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Sediment Geochemistry Influences Infaunal Invertebrate Community Composition and Population Abundances

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Abstract

Infaunal invertebrate communities are structured by various factors, including predation, resource availability, and environmental conditions. Given that these invertebrates live within sediment, it is not surprising that sediment properties play a critical role in many infaunal behaviours. When models explaining spatial and temporal variation in infaunal community composition are constructed using physical, biophysical, environmental, and sediment properties (salinity, detrital cover, elevation, particle size distribution, organic and water content, redox conditions, and penetrability), a considerable portion of the variation in the data is typically unaccounted for. This suggests that we do not fully understand all the variables that influence infaunal invertebrate communities. One suite of under-explored variables is the elemental composition/concentration of the sediments themselves. As such, we evaluated if sediment geochemistry improved model performance of the spatial variation in infaunal invertebrate communities on three intertidal mudflats in northern British Columbia, Canada. We observed that models including geochemistry data outperformed models that only included physical, biophysical, and environmental properties. Our results therefore suggest that some of the observed, and previously unaccounted for spatial variation in infaunal community composition may be a product of variation in sediment geochemistry. As such, sediment geochemistry should be accounted for when studying infaunal communities and assessing human impacts upon intertidal systems.

Key Words: Conservation, Estuary, Modelling, Restoration, Skeena, Infauna, Sediment Geochemistry

Introduction

Located at the interface between the land and the sea, intertidal ecosystems exist within a world of extremes. Oscillating between exposure and inundation, hot and cold, safety and danger, the intertidal is home to resilient and dynamic biological communities (Ferraro and Cole 2012; Musetta-Lambert et al. 2015; Delgado et al. 2018). Far from a uniform ecosystem, the intertidal is a mosaic of marshes (Virgin et al. 2020), rocky shores (Menge et al. 1997), and expanses of soft sediment, such as sandy beaches and mudflats (Barbeau et al. 2009). In coastal ecosystems, infaunal (animals that live within the sediment) are often used to study or identify disturbances (Fukuyama et al. 2014; Drylie et al. 2020; Gerwing et al. 2022a). For instance, biodiversity and total abundance of infauna (Sherman and Coull 1980; Campbell et al. 2019b) can be used to identify and study disturbances; however, infauna can respond to a disturbance in a variety of ways. For instance, amphipods, cumacea, and small bivalves are sensitive to disturbances, decreasing in abundances with disturbances (Sánchez-Moyano and García-Gómez 1998; Gerwing et al. 2022b). Conversely, Oligochaeta (Cowie et al. 2000), Nematoda (Mazzola et al. 2000), and *Capitella* species complex (Pearson and Rosenberg 1978; Gerwing et al. 2022b) are tolerant of disturbances, and can survive, or thrive in disturbed systems. Therefore, studying the population and community dynamics of these intertidal invertebrates is useful to advance the development of general ecological theories (Underwood and Fairweather 1989; Hamilton et al. 2006) and to undertake applied research, such as elucidating human impacts or the effectiveness of restoration strategies (Pearson and Rosenberg 1978; Borja et al. 2008).

Various factors influence the structure of infaunal invertebrate communities, including predation (Floyd and Williams 2004), resource availability (Hamilton et al. 2006), and environmental factors such as salinity, weather, and climate (Ghasemi et al. 2014; Gerwing et al.

2015b). While all of these variables are important, given the intimate nature of the relationship between infauna and the sediment they inhabit, it is not surprising that sediment properties have been observed to play a critical role in most infauna behaviours, including locomotion, foraging, reproduction, and larval settlement (Ólafsson et al. 1994; Lu and Grant 2008; Gerwing et al. 2020a). More specifically, sediment properties such as particle size distribution, water content, organic matter content, redox state, and sediment penetrability/consistency have all been observed to play important roles in shaping the composition of infaunal communities, by influencing infauna behaviour, survival, and physiology (Diaz and Trefry 2006; Valdemarsen et al. 2010; Pilditch et al. 2015a; Gerwing et al. 2018b; Gerwing et al. 2020a). These relationships are far from unidirectional, as infauna can greatly modify their sedimentary environment (De Backer et al. 2011; Quintana et al. 2013; Sizmur et al. 2013; Gerwing et al. 2017b).

Despite a wealth of information on the relationships between sediment properties/environmental conditions and infaunal communities, models constructed from the variables listed in the previous paragraph that predict the spatiotemporal variation in an infaunal community often leave a portion of the variation in the data (20-97%) unaccounted for (Chapman et al. 1987; Thrush et al. 2003; Dashtgard et al. 2014; Gerwing et al. 2015b; Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al. 2020a). While no model is perfectly representative of the process it is simulating, this unaccounted variation suggests that we do not fully understand all the factors that influence the structure of infaunal invertebrate communities. One suite of potentially important, but under-explored, variables are those related to sediment geochemistry (concentration of elements such as Hg, Mn, Ti, etc.). Especially since the abundance/concentration of some elements in intertidal sediments have been observed to influence infaunal invertebrate community composition and population size (Chapman et al. 1987; Waldock et al. 1999; Sizmur et al. 2019).

Elements that can negatively affect intertidal invertebrate communities are referred to as potentially toxic elements (PTEs). While PTEs are naturally occurring, human activities may elevate concentrations to levels that can induce deleterious impacts upon the physiology, behaviour, and survival of flora and fauna (Martinez-Colon et al. 2009; Pourret and Bollinger 2018; Sizmur et al. 2019). The concentration and availability of PTEs have generated substantial ecological insight in theoretical and applied settings (Chapman et al. 1987; Mermillod-Blondin and Rosenberg 2006; Spencer and Harvey 2012). However, interactions between invertebrates and sediment geochemistry are often studied in the context of contamination or pollution when the concentrations present are many times greater than ambient background values (Chapman et al. 1987; Yunker et al. 2011; Amoozadeh et al. 2014).

