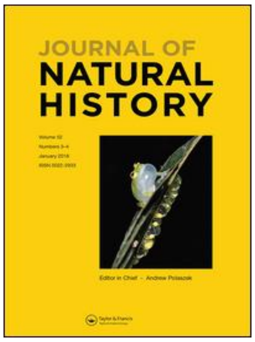

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Invertebrate communities, sediment parameters and food availability of intertidal soft-sediment ecosystems on the north coast of British Columbia, Canada

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ABSTRACT

The Skeena River estuary supports commercial and culturally important salmon fisheries. However, considerable development has occurred in the area, and more has been proposed. If anthropogenic development degrades this critical habitat, the Skeena salmon run, that every year contributes $110 million to local economies, may be negatively impacted. Benthic invertebrates are common indicator species, as they often respond to disturbances before commercial species, warning of potential impacts. Unfortunately, invertebrates in the Skeena estuary have not been extensively studied, and we lack the detailed understanding of their community structure and dynamics for them to serve as indicator species in this region. Therefore, present conditions of the Skeena estuary are established here (invertebrate community, sediment conditions and food availability), in order to provide the data required both to anticipate changes associated with potential anthropogenic disturbances and to detect changes in this system if development occurs.

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Biodiversity; estuary; intertidal habitats; invertebrates; Skeena River

Introduction

The Skeena River is British Columbia's second largest river, and its estuary provides important nursery habitats for juvenile Pacific salmon (Carr-Harris et al. 2015; Moore et al. 2016). Coastal areas to the north of the estuary surrounding the small port cities of Prince Rupert and Port Edward have been extensively developed, with industrial developments including an international port, a papermill and several historic canneries (Waldichuk and Bousfield 1962; Wilkes and Dwernychuk 1991; Campbell et al. 2019; Sizmur et al. 2019). Findings of previous surveys of the benthic invertebrates inhabiting the intertidal sediment in the Skeena estuary reveal an infaunal community (invertebrates living in sediment) that is relatively undisturbed at the estuary scale, but which still shows the scars of historic industrial developments at specific locations (Gerwing et al. 2017a, 2018b; Campbell et al. 2019; Sizmur et al. 2019). However,

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further developments have been proposed in the Skeena estuary, including oil and natural gas pipelines, super-tanker routes, potash loading facilities and a liquid natural gas terminal. The Skeena salmon run contributes an estimated 110 USD million dollars annually to the local economy (Nibr 2006), therefore, degradation of the Skeena Estuary could have devastating consequences on both the economy and the ecosystem (Higgins and Schouwenburg 1973; Hilborn and Walters 1977).

Benthic invertebrates are often used as indicator species as they are prey for many commercially important fish species, and often respond to disturbances (human or natural) before commercially viable species are negatively impacted, thus warning of potential future impacts at higher trophic levels (Gómez Gesteira and Dauvin 2000; Amoozadeh et al. 2014; Gerwing et al. 2017b). While some surveys of intertidal invertebrates, particularly infauna, have been conducted in the Skeena estuary, the spatiotemporal scope of this work was limited (Gerwing et al. 2017a, 2018b; Campbell et al. 2019; Sizmur et al. 2019). A more detailed understanding of the invertebrate community – including community composition, and spatiotemporal variation in populations – is required if we are to anticipate changes associated with anthropogenic disturbances, or to detect such changes after development occurs. Therefore, we quantified present conditions of the invertebrate community, sediment parameters and food availability at three intertidal mudflats within the Skeena Estuary, as well as at three intertidal sandy shores outside of the estuary.

Methods

Sampled habitats included intertidal mudflats (n = 3; sites whose sediment was dominated by silt/clay) in the Skeena River Estuary and intertidal sandy shores (n = 3; sites whose sediment was a mixture of silt/clay and sand) on Prescott Island (Figure 1).

Sampling scheme

At each site, five transects were established, stretching from the start of the mudflat or sandy shore to the low tide waterline (Gerwing et al. 2018a; Cox et al. 2019). Lengths of transects and distances between transects varied between sites. Mudflat beaches were Tyee Banks (TB; transects 150 m long, 100 m between transects), Wolfe Cove (WC; transects 60 m long, 25 m between transects) and Cassiar Cannery (CC; transects 60 m long, 100 m between transects). Sandy shores on Prescott Island were Boulder Beach (BO; transects 45 m long, 30 m between transects), Prescott Inlet (PI; transects 150 m long, 25 m between transects) and Coast Guard Beach (GU; transects 75 m long, 20 m between transects). All transects were stratified into three zones based upon relative distance from shore (near, middle and far (Gerwing et al. 2015a, 2018a)). Within each zone, one sampling location was randomly selected (n = 3 per transect, 15 per site) and a 1 m^2 quadrat was established. Sites were sampled four times throughout the summer of 2017 during the lowest low tides (Round A: 23 May 23–1 June. Round B: 21–26 June. Round C: 19–25 July . Round D: 18–24 August) for a total of 60 assessments per site.

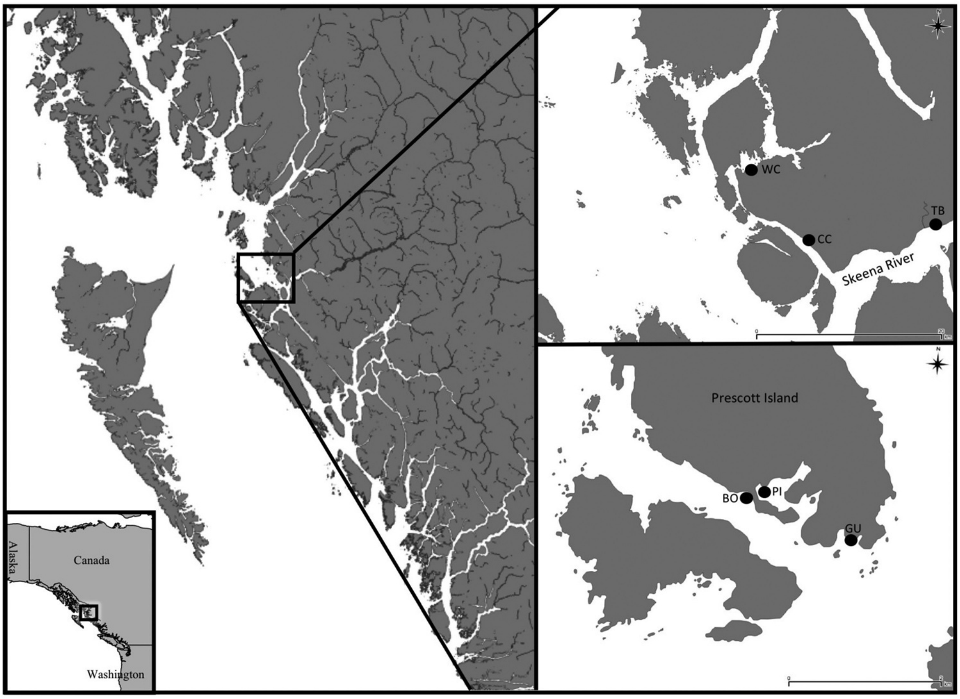

Figure 1. Map of intertidal mudflats and sandy shore study sties around Prince Rupert, and on Prescott Island, British Columbia, sampled during summer of 2017. Figure 1(a) shows mudflats close to the Skeena River (CC: Cassiar Cannery 54.1747, 130.1721; TB: Tyee Banks 54.2000, 129.9634; WC: Wolfe Cove 54.2424, 130.2730). Figure 1(b) shows sandy shores on Prescott Island (BO: Boulder Beach 54.0871, 130.5970; PI: Prescott Inlet 54.0709, 130.5950; GU: Coast Guard Beach 54.0659, 130.5757).

Invertebrate community

At each 1 m^2 quadrat, epifauna (invertebrates living on or above the sediment) were counted and infauna were collected with a corer 10 cm in length, and 7 cm in diameter. A 20 cm by 20 cm pit was also dug to a depth of 20 cm to obtain large or mobile specimens that may have been missed by the infaunal core. Following infaunal core collection, sediment was passed through a 250 µm sieve and stored in vials of 95% ethanol (Gerwing et al. 2015a, 2017a). 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 (Thrush et al. 2003a; Gerwing et al. 2017a).

Sediment parameters

At each quadrat, wood, macrophyte and eelgrass (*Zostera marina*) cover (%) of the quadrat were visually estimated, and 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 (Gerwing et al. 2015a). Depth the weight penetrated the sediment was measured as an indication of how easily water and animals can penetrate the sediment, therefore generating an index that can be compared between quadrats and sites. Additionally, water content and volume weighted mean particle size in the upper 1 cm of sediment were quantified by collecting a sediment core (4.5 cm diameter, 5 cm length) from each quadrat. Briefly, the top 1 cm of each core was weighed, placed in a drying oven at 110° C for 12 hours and re-weighed. Percent water-content was calculated as

$$(\text{mass wet sediment} - \text{mass dry sediment})/(\text{mass wet sediment}) \times 100$$

Volume-weighted mean particle-size of the sediment for each sample was determined using a Malvern Mastersizer 2000 (www.malvern.com). Particle size was measured in triplicate and a mean value per sample calculated (Gerwing et al. 2015a).

Depth of the apparent redox potential discontinuity (aRPD) was measured to the nearest 1 mm as an index of sediment pore water redox and dissolved oxygen content. aRPD depth was measured in the sediment void left by the removal of the 7 cm diameter infauna core. Sediment with a deeper aRPD has more available dissolved oxygen, and the sediment is more oxidised or less reduced than sediment with a shallower aRPD depth (Gerwing et al. 2013, 2015b, 2018c).

Food availability

Organic matter is a food source for invertebrates (Fauchald and Jumars 1979; Jumars et al. 2014) as well as an indicator of organic enrichment (Pearson and Rosenberg 1978; Subida et al. 2012); therefore, organic matter content was quantified from the sediment core as outlined by Gerwing et al. (2015a). Briefly, dried sediment samples were ashed in a muffle furnace at 550° C for 4 h and re-weighed. Percent organic matter content was calculated as

$$(\text{mass dry sediment} - \text{mass of ashed sediment})/(\text{mass of dry sediment}) \times 100$$

Additionally, a 2 cm diameter core was taken to determine the concentration of chlorophyll *a* in the top 2–3 mm of sediment as outlined by Coulthard and Hamilton (2011). Chlorophyll pigments were extracted from sediment samples via buffered acetone, with processing through a spectrophotometer to assess reflectance of chlorophyll pigments. Benthic diatoms are consumed by invertebrates, and chlorophyll *a* serves as a proxy for diatom abundance (Trites et al. 2005; Coulthard and Hamilton 2011).

Water column characteristics

Water temperature, dissolved oxygen (DO), salinity, conductivity and pH were measured at each beach on each sampling trip with a YSI multimeter in the water approximately 1 cm above the sediment surface. On mudflats, sites impacted by freshwater, a YSI reading was taken at high and low tide to quantify the impact of tides upon salinity (TB, WC, CC). At sandy shores, sites not impacted by freshwater, a YSI reading was only taken at high tide (BO, PI, GU).

Statistical analysis

Variables of interest were divided into three categories: invertebrate community (species composition and abundance), sediment parameters (aRPD depth, sediment water content, volume weighted mean particle size, penetrability, % macrophyte coverage, % wood coverage and % *Zostera marina* cover) and food availability (chlorophyll *a* concentration and sediment organic matter). For each category, statistical analyses were performed in a sequential manner (Figure 2), and all analyses were conducted in PRIMER with the PERMANOVA add-on (Anderson et al. 2008; Clarke and Gorley 2015). First, the divergent nature of the mudflat and sandy shore habitats suggest that all variables of interest are likely too different to pool mudflats and sandy shores together. As such, an Analysis of Similarities (ANOSIM) was used to test for significant differences between the invertebrate community, sediment paramaters and food availability in the two habitat types. As these habitats were significantly different for all variable groups (Table 1 and Figure S1), all downstream analyses separated mudflats and sandy shores.

Permutational Multivariate Analyses of Variance (PERMANOVAs) were used to elucidate how each variable group varied over space and time. Invertebrate abundances were fourth root ($x^{1/4}$) transformed to decrease the importance of very abundant species on the outcome of analyses and improve the assessment of less common species. Subsequently, Bray–Curtis distances were used to create a resemblance matrix (Clarke et al. 2006) for the PERMANOVA. Within this PERMANOVA, Site (3 levels) and Round (4 levels) were fixed factors, while Transect nested within Site (Transect(Site); 5 levels) was a random factor. *A priori* planned contrasts (contrasts of interest selected before analysis)

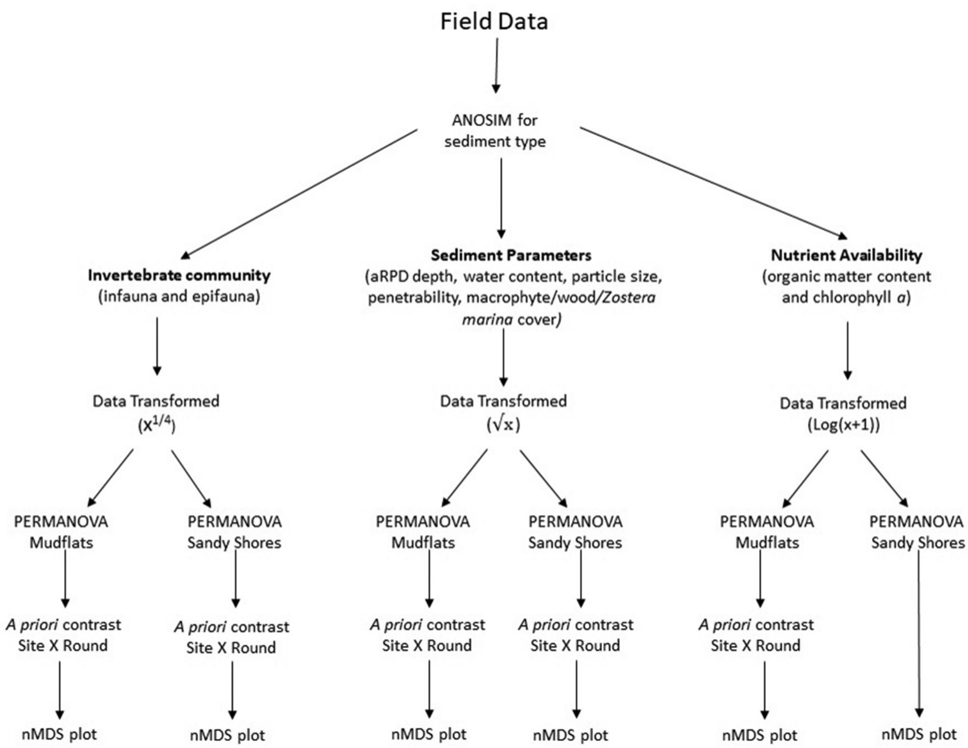

Figure 2. Flow chart demonstrating statistical analysis conducted on the biotic and abiotic variables sampled at intertidal mudflats (n = 3) and intertidal sandy shores (n = 3) on the north coast of British Columbia, Canada during the summer of 2017.

Table 1. Analysis of Similarity (ANOSIM) results quantifying the variation in the invertebrate community, sediment conditions and food availability between intertidal mudflats (n = 3) and intertidal sandy shores (n = 3) on the north coast of British Columbia, Canada during the summer of 2017. Significant p values (α < 0.05) are denoted in bold.

	Habitat type (mudflat versus sandy shore)	
	R	*p*
Invertebrate community	**0.50**	**0.0002**
Sediment parameters	**0.19**	**0.0002**
Food availability	**0.44**	**0.0002**

were conducted for Site X Round factors. For the sediment PERMANOVA, all variables were square root ($\sqrt{x}$) transformed to correct for skewed distributions. For the food matrix, all variables were log (Log(x + 1)) transformed. All variables in the sediment and food PERMANOVAs were normalised, and Euclidean distances were used to calculate a resemblance matrix. Factors and planned contrasts for both the sediment and food PERMANOVA were as described above in the infauna PERMANOVA. Sediment variables also had an *a priori* analysis conducted for Site X Round comparisons for both mudflats and sandy shores, whereas only mudflat sites had an *a priori* analysis conducted for Site X Round comparisons of food availability. An α of 0.05 for all analyses denotes significance (Beninger et al. 2012).

Similarity Percentages Analyses (SIMPER) were then used to examine the contribution of each variable (invertebrate, sediment, or food) to the observed differences among sites or sampling rounds (Clarke 1993). Increased percent dissimilarity indicates the greater dissimilarity between locations. The ratio of each variable's average dissimilarity to the standard deviation of dissimilarities (Diss/SD) for invertebrates, or average squared Euclidean distance to the standard deviation of squared distances (Sq.Dist/SD) for sediment and food variables were calculated. These values represent how consistently each variable contributed to the observed difference; variables with a ratio greater than 1 consistently contributed whereas those with a value below 1 did not (Gerwing et al. 2015a). Finally, non-metric multidimensional scaling (nMDS, 100 restarts) plots were used to visualise variation in infauna, sediment conditions and food availability between locations. All nMDS graphs had a stress of ~0.2 or less and were considered to be good two-dimensional representations (Clarke 1993).

Results/Discussion

Mudflat (Figures 3 and 4; Tables 2 and 3) and sandy shore (Figures 5 and 6; Table 7) invertebrate communities, sediment variables and food availability exhibited statistically significant spatiotemporal variation (Tables S1-S3) along the north coast of BC, Canada, near the Skeena River.

Invertebrate community

Percent dissimilarity of the mudflat invertebrate community varied among sites, ranging from 44% to 54% (Table 4). Four taxa consistently contributed to observed differences

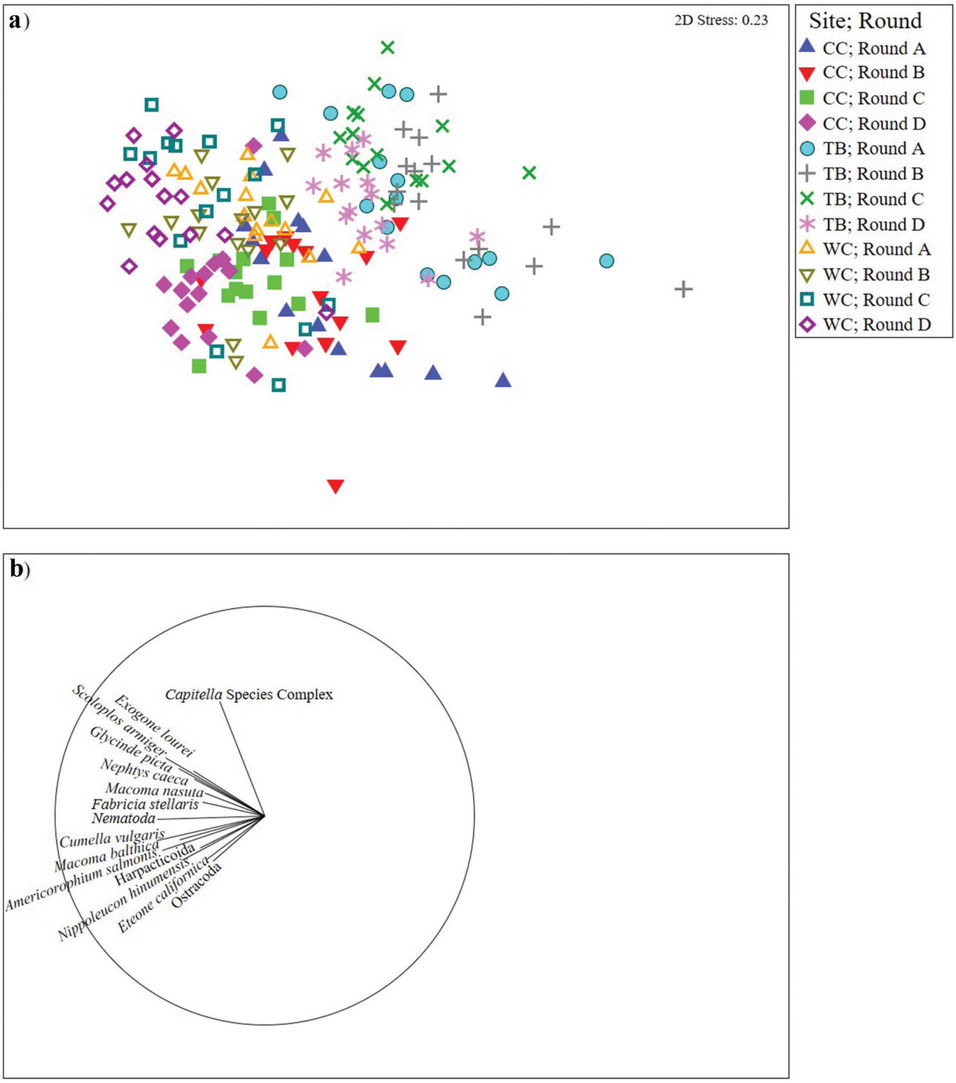

Figure 3. Non-metric multidimensional scaling (nMDS) graphs showing infaunal invertebrate community at three intertidal mudflats on the north coast of British Columbia, Canada during the summer of 2017. (a) the infaunal community by mudflat and sampling round and (b) the vector overlay indicates the direction of increased density, with correlations >0.3 shown. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. Round A: 23 May–June 1. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August.

among mudflats: Harpacticoida, *Capitella* Species Complex, Ostracoda and Nematoda. TB exhibited the lowest mean taxonomic richness of the three mudflats and the lowest average abundance of all taxa (Table 2 and Table S1). However, more oligochaetes were observed at TB than Wolfe Cove (densities four root transformed; 0.70 Vs 0.53 individuals/m^2 respectively), and more *Capitella* Species Complex, Isotomidae sp. and Chironomidae sp. were observed at TB than CC (4.82, 2.11, 1.43 Vs 4.25, 0.48, 0.32 individuals/m^2 respectively; Table 4). Percent dissimilarity of the infaunal community between sandy

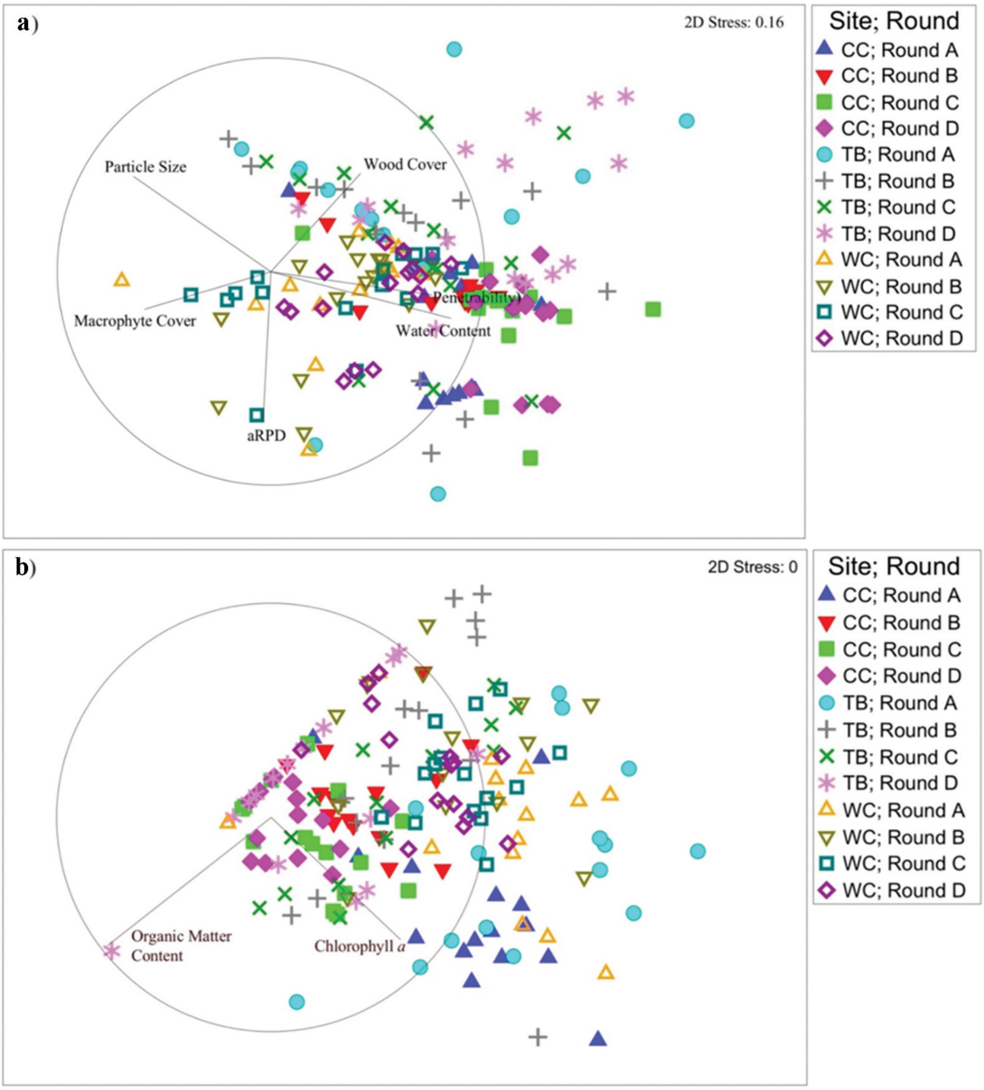

Figure 4. Non-metric multidimensional scaling (nMDS) plots of (a) sediment parameters (depth to the aRPD [apparent redox potential discontinuity], water content, particle size, penetrability, % macrophyte coverage, and % wood cover) by site and round and (b) the food availability (chlorophyll *a* and organic matter content) at three intertidal mudflats on the north coast of British Columbia, Canada during the summer of 2017. Vector overlays for sediment and food variables show the correlation between variables and nMDS axes, with each vector showing the direction of increased value. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. Round A: 23 May–1 June. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August.

shores varied between 50.50% and 54.46% (Table 8). Five taxa consistently contributed to observed differences between sites: Harpacticoida, *Leptochelia* spp. Nematoda, Oligochaeta and Ostracoda.

In general, abundances and taxonomic richness increased at all sites over the summer, peaking in Rounds C or D (July/August; Table S2). A similar temporal

Table 2. Observed taxonomic richness, divided by sediment type and site, as well as infaunal or epifaunal species richness. Species richness was calculated for each quadrat (n = 60) at each intertidal mudflat (n = 3) and intertidal sandy shore (n = 3) sampled on the north coast of British Columbia, Canada during the summer of 2017. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet.

Site	Mean taxonomic richness (epi/infaunal)	Highest taxonomic richness (epi/infaunal)	Lowest taxonomic richness (epi/infaunal)	Mean taxonomic richness (epifaunal)	Mean taxonomic richness (infaunal)
CC	7	12	2	0	7
TB	4	7	1	0	4
WC	11	15	5	0	10
BO	13	24	3	3	10
GU	4	10	2	0	4
PI	11	17	7	1	10
Mudflats	7	15	1	0	6
Sandy shores	10	24	2	1	9

Table 3. Permutational multivariate analysis of variance (PERMANOVA) tables quantifying the spatio-temporal variation in a) invertebrate community, and b) sediment variables (water content, sediment particle size, aRPR depth [apparent redox potential discontinuity], as well as cover of eelgrass, wood and macrophytes) and c) the food availability (organic matter content and chlorophyll *a* concentration) at three intertidal mudflats on the north coast of British Columbia, Canada, during the summer of 2017. Significant *p* values (α < 0.05) are denoted in bold. CC: Cassiar Cannery. TB: Tyee banks. WC: Wolfe Cove.

Source	df	MS	Pseudo-F	Unique permutations	*p*
A) Invertebrate community					
Site	**2**	**31,085.00**	**22.79**	**4897**	**0.0002**
Round	**3**	**7020.30**	**13.44**	**4981**	**0.0002**
Transect(site)	**12**	**1364.30**	**2.19**	**4965**	**0.0002**
Site X round	**6**	**2141.70**	**4.10**	**4973**	**0.0002**
Round A: CC vs TB	**1**	**6721.50**	**7.61**	**4990**	**0.0002**
Round A: CC vs WC	**1**	**4416.30**	**6.93**	**4985**	**0.0002**
Round A: TB vs WC	**1**	**9294.70**	**12.31**	**4987**	**0.0002**
Round B: CC Vs TB	**1**	**11,164.00**	**14.53**	**4990**	**0.0002**
Round B: CC vs WC	**1**	**3928.30**	**5.77**	**4985**	**0.0002**
Round B: TB vs WC	**1**	**16,246.00**	**23.04**	**4986**	**0.0002**
Round C: CC vs TB	**1**	**13,327.00**	**26.20**	**4985**	**0.0002**
Round C: CC vs WC	**1**	**6885.20**	**10.65**	**4987**	**0.0002**
Round C: TB vs WC	**1**	**10,088.00**	**17.62**	**4982**	**0.0002**
Round D: CC vs TB	**1**	**10,122.00**	**19.97**	**4982**	**0.0002**
Round D: CC vs WC	**1**	**7054.00**	**12.11**	**4983**	**0.0002**
Round D: TB vs WC	**1**	**13,283.00**	**21.87**	**4981**	**0.0002**
Round X transect(site)	36	522.46	0.84	4931	0.93
Residual	120	623.31			
Total	179				
B) Sediment parameters					
Site	**2**	**132.51**	**13.48**	**4909**	**0.0002**
Round	**3**	**16.16**	**5.46**	**4980**	**0.0002**
Transect(site)	**12**	**9.83**	**2.33**	**4957**	**0.0002**
Site X round	**6**	**4.81**	**1.62**	**4975**	**0.02**
Round A: CC vs TB	**1**	**24.14**	**4.51**	**4985**	**0.002**
Round A: CC Vs WC	**1**	**42.83**	**9.14**	**4984**	**0.0002**
Round A; TB vs WC	**1**	**17.81**	**3.19**	**4984**	**0.01**
Round B: CC vs TB	**1**	**28.67**	**5.52**	**4988**	**0.0008**
Round B: CC vs WC	**1**	**38.16**	**7.87**	**4982**	**0.0002**
Round B: TB vs WC	**1**	**28.16**	**5.41**	**4987**	**0.001**
Round C: CC vs TB	**1**	**31.29**	**6.14**	**4985**	**0.0004**

(*Continued*)

Table 3. (Continued).

Source	df	MS	Pseudo-F	Unique permutations	*p*
Round C: CC vs WC	**1**	**55.02**	**12.95**	**4987**	**0.0002**
Round C: TB vs WC	**1**	**19.66**	**3.57**	**4990**	**0.008**
Round D: CC vs TB	**1**	**35.08**	**7.07**	**4981**	**0.0002**
Round D: CC vs WC	**1**	**71.79**	**19.67**	**4985**	**0.0002**
Round D: TB vs WC	**1**	**32.85**	**6.52**	**4983**	**0.0006**
Round X transect(site)	36	2.96	0.70	4942	1.00
Residual	120	4.23			
Total	179				
C) Food availability					
Site	**2**	**21.62**	**10.94**	**4906**	**0.002**
Round	**3**	**30.52**	**41.62**	**4991**	**0.0002**
Transect(site)	12	1.98	1.49	4973	0.07
Site X round	**6**	**2.27**	**3.10**	**4986**	**0.002**
Round A: CC vs TB	1	3.22	1.65	4988	0.21
Round A: CC vs WC	**1**	**9.37**	**5.40**	**4988**	**0.003**
Round A: TB vs WC	1	1.90	0.95	4990	0.41
Round B: Site	2	3.42	1.57	4890	0.21
Round C: CC vs TB	**1**	**6.79**	**3.71**	**4983**	**0.03**
Round C: CC vs WC	**1**	**29.29**	**28.57**	**4984**	**0.0002**
Round C: TB vs WC	**1**	**11.39**	**6.84**	**4984**	**0.003**
Round D: CC vs TB	1	1.28	0.63	4979	0.55
Round D: CC vs WC	**1**	**28.08**	**26.28**	**4988**	**0.0002**
Round D: TB vs WC	**1**	**14.46**	**9.29**	**4991**	**0.0004**
Round X transect(site)	36	0.73	0.55	4950	1.00
Residual	120	1.33			
Total	179				

pattern was observed in other mudflats along the north coast of BC (Gerwing et al. 2018a; Campbell et al. 2019), as well as along Canada's Atlantic coast (Gerwing et al. 2015a). In both mudflats and sandy shores, we observed 76 taxa, 48 of which were infauna, while 28 were epifauna (Table 2 and Table S1). More epifaunal invertebrate taxa were observed at sandy shores than mudflats. Nineteen epifaunal taxa were observed only at sandy shores, whereas only one epifaunal taxa (*Crangon franciscorum*) was observed solely at a mudflat site. All mudflat sites had a mean epifaunal taxonomic richness of zero, whereas two of the sandy shore sites (BO and PI) had non-zero values. When epifauna and infauna were considered together, sandy shores had a mean taxonomic richness of 10 compared to 7 at mudflat sites. However, when examined by site, not all sandy shore sites had higher taxonomic richness compared to mudflat sites. For instance, GU had a mean taxonomic richness of 4, whereas CC had a mean taxonomic richness of 7, and both PI and WC had a mean taxonomic richness of 11 (Table 2).

Only six taxa were found at all six sites: Harpacticoida, Isotomidae sp., *Macoma balthica*, Nematoda, Oligochaeta and Ostracoda. Some taxa were found at all three sandy shores but not at any mudflat site (*Axiothella rubrocinata, Hemigrapsus nudus, Hemigrapsus oregonensis* and *Scoletoma zonata*). Only one taxon was found at all three mudflats but not at any sandy shore site (*Nippoleucon hinumensis*). Interestingly, this is an invasive species, common on mudflats along BC's north coast, and likely introduced via shipping sometime after the 1970 s (Akiyama and Yamamoto 2004; Gerwing et al. 2018a). Twelve of the observed taxa were found at two sandy shore sites but no mudflat site,

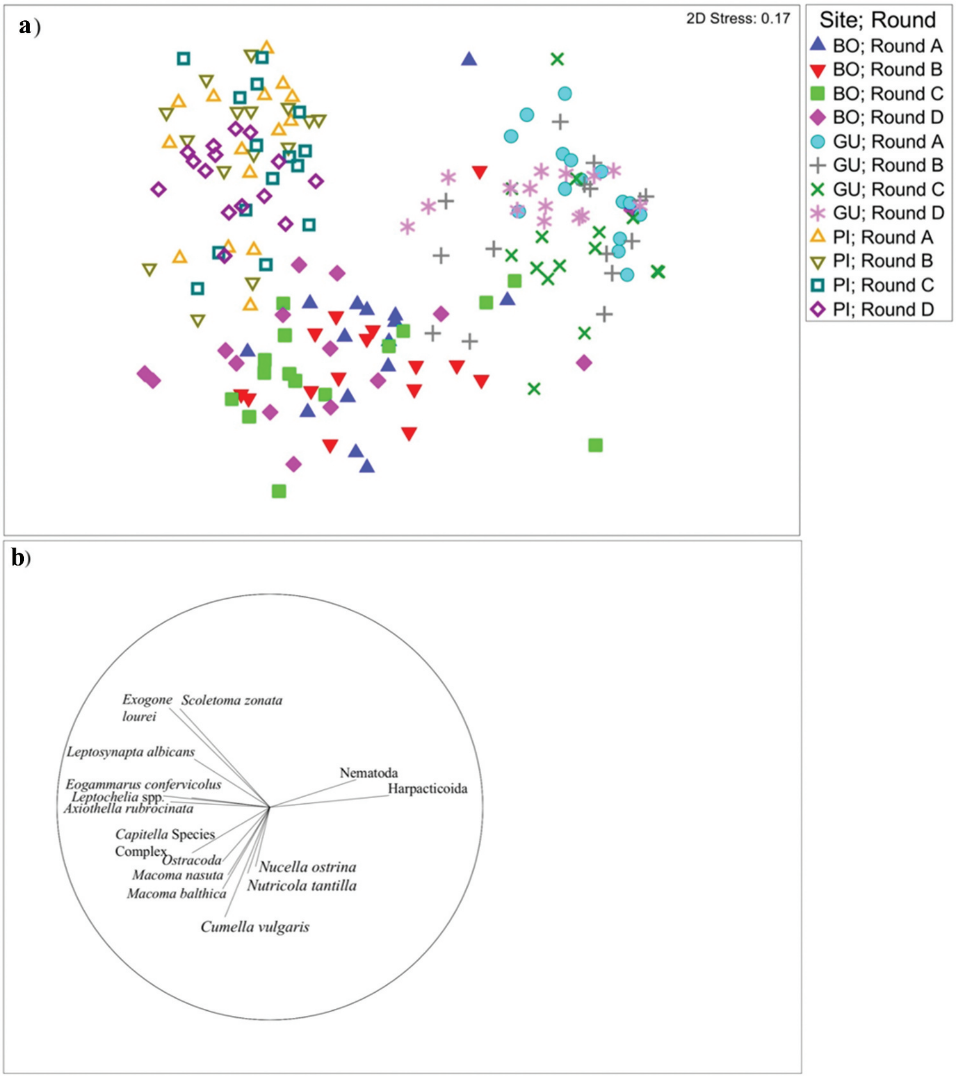

Figure 5. Non-metric multidimensional scaling (nMDS) plots showing infaunal invertebrate community at three intertidal sandy shore sites on the north coast of British Columbia, Canada during the summer of 2017. (a) the infaunal community by sandy shore site and sampling round and (b) the vector overlay indicates the direction of increased density, with correlations >0.3 shown. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet. Round A: 23 May–1 June. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August.

whereas no taxa were observed at two mudflat sites but no sandy shores. Twenty-five taxa were only found at one site, but only six of these taxa were found at a mudflat site (Table S1). It is not surprising that the mudflat and sandy shore habitats sampled in this study exhibited such a divergent invertebrate community (Tables 1 and 2, Tables S1-S3 and Figure S1). Differences between mudflats and sandy shores have been observed in numerous other studies (Peterson 1991; Thrush et al. 2003b; Dashtgard et al. 2008; Cox et al. 2017, 2019).

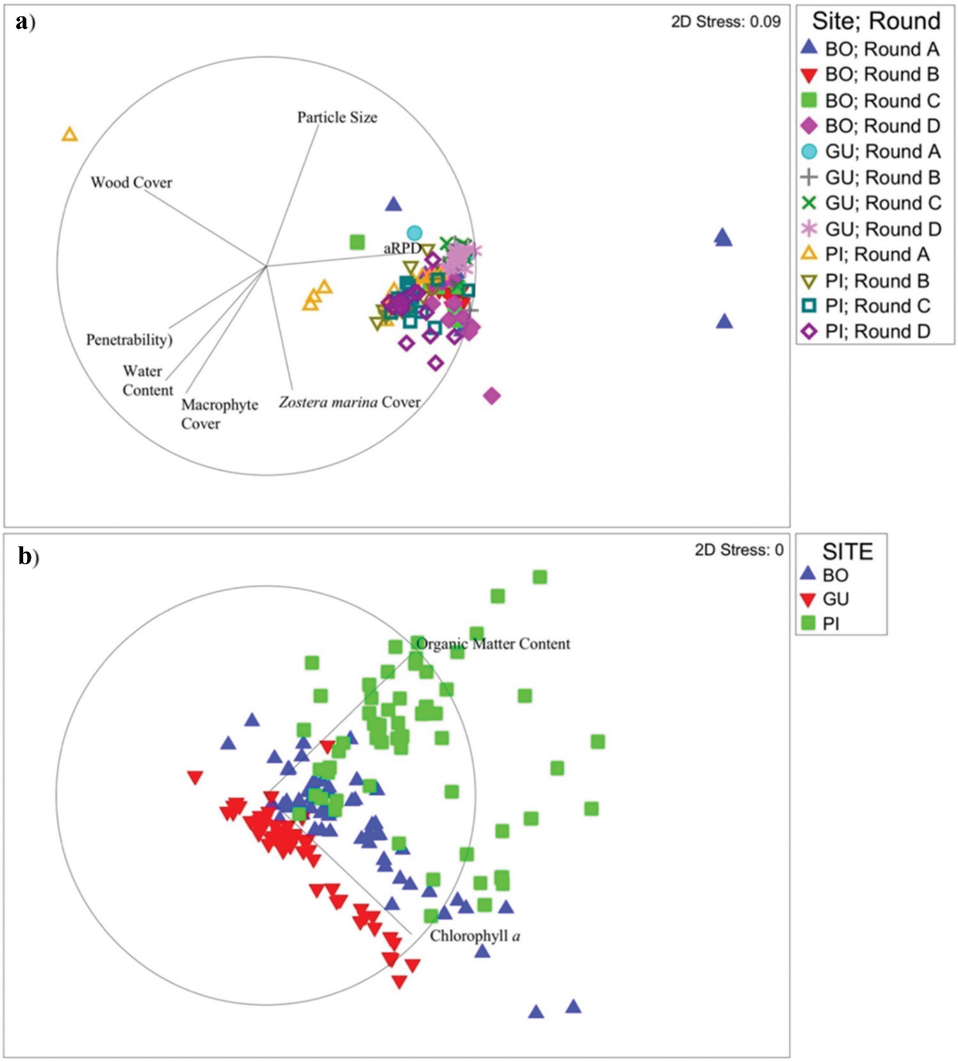

Figure 6. Non-metric multidimensional scaling (nMDS) plots of (a) sediment parameters (depth to the aRPD, water content, particle size, penetrability, % macrophyte coverage, % *Zostera marina* cover, and % wood cover) by site and round and (b) the food availability (chlorophyll *a* and organic matter content) at three intertidal sandy shore sites on the north coast of British Columbia, Canada during the summer of 2017. Vector overlays for sediment and food variables show the correlation between variables and nMDS axes, with each vector showing the direction of increased value. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet. Round A: 23 May 23–1 June. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August.

Overall, observed invertebrate species were similar to other soft-sediment habitats along the north coast of BC (Gerwing et al. 2018a; Campbell et al. 2019), and similar community structures, but different species, were observed at our study sites compared to similar habitats along BC's central coast (Cox et al. 2017, 2019), Canada's Atlantic Coast (Gerwing et al. 2015a, 2015c) and New Zealand (Thrush et al. 2003a, 2003b).

Table 4. SIMPER (Similarity Percentages) tables determining the contribution of each taxonomic grouping to the observed differences between intertidal mudflats on the north coast of British Columbia, Canada during summer of 2017. Diss/SD represents the ratio of the dissimilarity to the standard deviation. Values >1, denoted in bold, represent groups that consistently contribute to the observed differences between mudflats. Taxa with Diss/SD <1 did not consistently contribute to the observed differences between mudflats. Only groups that contributed ≥0.5% to the observed differences between mudflats are shown. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. Abundances are fourth root transformed.

CC vs TB Average dissimilarity = 51.52%	CC	TB				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Eteone californica	**4.13**	**0.00**	**5.73**	**1.63**	**11.13**	**11.13**
Harpacticoida	**6.89**	**5.03**	**5.58**	**1.19**	**10.83**	**21.95**
***Capitella* Species Complex**	**4.25**	**4.82**	**5.41**	**1.15**	**10.51**	**32.46**
Macoma balthica	**3.88**	**0.30**	**5.35**	**1.53**	**10.38**	**42.84**
Nematoda	**12.17**	**9.68**	**5.04**	**1.39**	**9.78**	**52.63**
Ostracoda	**3.37**	**1.67**	**4.30**	**1.09**	**8.35**	**60.98**
Nippoleucon hinumensis	2.79	0.37	3.55	0.89	6.90	67.87
Isotomidae sp.	0.48	2.11	3.07	0.70	5.96	73.83
Pygospio elegans	2.24	0.00	2.96	0.76	5.75	79.58
Americorophium salmonis	2.10	0.13	2.58	0.79	5.00	84.59
Oligochaeta	1.56	0.70	2.43	0.76	4.72	89.30
Chironomidae Larvae	0.32	1.43	2.24	0.71	4.34	93.64
Cumella vulgaris	1.30	0.00	1.52	0.59	2.96	96.60
Aricidea hartleyi	0.60	0.00	0.68	0.39	1.33	97.93
Balanus glandula	0.23	0.00	0.29	0.31	0.55	98.48
CC Vs WC Average dissimilarity = 43.94%	CC	WC				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Harpacticoida	**6.89**	**9.25**	**3.33**	**1.00**	**7.57**	**7.57**
***Capitella* species complex**	**4.25**	**6.19**	**3.33**	**1.11**	**7.57**	**15.15**
Ostracoda	**3.37**	**4.97**	**2.71**	**1.17**	**6.16**	**21.31**
Nematoda	**12.17**	**12.60**	**2.62**	**1.14**	**5.97**	**27.28**
Pygospio elegans	**2.24**	**2.45**	**2.52**	**1.08**	**5.74**	**33.01**
Nippoleucon hinumensis	2.79	0.66	2.42	0.92	5.50	38.52
Isotomidae sp.	0.48	2.61	2.36	0.82	5.37	43.89
Eteone californica	4.13	3.88	2.31	1.04	5.25	49.14
Chironomidae Larvae	0.32	2.40	2.29	0.83	5.20	54.34
Cumella vulgaris	1.30	2.40	2.26	0.98	5.14	59.47
Americorophium salmonis	2.10	1.04	2.01	0.90	4.57	64.04
Scoloplos armiger	0.00	2.40	1.97	0.83	4.49	68.53
Macoma balthica	3.88	3.82	1.96	1.00	4.47	73.00
Glycinde picta	0.07	1.99	1.67	0.85	3.79	76.79
Fabricia stellaris	0.00	1.85	1.55	0.75	3.52	80.31
Oligochaeta	1.56	0.53	1.52	0.74	3.46	83.77
Exogone lourei	0.00	1.88	1.50	0.65	3.42	87.19
Nephtys caeca	0.00	1.78	1.40	0.65	3.19	90.38
Eogammarus confervicolus	0.20	0.85	0.82	0.51	1.86	92.24
Macoma nasuta	0.00	0.75	0.61	0.55	1.40	93.63
Aricidea hartleyi	0.60	0.00	0.47	0.38	1.08	94.71
Scolelepis squamata	0.00	0.57	0.45	0.39	1.02	95.73
Balanus glandula	0.23	0.31	0.44	0.52	0.99	96.72
Alitta brandti	0.00	0.41	0.35	0.35	0.79	97.51
TB vs WC Average dissimilarity = 54.05%	TB	WC				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Harpacticoida	**5.03**	**9.25**	**5.10**	**1.26**	**9.43**	**9.43**
Ostracoda	**1.67**	**4.97**	**4.32**	**1.38**	**8.00**	**17.44**
Eteone californica	**0.00**	**3.88**	**4.31**	**1.55**	**7.97**	**25.41**

(*Continued*)

Table 4. (Continued).

TB vs WC Average dissimilarity = 54.05%	TB	WC				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
***Capitella* species complex**	**4.82**	**6.19**	**4.17**	**1.18**	**7.72**	**33.13**
Macoma balthica	**0.30**	**3.82**	**4.02**	**1.68**	**7.45**	**40.58**
Nematoda	**9.68**	**12.60**	**3.86**	**1.41**	**7.14**	**47.72**
Isotomidae sp.	2.11	2.61	3.54	0.94	6.55	54.27
Chironomidae larvae	1.43	2.40	2.92	0.95	5.41	59.68
Pygospio elegans	0.00	2.45	2.45	1.00	4.53	64.21
Cumella vulgaris	0.00	2.40	2.45	0.88	4.53	68.74
Scoloplos armiger	0.00	2.40	2.35	0.83	4.34	73.08
Glycinde picta	0.00	1.99	1.98	0.84	3.66	76.73
Fabricia stellaris	0.00	1.85	1.85	0.75	3.42	80.15
Exogone lourei	0.00	1.88	1.78	0.66	3.29	83.44
Nephtys caeca	0.00	1.78	1.65	0.66	3.06	86.50
Americorophium salmonis	0.13	1.04	1.14	0.54	2.11	88.62
Oligochaeta	0.70	0.53	1.14	0.54	2.11	90.73
Nippoleucon hinumensis	0.37	0.66	0.93	0.46	1.72	92.45
Eogammarus confervicolus	0.00	0.85	0.86	0.46	1.58	94.03
Macoma nasuta	0.00	0.75	0.73	0.55	1.35	95.38
Scolelepis squamata	0.00	0.57	0.53	0.39	0.98	96.36
Alitta brandti	0.07	0.41	0.47	0.37	0.87	97.23
Balanus glandula	0.00	0.31	0.36	0.42	0.66	97.89

Sediment parameters

Mudflat sediment parameters varied significantly for all site comparisons (Table 3). Particle size consistently contributed the most to comparisons including CC, but only consistently contributed to TB vs. WC comparisons in Sampling Round A, as shown by the Sq.Dist/SD ratio greater than 1 (Table 5). Sediment at CC had a smaller grain size than at other mudflats, indicating that it was composed of a higher proportion of silt and clay (Table S2). For TB vs. WC comparisons, macrophyte cover followed by wood cover contributed the most to the observed variation, although these were not consistent contributions as shown by the Sq.Dist/SD ratio smaller than 1 (Table 5). Differences between sites in macrophyte cover were driven by substantially higher values at WC, and we are unaware why macrophyte cover is so much higher at this site (Table S2). Conversely, the elevated amount of wood cover observed at TB is a result of accumulated sawdust on this mudflat, a product of a historical sawmill run in the area. Finally, no mudflat site had any *Zostera marina* cover; however, extensive eelgrass beds are located elsewhere in the Skeena estuary (Carr-Harris et al. 2015; Moore et al. 2016). Sandy shore sediment properties varied significantly for all site comparisons (Table 7). Particle size consistently contributed to differences in BO Vs GU comparisons and GU Vs PI comparisons, as shown by Sq.Dist/SD ratio greater than 1, although it did not necessarily contribute the largest percent of the variation (Table 9). Sediment particle size at GU was higher than at the other sandy shores, indicating that habitat comprised of a higher proportion of sand. Other sediment parameters did vary over time and space but did not vary in a systematic manner.

Considerable overlap between mudflat and sandy shores was observed for most sediment parameters, with the main observed difference between habitat types,

Table 5. SIMPER (Similarity Percentages) results showing percent contribution (%) of each sediment variable collected at each quadrat (normalised) to the dissimilarity in sediment conditions between three intertidal mudflats on the north coast of British Columbia, Canada, during summer of 2017. All variables were SQRT(X) transformed. Av. Sq. Dist: Average squared distance. Sq Dis/SD: Ratio of the average squared distance to the standard deviation. Values >1, denoted in bold, represent variables that consistently contribute to the observed differences between mudflats. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. aRPD: apparent redox potential discontinuity. Round A: 23 May–1 June. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August. Av.Sq.Dist: Average Squared Distance. Sq.Dist/SD: Squared Distance over standard deviation.

CC vs TB; Round A Average squared distance = 13.21				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**2.93**	**1.14**	**22.19**	**22.19**
Wood cover (%)	2.23	0.57	16.91	39.09
Water content (%)	2.12	0.71	16.06	55.15
aRPD (mm)	2.01	0.91	15.24	70.40
Penetrability (cm)	1.97	0.72	14.93	85.32
Macrophyte cover (%)	1.94	0.51	14.68	100.00
CC vs TB; Round B Average squared distance = 13.51				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size	**2.78**	**1.02**	**20.59**	**20.59**
Wood cover (%)	2.56	0.70	18.93	39.52
aRPD (mm)	2.14	0.46	15.85	55.37
Macrophyte cover (%)	2.07	0.30	15.32	70.69

CC Vs WC; Round A Average Squared Distance = 14.46				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle Size (µm)	**3.36**	**1.91**	**23.22**	**23.22**
Macrophyte Cover (%)	2.54	0.64	17.54	40.76
Water Content (%)	2.22	0.61	15.34	56.09
Penetrability (cm)	2.17	0.67	15.00	71.09
aRPD (mm)	2.13	0.92	14.71	85.80
Wood Cover (%)	2.05	0.32	14.20	100.00
CC Vs WC; Round B Average Squared Distance = 14.14				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**2.99**	**1.66**	**21.16**	**21.16**
Macrophyte cover (%)	2.79	0.78	19.70	40.85
Water content (%)	2.27	0.91	16.07	56.92
aRPD (mm)	2.14	0.46	15.14	72.06

TB vs WC; Round A Average squared distance = 12.79				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Macrophyte cover (%)	2.55	0.65	19.95	19.95
Wood cover (%)	2.30	0.57	17.99	37.94
Particle size (µm)	**2.04**	**1.01**	**15.98**	**53.92**
Penetrability (cm)	2.01	0.67	15.68	69.60
aRPD (mm)	1.95	0.59	15.27	84.87
Water content (%)	1.93	0.66	15.13	100.00
TB vs WC; Round B Average squared distance = 13.48				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Macrophyte cover (%)	3.08	0.82	22.83	22.83
Wood cover (%)	2.60	0.71	19.29	42.13
Particle size (µm)	1.97	0.76	14.61	56.74
Water content (%)	1.96	0.70	14.57	71.31

(*Continued*)

Table 5. (Continued).

CC vs TB; Round B Average squared distance = 13.51				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Water content (%)	2.02	0.75	14.94	85.62
Penetrability (cm)	1.94	0.66	14.38	100.00
CC vs TB; Round C Average squared distance = 13.69				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**2.81**	**1.07**	**20.51**	**20.51**
Water content (%)	2.43	0.77	17.72	38.23
Wood cover (%)	2.23	0.47	16.31	54.54
Penetrability (cm)	2.22	0.66	16.24	70.78
Macrophyte cover (%)	2.06	0.49	15.06	85.84
aRPD (mm)	1.94	0.58	14.16	100.00
CC vs TB; Round D Average squared distance = 13.94				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.26**	**1.32**	**23.39**	**23.39**
Wood cover (%)	2.38	0.75	17.05	40.44
aRPD (mm)	2.23	0.60	16.00	56.44
Penetrability (cm)	2.17	0.64	15.54	71.98
Water content (%)	1.97	0.79	14.12	86.10
Macrophyte cover (%)	1.94	0.36	13.90	100.00

CC Vs WC; Round B Average Squared Distance = 14.14				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Wood cover (%)	2.00	0.27	14.14	86.20
Penetrability (cm)	1.95	0.74	13.80	100.00
CC vs WC; Round C Average squared distance = 15.27				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.21**	**1.83**	**21.03**	**21.03**
Water content (%)	**3.17**	**1.10**	**20.79**	**41.82**
Macrophyte cover (%)	2.67	0.94	17.51	59.33
Penetrability (cm)	2.21	0.70	14.47	73.80
Wood cover (%)	2.06	0.36	13.52	87.32
aRPD (mm)	1.94	0.51	12.68	100.00
CC vs WC; Round D Average squared distance = 16.39				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.63**	**2.32**	**22.13**	**22.13**
Water content (%)	**3.30**	**1.18**	**20.13**	**42.25**
Macrophyte cover (%)	2.73	0.79	16.63	58.89
Penetrability (cm)	2.67	1.06	16.30	75.18
Wood Cover (%)	2.12	0.39	12.94	88.13
aRPD (mmc	1.95	0.75	11.87	100.00

TB vs WC; Round B Average squared distance = 13.48				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Penetrability (cm)	1.93	0.65	14.35	85.65
aRPD (mm)	1.93	0.64	14.35	100.00
TB vs WC; Round C Average squared distance = 12.91				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Macrophyte cover (%)	2.76	0.96	21.39	21.39
Wood cover (%)	2.35	0.47	18.20	39.59
Water content (%)	1.98	0.85	15.35	54.94
aRPD (mm)	1.95	0.62	15.09	70.04
Penetrability (cm)	1.93	0.85	14.99	85.02
Particle size	1.93	1.04	14.98	100.00
TB vs WC; Round D Average squared distance = 13.79				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Macrophyte cover (%)	2.74	0.79	19.87	19.87
Wood cover (%)	2.50	0.76	18.16	38.03
Water content (%)	2.42	0.94	17.58	55.61
aRPD (mm)	2.15	0.50	15.58	71.18
Penetrability (cm)	2.04	0.79	14.78	85.97
Particle size (µm)	1.93	0.97	14.03	100.00

Table 6. SIMPER (Similarity Percentages) results showing percent contribution (%) of food availability collected at each quadrat (normalised) to the dissimilarity in sediment conditions between three intertidal mudflats on the north coast of British Columbia, Canada, during summer of 2017. All variables were Log(X + 1) transformed. Av. Sq. Dist: Average squared distance. Sq Dis/SD: Ratio of the average squared distance to the standard deviation. Values >1, denoted in bold, represent variables that consistently contribute to the observed differences between mudflats. CC: Cassiar Cannery. TB: Tyee Banks. WC: Wolfe Cove. Round A: 23 May–1 June. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August. Av.Sq.Dist: Average Squared Distance. Sq.Dist/SD: Squared Distance over standard deviation.

CC vs WC; Round A Average squared distance = 4.49					CC vs TB; Round C Average squared distance = 4.32				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Organic matter content (%)	**2.46**	**1.07**	**54.79**	**54.79**	Organic matter content (%)	2.27	0.91	52.53	52.53
Chlorophyll *a* concentration (mg/ m^2)	2.03	0.61	45.21	100	Chlorophyll *a* concentration (mg/ m^2)	2.05	0.84	47.47	100
CC vs WC; Round C Average squared distance = 5.82					TB vs WC; Round C Average squared distance = 4.63				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Organic matter content (%)	**3.39**	**1.42**	**58.31**	**58.31**	Chlorophyll *a* concentration (mg/ m^2)	2.36	0.73	50.99	50.99
Chlorophyll *a* concentration (mg/ m^2)	2.43	0.78	41.69	100	Organic matter content (%)	2.27	0.83	49.01	100
CC vs WC; Round D Average squared distance= 5.74					TB vs WC; Round D Average squared distance = 4.83				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Organic matter content (%)	**3.45**	**1.56**	**60.17**	**60.17**	Organic matter content (%)	2.49	0.58	51.45	51.45
Chlorophyll *a* concentration (mg/ m^2)	2.29	0.91	39.83	100	Chlorophyll *a* concentration (mg/ m^2)	2.34	0.99	48.55	100

Table 7. Permutational multivariate analysis of variance (PERMANOVA) results quantifying the spatiotemporal variation in a) invertebrate community, and b) sediment variables (water content, sediment particle size, aRPR depth [apparent redox potential discontinuity], as well as cover of eelgrass, wood and macrophytes) and c) the food availability (organic matter content, and chlorophyll *a* concentration) at three intertidal sandy shores on the north coast of British Columbia, Canada during the summer of 2017. Significant *p* values (α < 0.05) are denoted in bold. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet.

Source	df	MS	Pseudo-F	Unique permutations	*p*
A) Invertebrate community					
Site	**2**	**51,149.00**	**32.73**	**4914**	**0.0002**
Round	**3**	**1740.10**	**3.21**	**4970**	**0.0002**
Transect(site)	**12**	**1562.60**	**2.75**	**4951**	**0.0002**
Site X round	**6**	**1663.70**	**3.07**	**4964**	**0.0002**
Round A: BO vs GU	**1**	**13,614.00**	**25.27**	**4986**	**0.0002**
Round A: BO vs PI	**1**	**10,617.00**	**17.00**	**4986**	**0.0002**
Round A: GU vs PI	**1**	**21,565.00**	**45.54**	**4979**	**0.0002**
Round B: BO vs GU	**1**	**9918.8**	**13.49**	**4984**	**0.0002**
Round B: BO vs PI	**1**	**11,329**	**16.54**	**4987**	**0.0002**
Round B: GU vs PI	**1**	**18,907**	**28.64**	**4982**	**0.0002**
Round C: BO vs GU	**1**	**12,073.00**	**16.15**	**4978**	**0.0002**
Round C: BO vs PI	**1**	**7992.20**	**11.02**	**4981**	**0.0002**
Round C: GU vs PI	**1**	**17,079.00**	**28.71**	**4987**	**0.0002**
Round D: BO vs GU	**1**	**12,258.00**	**16.92**	**4978**	**0.0002**
Round D: BO vs PI	**1**	**8833.90**	**12.75**	**4988**	**0.0002**
Round D: GU vs PI	**1**	**18,955.00**	**47.17**	**4978**	**0.0002**
Round X transect(site)	36	542.53	0.95	4929	0.67
Residual	120	568.16			
Total	179				
B) Sediment parameters					
Site	**2**	**236.21**	**36.66**	**4896**	**0.0002**
Round	**3**	**12.25**	**3.49**	**4979**	**0.0002**
Transect(site)	**12**	**6.44**	**1.57**	**4960**	**0.0038**
Site X round	**6**	**8.03**	**2.28**	**4975**	**0.0004**
Round A: BO vs GU	**1**	**59.93**	**11.73**	**4988**	**0.0002**
Round A: BO vs PI	**1**	**49.55**	**9.04**	**4977**	**0.0002**
Round A: GU vs PI	**1**	**76.07**	**30.90**	**4982**	**0.0002**
Round B: BO vs GU	**1**	**37.77**	**9.86**	**4983**	**0.0002**
Round B: BO vs PI	**1**	**57.37**	**18.33**	**4987**	**0.0002**
Round B: GU vs PI	**1**	**78.27**	**32.84**	**4983**	**0.0002**
Round C: BO vs GU	**1**	**48.28**	**13.98**	**4982**	**0.0002**
Round C: BO vs PI	**1**	**33.55**	**8.43**	**4984**	**0.0002**
Round C: GU vs PI	**1**	**83.37**	**37.88**	**4982**	**0.0002**
Round D: BO vs GU	**1**	**64.20**	**22.25**	**4985**	**0.0002**
Round D: BO vs PI	**1**	**42.00**	**11.42**	**4979**	**0.0002**
Round D: GU vs PI	**1**	**95.87**	**54.63**	**4983**	**0.0002**
Round X transect(site)	36	3.52	0.86	4934	0.93
Residual	120	4.1			
Total	179				
C) Food availability					
Site	**2**	**62.46**	**47.88**	**996**	**0.001**
BO vs GU	**1**	**82.66**	**62.79**	**4987**	**0.0002**
BO vs PI	**1**	**57.84**	**37.89**	**4989**	**0.0002**
GU vs PI	**1**	**84.05**	**64.42**	**4984**	**0.0002**
Round	**3**	**42.41**	**96.67**	**999**	**0.001**
Transect(site)	**12**	**1.3**	**2.26**	**999**	**0.002**
Site X round	6	0.84	1.91	998	0.052
Round X transect(site)	36	0.44	0.76	996	0.92
Residual	120	0.58			
Total	179				

Table 8. SIMPER (Similarity Percentages) tables determining the contribution of each taxonomic grouping to the observed differences between three intertidal sandy shores on the north coast of British Columbia, Canada during summer of 2017. Diss/SD represents the ratio of the dissimilarity to the standard deviation. Values >1, denoted in bold, represent groups that consistently contribute to the observed differences between sandy shores. Taxa with Diss/SD <1 did not consistently contribute to the observed differences between sandy shores. Only groups that contributed ≥0.5% to the observed differences between sandy shores are shown. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet. Abundances are fourth root transformed.

BO vs GU						
Average dissimilarity = 53.16%	BO	GU				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Cumella vulgaris	**7.95**	**0.13**	**6.65**	**2.56**	**12.51**	**12.51**
***Leptochelia* spp.**	**8.64**	**1.05**	**6.65**	**1.89**	**12.50**	**25.01**
Harpacticoida	**9.33**	**13.21**	**4.43**	**1.36**	**8.33**	**33.34**
Oligochaeta	**4.37**	**3.96**	**3.76**	**1.11**	**7.08**	**40.42**
Ostracoda	**5.13**	**2.15**	**3.54**	**1.30**	**6.65**	**47.08**
Nutricola tantilla	**4.41**	**1.24**	**3.40**	**1.27**	**6.39**	**53.47**
Nematoda	**12.63**	**15.17**	**3.16**	**1.29**	**5.94**	**59.41**
Capitella species complex	2.64	0.00	2.22	0.97	4.17	63.58
Macoma balthica	2.58	0.29	2.20	0.93	4.14	67.72
Exogone lourei	1.79	0.07	1.46	0.74	2.74	70.47
Isotomidae sp.	1.09	0.89	1.44	0.59	2.71	73.18
Chironomidae Larvae	1.13	0.21	1.00	0.60	1.88	75.06
Macoma nasuta	1.19	0.00	0.97	0.68	1.82	76.89
Axiothella rubrocinata	1.12	0.07	0.92	0.58	1.74	78.63
Balanus glandula	0.88	0.31	0.88	0.78	1.66	80.29
Littorina scutulata	0.71	0.16	0.64	0.85	1.20	81.49
Eogammarus confervicolus	0.76	0.00	0.60	0.44	1.14	82.62
Nephtys caecoides	0.74	0.00	0.59	0.44	1.12	83.74
Americorophium brevis	0.73	0.00	0.56	0.39	1.05	84.79
Eteone californica	0.50	0.13	0.47	0.40	0.88	85.67
Clinocardium nuttalii	0.35	0.24	0.46	0.45	0.87	86.53
Nucella ostrina	0.53	0.00	0.46	0.80	0.86	87.40
Owenia johnsoni	0.42	0.13	0.42	0.37	0.80	88.19
Saxidomus gigantea	0.45	0.00	0.40	0.45	0.76	88.95
Glycinde picta	0.27	0.19	0.35	0.32	0.67	89.62
Pagurus hirsutiusculus	0.39	0.00	0.34	0.68	0.64	90.26
Littorina sitkana	0.34	0.08	0.34	0.63	0.63	90.89
Eohaustorius washingtonianus	0.08	0.28	0.30	0.25	0.57	91.47
Hemigrapsus oregonensis	0.29	0.07	0.29	0.34	0.55	92.01
Leptosynapta albicans	0.35	0.00	0.29	0.30	0.54	92.55
Lottia pelta	0.33	0.02	0.29	0.50	0.54	93.09
Phoronis architecta	0.00	0.33	0.27	0.30	0.51	93.60
BO vs PI						
Average dissimilarity = 50.50%	BO	PI				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Exogone lourei	**1.79**	**8.69**	**4.90**	**1.87**	**9.71**	**9.71**
Cumella vulgaris	**7.95**	**1.78**	**4.33**	**1.87**	**8.57**	**18.28**
Oligochaeta	**4.37**	**9.15**	**3.86**	**1.46**	**7.64**	**25.92**
Harpacticoida	**9.33**	**4.52**	**3.53**	**1.32**	**7.00**	**32.92**
Scoletoma zonata	**0.08**	**5.01**	**3.35**	**1.61**	**6.63**	**39.55**
***Leptochelia* spp.**	**8.64**	**11.13**	**3.28**	**1.15**	**6.50**	**46.05**
Nutricola tantilla	**4.41**	**0.75**	**2.72**	**1.28**	**5.39**	**51.44**
Ostracoda	**5.13**	**4.55**	**2.59**	**1.22**	**5.13**	**56.57**
***Capitella* Species Complex**	**2.64**	**2.26**	**1.88**	**1.12**	**3.72**	**60.29**
Macoma balthica	**2.58**	**0.28**	**1.72**	**0.94**	**3.40**	**63.69**
Nematoda	**12.63**	**13.01**	**1.68**	**1.25**	**3.33**	**67.02**
Axiothella rubrocinata	**1.12**	**2.41**	**1.63**	**1.03**	**3.22**	**70.24**
Isotomidae sp.	1.09	1.72	1.51	0.76	2.99	73.23
Eogammarus confervicolus	0.76	2.10	1.50	0.87	2.97	76.20

(*Continued*)

Table 8. (Continued).

BO vs PI Average dissimilarity = 50.50%	BO	PI				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
Leptosynapta albicans	0.35	1.80	1.24	0.83	2.46	78.65
Macoma nasuta	1.19	0.48	0.91	0.78	1.80	80.46
Chironomidae Larvae	1.13	0.00	0.71	0.56	1.40	81.86
Balanus glandula	0.88	0.14	0.63	0.76	1.24	83.10
Armandia brevis	0.00	0.83	0.55	0.43	1.09	84.19
Eteone californica	0.50	0.41	0.53	0.48	1.05	85.24
Americorophium brevis	0.73	0.13	0.50	0.42	1.00	86.24
Littorina scutulata	0.71	0.13	0.49	0.86	0.96	87.20
Nephtys caecoides	0.74	0.04	0.48	0.46	0.96	88.16
Pagurus hirsutiusculus	0.39	0.52	0.39	1.03	0.78	88.93
Macoma inquinata	0.19	0.47	0.38	0.47	0.74	89.68
Nucella ostrina	0.53	0.00	0.35	0.81	0.70	90.38
Clinocardium nuttalii	0.35	0.22	0.35	0.46	0.70	91.08
Mediomastus californiensis	0.08	0.43	0.33	0.35	0.65	91.73
Saxidomus gigantea	0.45	0.04	0.33	0.47	0.65	92.38
Hemigrapsus oregonensis	0.29	0.20	0.30	0.39	0.60	92.98
Owenia johnsoni	0.42	0.00	0.26	0.33	0.52	93.50
Littorina sitkana	0.34	0.12	0.26	0.68	0.52	94.02
GU vs PI Average dissimilarity = 59.46%	GU	PI				
Species	Abundance	Abundance	Av.Diss	Diss/SD	Contribution (%)	Cumulative (%)
***Leptochelia* spp.**	**1.05**	**11.13**	**8.72**	**2.64**	**14.66**	**14.66**
Harpacticoida	**13.21**	**4.52**	**7.70**	**1.79**	**12.95**	**27.61**
Exogone lourei	**0.07**	**8.69**	**7.46**	**2.67**	**12.54**	**40.15**
Oligochaeta	**3.96**	**9.15**	**5.42**	**1.65**	**9.11**	**49.26**
Scoletoma zonata	**0.09**	**5.01**	**4.27**	**1.63**	**7.18**	**56.44**
Ostracoda	**2.15**	**4.55**	**3.32**	**1.25**	**5.58**	**62.02**
Nematoda	**15.17**	**13.01**	**2.77**	**1.37**	**4.65**	**66.67**
Axiothella rubrocinata	**0.07**	**2.41**	**2.01**	**1.00**	**3.37**	**70.05**
Capitella species complex	0.00	2.26	1.91	0.89	3.21	73.26
Isotomidae sp.	0.89	1.72	1.79	0.78	3.00	76.26
Eogammarus confervicolus	0.00	2.10	1.73	0.78	2.92	79.18
Cumella vulgaris	0.13	1.78	1.55	0.69	2.61	81.79
Leptosynapta albicans	0.00	1.80	1.51	0.80	2.53	84.32
Nutricola tantilla	1.24	0.75	1.35	0.73	2.27	86.59
Armandia brevis	0.00	0.83	0.69	0.44	1.17	87.75
Pagurus hirsutiusculus	0.00	0.52	0.45	0.94	0.75	88.51
Macoma balthica	0.29	0.28	0.44	0.37	0.74	89.25
Eteone californica	0.13	0.41	0.43	0.38	0.73	89.97
Macoma nasuta	0.00	0.48	0.43	0.40	0.73	90.70
Mediomastus californiensis	0.00	0.43	0.36	0.33	0.61	91.31
Macoma inquinata	0.00	0.47	0.36	0.40	0.61	91.92
Balanus glandula	0.31	0.14	0.36	0.44	0.61	92.53
Clinocardium nuttalii	0.24	0.22	0.36	0.39	0.60	93.13

particle size, unsurprisingly indicating that sandy shore sediment is composed of more sand (larger particle size) than mudflats (Tables 1 and 2, Tables S1-S3 and Figure S1). Another prominent difference between sites was the depth of the aRPD (Table S2). aRPD depth was deeper at mudflat sites when compared to sandy shores, primarily as the aRPD was often located at the surface of sandy shore sites. In general, observed sediment parameters were similar to those at similar habitats along the north coast of BC (Gerwing et al. 2018a). When compared to similar habitats along Canada's Atlantic coast (Gerwing et al. 2015a), intertidal sediment in our study exhibited a mixture of silt/clay and sand (≥63 μm), resulting in higher

Table 9. SIMPER (Similarity Percentages) results showing percent contribution (%) of each sediment variable collected at each quadrat (normalised) to the dissimilarity in sediment conditions between three intertidal sandy shores on the north coast of British Columbia, Canada during summer of 2017. All variables were SQRT(X) transformed. Av. Sq. Dist: Average squared distance. Sq Dis/SD: Ratio of the average squared distance to the standard deviation. Values >1, denoted in bold, represent variables that consistently contribute to the observed differences between sandy shores. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet. Round A: 23 May–June 1. Round B: 21–26 June. Round C: 19–25 July. Round D: 18–24 August. aRPD: apparent redox potential discontinuity.

BO vs GU; Round A Average squared distance = 17.53					BO vs PI; Round A Average squared distance = 16.84					GU vs PI; Round A Average squared distance = 14.74				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.52**	**1.63**	**20.06**	**20.06**	**Penetrability (cm)**	**2.99**	**1.04**	**17.75**	**17.75**	**Particle size (µm)**	**3.48**	**1.56**	**23.61**	**23.61**
Water content	**3.14**	**1.07**	**17.92**	**37.98**	**Macrophyte cover (%)**	**2.8**	**1.15**	**16.62**	**34.37**	**Water content**	**3.12**	**1.01**	**21.18**	**44.79**
Macrophyte cover (%)	2.53	0.91	14.46	52.44	Water content	2.64	0.79	15.65	50.02	**Macrophyte cover (%)**	**3.07**	**1.28**	**20.85**	**65.65**
Zostera marina Cover (%)	2.18	0.48	12.46	64.9	*Zostera marina* Cover (%)	2.18	0.48	12.97	62.99	**Penetrability (cm)**	**2.88**	**1.31**	**19.54**	**85.19**
aRPD (mm)	2.15	0.5	12.26	77.15	aRPD (mm)	2.15	0.5	12.76	75.75	Wood cover (%)	2.18	0.42	14.81	100
Penetrability (cm)	2	0.47	11.44	88.59	Wood cover (%)	2.08	0.45	12.37	88.12	aRPD (mm)	0	0	0	100
Wood cover (%)	2	0.27	11.41	100	Particle size (µm)	2	0.83	11.88	100	*Zostera marina* cover (%)	0	0	0	100

BO vs GU; Round B Average squared distance = 12.18					Bo vs PI; Round B Average squared distance = 13.49					GU vs PI; Round B Average squared distance = 14.88				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.5**	**1.62**	**28.71**	**28.71**	**Penetrability (cm)**	**3.25**	**1.42**	**24.06**	**24.06**	**Macrophyte cover (%)**	**3.46**	**1.55**	**23.25**	**23.25**
Water content (%)	2.59	0.77	21.24	49.95	**Macrophyte cover (%)**	**3.24**	**1.23**	**24.03**	**48.1**	**Penetrability (cm)**	**3.2**	**1.35**	**21.49**	**44.74**
Macrophyte cover (%)	2.11	0.78	17.35	67.3	Water content (%)	2.69	0.88	19.95	68.04	**Particle size (µm)**	**3.19**	**1.62**	**21.4**	**66.14**
Zostera marina Cover (%)	2.05	0.6	16.79	84.09	*Zostera marina* Cover (%)	2.35	0.62	17.41	85.45	**Water content (%)**	**3.04**	**1.04**	**20.42**	**86.56**

(*Continued*)

Table 9. (Continued).

BO vs GU; Round B Average squared distance = 12.18					Bo vs PI; Round B Average squared distance = 13.49					GU vs PI; Round B Average squared distance = 14.88				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Penetrability (cm)	1.94	0.81	15.91	100	Particle size (µm)	1.96	0.65	14.55	100	*Zostera marina* cover (%)	2	0.27	13.44	100
aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100
Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100

BO vs GU; Round C Average squared distance = 12.89					BO vs PI; Round C Average squared distance = 11.90					GU vs PI; Round C Average squared distance = 15.22				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.48**	**1.65**	**26.99**	**26.99**	**Macrophyte cover (%)**	**2.9**	**1.03**	**24.36**	**24.36**	**Particle size (µm)**	**3.38**	**1.62**	**22.19**	**22.19**
Water content (%)	2.97	0.98	23.04	50.03	**Water content (%)**	**2.65**	**1.18**	**22.28**	**46.64**	**Penetrability (cm)**	**3.34**	**1.46**	**21.95**	**44.14**
Macrophyte cover (%)	2.32	0.89	18	68.03	Penetrability (cm)	2.39	0.97	20.08	66.72	**Macrophyte cover (%)**	**3.31**	**1.41**	**21.72**	**65.85**
Penetrability (cm)	2.09	0.32	16.21	84.24	Particle size (µm)	2.03	0.71	17.03	83.75	**Water content (%)**	**3.17**	**1.51**	**20.85**	**86.7**
Zostera marina Cover (%)	2.03	0.45	15.76	100	*Zostera marina* Cover (%)	1.93	0.56	16.25	100	*Zostera marina* cover (%)	2.02	0.47	13.3	100
aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100
Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100

BO vs GU: Round D Average squared distance = 13.95					BO vs PI; Round D Average squared distance = 12.47					GU vs PI; Round D Average squared distance = 16.06				
Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)	Variable	Av.Sq. Dist	Sq.Dist/ SD	Contribution (%)	Cumulative (%)
Particle size (µm)	**3.58**	**1.81**	**25.67**	**25.67**	**Penetrability (cm)**	**3.19**	**1.22**	**25.56**	**25.56**	**Particle size (µm)**	**3.58**	**1.92**	**22.29**	**22.29**
Water content (%)	**3.25**	**1.25**	**23.31**	**48.98**	**Water content (%)**	**2.83**	**1.31**	**22.7**	**48.26**	**Penetrability (cm)**	**3.56**	**1.79**	**22.17**	**44.46**
Macrophyte cover (%)	2.42	0.76	17.34	66.32	Macrophyte cover (%)	2.47	0.91	19.85	68.11	**Macrophyte cover (%)**	**3.47**	**1.66**	**21.61**	**66.07**
Penetrability (cm)	2.37	0.73	17	83.32	Particle size (µm)	2.02	0.71	16.18	84.3	**Water content (%)**	**3.2**	**1.53**	**19.91**	**85.98**
Zostera marina Cover (%)	2.33	0.57	16.68	100	*Zostera marina* Cover (%)	1.96	0.7	15.7	100	*Zostera marina* cover (%)	2.25	0.59	14.02	100
aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100	aRPD (mm)	0	0	0	100
Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100	Wood cover (%)	0	0	0	100

Table 10. SIMPER (Similarity Percentages) results showing percent contribution (%) of food availability collected at each quadrat (normalised) to the dissimilarity in sediment conditions between three intertidal sandy shores on the north coast of British Columbia, Canada during summer of 2017. All variables were Log(X + 1) transformed. Av. Sq. Dist: Average squared distance. Sq Dis/SD: Ratio of the average squared distance to the standard deviation. Values >1, denoted in bold, represent variables that consistently contribute to the observed differences between sandy shores. BO: Boulder Beach. GU: Coast Guard Beach. PI: Prescott Inlet.

BO vs GU
Average squared distance= 5.34

Variable	Av.Sq.Dist	Sq.Dist/SD	Contribution (%)	Cumulative (%)
Organic matter content (%)	**3.34**	**1.29**	**62.41**	**62.41**
Chlorophyll *a* voncentration (mg/m^2)	2.01	0.58	37.59	100
BO vs PI				
Average squared distance = 4.93				
Organic matter content (%)	2.94	0.82	59.68	59.68
Chlorophyll *a* concentration (mg/m^2)	1.99	0.63	40.32	100
GU vs PI				
Average squared distance = 5.37				
Organic matter content (%)	**3.38**	**1.14**	**62.89**	**62.89**
Chlorophyll *a* concentration (mg/m^2)	1.99	0.72	37.11	100

observed particle sizes (~173 µm). Finally, the aRPD was deeper and penetrability, water content as well as organic matter content were all higher on the Atlantic coast than observed in our study area (Gerwing et al. 2015a).

Food availability

Food availability at mud and sandflats was also variable through space and time (Table 3). Sampling Round B had no significant Site term (p = 0.21), whereas all Site comparisons were significant for Round C (p = 0.0002). For Rounds A and D, only certain site comparisons were significantly different (CC Vs WC for Round A; CC Vs WC and WC Vs TB for Round D). Organic matter content consistently contributed to differences between CC and WC, with sediment at CC exhibiting a higher organic matter content than at WC. Chlorophyll *a* content was highly variable over space and time, peaking at all mudflats in Round A and then decreasing to low levels for the rest of the summer (Table 6 and Table S2). Food availability at sandy shores showed spatiotemporal variation, but not a significant Round X Site interaction (p = 0.052; Table 6). Organic matter content (%) accounted for the largest proportion of the variation between sites, although it did not consistently contribute to observed variation between BO and PI (Table 9). In general, sediment organic matter content was highest at PI and lowest at GU. As with mudflats, sandy shore Chlorophyll *a* peaked in Round A and then declined to low levels for the rest of the summer (Table S3).

Organic matter tended to be observed in higher amounts at mudflats than sandy shores, while Chlorophyll *a* concentration exhibited the opposite pattern, with higher concentrations observed at sandy shores (Table S3). Similar organic matter content values were observed along BC's north coast (Gerwing et al. 2018a), as well as Canada's Atlantic coast (Gerwing et al. 2015a). Chlorophyll *a* concentrations observed in our study are similar to the lowest values observed along Canada's Atlantic coast; however, the

Table 11. Water column values (approximately 1 cm from sediment surface) at three mudflats near Prince Rupert and three sandy shores on Prescott Island, British Columbia during summer of 2017. "-" indicates that no data were collected from the sandy shores at low tide. As these habitats were not influenced by rivers, water chemistry did not need to be calculated at different points in the tidal cycle.

		Temperature (°C)		SpCond (µS/cm)		Salinity (ppt)		pH	
Site	Date	High tide	Low tide	High tide	Low tide	High tide	Low tide	High tide	Low tide
Cassiar Cannery	26-5-2017	8.88	8.38	23.15	7.95	13.96	4.39	7.70	8.10
	22-6-2017	10.34	10.08	14.44	7.09	8.39	3.91	7.63	7.78
	21-7-2017	12.17	12.85	28.56	20.18	17.63	120.08	7.68	7.70
	20-8-2017	12.17	12.30	26.40	21.18	16.18	13.14	7.88	7.91
Tyee Banks	23-5-2017	9.16	10.40	1.80	0.28	0.92	0.13	7.64	7.81
	21-6-2017	10.25	9.99	0.78	0.58	0.39	0.28	7.39	7.75
	19-7-2017	13.16	13.56	2.98	0.14	1.56	0.06	7.57	7.87
	18-8-2017	13.51	12.34	3.43	0.37	1.18	0.18	7.69	9.38
Wolfe Cove	25-5-2017	9.43	9.72	39.01	39.64	24.70	25.16	7.76	7.92
	23-6-2017	11.13	12.00	39.44	37.61	25.08	24.53	7.87	8.00
	20-7-2017	12.78	12.68	39.99	40.61	25.52	25.95	7.48	7.64
	19-8-2017	12.21	12.12	41.02	41.49	26.23	26.56	7.64	7.67
Boulder Beach	31-5-2017	10.86	-	48.69	-	31.65	-	7.27	-
	25-6-2017	10.99	-	56.64	-	46.64	-	806.00	-
	25-7-2017	12.24	-	47.57	-	47.57	-	8.20	-
	21-8-2017	12.34	-	45.95	-	45.95	-	7.87	-
Coast Guard Beach	1-7-2017	11.54	-	48.29	-	31.69	-	8.01	-
	26-6-2017	11.71	-	45.04	-	29.06	-	8.24	-
	24-7-2017	11.95	-	46.89	-	30.40	-	7.88	-
	23-8-2017	12.04	-	47.20	-	30.63	-	8.09	-
Prescot Inlet	28-5-2017	10.16	-	46.46	-	30.01	-	7.95	-
	24-6-2017	11.55	-	46.59	-	30.24	-	7.98	-
	23-7-2017	12.00	-	46.95	-	30.45	-	7.73	-
	24-8-2017	12.33	-	46.09	-	29.84	-	8.29	-

temporal pattern of peaks in early spring followed by declines over the summer was also observed on Atlantic mudflats (Gerwing et al. 2015a).

Water column characteristics

Water properties varied greatly among site type, site, sampling date and tide (Table 11); however, some trends were evident. Salinity and specific conductivity were consistently higher at the sandy shores (BO, PI, GU) than mudflats (CC, TB, WC), although the exact amount fluctuated between site and sampling date comparisons. This was expected as mudflat sites were influenced by freshwater inputs from the Skeena River, while sandy shores were entirely marine. When comparing individual sites, the difference in salinity at PI versus CC varied between 12.82ppt and 21.85ppt, whereas the difference in salinity at PI versus TB showed a narrower range but larger values (between 28.03ppt and 29.09ppt). The salinity and specific conductivity of marine sandy shores averaged 34.5ppt and 46.9 µS/cm, respectively, whereas estuarine beaches averaged 12.4ppt and 20.0 µS/cm across the site, sampling date and tide. TB consistently had the lowest salinity and specific conductivity of all the beaches (average of 0.7ppt and 1.3 µS/cm, respectively). pH was also higher at low tide compared to high tide (CC, TB, WC). The difference between high and low tide varied between 0.03 and 1.69, with TB showing the largest difference (average of 0.63) for all sampling times except for May where CC had a larger difference (0.40 compared to 0.17).

At CC and TB salinity and specific conductivity decreased at low tide, but this was not the case for WC. Instead, the salinity and specific conductivity at WC increased at low tide in May, July and August, and only decreased in June. This result was unexpected; however, WC showed the smallest change between high and low tide (>1ppt and 1 µS/cm). It is, therefore, possible that this is a result of the creek at the site, providing a constant influx of freshwater kept the salinity more constant than other beaches.

Conclusion

This study aimed to elucidate present conditions of invertebrate communities, sediment parameters and food availability of intertidal habitats located near the Skeena estuary. The Skeena salmon run contributes an estimated 110 USD million dollars annually to the local economy (Nibr 2006), therefore, degradation of the Skeena Estuary could have devastating consequences on both the economy and the ecosystem (Higgins and Schouwenburg 1973; Hilborn and Walters 1977). Given the history of development in the area, as well as the number of proposed future developments, the present conditions described above are critical to enhance our understanding of the Skeena river estuary. These data can be used to not only predict the impact of future development, but also to detect changes that may occur following development or disturbances. Comparisons to conditions presented here can hopefully alert land-use managers in the Skeena estuary to disturbances. This is particularly true with regards to the examined invertebrates, as they can be used as indicator species (Gómez Gesteira and Dauvin 2000; Amoozadeh et al. 2014; Gerwing et al. 2017b), alerting conservationists to potential impacts before commercial species, such as Pacific salmon, are impacted.

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