

# Structuring forces of intertidal infaunal communities on the northern coast of British Columbia, Canada: assessing the relative importance of top-down, bottom-up, middle-out, and abiotic variables

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## Abstract

While trophic and habitat-related abiotic variables (predation, competition, tolerance, etc.) are known to influence community structure in many ecosystems, some systems appear to be only minimally influenced by these variables. Sampling multiple tidal flat communities in northern BC, Canada, we investigated the relative importance of top-down and middle-out (mesopredators) variables, competition for resources (bottom up), and abiotic variables in structuring an infaunal community (invertebrates living in sediment). Similar to previous studies on mudflats in the Bay of Fundy (also at a north temperate latitude), we determined that these variables accounted for a minor (0%–9%) proportion of the observed variation in this infaunal community, suggesting that these variables play a small role in structuring this community. Based on the results of our study and in combination with previous experiments on infaunal recovery patterns post disturbance, we posit that the main factors influencing these infaunal communities likely operate at a scale of sites (kilometres) and/or plot (metres or less) but not transects (10–100 m within site). Candidate forces structuring these intertidal communities that need future examination include regional species pools and the variables that affect these pools, sediment biogeochemistry, and disturbance/recovery history of a site. The similarity of our Pacific coast findings to those from the north temperate Atlantic coast suggests some similarity in the processes structuring these distinct infaunal communities.

**Key words:** biological community, north Pacific coast, soft-sediment coastal ecosystem, species performance, tidal flats

## Introduction

An important goal in ecology is the development of general theories that can explain observed spatiotemporal variation in biological communities (Pearson and Rosenberg 1978; Hubbell 2005; Huston 2014). These then enhance our ability to predict outcomes of natural or anthropogenic disturbances (Pearson and Rosenberg 1978; Orwin et al. 2016), as well as of restoration following disturbance (Campbell et al. 2019a). Frameworks for theory on forces underlying community composition and dynamics include niche vs. neutral dynamics (Hubbell 2005) and the designation of such forces into categories related to habitat availability, species availability, and species performance once in the habitat (such as predation, competition, and tolerance to environmental conditions) (Pickett et al. 1987; Meiners et al. 2015), among other frameworks.

Here, we examine possible species performance forces (predation, competition, and response to certain abiotic conditions) underlying community structure. For instance, envi-

ronmental or abiotic variables, such as water salinity, temperature, or sediment properties, coupled with variations in exhibited tolerances of organisms for these conditions (Stillman 2002; Lu et al. 2008; Dashtgard et al. 2014; Sizmur et al. 2019) can play an important role in structuring communities (Kelaheer et al. 2001; Ferguson et al. 2013; Gerwing et al. 2022a). As well, interactions among the living components of an ecosystem can affect communities, namely top-down predation, which in our analysis, and as discussed below, may be indistinguishable from bioturbation (Heck Jr. and Valentine 2007; Hughes et al. 2014; Johnson et al. 2014) and bottom-up forces, such as the availability and competition for nutrients (Davis et al. 2014; Schuldt et al. 2014; Pilditch et al. 2015a). Many communities appear shaped by a combination of top-down and bottom-up forces (Hamilton et al. 2006; Bracken et al. 2014; Greenville et al. 2014). Added complexity is observed in systems with mesopredators (mid-trophic level predators) (Prugh et al. 2009), which act both as predator and prey (Ambrose Jr. 1991; Marczak et al. 2011). These species

can exert strong structuring influences upon a community via predation, bioturbation, and competition in a middle-out manner (Elmhagen and Rushton 2007; Quijón and Snelgrove 2008; Cunningham et al. 2020). Designing studies to elucidate the individual role of abovementioned forces in structuring a community is relatively straightforward; however, it is more difficult to quantify the relative importance of these forces, occurring concurrently, in determining community structure and dynamics (Wootton 1994; Agrawal et al. 2007; Dray et al. 2012; Gerwing et al. 2022b).

While trophic and habitat-related abiotic variables are known to influence community structure in many ecosystems, some systems appear to be only minimally influenced by them. For instance, ephemeral freshwater habitats, such as floodplains, can act as resource-pulse ecosystems (Crook et al. 2020; Nelson et al. 2021). In such systems, amply available resources, whose availability is temporally limited, trigger a cascading response throughout the ecosystem, minimizing the controlling influence of competition for resources, predation, and an individual species' preference for abiotic conditions (Tilman 2004; Letnic and Dickman 2010; Greenville et al. 2014). In resource-pulse systems, more research is required to better understand how these communities are structured. Another study, pertinent to our current study, focused on intertidal mudflats in the upper Bay of Fundy (NB and NS, Canada). Gerwing et al. (2016) assessed the relative importance of top-down, bottom-up, middle-out, and sediment-related abiotic variables in structuring the infaunal community (invertebrates living in the sediment). They observed that while top-down, bottom-up, middle-out, and abiotic variables accounted for a statistically significant proportion of the observed community variation (1%–11%), the majority of that variation (79%) was accounted for by spatial factors, such as study site or patch.

Gerwing et al. (2016) suggested two sets of hypotheses for their observed patterns. First, high abundance of resources on the expansive Bay of Fundy mudflats may both minimize bottom-up control (e.g., by limiting competition for nutrients from sediment organic matter and benthic diatoms) and support a sufficiently dense population of potential prey items to dilute the importance of top-down and middle-out predation/bioturbation. Furthermore, the relatively low importance of abiotic variables in structuring the infaunal community could be a result of generally low horizontal physical heterogeneity observed on their study sites, as well as high nutrient concentrations that limit the influence of abiotic factors by attracting animals to patches with abiotic characteristics that would normally reduce occupancy. Pulses of amply available resources may result in intertidal mudflats operating as a resource-pulse ecosystem. Secondly, Gerwing et al. (2016) also hypothesized that since mudflats are a relatively benign environment for organisms adapted to living in mud, the inhabiting communities were not predominantly structured by top-down, bottom-up, middle-out, or abiotic factors. Instead, these communities may reflect priority effects or a “first come, first served” process (Sutherland 1974; Connell and Slatyer 1977). Initial delivery of larvae or colonization by juveniles and adults may play a predominant role in explaining the observed spatiotemporal variation in this type of com-

munity (Snelgrove et al. 1999; Pilditch et al. 2015a;2015b). In contrast to the resource-pulse hypothesis, priority effects imply some competition for resources.