Another important group of elements found in intertidal sediments (which overlap with PTEs) are essential elements. Essential elements are those that are required in specific stochiometric ratios for organisms to complete their life cycle (Karimi and Folt 2006; Bradshaw et al. 2012). Previous investigations have focused upon the interaction between specific infaunal species and the presence or availability of a few, albeit important, elements (Christensen et al. 2000; Teal et al. 2013; Kalman et al. 2014). What is currently lacking is a holistic understanding of how sediment geochemistry, influences entire infaunal communities (Sizmur et al. 2019; Eccles et al. 2020), and if the geochemical composition of sediments plays a greater role than other sediment parameters in structuring infaunal communities.

To better understand how sediment geochemistry influences infaunal communities, we quantified whether adding sediment geochemistry data (elemental concentrations) to models containing traditionally studied sediment and environmental variables (salinity, detritus cover, distance from shore, particle size distribution, organic and water content, redox conditions, and penetrability) improved their performance when modelling infaunal community composition and population abundances. We then explored in more detail how specific elements were associated with the observed variation in specific members of an infaunal invertebrate community. A better understanding of how sediment geochemistry influences infaunal community species composition and abundances will expand our theoretical knowledge of the processes that structure these communities. Such information will also inform interpretations of human impacts on intertidal systems.

Methods

Study Sites

Our study focused on three intertidal mudflats surrounding the Skeena River estuary in northern British Columbia, Canada (Figure 1; ~3m tidal amplitude): Cassiar Cannery (CC), Wolfe Cove (WC), and Tyee Banks (TB). Cassiar Cannery (N54˚ 10’ 40.4, W130˚ 10’ 40.4) is a mudflat adjacent to a former salmon cannery that closed in 1983 and is now an ecotourism lodge. Wolfe Cove (N54˚ 14’ 33.0, W130˚ 17’ 34.5) is a mudflat located approximately 1 km from a decommissioned papermill. The papermill was closed in 2001, ceasing all operations and discharge (Yunker et al. 2011; Sizmur et al. 2019). Tyee Banks (N54˚ 11’ 59.1, W129˚ 57’ 36.7) is a large intertidal mudflat 20 km upstream of the mouth of the Skeena River, that previously had a small-scale sawmill operating and accumulations of sawdust and woodchips are still present in the upper intertidal sediment. All three sites have a diverse and abundant infaunal community (Campbell et al. 2020), with the infaunal community dominated by Cumacea (primarily *Nippoleucon hinumensis* with *Cumella vulgaris* observed less frequently), Polychaetes

(Families Phyllodocidae [*Eteone californica*], Capitellidae [*Capitella* Species Complex], and Spionidae [*Pygospio elegans*]), Oligochaetes (*Paranais litoralis*), Nematodes, Copepods (order Harpacticoida), Amphipods (*Americorophium salmonis*), and the bivalve *Macoma balthica* (Gerwing et al. 2017a; Campbell et al. 2020) (Supplemental Table S1). Average volume weighted sediment particle size varied from 60-180 µm, organic matter content varied from 2.5-4.5%, and sediment water content from 28-37% (Campbell et al. 2020). No evidence of PTE concentrations above naturally occurring levels was observed in the top 20 cm of sediment (Sizmur et al. 2019). Observed elemental concentrations and all abiotic variables are detailed in Supplemental Table S2. More details on these sites are available in Sizmur et al. (2019) and Campbell et al. (2020).

Sampling Scheme

At each mudflat, transects were established running from the landward start of the mudflat to the low water line (five transects per site, separated by ~25m and 60-200m long). Transects were stratified into zones based on distance from shore (near, middle, and far). Within each zone, one sampling location was randomly selected from which all data types, detailed below, were collected (n = 3 per transect, 15 per site; 45 overall). Samples were collected July 13-25, 2017, on one of the lowest low tides of the year. More details of the sampling scheme can be found in Campbell et al. (2020).

Infauna, Sediment, and Environmental Parameter Sampling

At each sampling location, a 1 m^2 plot was established and infauna were collected with a corer 10 cm in length, and 7 cm in diameter. (Campbell et al. 2020). A pit (20 cm long, by 20 cm wide, by 20 cm deep) was also dug in the plot where the core was taken to sample and identify larger or more mobile specimens *in situ* (Campbell et al. 2019b) that may have been missed by the infaunal core. Sediment from the core was passed through a 250 μm sieve, and the infauna retained by the sieve were stored in vials of 95 % ethanol (Campbell et al. 2020). Specimens were identified to the lowest possible taxonomic unit, as follows: cumaceans, amphipods, tanaids, polychaetes, nemerteans and bivalves were identified to species; chironomids (larvae) to family; copepods to order; ostracods to class; and nematodes to phylum (Campbell et al. 2020; Gerwing et al. 2020b). Observed abundances from the pit and cores were combined, making note of the processed sediment from each method (Gerwing et al. 2022a), and converted to density per m^2.

At each sampling location, sediment penetrability was assessed by dropping a metal weight (15 cm long, 1.9 cm diameter, 330 g) from a height of 0.75 m above the sediment and measuring how far it penetrated into the sediment (Meadows et al. 1998; Gerwing et al. 2020a). Penetrability is an integrative variable that reflects the overall *in situ* conditions experienced by biota. Increased penetrability indicates finer-grained sediment with high water content, and fewer rocks or shell hash present in or on the sediment. Sediment characterised by low penetrability is indicative of larger-grained sediment with low water content and with more rocks or shell hash present (Gerwing et al. 2020a). A sediment core (4.5 cm diameter, 5 cm depth) was collected from each sampling location. From this core, the top 1 cm was processed to determine sediment water content (mass lost by drying at 110 °C for 12 h), organic matter content (mass lost by ashing at 550 °C for 4 h) and volume-weighted average particle size (Malvern Mastersizer 2000). More details of these processes can be found in Campbell et al. (2020). While in the field, the void created in the sediment from the collection of the infaunal core was used to determine the depth to the apparent redox potential discontinuity, aRPD (Gerwing et al. 2013). aRPD depth is a relative measure of sediment porewater dissolved oxygen and redox conditions. Sediment with a deeper aRPD has more available dissolved oxygen, and the sediment is more oxidized, or less reduced, than sediment with a shallower aRPD depth (Gerwing et al. 2015a; Gerwing et al. 2018b). We refer to these variables as physical variables.

The proportion of each 1 m^2 plots covered in woody debris, as well as deposited algae and eelgrass (*Zostera* spp.) debris was also quantified visually, as this debris can create hypoxic conditions and smother infauna. Such debris are commonly observed in the area. No eelgrass detritus was observed at these sites during this period; therefore, eelgrass cover was not used in any analyses. These variables are referred to as biophysical variables. Salinity was measured at each transect in each tidal flat on each sampling trip with a YSI multimeter in the water approximately 1 cm above the sediment surface at high tide (n = 5). Finally, relative distance of each plot from the start of the mudflat (transition of saltmarsh, bedrock, or sandy beaches to mud (see Gerwing et al. (2016)) was included for each plot, as a proxy for intertidal elevation or duration of inundation. These variables are referred to as environmental variables.

Sediment Geochemistry Sampling

At each sample location, sediment samples of the top 5 cm were collected from each site using polycarbonate cores (5 cm diameter, 20 cm length). Samples were dried at 40 ˚C, digested in reverse aqua regia following US EPA Method 3051A, and the concentration of elements (Al, As, Ca, Cd, Co, Cr, Cu, Fe, K, Mg, Mn, Mo, Na, Ni, P, Pb, S, Sr, Ti, and Zn; a mixture of elements that are broadly representative of the lithophile, siderophile, and chalcophile geochemical groups (Goldschmidt 1937)). determined by ICP-OES (Inductively Coupled Plasma Optical Emission Spectroscopy) or ICP-MS (Inductively Coupled Plasma Mass Spectrometry). The total concentration of Hg in sediments was determined using thermal degradation–gold amalgamation atomic absorbance spectroscopy as outlined in EPA Method 7473 using a Nippon

MA-3000 analyser (Sizmur et al. 2019). These elemental variables are then referred to as geochemical variables.

Data Analysis

Prior to analysis, we assessed possible correlations between all pairs of covariates by calculating univariate Pearson's correlation coefficients. We used a threshold of 0.95 (Clarke and Ainsworth 1993) for variables too correlated to be considered independent. Since the highest correlation coefficient observed was 0.76, all variables were included in our models.

Data Visualization

Statistical analyses (sequential analysis procedures are detailed in Supplemental Figure S1) were conducted in PRIMER with the PERMANOVA add-on (Anderson et al. 2008; Clarke and Gorley 2015). First, non-metric multidimensional scaling (nMDS) plots were used to visualize variation in infaunal communities (Supplemental Table S1) and sediment geochemistry as well as environmental parameters (Supplemental Table S2) between sites (100 restarts; infaunal community resemblance matrix calculated using Brays-Curtis similarities on fourth root transformed density data, and geochemical or environmental resemblance matrix calculated using Euclidean distances after square root transforming Sr to correct for a skewed distribution). Vector overlays were used to identify which infauna and elements had a Pearson's univariate correlation coefficient of 0.2 or greater (Clarke 1993).

Assessing Model Performance with Inclusion of Sediment Geochemistry

To determine if models of the infaunal community (all species) that included sediment geochemistry performed better than models that included other traditionally measured physical, biophysical, and environmental parameters (distance from shore, salinity, algae, eelgrass, and woody debris cover, sediment water content, organic matter content, mean particle size, aRPD depth, and penetrability) a distance based linear model (DISTLM) was created using the BEST routine (9999 permutations) was used. Infaunal data were fourth root transformed, while Sr was square root transformed, and aRPD depth, water content, and mean particle size were fourth root transformed to correct for skewed distributions. All physical, biophysical, and environmental variables were normalized; however, variation exists in the precision of our variables. For instance, the precision of visual estimates of detrital cover or organic matter content analyzed via combustion is lower than that obtained from the spectrometry used to elucidate elemental concentrations. We evaluated candidate models using the Information Theoretic Model Selection Approach (Burnham and Anderson 2001; Burnham and Anderson 2002). This approach utilizes multiple lines of evidence to select the “top” performing or “best” model from amongst a series of candidate models designed a priori. All possible permutations of physical, biophysical, and environmental variables were assessed. Candidate top-ranked models were selected by calculating Akaike Information Criterion, corrected for small sample sizes (AICc) values. Models within 2 AICc units of each other were considered to be equivalent (Burnham and Anderson 2001; Burnham and Anderson 2002). Model performance was further assessed using the R^2 value, which denotes the proportion of explained variation for the model (Anderson et al. 2008). R^2 values were contrasted between models only containing traditional physical, biophysical, and environmental parameters, those only containing elements, and those containing all variables.

