mud, with the mud content displaying cohesive qualities (Dyer et al., 2000). The proportions of sand and mud can vary, resulting in different mudflat characteristics that support diverse populations (Gerwing, 2016). Generally, high levels of organic matter such as plant residue can influence carbonate chemistry by decreasing pH as organic matter breaks down and releases acidic compounds (Leifeld et al., 2008; Rukshana et al., 2012). Chemical processes in the sediment linked to microbe respiration, can lead to overconsumption of oxygen, creating anaerobic conditions and increasing alkalinity (Kirchman, 2018). The extent of wave exposure varies by location, with mudflats along exposed coastlines experiencing greater wave action than those located in enclosed areas (Dyer et al., 2000). Wave action erodes soluble substances, gradually transforming larger particles into smaller grains over time, and exerts a significant influence on environmental factors, such as grain size. Tidal range can also influence various ecological factors of mudflats, including topography, physiographic features, morphology, and classification. (Dyer et al., 2000; McFall, 2019).

Mudflats support a wide variety of species, including infaunal organisms (Shen et al., 2006), which live buried in sediments (Banta & Andersen, 2003). These organisms have developed the necessary adaptations to live surrounded by sediment, as they must be able

to burrow, move, respire, and some process sediment particles to feed (Banta & Andersen, 2003). Faunal diversity in these environments can range from highly diverse populations to a limited number of species (Dyer, 1998). Soft sediments exposed to strong wave energy are highly dynamic, preventing many organisms from living in them. On the contrary, wave sheltered soft sediments are usually more suitable for a larger diversity of invertebrates (Bertness, 1999). On mudflats, the most abundant macrofaunal invertebrate groups of the Gulf of Maine include oligochaetes, mollusks, polychaetes and amphipods (Larsen & Doggett, 1991). Invertebrate communities play crucial roles in mudflat ecosystems, contributing to essential processes such as nutrient cycling and overall ecosystem biodiversity (Ieno et al., 2006, Lohrer et al., 2010), benthic-pelagic coupling through suspension-feeding bivalves, and serving as a food source for predators such as migrating shorebirds, crustaceans, and fish foraging at high tide (Nguyen, 2018). They also contribute to sediment processes (Lohrer et al., 2010) and energy transfer across different trophic levels (Snelgrove et al., 1997).

Both biotic and abiotic factors, can influence mudflat community composition and spatiotemporal dynamics (Gerwing et al., 2016). The present study focuses on abiotic factors, that have been shown to have effects on invertebrates (Jones et al., 2017) including sediment organic content (Bolam et al., 2004), carbonate chemistry (McGarrigle, 2023), pH (Rosemond et al., 1992) and sediment particle size (Meadows, 1964). Organic content significantly influences infaunal community structure, as it impacts species diversity and composition (Widdicombe & Austen, 2001). Furthermore, organic content is important for deposit feeders, as it serves as a food source (Snelgrove & Butman, 1994). However, research has shown that infaunal diversity decreases as

organic content increases, as anoxic conditions arise with high organic content due to anaerobic decomposition. This can be mitigated by the bioturbation of the substrate by organisms, which can enhance oxygen penetration into deeper sediment layers, benefiting microbial activity and facilitating the breakdown of organic material. Increased oxygen availability mitigates the detrimental effects of low oxygen on larger animals and enhances the activity of aerobic (oxygen-requiring) microbes, facilitating the breakdown of organic molecules containing carbon (Widdicombe & Austen, 2001). Nevertheless, if carbon degradation continues to escalate due to high organic material, it can lead to anoxic conditions, which may harm the community (Widdicombe & Austen, 2001).

Additionally, invertebrate communities are negatively affected by changes in carbonate chemistry, including decreased pH and increased alkalinity (Rosemond et al., 1992, Victoria et al., 2008). Studies suggest that seawater pH is crucial in determining infaunal community structure, with some species being more sensitive to acidic environments (Rosemond et al., 1992). For example, it has been reported that calcification in *Mercenaria mercenaria* decreased as acidification in the water column intensified (Ries et al., 2009) as there are less carbonate ions available for shell formation because carbonate ions bond with hydrogen ions (Green et al., 2004, Green et al., 1993). While fewer studies have examined sediment carbonate chemistry (pH and alkalinity), and their effects on growth, development, and calcification of marine bivalves compared to seawater carbonate chemistry, it is suggested that sediment carbonate chemistry may influence invertebrate and bivalve abundance (Meseck et al., 2018, Clements & Hunt, 2017). For example, *Mercenaria mercenaria* and other burrowing species showed shell dissolution when exposed to sediment with decreased pH and low levels of calcite and

aragonite, which are the main forms of calcium carbonate found in organisms. Carbonate chemistry and sediment acidification appears to affect bivalve settlement, indicating a need for further research to understand seasonal and yearly variability (Meseck et al., 2018, Clements & Hunt, 2017).

Additionally, species within the community show preferences for different grain sizes (Pomory et al., 1995). Firm mud typically supports the greatest diversity and density of infaunal organisms. As grain size increases, conditions may become less favorable for organisms to maintain their burrows, and bivalves may find it difficult to sustain their burrowing depth (Dashtgard et al., 2007). For some species, a larger grain size means less protection from predators because there are less grain boundaries which allow for freer movement for burrowing and digging, and fewer sources of food, as there is less organic matter available for feeding (Grant, 1981). Diversity and density of infauna generally increase from onshore to offshore, where mud deposits are more prevalent, and in other areas where substrate grain size decreases (Dashtgard et al., 2007).

This study aims to assess the spatial variation of abundance of the amphipod *Corophium volutator*, the clam *Macoma balthica*, the oligochaete *Tubificoides benedii* and the polychaete *Hediste diversicolor* between different intertidal mudflats in the Northwest Fundy shore, Bay of Fundy. This study also examines how the abundance of these species relates to environmental factors: sediment pH, alkalinity, organic matter, carbonate content and grain size. By investigating how the sediment chemistry and characteristics influence infaunal communities, this research aims to enhance our understanding of species distribution and abundance. By examining the strength of these

relationships, the study will provide valuable groundwork for future research focused on specific species or environmental aspects.

Materials and methods

Study Sites

Sampling was conducted at ten different sites along the Northwest Fundy shore in the upper Bay of Fundy, New Brunswick, Canada. The Bay of Fundy is known for its distinctive rise and fall of tides, with diurnal cycles and tidal ranges exceeding 15 meters (Desplanque & Mossman, 1972); the tidal range of my study sites is from 6 to 8 meters. The selected sites varied in composition, with some consisting of sandy beaches and others of mudflats. The ten selected sites were as follows (Figure 1): Bar Road, Saint Andrews, Charlotte County (BR, 45°06'02"N, 67°03'09"W); Pagan Point, Saint Andrews, Charlotte County (PP, 45°04'24"N, 67°02'07"W); Letang (Limekiln Rd.), Charlotte County (LR, 45°04'42"N, 66°44'07"W); Beaver Harbour Basin, Charlotte County (BH, 45°07'36"N, 66°44'28"W); Red Head Road, Charlotte County (RH, 45°04'09"N, 66°49'21"W); Pocologan, Charlotte County (POC, 45°06'49"N, 66°36'37"W); Maces Bay (Cassidy Ln), NB (CL, 45°07'29"N, 66°28'14"W); Little Dipper Harbour, NB (LDH, 45°04'24"N, 67°02'07"W); Little Lepreau, NB (LL, 45°07'52"N, 66°28'26"W); and Musquash, Saint John County (MUS, 45°10'51"N, 66°14'13"W).

Figure 1. Map of the ten sites in southwestern New Brunswick, sampled during fall of 2023. Furthest distance between sites is 65.7km (Google, 2025).

