FEATURE ARTICLE

Living under Arctic kelp forests: linking soft-bottom communities to kelp cover in the Canadian Arctic

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ABSTRACT: Kelp forests are dominant habitats along Canadian Arctic coastlines. While their extent and productivity are expected to change dramatically due to global warming, their role in supporting Arctic coastal biodiversity remains poorly explored. Leveraging an extensive data set encompassing core samples, video transects, and environmental data, this study explores the patterns and drivers of benthic diversity, particularly focusing on kelp cover, across 4 Eastern Canadian Arctic regions. We show that the widespread soft bottoms in many subtidal coastal Arctic areas are associated with high densities of the kelp *Saccharina latissima*, often growing in mixed stands with *Laminaria solidungula* and *Alaria esculenta*. These kelps enhance the diversity of invertebrate communities thriving in the sediment below, increasing densities in specific groups and promoting subsurface feeding activity. Interregional comparisons indicate that high turbidity conditions typically lead to low macroalgal cover and low invertebrate richness, whereas extensive sea ice cover can favor high macroalgal abundance and unique diverse communities. Conditions of intermediate open-water duration and high water clarity support tall kelp forests, hosting approximately 70% of local rare taxa. Based on these surveys, we provide a list of Arctic invertebrate taxa according to their level of selectivity for kelp forests as habitats. Despite variation among regions, kelp forests enhance biodiversity and drive unique ben-
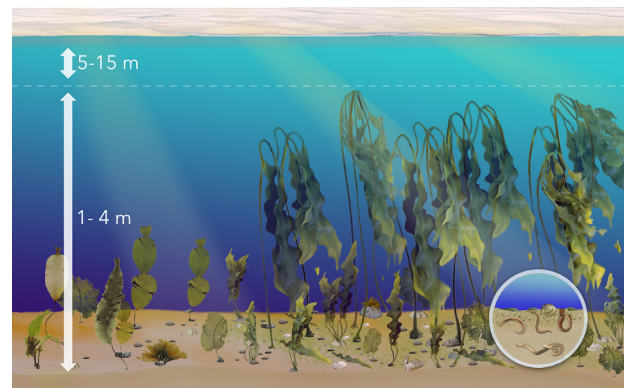
Tall kelp forests of the Canadian Arctic growing attached to pebbles and cobbles amidst soft sediment, increasing local biodiversity and providing habitat for subsurface deposit feeders.

Illustration: ArcticKelp Canada

thic communities in the Canadian Arctic. Due to their ecological significance and potential vulnerability, we recommend efforts to integrate kelp forests into marine protected areas and minimize human-induced damaging activities within or near these habitats.

KEY WORDS: Arctic coastal habitats · Kelp forests · Biodiversity · Benthic communities · Functional traits · Feeding mode · Invertebrates · Endofauna · Ocean warming

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1. INTRODUCTION

The Canadian Arctic and its Archipelago represent a vast territory that incorporates two-thirds of Canada's coastline and shallow areas (162 000 km linear coastline (Arctic Institute 2024) and >10 % of the global coastline (Nicholls et al. 2021). This territory is characterized by a mosaic of seascapes and oceanographic conditions, shaping regional patterns in benthic diversity (Spalding et al. 2007, Piepenburg et al. 2011). Like most systems, this diversity is influenced by local variables including substratum type, water chemistry, land discharges, wave energy, sea-ice cover and scouring, seasonal patterns, and increasingly, effects of climate change, which are exacerbated in the Arctic (Gutt 2001, Overland et al. 2019, Irrgang et al. 2022).

As most shallow (0–40 m) Canadian Arctic areas are generally inaccessible to large research vessels, the sampling records for coastal benthic fauna tend to be localized and limited relative to the deeper shelf areas of the Arctic; thus, many Arctic coastal ecological processes remain poorly known (Piepenburg et al. 2011). Furthermore, even though the 0–5 m depth range undergoes substantial disturbance from ice scouring (Conlan et al. 1998, Barnes 1999, Dale & Leontowich 2006), there is no evidence to indicate that beyond this depth range, the diversity in the shallow euphotic zone is not as extensive as that reported for deeper shelf areas (Thomson 1982, Gray et al. 1997). In fact, a recent campaign using benthic trawls reported as many as 900 epibenthic taxa in the shallow coastline of the Eastern Canadian Arctic alone (Gianasi et al. 2022b), which represents one-third of the latest panarctic inventory (Piepenburg et al. 2011). Gianasi et al. (2022b) also pointed to a lack of connections between benthic communities and environmental variables and emphasized the necessity for additional assessments that could include coastal habitats.

Recent surveys have found extensive kelp forests along shallow Arctic coasts, with the Eastern Canadian Arctic section alone potentially representing as much as 9 % of the estimated global distribution of kelp (312 000 of 1 500 000–2 500 000 km^2) (Goldsmit et al. 2021, Filbee-Dexter et al. 2022). This massive source of benthic productivity contrasts with terrestrial vegetation patterns in Arctic Canada, where continental forests stop at the tree line (between 54° and 68° N) and transition to low-lying or minimal vegetation, whereas dense kelp forests are recorded as far north as Ellesmere Island (>75° N) (Filbee-Dexter et al. 2022). Favorable conditions, including clear waters in summer and low grazing pressure over much of the Arctic coastal zones (5–40 and up to 60 m in depth; Krause-Jensen et al. 2019), promote this productivity, since most kelp species and other macroalgae including Desmarestiales, Fucales, and a variety of fleshy red algae from genera like *Odonthalia*, *Phycodrys*, and *Dilsea*, thrive in cold temperatures (on average from –1 to 4°C), and are well adapted to the long period under sea-ice cover (Wiencke et al. 2009, Scheschonk et al. 2019, Bringloe et al. 2022, Filbee-Dexter et al. 2022).

Kelp forests are well known for hosting high benthic and pelagic diversity (Teagle et al. 2017, UNEP & NBFN 2023). Research, largely from temperate areas of the world, using manipulative clearing experiments (Graham 2004, Vanella et al. 2007, Deza & Anderson 2010), artificial substrates (Bologna & Steneck 1993, Norderhaug et al. 2002, Almanza et al. 2012), modeling (Miller et al. 2018), or comparisons of observations from inside and outside of kelp forests (Konar & Estes 2003, Schaffer 2004), has provided strong evidence that kelp forests enhance coastal biodiversity. Like terrestrial forests, kelp forests add spatial heterogeneity and dimensionality to their environment (Pessarrodona et al. 2021), which is key to the establishment of a diverse fauna and complex ecological interactions (Keats et al. 1987, Shaffer 2004, Miller et al. 2018). Furthermore, as their density increases, kelps can also modify the physical and chemical processes in their immediate environment, including dampening water currents and waves (Eckman et al. 1989, Mork 1996, Hurd 2000), increasing dissolved O_2, pH, and DOC (Krause-Jensen et al. 2016, Kosek & Kukliński 2023), and shading the seafloor (Clark et al. 2004), all of which can facilitate the establishment of certain species of invertebrates, fish, and understory algae (Duggins et al. 1990, Connell 2003). Finally, their high primary productivity can, to some extent, supply local food webs (Dunton & Schell 1987, McMeans et al. 2013, von Biela et al. 2016) and enhance secondary productivity through filter feeders (Duggins & Eckman 1994, Gaillard et al. 2017), grazers, and phytodetritivores that feed on live and detrital kelp material (Fredriksen 2003, Renaud et al. 2015).

In the context of global warming, Arctic kelp forests are undergoing various transformations. In some regions, they may increase in biomass and productivity due to increased light or expand their ranges, colonizing the substrate where the ice recedes, such as along coastal strips or at higher latitudes with declining multi-year sea ice (Goldsmit et al. 2021, Assis et al. 2022, Castro de la Guardia et al. 2023). In other regions, the picture is more pessimistic, with increased wave activity, thawing permafrost, and shoreline erosion leading to increased nutrient discharge and tur-

bidity, all of which may negatively affect kelp growth (Shaffer & Parks 1994, Muth 2012, Bartsch et al. 2016, Bonsell & Dunton 2018). Warmer water could also encourage herbivory and interspecific competition between macroalgae that may lead to the extinction of endemic Arctic taxa, such as *Laminaria solidungula*, and dominance by more temperate species, such as *Agarum clathratum* or *Saccharina latissima* (Franco et al. 2015, Goldsmit et al. 2021, Bringloe et al. 2022).