Exploring Relationships Between Elements and the Infaunal Community

While DISTLMs are effective at comparing models, they are not able to determine the relative importance of variables included in a model (Supplemental Figure S1). As such, a permutational multivariate analysis of covariance (PERMANCOVA; 9999 permutations) was also used to quantify the relationship between the infaunal community and physical, biophysical, environmental, and geochemical variables (Gerwing et al. 2016). The multivariate response was a resemblance matrix of the densities of the infaunal community, calculated using Bray-Curtis similarity. Taxa densities were fourth root transformed to better equalize the influence of abundant and rare species on the outcome of the analysis. Within the PERMANCOVA, site (three levels; fixed factor), and transect nested within site (transect(site); five per site; random factor) were included. Geochemical, as well as physical, biophysical, and environmental variables were included as covariates. As part of the PERMANCOVA, we quantified components of variation, the proportion of the multivariate variation accounted for by each independent variable (Searle et al. 1992; Anderson et al. 2008; Gerwing et al. 2016). An α of 0.05 was used to determine statistical significance for all analyses (Beninger et al. 2012). Elements identified as accounting for a statistically significant proportion of the variation in the infaunal community were retained for downstream analysis (Pearson's univariate correlation assessment).

As we were primarily interested in differences between sites, to reduce the number of taxa included in downstream analyses (Supplemental Figure S1), Similarity Percentages Analyses (SIMPER) were then used to determine which infaunal species were responsible for the observed variation between sites (Clarke 1993). Only species that accounted for $\geq$5 % of the dissimilarity between sites were retained for the next analytical step, as these taxa are the drivers of the observed variation in the infaunal community between sites. Finally, Pearson's univariate correlation coefficient was used to assess if the elements and infaunal species identified above had a positive or negative relationship (Gerwing et al. 2016; Campbell et al. 2020).

Results

Infaunal community composition and sediment parameters varied between sites, with all variables tending to cluster by site (Figures 2 and 3; Supplemental Tables S1, 2 and 3). More details on the biotic and abiotic parameters can be found in Sizmur et al. (2019) and Campbell et al. (2020).

Assessing Model Performance with Inclusion of Sediment Geochemistry Data

Models containing only physical (penetrability, aRPD depth, water/organic matter content, and mean particle size), environmental variables (distance from shore, salinity), or biophysical variables (detrital cover), performed the worst, explaining only 0.01-0.50 (Supplemental Table S4) of the variation in the model (R^2). Models that included only sediment geochemistry performed moderately well (R^2: 0.38-0.55), while models including all variables (R^2: 0.40-0.60) performed the best (Supplemental Table S4).

Exploring Relationships Between Sediment Properties and the Infaunal Community

The PERMANCOVA (Table 1) identified that a mixture of environmental variables (distance from shore, and salinity) and elements (K, Mn, P, SR, and Ti) were significantly correlated to the observed variation in the infaunal community composition. No physical or biophysical variables were statistically significant in this model. Environmental variables accounted for 5% of this variation, while geochemistry accounted for 65%. The strongest relationship was observed with Ti, with this single element accounting for 33% of the variation in the infaunal community composition. Differences in the infaunal community between sites and transects were not statistically significant, but the infaunal community varied between plots (6%).

With regards to differences between sites, taxa that accounted for ≥ 5% of the dissimilarity in the SIMPER analysis (Supplemental Table S3), and were thus retained for downstream analyses, included: *Americorophium salmonis*, *Cumella vulgaris*, *Nippoleucon hinumensis*, *Eteone californica*, *Capitella* Species Complex, *Fabricia stellaris*, *Pygospio elegans*, *Macoma balthica*, Harpacticoida, Ostracoda, and Nematoda. Table 2 summarizes the Pearson's correlation coefficients between the concentrations of individual elements measured in sediments and the infaunal community composition. In general, the infaunal community had a complex relationship with sediment geochemistry, with some taxa having a positive correlation (increasing population density with increasing element concentration) with some elements, and a negative correlation with others (decreasing population density with increasing element concentration). However, Ti and K had a strong negative correlation with most taxa.

Discussion

To create models explaining infaunal community composition, the relationship between the intertidal invertebrate communities of three intertidal mudflats in the Skeena River estuary and sediment/environmental properties was explored.

Assessing Model Performance with Inclusion of Sediment Geochemistry

Inclusion of sediment geochemistry into models explaining the infaunal community composition produced models that preformed the best. These models were either comprised exclusively of geochemical data, or a combination of geochemistry, physical, biophysical, and environmental variables. Previous studies reporting models to explain the observed spatiotemporal variation in the infaunal community using physical, biophysical, and environmental variables, often leave a portion of the variation (20-97%) unaccounted for (Thrush et al. 2003; Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al. 2020a; Norris 2021; Norris et al. 2022). However, our results indicate that including sediment geochemistry into such models, alongside sediment and environmental variables, will produce better preforming models. Further research exploring these relationships, as well as the interaction between sediment geochemistry and other physical/environmental properties, will offer greater insight into how the elemental composition of sediments influences infaunal community composition and dynamics. Note, R^2 values can be sensitive to overfitting, with models with a higher number of terms performing better, in some situations (Anderson et al. 2008). However, this does not seem to be the case in our data, as models with more terms do not consistently perform better than more parsimonious models (Supplemental Table S4). Further, AICc values were also used to evaluate model performance, and AICc values penalize for every term included. As such, AICc values also suggest that our models do not suffer from overfitting.

