Assessment of Sediment Penetrability as an Integrated *In Situ* Measure of Intertidal Soft-Sediment Conditions

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Abstract

Infauna have an intimate relationship with the sediments they inhabit, and any study conducted upon infauna must, at the very least, describe sediment conditions. Common sediment assessments in intertidal systems include particle size distribution, as well as water and organic matter contents. These measures require extracting and processing a sediment core, and this disturbance may result in data that do not necessarily reflect *in situ* conditions. Sediment penetrability measured *in situ* by using a penetrometer can circumvent this limitation. However, relationships between sediment penetrability and other sediment variables are poorly understood, especially in coastal systems. We evaluated the relationship between sediment penetrability and other variables – depth to the apparent redox potential discontinuity, mean particle size, organic matter content, and water content – on tidal flats along the Pacific and Atlantic coasts of Canada. We also assessed if adding penetrability into environmental models of the infaunal community improved model performance. We observed that while penetrability is statistically related to other sediment variables, relationships to covariates were weak. Further, inclusion of penetrability with other sediment variables improved the performance of models predicting infaunal community composition. Therefore, penetrability can be considered a separate variable, and contributes to an integrated assessment of environmental conditions experienced by biota. Finally, since we evaluated this method in different soft-sediment intertidal ecosystems (mudflats to sandflats), this method is applicable to a range of systems in other geographical areas.

Key Words: Bay of Fundy, Infauna, Invertebrates, Skeena River, Soft sediment, Tidal Flats

1 Introduction

Given the intimate nature of the relationship between sediment and organisms living on or in sediment (infauna), it is not surprising that sediment conditions impact all aspects of their life histories. For example, sediment conditions have been observed to play an important role in processes such as larval settlement, foraging, reproduction, and locomotion of infauna, (Ólafsson et al. 1994, Lu & Grant 2008, Lu et al. 2008, Dashtgard et al. 2014, Gerwing et al. 2016). This relationship is far from unidirectional, as infauna are able to greatly modify their sedimentary environment (Woodin et al. 2010, De Backer et al. 2011, Godbold et al. 2011, Quintana et al. 2013, Gerwing et al. 2017b). As such, any study conducted on infauna must include some measure of sediment variables to comprehensively understand or describe these systems.

Common assessments of intertidal sediment conditions, such as particle size distribution, as well as water and organic matter content, require extracting a sediment core that is transported back to the laboratory for processing (Valdemarsen et al. 2010, Ghasemi et al. 2014, Pilditch et al. 2015, Gerwing et al. 2016). This extraction and movement can potentially alter physical, chemical, and biological sediment characteristics; for example, cores can begin to dry out, or water can move within the core influencing the results of depth profile analyses. Moreover, large rocks and shells are often removed from samples, and biogenic structures such as burrows are destroyed during sediment homogenization prior to processing. (Kristensen et al. 2011, Queirós et al. 2013). All these aspects may influence measurements, and results may not be accurate representations of *in situ* sediment conditions.

There is a need for an *in situ* method to assess sediment conditions to supplement existing variables. One potential candidate is sediment penetrability, that can easily be measured *in situ* by, for example, dropping an object of known weight from a known height and measuring how far it penetrates into sediment (Hsu et al. 2009, Gerwing et al. 2015a, Campbell et al. In press). Devices that measure sediment penetrability are referred to as penetrometers. They have a long history of consistent use in terrestrial systems (Perumpral 1987, Lowery & Morrison 2002, da Veiga et al. 2007, Heneberg 2009, Fleischer et al. 2014), but have been used only sporadically in coastal systems (Chapman & Newell 1947, Chapman 1949, Grant 1984, Thrush et al. 2003b, Hsu et al. 2009, Virgin et al. 2020). Sediment penetrability, also termed sediment compressive strength, penetrability resistance, or sediment hardness, is typically acknowledged as a quick and inexpensive way to assess sediment conditions, either independently or in conjunction with other sediment variables. Penetrability has also been used to assess sediment compaction, an indicator of deterioration of sediment conditions (Chapman 1949, Greenwood et al. 1997, Herrick & Jones 2002, Hsu et al. 2009, Spencer et al. 2017).