Species selected for the study

Four species were selected for this study: *Tubificoides benedii*, *Corophium volutator*, *Macoma balthica*, and *Hediste diversicolor*. These four species were chosen based on their ease of identification and abundance in samples collected in the field. According to Giere et al. (1998), the oligochaete *T. benedii* is a deposit feeder typically found in polluted, eutrophic coastal environments. These high-stress habitats often feature elevated levels of hydrogen sulfide, suggesting that *T. benedii* is capable of tolerating anoxic conditions. Its ability to maintain high oxygen regulatory capacity and engage in aerobic respiration under low oxygen levels enables it to thrive in sulfidic environments (Giere et al., 1999). *C. volutator* is a common amphipod and a dominant deposit feeder in the Bay of Fundy/Gulf of Maine and Northwest Europe. It plays a key role in linking primary producers to higher trophic levels and serves as prey for coastal birds and ground-feeding fish (Murdoch et al., 1986). *M. balthica* is a small, thin-shelled clam common in estuaries and muddy habitats on the East Coast of the US. Its shell size does not exceed 40 mm, and it feeds on small particles on the surface layer of the

sediment. *H. diversicolor* is a common ragworm from the polychaete group, found in shallow, marine brackish waters in temperate zones. When burrowing, it forms a U- or Y-shaped structure in the sediment (Scaps, 2002) and exhibits various feeding behaviors, such as carnivory, scavenging, filter feeding, and deposit feeding (Beyer & Sundt, 2006). This species is frequently used as bait for commercial purposes (Rasines et el., 2023). It is an important component of the food web, as it is preyed upon by fish and crustaceans (Long et al., 2008).

Field sampling design

Sampling for this project was completed in Fall 2023 over a two-week period (Oct 31st - Nov 8th) during low tide. The invertebrate community was characterized, and abiotic environmental variables, including sediment carbonate chemistry (pH and alkalinity) and sediment characteristics (organic content and grain size) were recorded for analysis.

Upon arrival at each site, a 25m transect was placed perpendicular to the waterline in the mid intertidal zone. Sampling was conducted on one side of the transect to ensure that the opposite side remained undisturbed. Sediment and alkalinity samples were collected at six randomly assigned meter marks per site, which were pre-determined using a random number generator in Excel. No repeats were made at any given mark. Sediment samples for pH were obtained using a core, by pressing it into the sediment. The sample was then transferred into the core jar (diameter 6.4 cm, depth 5 cm), ensuring that the surface remained undisturbed. A second sediment sample was collected at the same meter location using the same procedure for sediment characteristics analysis. For alkalinity measurements, a metal scoop was used to collect surface sediment at each location, which was then placed in a vial (15 mL; 1.6 cm diameter × 11.8 cm height).

At the same random meter locations, a 0.015m² quadrat was haphazardly placed near the core collection point. A 10cm deep hole was dug evenly within the quadrat, and the sediment was placed in a bucket. The sediment was then taken to a water source, where it was sieved through a 4mm mesh sieve. Any macrofauna larger than 4 mm (excluding worms, due to identification challenges in the field) were measured using calipers and then released back to the environment. Once sieving was complete, the remaining material in the sieve was transferred into plastic jars for further analysis. All core jars and water samples were transported in a cooler with ice to keep samples cool, as pH measurements could be affected by temperature changes. Samples for sediment characteristics were placed in the freezer for storage, and the quadrat samples were preserved in ethanol.

Laboratory analyses

pH analysis was conducted using a Unisense microelectrode pH-500 probe and a Unisense pH/Redox Uniamp meter. All pH profiling was completed within six hours of sample collection. Sediment pH measurements were taken at depth intervals of 0.5cm, extending from the surface to 3cm into the sediment core. Three holes were haphazardly created in the sediment to check for obstructions and avoid damaging the probe. The profile was conducted at the edge of each of the three holes, resulting in a total of three profiles per core. A motorized arm, holding the probe, was moved down to the corresponding depth, while the core was positioned below the arm. The tip of the probe was placed right next to the previously made hole. pH readings were recorded at each interval, with temperature only recorded at the surface. If an obstruction was encountered in the sediment, the profile was discontinued. The pH probe was calibrated before use

with 4.0, 7.0, and TRIS buffer solutions for pH value correction. After completing the pH profiles, all sediment samples were sieved through a 500µm sieve and stored in core jars with ethanol, properly labeled for future invertebrate analysis.

Alkalinity was measured using spectrometry following the method outlined by Sarazin et al., (1999). Sediment samples were processed in a centrifuge at a speed of 5 for 12 minutes to extract the porewater. A standard curve for conversion of absorbance to alkalinity was created, using seawater with known alkalinity levels and a colour reagent composed of formic acid, bromophenol blue solution, and sodium chloride. The amount of seawater standard (with known alkalinity) was varied by adjusting the NaCl-to-seawater ratio to create the calibration curve. Mixtures were added and mixed using a micropipette. Once the calibration curve was established, the spectrophotometer was ready for processing the porewater samples. After centrifuging the mud samples and extracting the porewater from the sediment samples, the same reagent mixture used previously was added to the porewater using a micropipette. The prepared samples were then placed in the VWR V-1200 spectrophotometer set to 590nm, and the absorbance readings were recorded. Finally, the absorbance readings were converted to alkalinity values based on the curve developed.

Grain size analysis was performed by preparing approximately 150–175g of the frozen sediment samples, by thawing and drying them at 105˚C for 24h, and then pulverizing them with a mortar and pestle. The samples were passed through a stack of sieves with mesh sizes of 63µm, 125µm, 500µm, 710µm, 1mm, 2mm, and 4mm and shaken using a sieve shaker at 20min intervals. After shaking, the material from each sieve was carefully

poured into a plastic plate and weighed to calculate the mean grain size using the GRADISTATv8 template in Excel (Blott & Pye, 2001).

Organic content was analyzed using the loss on ignition method. Approximately 2–3g of each sediment sample was first dried in an oven at 105˚C for 24h, then burned in a muffle furnace at 550˚C for 4h. Afterward, the samples were burned again at 950˚C for two hours. The percentage weight difference before and after the 550˚C and 950˚C burning periods indicated the relative amounts of organic content and carbonate content in the sediment, respectively.

Invertebrate counts were performed on both the core and quadrat samples. For the quadrats, which had been sieved using a 4mm sieve, the sample was poured into a tray where organisms > 4mm were counted. These organisms were measured using calipers or, when necessary, an ocular micrometer on a dissecting microscope, which was also used for taxonomic identification. Core samples were sieved using a 500µm sieve, and the organisms were counted and identified using a dissecting microscope.

Statistical analyses

Due to the varying sizes of the species of interest, cores and quadrats were selected for analysis based on which method yielded the highest abundance for each species. Core samples were used for *T. benedii*, *C. volutator*, and *H. diversicolor*, while quadrat samples were used for *M balthica*.

All statistical analyses and graphs were conducted using RStudio (version 4.3.2). The effect of site on abundance of each species was assessed first. The data failed to meet the assumptions of homogeneity of variance and normality of residuals for ANOVA, tested

using the "leveneTest" function from the "car" package for homogeneity and the "shapiro.test", "qqnorm", and "qqline" functions from the "stats" package for normality. As a result, a generalized linear model (GLM), with negative binomial distribution, from the "glm" function in the "stats" package was used. To determine if site had a significant effect on species abundance, the “Anova” function from the “car” package was used to do likelihood ratio Chi-square tests. To make posthoc pairwise comparisons between sites, the "emmeans" function from the "emmeans" package was used. To illustrate the relationship between site and species abundance, one boxplot graph per species was created using the "ggplot2" package from the "tidyverse" collection of packages.

To examine which environmental variables—sediment carbonate content, pH, alkalinity, organic matter, and grain size—had the greatest influence on species abundance, a generalized linear mixed model (GLMM) was used, with site as a random variable. Using the "check_overdispersion" function from the "DHARMa" package, it was determined that the data were overdispersed. Therefore, a GLMM with a negative binomial distribution was used, employing the "glmmTMB" function from the "glmmTMB" package, with site as a random variable. Since pH depth was measured in 0.5cm intervals, the data were filtered to create one dataset per mean pH depth with the rest of the variables in it, resulting in seven models in total per species. These models were compared using the "AIC" function from the "stats" package to identify the depth at which pH best explained abundance for each species. The Akaike Information Criterion (AIC) indicated that for *T. benedii* and *C. volutator*, the depth that best explained their abundance was 1.5cm; for *M. balthica* and *H. diversicolor*, the chosen depths were 2.5cm and 0cm, respectively.

For each species, candidate models with different combinations of environmental variables, including pH at the selected depth were created using the “glmmTMB” function and compared using the same AIC function (Table A1). The top three models for each species are presented in the results section (Table 2). Finally for all species the pseudo-R^2 value was calculated using the function “logLik”, “calc_pseudo_r2() and “glmmTMB” with “nbinom2” distribution from the package “glmmTMB”. Scatterplots of abundance in relation to environmental variables were created for each environmental variable included in the three best models, using the “ggplot” function from the “ggplot2” package.

Results

Species abundance relative to site

The four species showed different patterns of abundance across sites. *C. volutator* was the species present at the most sites, and *H. diversicolor* was the least present across sites, only collected in three out of ten sites (Figure 2.). *M. balthica* and *T. benedii* were present at four out of ten sites. Although abundances varied, all four species were present at Red Head (RH) (Figure 2.). There was a significant effect of site on species abundances (Table 1.).

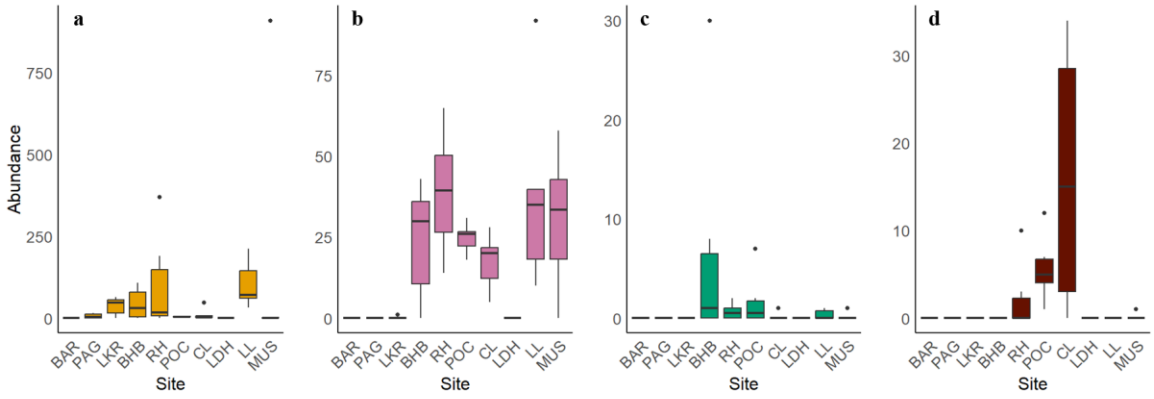

Figure 2. Boxplots of abundance of a) *T. benedii*, b) *C. volutator*, c) *M. balthica* and d) *H. diversicolor* at ten different sites during the fall of 2023 in the Northwest Fundy shore. a), b) and d) expressed as abundance per core and c) expressed as abundance per quadrat.

Table 1. The Chi-square statistic, degrees of freedom and P-value from GLMs of the effect of site on abundance of *T. benedii*, *C. volutator*, *M. balthica*, and *H. diversicolor*. *** represents statistical significance at an alpha level of 0.05.

Species	**Chi-square statistic**	**Degrees of freedom**	**P-value**
Tubificoides benedii	68.32	9	3.234e-11 ***
Corophium volutator	257.4	9	< 2.2e-16 ***
Macoma balthica	48.87	9	1.749e-07 ***
Hediste diversicolor	107.38	9	< 2.2e-16 ***

Tubificoides benedii

T. benedii was abundant at Beaver Harbor Basin (BHB), Limekiln Road (LKR), Read Head (RH) and Little Lepreau (LL) (Figure 2). There was more abundance variation among samples at RH than LL, indicated by the longer boxplot length (Figure 2.). The boxplot from LKR and BHB is short, showing little variation, and BHB exhibited symmetrical distributed data (Figure 2). There was a significant variation among sites in *T. benedii* abundance (Table 1). When comparing the abundance of *T. benedii* among the ten sites, all the sites varied significantly form each other, except for Bar Road (BAR) and Little Dipper Harbour (LDH) (Table A2).

Corophium volutator

Among all the species of interest, *C. volutator* exhibited the highest abundance across multiple sites (Figure 2). There was the greatest abundance variation among samples at Beaver Harbour Basin (BHB), Musquash (MUS), and Red Head (RH). RH and MUS showed a more symmetrical distributed abundance across samples. Data from BHB, Pocologan (POC), Cassidy Lane (CL) and Little Lepreau (LL) was positively skewed

(Figure 2). There was significant variation in the abundance of *C. volutator* across different sites (Table 1). The abundance of *C. volutator* among the ten sites, varied significantly for all pairs of sites, except for Bar Road (BAR), Little Dipper Harbour (LDH) and Pagan Point (PAG) (Table A3).

Macoma balthica

Beaver Harbour Basin (BHB) had the highest abundance of *M. balthica* among all sites (Figure 2). Red Head (RH), Pocologan (POC) and Little Lepreau (LL) showed abundance levels greater than zero but lower than those observed at BHB. No *M. balthica* were detected in quadrats at the rest of the sites (Figure 2). There was significant variation among sites in *M. balthica* abundance (Table 1). When comparing the abundance of *M. balthica* among the ten sites, it varied significantly between most pairs of sites but not between Bar Road (BAR), Little Dipper Harbour (LDH), Limekiln Road (LKR) and Pagan Point (PAG) (Table A4). Note that the abundance of *M. balthica* is shown per quadrat; therefore, its overall density is lower than the other species.

Hediste diversicolor

H. diversicolor was only present at Red Head (RH), Pocologan (POC) and Cassidy Lane (CL) (Figure 2). CL exhibited the highest abundance and the greatest variation among samples; abundance values appear to be evenly distributed across samples. RH and POC had lower abundance than CL, values were negatively skewed (Figure 2). There was significant variation in the abundance of *H. diversicolor* across sites (Table 1). The abundance of *H. diversicolor* compared among the ten sites only varied significantly between Pocologan (POC) and Musquash (MUS) (Table A5).

Abiotic variables in mudflats

Abiotic variables varied across the different sites (Figure 3). For instance, sediment carbonate content generally ranged from 0.0% to 0.5%, but BAR, PAG, and LKR had values that ranged up to 2.0% (Figure 3). BAR had the highest mean grain size, followed by LL, while the other sites had grain sizes ranging from 100µm to about 500µm (Figure 3). The highest sediment pH values were found at BAR and PAG, while pH at the remaining sites ranged from just above 7.00 to approximately 7.50 (Figure 3). Sediment at LKR had the highest organic content percentage, while PAG had the lowest (Figure 3). Lastly, sediment alkalinity was lowest at BAR and highest at LL, with the other sites showing intermediate values (Figure 3).