Exploring Relationships Between Individual Variables and the Infaunal Community

The infaunal community composition was statistically correlated (Table 1) with environmental variables (5%; distance from shore, and salinity) as well as sediment geochemistry (65%). Physical, and biophysical variables were not statistically correlated to observed variation within the infaunal community. Interestingly, when similar analyses, excluding sediment geochemistry, were conducted upon similar communities along Canada's Pacific and Atlantic coasts (Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al. Submitted), physical, and biophysical parameters were significantly related to the infaunal community and accounted for 9-11% of the observed. As discussed above, our findings here may suggest that when sediment geochemistry is included in models, traditionally studied physical and biophysical parameters (particle size, organic matter and water content penetrability, and aRPD depth) may not be as important in explaining the structure of an infaunal community. However, sediment variables exert a known influence upon infaunal communities, (Diaz and Trefry 2006; Valdemarsen et al. 2010; Pilditch et al. 2015a; Gerwing et al. 2018b; Gerwing et al. 2020a), and it seems likely that sediment biophysical and geochemical properties both influence infaunal community composition and population dynamics. More research is required to better understand the relative importance of each variable, as well as how and why this varies spatially and temporally.

In our analysis the site term was non-significant and accounted for none of the infaunal community variation, while the transect term was also not significant, and the plot term only accounted for 8% of the variation (Table 1). The plot and transect terms are likely a product of local hydrology and delivery of larvae, intra and interspecific interactions, as well as post-settlement dispersal and mortality (Flach and Beukema 1995; Bringloe et al. 2013; Drolet et al. 2013; Pilditch et al. 2015b; Gerwing et al. 2016; Sizmur et al. 2019; Norris et al. 2022). The lack of statistical differences observed between sites, is in stark contrast to the apparent site level clustering of infaunal communities observed between sites in Figure 2 (nMDS plot). The results of similar investigations, that did not include elemental data, reported that the site term accounted for 32-35% of the infaunal community variation, and the plot term 33-37% (Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al. Submitted). These authors hypothesized that the observed variation in the infaunal community associated with this site term site term was likely a product of processes such as larval supply (Weersing and Toonen 2009; Einfeldt and Addison 2013), post-settlement dispersal and mortality (Pilditch et al. 2015b), unmeasured site variables such as hydrology, elemental concentrations (Sizmur et al. 2019), and exposure to waves/tides (Williams et al. 2013; Gerwing et al. 2015b; Rubin et al. 2017), or disturbance and human development history (Gerwing et al. 2017c; Gerwing et al. 2018a; Campbell et al. 2019a; Cox et al. 2019). However, in our study, when sediment geochemistry was included in models of the infaunal community, the variation attributed to the site and plot terms decreased and in the case of our site term, became statistically insignificant. When taken together, these results suggest that some, or even most, of the previously observed variation between sites and plots in infaunal communities (as seen in Figure 2) may not be purely spatial in nature, nor the product of unmeasured or unknown variables that vary at these spatial scales. Instead, this infaunal community variation previously accounted for by spatial terms such as site or plot, may be the product of variation in sediment geochemistry.

Of the elements identified as of interest in the PERMANCOVA (Table 1), only K (17%), Mn (2%), P (4%), Sr (6%), and Ti (36%) accounted for a significant portion of the variation in the infaunal community. Of these elements, K, Mn, and P are essential elements for life whereas Sr and Ti are not known to play any biological role. While K and P are elements that are essential for survival, excess concentrations can have deleterious effects (Yool et al. 1986; Tyrrell 1999; Nath et al. 2011; Chiarelli and Roccheri 2014). Mn and Sr are common contaminants in marine ecosystems, with known deleterious effects on many species (Mejía-Saavedra et al. 2005; Blaise et al. 2008; Pinsino et al. 2012; Whiteway et al. 2014).

Sediment geochemistry can also be used to identify the provenance of sediments (Zhang et al. 2014) and may indicate that the provenance of the sediment in an intertidal mudflat influences the composition of the infaunal community. Whereas K, P, and to a certain extent Mn, may be applied as fertilisers within the Skeena watershed and their enrichment representative of sediments eroded from farmland, Ti (the element responsible for the greatest variation in infaunal community composition) is a lithogenic element that has previously been found to correlate positively with grain size (Bábek et al. 2015). It may therefore be the case that Ti concentrations are a sensitive indicator of sediment grain size, which is already known to be a property that shapes the composition of benthic infaunal communities (Coblentz et al. 2015). Interestingly, when Ti and particle size were included in our analyses (Table 1) Ti was significantly correlated with the infaunal community, while particle size was not. Nor was Ti correlated with sediment particle size in our dataset (Pearson univariate correlation; n = 45, p = 0.13). Conversely, Ti can also have acute and chronic deleterious effects upon invertebrates (Das et al. 2013). Finally, all of our measured elements and environmental variables could be correlated with another, unmeasured variable, that is driving the observed infaunal change. For instance, TB was characterized by lower infaunal abundances and higher concentrations of Ti, K and S, lower concentrations of Mn, as well as lower salinity than the other sites. It is possible that an unmeasured variable resulted in this variation, andmore research is required to better understand these relationships. Specifically, future studies should not only include more study sites, spanning a broader range of environmental conditions, but also include more samples per site to increase analytical resolution.

At the level of the infaunal invertebrate populations and individual elements, a complex relationship was detected between sediment geochemistry and infaunal species, with a mixture of positive and negative correlations observed (Table 2). Many of these elements are known to have positive and negative impacts upon infaunal species (Smith 1984; Vitousek and Howarth 1991; Tyrrell 1999; Little et al. 2017), but these impacts can vary between species and at different concentrations (Pourret and Bollinger 2018; Sizmur et al. 2019; Eccles et al. 2020). Given the correlational nature of the data presented in Table 2, we will not attempt to postulate causal mechanisms. Especially as *in situ* context, such as information regarding nuanced ecological interactions between species and covariates, is lacking. For instance, an observed positive correlation could suggest that increasing concentrations of a given element induces immigration into an area, enhances reproductive output, or has positive impacts upon survival and physiological processes. Conversely, the element itself may have negative impacts upon a species, however, it may have greater effects on a competitor, leading to competitive release. As such, instead of postulating causal relationships, we suggest that more research incorporating more study sites and more samples per site is required to untangle the complicated positive and negative relationships observed in our study, between infaunal invertebrate community composition and sediment geochemistry.