Correlations between sediment penetrability and infaunal communities in soft-sediment coastal habitats have been observed previously (Chapman 1949, Thrush et al. 2003a, Hsu et al. 2009, Gerwing et al. 2016). Although these earlier studies suggest value in measuring sediment penetrability, relationships with other sediment variables in intertidal habitats, as well as with the infaunal community, are poorly understood. It is possible that penetrability is merely a product of other factors that influence tidal flat communities and is not contributing independent information. Furthermore, it is unclear if using sediment penetrability improves our ability to predict infaunal community structure based upon sediment conditions. Therefore, on both the Pacific and Atlantic coasts of Canada, we examined the relationship between sediment penetrability, other sediment variables (mean particle size, water content, organic content, as well as a measure of porewater redox and dissolved oxygen content), and infaunal community structure to determine if penetrability should be included when assessing environmental conditions. More specifically, we addressed the following questions: (1) Should sediment penetrability be considered as a separate, complementary, variable when assessing sediment conditions; (2) what environmental conditions might sediment penetrability be representing; and (3) does inclusion of sediment penetrability improve empirical model performance when evaluating relationships between sediment variables and the infaunal community?

2 Materials and Methods

While data used here have been published before (Gerwing et al. 2015a, Gerwing et al. 2016, Campbell et al. In press), the relationship between sediment penetrability and other sediment variables has not been explored, and the extent to which adding penetrability to other sediment measures improves model performance has not been considered.

2.1 Penetrometer (Guide Bar and Weight)

Sediment penetrability in our studies was measured using a guide bar and weight (Gerwing et al. 2015a, Gerwing et al. 2016, Campbell et al. In press). The guide bar is comprised of a 1m long metal angler (90°), with a hollow cylindrical tube ~15cm long secured within (Figure S1). The top of the cylinder is 0.75m from the bottom of the guide bar. As this creates an asymmetrical design, the top of the guide bar is marked. A cylindrical rod of steel was then cut to form the weight (15cm long with a 1.9cm diameter and weighing 333g). When assessing sediment penetrability, the guide bar is placed flush against the sediment surface and the top of the weight dropped from 0.75m, passing through the tube and along the angler, penetrating the sediment. Depth of penetration is marked on the weight and measured (mm); we used this depth as our measure of sediment penetrability. Note that this measure of penetrability (depth) can be converted to average impact force per unit area by assuming that all the initial potential energy

(2.204 Joules) of the weight is converted to kinetic energy immediately before impact. Materials for our penetrability device cost under $50 (CDN) and construction took less than 1 h. Certain commercial devices (such as the Pocket Penetrometer) can also be used (Grant 1984).

2.2 Study Sites

The present study was conducted on tidal flats on both the Pacific and Atlantic coasts of Canada (Figure 1). Six intertidal areas were examined along the Pacific coast near the Skeena River (WC: Wolfe Cove. CC: Cassiar Cannery. TB: Tyee Banks. BO: Boulder Beach. PI: Prescott Inlet. GU: Coast Guard Beach), while eight were studied along the Atlantic coast in the upper Bay of Fundy (MP: Mary's Point. DF: Daniels Flats. GA: Grande Anse. PC: Pecks Cove. MN: Minudie. MC: Moose Cove. AV: Avonport. SP: Starrs Point). Intertidal sediments along the Atlantic coast were predominantly composed of silt and clay (< 63µm), resulting in a small observed volume-weighted mean particle size (~46µm). Intertidal sediments along the Pacific coast were a mixture of silt/clay and sand (≥ 63µm), resulting in higher observed volume-weighted mean particle sizes (~173µm; Table 1). However, considerable variation exists among sites, with tidal flats dominated by clay/silt, mixtures of silt/clay and sand, or composed mostly of sand (Table S1). In addition, the apparent redox potential discontinuity (aRPD) was deeper, and penetrability, water content, and organic matter content of the sediments were all higher on the Atlantic coast (Table 1 and Table S1). More information on these sites can be found in Gerwing et al. (2015a) and Campbell et al. (In press).

2.3 Sampling Scheme

At each mudflat, transects were established running from the landward start of the mudflat to the low water line (Pacific: five transects per site, separated by ~25m, and 60-200m long; Atlantic: two transects per site, separated by 700-1000m, and 700-1800m long). Transects were stratified into zones based on distance from shore, with four zones in the longer transects of the Atlantic coast, and three zones in those of the Pacific. Within each zone, one sampling location was randomly selected (Pacific coast: n = three per transect, 15 per site; Atlantic coast: n = four per transect, eight per site). On the Pacific coast, sites were sampled four times throughout the summer of 2017 (May 23-June 1, June 21-26, July 19-25, and August 18-24) on the lowest low tides (Cox et al. 2017, Gerwing et al. 2018a, Campbell et al. In press). On the Atlantic coast, sites were sampled sixteen times between 2009-2011, approximately every 3-6 weeks (sampling rounds were conducted over 4-5 days starting on the following dates: June 3, June 20, July 13, August 4, August 30, October 2, and December 8 in 2009, March 10, May 31, June 22, July 14, August 3, October 15, December 4 in 2010, and March 11 in 2011). Individual sampling trips are hereafter referred to as rounds. On the Pacific coast 360 sampling locations were assessed, while on the Atlantic coast 1021 were assessed. More details of the sampling scheme can be found in Gerwing et al. (2015a) and Campbell et al. (In press).

2.4 Sediment Properties

At each sampling location, sediment penetrability was measured, and a sediment core (3cm diameter, 5cm depth on the Atlantic Coast, 4.5cm diameter, 5cm depth on the Pacific Coast) was collected as close by as possible to determine sediment properties. From this core, the top 1cm was processed to determine sediment water content (drying at 110°C for 12 h), organic matter content (ashing at 550°C for four h) and volume-weighted average particle size (Malvern Mastersizer 2000). More details of this process can be found in Gerwing et al. (2015a) and in the online supplement (Text S1). Particle size distribution, water content and organic matter content deeper than 1cm within cores were seldom greatly divergent from the top 1cm (Savoie 2009, Cox et al. 2019, Sizmur et al. 2019), and so we only analysed the top 1cm. While in the field, a second core (7cm diameter and 5-10cm depth) was used to create a void in the sediment from which the depth to the aRPD was visually determined (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. 2015b, Gerwing et al. 2018b).

2.5 Infaunal Community

At each 1m^2 quadrat, infauna were collected with a corer 10cm in length, and 7cm in diameter. Sediment was passed through a 250μm sieve, and the content in the sieve was stored in vials of 95% ethanol (Gerwing et al. 2015a, Gerwing et al. 2017a, Campbell et al. In press). On the Pacific coast, 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 (Gerwing et al. 2017a, Gerwing et al. 2020, Campbell et al. In press). On the Atlantic coast, polychaetes were identified to family, bivalves and amphipods to species, copepods to order, ostracods to class, and nematodes to phylum (Gerwing et al. 2015a, Gerwing et al. 2016). Different taxonomic resolution should not impair our ability to compare between coasts, as Gerwing et al. (2020) showed that analyzing infauna community composition data with specimen identified to different taxonomic levels produced similar results.

2.6 Statistical Analysis

2.6.1 Relationship between Sediment Penetrability and other Sediment Variables

Scatter plots (Figures S2 and S3) suggested that potential relationships between sediment penetrability and other sediment variables were linear; therefore, only linear relationships were explored. Relationships between penetrability as the response variable, and either aRPD depth, mean particle size, water content, organic matter content or some combination as predictor variables were assessed using generalized linear mixed effects models (Burnham et al. 2011), corrected for a skewed distribution by using a Poisson distribution (Richards 2008, O'Hara & Kotze 2010). Models were constructed in R Version 3.6.1. A threshold Pearson correlation coefficient of 0.95 was used to decide if sediment variables were too correlated to be considered independent and included together in models (Clarke & Ainsworth 1993). Since the highest correlation coefficient observed was 0.86, all variables were included in our models. Based upon our previous experience examining relationships between infaunal communities and sediment conditions (Barbeau et al. 2009, Savoie 2009, Gerwing et al. 2016, Cox et al. 2019, Sizmur et al. 2019), a candidate suite of models of interest were constructed *a priori* (Anderson et al. 2000, Burnham & Anderson 2002). This suite of models includes all sediment variables individually, all variables in a single model, and a model including water content, mean particle size and their interaction. A separate suite of models was constructed for the Pacific and Atlantic coasts. In all models, residuals were examined for heteroscedasticity and no corrections were required. Models from the Pacific coast included site (six sites), transect nested within site, and round (four rounds) as random factors. Models from the Atlantic coast included site (eight sites), transect nested within site, year (two years), and round nested within year (eight rounds) as random factors (Burnham et al. 2011, Gerwing et al. 2012). Since all models include these random factors, and it is the sediment variables that are of interest, we do not present coefficients or *p* values for random factors. Further, since models were constructed to visualize relationships between sediment variables, not to select a top-ranked model, criteria such as AIC_c are not presented. Rather, model performance is elucidated using marginal R^2, not conditional R^2. Marginal R^2 values describe the proportions of variance explained by sediment variables of interest (the fixed effect), while conditional R^2 values also include the random factors. Therefore, marginal R^2 enables us to properly model the spatiotemporal nature of the variables using random effects, while assessing the fit of the fixed effect(s) of interest (Edwards et al. 2008, Nakagawa & Schielzeth 2013).