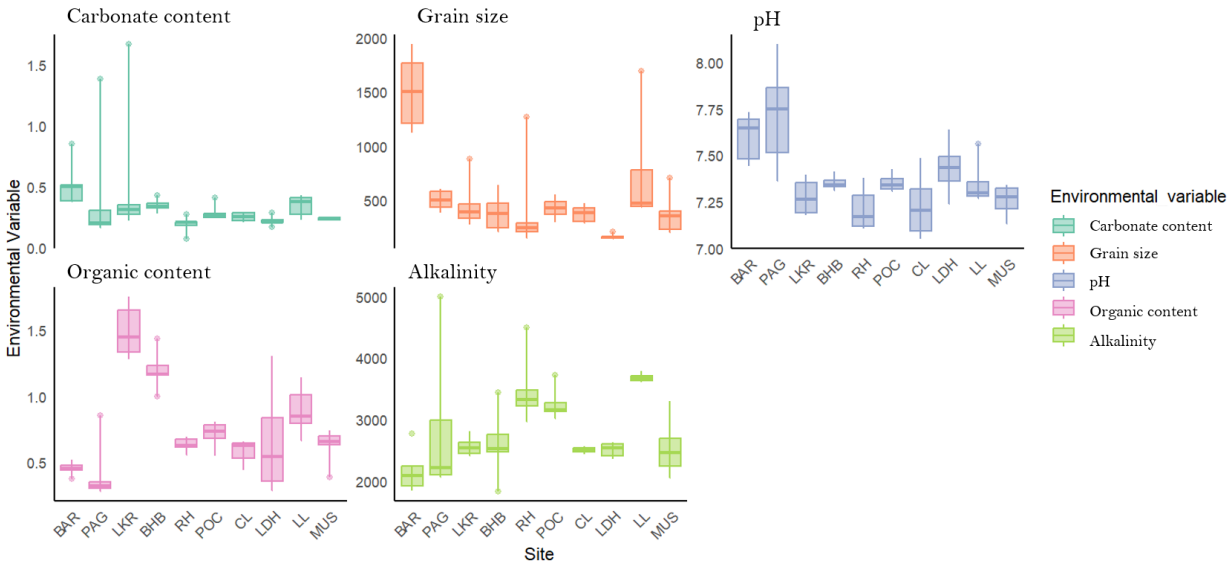

Figure 3. Boxplots of environmental variables (carbonate content, grain size, pH, organic content and alkalinity) measured in the sediment at ten different sites (Bar Road (BAR), Pagan Point (PAG), Limekiln Road (LKR), Beaver Harbour Basin (BHB), Red Head (RH), Pocologan (POC), Cassidy Lane (CL), Little Dipper Harbour (LDH), Little Lepreau (LL) and Musquash (MUS) in the Northwest Fundy shore, New Brunswick, Canada).

Species abundance relative to environmental factors

Tubificoides benedii

T. benedii abundance was greatest at intermediate levels of alkalinity and had a negative trend with the rest of the abiotic variables (Figure 4). Higher abundance values were more clustered towards lower carbonate content percentages and smaller grain sizes. *T. benedii* abundance varied across the range of sediment organic content, alkalinity and pH values (Figure 4).

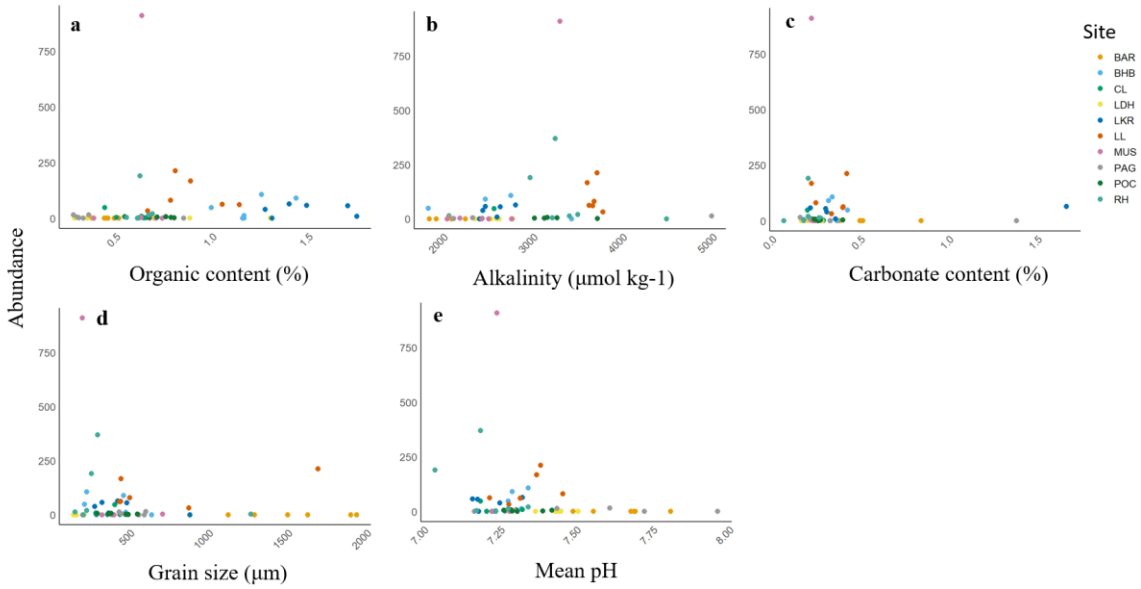

Figure 4. Scatterplot of abundance of *T. benedii* relative to a) organic content (%), b) alkalinity (µmol kg-1), c) carbonate content (%), d) grain size (µm) and e) pH of sediment in ten different sites during the fall of 2023 in the Northwest Fundy shore. Abundance of T. *benedii* per core (diameter 6.4 cm, depth 5 cm).

The top model of the relationship between *T. benedii* abundance and environmental variables included sediment organic content and alkalinity, while the second-best model, included carbonate content and alkalinity (Table 2). The third-best model, the global model, included all the abiotic variables—organic content, carbonate content, alkalinity,

grain size, and pH (Table 2). According to the pseudo-R^2, these models explain only between 4% and 17% of the variation in the data (Table 2).

Table 2. Top three models based on Akaike Information Criterion (AIC) results for Generalized Linear Mixed Models (GLMM) of relationships between abundance of *T. benedii*, *C. volutator*, *M. balthica,* and *H. diversicolor* and abiotic variables, with site as a random variable. Data from the fall 2023 sampling, Northwest Fundy shore.

Species	**pH depth (cm)**	**Variables**	**Delta**	**AICc**	**df**	**Loglik**	**K**	**Pseudo-R2**
Tubificoides benedii	1.5	Organic content and alkalinity	0.00	377.46	5	-183.01	5	0.04
		Carbonate content and alkalinity	0.74	378.20	5	-183.39	5	0.04
		Alkalinity, organic content, carbonate content, grain size and pH	1.90	379.35	8	-179.83	8	0.17
Corophium volutator	1.5	Carbonate content and alkalinity	0.00	307.14	5	-147.86	5	0.17
		Organic content and alkalinity	1.64	308.78	5	-148.68	5	0.16
		Alkalinity, organic content, carbonate content,	8.16	315.31	8	-147.81	8	0.17

		grain size and pH						
Macoma balthica	2.5	Alkalinity	0.00	95.11	4	-43.10	4	0.21
		Organic content and alkalinity	0.38	95.48	5	-42.03	5	0.23
		Carbonate content and alkalinity	1.58	96.69	5	-42.63	5	0.22
Hediste diversicolor	0	Alkalinity and pH	0.00	75.37	5	-32.00	5	0.51
		Carbonate content and alkalinity	1.24	76.61	5	-32.61	5	0.50
		Organic content and alkalinity	1.68	77.05	5	-32.83	5	0.50

Corophium volutator

There was a positive trend between *C. volutator* abundance and sediment carbonate content. There were no *C. volutator* at the highest and lowest organic content percentages. There was a negative relationship between abundance and alkalinity, grain size and pH (Figure 5). Abundance values were greater and mostly concentrated at lower carbonate content percentages and at intermediate pH values (Figure 5).

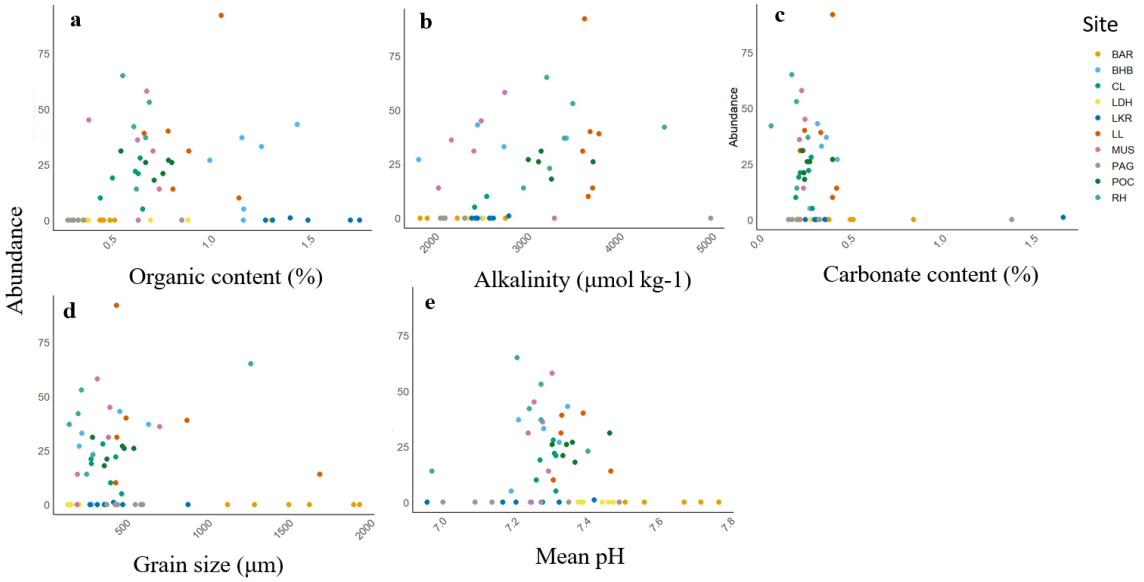

Figure 5. Abundance of *C. volutator* relative to a) organic content (%), b) alkalinity (µmol kg-1), c) carbonate content (%), d) grain size (µm) and e) pH of sediment in ten different sites during the fall of 2023 in the Northwest Fundy shore. Abundance of *C. volutator* per core (diameter 6.4 cm, depth 5 cm).

The model that best explained *C. volutator* abundance included sediment carbonate content and alkalinity, while the second-best model included organic content and alkalinity. The third-best model, the global model, included all the abiotic variables—organic content, carbonate content, alkalinity, grain size, and pH (Table 2). According to the pseudo-R^2, these models explain about 17% of the variation in the data (Table 2).

Macoma balthica

M. balthica showed the lowest abundance values out of the four species with no linear relationship to the abiotic variables (Figure 6). *M. balthica* were found mostly at lower levels of organic and carbonate content and moderate alkalinity values (Figure 6).

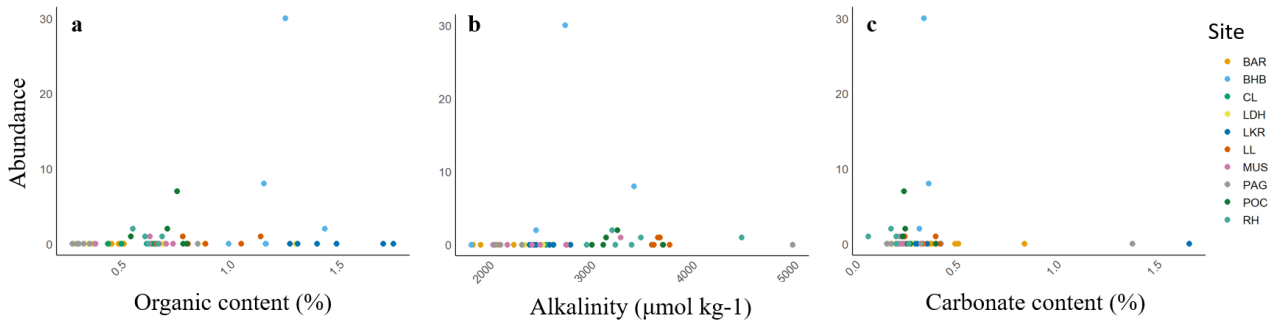

Figure 6. Abundance of *M. balthica* relative to a) organic content (%), b) alkalinity (µmol kg-1) and c) carbonate content (%) at sediment in ten different sites during the fall of 2023 in the Northwest Fundy shore. Abundance of *M. balthica* per quadrat (0.015m2).

The model that best explained *M. balthica* abundance included only sediment alkalinity, while the second-best model included organic content and alkalinity (Table 2). The third-best model included carbonate content and alkalinity (Table 2). Based on the pseudo-R^2, these models explained 21% to 23% of the variation in the data (Table 2).

Hediste diversicolor

Abundance values of *H. diversicolor* were greater at lower levels of organic content, carbonate content, and pH (Figure 7). Abundance values, especially at Pocologan and Red Head were greatest at moderate levels of organic content, pH and alkalinity, and

lower levels of carbonate content (Figure 7).

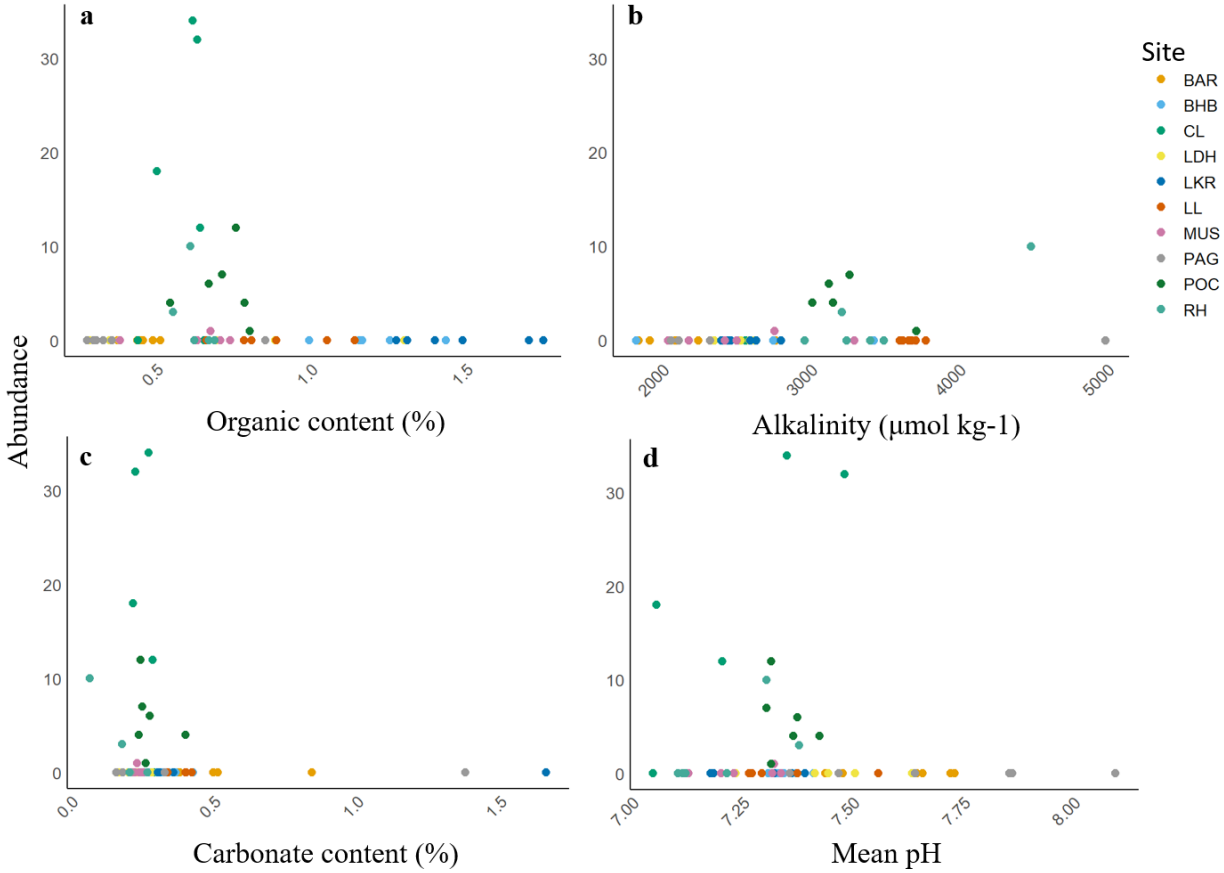

Figure 7. Abundance of *H. diversicolor* relative to a) organic content (%), b) alkalinity (µmol kg-1), c) carbonate content (%) and d) pH in sediment at ten different sites during the fall of 2023 in the Northwest Fundy shore. Abundance of *H. diversicolor* per core (diameter 6.4 cm, depth 5 cm).

The model that best explained *H. diversicolor* abundance included alkalinity and pH while the second best model included carbonate content and alkalinity. The third-best model included organic content and alkalinity (Table 2). According to the pseudo-R^2, these models explained about 50% of the variation in the data (Table 2).

Influence of abiotic variables on species abundance

While different environmental variables had an impact on the four species, the abiotic variables which were included in the best models of species abundance most often were organic content, carbonate content and alkalinity (Table 2).

Overall, sediment alkalinity was found in the best model for all 4 species. Sediment organic content and carbonate content were in at least one of the three best models for all the species. Finally, sediment pH was in the top model for *H. diversicolor*. The models of relationships between abundance and abiotic variables explained the most variance for *H. diversicolor* (~50%), and the least variation for *T. benedii* (4-17%), with models for *C. volutator* and *M. balthica* having pseudo-R^2 that ranged between 16-23%.

Discussion

Abundances of *T. benedii*, *C. volutator*, *M. balthica* and *H. diversicolor* varied significantly across the study sites. The species were patchy in their distribution or were not found at all at some sites. The study sites exhibited variation in environmental variables, including sediment carbonate content, grain size, pH, organic content, and alkalinity. Overall, based on the GLMM models, abundance of the four species of interest in this study were consistently related to sediment alkalinity, while abundance of some species was also related to organic content or carbonate content. For *T. benedii*, the best fit model included organic content and alkalinity. For *C. volutator*, the best fit model featured carbonate content and alkalinity. The best model for *M. balthica* only included alkalinity, while for *H. diversicolor*, alkalinity and pH were included.

Alkalinity was present in the best fit model of all four species, and pH in the best fit model for *H. diversicolor*. Both of these variables are related to carbonate chemistry. My study showed that species abundance was mostly centered at a low to moderate alkalinity, and moderate pH levels. Fewer studies have focused on sediment carbonate chemistry (pH and alkalinity) compared to studies on water column pH and alkalinity, but it is known that a decline in sediment pH can negatively affect survival rates and calcification in infaunal species (Guzman-Guevara et al., 2018). If tolerance ranges are exceeded, acidification can dissolve calcium-based body structures, such as the shells of *M. balthica* and other bivalves, or impair the development of their larvae (Jansson et al., 2013). For example, Green et al., 2004 found that mortality of *Mercenaria mercenaria* juveniles increased at low carbonate levels when their shells started to dissolve due to the low concentration of biogenic aragonite, which makes up their shell. A previous study on

intertidal mudflat communities found that carbonate chemistry played a critical role, with sediment pH and water alkalinity being the best explanatory variables for multivariate community variation (McGarrigle & Hunt, 2024).

Organic content also appeared to influence species abundance as it was found in the top three models of all 4 species. For example, as organic content increased, the abundance of *T. benedii* increased. This is likely because *T. benedii*, a deposit feeder, relies on organic matter in the sediment for food (Dubilier & Giere, 1995). This species is known to hold its tail to the surface for respiration while foraging in deeper, organic-rich sediment (Dubilier & Giere, 1995). *C. volutator* and *M. balthica*, deposit feeders, also depend on organic matter such as particulate matter, organic detritus, and diatoms for survival (Icely & Nott, 1985). Results from my study showed that the abundance of the four species was higher in areas with low to moderate organic matter. Although it is known that organic content in sediment is associated with food availability for infaunal organisms, high levels of organic content are related to oxygen depletion in the environment (Levin & Gage, 1998), which may harm the community (Widdicombe, 2001). More research on polychaetes and oligochaetes such as *T. benedii* and *H. diversicolor* is needed as there was limited information compared to *C. volutator* and *M. balthica* to fully understand how these species are affected by different environmental variables.

In my study, there was little evidence for the importance of grain size compared to the other abiotic variables, which is different than what I would expect based on past studies of these species. It was only included in the third best model for *T. benedii* and *C. volutator*. Although there was not a clear relationship, *T. benedii* and *C. volutator*

abundance was higher in finer grain sizes. Fenchel et al. (1975) noted that *C. volutator* utilizes specific-sized bacteria attached to clay particles in the sediment as a food source. Smaller particle sizes also provide better protection from predators for different species of invertebrates (Fenchel et al., 1975), as some are predated upon by shorebirds and benthic fish (Meadows, 1964; McCurdy et al., 2005). It is possible that the relationship to grain size for the 4 species of interest was not very clear in this study because the species might have adapted to thrive in different grain sizes. They might be able to burrow into finer or coarser sediments, without being strongly impacted by the exact grain size.

Even though the top models for all species included similar environmental variables, the pseudo-R^2 values indicated that the variables explained more of the variation in abundance for some species than others. The models for *H. diversicolor* explained about 50% of the variation, in contrast to *T. benedii*, where the models explained only 4–17% of the variation. *C. volutator* and *M. balthica* showed intermediate values compared to the other two species. This could be an indicator that the distribution and abundance of the species with lower pseudo-R^2 values are more strongly influenced by abiotic or biotic factors not considered in this study. Other environmental variables not included in this study, such as salinity, temperature, wave action, and air exposure, might also affect species abundance and could explain more variation. Additionally, biotic factors, such as the abundance of predators, competitors, or food availability, may also influence species abundance.

In conclusion, sediment organic content, carbonate content, and alkalinity emerged as the environmental variables most strongly related to the abundance of *T. benedii*, *C. volutator*, *M. balthica*, and *H. diversicolor*. Significant spatial variation in species

abundance was observed across sites, highlighting the importance of local environmental factors. Understanding how these factors differ across sites is crucial for comprehending the spatial distribution of species. Specifically, sediment alkalinity appeared to play a role in shaping the abundance patterns of all four species, emphasizing its significance in their ecological patterns. Future directions for research on infaunal invertebrates in this region include investigating in greater depth the extent to which alkalinity affects the infaunal community and identifying other variables that influence the abundance of different species. Collecting data on more variables so that they can be included in models, in addition to those studied here, could provide a better understanding of why the infaunal community varies spatially and under different conditions.

Contributions to Thesis

This honours project is part of a larger project, which consists of three sampling periods: fall 2023, summer 2024 and fall 2024. The data for my thesis comes from the fall 2023 sampling period only. Field work, pH and alkalinity analyses were conducted by Dr. Heather Hunt, Mia Francis and Krista Beardy. Amanda Fenech and I did invertebrate counts and identification for the fall 2023 data. I carried out the statistical analyses for this honours project. I participated in field sampling and laboratory sample processing for the second sampling period and contributed to the laboratory sample processing for the third sampling period.

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Appendix

Table A1. Candidate models for the species *T. benedii*, *C. volutator*, *M. balthica* and *H. diversicolor*. Average pH at a single depth was included in the models: *T. benedii* (1.5cm), *C. volutator* (1.5cm), *M. balthica* (2.5cm), and *H. diversicolor* (0cm).

Models	**Variables**
Global model	Abundance ~ Organic content + Carbonate content + pH + Grain size + Alkalinity
Model #1	Abundance ~ Organic content
Model #2	Abundance ~ Carbonate content
Model #3	Abundance ~ pH
Model #4	Abundance ~ Grain size
Model #5	Abundance ~ Alkalinity
Model #6	Abundance ~ Organic content + carbonate content
Model #7	Abundance ~ Organic content + pH
Model #8	Abundance ~ Organic content + Grain size
Model #9	Abundance ~ Organic content + alkalinity
Model #10	Abundance ~ Carbonate content + pH
Model #11	Abundance ~ Carbonate content + Grain size
Model #12	Abundance ~ Carbonate content + Alkalinity
Model #13	Abundance ~ pH + Grain size

Model #14	Abundance ~ pH + Alkalinity
Model #15	Abundance ~ Grain size + Alkalinity

Table A2. Pairwise comparisons of abundance of *T. benedii* between sites: Bar Road, Saint Andrews, Charlotte County (BR); Pagan Point, Saint Andrews, Charlotte County (PP); Letang (Limekiln Rd.), Charlotte County (LR); Beaver Harbour Basin, Charlotte County (BH); Red Head Road, Charlotte County (RH); Pocologan, Charlotte County (POC); Maces Bay (Cassidy Ln), NB (CL); Little Dipper Harbour, NB (LDH); Little Lepreau, NB (LL) and Musquash, Saint John County (MUS)

Site comparison	**Estimate**	**SE**	**z.ratio**	**P-value**
BAR-BHB	-18.05	315.89	-0.05	1
BAR-CL	-16.66	315.89	-0.05	1
BAR-LDH	0	446.74	0	1
BAR-LKR	-17.91	315.89	-0.05	1
BAR-LL	-18.92	315.89	-0.06	1
BAR-MUS	-19.32	315.89	-0.06	1
BAR-PAG	-16.06	315.89	-0.05	1
BAR-POC	-15.72	315.89	-0.05	1
BAR-RH	-18.90	315.89	-0.06	1
BHB-CL	1.39	0.13	9.95	<0.0001
BHB-LDH	18.05	315.89	0.05	1
BHB-LKR	0.14	0.09	1.55	0.87
BHB-LL	-0.86	0.07	-11.69	<0.0001
BHB-MUS	-1.26	0.07	-17.93	<0.0001
BHB-PAG	1.99	0.18	11.06	<0.0001
BHB-POC	2.33	0.20	11.12	<0.0001

BHB-RH	-0.84	0.07	-11.29	<0.0001
CL-LDH	16.66	315.89	0.53	1
CL-LKR	-1.24	0.14	-8.80	<0.0001
CL-LL	-2.25	0.13	-17.2	<0.0001
CL-MUS	-2.65	0.12	-20.54	<0.0001
CL-PAG	0.60	0.21	2.87	0.11
CL-POC	0.94	0.23	3.98	0.0027
CL-RH	-2.23	0.13	-16.97	<0.0001
LDH-LKR	-17.91	315.89	-0.05	1
LDH-LL	-18.92	315.89	-0.06	1
LDH-MUS	-19.32	315.89	-0.61	1
LDH-PAG	-16.06	315.89	-0.05	1
LDH-POC	-15.72	315.89	-0.05	1
LDH-RH	-18.90	315.89	-0.06	1
LKR-LL	-1.01	0.07	-12.93	<0.0001
LKR-MUS	-1.40	0.07	-18.85	<0.0001
LKR-PAG	1.85	0.18	10.18	<0.0001
LKR-POC	2.18	0.21	10.36	<0.0001
LKR-RH	-0.98	0.07	-12.54	<0.0001
LL-MUS	-0.39	0.05	-7.60	<0.0001
LL-PAG	2.86	0.17	16.47	<0.0001
LL-POC	3.19	0.20	15.68	<0.0001
LL-RH	0.02	0.05	0.46	1
MUS-PAG	3.26	0.17	18.92	<0.0001

MUS-POC	3.59	0.20	17.74	<0.0001
MUS-RH	0.42	0.05	8.04	<0.0001
PAG-POC	0.33	0.26	1.28	0.95
PAG-RH	-2.83	0.17	-16.31	<0.0001
POC-RH	-3.17	0.20	-15.54	<0.0001

Table A3. Pairwise comparisons of abundance of *C. volutator* between sites: Bar Road, Saint Andrews, Charlotte County (BR); Pagan Point, Saint Andrews, Charlotte County (PP); Letang (Limekiln Rd.), Charlotte County (LR); Beaver Harbour Basin, Charlotte County (BH); Red Head Road, Charlotte County (RH); Pocologan, Charlotte County (POC); Maces Bay (Cassidy Ln), NB (CL); Little Dipper Harbour, NB (LDH); Little Lepreau, NB (LL) and Musquash, Saint John County (MUS)

Site comparison	**Estimate**	**SE**	**z.ratio**	**P-value**
BAR-BHB	-20.48	1.42E+03	-0.01	1
BAR-CL	-20.16	1.42E+03	-0.01	1
BAR-LDH	0	2.00E+03	0	1
BAR-LKR	-15.51	1.42E+03	-0.01	1
BAR-LL	-20.93	1.42E+03	-0.01	1
BAR-MUS	-20.72	1.42E+03	-0.01	1
BAR-PAG	0	2.00E+03	0	1
BAR-POC	-20.51	1.42E+03	-0.01	1
BAR-RH	-20.96	1.42E+03	-0.01	1
BHB-CL	0.32	1.28E-1	2.51	0.25
BHB-LDH	20.48	1.42E+03	0.01	1
BHB-LKR	4.97	1.00E+00	4.96	<0.0001
BHB-LL	-0.44	1.06E-01	-4.17	0.0013
BHB-MUS	-0.23	1.11E-01	-2.14	0.49

BHB-PAG	20.48	1.42E+03	0.01	1
BHB-POC	-0.02	1.17E-01	-0.23	1
BHB-RH	-0.47	1.06E-01	-4.52	0.0003
CL-LDH	20.48	1.42E+03	0.014	1
CL-LKR	4.65	1.00E+00	4.63	0.0002
CL-LL	-0.76	1.18E-01	-6.49	<0.0001
CL-MUS	-0.56	1.22E-01	-4.58	0.0002
CL-PAG	20.16	1.42E+03	0.01	1
CL-POC	-0.35	1.27E-01	-2.74	0.1552
CL-RH	-0.80	1.17E-01	-6.82	<0.0001
LDH-LKR	-15.51	1.42E+03	-0.01	1
LDH-LL	-20.93	1.42E+03	-0.01	1
LDH-PMUS	-20.72	1.42E+03	-0.01	1
LDH-PAG	0	2.00E+03	0	1
LDH-POC	-20.51	1.42E+03	-0.01	1
LDH-RH	-20.96	1.42E+03	-0.01	1
LKR-LL	-5.42	1.00E+00	-5.40	<0.0001
LKR-MUS	-5.21	1.00E+00	-5.20	<0.0001
LKR-PAG	15.51	1.42E+03	0.01	1
LKR-POC	-5	1.00E+00	-4.98	<0.0001
LKR-RH	-5.45	1.00E+00	-5.44	<0.0001
LL-MUS	0.20	9.93E-02	2.07	0.5485
LL-PAG	20.93	1.42E+03	0.015	1
LL-POC	0.41	1.05E-01	3.94	0.0032
LL-RH	-0.03	9.33E-02	-0.37	1

MUS-PAG	20.72	1.42E+03	0.01	1
MUS-POC	0.21	1.10E-01	1.91	0.6592
MUS-RH	0.24	9.85E-02	-2.44	0.302
PAG-POC	-20.51	1.42E+03	-0.01	1
PAG-RH	-20.96	1.42E+03	-0.01	1
POC-RH	-0.45	1.05E-01	-4.30	0.0007

Table A4. Pairwise comparisons of abundance of *M. balthica* between sites: Bar Road, Saint Andrews, Charlotte County (BR); Pagan Point, Saint Andrews, Charlotte County (PP); Letang (Limekiln Rd.), Charlotte County (LR); Beaver Harbour Basin, Charlotte County (BH); Red Head Road, Charlotte County (RH); Pocologan, Charlotte County (POC); Maces Bay (Cassidy Ln), NB (CL); Little Dipper Harbour, NB (LDH); Little Lepreau, NB (LL) and Musquash, Saint John County (MUS)

Site comparison	**Estimate**	**SE**	**z.ratio**	**P-value**
BAR-BHB	-20.2	2334.17	-0.009	1
BAR-CL	-16.51	2334.17	-0.007	1
BAR-LDH	0	3301.02	0	1
BAR-LKR	0	3301.02	0	1
BAR-LL	-17.20	2334.17	-0.007	1
BAR-MUS	-16.51	2334.17	-0.007	1
BAR-PAG	0	3301.02	0	1
BAR-POC	-18.81	2334.17	-0.008	1
BAR-RH	-17.89	2334.17	-0.008	1
BHB-CL	3.68	1.01	3.64	0.01
BHB-LDH	20.2	2334.17	0.009	1
BHB-LKR	20.2	2334.17	0.009	1

BHB-LL	2.99	0.72	4.13	0.0015
BHB-MUS	3.68	1.01	3.64	0.01
BHB-PAG	20.2	2334.17	0.009	1
BHB-POC	1.38	0.35	3.92	0.0035
BHB-RH	2.30	0.52	4.39	0.0005
CL-LDH	16.51	2334.17	0.007	1
CL-LKR	16.51	2334.17	0.007	1
CL-LL	-0.69	1.22	-0.56	0.99
CL-MUS	0	1.41	0	1
CL-PAG	16.51	2334.17	0.007	1
CL-POC	-2.30	1.04	-2.19	0.45
CL-RH	-1.38	1.11	-1.24	0.96
LDH-LKR	0	3301.02	0	1
LDH-LL	-17.20	2334.17	-0.007	1
LDH-PMUS	-16.51	2334.17	-0.007	1
LDH-PAG	0	3301.02	0	1
LDH-POC	-18.81	2334.17	-0.008	1
LDH-RH	-17.89	2334.17	-0.008	1
LKR-LL	-17.20	2334.17	-0.007	1
LKR-MUS	-16.51	2334.17	-0.007	1
LKR-PAG	0	3301.02	0	1
LKR-POC	-18.81	2334.17	-0.008	1
LKR-RH	-17.89	2334.17	-0.008	1
LL-MUS	0.69	1.22	0.56	0.99
LL-PAG	17.20	2334.17	0.007	1

LL-POC	-1.60	0.77	-2.07	0.54
LL-RH	-0.69	0.86	-0.8	0.99
MUS-PAG	16.51	2334.17	0.007	1
MUS-POC	-2.30	1.04	-2.19	0.45
MUS-RH	-1.38	1.11	-1.24	0.96
PAG-POC	-18.81	2334.17	-0.008	1
PAG-RH	-17.89	2334.17	-0.008	1
POC-RH	0.91	0.59	1.54	0.87

Table A5. Pairwise comparisons of abundance of *H. diversicolor* between sites: Bar Road, Saint Andrews, Charlotte County (BR); Pagan Point, Saint Andrews, Charlotte County (PP); Letang (Limekiln Rd.), Charlotte County (LR); Beaver Harbour Basin, Charlotte County (BH); Red Head Road, Charlotte County (RH); Pocologan, Charlotte County (POC); Maces Bay (Cassidy Ln), NB (CL); Little Dipper Harbour, NB (LDH); Little Lepreau, NB (LL) and Musquash, Saint John County (MUS)

Site comparison	**Estimate**	**SE**	**z.ratio**	**P-value**
BAR-BHB	0	3301.02	-0.009	1
BAR-CL	-21.075	2334.17	0	1
BAR-LDH	0	3301.02	0	1
BAR-LKR	0	3301.02	0	1
BAR-LL	0	3301.02	-0.007	1
BAR-MUS	-16.51	2334.17	0	1
BAR-PAG	0	3301.02	-0.009	1
BAR-POC	-20.03	2334.17	-0.008	1
BAR-RH	-19.07	2334.17	-0.009	1
BHB-CL	-21.07	2334.17	0	1

BHB-LDH	0	3301.02	0	1
BHB-LKR	0	3301.02	0	1
BHB-LL	0	3302.02	-0.007	1
BHB-MUS	-16.51	2334.17	0	1
BHB-PAG	0	3302.02	-0.009	1
BHB-POC	-20.03	2334.17	-0.008	1
BHB-RH	-19.07	2334.17	0.009	1
CL-LDH	21.07	2334.17	0.009	1
CL-LKR	21.07	2334.17	0.009	1
CL-LL	21.07	2334.17	4.54	1
CL-MUS	4.56	1	0.009	0.0002
CL-PAG	21.07	2334.17	5.20	1
CL-POC	1.03	0.2	6.76	<0.0001
CL-RH	1.99	0.29	0	<0.0001
LDH-LKR	0	3301.02	0	1
LDH-LL	0	3301.02	-0.007	1
LDH-PMUS	-16.51	2334.17	0	1
LDH-PAG	0	3301.02	-0.009	1
LDH-POC	-20.03	2334.17	-0.008	1
LDH-RH	-19.07	2334.17	0	1
LKR-LL	0	3301.02	-0.007	1
LKR-MUS	-16.51	2334.17	0	1
LKR-PAG	0	3301.02	-0.009	1
LKR-POC	-20.03	2334.17	-0.008	1
LKR-RH	-19.07	2334.17	-0.007	1

LL-MUS	-16.51	2334.17	0	1
LL-PAG	0	3301.02	-0.009	1
LL-POC	-20.03	2334.17	-0.008	1
LL-RH	-19.07	2334.17	0.007	1
MUS-PAG	16.51	2334.17	-3.47	1
MUS-POC	-3.52	1.01	-2.47	0.01
MUS-RH	-2.56	1.038	-0.009	0.28
PAG-POC	-20.03	2334.17	-0.008	1
PAG-RH	-19.07	2334.17	2.94	1
POC-RH	0.96	0.32	2.94	0.09