Conclusions

Focusing on three intertidal mudflats in the Skeena estuary, we observed complex relationships between sediment geochemistry and the infaunal community composition. Despite these complicated relationships, combining sediment geochemistry data with traditionally studied physical, biophysical and environmental variables (salinity, distance from shore, detrital cover, penetrability, aRPD depth, organic matter/water content, mean particle size) produced models that outperformed models that contained only traditional sediment and environmental parameters. Our results suggest that some of the observed, and previously unaccounted for, spatial variation (between sites and plots) in infaunal community composition may be a product of variation in sediment geochemistry. As such, *in situ* sediment chemical composition should be integrated into how we study infaunal communities, as well as how we interpret human impacts upon intertidal systems, and assess the success of restoration and conservation projects.

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Declarations

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Conflict of Interest

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval

No animal welfare approval was required as we were working with common invertebrates.

Data/Code Availability

Available upon reasonable request

Authors' Contribution

TGG and TM designed the study, collected data, and wrote the paper. KD and LC helped collect data and write the paper. AMAG, MMD, JK, HMT helped analyze the data and write the paper. JK and SC helped analyze samples and write the paper. FJ and SED helped design the study, provided supervision, and write the paper.

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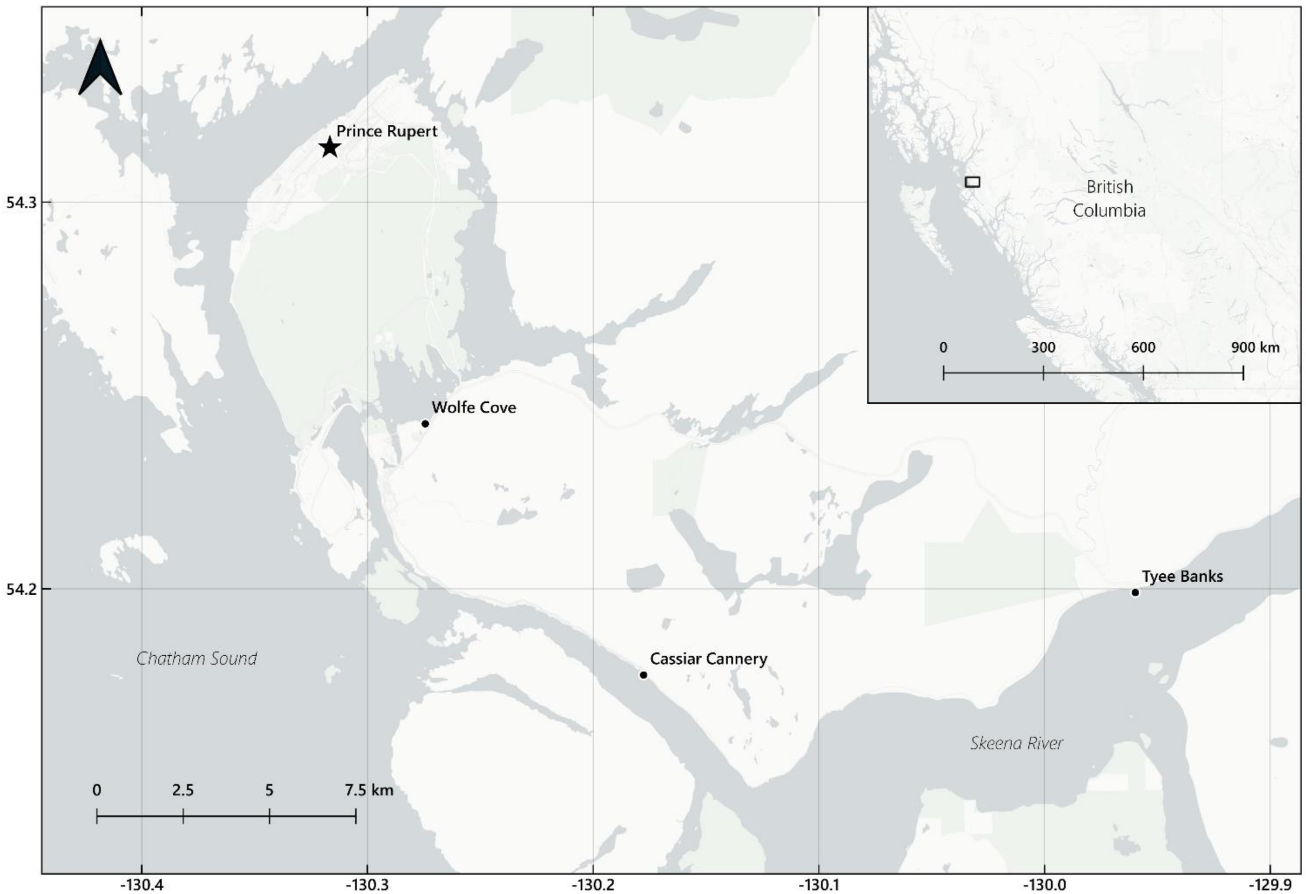
Figure 1: Location of three intertidal mudflat study sites in the Skeena Estuary, northern British Columbia, Canada. WC: Wolfe Cove (N54˚ 14’ 33.0, W130˚ 17’ 34.5). CC: Cassiar Cannery (N54˚ 10’ 40.4, W130˚ 10’ 40.4). TB: Tyee Banks (N54˚ 11’ 59.1, W129˚ 57’ 36.7).