While these transformations are predicted or already underway, we still have very little baseline knowledge of the faunal diversity, patterns, and ecological functions associated with kelp in the polar regions. Given their demonstrated importance in other regions, future changes to kelp habitats are expected to affect Arctic coastal ecosystems and the predominately Indigenous human populations who rely on coastal resources (Smale et al. 2013, Eger et al. 2023). Moreover, kelp forests were recently targeted as ecological features of interest in supporting the creation of a marine protected area around Southampton Island in Hudson Bay (Loewen et al. 2020). This type of exercise, soon to be repeated in other regions of the Canadian Arctic (Fisheries and Oceans Canada 2024), also underscores the necessity of expanding our understanding of kelp ecology and its different roles, such as supporting biodiversity in Arctic and high-Arctic climatic and oceanographic conditions.

Here, we explored the zoobenthic diversity, mostly infauna and small epifauna, associated with kelp forests in the Eastern Canadian Arctic. Unlike temperate kelp forests, which are predominantly associated with hard substrata, a large proportion of kelp in the Canadian Arctic can form tall (~3—5 m height) and high-biomass forests on soft substrata, where the kelps attach to sparse pebbles or cobbles (Filbee-Dexter et al. 2022). These unique habitats are also ideal for the establishment of soft-bottom invertebrate communities. We tested the hypothesis that variability in kelp abundance (with kelp percent cover as a proximal metric) should produce differing patterns of benthic diversity, with the prediction that stations with high kelp cover would host greater richness and distinct communities characterized by their own sets of functional traits. Leading to this, our specific objectives were to (1) explore the patterns of Arctic nearshore benthic (infauna and small epifauna) diversity and kelp abundance at regional and local scales, (2) determine if kelp (and other macroalgae) cover influences invertebrate community diversity and composition, and (3) describe the community assemblages and functional trait variability associated with differences in kelp/macroalgal abundance.

2. MATERIALS AND METHODS

2.1. Sample collection (cores and videos)

Fieldwork took place during the summers of 2011 and 2012 in 4 different regions of the Eastern Canadian Arctic: Churchill (Manitoba), Deception Bay (Quebec), and Iqaluit and Steensby Inlet (Nunavut), as part of a Fisheries and Oceans Canada led project through the Canadian Aquatic Invasive Species Network (CAISN) to catalogue a biodiversity baseline of benthic fauna in coastal areas (Goldsmit et al. 2014, Goldsmit 2016). The 4 regions are far away from each other, with the greatest distance being 1470 km between Churchill and Steensby Inlet, and are influenced by differing currents and water masses (Fig. 1).

To maintain optimal proximity to the surveyed habitats and ensure sampling consistency among regions, zoobenthos samples were collected by divers at depths ranging from 4 to 20 m using cylindrical cores (diameter = 10 cm, length = 15 cm, volume = 1178 cm^3). At each station, divers followed a 50 m long transect line (N = 10 per region except for Iqaluit, where N = 7), and while filming the habitat at ~1 m above the seafloor, they collected cores at random locations along the line (4 core replicates for each of the 37 transects = 148 total samples). When in the presence of a kelp forest or algae bed, the cores were planted directly under the canopy, but algae/holdfasts were avoided. All cores were sieved to a minimum of 500 μm and organisms were preserved in a 4% buffered formaldehyde solution. The organisms were later sorted, weighed (wet blotted, per species biomass per sample), and identified to the lowest practical taxonomic level. The cores contained mostly fauna living in the sediment (infauna), but also specimens attached to or living on the surface of the sediment (small epifauna). All species names were standardized to the World Register of Marine Species (WoRMS; Appeltans et al. 2012). The term 'taxa' refers to species and generic-level identifications unless otherwise noted. Some groups, including Foraminifera, Oligochaeta, Nematoda, and Nemertea, were not identified to lower levels due to the level of taxonomic specialization required (but see Gianasi et al. 2022a for further details on nematodes).

The transect videos were used to obtain kelp, macroalgal, and substratum percent cover for each station. A subset of 10—12 images was selected at regularly spaced intervals along each video (~20—30 s, depending on total video time), and only high-quality images with a clear view of the canopy/sub-canopy or seafloor were used. Using ImageJ, we overlaid 49
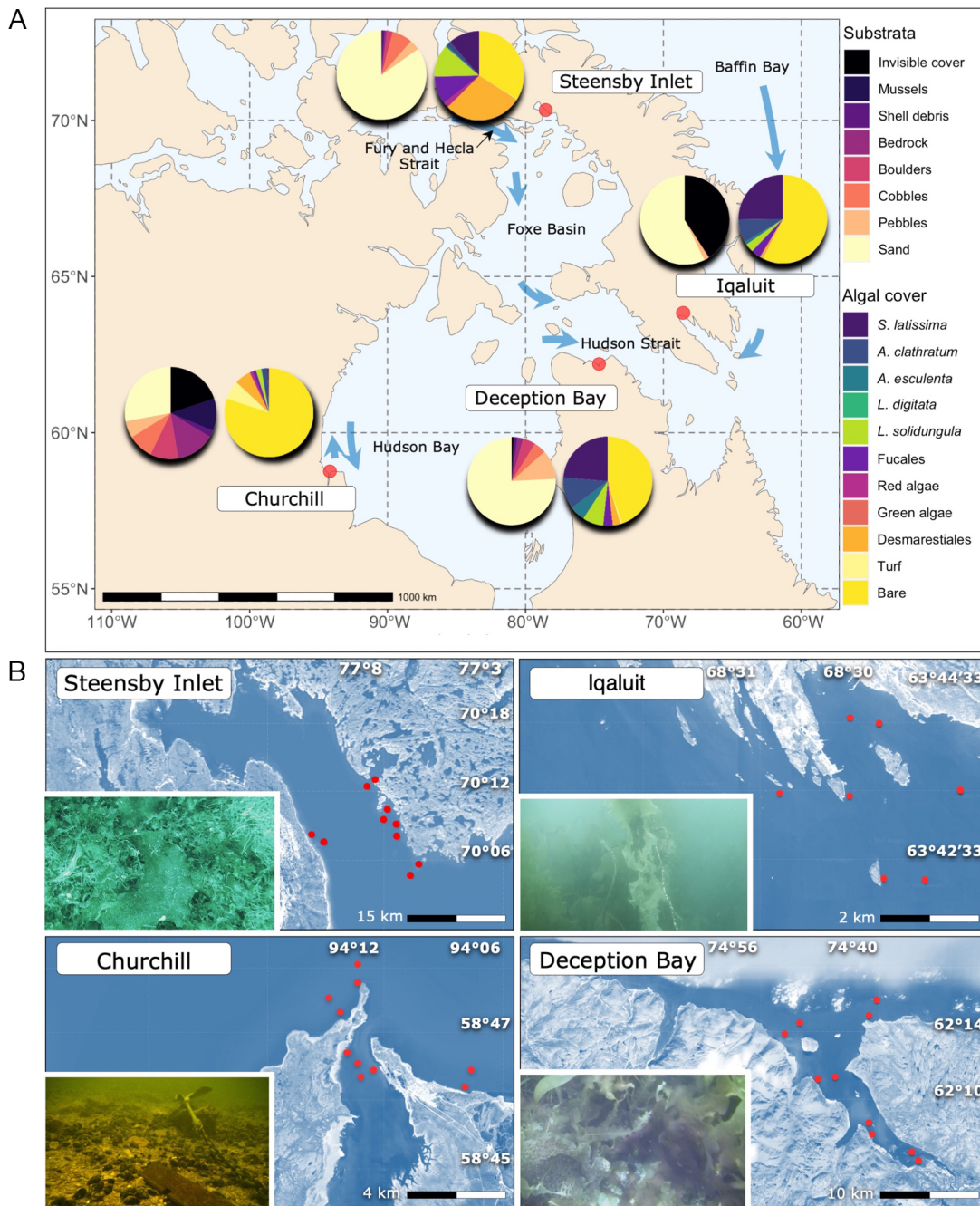
Fig. 1. (A) Locations of the 4 regions surveyed. Pie charts indicate the average (%) of substratum type (left) and algal cover (right) at the regional level. Blue arrows represent the direction of the dominant currents. The category 'Invisible cover' was used for images on which the substratum was invisible due to low visibility or high algal densities. (B) Overview of the positions of the sampling stations within each region along with photos of the typical seascapes from the transect videos

points over each image and identified the macroalgae or substratum type under each point and calculated a percent cover (Schindelin et al. 2012, Filbee-Dexter et al. 2022). Seaweeds were separated into kelps (*Agarum clathratum*, *Alaria esculenta*, *Laminaria digitata*, *L. solidungula*, *Saccharina latissima*), Fucales, Des-

marestiales, red and green algae, and turf algae. The substratum type (fine sediment [sand or silt], pebbles, cobbles, boulders, bedrock) was defined according to a simplified version of the Wentworth scale (Fig. 1). Field notes and dive logs were used to countercheck and complete some gaps from the video analysis.

2.2. Regional characteristics

Churchill (Manitoba) was sampled in August 2011, at 10 stations ranging from 6 to 17 m depth (Fig. 1). The area is located at the southern limits of the Canadian Arctic but experiences a full Arctic climate involving cold and strong winds, inducing the formation of thick landfast sea ice in the coastal area (1.2–1.6 m of ice) extending out to a water depth of about 15 m (Kuzyk et al. 2008). The Churchill River influences the local coastal area as it discharges great volumes of fresh water (566 m^3 s^{-1}) and nutrients into Hudson Bay (Pratte 1977, Prinsenberg 1986b, Kuzyk et al. 2008). The extremely brackish waters made the evaluation of substratum and kelp/macroalgal cover challenging due to poor visibility in many videos from this location.

Deception Bay (northern Quebec), located 40 km east of the village of Salluit, was sampled in July 2012 at 10 stations ranging from 6 to 20 m depth. At the time of data collection, there were no permanent installations in the bay except a deep-water port used by the Raglan Mine nickel shipping operations. The water in the bay is mostly influenced by westbound currents flowing through Hudson Strait from Hudson Bay and Foxe Basin (Dufour-Beauséjour et al. 2020).

Iqaluit (Nunavut) was sampled in August 2011 at 7 stations ranging from 4 to 15 m depth. The community, located on southern Baffin Island in Frobisher Bay, is the largest in Nunavut, with a current population of about 7400 inhabitants (Statistics Canada 2023). The region is uniquely characterized by having among the highest tidal amplitudes in the Canadian Arctic (up to 12 m; CHS 2020), which impacts sedimentary processes around the tidal flats (Dale et al. 2002, Hatcher et al. 2022). The water around the region is mostly influenced by the cold and saline Baffin Bay Current that flows southward (Stewart et al. 2015).

Steensby Inlet (Nunavut) was sampled in August 2012 at 10 stations ranging from 7 to 16 m depth. The inlet mainly receives Arctic water transported through Fury and Hecla Strait, south into Foxe Basin (Prinsenberg 1986a). Steensby Inlet falls inside the Arctic circle and experiences 3 mo of polar night from November to January. The inlet is currently uninhabited and has limited infrastructure (but see CBC News 2023). During dives in mid-August 2012, a thick layer of sediment, similar to that described in Alaska by Dunton et al. (1982), and probably typical of thick ice sheets, was visible and covered most algae beds. Additional details on regional characteristics are available in Table S1 in the Supplement at www.int-res.com/articles/suppl/m740p001_supp.pdf.

We used satellite-derived data to compare general trends in light availability at the seafloor among the 4 regions, as light is often the most limiting factor for kelp and macroalgae settlement and growth in the Arctic (Aumack et al. 2007, Dunton et al. 2009, Krause-Jensen et al. 2012, Castro de la Guardia et al. 2023). Specific satellite products included sea-ice concentration, particulate organic carbon (POC), photosynthetic active radiation (PAR), and diffuse attenuation coefficient (k_{d490}), which represents the rate at which light at 490 nm is attenuated with depth (Figs. S1 & S2 in the Supplement). We focused on light during the spring–summer period, which is a key period for photosynthesis and/or growth in the Arctic, to determine regional differences in light availability before and during the sea-ice melt. Typically, PAR values are beyond saturation requirements for kelp growth (>13 E m^{-2} d^{-1} for *S. latissima* and >3.3 for *L. solidungula*; Dunton & Jodwalis 1988) in spring, whereas light diminishes quickly below the saturation point in autumn before the sea-ice formation. Monthly averages of PAR, POC, and k_{d490} were obtained at a resolution of 4 km from the Moderate Resolution Imaging Spectroradiometer (MODIS) mounted on the Aqua Satellite (Level 3 data). These data were downloaded from the NASA Ocean Biology Distributed Active Archive Center (NASA Ocean Biology Processing Group 2019). The averages and standard deviations around each region were calculated using all pixels falling into 25 km buffers from a theoretical point located at the center of all stations in each region. Sea-ice concentrations between 2006 and 2011 were calculated using the ARTIST Sea Ice (ASI) algorithm (www.seaice.de) at a resolution of 3.125 km, with data obtained from the National Snow and Ice Data Center with the Advanced Microwave Scanning Radiometer (AMSR-E) (Cavalieri et al. 2014). Similarly, sea-ice concentrations were averaged using 25 km buffers around each region.

2.3. Data analysis

2.3.1. Patterns of benthic (infauna and small epifauna) diversity and kelp abundance at regional and local scales

Analyses of the core collections, including 4 biological replicates for each of the 37 stations (148 samples), were performed using R 4.4.2 (R Core Team 2023). To test how the sampling effort was representative of the regional diversity and compare potential diversity among regions, we built taxa accumulation curves and calculated Chao 1 estimates using the 'iNext' package (interpola-
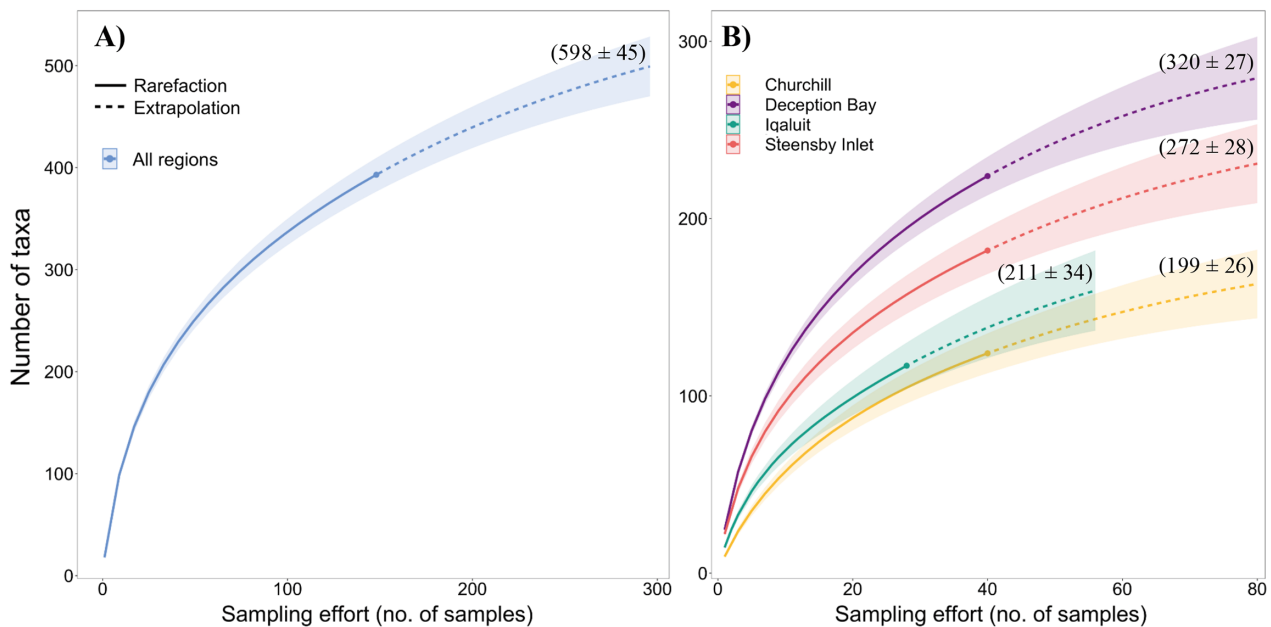
Fig. 2. Taxa accumulation (rarefaction and extrapolation) curves for (A) all regions combined (148 cores) and (B) each individual region, with 95% confidence intervals. Numbers in parentheses correspond to Chao 1 ($\pm$ SE) estimates

tion and extrapolation of species richness) (Chao et al. 2014, Hsieh et al. 2016) (Fig. 2). To evaluate the extent to which taxa were shared among regions, we created Venn diagrams using the 'ggvenn' package (Yan & Yan 2021) (Fig. S3 in the Supplement). Main interregional class-level differences were assessed using density calculations (Fig. S4 in the Supplement) (and see Table S3 in the Supplement for species list by region).

For each station (of 4 core replicates) and region, we calculated the following community metrics: density (mean number of specimens per m^{-2}), biomass (g m^{-2}), taxa richness (*S*, cumulative number of taxa), Shannon-Wiener diversity index (*H'*, using log$_e$), and Pielou's evenness index (*J'*). Regional means ($\pm$SE) for each community metric were calculated using station-specific means (Table 1). ANOVAs, followed by post hoc Tukey's HSD tests, were conducted on the station-specific means to assess differences among the 4 regions. ANOVA tests that violated assumptions of normality or homogeneity of variance (based on the examination of residual plots) were discarded.

Table 1. Benthic community characteristics across the regions sampled (mean $\pm$ SE), where *S* is taxa richness (shown as total taxa number and range across stations), *H'* is the Shannon-Wiener index, and *J'* is Pielou's evenness index. Kelp cover includes only species from the order Laminariales. Letters refer to groups that differ significantly following ANOVA and post hoc Tukey results

|	Density (ind. m^{-2})	Wet biomass (g m^{-2})	*S*	*H'*	*J'*	Kelp cover (%)	Algal cover (%)
Churchill (N = 10)	14174 $\pm$ 6395 (a)	1587 $\pm$ 857 (a)	123 (9—43) (c)	1.32 $\pm$ 0.2 (b)	0.44 $\pm$ 0.07	4.33 $\pm$ 2.6 (0—19) (b)	17.36 $\pm$ 5.6 (0—38) (b)
Deception Bay (N = 10)	29711 $\pm$ 6906 (a)	517 $\pm$ 138 (a)	225 (12—91) (a)	2.04 $\pm$ 0.2 (a)	0.52 $\pm$ 0.04	44.56 $\pm$ 9.4 (0—86) (a)	51.62 $\pm$ 8.4 (0.5—86) (a)
Iqaluit (N = 7)	24433 $\pm$ 11635 (a)	380 $\pm$ 142 (a)	118 (18—46) (b,c)	1.49 $\pm$ 0.2 (a,b)	0.44 $\pm$ 0.07	37.88 $\pm$ 13.0 (0—80) (a)	42.69 $\pm$ 12.7 (2—85) (a,b)
Steensby Inlet (N = 10)	22701 $\pm$ 4944 (a)	320 $\pm$ 110 (a)	183 (31—83) (a,b)	2.03 $\pm$ 0.1 (a)	0.52 $\pm$ 0.03	20.99 $\pm$ 6.4 (0—52) (a,b)	71.50 $\pm$ 8.2 (31—100) (a)
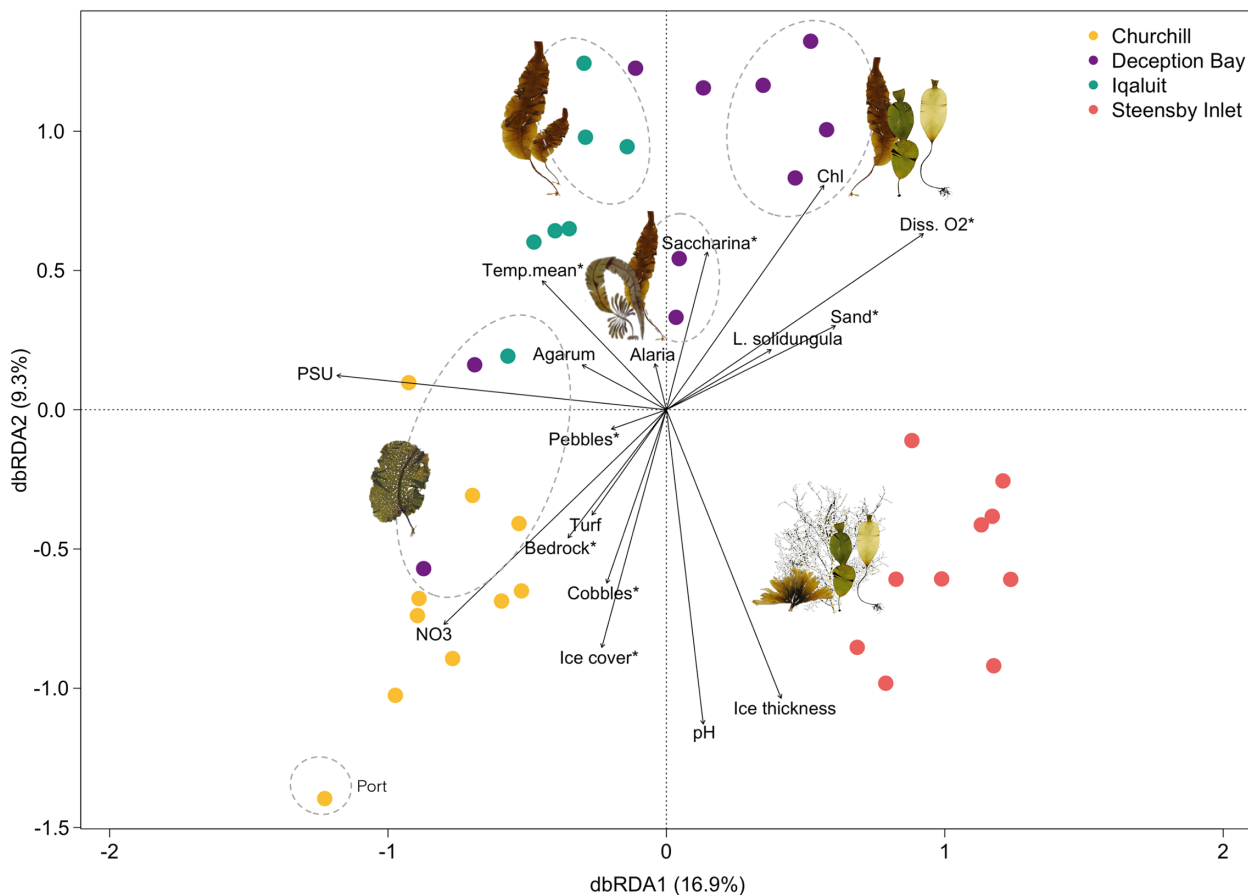
Fig. 3. Distance-based redundancy analysis performed on Bray-Curtis similarity matrices of the log-transformed station-specific density data (invertebrate communities) with the relative influence of the local environmental parameters (2006—2014 minimum depth averages obtained from BioORACLEv2.1; Assis et al. 2018). Communities that share similarities in terms of their macroalgal assemblages are circled. PSU: practical salinity unit; asterisks indicate significant vectors

A distanced-based redundancy analysis (dbRDA; Legendre & Anderson 1999) was used to identify patterns in zoobenthic community composition and evaluate the potential effects of environmental factors, including macroalgal assemblage, substratum type, and station-specific physical parameters (Fig. 3). We based the dbRDA on log-transformed station-specific density data (log (mean ind. m^{-2} + 1)), using the 'capscale' function based on a Bray-Curtis distance matrix using the 'vegan' package (Oksanen et al. 2022). The physical parameters used for the dbRDA were obtained from BioORACLE v2.1 (Assis et al. 2018) using data from the nearest-neighbor point to each study station (at minimum depth) and extracted as multi-year means for the period 2006—2014. We retained parameters likely to influence benthic biotic communities, including sea-ice cover and thickness, dissolved O$_2$, nitrate and chlorophyll concentrations, pH, and sea surface temperature (SST). A permutation-based ANOVA (by axis and by terms) was used

to evaluate the significance of the axes and vectors selected by the models (Legendre et al. 2011, Legendre & Legendre 2012).

2.3.2. Kelp (and other macroalgae) abundance influences on invertebrate community diversity and composition

Station-specific means of all invertebrate community metrics (presented in Table 1) were evaluated to see if they varied as a function of kelp percent cover for all regions combined (with region as a random factor) using linear mixed-effects models (LMER) or generalized linear mixed-effects models (GLMER), and within each region using linear models (LM) or generalized linear models (GLM) (Table 2, Fig. 4). GLM/GLMER were used on untransformed taxa richness (S) data to account for the Poisson distribution, LM/LMER with log+1 or sqrt+1 transformations were

Table 2. Slope, with adjusted R^2/p-values (in brackets) from multiple regressions testing the effect of kelp percent cover on benthic univariate statistics. Failing models (−) were discarded. Significant results with notable effect sizes are indicated in **bold**

	Churchill	Deception Bay	Iqaluit	Steensby Inlet	All
Density (ind. m^{-2})	−12.99 (0.06/0.32)	—	—	496.9 (0.34/0.09)	—
Biomass (g m^{-2})	—	—	0.96 (0.18/0.41)	12.56 (0.13/0.15)	−8.457 (0.11/0.52)
S	1.01 (0.29/0.15)	**1.01 (0.82/<0.001)**	**1.01 (0.89/0.004)**	1.00 (0.29/0.14)	**1.01 (0.54/<0.001)**
H'	0.06 (0.49/0.32)	0.01 (0.25/0.05)	—	−0.02 (0.70/0.02)[a]	0.01 (0.15/0.18)
J'	0.02 (0.23/0.22)	—	0.00 (0.70/0.70)	−0.01 (0.87/0.002)[b]	—

[a]Significant depth effects: 0.04 (0.87/0.003)
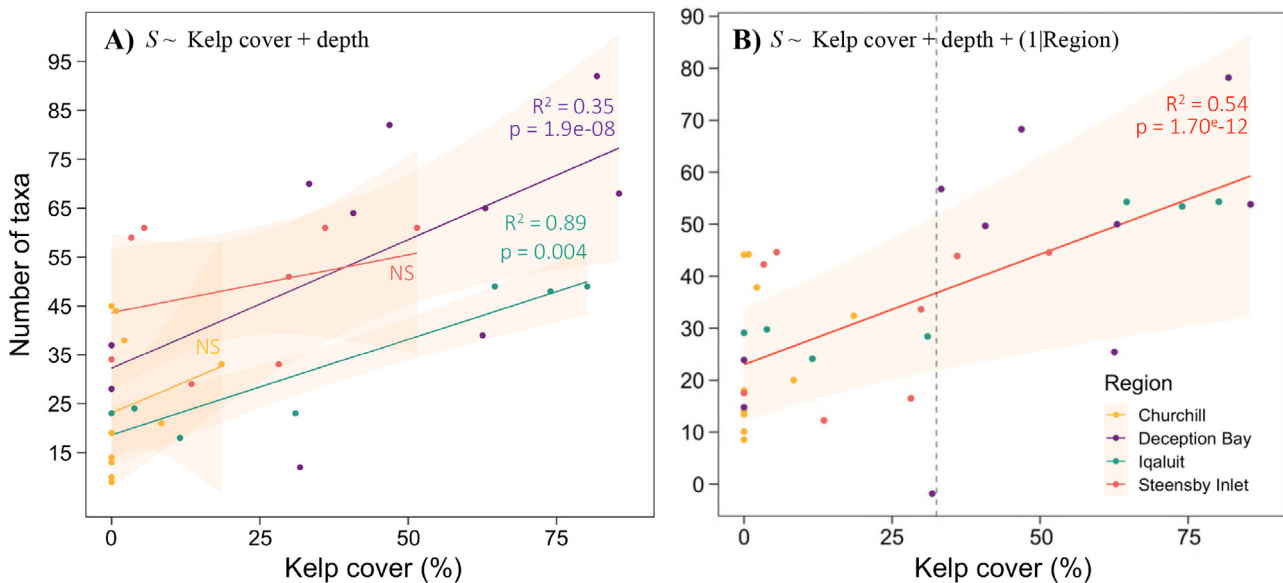[b]Significant depth effects: 0.15 (0.70/0.01)

Fig. 4. Number of taxa (S) relative to kelp percent cover (A) by region and (B) for all regions combined. Points represent values at specific stations and corresponding lines represent associated regressions. Shaded bands around the regression lines indicate the standard error (SE) around the predictions. The dashed vertical line in (B) indicates a possible threshold at around 30%, from which kelp abundance could affect faunal diversity. NS: not significant

used on density and biomass data, and LM/LMER were applied to untransformed indexes. Depth was included as a covariate in all models and corrected for tidal height using data from the Canadian Hydrographic Service (CHS 2020). Possible collinearity between kelp cover and depth was verified using the variance inflation factor (VIF). Models that could not be fitted and that violated assumptions of normality or homogeneity of variance (based on examination of residual plots) were discarded.

Table 3. Permutational multivariate analyses of variance, based on Bray-Curtis similarity matrices of log-transformed station-specific density data (invertebrate communities) within each region including the effects of kelp cover, substratum type, and depth. Failing models (−) were discarded. Significant effects are indicated in **bold**

	Churchill			Deception Bay			Iqaluit			Steensby Inlet			All		
	R^2	pseudo-F	p	R^2	pseudo-F	p	R^2	pseudo-F	p	R^2	pseudo-F	p	R^2	pseudo-F	p
Kelp (%)	—	—	—	0.18	2.74	**0.003**	0.25	1.63	**0.05**	—	—	—	0.06	2.17	**0.013**
Substratum	—	—	—	0.47	2.36	**0.003**	—	—	—	—	—	—	0.16	1.87	**0.012**
Depth	—	—	—	0.09	1.29	0.230	0.13	0.87	0.65	—	—	—	0.02	0.98	0.375

A permutational multivariate analysis of variance (PERMANOVA) based on the principles of McArdle & Anderson (2001) (and see Bakker 2024, https://uw. pressbooks.pub/appliedmultivariatestatistics/chapter/ permanova/), using the 'adonis2' function in the 'vegan' package, was used to test the specific effects of kelp cover, substratum type, and depth on benthic communities within each region (Table 3). Kelp cover and depth were added as continuous variables to the models (df = 1), while the substratum was reclassified at the transect level into 4 categories: silty, sandy, mixed (pebbles with sand and/or silt), and rocky (with mainly cobbles). Substratum type could not be used in Iqaluit and Steensby Inlet due to high uniformity amongst transects. The test was carried out on a Bray-Curtis distance matrix calculated from log-transformed station-specific density data (log (mean ind. m^{-2} + 1)). Test assumptions were checked using the 3-step method proposed by Bakker (2024) (https://uw.pressbooks. pub/appliedmultivariatestatistics/chapter/complex-models/) which is to (1) fit the model using a univariate response in a regular mixed-model including our 3

variables (here we used the taxa richness tested previously), (2) analyze the same univariate response in a PERMANOVA using a Euclidian distance matrix and check for matching results, and (3) re-run the PERM-ANOVA using the community matrix and the Bray-Curtis distance measure. Failing models were discarded.

2.3.3. Community assemblages and functional trait variability associated with differences in kelp/macroalgal abundance

We applied a further functional trait-based approach, using both feeding traits and taxonomic groups (Martini et al. 2021), to better understand relationships between kelp cover and zoobenthic assemblages within regions (Figs. 5 & 6, Table 4; Figs. S5 & S6 in the Supplement). Based on the methodology developed by Degen & Faulwetter (2019), we undertook a literature review on the feeding habits of each of the benthic species and classified them into 1 of 6
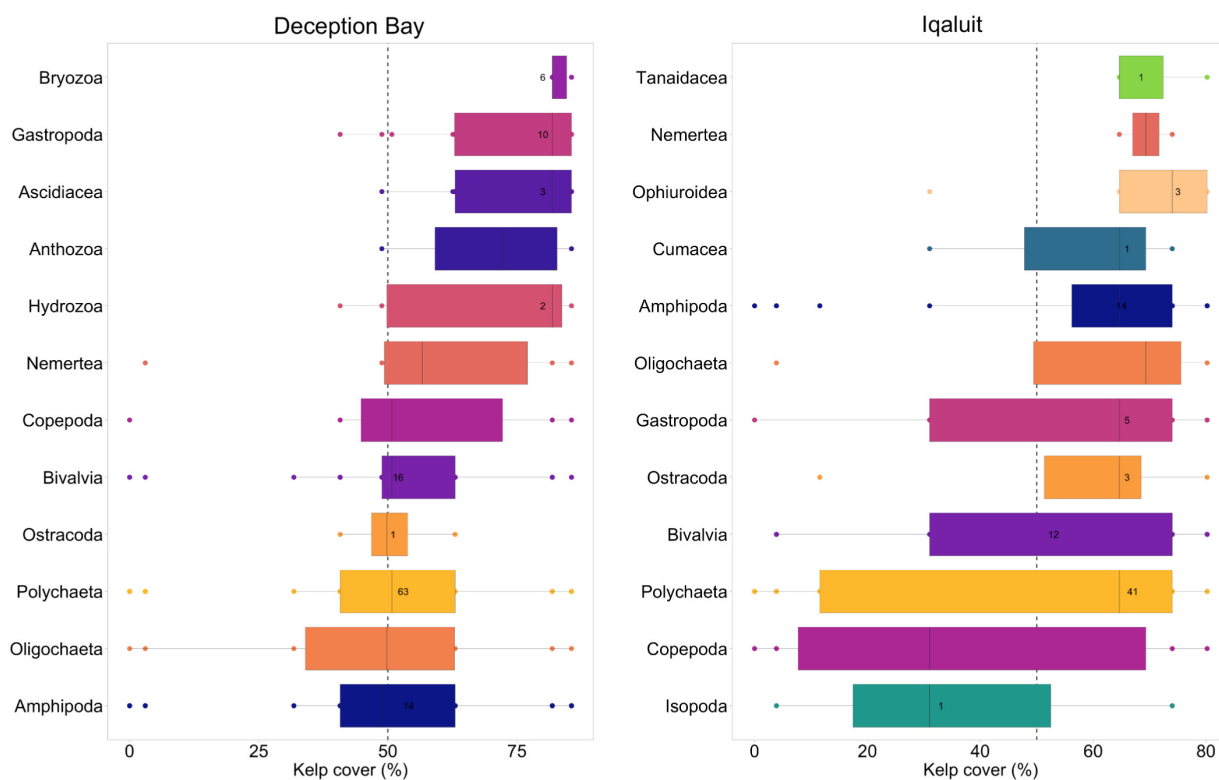

Fig. 5. Densities of invertebrates in different taxonomic groups (class level) relative to percent kelp cover in Deception Bay (N = 10) and Iqaluit (N = 7). Vertical dashed lines indicate 50% kelp cover. Density boxes highlight the stations with the highest invertebrate densities. Size of the boxes represents the spread of the middle 50% of the data (interquartile range). Lines inside the boxes denote the median (50th percentile) of the data, where 50% of the values lie above and 50% below this line. Single dots represent the presence of the invertebrate group at lower densities. When available, the number of taxa (at lowest level of identification) per group is indicated within boxes; detailed results broken down to lowest taxonomic level are shown in Fig. S5

Table 4. Partial taxa classification based on kelp cover affinity. Taxa common to Deception Bay and Iqaluit are displayed; singletons were eliminated. Where available, supporting literature is included. Nemertea and Nematoda, which were not identified at the species level, were omitted

Externals	Ubiquitous	Kelp-related
Euchone sp./ *Euchone analis* (Petrowski et al. 2016)	*Chaetozone* sp. (Włodarska-Kowalczuk & Pearson 2004, Petrowski et al. 2016, Pavlova et al. 2023)	*Hiatella arctica* (Różycki & Gruszczyński 1986, Fredriksen 2003, McMeans et al. 2013, Bluhm et al. 2022)
Mya truncata (Petrowski et al. 2016)	*Eteone* sp. (Pavlova et al. 2023)	*Dipolydora quadrilobata* (Petrowski et al. 2016)
Spio/Pygospio sp. (Petrowski et al. 2016)	*Capitella capitata* (Petrowski et al. 2016, Pavlova et al. 2023)	*Testudinalia testudinalis* (McMeans et al. 2013)
Chone sp.		*Scalibregma inflatum*
Pholoe sp.	*Praxillella praetermissa*	Serpulidae spp./ *Spirorbis* sp. (Lippert et al. 2001, Carlsen et al. 2007)
	Protomedeia fasciata	*Margarites helicinus* (Lippert et al. 2001, Dale & Leontowich 2006, Carlsen et al. 2007, Włodarska-Kowalczuk et al. 2009)
Sarsicytheridae spp.		*Eunnucula tenuis*
Lysianassidae spp.		*Harmothoe* sp. (Różycki & Gruszczyński 1986, Lippert et al. 2001, Dale & Leontowich 2006, Visch et al. 2020)

functional groups: subsurface deposit feeder, surface deposit feeder, chemosymbiont, predator/scavenger, omnivore/detritivore (opportunists), filter/suspension feeder, or grazer. We then examined how the different groups were distributed along the kelp cover gradient. As a final step, we used multiple regressions (LM, same method as in Section 2.3.2) on specific invertebrate classes to test if their density, biomass, or mean individual biomass varied significantly with kelp cover (Figs. S7–S9 in the Supplement). Note that the analyses in this section were conducted exclusively for Iqaluit and Deception Bay, where a wide range of kelp cover (ranging from approximately 0 to 100 %) was observed across stations (refer to Section 3, Table 2, and Fig. 4A). The detailed list of species and the references supporting classification decisions are available in Table S3.

3. RESULTS

3.1. Regional and local patterns — environmental factors and benthic diversity

Interregional comparisons revealed great variations in oceanographic and environmental conditions across the 4 Arctic regions, which were reflected by distinctive benthic communities in terms of both flora and fauna.

Analysis of satellite data showed clear differences between regions in terms of variables associated with light availability (Figs. S1 & S2). PAR and sea-ice concentration values followed a latitudinal gradient, starting with Churchill receiving the most light, followed by Deception Bay, Iqaluit, and then Steensby Inlet, with a melting period staggered by 2 wk between regions. In contrast, differences in POC and k_{d490} values among regions were more related to local oceanography including land discharges and productivity. All satellite measurements aligned with observations made by divers and from transect videos; during the open-water season, Churchill had the most turbid waters, followed by Iqaluit, Deception Bay, and then Steensby Inlet.

SSTs differed among regions but were limited to a relatively narrow range throughout the year, ranging from −1.0 to 3.6°C (Table S1). During the ice-free season, Churchill and Deception Bay experienced average temperatures above 0°C, while Iqaluit and Steensby Inlet remained mostly below 0°C. All regions experienced very low minimum depth water velocities (<0.04 m s^{-1}) (Table S1).

The sea floor substratum in most sampled locations was flat and largely composed of fine sediment, mainly

sand or silt with scattered pebbles and cobbles on the surface (Fig. 1). Soft sediment did not seem to prevent substantial macroalgal coverage, including kelp, at most of the stations, especially in Deception Bay, Iqaluit, and Steensby Inlet. Iqaluit and Deception Bay had the highest macroalgal cover and hosted tall (3−4 m high), erected kelp forests, whereas Steensby Inlet was dominated mainly by Desmarestiales (28.5%) low-lying kelp (25.5%), and Fucales (10%) (mainly *Fucus distichus*). Conversely, although many stations around Churchill had the highest cover of rocky substratum, they also had the lowest macroalgal cover.

As for invertebrates, a total of 23 000 specimens, representing 422 taxa and 208 genera, were identified in the 148 cores examined. Despite sustained sorting and taxonomical efforts, taxa accumulation plots failed to reach an asymptote, both when considering all regions collectively (Chao 1 estimate climbed up to 600 taxa) and when examining each region individually (Fig. 2). A small percentage (7.3%) of the taxa were shared among the 4 regions (Fig. S3). Deception Bay had the highest number of unique species (88), followed by Steensby Inlet (74), while Churchill (39) and Iqaluit (31) had the lowest. Deception Bay and Steensby Inlet shared the most taxa (23.6%) while Churchill and Iqaluit shared the fewest (12.5%). A complete list of taxa by region is available in Table S2 in the Supplement.

Densities varied between ~14 000 and 30 000 ind. m^{-2} and wet biomass varied between ~300 and 1600 g m^{-2}, with high within-region variability and no significant difference between regions (Table 1). Nematodes clearly dominated most samples and reached abundances over 10 000 ind. m^{-2} in Deception Bay and Iqaluit (Fig. S4). They were outnumbered only in Steensby Inlet, where Foraminifera (9170 ind. m^{-2}) dominated. The latter were absent in Churchill and Iqaluit and represented only a small fraction in the samples in Deception Bay (293 ind. m^{-2}). Bivalves (~231−1540 g m^{-2}) and polychaetes (21−87 g m^{-2}) accounted for the bulk of the biomass in all regions. Isopoda (24.9 g m^{-2}), Cirripedia (24.6 g m^{-2}), Gastropoda (17.8 g m^{-2}), and Polyplacophora (12.4 g m^{-2}) accounted for the third greatest biomass in Iqaluit, Deception Bay, Steensby Inlet, and Churchill, respectively.

The dbRDA of benthic assemblages across all stations showed general clustering by regions, with only moderate effects of local environment variables (25.3% of the variation among groupings was explained by both axes) (Fig. 3). Vectors including substratum type, *Saccharina latissima* percent cover, sea-ice cover, water temperature, pH, and dissolved O$_2$ were significant, although many of them essentially reflected re-

gional trends. Two stations in Deception Bay grouped with stations in Churchill, revealing the possible effect of similar harder bottoms (having a higher cover of pebbles and cobbles) on invertebrate communities. We also detected a change in dominant kelps among areas with different substrata, with *S. latissima*, *Laminaria solidungula*, and *Alaria esculenta* associated with soft sediment habitats and concurrent faunal assemblages, while *Agarum clathratum* was associated with rockier seafloors (see also Filbee-Dexter et al. 2022). A detailed account of each region follows.

3.1.1. Churchill

The mean (±SE) macroalgal cover in Churchill was the lowest among all regions (17.36 ± 5.6%) and was dominated by turf algae and Desmarestiales (Fig. 1, Table 1). Satellite data showed that this region had the longest PAR availability and an early sea-ice break-up in the spring (mid-June), but very poor water clarity compared to the other regions, with much higher k_{d490} (up to 0.6 m^{-1}) and POC (up to 800 mg m^{-3}) values (Figs. S1 & S2). Churchill was characterized by generally low richness and densities of invertebrates, but with high abundances in certain groups such as ascidians (*Ascidia* spp.), bivalves (mainly *Macoma balthica* and *Mytilus* sp.), ophiuroids (mainly *Ophiura robusta*), and polychaetes (*Cistenides granulata* and *Ophelia limacina*) (Fig. S4). Of particular note were the exceptionally dense mussel (*Mytilus* sp.) aggregations observed at stations around the port (depths of 10.4−11.0 m) in the Churchill River estuary, whereas they were virtually absent from all other stations and regions. The significantly higher bivalve biomass accounted for the disparity in mean biomass (~3- to 5-fold higher; Table 1) between Churchill and the other regions.

3.1.2. Deception Bay

The mean macroalgal cover in Deception Bay was the second highest (after Steensby Inlet) at 51.62 ± 8.4% and was dominated by Laminariales: *S. latissima*, followed by *A. clathratum*, *L. solidungula*, and *A. esculenta* attached to scattered cobbles and pebbles (Fig. 1, Table 1). Satellite data revealed that the average sea-ice break-up occurred in early July, 2 wk after Churchill, with high water clarity values (k_{d490} < 0.1) (Figs. S1 & S2). Deception Bay had the highest mean faunal density and diversity (Table 1), and the highest densities in most taxa groups including poly-

chaetes (mainly Cirratulidae spp. and *Chaetozone* sp.), amphipods (dominated by *Monoporeia affinis*), gastropods (mainly Hydrobiidae spp.), and bivalves (mainly *Hiatella arctica*) (Fig. S4).

3.1.3. Iqaluit

The mean macroalgal cover around Iqaluit was almost as high as in Deception Bay (42.69 ± 12.7%) and had a similar composition, dominated by tall forests of *S. latissima* mixed with lower proportions of other species, including *A. clathratum*, *L. solidungula*, and *A. esculenta* (Fig. 1, Table 1). Although Iqaluit is close to Deception Bay and has similar PAR availability, the sea-ice break-up occurs, on average, 2 wk later (mid-July), with waters reaching k_{d490} values of ~0.3, indicating moderate turbidity (Shi & Wang 2010) (Figs. S1 & S2). In terms of invertebrate diversity, fewer stations were sampled in Iqaluit (N = 7) compared to the other regions (N = 10), most likely leading to an artificially low observed species richness (118). It was nonetheless characterized by a higher Shannon-Wiener index as well as a slightly higher taxa accumulation curve and Chao 1 estimate than Churchill (Table 1, Fig. 2). Total invertebrate densities were almost as high as in Deception Bay (~24 000 m^{-2}), mostly because of nematodes. The region was otherwise dominated by polychaetes (mainly *Chaetozone* sp., Capitellidae spp., and *Eteone* sp.), amphipods (largely *Protomedeia fasciata*), copepods (harpacticoids), and ophiuroids (mainly *Stegophiura nodosa*).

3.1.4. Steensby Inlet

Steensby Inlet was distinct both in terms of seascape and biodiversity. Most transects were covered with dense *Desmarestia* sp. mats over a silty to sandy bottom. The other algae encountered were mainly Fucales (mostly *F. distichus*) and low-lying *L. solidungula* and *S. latissima* sprinkled with ice-flow deposits (Fig. 1, Table 1). Total macroalgal cover was the highest among regions and averaged 71.5 ± 8.2%. Satellite data highlighted the opposite pattern to Churchill, with the shortest PAR season and the latest sea-ice break-up (August), which prevented satellite measurements during many months, but with the highest water clarity (k_{d490} < 0.1) (Figs. S1 & S2). The observed benthos was highly diverse and had few taxa in common with the other regions, with large numbers and varieties of ostracods (principally *Sarsicytheridea* spp.,

Cytheroidea spp., and *Robertsonites* spp.), polychaetes (mainly Cirratulidae spp., *Spio* sp., and *Pholoe longa*), amphipods (*Ischyrocerus anguipes*), and, especially, large numbers of Foraminifera (Fig. S4).

3.2. Kelp cover (and other macroalgae) influences on invertebrate communities

Overall, there was a significant relationship between kelp percent cover and taxa richness, as station-specific richness increased with kelp cover for all regions combined and within 2 of the regions (GLM; Table 2, Fig. 4). The pattern was particularly evident in Deception Bay and Iqaluit, where tall *S. latissima* forests reached 80% cover at some stations and hosted more than twice as many taxa compared to exposed stations with less kelp. In Iqaluit, taxa richness varied from ~20 taxa at stations without kelp to ~45 taxa at kelp-covered stations, while in Deception Bay, richness ranged from ~30 to ~75 taxa per station. Point clusters in Fig. 4B for all regions combined suggest a possible threshold around 30% cover, from which kelp abundance could affect faunal diversity. In Churchill, and especially in Steensby Inlet, more than half the flora consisted of Desmarestiales or Fucales macroalgae that were not part of the true kelps (Laminariales). Consequently, we tested the taxa richness against both total kelp cover and total macroalgal cover for these 2 regions. However, none of the relationships with either kelp or macroalgal cover were statistically significant. Despite generally strong correlations between kelp cover and invertebrate richness (R^2 = 0.5, p < 0.0001), there were similar average densities and biomasses of invertebrates across different levels of kelp cover at both intra- and inter-regional levels, and kelp cover did not significantly affect either Shannon-Wiener or Pielou's indices (Table 2).

The PERMANOVA indicated that local variations in kelp percent cover was a significant driver of benthic assemblages in both Iqaluit and Deception Bay (Table 3). These 2 regions had dense *S. latissima* forests and a gradient of kelp cover across stations (Fig. 4A). The substratum type was only a significant driver in Deception Bay, where it co-varied with kelp cover in driving benthic assemblages. Finally, while benthic assemblages in Steensby Inlet clearly differed from other regions, stations within this region were rather uniform in many environmental aspects (Fig. 3), including substratum and macroalgal cover, making it difficult, with limited data, to identify the cause of any intraregional variation.
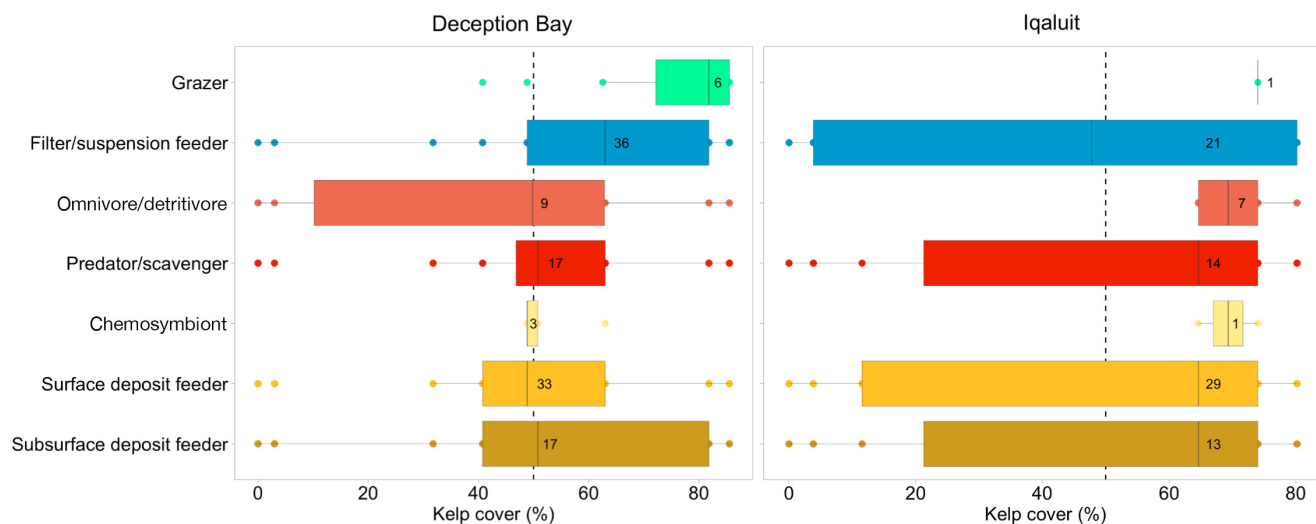
Fig. 6. Densities of invertebrates in different feeding guilds relative to kelp percent cover in Deception Bay (N = 10) and Iqaluit (N = 7). The number of taxa per guild is indicated within boxes; detailed results broken down to lowest taxonomic level are shown in Fig. S6. See Fig. 5 for other details

3.3. Invertebrate assemblages and functional trait variability associated with differences in kelp/macroalgal abundance (Deception Bay and Iqaluit)

Given the PERMANOVA results, and because stations in Deception Bay and Iqaluit occurred across a continuous gradient of kelp cover among the sampled stations, we undertook a detailed functional group approach to explore relationships of kelp cover with densities of invertebrates in different taxonomic groups (Fig. 5; Fig. S5) and feeding guilds (Fig. 6; Fig. S6).

At the class/order level, most taxa were ubiquitous across stations of varying kelp cover in both regions. However, for more than two-thirds of the taxa, higher densities were associated with higher kelp cover (Fig. 5). Among the groups present across most sites, Gastropoda (p = 0.03), Nemertea (found only in kelp), Oligochaeta (p = 0.01), and Bivalvia (p = 0.07) abundances had significant (or marginally significant) positive relationships with kelp cover, while Gastropoda (p = 0.07) and Oligochaeta (p = 0.02) also had higher overall and individual biomasses with increasing percent kelp cover (Figs. S7—S9). Deception Bay and Iqaluit exhibited regional differences concerning certain groups associated with kelp. In Deception Bay, Hydrozoa, Ascidiacea, Bryozoa (the bulk of filter feeders), and Anthozoa were found exclusively at stations with over 60% kelp cover. In contrast, in Iqaluit, Tanaidacea, Cumacea, Ophiuroidea, and Ostracoda were found at stations with over 70% kelp, although the latter were represented by only a few taxa (Fig. S5).

A closer look at the detailed taxa list in relation to kelp cover in both Deception Bay and Iqaluit (Fig. S6) showed 2 key trends: (1) most of the rare taxa (70%) were found in the densest kelp habitats (over 50% cover) and (2) species/taxa fell into 3 predominant groups: species that tended to reside outside the kelp (~15), ubiquitous species found at all stations (~20—30), and species that were predominantly present in areas with high kelp cover (~40—55). When considering only species/taxa common to both Deception Bay and Iqaluit (with the exclusion of singletons), we could categorize some of the species/taxa with a higher confidence level (Table 4). This categorization was further supported by relevant literature where available.

There were also important differences in feeding traits between invertebrate taxa found in Deception Bay and Iqaluit, and clear associations between some invertebrate functional groups and kelp abundance (Fig. 6; Fig. S6). In Deception Bay, most feeding groups (filter feeders, predators, and subsurface deposit feeders) were more abundant at stations with high kelp cover, while in Iqaluit, there was a wider distribution of these groups along the kelp cover gradient, probably related to increased substrata uniformity between stations compared to Deception Bay. Interestingly, almost all functional groups in the 2 regions included a similar total number of taxa, except for grazers and filter feeders, for which there were nearly twice as many taxa in Deception Bay. The main grazers were a few species of mollusks, either patellids or small gastropods, limited to stations with high kelp cover in both regions. Omnivorous taxa, largely represented by am-

phipods (Oedicerotidae spp.), tended to be ubiquitous in Deception Bay, but were found exclusively at kelp stations in Iqaluit. The few omnivorous polychaetes (Dorvilleidae spp. and *Harmothoe* sp.) were found at kelp-dominated stations in both regions. Among predators, the taxa list differed greatly between the 2 regions, and while most of them exhibited a wide distribution in Iqaluit, they tended to be restricted to a small subset of stations with moderate kelp cover in Deception Bay. Among predatory taxa, nemerteans showed a distinct preference for kelp habitats. Finally, surface and subsurface deposit feeders were represented almost exclusively by polychaetes, with variable degrees of habitat selectivity; many were ubiquitous taxa from the families Cirratulidae and Capitellidae. One of the key findings is that higher abundances of subsurface deposit feeders were found at kelp-dominated stations in both regions (Fig. 6; see depiction in Fig. S11 in the Supplement).

4. DISCUSSION

Our study revealed unique characteristics of Arctic nearshore habitats, where kelp forests are found over soft sediment and exert local influence on infauna and small epifauna. Initially, we presented an overview of the primary regional patterns and factors shaping the benthic fauna in Arctic nearshore areas. Invertebrate diversity, community assemblages, and composition were partly driven by the background environmental conditions defining each region, but also, at a local scale, by the abundance of habitat-forming kelp and the substratum type. Soft sediment, dominant in many regions, did not seem to prevent substantial kelp coverage and was also an ideal matrix for dense infaunal communities. As for the specific role of kelp on community structure, we found interesting patterns, especially in Deception Bay and Iqaluit, where tall *Saccharina latissima* forests hosted the highest observed invertebrate diversity and were associated with unique taxa traits and composition, including an important component of the community comprised of subsurface deposit feeders. Among other regions, benthic communities in Steensby Inlet were the most distinctive and reflected High-Arctic characteristics, while the communities in Churchill primarily reflected disturbances originating from high POC discharges. Overall, it appears that suitable conditions of light are conducive to the emergence of kelp habitats in the Arctic, which are in turn driving local invertebrate community structure shifts and enhancing benthic diversity.

4.1. Regional patterns: general environment and benthic diversity

4.1.1. Turbidity and access to light

Regional comparisons suggested that turbidity and access to light are key variables that influence benthic community structure. Around Churchill, it is plausible that the reduced levels of kelp and other macroalgae, and lower invertebrate richness and densities, are the result of very high spring turbidity (k_{d490} = 0.625) due to the influence of the Churchill River. Despite having the earliest sea-ice break-up (late May) and the highest PAR of the 4 studied regions, high turbidity in Churchill likely imposes important limitations for kelp photosynthesis and development (Blain et al. 2021, Picard et al. 2022). The effect of turbidity is particularly high during spring in the Arctic, while high nutrient concentrations and deposition associated with turbid waters may impact benthic diversity, selecting for resistant filter feeders, including larger bivalves or ascidians, potentially explaining the lower observed taxa richness and dominance of *Mytilus* sp. (Grall & Chauvaud 2002, Włodarska-Kowalczuk et al. 2005, Norderhaug et al. 2015, Gammal et al. 2023). Other factors may also contribute to low invertebrate diversity in Churchill, including the intensity of human activities around the port and the fact that waters of southern Hudson Bay in general are known to host lower benthic diversity (Pierrejean et al. 2020). The lower benthic marine invertebrate diversity observed in Churchill is also supported by previous eDNA and specimen-based studies (Leduc et al. 2019, Gianasi et al. 2022b).

In contrast, Steensby Inlet exhibits typical High-Arctic characteristics with the greatest water clarity but also the shortest growth season for algae based on the combined ice-free period and PAR availability. Many factors could contribute to the overall water clarity and low POC values in the region, including oligotrophic waters originating from the central regions of Canadian Arctic Archipelago (Ardyna et al. 2011), long seasonal sea-ice cover (Bonsell & Dunton 2018), and the absence of coastal infrastructure. These conditions have likely led to rich benthic assemblages distinct from those seen in other regions; we observed ~60 more taxa in Steensby Inlet than in Iqaluit and Churchill in this study, and almost 100 more than that observed in Gjoa Heaven (66) and Sachs Harbor (73) by Brown et al. (2011) with a similar sampling effort; