

RESEARCH ARTICLE

Eelgrass-associated invertebrate biodiversity patterns in a subarctic seascape

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Abstract

Abiotic, biotic, and spatial processes shape patterns of biodiversity in coastal ecosystems. In this study, we test how these processes influence eelgrass-associated invertebrate diversity in a subarctic seascape. We sampled invertebrate assemblages in 12 meadows along 300 km of coastline in James Bay, Canada, and tested the relative contributions of abiotic conditions, spatial arrangement, and meadow attributes in explaining variation in invertebrate community composition, abundance, and diversity within and among meadows. We found that eelgrass meadows in James Bay support diverse invertebrate communities comprising at least 72 taxa. Greater invertebrate abundance was associated with higher epiphyte load and clearer water (lower turbidity). Invertebrate diversity increased with aboveground eelgrass biomass and epiphyte loads, and species richness increased in clearer water. Invertebrate communities in very salty and very fresh waters contributed the most to regional beta diversity. Variation in taxonomic composition across the seascape was notable; no species was observed at every site, and most taxa were observed at 3–5 sites. The most widely distributed taxa were the arctic amphipod *Gammarus setosus* and the bivalves *Mytilus trossulus* and *Macoma balthica*, each observed at 11 of the 12 sites. Variation in taxonomic composition among meadows was partially explained by meadow spatial arrangement and local abiotic conditions (salinity, fetch, temperature, and turbidity) but not meadow attributes such as eelgrass biomass or shoot size. We conclude that both local conditions and regional ecological processes such as spatially structured population dynamics and species interactions may be important for regional-scale biodiversity patterns on this coastline.

Marine habitat-forming species such as seagrasses and corals create discrete patches of habitat that support diverse faunal communities. The abundance, diversity, and taxonomic composition of these communities depend on three types of processes: abiotic effects on population dynamics, biotic effects on population dynamics such as species interactions, and spatial processes such as dispersal and immigration (Thompson et al. 2020). Each

of these processes can be shaped by the extent and physical structure of the biogenic habitats these species create (Hauser et al. 2006; Murphy et al. 2021; Swaminathan et al. 2024). The relative importance of habitat, local abiotic conditions, and dispersal in maintaining biodiversity can influence the stability of communities and how they recover from disturbance (Leibold et al. 2004). Understanding the interplay of regional and local processes is an important component of managing habitat at the scales appropriate to support biodiversity (Boström et al. 2006; Thompson et al. 2017).

The relative influences of foundation species attributes, abiotic conditions, and the spatial arrangement of habitat on communities are difficult to disentangle because they are spatially autocorrelated and interdependent (Legendre and Fortin 1989; Dray et al. 2012). For example, communities in

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nearby patches may be more similar than those in distant patches because nearby patches experience similar abiotic conditions, because they are strongly connected by dispersal, or both (Leibold et al. 2004). Similarly, local abiotic conditions may influence communities directly by altering population dynamics, or indirectly through their effects on foundation species. In both examples, strong associations between abiotic conditions, foundation species attributes, and spatial arrangement challenge our ability to assess how biodiversity is generated and maintained.

Eelgrass (*Zostera marina*) is a habitat-forming marine plant that supports rich and productive food webs along coastlines throughout the Northern Hemisphere. In these systems, invertebrates that live on and among eelgrass leaves consume epiphytic algae and are prey to diverse assemblages of fish and larger invertebrates (Duffy 2006). Grazing of algae by epifaunal invertebrates can control epiphyte load and facilitate eelgrass growth under some conditions (Orth and Van Montfrans 1984; Duffy 2006; Lewis and Boyer 2014). The energy that flows through these food webs not only supports numerous fish and invertebrates that are of commercial and recreational value, but also supports waterbirds and marine mammals (Huang et al. 2015).

Eastern James Bay, Québec, is a subarctic region that historically supported some of the largest eelgrass meadows recorded in North America (Fig. 1) (Lalumière et al. 1994). Now eelgrass meadows occupy just a portion of their historical range following local and regional disturbances including changes associated with regional hydroelectric development and severe marine heat waves in the 1980s and 1990s (Leblanc et al. 2022; Idrobo et al. 2024; Kuzyk et al. 2026). Thirty years later, eelgrass has not returned in many locations along the coastline (Idrobo et al. 2024). In surviving meadows, eelgrass density is 60% less than historical recorded values (213 vs. 537 shoots m^{-2} on average), aboveground biomass is 81% less, and maximum shoot length has decreased from 2.5 to 1 m (Leblanc et al. 2022; Idrobo et al. 2024). Coastal waters are also now more turbid in many places; the geographical distribution of freshwater input to the bay has shifted following river diversions implemented during hydroelectric development, and the frequency of marine heat waves has increased (Peck et al. 2022; Bruneau et al. 2025; Kuzyk et al. 2026). Eelgrass is valued in the region for its role as a foundation species, but the biodiversity supported by eelgrass along this coastline has not been assessed at spatial extents that could capture local and regional processes. Invertebrate diversity associated with James Bay has never been broadly censused apart from reports of the presence of a small number of taxa (bivalves, polychaetes, gastropods) from a few locations preceding eelgrass declines (Lalumière et al. 1994).

Here we provide the first comprehensive description and assessment of eelgrass-associated invertebrate biodiversity from James Bay, Québec (Fig. 1). We evaluated the influence of meadow spatial arrangement, local abiotic conditions, and meadow attributes (aboveground biomass, epiphyte

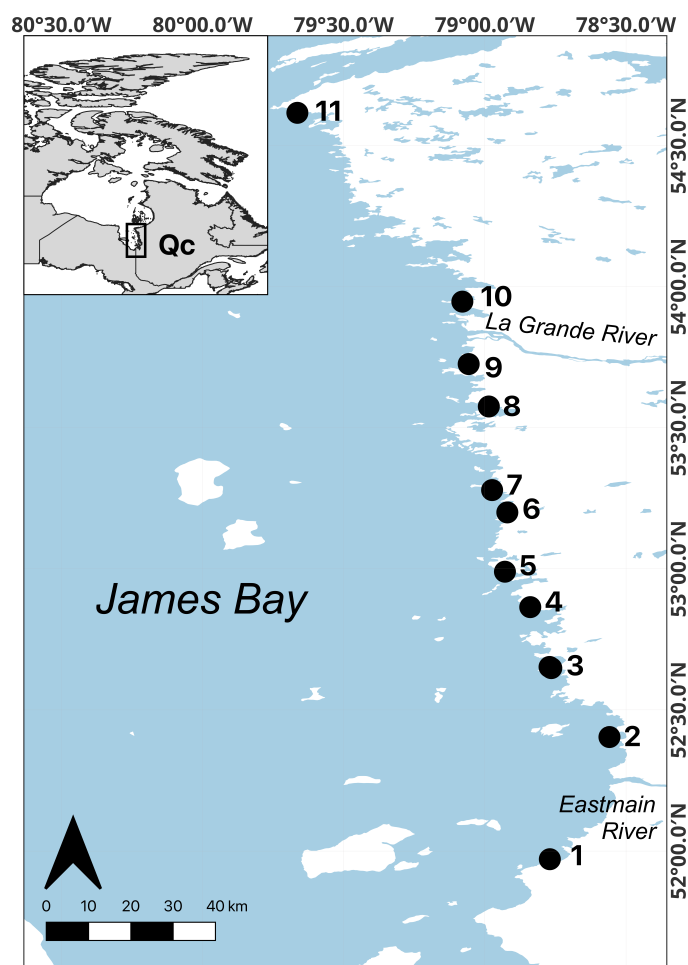


Fig. 1. Eastern coast of James Bay, Canada, Québec, marked with the sampling sites included in this study. Number 3 represents two sites (3a and 3b) located less than 1 km apart.