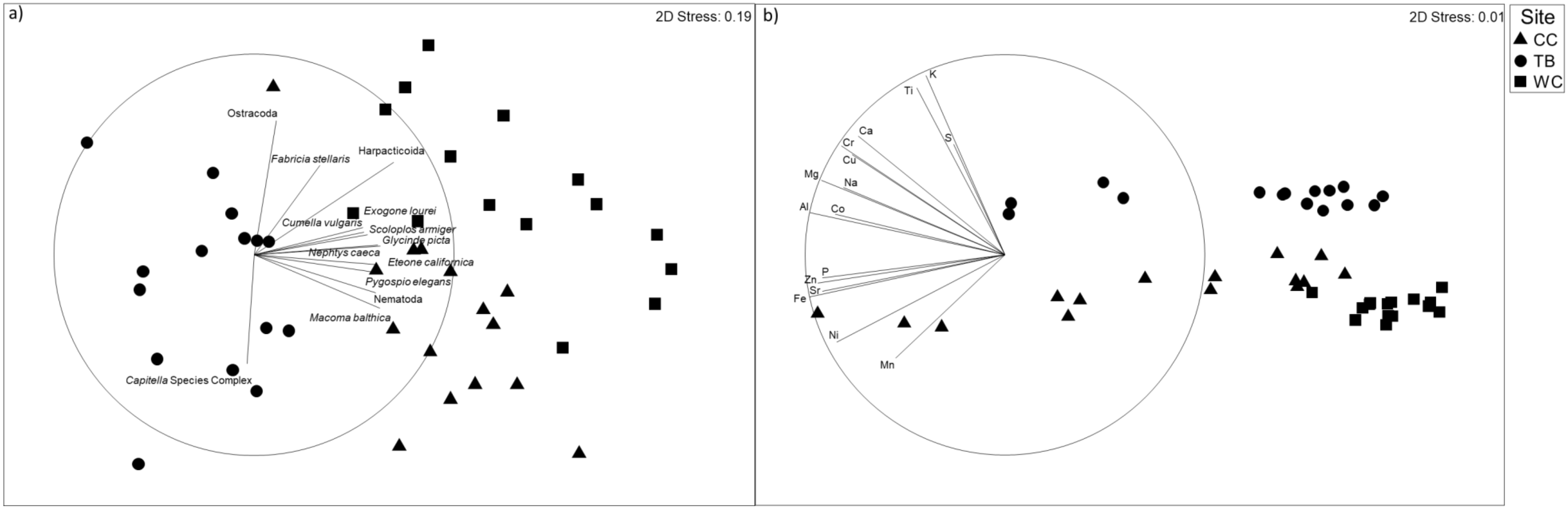


Figure 2: Non-metric multidimensional scaling (nMDS) plots exploring the variation in the infaunal community (a) and sediment geochemistry (b) at three intertidal mudflats near the Skeena Estuary in northern British Columbia, Canada. Vector overlays are overlain, and longer lines indicate greater values associated with that species or element along that axis. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove.