2.6.2 Relationship between Infaunal Communities and Sediment Variables

Relationships between the infaunal community and sediment variables were examined using three multivariate analyses in PRIMER with the PERMANOVA add-on (Anderson et al. 2008, Clarke & Gorley 2015). First, distance-based linear models (DISTLM; (McArdle & Anderson 2001, Anderson et al. 2008) were constructed to assess linear relationships between infauna and all combinations of sediment variables, including models with and without sediment penetrability. Second, since biota could have a non-linear relationship with some of the sediment variables, we conducted PRIMER's RELATE test (Clarke & Gorley 2015) to explore concordance in patterns between infauna and sediment variables. If the RELATE test was significant, then PRIMER's BEST routine (BIO-ENV, Spearman correlation) was used to identify which sediment variable(s) was/were associated with the infaunal community (Clarke & Ainsworth 1993, Clarke et al. 2006). Third, a permutational multivariate analysis of covariance (PERMANCOVA) was also conducted (Gerwing et al. 2016) to incorporate the spatial and temporal categorical structure of the data sets (which the DISTLM and RELATE did not) as random factors (similar to the univariate mixed effects models above). The PERMANCOVA is presented in the supplement (Supplemental Table S2) as results do not differ from those presented here.

Multivariate relationships from the Pacific and Atlantic coasts were analysed separately. Infaunal densities were fourth root transformed (to better balance the influence of rare and common taxa on the resemblance matrix), and the resemblance matrix was constructed using Bray-Curtis similarity (a dummy variable of "1," a value below our threshold of detection, was added to ensure proper calculation of resemblance for patches devoid of infauna). For the sediment variables for the Pacific coast, mean particle size, water content, and organic matter content were square-root transformed, while for the Atlantic coast, mean particle size was log(datum+1) transformed, aRPD depth was fourth-root transformed, and water content and organic matter content were square-root transformed to correct for skewed distributions. Sediment variables were then normalized, and a resemblance matrix constructed using Euclidean distances. In the DISTLM, since we are now interested in selecting top-ranked models, model performance was assessed using Akaike Information Criterion, corrected for small sample sizes (AIC_c), as well as R^2 values (Burnham & Anderson 2001, Burnham & Anderson 2002, Anderson et al. 2008). Models with a ΔAIC_c of 2 were considered to be equivalent (Burnham & Anderson 2002, Burnham et al. 2011).

3 Results

3.1 Relationship between Sediment Penetrability and other Sediment Variables

While univariate regressions identified statistically significant relationships between sediment penetrability and all other sediment variables, sediment variables accounted for a minor portion of observed variation in penetrability (Table 2; Figures S2 and S3). In general, higher R^2

values were observed along the Pacific coast than the Atlantic; however, all values were below 10%, and only water content in Pacific sediment was higher than 5%. On both coasts, as water content and organic matter content of sediments increased, so did penetrability. Conversely, as mean particle size decreased, penetrability increased on both coasts. The only property that exhibited a mixed trend (positive and negative coefficients between coasts) was aRPD depth. aRPD depth accounted for a very small portion of the observed variation in penetrability (0.1-1.2%).

3.2 Relationship between Infaunal Communities and Sediment Variables

When linear relationships between the infaunal community and sediment variables were examined, sediment penetrability was included in almost all top ranked models (Table 3). While none of the models explained a large portion of the variation observed in infaunal communities (2-8% for the top-ranked models, down to 0.3 for the other models examined), penetrability accounted for a similar or greater portion of the infaunal community variation than other single sediment variables.

Assessment of pattern concordance to gain insight on possible non-linear relationships between sediment variables and the infaunal community revealed no relationship on the Pacific coast (RELATE rho: 0.009; $p = 0.69$). A significant pattern concordance between infaunal community and sediment variables was observed on the Atlantic coast (RELATE rho: 0.15; $p = 0.0001$). While the sediment variable that grouped best with the infaunal community on the Atlantic Coast was mean particle size (Table 4), penetrability was included in the top correlations (Spearman correlation coefficient: 0.15-0.16). The outcome of this multivariate correlation analysis did not differ greatly from the DISTLM analysis, suggesting that there are no strong non-linear associations underlying the relationship between infaunal community and sediment variables in our datasets.

4 Discussion

Infauna live within sediment, therefore, sediment conditions can have a large impact upon them, at all stages in their life cycle (Lu & Grant 2008, Lu et al. 2008, Dashtgard et al. 2014). Elucidating sediment conditions is thus necessary to fully understand infaunal communities and intertidal systems in general. We evaluated the relationship between commonly studied sediment variables, namely aRPD depth, mean particle size, organic matter content, water content, and sediment penetrability, along the Pacific and Atlantic coasts of Canada. Our objective was to determine whether penetrability measures a different aspect of intertidal sediment conditions when compared to other sediment variables. We also examined if penetrability is an important variable to include when modelling infaunal community dynamics, as well as gave thought to what sediment penetrability may be representing.