availability) on local and regional patterns of biodiversity. First, we tested the hypothesis that the spatial arrangement of meadows across the region shapes invertebrate communities by comparing invertebrate taxonomic composition, diversity, and abundance among meadows. Because eelgrass meadows along the coastline have become smaller and further apart (Idrobo et al. 2024), we predicted that we would observe a strong effect of meadow arrangement on invertebrate assemblages. Second, we tested the hypothesis that local abiotic conditions explain variation in invertebrate composition and meadow-scale abundance and diversity. We tested the prediction that low salinity, in particular, is associated with decreased invertebrate abundance and diversity (Yamada et al. 2007). Third and finally, we tested the hypothesis that meadow attributes (particularly aboveground eelgrass biomass) explain variation in invertebrate meadow-scale abundance and diversity (Reed and Hovel 2006). We predicted that invertebrate abundance and diversity would increase with eelgrass biomass.

Materials and methods

Study area

In subarctic Québec, the eastern James Bay shore stretches from 51°N to 54°N and is the traditional territory of the Cree First Nations of James Bay (Eeyou Istchee; Fig. 1). *Zostera marina* (shikaapaashkwh in Cree) (Linnaeus, 1753) is the primary meadow-forming seagrass species in the region; however, *Ruppia maritima* (Linnaeus, 1753) is also present at some river mouths. Eelgrass meadows in eastern James Bay are found in shallow subtidal lagoons (typically 1–2 m depth), protected bays, and small estuaries where the tidal flats and subtidal slopes are gentle (Lalumière et al. 1994; Leblanc et al. 2022). Seasonal ice scouring appears to be an important source of local disturbance (Lalumière et al. 1994). The ice-free or summer eelgrass growing season is short, with onset marked by ice melting in mid-May to early June and ending with ice formation beginning in October and November (Taha et al. 2019). Along the Eastern James Bay coastline, mean growing season temperature, ice dynamics and salinity do vary, but there is not a distinct latitudinal gradient in these conditions likely due to water circulation patterns, coastline configuration, water depth and the presence of numerous rivers (de Melo et al. 2022).

Sampling design and sample collection

In the summer of 2019, we collected eelgrass and epifaunal invertebrates at 12 sites (Fig. 1). Northern and southern sections of the coastline were sampled concurrently by two teams between late July to mid-August. Sites were at comparable depths (1–1.5 m). We prioritized sites that had supported eelgrass for a long time based on Cree local knowledge (Leblanc et al. 2022; Fink-Mercier et al. 2024; Idrobo et al. 2024). At each site, we used SCUBA to collect aboveground eelgrass biomass and invertebrates. We collected eelgrass from nine 0.0625 m² quadrats per site, in three sets of three quadrats. Sets of quadrats were spaced 20 to 30 m apart, and within each set quadrats were at least 2 m apart. In each quadrat, we broke off eelgrass by hand at the sediment-water column interface and immediately placed it into a 300-μm mesh bag to retain mobile invertebrates (following Whippo et al. 2018). We also collected one additional shoot from outside each sampling quadrat ($n = 9$ per site) to quantify epiphyte load, which we placed into plastic bags on ice.

Invertebrate processing

Within 36 h of sample collection, we separated invertebrates from eelgrass and algae using forceps and by rinsing samples with freshwater through a 0.5-mm sieve. We preserved all invertebrates in 95% ethanol. We then used a dissecting microscope to identify and count every individual from at least six of the nine samples collected from each site, with the exception of site 5 ($n = 2$). To assess how well our sampling captured site-level species richness, we used the

iNEXT R package (Hsieh et al. 2016) to generate rarefaction curves and estimate saturating species richness for each quadrat (Supporting Information Fig. S1). We identified individuals to the lowest taxonomic level possible, often family or order, though sometimes species. To identify taxa we used subarctic or arctic taxonomic references as frequently as possible; when such keys were unavailable, we used more general references and identified taxa to higher taxonomic levels (Supporting Information Table S1).

Quantifying meadow characteristics

To test whether characteristics of eelgrass meadows are associated with invertebrate community properties, we quantified eelgrass morphological characteristics and epiphytic algal abundance for each meadow sampled. In the lab, we measured shoot density, shoot morphology, and aboveground biomass of eelgrass in each quadrat. We first cleaned each shoot to remove epiphytes and invertebrates (described above). To characterize shoot morphology, we counted the number of leaves on each shoot and measured the length and width of the longest leaf for five shoots (including the shoot collected from outside each quadrat to estimate epiphyte load). We then used these values to calculate leaf area as (sheath length $\times$ sheath width $\times$ 2) + (leaf length $\times$ leaf width $\times$ 2 $\times$ number of leaves). We quantified aboveground biomass as dry weight to the nearest 0.001 g after drying cleaned shoots at 60°C for 48 h.

We quantified epiphyte load by gently scraping epiphytes off each of the shoots collected for epiphyte analysis into seawater from the sampling site with a glass microscope slide. We then filtered the combined water and epiphytes through a 0.7-μm GF/F filter. We extracted chlorophyll *a* (Chl *a*) in 90% acetone at 4°C in the dark for approximately 18 h. We then measured Chl *a* concentrations using an Aquaflor Handheld Fluorometer (Turner Designs Inc.) calibrated for the non-acidification method. For each estimate of epiphyte chlorophyll, we subtracted the estimated Chl *a* concentrations from the water column of the site where the sample was collected. We standardized epiphyte load to the leaf area of each shoot ($\mu\text{g chlorophyll} \times \text{cm}^{-2}$ eelgrass surface area).

Quantifying local environmental conditions

To test the hypothesis that local abiotic conditions explain variation in invertebrate communities, we compared observations of water column measurements taken the same day that we collected eelgrass and invertebrate samples. The remoteness of the region and sites precluded installing sensors to gain a longer-term estimate of environmental conditions. We measured salinity (unitless), temperature (°C) and turbidity (nephelometric turbidity units) using an EXO-1 YSI multi-parameter probe (YSI Inc. Xylem Inc.). We estimated Chl *a* concentrations of the water column at each site by collecting water samples that we then filtered onto GF/F filters with a 0.7 μm pore size. Filters were stored in 10 mL of 90% acetone

at 4°C in the dark for 18–24 h. We corrected water column samples for the influence of phaeopigments by acidifying with 5% hydrochloric acid (Butler 1984) and calculated the concentration of Chl *a* (Holm-Hansen et al. 1965).

We also quantified fetch and growing period, variables that likely impact local water column properties, eelgrass habitat, and local community composition (Boström et al. 2006; Robinson et al. 2011). Fetch, defined as the distance over which wind can travel across water without obstruction, can limit wave magnitude (Hill et al. 2010). Fetch is typically calculated as the distance from a point to the nearest land in a given direction (Marchand and Gill 2017). We estimated fetch for each meadow included in our analyses using the *waver* package in R (Marchand and Gill 2017). We did not use a more comprehensive estimate of exposure such as relative exposure index (O'Brien et al. 2022) that includes wind values because of the limited number of weather stations in the region. We estimated fetch at 36 main compass bearings spaced 10° apart. Each main bearing was the average of 11 sub-bearings spaced around the main bearing, weighted by cos(angle between main and sub-bearing). We then summed the fetch estimates across all of the main bearings to produce a single estimate of fetch for that meadow.

We estimated growing period as the number of days between ice breakup that year and the date that each meadow was sampled. The number of ice-free days was determined at each site from 1058 multispectral optical images acquired by the satellites Landsat-7 ETM+, Landsat-8 OLI, Sentinel-2A, Sentinel-2B, Sentinel-3A, and Sentinel-3B, as well as 236 synthetic-aperture radar imagery acquired by Sentinel-1A and Sentinel-1B. The images were orthorectified, filtered, and photo-interpreted to determine dates (day of year) of sea-water freeze-up and ice breakup (see Kuzyk et al. 2023 for full description of methods).

Spatial descriptors of invertebrate communities

To test the hypothesis that the spatial arrangement of meadows influences invertebrate communities, we used a method that identifies spatial correlation among habitats at broad to fine spatial scales called distance-based Moran's Eigenvector Maps (dbMEMs; formerly known as principal coordinates of neighbor matrices) (Borcard and Legendre 2002). A dbMEM is a variable that hypothesizes spatial correlation at a given scale for a set of n spatially structured samples. A set of n samples produces $n - 1$ dbMEMs, each of which represents a different hypothesis about the scale of positive or negative spatial correlation ranging from broad to fine spatial scales (Legendre and Legendre 2012).

We generated dbMEMs to test if spatial correlation at different scales explains variation in invertebrate abundance, richness, diversity, and composition between meadows. We generated these dbMEMs from a matrix of geographic distances between quadrats (Borcard et al. 2018). From a distance matrix of the 80 quadrats we sampled, we generated 79 eigenvectors with the *dbmem()* function from the *adespatial*

package using the maximum edge length of the minimum spanning tree as the truncation level (Dray et al. 2024). Of these 79 eigenvectors, only six represented positive spatial correlation (Legendre and Legendre 2012). We retained only these eigenvectors describing positive spatial correlation for our analyses, as we were not interested in processes that can cause negative correlation (Borcard et al. 2018). dbMEMs produced by irregularly spaced samples may not capture spatial structures occurring at finer scales (Borcard et al. 2018); the dbMEMs produced from a distance matrix of all of the quadrats in our study only described spatial structures occurring among and not within meadows. We classified the six positive dbMEMs as broad-scale predictors (describing spatial structures at the scale of hundreds of kilometers) and medium-scale predictors (describing spatial structures occurring at tens of kilometers) based on spatial correlograms and maps of each dbMEM (Supporting Information Fig. S15). We included all six positive dbMEMs as predictors in our analyses of invertebrate communities.

Statistical analyses

All statistical analyses were conducted in R 4.3.2 (R Core Team 2023). To test how the local abiotic environment and meadow attributes influence invertebrate diversity, we characterized the quadrat-level diversity of invertebrate communities within each meadow by estimating Hill–Simpson diversity using the R package *vegan* (Oksanen et al. 2020). We chose to use Hill–Simpson diversity because it is expressed in units of effective number of species, and compared to the Hill–Shannon diversity index it is relatively insensitive to sampling effort as it weights common species more heavily (Roswell et al. 2021). To standardize our estimates of species richness to sampling effort, we used the *iNEXT* package to estimate Chao richness for each quadrat (Hsieh et al. 2016). We assessed species' evenness within meadows using Pielou's J (Pielou 1969). We assessed beta diversity within and across meadows using the *adespatial* function *beta.div.comp()* (Dray et al. 2024) with the Ruzicka index (Podani et al. 2013). We used the estimates of beta diversity from these analyses to quantify the local contribution to beta diversity of each quadrat and meadow using the local contribution to beta diversity metric, and the *LCBD.comp()* function (Dray et al. 2024; Legendre 2014). The local contribution to beta diversity metric estimates the ecological uniqueness of a sample or site compared to the mean site composition of the dataset. High values indicate that a sample has a distinct species assemblage relative to other samples (Legendre 2014). We multiplied local contributions to beta diversity by 100 to facilitate visualization and parameter estimation.

To test whether variation in abiotic conditions explains variation in meadow attributes, we used a partial redundancy analysis with site as a covariable. We centered and standardized all variables prior to analysis. To identify significant predictor variables, we used a forward selection procedure with

the proportion of explained variance (R^2) of the full model as a cutoff. To identify relationships among different abiotic conditions and among different meadow attributes, we used principal component analysis of local abiotic conditions and a principal component analysis of meadow attributes.

To test whether variation in local abiotic conditions and meadow characteristics explain variation in invertebrate abundance and diversity, we modeled quadrat-level invertebrate abundance and quadrat-level diversity using generalized linear mixed-effect models. For each response variable, we tested meadow-scale abiotic predictors (water temperature, salinity, turbidity, growing period, ice off date, and fetch), quadrat-scale habitat predictors (aboveground eelgrass biomass, shoot density, shoot length and width, epiphyte load, and water column Chl *a* [site level]), and our broad- and medium-scale spatial predictors (dbMEMs). To check for non-linear relationships, we plotted raw predictor variables against response variables transformed using the same transformation as employed by the generalized linear mixed-effect model. In instances with non-linear relationships, we log-transformed predictor variables to fully linearize the relationship. For all models, we centered and standardized predictor variables prior to analysis to facilitate interpretation. We included site (meadow ID) as a random effect in all models.

We used the Bayesian package *brms* to model each response variable (Bürkner 2017). We modeled abundance and species richness using a negative binomial distribution, Hill-Simpson diversity using the gamma distribution, local contribution to beta diversity using a student distribution, and Pielou's *J* using a beta distribution. We used posterior predictive checks and Pareto-smoothed importance sampling leave-one-out cross validation to ensure that the selected models effectively captured the structure of the data (Vehtari et al. 2017). We also used model weights calculated from leave-one-out values to identify the best-performing model (Vehtari et al. 2017).

To test the hypotheses that invertebrate community composition depends on meadow characteristics, abiotic conditions and the spatial arrangement of meadows, we conducted variation partitioning and partial redundancy analyses using the *vegan* package (Oksanen et al. 2020) and following the steps in Borcard et al. (2018). Variation partitioning analyses are used in ecology to estimate how much variation in a multivariate dataset (in this case, community composition data) is attributable to different sets of explanatory variables (Borcard et al. 2018). Often, variation can be explained jointly by two or more sets of explanatory variables. For example, variation explained jointly by a set of abiotic predictors and a set of spatial predictors can reflect spatial structuring of those abiotic predictors (Borcard et al. 2018). For our analysis of invertebrate community composition, we tested four sets of explanatory variables: site-scale local abiotic conditions, quadrat-scale meadow attributes, medium-scale spatial correlation and broad-scale spatial correlation.

Prior to using the variation partitioning function, we used a forward-selection procedure on all four sets of explanatory variables to identify significant explanatory variables within each set. For the forward-selection procedure, we tested each set of variables on Hellinger-transformed invertebrate abundance data (Legendre and Gallagher 2001). We also centered and standardized all abiotic and meadow predictors. For each of our four sets of variables, we first ran a redundancy analysis to estimate how much variation in invertebrate composition was explained by the full set of variables (R^2). We then used the `forward.sel()` function from the *adespatial* package to test which variables from the full set explained significant variation in the invertebrate data, adding one variable at a time until the forward-selection model explained as much variation in the data as the full set of variables (Dray et al. 2024). The significant variables were included in the variation partitioning analyses. For our two sets of spatial explanatory variables, we ran these analyses on the spatially detrended, Hellinger-transformed invertebrate data following Borcard et al. (2018). We also tested whether our invertebrate data included a significant linear spatial trend, which is not captured by dbMEMs, that should be included in our set of broad-scale spatial predictors. We tested this by conducting an additional redundancy analysis with the Hellinger-transformed invertebrate composition data as our response matrix and the sample coordinates as our explanatory matrix.

We conducted the variation partitioning procedure with all four sets of variables (abiotic conditions, meadow attributes, and broad- and medium-scale variation) using the `varpart()` function (Oksanen et al. 2020). We then tested whether each set of predictors uniquely explained a significant amount of variation in invertebrate composition after accounting for all other predictors. For each significant block of predictors, we used a partial redundancy analysis with that block of predictors as the explanatory matrix and all other predictors included as covariables to identify the predictors within each set that explained the most variation in the data (Borcard et al. 2018).

Results

Invertebrate diversity and abundance

We identified a total of 16,029 individuals representing at least 72 taxa. On average, we observed 10.3 taxa (± 4.8 SD; range 1–21 taxa) in a 0.0625 m² plot of eelgrass and 21.7 taxa (± 6.5 SD; range 9–33 taxa) in a meadow. Rarefaction curves indicated that despite collecting nine samples at most meadows, we likely undersampled species richness in some meadows based on the extrapolations of saturating species richness (Supporting Information Fig. S1). Annelids, crustaceans, and bivalves, taxa commonly associated with eelgrass meadows, were observed at all sites (Fig. 2). We observed gastropods, chironomids, foraminifera, nematodes, and halacarid mites at most sites. Higher latitude sites were numerically

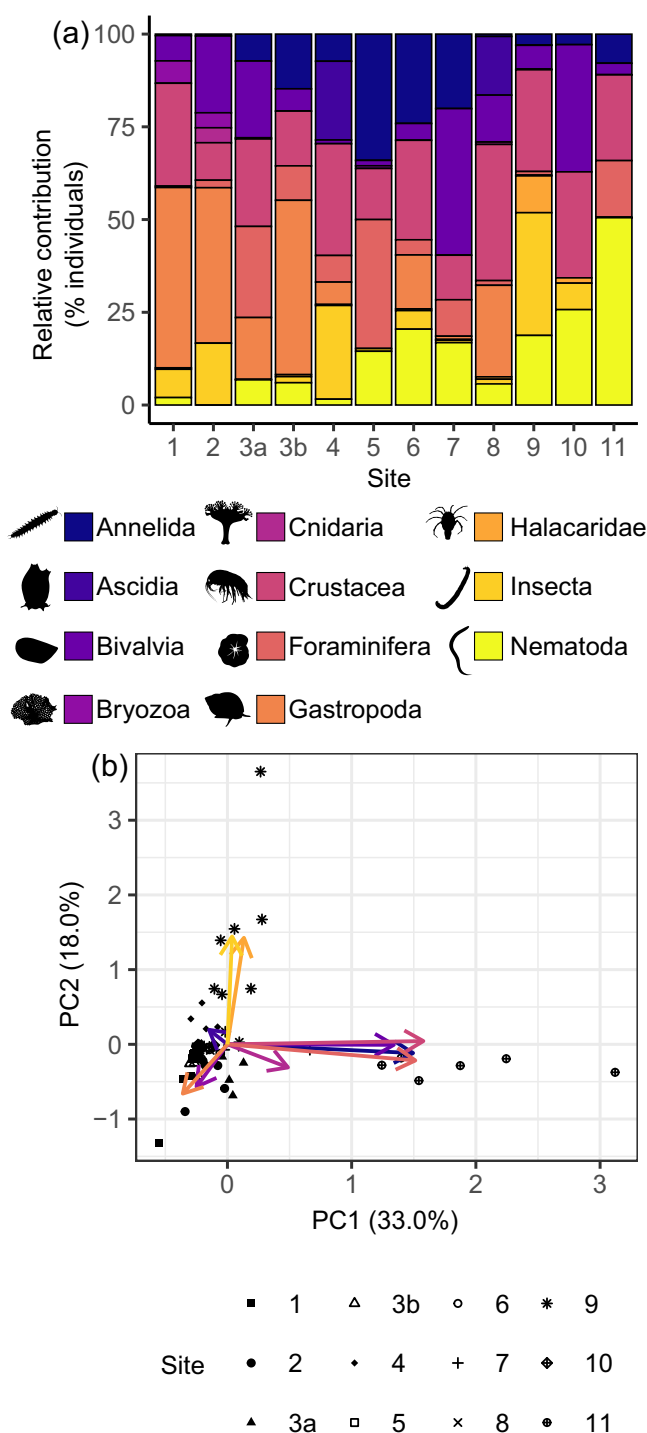


Fig. 2. (a) Relative contribution (%) of 11 taxonomic groups. Sites are numbered from south (1) to north (11). (b) Variation in the scaled abundances of each taxonomic group across quadrats in a principal component analysis. Figures only include taxonomic groups that had >10 individuals across the dataset. In (b), scaling is Type 2, meaning that the angles between the response and explanatory variables (or between response variables) reflect their correlations, where an angle of 0° means a perfect positive correlation, 90° means no correlation, and 180° means a perfect negative correlation (Borcard et al. 2018).

dominated by nematodes, while lower latitude sites were dominated by gastropods (Fig. 2). Most taxa were relatively rare: 57 of 72 taxa were each represented by fewer than 100 individuals across all samples (<1% of all individuals). Nematodes constituted the most abundant taxon (38.1% of all individuals), but this was driven by extremely high nematode abundance at sites 11 (89% of all nematodes) and 9 (7% of all nematodes).

Invertebrate abundance in each 0.0625 m² plot ranged from 1 to 4236 individuals (median: 32; interquartile range: 16–112). After standardizing for available habitat in each quadrat (i.e., aboveground eelgrass dry mass), plot-level invertebrate density ranged over three orders of magnitude from 1 individuals g⁻¹ eelgrass to 697 individuals g⁻¹ eelgrass (median: 29; interquartile range: 9–136).

Variation in eelgrass habitat and abiotic conditions

Temperature varied from 9°C to 16°C among meadows, and salinity from 9.4 to 20.7. Turbidity varied from 1 to 11.6 nephelometric turbidity units and fetch from 30 to 230 km among eelgrass meadows (Fig. 3a). Sites with greater fetch were associated with warmer and fresher water on these summer sampling dates, but no other clear correlations emerged among these variables. A redundancy analysis using meadow attributes as a response matrix and abiotic conditions as explanatory variables found that meadows with longer shoots and more blades per shoot were associated with a longer growing period, but no evidence of associations between other local abiotic conditions and meadow attributes. Quadrats comprising larger eelgrass shoots were weakly associated with greater quadrat-level eelgrass density and biomass (Fig. 3b). The amount of epiphytes on eelgrass blades was weakly associated with more chlorophyll in the water column and narrower eelgrass shoots (Fig. 3b). Latitude did not explain variation in eelgrass habitat or abiotic conditions.

Variation in invertebrate diversity, abundance, and composition

Local abiotic conditions and meadow attributes explained variation in invertebrate abundance and diversity (Figs. 4, 5). Invertebrate abundance was lowest at sites with high turbidity (Fig. 4a) and low epiphyte load (Fig. 5a). However, invertebrate abundance at site 11 was greater than expected based on abiotic differences alone; the best abundance model included a broad-scale spatial eigenvector accounting for this difference (Supporting Information Table S3). Invertebrate richness was negatively associated with turbidity (Fig. 4b); additional variation was explained by a broad-scale eigenvector (Supporting Information Table S3). Invertebrate evenness (Pielou's *J*) was positively associated with turbidity (Fig. 4c). A broad-scale eigenvector in the selected model indicated that evenness was lower than expected from turbidity at site 11, a site that was heavily dominated by nematodes (50% of all invertebrates). Hill–Simpson diversity was greatest at sites with high

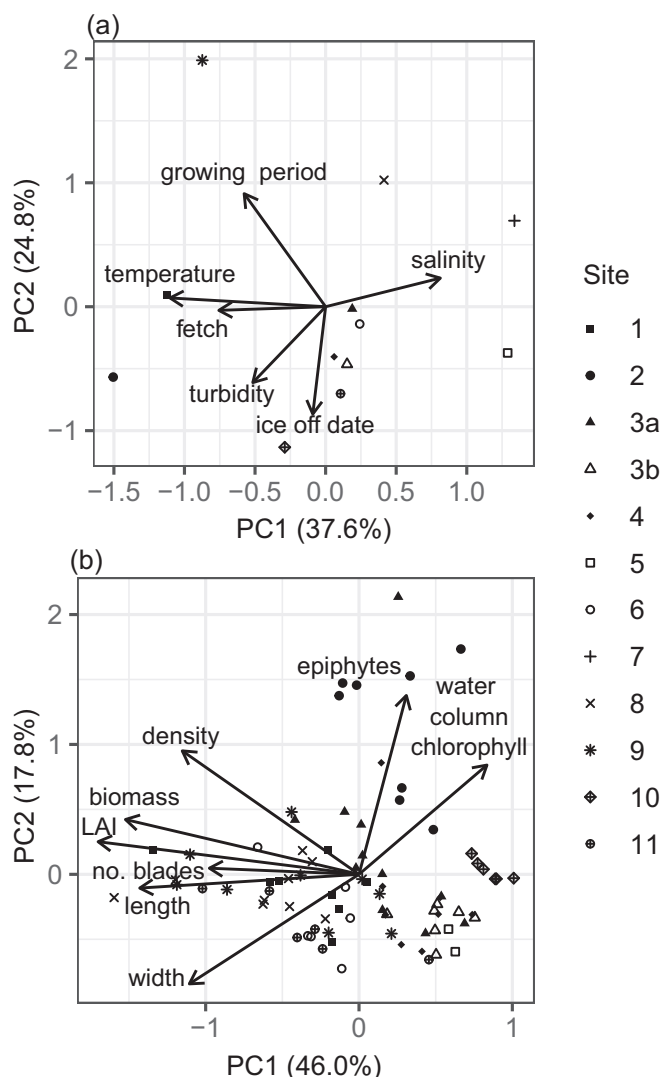


Fig. 3. Variation in (a) meadow-level abiotic conditions ($N=12$ meadows) and (b) eelgrass attributes ($N=80$ quadrats) visualized in a principal components analysis. In both (a) and (b), scaling is Type 2.

eelgrass and epiphyte biomass (Fig. 5b,c). Local contributions to beta diversity were highest in very salty (salinity greater than 18) or very fresh (salinity less than 10) waters; communities in warmer waters contributed less to beta diversity (Fig. 4d,e). The best selected model of local contributions to beta diversity also included a broad-scale spatial eigenvector indicating that site 11 contributed disproportionately more to beta diversity than expected from local abiotic conditions (Supporting Information Table S3).

Our spatial analyses identified significant regional patterns of invertebrate biodiversity. Invertebrate community composition was more dissimilar among meadows (mean Ruzicka dissimilarity = 0.93 ± 0.08 SD) than within meadows (mean Ruzicka dissimilarity = 0.74 ± 0.15 SD). After accounting for local abiotic conditions and meadow attributes, broad-scale spatial structures occurring at the scale of hundreds of

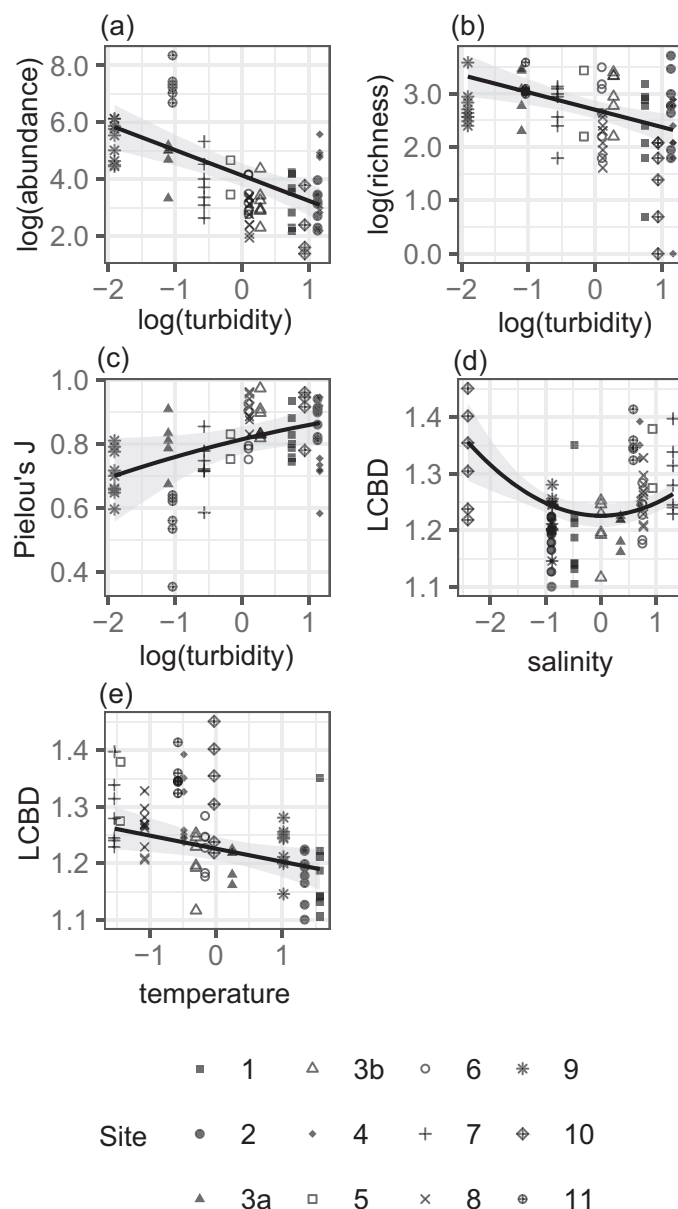


Fig. 4. Results of generalized linear mixed-effect models describing relationships between invertebrate communities and standardized local abiotic conditions. Lines and shaded areas show model-predicted means and 95% credibility intervals, respectively. LCBD is local contribution to beta diversity and richness is Chao richness.

kilometers explained 10.3% of variation in invertebrate community composition ($p < 0.01$), whereas medium-scale spatial structures occurring over tens of kilometers explained only 2% of variation in invertebrate community composition ($p = 0.02$; Fig. 6a).

When considering local abiotic conditions, meadow attributes, and broad- and medium-scale spatial structures, we found that altogether these conditions explained less than half of the variation in invertebrate community composition (Fig. 6a). Local abiotic conditions including growing period,

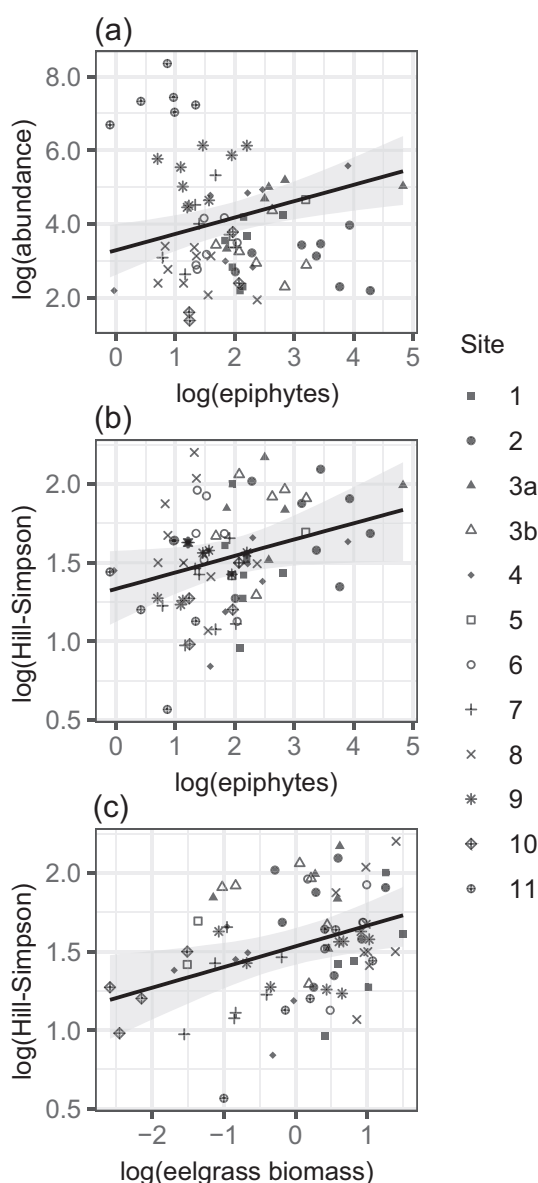


Fig. 5. Results of generalized linear mixed-effect models describing relationships between invertebrate communities and standardized meadow attributes. Lines and shaded areas show model-predicted means and 95% credibility intervals, respectively.

salinity, temperature, fetch, and turbidity, but not ice-off date, explained the largest significant unique fraction of variation in invertebrate composition (Fig. 6b; $p = 0.001$). After accounting for the influence of the abiotic environment and spatial position, meadow attributes including eelgrass biomass, epiphyte biomass, eelgrass morphology, and water-column chlorophyll did not independently explain variation in invertebrate composition ($p = 0.198$), but the analyses did suggest that there is variation in invertebrate community composition jointly explained by meadow attributes and abiotic conditions (Fig. 6a).

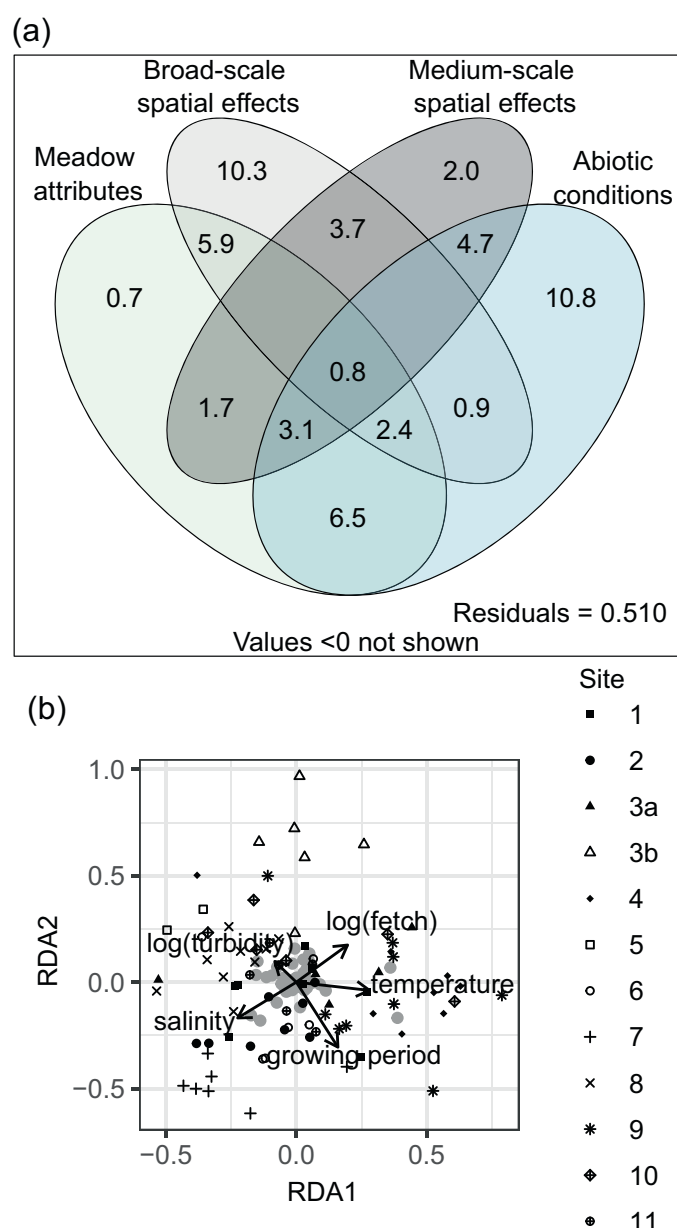


Fig. 6. (a) Variation partitioning results for invertebrate community composition data. Values represent percentages of variation in community composition explained by eelgrass meadow attributes, the abiotic environment, the spatial arrangement of meadows at broad (100s of km) and medium (10s of km) spatial scales, or some combination thereof (areas of overlap). Colors represent different sets of explanatory variables. (b) Partial RDA showing the effects of variation of different environmental factors on invertebrate communities after accounting for the effects of spatial arrangement and meadow attributes. In (b), scaling is Type 2.

Discussion

We conducted the first comprehensive survey of eelgrass-associated invertebrates in eastern James Bay to describe these communities and explore how they are shaped by local abiotic conditions, meadow arrangement, and meadow attributes.

Our analyses revealed that each of these factors influences eelgrass-associated invertebrate biodiversity patterns in different ways. Invertebrate abundance and species richness declined with increasing turbidity, and local contributions to beta diversity were lower in warmer waters and highest in very fresh or very salty waters (Fig. 4). These abiotic conditions also influenced invertebrate composition (Fig. 6). The spatial arrangement of meadows explained differences in invertebrate composition across 10s to 100 s of km (Fig. 6). Meadow attributes did not independently explain significant variation in invertebrate composition (Fig. 6a), but invertebrate abundance and diversity increased with eelgrass epiphytes and invertebrate diversity increased with aboveground eelgrass biomass (Fig. 5). Altogether, these results strongly suggest that local conditions alone do not explain variation in invertebrate communities, and that the spatial arrangement of eelgrass meadows along the coastline is an important component of sustaining regional biodiversity.

Consistent with the predictions we tested, invertebrate composition was strongly influenced by local abiotic conditions, particularly salinity, temperature and growing period (Fig. 6b). Salinity in James Bay ranges from <5 to >20 depending the location and season, with local influences from rivers (Peck et al. 2022). In recent decades, hydroelectric development has redirected rivers, increasing freshwater output in the northern part of the coastline (Kuzyk et al. 2026). Many marine species cannot osmoregulate in low salinities, which can lead to lower diversities and abundances of marine organisms in fresher environments (Yamada et al. 2007; Barnes and Ellwood 2012). It is possible that we did not observe a positive association between salinity and invertebrate diversity because the salinity gradient over which we sampled (9.4–20.7) was too narrow. In the Baltic Sea, eelgrass exists over a wide salinity gradient (1–25), and in this region, benthic macrofauna (not exclusive to eelgrass habitats) diversity is much lower in lower salinity environments (Zettler et al. 2014). This has been found in other regions as well (e.g., Yamada et al. 2007). Though we did not observe a positive association between salinity and invertebrate diversity, contrary to our prediction, we found that meadows in fresher (salinity less than 10) or saltier (salinity greater than 18) waters were more ecologically unique (Fig. 4d). Fresher waters were particularly associated with chironomids (midges) and harpacticoid copepods, whereas salty waters were associated with bristle worms and the amphipod *Ischyrocerus anguipes*.

Differences in temperature also explained variation in invertebrate composition (Fig. 6b); communities in warmer waters contributed less to regional beta diversity (Fig. 4e). It is possible that some invertebrate species are negatively impacted by warmer or more variable temperatures, as has been observed in other regions (Stark et al. 2020; Murphy et al. 2021). Growing period also influenced invertebrate composition in James Bay (Fig. 6b), consistent with prior findings

that composition changes as species reproduce and recruit throughout the growing season (e.g., Whippo et al. 2018).

Sites with higher turbidity in July were associated with lower epifaunal abundance, lower species richness and greater species evenness (Fig. 4a–c) and turbidity influenced invertebrate composition (Fig. 6b). In other systems, turbidity has been identified as an influence on animal abundance and composition through its effects on predator–prey interactions (Lunt and Smee 2020), but interpreting the influence of turbidity on invertebrate communities in James Bay is not possible from this comparative analysis. In James Bay, turbidity during the ice-free summer is influenced by local, short-term conditions such as wind and other weather events (Kuzyk et al. 2026). Local turbidity is also likely influenced by site-level vulnerability to sediment resuspension, which is in turn affected by numerous environmental conditions including sediment size, wave action, and meadow extent, canopy height and density (Adams et al. 2016).

Invertebrate communities exhibited greater Hill–Simpson diversity in meadows with high eelgrass biomass (Fig. 5c), consistent with a general positive association observed between diversity and habitat availability (Hauser et al. 2006; Moore and Hovel 2010). However, eelgrass biomass did not significantly explain variation in invertebrate abundance, contrasting with our prediction. A possible explanation for this disconnect is that eelgrass in James Bay grows rapidly in the early part of the growing season (Davis et al. 2024), and local invertebrate population growth or immigration may not have saturated the available habitat that reflects recent seasonal growth. In the Baltic, eelgrass biomass is positively associated with invertebrate abundance only after the eelgrass canopy has regrown following ice break up (Włodarska-Kowalczyk et al. 2014). Eelgrass-associated epiphyte abundance, which was positively associated with invertebrate abundance and diversity (Fig. 5a,b), explained more variation in invertebrate abundance than did eelgrass biomass. Higher epiphyte load may indicate higher epiphyte productivity, and could reflect a bottom-up influence on grazer abundance (Amundrud et al. 2015), but the causality in this case remains unclear.

Our variation partitioning analysis did not detect an independent influence of meadow characteristics on invertebrate composition, but it did identify variation *jointly* explained by meadow characteristics, abiotic conditions and spatial structure (Fig. 6a; overlapping areas of Venn diagram), reflecting covariation between these sets of variables. Thus, it may be that meadow characteristics were directly associated with differences in invertebrate communities, as has been observed in other studies (Hall and Bell 1988; Knight et al. 2015; Stark et al. 2020), but these associations are masked by covariation. For example, variation in eelgrass morphology (meadow attribute) was associated with the duration of the growing period (abiotic condition) prior to sampling.

The spatial arrangement of meadows across the region influenced invertebrate composition among meadows, particularly at broad scales (100 s of km; Supporting Information Figs. S15, S18; Fig. 6a), supporting our prediction. This spatial structure could reflect different underlying environmental or ecological mechanisms. It is possible that spatially structured, unmeasured environmental variation causes these patterns rather than purely spatial processes (Borcard et al. 2018). It is also possible that dispersal limitation over broad scales contributes to the observed spatial structure: the James Bay coastline features complex currents that may form geographic barriers to dispersal and fragment connectivity along the coastline. Moreover, eelgrass meadows in James Bay are substantially smaller and more isolated than before declines in the 1990s (Idrobo et al. 2024; Kuzyk et al. 2026); smaller and more distant habitat patches reduce the probability of successful colonization (i.e., reduce connectivity) between meadows (Macarthur and Wilson 1967; Thompson et al. 2017; Carroll and Freestone 2023). Connectivity between meadows may be further influenced by future climate change through the loss or modification of eelgrass habitat (Krause-Jensen et al. 2020; Wernberg et al. 2024). In James Bay, eelgrass is predicted to be particularly vulnerable to degradation and loss from warming because of low genetic diversity (Jeffery et al. 2024), putting its associated biodiversity at risk. We also note that a spatial eigenvector selected by our models (dbMEM3, Supporting Information Fig. S14) indicates that invertebrate assemblages in site 11, near the mouth of James Bay, were more abundant, more unique, and less even than expected from local abiotic conditions and meadow attributes. It is possible that these differences reflect the influence of the adjacent Hudson Bay.

The spatial arrangement of meadows along the coastline, whether through spatially structured environmental variation or dispersal limitation, appears to have a greater influence on eelgrass-associated invertebrate communities in James Bay than in other regions. For example, in British Columbia invertebrate communities > 1000 km apart may be just as similar as nearby meadows (Stark et al. 2020). Network analysis of invertebrate communities in the region (using a biophysical model to simulate dispersal) has suggested that this high regional similarity among meadows is not due to direct connections between distant meadows, but more likely that dispersal between distant meadows is multi-generational and mediated by “stepping-stone” meadows (Cristiani et al. 2021), the loss of which can cause large and nonlinear declines in regional biodiversity (Thompson et al. 2017). A deeper understanding of dispersal and population connectivity in this region will require the use of such a biophysical model to estimate currents and dispersal, but our finding that invertebrate communities are spatially structured at broad spatial scales may reflect an impact of widespread habitat loss on the potential for this type of multigenerational, long-distance dispersal.

We found no historical survey of similar scale and methods with which to assess changes in the biodiversity of these

communities over time. When comparing our inventory with the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS), and given the limited historical surveys in this region, we find that ours are the first observations of two species in the shallow coastal habitats of this region: polychaete *Harmothoe imbricata* and the amphipod *Caprella septentrionalis*. When comparing with what records are available in the literature, we note the absence of any limpets in our observations. Limpets were recorded in the region on eelgrass leaves in samples collected between 1986 and 1991 (Lalumière et al. 1994). Though the exact location of those collections is not known, one of the five stations where invertebrates were observed by Lalumière et al. (1994) is our Site 9 (Fig. 1). Because limpets are morphologically very distinct from other taxa, it is unlikely these were missed in our collections if they were indeed present. The absence of limpets from our entire collection is notable and a potential indication of its loss from the region. The limpet was reported by Lalumière et al. (1994) as *Testudinalia testudinalis*, but we note that *T. testudinalis* is typically found on rocks and boulders, not eelgrass, and has historically been conflated with other limpet species (Carlton et al. 1991). Eelgrass-associated limpets have been reported in the literature, and there are reports of their extinction (Carlton et al. 1991) or near-extinction (Pillay et al. 2010) following eelgrass crashes. For example, the limpet *Lottia alveus*, an eelgrass specialist on Atlantic shores, is considered extinct following widespread die-offs of *Zostera marina* in the 1930s caused by the slime mold *Labyrinthula zosterae* (Carlton et al. 1991; Carlton 2023).

Subarctic and arctic systems are on the front lines of global change. Climate change is not only driving significant warming (Rantanen et al. 2022), but changing the timing of major seasonal events such as ice break-up and ice formation and causing increased climatic anomalies such as marine heat waves (Taha et al. 2019; Bruneau et al. 2025). Warming-driven increases in ice melt and run-off can also increase coastal turbidity (Krause-Jensen et al. 2020; Pecuchet et al. 2025). In our study, warmer waters were associated with less unique invertebrate assemblages, and more turbid waters were associated with less abundant and species-rich assemblages (Fig. 4), suggesting that continued increases to temperature and turbidity may negatively impact eelgrass-associated biodiversity. Climate change may also impact eelgrass-associated biodiversity in the sub-Arctic and Arctic through its effects on the expansion or loss of eelgrass habitat (Krause-Jensen et al. 2020; Wernberg et al. 2024). Despite these rapid and relevant changes, subarctic marine biodiversity in many regions remains understudied. Increased attention to these systems is essential to steward them through the consequential changes that lie ahead.

Biodiversity patterns in the coastal waters reflect local abiotic conditions, movement among habitat patches, and interactions between foundation species and associated fauna. Our analyses showed that in eastern James Bay, these processes influence different aspects of local and regional biodiversity.

At the local scale, meadow characteristics explained overall invertebrate diversity, whereas salinity, temperature, and turbidity had a greater impact on invertebrate composition. At the regional scale, diversity increased because of broad-scale spatial structuring as well as differences between the abiotic conditions in which meadows were found. Overall, our findings contribute to a growing literature demonstrating the importance of local and regional processes for maintaining biodiversity in coastal foundation species and underscore the need for process-based understanding of biodiversity patterns.

Author Contributions

All individuals listed as authors have agreed to be listed on this manuscript and have approved the submitted version of the manuscript. Each author contributed to the manuscript as follows: Mary I. O'Connor, Fanny Noisette, Melanie-Louise Leblanc, Nicole S. Knight, and Elliot Dreujou contributed ideas to the manuscript; Nicole S. Knight, Mélanie-Louise Leblanc, and Mary I. O'Connor co-wrote the submitted manuscript; Nicole S. Knight conducted the statistical analyses; Mélanie-Louise Leblanc, Kaleigh E. Davis, Fanny Noisette, and Mary O'Connor collected the data; Felipe Amadeo identified all invertebrates; Armand LaRocque estimated ice-break dates at sampling sites. All authors contributed to editing the final manuscript draft.

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Conflicts of Interest

None declared.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at <http://doi.org/10.5281/zenodo.17781637>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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