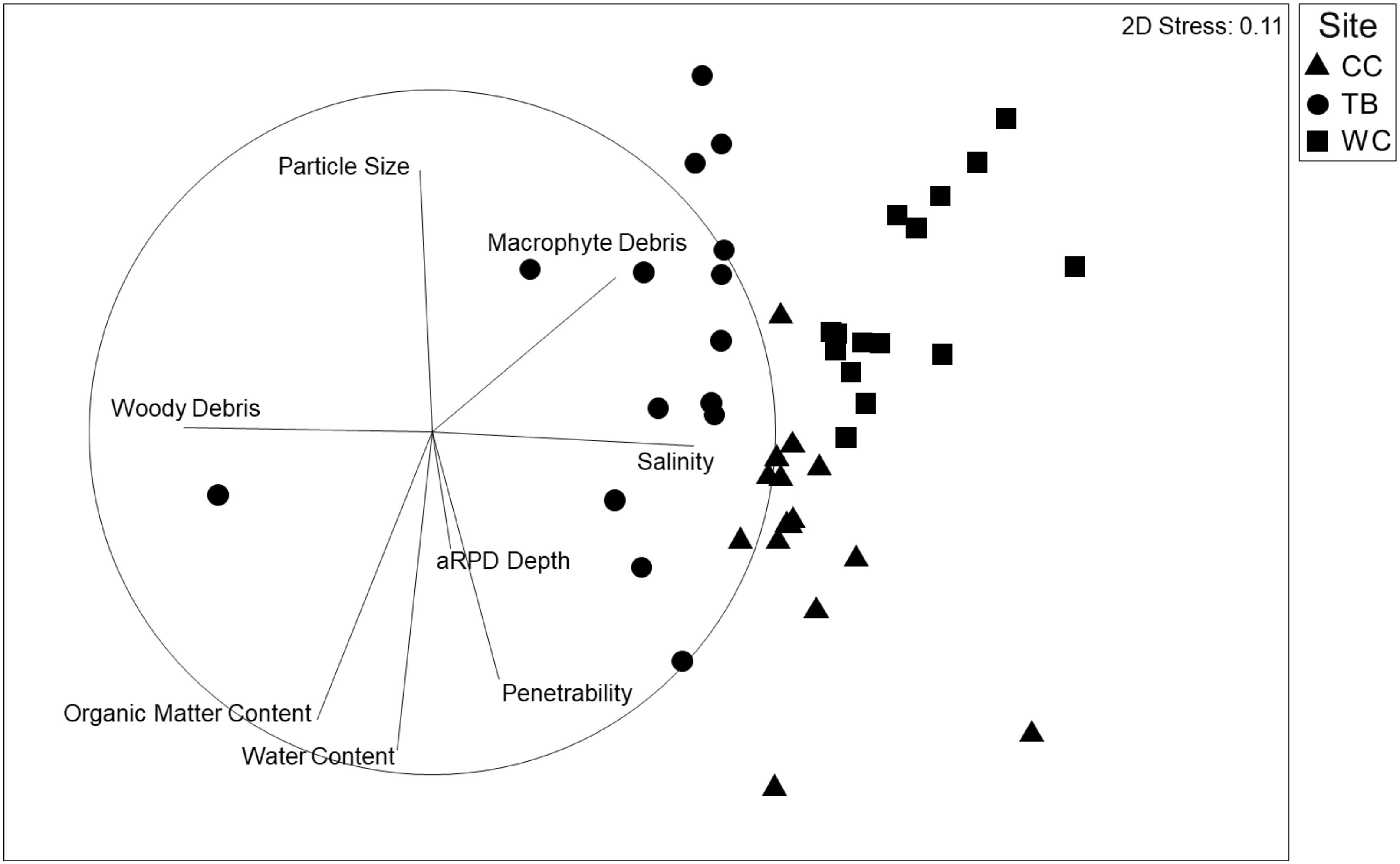


Figure 3: Non-metric multidimensional scaling (nMDS) plots exploring the variation in environmental parameters at three intertidal mudflats near the Skeena Estuary in northern British Columbia, Canada. Vector overlays are overlain, and longer lines indicate greater values associated with that paramater along that axis. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove.

Table 1: Permutational multivariate analysis of covariance (PERMANCOVA) results assessing the relative importance of sediment parameters and geochemical elements in shaping infaunal communities on tidal flats in northern British Columbia in 2017. Significant sources of variation are in bold (α = 0.05).

Source	df	MS	Pseudo-F	Unique Permutations	*p*	Variance Components (%)
Salinity	**1**	**13469.00**	**10.20**	**9929**	**0.0001**	**4.27**
Wood Cover	1	81.75	0.18	9955	0.86	0.00
Macrophyte cover	1	1556.60	2.01	9944	0.10	0.40
Distance from Shore	**1**	**2027.00**	**5.13**	**9963**	**0.008**	**0.82**
Sediment Particle Size	1	537.19	1.06	9951	0.39	0.00
Penetrability	1	183.13	0.37	9946	0.76	0.00
aRPD Depth	1	417.68	0.88	9962	0.47	0.00
Water Content	1	811.70	1.60	9941	0.22	0.23
Organic Matter Content	1	915.77	1.92	9967	0.15	1.67
Hg	1	1470.70	1.58	9952	0.16	0.32
Pa	1	537.19	1.06	9951	0.39	0.03
Al	1	331.95	0.66	9958	0.62	0.00
Ca	1	525.00	1.11	9951	0.36	0.25
Co	1	996.50	1.97	9959	0.15	1.77
Cr	1	126.83	0.26	9966	0.81	0.00
Cu	1	797.60	1.34	9954	0.27	6.33
Fe	1	256.00	0.52	9953	0.71	0.00
K	**1**	**1367.10**	**2.08**	**9952**	**0.05**	**17.06**
Mg	1	405.57	0.95	9946	0.44	0.00
Mn	**1**	**1417.40**	**2.90**	**9958**	**0.05**	**2.19**
Na	1	708.75	1.59	9966	0.21	1.24
Ni	1	927.92	1.76	9947	0.17	9.73
P	**1**	**1250.00**	**2.64**	**9955**	**0.04**	**4.20**
S	1	393.54	0.79	9953	0.49	0.00
Sr	**1**	**773.23**	**1.63**	**9953**	**0.04**	**5.96**
Ti	**1**	**790.51**	**1.77**	**9947**	**0.0001**	**35.75**
Zn	1	406.68	0.92	9961	0.43	0.00
Site	1	555.12	1.01	9951	0.44	0.25
Transect(Site)	11	512.45	1.36	9926	0.22	1.85
Residual (A.K.A Plot)	6	376.48				5.68
Total	44					

Table 2: Pearson's univariate correlation coefficient between key infaunal species and sediment geochemical elements at three intertidal mudflats near the Skeena Estuary in northern British Columbia, Canada.

Category	Species	K	Mn	P	Sr	Ti
Errant Arthropods	*Americorophium salmonis*	-0.21	0.21	0.26	0.29	-0.24
	Cumella vulgaris	-0.10	0.31	0.50	0.52	-0.11
	Nippoleucon hinumensis	-0.41	0.16	-0.14	-0.09	-0.33
Errant Polychaete	*Eteone californica*	-0.45	0.31	0.21	0.32	-0.46
	Capitella Species Complex	0.38	-0.33	0.03	-0.10	0.31
Sessile Polychaetes	*Fabricia stellaris*	-0.38	-0.12	-0.31	-0.31	-0.31
	Pygospio elegans	-0.35	0.16	0.14	0.21	-0.37
Bivalve	*Macoma balthica*	-0.59	0.25	-0.13	-0.07	-0.52
Harpacticoida	Harpacticoida	-0.33	-0.19	-0.23	-0.23	-0.29
Ostracoda	Ostracoda	-0.38	0.38	0.11	0.16	-0.37
Nematoda	Nematoda	-0.15	0.25	0.12	0.22	-0.19