

*Sediment geochemistry influences
infaunal invertebrate community
composition and population abundances*

Article

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1 Sediment Geochemistry Influences Infaunal Invertebrate Community Composition and
2 Population Abundances

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14

15 **Abstract**

16 Infaunal invertebrate communities are structured by various factors, including predation,
17 resource availability, and environmental conditions. Given that these invertebrates live within
18 sediment, it is not surprising that sediment properties play a critical role in many infaunal
19 behaviours. When models explaining spatial and temporal variation in infaunal community
20 composition are constructed using physical, biophysical, environmental, and sediment properties
21 (salinity, detrital cover, elevation, particle size distribution, organic and water content, redox
22 conditions, and penetrability), a considerable portion of the variation in the data is typically

23 unaccounted for. This suggests that we do not fully understand all the variables that influence
24 infaunal invertebrate communities. One suite of under-explored variables is the elemental
25 composition/concentration of the sediments themselves. As such, we evaluated if sediment
26 geochemistry improved model performance of the spatial variation in infaunal invertebrate
27 communities on three intertidal mudflats in northern British Columbia, Canada. We observed
28 that models including geochemistry data outperformed models that only included physical,
29 biophysical, and environmental properties. Our results therefore suggest that some of the
30 observed, and previously unaccounted for spatial variation in infaunal community composition
31 may be a product of variation in sediment geochemistry. As such, sediment geochemistry should
32 be accounted for when studying infaunal communities and assessing human impacts upon
33 intertidal systems.

34

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

37

38 **Introduction**

39 Located at the interface between the land and the sea, intertidal ecosystems exist within a
40 world of extremes. Oscillating between exposure and inundation, hot and cold, safety and
41 danger, the intertidal is home to resilient and dynamic biological communities (Ferraro and Cole
42 2012; Musetta-Lambert et al. 2015; Delgado et al. 2018). Far from a uniform ecosystem, the
43 intertidal is a mosaic of marshes (Virgin et al. 2020), rocky shores (Menge et al. 1997), and
44 expanses of soft sediment, such as sandy beaches and mudflats (Barbeau et al. 2009). In coastal
45 ecosystems, infaunal (animals that live within the sediment) are often used to study or identify
46 disturbances (Fukuyama et al. 2014; Drylie et al. 2020; Gerwing et al. 2022a). For instance,
47 biodiversity and total abundance of infauna (Sherman and Coull 1980; Campbell et al. 2019b)
48 can be used to identify and study disturbances; however, infauna can respond to a disturbance in
49 a variety of ways. For instance, amphipods, cumacea, and small bivalves are sensitive to
50 disturbances, decreasing in abundances with disturbances (Sánchez-Moyano and García-Gómez
51 1998; Gerwing et al. 2022b). Conversely, Oligochaeta (Cowie et al. 2000), Nematoda (Mazzola
52 et al. 2000), and *Capitella* species complex (Pearson and Rosenberg 1978; Gerwing et al. 2022b)
53 are tolerant of disturbances, and can survive, or thrive in disturbed systems. Therefore, studying
54 the population and community dynamics of these intertidal invertebrates is useful to advance the
55 development of general ecological theories (Underwood and Fairweather 1989; Hamilton et al.
56 2006) and to undertake applied research, such as elucidating human impacts or the effectiveness
57 of restoration strategies (Pearson and Rosenberg 1978; Borja et al. 2008).

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

61 2015b). While all of these variables are important, given the intimate nature of the relationship
62 between infauna and the sediment they inhabit, it is not surprising that sediment properties have
63 been observed to play a critical role in most infauna behaviours, including locomotion, foraging,
64 reproduction, and larval settlement (Ólafsson et al. 1994; Lu and Grant 2008; Gerwing et al.
65 2020a). More specifically, sediment properties such as particle size distribution, water content,
66 organic matter content, redox state, and sediment penetrability/consistency have all been
67 observed to play important roles in shaping the composition of infaunal communities, by
68 influencing infauna behaviour, survival, and physiology (Diaz and Trefry 2006; Valdemarsen et
69 al. 2010; Pilditch et al. 2015a; Gerwing et al. 2018b; Gerwing et al. 2020a). These relationships
70 are far from unidirectional, as infauna can greatly modify their sedimentary environment (De
71 Backer et al. 2011; Quintana et al. 2013; Sizmur et al. 2013; Gerwing et al. 2017b).

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

83 influence infaunal invertebrate community composition and population size (Chapman et al.
84 1987; Waldock et al. 1999; Sizmur et al. 2019).

85 Elements that can negatively affect intertidal invertebrate communities are referred to as
86 potentially toxic elements (PTEs). While PTEs are naturally occurring, human activities may
87 elevate concentrations to levels that can induce deleterious impacts upon the physiology,
88 behaviour, and survival of flora and fauna (Martinez-Colon et al. 2009; Pourret and Bollinger
89 2018; Sizmur et al. 2019). The concentration and availability of PTEs have generated substantial
90 ecological insight in theoretical and applied settings (Chapman et al. 1987; Mermillod-Blondin
91 and Rosenberg 2006; Spencer and Harvey 2012). However, interactions between invertebrates
92 and sediment geochemistry are often studied in the context of contamination or pollution when
93 the concentrations present are many times greater than ambient background values (Chapman et
94 al. 1987; Yunker et al. 2011; Amoozadeh et al. 2014).

95 Another important group of elements found in intertidal sediments (which overlap with
96 PTEs) are essential elements. Essential elements are those that are required in specific
97 stoichiometric ratios for organisms to complete their life cycle (Karimi and Folt 2006; Bradshaw
98 et al. 2012). Previous investigations have focused upon the interaction between specific infaunal
99 species and the presence or availability of a few, albeit important, elements (Christensen et al.
100 2000; Teal et al. 2013; Kalman et al. 2014). What is currently lacking is a holistic understanding
101 of how sediment geochemistry, influences entire infaunal communities (Sizmur et al. 2019;
102 Eccles et al. 2020), and if the geochemical composition of sediments plays a greater role than
103 other sediment parameters in structuring infaunal communities.

104 To better understand how sediment geochemistry influences infaunal communities, we
105 quantified whether adding sediment geochemistry data (elemental concentrations) to models

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

115 **Methods**

116 **Study Sites**

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

129 (Families Phyllodocidae [*Eteone californica*], Capitellidae [*Capitella* Species Complex], and
130 Spionidae [*Pygospio elegans*]), Oligochaetes (*Paranais litoralis*), Nematodes, Copepods (order
131 Harpacticoida), Amphipods (*Americorophium salmonis*), and the bivalve *Macoma balthica*
132 (Gerwing et al. 2017a; Campbell et al. 2020) (Supplemental Table S1). Average volume
133 weighted sediment particle size varied from 60-180 μm , organic matter content varied from 2.5-
134 4.5%, and sediment water content from 28-37% (Campbell et al. 2020). No evidence of PTE
135 concentrations above naturally occurring levels was observed in the top 20 cm of sediment
136 (Sizmur et al. 2019). Observed elemental concentrations and all abiotic variables are detailed in
137 Supplemental Table S2. More details on these sites are available in Sizmur et al. (2019) and
138 Campbell et al. (2020).

139 **Sampling Scheme**

140 At each mudflat, transects were established running from the landward start of the
141 mudflat to the low water line (five transects per site, separated by ~25m and 60-200m long).
142 Transects were stratified into zones based on distance from shore (near, middle, and far). Within
143 each zone, one sampling location was randomly selected from which all data types, detailed
144 below, were collected ($n = 3$ per transect, 15 per site; 45 overall). Samples were collected July
145 13-25, 2017, on one of the lowest low tides of the year. More details of the sampling scheme can
146 be found in Campbell et al. (2020).

147 **Infauna, Sediment, and Environmental Parameter Sampling**

148 At each sampling location, a 1 m^2 plot was established and infauna were collected with a
149 corer 10 cm in length, and 7 cm in diameter. (Campbell et al. 2020). A pit (20 cm long, by 20 cm
150 wide, by 20 cm deep) was also dug in the plot where the core was taken to sample and identify
151 larger or more mobile specimens *in situ* (Campbell et al. 2019b) that may have been missed by

152 the infaunal core. Sediment from the core was passed through a 250 μm sieve, and the infauna
153 retained by the sieve were stored in vials of 95 % ethanol (Campbell et al. 2020). Specimens
154 were identified to the lowest possible taxonomic unit, as follows: cumaceans, amphipods,
155 tanaids, polychaetes, nemertean and bivalves were identified to species; chironomids (larvae) to
156 family; copepods to order; ostracods to class; and nematodes to phylum (Campbell et al. 2020;
157 Gerwing et al. 2020b). Observed abundances from the pit and cores were combined, making note
158 of the processed sediment from each method (Gerwing et al. 2022a), and converted to density
159 per m^2 .

160 At each sampling location, sediment penetrability was assessed by dropping a metal
161 weight (15 cm long, 1.9 cm diameter, 330 g) from a height of 0.75 m above the sediment and
162 measuring how far it penetrated into the sediment (Meadows et al. 1998; Gerwing et al. 2020a).
163 Penetrability is an integrative variable that reflects the overall *in situ* conditions experienced by
164 biota. Increased penetrability indicates finer-grained sediment with high water content, and fewer
165 rocks or shell hash present in or on the sediment. Sediment characterised by low penetrability is
166 indicative of larger-grained sediment with low water content and with more rocks or shell hash
167 present (Gerwing et al. 2020a). A sediment core (4.5 cm diameter, 5 cm depth) was collected
168 from each sampling location. From this core, the top 1 cm was processed to determine sediment
169 water content (mass lost by drying at 110 $^{\circ}\text{C}$ for 12 h), organic matter content (mass lost by
170 ashing at 550 $^{\circ}\text{C}$ for 4 h) and volume-weighted average particle size (Malvern Mastersizer 2000).
171 More details of these processes can be found in Campbell et al. (2020). While in the field, the
172 void created in the sediment from the collection of the infaunal core was used to determine the
173 depth to the apparent redox potential discontinuity, aRPD (Gerwing et al. 2013). aRPD depth is a
174 relative measure of sediment porewater dissolved oxygen and redox conditions. Sediment with a

175 deeper aRPD has more available dissolved oxygen, and the sediment is more oxidized, or less
176 reduced, than sediment with a shallower aRPD depth (Gerwing et al. 2015a; Gerwing et al.
177 2018b). We refer to these variables as physical variables.

178 The proportion of each 1 m² plots covered in woody debris, as well as deposited algae
179 and eelgrass (*Zostera* spp.) debris was also quantified visually, as this debris can create hypoxic
180 conditions and smother infauna. Such debris are commonly observed in the area. No eelgrass
181 detritus was observed at these sites during this period; therefore, eelgrass cover was not used in
182 any analyses. These variables are referred to as biophysical variables. Salinity was measured at
183 each transect in each tidal flat on each sampling trip with a YSI multimeter in the water
184 approximately 1 cm above the sediment surface at high tide (n = 5). Finally, relative distance of
185 each plot from the start of the mudflat (transition of saltmarsh, bedrock, or sandy beaches to mud
186 (see Gerwing et al. (2016)) was included for each plot, as a proxy for intertidal elevation or
187 duration of inundation. These variables are referred to as environmental variables.

188 **Sediment Geochemistry Sampling**

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

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

200 **Data Analysis**

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

205 **Data Visualization**

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

216 **Assessing Model Performance with Inclusion of Sediment Geochemistry**

217 To determine if models of the infaunal community (all species) that included sediment
218 geochemistry performed better than models that included other traditionally measured physical,
219 biophysical, and environmental parameters (distance from shore, salinity, algae, eelgrass, and

220 woody debris cover, sediment water content, organic matter content, mean particle size, aRPD
221 depth, and penetrability) a distance based linear model (DISTLM) was created using the BEST
222 routine (9999 permutations) was used. Infaunal data were fourth root transformed, while Sr was
223 square root transformed, and aRPD depth, water content, and mean particle size were fourth root
224 transformed to correct for skewed distributions. All physical, biophysical, and environmental
225 variables were normalized; however, variation exists in the precision of our variables. For
226 instance, the precision of visual estimates of detrital cover or organic matter content analyzed via
227 combustion is lower than that obtained from the spectrometry used to elucidate elemental
228 concentrations. We evaluated candidate models using the Information Theoretic Model Selection
229 Approach (Burnham and Anderson 2001; Burnham and Anderson 2002). This approach utilizes
230 multiple lines of evidence to select the “top” performing or “best” model from amongst a series
231 of candidate models designed a priori. All possible permutations of physical, biophysical, and
232 environmental variables were assessed. Candidate top-ranked models were selected by
233 calculating Akaike Information Criterion, corrected for small sample sizes (AICc) values.
234 Models within 2 AICc units of each other were considered to be equivalent (Burnham and
235 Anderson 2001; Burnham and Anderson 2002). Model performance was further assessed using
236 the R^2 value, which denotes the proportion of explained variation for the model (Anderson et al.
237 2008). R^2 values were contrasted between models only containing traditional physical,
238 biophysical, and environmental parameters, those only containing elements, and those containing
239 all variables.

240 **Exploring Relationships Between Elements and the Infaunal Community**

241 While DISTLMs are effective at comparing models, they are not able to determine the
242 relative importance of variables included in a model (Supplemental Figure S1). As such, a

243 permutational multivariate analysis of covariance (PERMANCOVA; 9999 permutations) was
244 also used to quantify the relationship between the infaunal community and physical, biophysical,
245 environmental, and geochemical variables (Gerwing et al. 2016). The multivariate response was
246 a resemblance matrix of the densities of the infaunal community, calculated using Bray-Curtis
247 similarity. Taxa densities were fourth root transformed to better equalize the influence of
248 abundant and rare species on the outcome of the analysis. Within the PERMANCOVA, site
249 (three levels; fixed factor), and transect nested within site (transect(site); five per site; random
250 factor) were included. Geochemical, as well as physical, biophysical, and environmental
251 variables were included as covariates. As part of the PERMANCOVA, we quantified
252 components of variation, the proportion of the multivariate variation accounted for by each
253 independent variable (Searle et al. 1992; Anderson et al. 2008; Gerwing et al. 2016). An α of
254 0.05 was used to determine statistical significance for all analyses (Beninger et al. 2012).
255 Elements identified as accounting for a statistically significant proportion of the variation in the
256 infaunal community were retained for downstream analysis (Pearson's univariate correlation
257 assessment).

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

266 **Results**

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

271 **Assessing Model Performance with Inclusion of Sediment Geochemistry Data**

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

278 **Exploring Relationships Between Sediment Properties and the Infaunal Community**

279 The PERMANCOVA (Table 1) identified that a mixture of environmental variables
280 (distance from shore, and salinity) and elements (K, Mn, P, SR, and Ti) were significantly
281 correlated to the observed variation in the infaunal community composition. No physical or
282 biophysical variables were statistically significant in this model. Environmental variables
283 accounted for 5% of this variation, while geochemistry accounted for 65%. The strongest
284 relationship was observed with Ti, with this single element accounting for 33% of the variation
285 in the infaunal community composition. Differences in the infaunal community between sites
286 and transects were not statistically significant, but the infaunal community varied between plots
287 (6%).

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

299 **Discussion**

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

303 **Assessing Model Performance with Inclusion of Sediment Geochemistry**

304 Inclusion of sediment geochemistry into models explaining the infaunal community
305 composition produced models that performed the best. These models were either comprised
306 exclusively of geochemical data, or a combination of geochemistry, physical, biophysical, and
307 environmental variables. Previous studies reporting models to explain the observed
308 spatiotemporal variation in the infaunal community using physical, biophysical, and
309 environmental variables, often leave a portion of the variation (20-97%) unaccounted for (Thrush

310 et al. 2003; Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al. 2020a; Norris 2021; Norris
311 et al. 2022). However, our results indicate that including sediment geochemistry into such
312 models, alongside sediment and environmental variables, will produce better performing models.
313 Further research exploring these relationships, as well as the interaction between sediment
314 geochemistry and other physical/environmental properties, will offer greater insight into how the
315 elemental composition of sediments influences infaunal community composition and dynamics.
316 Note, R^2 values can be sensitive to overfitting, with models with a higher number of terms
317 performing better, in some situations (Anderson et al. 2008). However, this does not seem to be
318 the case in our data, as models with more terms do not consistently perform better than more
319 parsimonious models (Supplemental Table S4). Further, AICc values were also used to evaluate
320 model performance, and AICc values penalize for every term included. As such, AICc values
321 also suggest that our models do not suffer from overfitting.

322 **Exploring Relationships Between Individual Variables and the Infaunal Community**

323 The infaunal community composition was statistically correlated (Table 1) with
324 environmental variables (5%; distance from shore, and salinity) as well as sediment
325 geochemistry (65%). Physical, and biophysical variables were not statistically correlated to
326 observed variation within the infaunal community. Interestingly, when similar analyses,
327 excluding sediment geochemistry, were conducted upon similar communities along Canada's
328 Pacific and Atlantic coasts (Gerwing et al. 2016; Campbell et al. 2020; Gerwing et al.
329 Submitted), physical, and biophysical parameters were significantly related to the infaunal
330 community and accounted for 9-11% of the observed. As discussed above, our findings here may
331 suggest that when sediment geochemistry is included in models, traditionally studied physical
332 and biophysical parameters (particle size, organic matter and water content penetrability, and

333 aRPD depth) may not be as important in explaining the structure of an infaunal community.
334 However, sediment variables exert a known influence upon infaunal communities, (Diaz and
335 Trefry 2006; Valdemarsen et al. 2010; Pilditch et al. 2015a; Gerwing et al. 2018b; Gerwing et al.
336 2020a), and it seems likely that sediment biophysical and geochemical properties both influence
337 infaunal community composition and population dynamics. More research is required to better
338 understand the relative importance of each variable, as well as how and why this varies spatially
339 and temporally.

340 In our analysis the site term was non-significant and accounted for none of the infaunal
341 community variation, while the transect term was also not significant, and the plot term only
342 accounted for 8% of the variation (Table 1). The plot and transect terms are likely a product of
343 local hydrology and delivery of larvae, intra and interspecific interactions, as well as post-
344 settlement dispersal and mortality (Flach and Beukema 1995; Bringloe et al. 2013; Drolet et al.
345 2013; Pilditch et al. 2015b; Gerwing et al. 2016; Sizmur et al. 2019; Norris et al. 2022). The lack
346 of statistical differences observed between sites, is in stark contrast to the apparent site level
347 clustering of infaunal communities observed between sites in Figure 2 (nMDS plot). The results
348 of similar investigations, that did not include elemental data, reported that the site term
349 accounted for 32-35% of the infaunal community variation, and the plot term 33-37% (Gerwing
350 et al. 2016; Campbell et al. 2020; Gerwing et al. Submitted). These authors hypothesized that the
351 observed variation in the infaunal community associated with this site term site term was likely a
352 product of processes such as larval supply (Weersing and Toonen 2009; Einfeldt and Addison
353 2013), post-settlement dispersal and mortality (Pilditch et al. 2015b), unmeasured site variables
354 such as hydrology, elemental concentrations (Sizmur et al. 2019), and exposure to waves/tides
355 (Williams et al. 2013; Gerwing et al. 2015b; Rubin et al. 2017), or disturbance and human

356 development history (Gerwing et al. 2017c; Gerwing et al. 2018a; Campbell et al. 2019a; Cox et
357 al. 2019). However, in our study, when sediment geochemistry was included in models of the
358 infaunal community, the variation attributed to the site and plot terms decreased and in the case
359 of our site term, became statistically insignificant. When taken together, these results suggest that
360 some, or even most, of the previously observed variation between sites and plots in infaunal
361 communities (as seen in Figure 2) may not be purely spatial in nature, nor the product of
362 unmeasured or unknown variables that vary at these spatial scales. Instead, this infaunal
363 community variation previously accounted for by spatial terms such as site or plot, may be the
364 product of variation in sediment geochemistry.

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

373 Sediment geochemistry can also be used to identify the provenance of sediments (Zhang
374 et al. 2014) and may indicate that the provenance of the sediment in an intertidal mudflat
375 influences the composition of the infaunal community. Whereas K, P, and to a certain extent Mn,
376 may be applied as fertilisers within the Skeena watershed and their enrichment representative of
377 sediments eroded from farmland, Ti (the element responsible for the greatest variation in
378 infaunal community composition) is a lithogenic element that has previously been found to

379 correlate positively with grain size (Bábek et al. 2015). It may therefore be the case that Ti
380 concentrations are a sensitive indicator of sediment grain size, which is already known to be a
381 property that shapes the composition of benthic infaunal communities (Coblentz et al. 2015).
382 Interestingly, when Ti and particle size were included in our analyses (Table 1) Ti was
383 significantly correlated with the infaunal community, while particle size was not. Nor was Ti
384 correlated with sediment particle size in our dataset (Pearson univariate correlation; $n = 45$, $p =$
385 0.13). Conversely, Ti can also have acute and chronic deleterious effects upon invertebrates (Das
386 et al. 2013). Finally, all of our measured elements and environmental variables could be
387 correlated with another, unmeasured variable, that is driving the observed infaunal change. For
388 instance, TB was characterized by lower infaunal abundances and higher concentrations of Ti, K
389 and S, lower concentrations of Mn, as well as lower salinity than the other sites. It is possible
390 that an unmeasured variable resulted in this variation, and more research is required to better
391 understand these relationships. Specifically, future studies should not only include more study
392 sites, spanning a broader range of environmental conditions, but also include more samples per
393 site to increase analytical resolution.

394 At the level of the infaunal invertebrate populations and individual elements, a complex
395 relationship was detected between sediment geochemistry and infaunal species, with a mixture of
396 positive and negative correlations observed (Table 2). Many of these elements are known to have
397 positive and negative impacts upon infaunal species (Smith 1984; Vitousek and Howarth 1991;
398 Tyrrell 1999; Little et al. 2017), but these impacts can vary between species and at different
399 concentrations (Pourret and Bollinger 2018; Sizmur et al. 2019; Eccles et al. 2020). Given the
400 correlational nature of the data presented in Table 2, we will not attempt to postulate causal
401 mechanisms. Especially as *in situ* context, such as information regarding nuanced ecological

402 interactions between species and covariates, is lacking. For instance, an observed positive
403 correlation could suggest that increasing concentrations of a given element induces immigration
404 into an area, enhances reproductive output, or has positive impacts upon survival and
405 physiological processes. Conversely, the element itself may have negative impacts upon a
406 species, however, it may have greater effects on a competitor, leading to competitive release. As
407 such, instead of postulating causal relationships, we suggest that more research incorporating
408 more study sites and more samples per site is required to untangle the complicated positive and
409 negative relationships observed in our study, between infaunal invertebrate community
410 composition and sediment geochemistry.

411 **Conclusions**

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

423

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433 **Conflict of Interest**

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

435 **Ethics approval**

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

437 **Data/Code Availability**

438 Available upon reasonable request

439 **Authors' Contribution**

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

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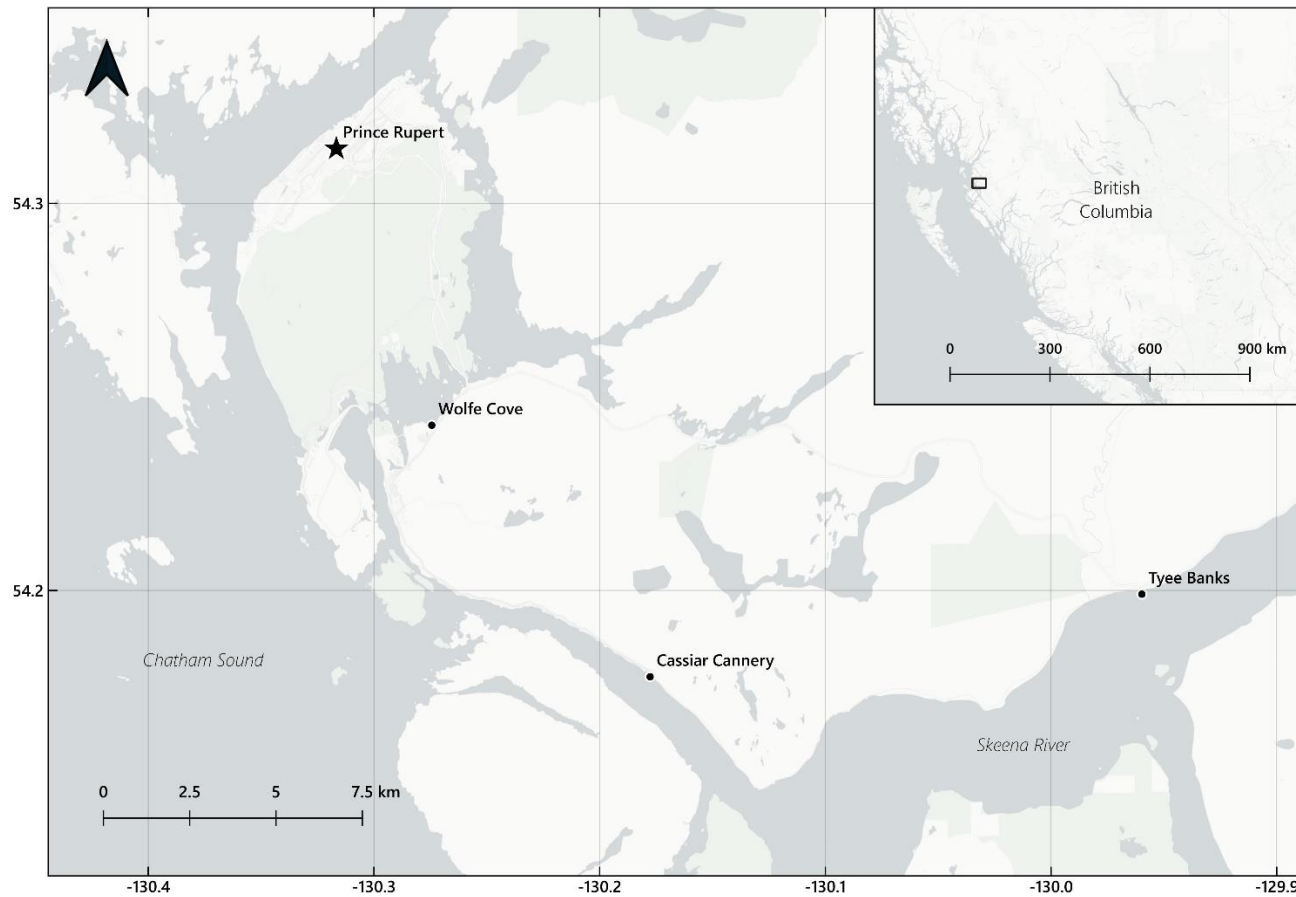
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716

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



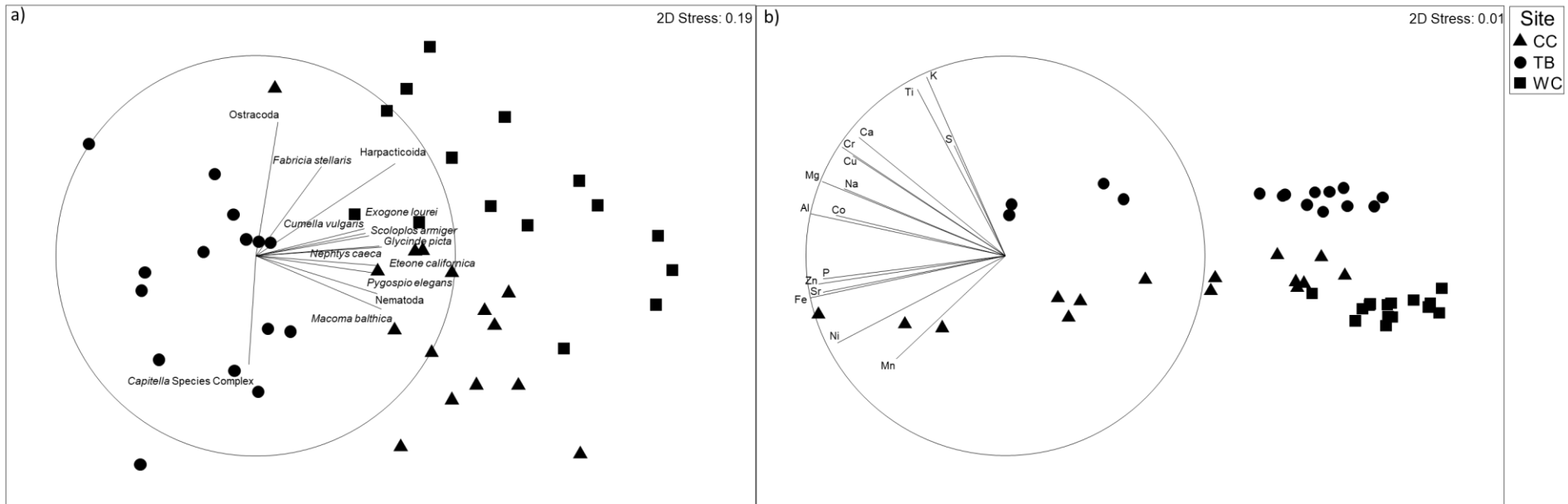


Figure 2: Non-metric multidimensional scaling (nMDS) plots exploring the variation in the infaunal community (a) and sediment geochemistry (b) at three intertidal mudflats near the Skeena Estuary in northern British Columbia, Canada. Vector overlays are overlain, and longer lines indicate greater values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

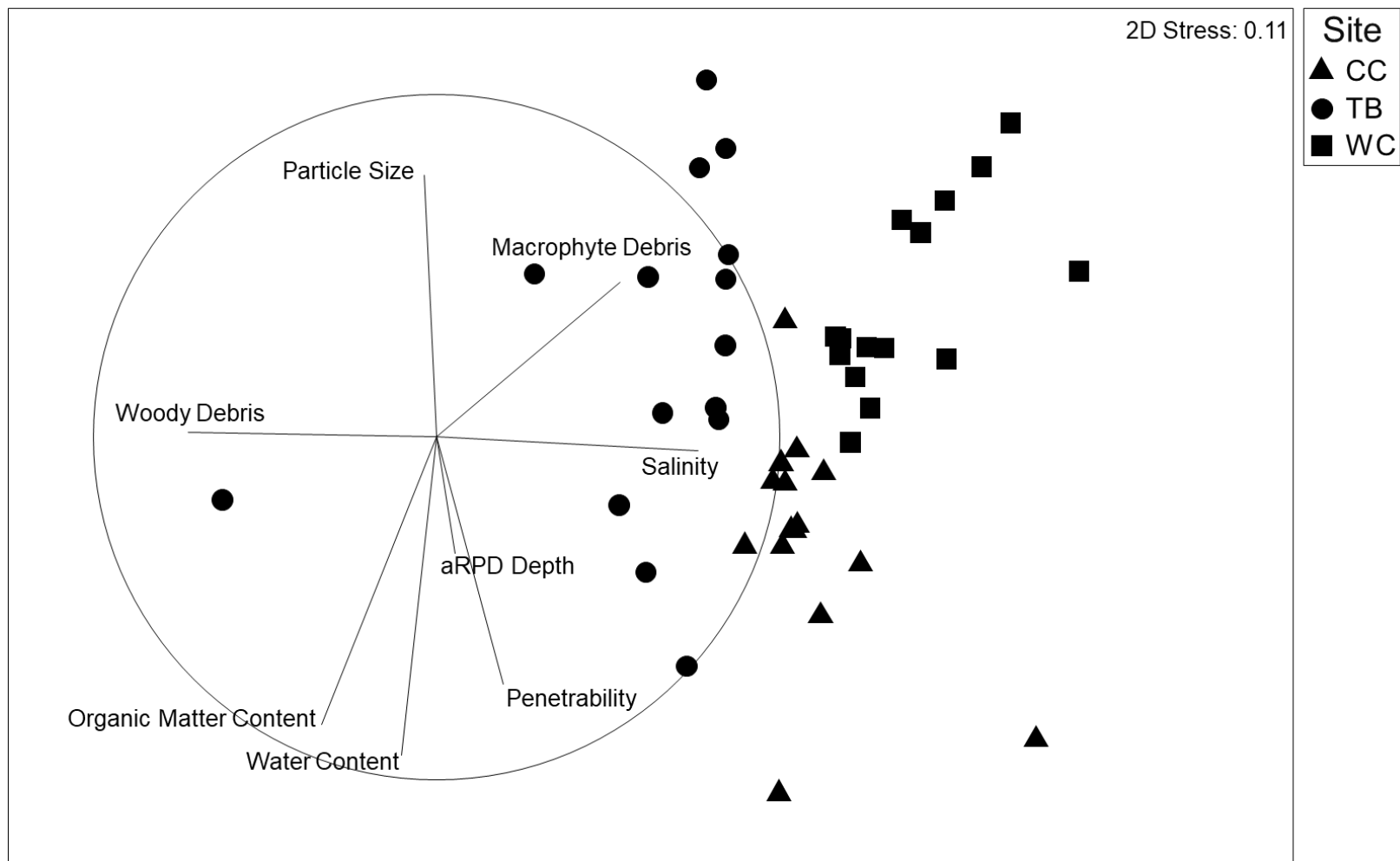


Figure 3: Non-metric multidimensional scaling (nMDS) plots exploring the variation in environmental parameters at three intertidal mudflats near the Skeena Estuary in northern British Columbia, Canada. Vector overlays are overlain, and longer lines indicate greater values associated with that parameter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

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

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

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

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