4.1 Relationship between Sediment Penetrability and other Sediment Variables

We observed that while sediment penetrability is statistically related to other sediment properties, relationships were weak. Therefore, penetrability can be considered as a separate, complementary variable when quantifying sediment conditions in intertidal systems. The positive relationship observed between penetrability and water content, as well as the negative relationship observed with mean particle size were expected (Chapman & Newell 1947, Chapman 1949, Grant 1984, Perumpral 1987, Vaz et al. 2001, Hsu et al. 2009, Fleischer et al. 2014). Sandy sediment resists the impact force of the dropped weight more than sediment composed of silt/clay, as does sediment with a lower water content (Perumpral 1987, Vaz et al.

2001, Hsu et al. 2009, Fleischer et al. 2014). As such, penetration is lower on sandflats when compared to mudflats, and higher in sediment containing more water. Our cursory field observations in mudflat areas with high water content confirm the latter: “soupy” sediments exhibit high penetration values. However, the relationship between particle size and penetrability is complex, as finer grained sediments will contain more silt and clay. Clay has electromagnetic properties and causes sediment particles to bind together. In dry, terrestrial systems, clay cements and hardens the soil, but in wet systems clay can remain in suspension and be colloidal, making sediment soupier (Chapman & Newell 1947, Yates et al. 1993, Dashtgard et al. 2008). So, the relationship between sediment penetrability and clay content is complex and will require further research.

Currently, the nature of the weak positive relationship observed between sediment organic matter content and sediment penetrability in our study is unclear. This relationship could be a result of bioturbation by small infauna or meiofauna such as copepods and ostracods that would have been present in the sediment cores (hence increasing organic matter content) and could increase penetrability. However, the opposite relationship could also be expected (decreased penetrability with increased organic matter content), as organic matter in the form of extracellular polymeric substances (EPS) increases the sediment’s resistance to disturbance and erosion (Underwood et al. 1995, Paterson & Hagerthey 2001). More research is required to better understand this penetrability-organic matter content relationship.

The only sediment variable that exhibited both a positive and negative relationship between coasts with sediment penetrability was aRPD depth. aRPD depth is a relative indicator of sediment porewater redox and dissolved oxygen conditions (Gerwing et al. 2015b, Gerwing et al. 2018b). Based upon the positive and negative coefficients, as well as the small portion of the observed variation each term accounted for (Table 2), we suggest that no meaningful relationship exists between aRPD depth and sediment penetrability. Statistical significance in this case is likely a result of high statistical power that detected small random trends.

When these relationships are examined together, and despite the observed correlations between sediment penetrability and other sediment variables, the weak nature of the associations indicates that penetrability can be considered as a separate, complementary variable when quantifying sediment conditions in intertidal systems.

4.2 What Environmental Conditions Might Sediment Penetrability be Representing?

Sediment penetrability has been used to measure or infer various sediment conditions in different habitats. From an agricultural perspective, soil penetrability is affected by clay content, soil moisture, and compaction by machinery traffic. Such terrestrial studies have used soil penetrability as an assessment of plant root restriction and soil degradation due to machinery traffic (da Veiga et al. 2007). From a geotechnical engineering perspective, penetrability is used as an indication of the relative density of granular deposits, such as sands and gravels from which it is virtually impossible to obtain undisturbed samples (Chapman & Newell 1947, Chapman 1949, Perumpral 1987). In coastal systems, penetrability has been used to assess sediment compaction, an indicator of deterioration of sediment conditions (Chapman 1949, Greenwood et al. 1997, Herrick & Jones 2002, Hsu et al. 2009, Spencer et al. 2017).

Beyond generalities, penetrability has also been used in various specific contexts in coastal habitats. Grant (1984) assessed the penetrability of coastal sediment as an indication of resistance of sediment to bill probing by shorebirds. Similarly, sediment penetrability has been used to measure the force required for infauna to burrow into the sediment, with increased penetrability indicating sediment requiring more force (Chapman & Newell 1947, Chapman 1949). Other studies have used sediment penetrability to measure catastrophic deposition of terrestrial sediment on intertidal mudflats; specifically, sediments more difficult to penetrate reflected disturbance, and sediments with higher penetrability values reflected those undergoing recovery (Thrush et al. 2003a, Thrush et al. 2003b). Virgin et al. (2020) used sediment penetrability to measure certain aspects of salt marsh restoration; sediments at the bottom of salt pools in newly restored marshes were unconsolidated and easily penetrable, but hardened and became less penetrable as recovery progressed. Conversely, consolidated sediment that is difficult to penetrate on mudflats or on marsh surfaces may act as a barrier to water penetration and subsurface flow, impact drainage, and promote formation of cyanobacteria mats. All factors that hinder restoration of estuaries and saltmarshes (Underwood 1997, Crooks et al. 2002, Morris et al. 2014, Spencer et al. 2017, Lawrence et al. 2018). Finally, in our previous studies, we postulated that sediment penetrability is a relative measure of how easily infauna can burrow and water pass into the sediment (Gerwing et al. 2015a, Gerwing et al. 2016, Gerwing et al. 2017c, Gerwing et al. 2018a, Campbell et al. In press).

Sediment penetrability is also associated with sediment shear strength in coastal systems (Deans et al. 1982, Berlamont et al. 1993, Grant & Daborn 1994, Fernandes et al. 2006). Shear stress is the stress component parallel to a given surface, such as by tidal currents for marine sediments. Sediments with higher shear strength are more stable and more resistant to penetration (Berlamont et al. 1993, Grant & Daborn 1994, Haralampides & Rodriguez 2006, Wu et al. 2011, Grabowski 2014). While shear stress was not evaluated in this study, the penetrability measure described here could be a good indicator of shear stress. Further research is required to explore this relationship.

Our results build upon and refine these previous interpretations of sediment penetrability in coastal systems. We suggest that sediment penetrability is an integrative variable that reflects the overall *in situ* conditions experienced by biota. Increased penetrability is indicative of finer-grained sediment with high water content, with few rocks or shell hash present in or on the sediment, resulting in sediment that is easier to burrow or penetrate. Habitat characterised by low penetrability is indicative of larger-grained sediment with low water content, and with more rocks or shell hash present, resulting in sediment that requires more energy to burrow or penetrate. While sediment exhibiting lower penetrability is more difficult to burrow into than finer-grained sediment with increased penetrability, biogenic structures will be inherently more stable (Kristensen et al. 2011, Queirós et al. 2013). Finally, infauna can also modify the sediment environment they inhabit via burrowing and foraging, often called bioturbation (Teal et al. 2010, Birchenough et al. 2012, Teal et al. 2013, Queirós et al. 2015); therefore infauna may also influence sediment penetrability. Sediment experiencing increased bioturbation is likely to exhibit increased penetrability, especially in muddy sediment with high water content. However, more research is required to elucidate how levels of bioturbation influences sediment penetrability, and if this varies between muddy and sandy sediment.

4.3 Relationship between Infaunal Communities and Sediment Variables

When relationships between infaunal community composition and sediment variables on tidal flats along the Pacific and Atlantic coasts were assessed, sediment penetrability was at least as informative as the more commonly used measures of sediment conditions, and inclusion of penetrability created better performing models of the infaunal community. Other studies have also observed weak to strong relationships between sediment penetrability and infaunal community structure and population densities (Thrush et al. 2003a, Hsu et al. 2009, Gerwing et al. 2016). In our study, none of the top-ranked linear models (4-8%) accounted for a large portion of the observed variation in the infaunal community, and when modelled independently, penetrability only accounted for a minor proportion of the infaunal community variation (0.6-2%). Models explaining a low proportion of the observed community variation are not surprising, since stochastic larval settlement processes (Jones & Ricciardi 2014), inter- and intraspecies interactions (Drolet et al. 2013, Greenville et al. 2014), and other regional variables that operate on broad spatial and temporal scales can have large effects on community structure. Moreover, weak detected relationships may also be a product of the coarse measures of invertebrate density used in our study. Stronger associations would likely be observed if we examined more focused relationships, such as those between sediment variables and larval settlement, burrowing activity (Chapman & Newell 1947), or if we contrasted sediment variables in inhabited patches versus uninhabited patches (Meadows 1964, Ólafsson et al. 1994, Pilditch et al. 2015). Regardless, penetrability accounted for similar or greater proportions of the infaunal community variation when compared to sediment particle size, organic matter content, and water content (Tables 3 and 4); variables whose influence on infaunal communities is more well known (Meadows 1964, Schlüter 1991, Ólafsson et al. 1994, Snelgrove et al. 1999, Lu & Grant 2008, Lu et al. 2008, Dashtgard et al. 2014, Pilditch et al. 2015, Gerwing et al. 2016). Therefore, our results show that sediment penetrability is at least as informative as the more commonly used measures of sediment conditions, and inclusion of penetrability creates better performing models of the infaunal community. As such, sediment penetrability is an important variable to include when assessing infauna or intertidal sediment conditions.

4.4 Conclusions

Even though sediment penetrability is correlated with other sediment variables, the weak nature of these relationships indicates sediment penetrability can be used as a separate, complementary assessment of sediment conditions. Specifically, penetrability is an *in situ*, integrative measure of conditions experienced by biota. As such, it is an informative and useful variable to include in future studies that assess soft sediment conditions and infaunal communities in intertidal habitats. Penetrability is not often measured in intertidal studies, and we suggest that its inclusion will allow for a better understanding of intertidal sediment conditions. Finally, we evaluated an inexpensive and easy-to-use method in a large range of soft-sediment intertidal ecosystems (mudflats to sandflats) in two geographically distinct regions, indicating that this method may be informative in other geographical regions.

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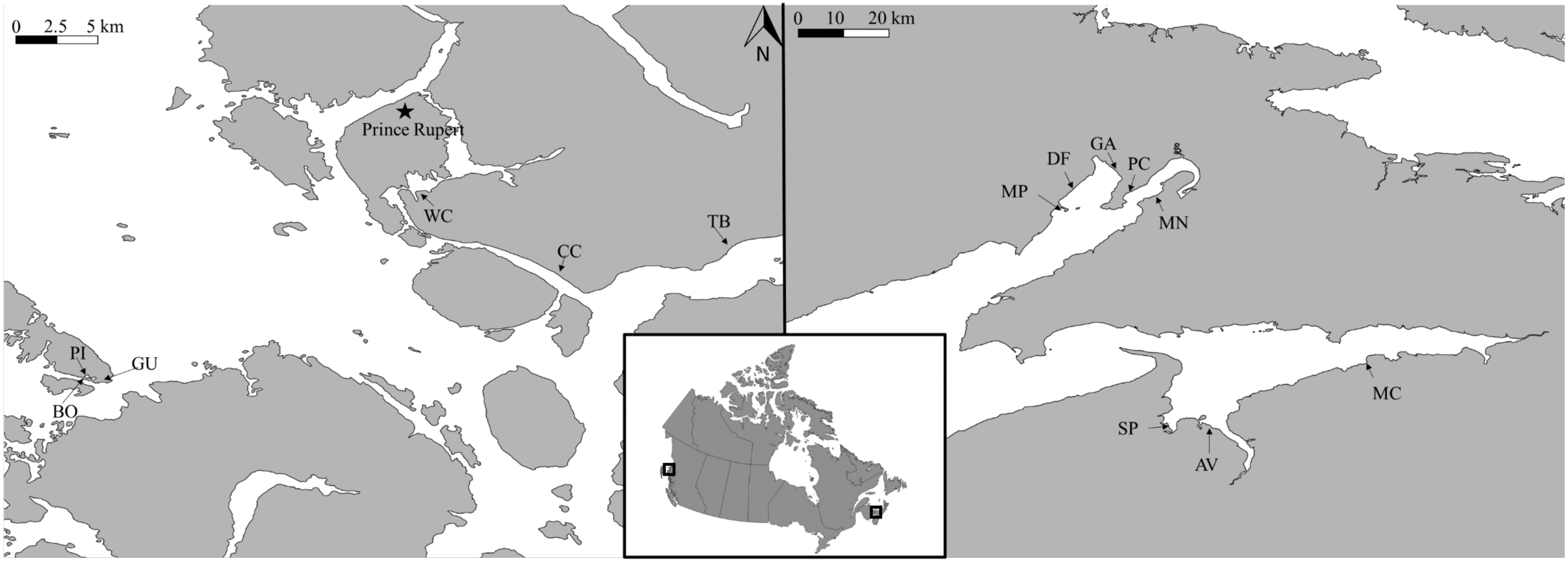

Figure 1: Map of study sites on the Pacific and Atlantic coasts of Canada, made using QGIS (QGIS 2019). WC: Wolfe Cove. CC: Cassiar Cannery. TB: Tyee Banks. BO: Boulder Beach. PI: Prescott Inlet. GU: Coast Guard Beach. MP: Mary's Point. DF: Daniels Flats. GA: Grande Anse. PC: Pecks Cove. MN: Minudie. MC: Moose Cove. AV: Avonport. SP: Starrs Point.

Table 1: Summary of sediment variables of tidal flats along the Pacific and Atlantic coasts of Canada. N: sample size. SE: standard error. aRPD: apparent redox potential discontinuity. See Table S1 for more detail.

	Pacific Coast		Atlantic Coast	
Variable	N	Mean ± SE	N	Mean ± SE
Sediment Penetrability (mm)	360	30.31 ± 1.17	1021	66.81 ± 1.01
Depth to aRPD (mm)	360	0.11 ± 0.02	1021	37.78 ± 0.84
Water Content (%)	360	28.08 ± 0.45	1021	37.91 ± 0.31
Organic Matter Content (%)	360	2.42 ± 0.09	1021	3.30 ± 0.04
Mean Particle Size (µm)	360	173.02 ± 4.16	1021	46.56 ± 1.45

Table 2: Summary of the generalized linear mixed effects models assessing the relationship between sediment penetrability and other sediment variables of tidal flats along the Pacific and Atlantic coasts of Canada. SE: standard error. R^2: marginal coefficient of determination. Particle size: mean particle size; aRPD: apparent redox potential discontinuity.

Coast	Model	R^2	Terms	*p*
Pacific	Particle Size, Water Content, and Interaction	8.74	3	> 0.0001
	Water Content	8.45	1	0.001
	All Variables	8.24	4	> 0.0001
	Particle Size	5.71	1	0.001
	Organic Matter Content	5.31	1	0.001
	aRPD Depth	0.07	1	0.01
Atlantic	All Variables	4.54	4	> 0.0001
	Particle Size, Water Content, and Interaction	3.29	3	> 0.0001
	Particle Size	3.00	1	0.001
	Water Content	2.65	1	0.001
	Organic Matter Content	2.18	1	0.001
	aRPD Depth	1.22	1	0.001

Table 3: Summary of distance-based linear models (DISTLM) evaluating model performance of sediment variables on infaunal communities of tidal flats along the Pacific and Atlantic coasts of Canada. Top ranked models are indicated in bold. Particle size: mean particle size; aRPD: apparent redox potential discontinuity.

Coast	Model	ΔAIC_c	AIC_c	R^2	# Terms
Pacific	**Organic Matter Content, Particle Size, Penetrability**	**0**	**2555.10**	**3.22**	**3**
	aRPD Depth, Organic Matter Content, Particle Size, Penetrability	**0.70**	**2555.80**	**3.59**	**4**
	Water Content, Organic Matter Content, Particle Size, Penetrability	**0.70**	**2555.80**	**3.59**	**4**
	All	**1.50**	**2556.60**	**3.93**	**5**
	Water Content, Organic Matter Content, Particle Size	**1.60**	**2556.70**	**2.78**	**3**
	Organic Matter Content, Penetrability	**1.70**	**2556.80**	**2.21**	**2**
	Water Content, Organic Matter Content, Penetrability	2.10	2557.20	2.64	3
	Organic Matter Content, Particle Size	2.20	2557.30	2.09	2
	aRPD Depth, Organic Matter Content, Penetrability	2.40	2557.50	2.58	3
	aRPD Depth, Water Content, Organic Matter Content, Particle Size	2.50	2557.60	3.11	4
	Organic Matter Content	4.50	2559.60	0.89	1
	Penetrability	5.60	2560.70	0.59	1
	Particle Size	5.90	2561.00	0.50	1
	Water Content	5.90	2561.00	0.49	1
	aRPD Depth	6.50	2561.60	0.33	1
Atlantic	**All**	**0**	**7293.60**	**7.95**	**5**
	Particle Size, Water Content, aRPD Depth, Penetrability	7.80	7301.40	7.06	4
	Particle Size, Water Content, Organic Matter Content, Penetrability	10.10	7303.70	6.85	4
	Water Content, Organic Matter Content, aRPD Depth, Penetrability	13.00	7306.60	6.59	4
	Particle Size, Water Content, Organic Matter Content, aRPD Depth	13.80	7307.40	6.51	4
	Particle Size, Organic Matter Content, Penetrability	18.80	7312.40	5.86	3
	Particle Size, Organic Matter Content, aRPD Depth	19.30	7312.90	5.82	3

Particle Size, Water Content, aRPD Depth, Penetrability	19.90	7313.50	5.95	4
Particle Size, Water Content, Organic Matter Content	21.90	7315.50	5.58	3
Organic Matter Content, aRPD Depth, Penetrability	22.30	7315.90	5.54	3
Organic Matter Content	47.70	7341.30	2.78	1
Penetrability	53.40	7347.00	2.24	1
Water Content	55.60	7349.20	2.03	1
Particle Size	57.40	7351.00	1.85	1
aRPD Depth	65.80	7359.40	1.04	1

Table 4: Correlation (BEST BIO-ENV, 9999 permutations) between the infaunal community of mudflats along the Atlantic coast and sediment variables to gain insight on possible non-linear relationships.

# Variables	Correlation	Variables
2	0.16	Particle Size, Organic Matter Content
3	0.16	Particle Size, Organic Matter Content, Penetrability
3	0.16	Particle Size, Organic Matter Content, aRPD Depth
4	0.16	Particle Size, Organic Matter Content, aRPD Depth, Penetrability
1	0.16	Particle Size
2	0.15	Particle Size, Penetrability
5	0.15	Particle Size, Water Content, Organic Matter Content, aRPD Depth, Penetrability
4	0.15	Particle Size, Water Content, Organic Matter, Penetrability
3	0.15	Particle Size, Water Content, Penetrability
4	0.15	Particle Size, Water Content, Organic Content, aRPD Depth
1	0.10	Organic Matter Content
1	0.09	Water Content
1	0.07	Penetrability
1	0.07	aRPD Depth