While these sets of hypotheses are intriguing, there are questions about their applicability to other tidal flat systems. The Bay of Fundy is home to the largest tides in the world, a phenomenon that results in considerable amounts of sediment being suspended in the water column each day (Wu et al. 2011). Sediment dynamics may be partly responsible for the relatively limited biodiversity exhibited on the upper Bay of Fundy mudflats, by filtering out species unable to survive in such situations. For instance, the community of these Bay of Fundy mudflats is composed of roughly 10 infaunal taxa, 3 top-down predators, and 3 mesopredators (Gerwing et al. 2015a). Conversely, mudflat communities on the Pacific coast of BC, Canada, are composed of roughly 39 infaunal taxa, 8 top-down consumers, and 12 mesopredators (Campbell et al. 2020). Given the unique characteristics of Bay of Fundy mudflats, it is unclear whether the hypotheses of Gerwing et al. (2016) can be applied to other mudflat or tidal flat communities. Moreover, field studies focused on infaunal community recovery from anthropogenic and natural disturbances along the Pacific and Atlantic coasts suggest that priority effects may not be the predominant force structuring these communities (Norris et al. 2022). Instead, community trajectories may be strongly influenced by species availability, particularly regional species pools (Beukema et al. 1999; Thrush et al. 2003; Gerwing et al. 2017a; Campbell et al. 2019a; Cox et al. 2019; Gerwing et al. 2022c; Norris et al. 2022). As such, more work is required to better understand the suite of forces structuring infaunal communities.

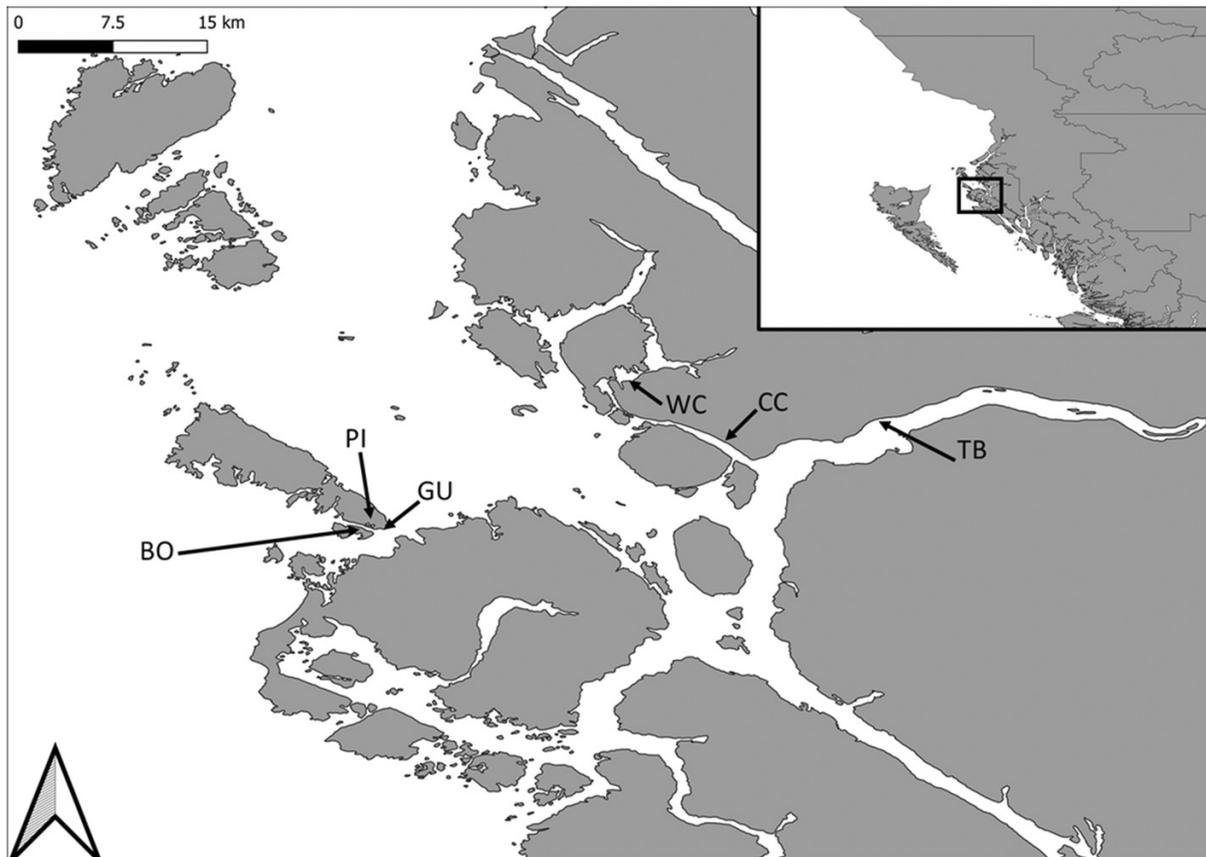
Our goal for the present paper was to use community and population level correlations to investigate the potential relative importance of top-down, bottom-up, middle-out, and abiotic variables in structuring the infaunal community of tidal flats (both sand and mudflats) of the north coast of BC (Supplementary Table S1). We hypothesized that, as observed in Gerwing et al. (2016), top-down, bottom-up, middle-out, and abiotic variables would not associate well with the infaunal community. If top-down, bottom-up, middle-out, and abiotic variables have only a minor influence in structuring tidal flat communities on the Pacific coast, as inferred by Gerwing et al. (2016) on the Atlantic coast, it is possible that similar processes are operating in other infaunal communities elsewhere, thus expanding our empirical understanding of the relative importance of the forces that structure soft-sediment intertidal communities.

## Methods

### Study sites

Six tidal flats (termed sites) were examined along the north coast of BC (Fig. 1), near the Skeena River (WC, Wolfe Cove; CC, Cassiar Cannery; TB, Tyee Bank; BO, Boulder Beach; PI, Prescott Inlet; GU, Coast Guard Beach). Typical amplitude of the semi-diurnal tides is 5–6.5 m. Sediment at WC, CC, and TB is primarily composed of silt and clay (mud), while that at BO, PI, and GU has a higher predominance of sand

**Fig. 1.** Tidal flat sites along the north Pacific coast of BC, Canada. CC, Cassiar Cannery 54.1747°N, 130.1721°W; TB, Tye Banks 54.2000°N, 129.9634°W; WC, Wolfe Cove 54.2424°N, 130.2730°W; BO, Boulder Beach 54.0871°N, 130.5970°W; PI, Prescott Inlet 54.0709°N, 130.5950°W; GU, Coast Guard Beach 54.0659°N, 130.5757°W. Map made using QGIS (QGIS 2019).



(Campbell et al. 2020; Gerwing et al. 2020a); amounts of gravel and cobble are low. Additional details about the sites are provided in Supplementary Table S1. The intertidal area in the region has a history of disturbance associated with human development, particularly from pulp mill effluent (operations ceased in 2001). Despite this history, tidal flats have naturally recovered from these disturbances (though indications of previous disturbance remain), with top layers of sediment (~20 cm) currently uncontaminated by metal pollutants and host to an abundant and diverse invertebrate community (Campbell et al. 2019a, 2019b; Sizmur et al. 2019; Gerwing et al. 2020b). Our tidal flats are not main foraging areas for migrating shorebirds, such as the Western Sandpipers (*Calidris mauri* (Cabanis, 1857)); however, small flocks of 10–100 birds are observed in spring (T.G. Gerwing, personal observation).

### Sampling design

At each site, 5 randomly selected transects (60–200 m long; depending on mudflat cross-shore width) were established running from the landward start of the tidal flat to the low water line, separated by ~20–100 m. Transects were stratified into equisized zones based on distance from shore (near, middle, and far). Within each zone, one sampling location was randomly selected ( $n=3$  per transect, 15 per site). Sites were

sampled four times in summer 2017 (Round A: 23 May–1 June, Round B: 21–26 June, Round C: 19–25 July, Round D: 18–24 August; 15 samples per site per round) on the lowest low tides of the year for a total of 60 samples per site and 360 total over all rounds. More details of the sampling design can be found in Campbell et al. (2020).

### Biotic variables

At each sampling location, a 1 m<sup>2</sup> plot was established to count epifauna (invertebrates living on the sediment), within which infauna were collected using a sediment core (10 cm length and 7 cm in diameter). For the latter, the sediment was passed through a 250 μm sieve, and the content stored in vials with 95% ethanol for later identification (Campbell et al. 2020). A pit (20 cm long, 20 cm wide, and 20 cm deep) was also dug in the plot where the core was taken to sample and identify larger or more mobile specimens that may have been missed by the infaunal core; these individuals were scarce and were integrated with abundances from core samples in the estimation of densities (standardized to numbers per m<sup>2</sup>). All infaunal specimens were identified to the lowest possible taxonomic unit as follows: cumaceans, amphipods, tanaids, polychaetes, nemerteans, and bivalves to species; chironomid larvae to family; copepods to order; ostracods to class; and nematodes to phylum (Campbell et al. 2020).

Variable taxonomic resolution does not impair contrasts between sites, as Gerwing et al. (2020b) showed that analyzing infauna community data with specimens identified to different taxonomic levels produced similar results. In addition, a small sediment core (2–3 mm deep, 2 cm diameter) was taken adjacent to the infaunal core to measure abundance of benthic diatoms by determining concentration of chlorophyll *a*. Chlorophyll *a* pigment was extracted from sediment samples using buffered acetone, and its reflectance quantified using a spectrophotometer (Coulthard and Hamilton 2011).

## Abiotic variables

At each sampling location, sediment properties were also measured. Sediment penetrability, an integrative variable that reflects the overall in situ physical conditions experienced by biota (Meadows et al. 1998; Gerwing et al. 2020a), was assessed by dropping a metal weight (15 cm long, 1.9 cm diameter, 330 g) from a height of 0.75 m above the sediment and measuring how far it penetrated into the sediment. Higher penetrability indicates finer-grained sediment with high water content, with few rocks or shell hash present in or on the sediment. Lower penetrability is indicative of larger-grained sediment with low water content, with more rocks or shell hash present (Hsu et al. 2009; Gerwing et al. 2020a). Water content (drying at 110 °C for 12 h), organic matter content (ashing at 550 °C for 4 h), and volume-weighted average particle size in the sediment's top 1 cm were measured from sediment cores (5 cm depth, 4.5 cm diameter), collected adjacent to the abovementioned infaunal cores; more details of these processes can be found in Campbell et al. (2020). In the field, the void created in the sediment from the corer to collect infauna was used to measure depth to the apparent redox potential discontinuity, aRPD (Gerwing et al. 2013). aRPD depth is a relative measure of sediment porewater dissolved oxygen and redox conditions. Sediment with a deeper aRPD has more available dissolved oxygen than that with a shallower aRPD depth (Gerwing et al. 2018b). The proportion of each 1 m<sup>2</sup> plot covered in woody debris, as well as deposited algae and eelgrass (*Zostera* spp.) debris, was also quantified, as this debris can create hypoxic conditions and smother infauna. Salinity was measured at the seaward end of each transect on each tidal flat on each sampling trip with a YSI multimeter in the water approximately 1 cm above the sediment surface at high tide. Finally, relative distance of each plot from the start of the mudflat (transition of saltmarsh, bedrock, or sandy beaches to mud (Gerwing et al. 2016)) was used as a proxy for intertidal elevation or duration of inundation for each plot location.

## Data analysis

Analyses were conducted in the program PRIMER V7 (Clarke and Gorley 2015), with the PERMANOVA add on (Anderson et al. 2008). A permutational multivariate analysis of covariance (ANCOVA) (PERMANCOVA; 9999 permutations) was used to quantify the relationship between the infaunal community and top-down, bottom-up, middle-out, and abiotic variables (Gerwing et al. 2016). The multivariate response was a resemblance matrix of the densities of 39 taxa

of infaunal invertebrates, calculated using Bray-Curtis similarity. Taxa densities were fourth root transformed to better consider the influence of abundant and rare species on the outcome of the analysis. A dummy variable of 0.01, below our threshold of detection, was added to address plots with no observed infauna (Anderson et al. 2008). Within the PERMANCOVA, round (four levels), site (six levels), and transect nested within site (five transects per site) were included as random factors and hereafter referred to as structural variables (since they reflect the structure of our sampling design).

Top-down, bottom-up, middle-out, and abiotic variables were included as covariates. Top-down predators (or bioturbators) included eight species whose diet could include infaunal taxa, or who would influence infauna through bioturbation (Pagliosa 2005; Light 2007; Jumars et al. 2015), but were unlikely to experience high levels of predation themselves during low tide (snails, crabs, and hermit crabs: *Littorina sitkana* Philippi, 1846; *Littorina scutulata* Gould, 1849; *Cancer productus* Randall, 1840; *Cancer magister* Dana, 1852; *Hemigrapsus oregonensis* (Dana, 1851); *Pagurus hirsutiussculus* (Dana, 1851); *Pagurus granosimanus* (Stimpson, 1859); and *Hemigrapsus nudus* (Dana, 1851). Middle-out variables, or mesopredators, were composed of four species (ribbon worms and sea cucumbers: *Emplectonema gracile* (Johnston, 1837); *Paranemertes peregrina* Coe, 1901; *Leptosynapta albicans* (Selenka, 1867); and *Tubulanus polymorpha* Renier, 1804, which are predominantly found on the sediment surface and may act as both predator and prey (Light 2007). This category does not include eight species of infaunal polychaete mesopredators (*Hemigrapsus oregonensis*; *Eteone californica* Hartman, 1936; *Alitta brandti* Malmgren, 1865; *Scoletoma zonata* (Johnson, 1901); *Nephtys caeca* (Fabricius, 1780); *Nephtys caecoides* Hartman, 1938; *Glycera macrobranchia* Moore, 1911; and *Exogone lourei* Berkeley & Berkeley, 1938), which in this analysis were classified as part of the infaunal community to better understand this community as a whole. We did this because these infaunal mesopredators could not be included both as covariates and in the multivariate response variable. However, these predatory polychaete worms were included as covariates in the subsequent individual species analyses detailed below. We also included two nutrient-based resources as bottom-up variables (chlorophyll *a* concentration and sediment organic matter content) and seven abiotic variables [sediment penetrability, water content, volume-weighted mean particle size, aRPD depth, water salinity, and possible causes of hypoxic conditions (% cover by algae and eelgrass)].

Prior to analysis, we assessed possible correlations between all pairs of covariates by calculating univariate Pearson's correlation coefficients. We used a threshold of 0.95 (Clarke and Ainsworth 1993) for variables too correlated to be considered independent. Since the highest correlation coefficient observed was 0.76, all variables were included in our models. All covariates (except relative distance from shore) were fourth root transformed to correct for skewed distributions and then normalized.

As part of the PERMANCOVA, we quantified components of variation, the proportion of the multivariate variation accounted for by each independent variable (Searle et al. 1992;

Anderson et al. 2008; Gerwing et al. 2016). An  $\alpha$  of 0.05 was used to determine statistical significance for all analyses (Beninger et al. 2012). Finally, covariates that did not account for any variation in the multivariate response were removed (Fletcher and Underwood 2002; Gerwing et al. 2016).

Since multivariate analyses can obscure key taxa-specific relationships (Spasojevic and Suding 2012; Murray et al. 2014; Gerwing and Hawkes 2021), a PERMANCOVA (which also works well as a univariate analysis) was conducted for selected infaunal taxa. This selection was conducted via similarity percentages analyses (SIMPER; Clarke 1993), which identify taxa contributing the most to observed community variation between sites and rounds. Only taxa that accounted for  $\geq 5\%$  of the observed community variation between sites in the SIMPER analysis were retained for subsequent univariate analyses (*Americorophium salmoneis* (Stimpson, 1857); *Capitella* species complex; *Cumella vulgaris* Hart, 1930; *Eteone californica*; *Exogone lourei*; Harpacticoida, *Leptochelia* spp.; *Macoma balthica* (Linnaeus, 1758); Nematoda, *Nippoleucon hinumensis* (Gamo, 1967); *Nutricola tantilla* (Gould, 1853); Oligochaeta, Ostracoda, *Pygospio elegans* Claparède, 1863; and *S. zonata*). Resemblance matrices were constructed and PERMANCOVA performed as detailed above with one exception. In taxa-specific PERMANCOVA, all middle-out variables could be included (11–12 species). Univariate Pearson's correlation test was then calculated to determine the nature of the relationship between covariates and a given response taxon (+/–).

## Results

Structural factors accounted for most of the observed variation in the infaunal community (81%), with site (our largest spatial scale, 35%) and plot (our smallest spatial scale, 33%) accounting for the most (Table 1). Transect, which was intermediate in spatial scale and integrated across intertidal depth, accounted only for  $\sim 3\%$  of the community variation. While most of the relationships central to our study were statistically significant, top-down consumers only accounted for 0.4% of the variation, middle-out predators 0.2%, and abiotic variables 9% (Table 1). The covariate that accounted for the highest proportion of the variation was water salinity (7%). Bottom-up variables (nutrients) did not have a significant influence.

Individual taxa exhibited a similar trend, with the majority of the variation accounted for by structural factors (Table 2). However, several key exceptions were noted, where covariates accounted for  $\geq 10\%$  of the observed variation in an infaunal taxon. These exceptions were correlations between water salinity and *Cumella vulgaris* (16%), *Leptochelia* spp. (28%), Oligochaeta (11%), Nematoda (12%), and *Nutricola tantilla* (15%); sediment organic matter content correlated with *Nippoleucon hinumensis* (22%) and *Capitella* species complex (12%); algal cover correlated with *S. zonata* (31%) and *Exogone lourei* (17%); and sediment particle size correlated with *Macoma balthica* (17%). Finally, a mixture of positive and negative correlations was observed between covariates and individual populations (Table 2).

## Discussion

For tidal flat systems on the north coast of BC, we attempted to elucidate the relative importance of top-down, bottom-up, middle-out, and abiotic variables in potentially structuring an infaunal community. In general, we observed that these variables accounted for a minority of the observed variation in this community; however, some differences were observed between individual taxa and community-level results.

### Dominance of structural factors on observed community variation

Overall, spatial structural factors, namely site and plot, accounted for the majority (81%) of our observed variation in the infaunal community (Table 1; Fig. 2). As in other studies, the infaunal community varied significantly with top-down (Heck Jr. and Valentine 2007; Hughes et al. 2014), middle-out (Prugh et al. 2009; Johnson et al. 2014), and abiotic variables (Lu et al. 2008; Dashtgard et al. 2014), but these variables accounted for a minority of the community variation (0%–9% each; 10% total). The overall low proportion of the variation accounted for by these covariates does not mean that these variables are unimportant in structuring the infaunal community, since our analyses use correlational data to report on relative importance and not on absolute effect size. Other studies have observed that top-down, bottom-up, middle-out, and environmental variables may exert structuring influences upon infaunal communities at limited spatiotemporal scales (Commito and Ambrose Jr. 1985; Wilson 1990; Lindsay et al. 1996; Williams et al. 2004; Hamilton et al. 2006; Cheverie et al. 2014; Gerwing et al. 2022b). However, our findings suggest that at broad spatiotemporal scales, infaunal communities are relatively uncoupled from the controlling influences of top-down, bottom-up, middle-out, and a number of sediment abiotic variables.

In habitats where predation and attendant bioturbation are common, if the prey base is large enough or predation/bioturbation is patchy, predation and bioturbation can have a minor effect on the prey community (Tilman 2004; Letnic and Dickman 2010; Greenville et al. 2014). Community dynamics that are relatively independent from predation/bioturbation (top down or middle out) have been observed before in infaunal communities (Gerwing et al. 2016), as well as in resource-pulse ecosystems. In the latter ecosystems, large increases in prey populations stimulated by pulses of resources result in a prey community so large that predators exert little influence over the density or dynamics of the prey species (Gray et al. 2002; Greenville et al. 2014; Crook et al. 2020). Tidal flats (at least in north temperate latitudes) experience regular pulses in nutrients in the form of benthic diatoms and organic matter, mainly during spring and summer (de Jong and de Jonge 1995; Gerwing et al. 2015a; Campbell et al. 2020; Schnurr et al. 2020). These resource pulses result in a rapid increase in infaunal density and richness. We posit that these increases are so large that predation and bioturbation, both top down and middle out (epifaunal and mesopredators), have a minor impact upon this infaunal community (Gerwing et al. 2016). While some

**Table 1.** Permutational multivariate ANCOVA (PERMANCOVA) results assessing the relative importance of species performance (top-down, bottom-up, middle-out, and sediment-related abiotic variables) covariates and structural factors (reflecting the design of the sampling program) in shaping infaunal communities on tidal flats in northern BC in 2017.

Category	Source	df	MS	Pseudo-F	Unique permutations	p	Variance components (%)
Top down (0.40%)	<i>Cancer magister</i>	1	1361.10	1.34	9957	0.25	0.06
	<i>Littorina sitkana</i>	1	1617.00	1.09	9944	0.39	0.02
	<i>Hemigrapsus nudus</i>	1	<b>3574.50</b>	<b>2.66</b>	<b>9944</b>	<b>0.02</b>	<b>0.40</b>
Mesopredators (0.19%)	<b><i>Emplectonema gracile</i></b>	<b>1</b>	<b>2203.30</b>	<b>1.89</b>	<b>9959</b>	<b>0.08</b>	<b>0.19</b>
	<i>Paranemertes peregrina</i>	1	1636.90	1.56	9956	0.17	0.10
	<i>Leptosynapta albicans</i>	1	5596.00	1.60	9948	0.15	0.45
	<i>Pagurus granosimanus</i>	1	1984.40	1.77	9946	0.14	0.15
Nutrients (0%)	Organic matter content	1	21 447.00	1.74	9950	0.12	2.59
	Chlorophyll a	1	5414.00	1.17	9957	0.35	0.15
Abiotic (9.17%)	<b>Penetrability</b>	<b>1</b>	<b>8290.30</b>	<b>2.25</b>	<b>9952</b>	<b>0.04</b>	<b>1.18</b>
	<b>aRPD depth</b>	<b>1</b>	<b>2912.80</b>	<b>2.17</b>	<b>9950</b>	<b>0.04</b>	<b>0.29</b>
	Water content	1	1759.60	1.31	9949	0.27	0.49
	Sediment particle size	1	18 025.00	1.53	9951	0.18	2.72
	<b>Water salinity</b>	<b>1</b>	<b>79 861.00</b>	<b>2.25</b>	<b>9941</b>	<b>0.03</b>	<b>7.70</b>
	Algal cover	1	32 780.00	1.82	9939	0.11	2.83
	Eelgrass cover	1	3760.50	1.36	9946	0.23	0.18
Structural (80.51%)	<b>Site</b>	<b>5</b>	<b>19 578.00</b>	<b>9.83</b>	<b>9857</b>	<b>0.0001</b>	<b>35.34</b>
	<b>Round</b>	<b>3</b>	<b>5343.30</b>	<b>3.62</b>	<b>9929</b>	<b>0.0001</b>	<b>3.49</b>
	<b>Transect (site)</b>	<b>24</b>	<b>1132.80</b>	<b>2.31</b>	<b>9787</b>	<b>0.0001</b>	<b>3.53</b>
	<b>Site × round</b>	<b>14</b>	<b>1581.20</b>	<b>3.26</b>	<b>9842</b>	<b>0.0001</b>	<b>4.86</b>
	Round × transect (site)	72	485.06	0.90	9665	0.89	0.00
	<b>Residual (a.k.a. plot)</b>	<b>225</b>	<b>539.16</b>				<b>33.29</b>
	Total	359					

**Note:** Significant sources of variation are in bold ( $\alpha = 0.05$ ). The % in parentheses is the sum of the statistically significant components of variation associated with that category.

predators/bioturbators may have localized and short-term effects upon certain taxa (Drolet et al. 2009; Cheverie et al. 2014), induced mortality is likely compensatory (Pöysä 2004). Abundances in infaunal communities located in north temperate latitudes, like ours, decline naturally each year as winter approaches (Reise 1991; Gerwing et al. 2015a; Campbell et al. 2020). Therefore, predators are likely consuming soon-to-die individuals (compensatory mortality, sensu (Hamilton et al. 2006)), further minimizing the impact of predation upon these populations and communities.

Infaunal community structure and dynamics were also uncoupled from availability of nutrients (chlorophyll *a* concentration and sediment organic matter content; Table 1). High primary productivity of intertidal flats in spring and summer (Hargrave et al. 1983; Gerwing et al. 2015a; Campbell et al. 2020) likely limits the role exploitative competition plays in structuring the infaunal community, a relationship that is also commonly observed in resource-pulse ecosystems (Letnic and Dickman 2010; Greenville et al. 2014; Crook et al. 2020).

Abiotic variables mainly related to sediment properties and salinity only accounted for 9% of the infaunal community variation (Table 1). Gerwing et al. (2016) observed a similar phenomenon and partially attributed this observation to the limited range of sediment abiotic conditions observed in their study sites. However, our study included a broader

range and variation of abiotic conditions (both between and within sites; Supplementary Table S1). Moreover, the most important abiotic covariate in our study was water salinity, which accounted for 8% of the infaunal community variation. The influence of salinity upon invertebrate community structure is well known (Rosenberg et al. 1992; Owen and Forbes 1997; Rutger and Wing 2006; Lu et al. 2008). Despite this variable not being included within Gerwing et al.'s (2016) analysis, our study reported a similar influence of abiotic variables upon the infaunal community (Table 3; 9%–11%). Thus, it is unlikely that the low proportion of the community variation accounted for by abiotic variables (related to tidal flat environments) is a product of low variability in sediment conditions or missing variables within Gerwing et al.'s (2016) analysis.

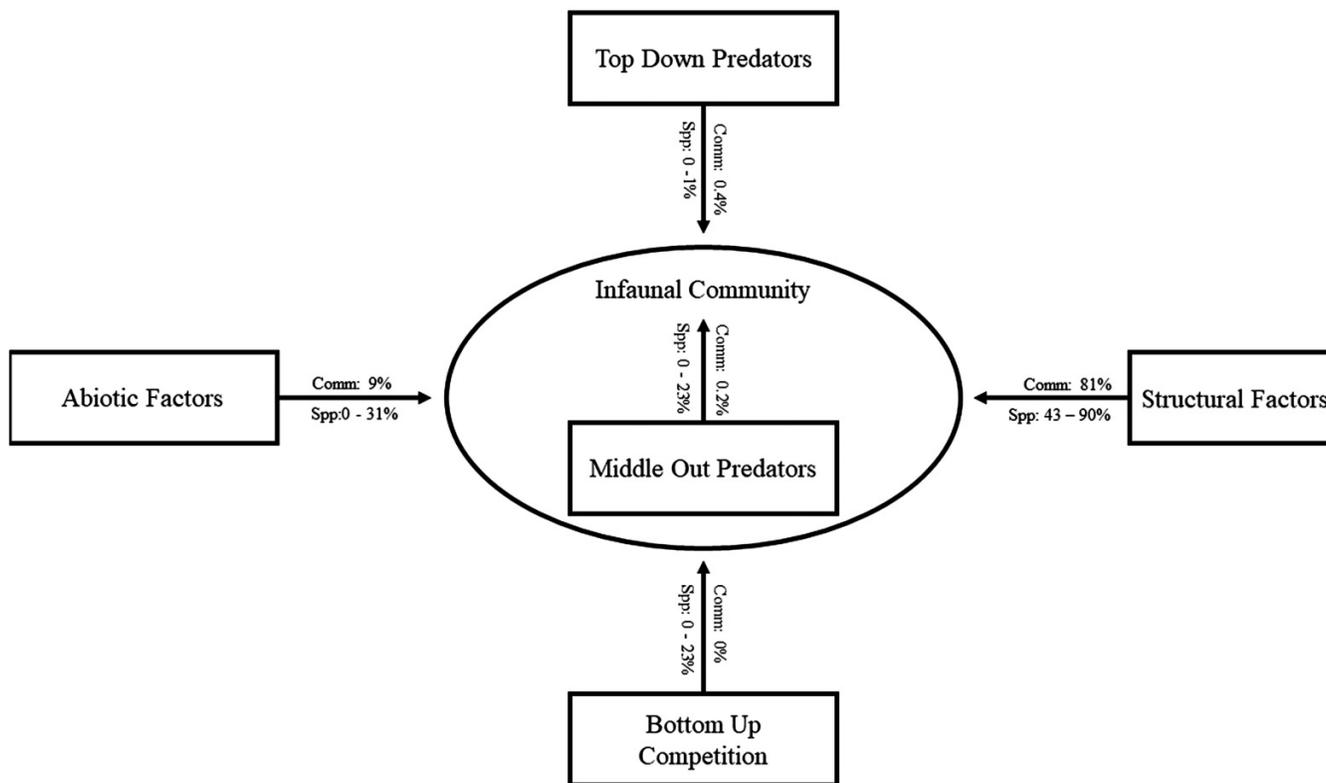
Structural factors, which accounted for 81% of the observed variation in the infaunal community (Table 1), are challenging to quantify. For instance, the temporal term round (3%) may represent interactions between the time of year and weather or climate patterns (Scholz and Liebezeit 2012; Drolet et al. 2013b). In our study, plots (1 m<sup>2</sup>) accounted for 33% of the observed community variation. This factor may represent localized hydrology and delivery of larvae, post-settlement dispersal, small-scale (within-plot) unmeasured intra- and interspecific interactions, and(or) availability of

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**Table 2.** Results of the components of variation from permutational multivariate ANCOVA (PERMANCOVA assessing the relative importance of top-down, bottom-up, middle-out, and sediment-related abiotic covariates (species performance variables) and structural factors on densities of infaunal populations on tidal flats in northern BC in 2017. Only significant sources of variation are indicated ( $\alpha = 0.05$ ). +/- refers to the result of Pearson's correlation test between two variables.

Category	Variables	Americorophium salmonis	Cumella vulgaris	Nippoleucon hinumensis	Leptochelia spp.	Eteone californica	Scoletoma zonata	Exogone lourei	Pygospio elegans	Capitella species complex	Oligochaete	Nematoda	Harpacticoida	Ostracoda	Macoma balthica	Nutricula tantilla	
Top Down	<i>Cancer productus</i>																0.59% (+)
	<i>Hemigrapsus oregonensis</i>				0.23% (-)												
	<i>Pagurus hirsutiusculus</i>				0.91% (+)												
	<i>Pagurus granosimanus</i>				0.64% (-)												1.1% (-)
	<i>Hemigrapsus nudus</i>						0.37% (+)										
Mesopredator	<i>Glycinde picta</i>								9.64% (+)								
	<i>Scoletoma zonata</i>				2.68% (+)			6.45% (-)			4.87% (-)						
	<i>Eteone californica</i>		1.12% (-)														
	<i>Nephtys caeca</i>							2.07% (+)	4.39% (+)								
	<i>Nephtys caecoides</i>																
	<i>Glycyera macrobranchia</i>		2.05% (-)		0.54% (-)												
	<i>Exogone lourei</i>				2.08% (-)		22.59% (-)										
	<i>Paranemertes peregrina</i>				1.70% (+)												
	<i>Leptosynapta albicans</i>								1.31% (+)								
Nutrients	Organic matter content	6.85% (+)		22.03% (+)						12.00% (+)							
	Chlorophyll a									1.39% (-)							
Abiotic	Penetrability						1.55% (-)										
	aRPD	0.99% (+)							1.00% (+)				1.44% (-)				
	Salinity		16.05% (+)		28.23% (+)						10.68% (+)	12.21% (+)					14.53% (+)
	Algae cover						30.88% (+)	17.38% (+)									
	Sediment particle size			4.15% (-)												16.92% (-)	
Structural	Round											3.19%				25.57%	
	Site	9.63%	20.81%		34.45%	45.36%	15.37%	25.44%	21.62%	18.78%	16.35%	15.57%	13.12%	8.29%			18.04%
	Transect (site)			6.12%	0.65%			2.18%			6.15%	5.63%	3.37%				
	Round × site	16.72%	10.12%	21.45%	0.91%						3.94%		9.24%				5.46%
	Round × transect (site)						7.40%										
Residual (a.k.a plot)	61.68%	39.81%	39.13%	20.13%	41.87%	20.09%	34.63%	52.94%	62.27%	50.60%	58.65%	64.53%	77.40%	40.94%	57.36%		

**Fig. 2.** Summary of the forces that are statistically associated with the infaunal community on tidal flats in northern BC, sampled in 2017. Abiotic variables examined are mostly those related to sediment properties. We posit that the regional species pool is a main process underlying the effects of our structural factors (site, round, and plot); we did not evaluate this hypothesis in the present study. “Comm” refers to the community results (Table 1) and “Spp” the individual species results (Table 2).



**Table 3.** Summary comparing the % of the infaunal community variation accounted for by top-down and middle-out predators, available resources (bottom-up forces), abiotic sediment conditions, and the structural factors of the model (year, round, site, transect, and plot) on tidal flats on the Pacific coast (Skeena estuary, this study) and the Atlantic coast (upper Bay of Fundy, Gerwing et al. (2016)).

Variables	Pacific coast	Atlantic coast
Top down	0.4%	6%
Middle out	0.5%*	1%*
Bottom up	0%	1%
Abiotic	9%	11%
Structural	81%	79%

\*Middle-out variables are averaged (from Table 2 in the present study and Table 2 in Gerwing et al. (2016)), since mesopredators are also a component of the infaunal community, and so had to be analyzed separately.

supply (Weersing and Toonen 2009), post-settlement dispersal (Pilditch et al. 2015b), as well as unmeasured site variables such as hydrology, biogeochemistry, exposure to waves and tidal currents (Williams et al. 2013; Gerwing et al. 2015b; Rubin et al. 2017; Gerwing et al. 2022a), or site-specific histories, such as previous disturbance and human development (Gerwing et al. 2017c; Campbell et al. 2019a; Sizmur et al. 2019).

### Patterns at the level of an individual taxon

In general, a similar pattern was observed when this infaunal community was analyzed as a whole and as individual taxa: the majority of the variation was accounted for by spatial structural factors (Tables 1 and 2; Fig. 2). This further supports the idea that these infaunal species are mostly uncoupled from the controlling influence of top-down, bottom-up, middle-out, and abiotic variables. In particular, none of the measured top-down variables accounted for more than 1% of the observed variation of an individual infaunal taxon (Table 2). When combined with the results from the community-level analysis, it appears that top-down variables may not play a major role in structuring these infaunal taxa, nor the community as a whole.

Nevertheless, some stronger relationships were noted, and these identify areas for further research, as well as poten-

biogeochemical elements in the sediment (Drolet et al. 2013a; Pilditch et al. 2015b; Sizmur et al. 2019; Gerwing et al. 2022a, 2022b). Site, representing spatial variation on the scale of kilometres, is likely a product of processes such as larval

tially useful indicator species. For example, *Capitella* species complex, a sessile polychaete worm, was positively associated with sediment organic matter content (12%; Table 2). This relationship was not unexpected since this capitellid family is a known indicator of organic enrichment, often found thriving in areas with elevated levels of sediment organic matter (Pearson and Rosenberg 1976, 1978; Gerwing et al. 2018a; Campbell et al. 2019a). As such, this observation suggests that these polychaetes can be used as indicators of organic enrichment in this Pacific intertidal system as well.

With regard to abiotic variables, water salinity had a positive correlation with five taxa: *Cumella vulgaris* (16%), *Leptochelia* spp. (28%), *Oligochaeta* (11%), *Nematoda* (12%), and *Nutricola tantilla* (15%) (Table 2). As mentioned above, the influence of salinity upon infaunal community composition and density is well reported (Rosenberg et al. 1992; Owen and Forbes 1997; Rutger and Wing 2006; Lu et al. 2008). In our study, the positive correlations between these taxa and salinity suggest that these taxa increase in density the further away the intertidal site was from the influence of the Skeena River's freshwater input. Finally, a negative correlation was observed between *Macoma balthica* (17%) and sediment particle size, indicating that in our study area, *M. balthica* was more common on flats composed of mud than sand (Campbell et al. 2020). This observation has been made before (Cranford et al. 1985; Gerwing et al. 2015a, 2015b).

While middle-out variables may be relatively unimportant in structuring our infaunal community as a whole, at the level of individual taxa, we detected certain interactions that may be important to individual species at fine spatiotemporal scales. We observed 13 correlations between mesopredators and individual infaunal taxa, accounting for 1%–23% of infaunal population variation (Table 2). This suggests that mesopredators may play a minor but meaningful role in structuring infaunal communities and populations, a conclusion that has been reached by other studies of intertidal infauna (Ambrose Jr. 1984a, 1984b; Commito and Ambrose Jr. 1985; Commito and Shrader 1985; Ambrose Jr. 1991; Gerwing et al. 2022b). However, only one correlation was observed to exceed 10% of the infaunal variation: a negative correlation between *S. zonata* and *Exogone lourei* (23%). Interestingly, this relationship was unidirectional. When we assessed the variables associated with the spatiotemporal variation of *S. zonata*, a strong negative correlation with *Exogone lourei* was observed. However, when we assessed the variables associated with the spatiotemporal variation of *Exogone lourei*, no correlation with *S. zonata* was observed. This relationship could be the result of predation or competition, and more research is required to better elucidate the nature of this interaction.

## Other hypotheses on predominant structuring forces of infaunal communities in tidal flats

Early studies examining forces that influence community variation in soft-sediment marine ecosystems (including tidal flats) questioned the importance of local interactions (i.e., species performance drivers) (Grassle and Sanders 1973; Thistle 1981). Based upon their recent work in the Bay of Fundy mudflats, Gerwing et al. (2016) also reasoned that in-

tertidal infaunal communities are not predominantly structured by top-down, bottom-up, middle-out, or sediment variables (considered species performance forces). Despite being conducted in tidal flats that exhibited greater biological diversity and abiotic differences, the results of our current study mirrored those of Gerwing et al. (2016). Such similarity in results from disparate study sites on the Atlantic and Pacific coasts of Canada suggests some similarity in the main structuring forces of these infaunal communities. It would be interesting to re-examine whether other tidal flat infaunal communities in north temperate latitudes, such as those in the Wadden Sea (Flach and Beukema 1995) and the UK (Waldock et al. 1999), are structured in a similar manner. Overall, these results continue to raise questions about the primary drivers of infaunal community structure.

Our data suggest that unmeasured or unidentified spatial terms, operating at the site or plot level, may be the dominant structuring factors. Gerwing et al. (2016) postulated that intertidal infaunal communities may be structured by a first-come-first-served process (priority effects) following a disturbance, as can be observed in rocky shores when recruitment is low (Sutherland 1974; Bertness 2007; Fukami 2015). Under such a process, delivery of larvae and dispersing propagules as well as movement by juveniles and adults (Stocks 2002; Drolet et al. 2012; Bringloe et al. 2013; Pilditch et al. 2015b) may play important structuring roles at the spatial scale of the plot (metres) and site (hundreds of metres to kilometres) following the disturbance. This process could explain the large proportion of the variation accounted for by structural terms in our results (Tables 1 and 2), as well as in the results of Gerwing et al. (2016) (Table 3). Once individuals are established, they may be able to resist colonization by subsequent dispersing of individuals via pre-emptive competition or inhibition (Ambrose Jr 1984a; Loeuille and Leibold 2008), resulting in priority effects dominating infaunal community structure and dynamics.

However, studies of infaunal community recovery from anthropogenic and natural disturbances along the Pacific and Atlantic coasts of Canada suggest that priority effects may not be the predominant force structuring these communities (Norris et al. 2022). Instead, community trajectories appeared to be strongly influenced by species availability, particularly regional species pools, and not by the order of species arrival. Following disturbance and then establishment, infaunal community structure (species composition and abundances) increased in similarity to the surrounding areas (Beukema et al. 1999; Thrush et al. 2003; Gerwing et al. 2017a; Campbell et al. 2019a; Cox et al. 2019; Gerwing et al. 2022c; Norris et al. 2022). Regional species pools have been implicated in structuring other marine invertebrate communities (Weslawski 2003; Witman et al. 2004; Somerfield et al. 2009; de Juan and Hewitt 2011), and we posit that they may play a substantial role in structuring intertidal infaunal communities both on small and large scales.

Another set of hypotheses about drivers of infaunal community structure, related to species performance, that we only superficially mention in our study is the modification of the sedimentary environment by infauna (Reise 2002; Woodin et al. 2010). While our study mostly considered

trophic-related variables, infauna can also stabilize sediments (e.g., bioconstruction), destabilize sediments (including bioturbation), cause bioadvection of porewater (affecting local distribution of dissolved oxygen and various other chemicals) while undertaking all sorts of behaviours, and subsequently facilitate or inhibit other community members (Rhoads and Young 1970; Reise 2002; Woodin et al. 2010; Gerwing et al. 2017b). Sediment geochemistry (whether mediated by biota or not) could affect communities at the patch level or site level, where the presence/absence and concentrations of key elements within the sediment may influence infaunal survival, physiology, behaviour, and abundance (Volkenborn et al. 2012; Sizmur et al. 2013; Chiarelli and Roccheri 2014; Sizmur et al. 2019; Gerwing et al. 2022a). More research is required to evaluate these various hypotheses related to non-trophic species performance (such as facilitation), species availability (such as the regional species pool), and habitat availability (such as disturbance type, scale, and frequency) on tidal flats in northern BC as well as in the Bay of Fundy.

## Conclusions

Using intertidal soft-sediment communities in northern BC, we investigated relationships among top-down, bottom-up, middle-out, and abiotic variables with infaunal community composition. As in Gerwing et al.'s (2016) work in a similar ecosystem in the Bay of Fundy, we observed that these forces accounted for a minor proportion of the observed variation in infaunal community, suggesting a minor role in structuring this community. We posit that regular pulses of nutrient-related resources on tidal flats enable them to act like resource-pulse ecosystems. Where freely available and abundant, these resources contribute to limiting the effects of top-down, bottom-up, middle-out, and abiotic variables as structuring forces. Gerwing et al. (2016) also hypothesized that priority effects (pre-emptive competition) may be a primary force structuring infaunal communities. However, we now suggest, based on our present study in combination with recent studies on recovery of the infaunal community following various disturbances (Thrush et al. 2003; Gerwing et al. 2017a, 2018a; Cox et al. 2019; Sizmur et al. 2019; Campbell et al. 2019a; Gerwing et al. 2022c; Norris et al. 2022) that colonizers and subsequent infaunal community composition may reflect regional species pools and the variables that influence these pools. More research is required to evaluate this hypothesis.

## Acknowledgements

Field work was done with assistance from D Parker, J Starr, and Z Starr. Funding was provided by the Kitsumkalum First Nation to TGG, a Natural Sciences and Engineering Research Council (NSERC) of Canada Engage grant to TGG and FJ, a MITACS Elevate grant, partnered with the Hakai Institute, to TGG, and an NSERC CGS M to LC. Cassiar Cannery provided further support to TGG and LC. We dedicate this paper to the memory of Mark Bell. Wherever you are Mark, we know that

the beer is cold, the fishing is good, and the boats are made of cedar. Sleep well my friend.

## Article information

### Editor

Dr. S.J. Cooke

### History dates

Received: 10 September 2022

Accepted: 6 February 2023

Version of record online: 4 June 2023

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### Data availability

Data is available upon reasonable request to the corresponding author.

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### Competing interests

The authors have no competing interests or conflicts of interest to declare.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/facets-2022-0199>.

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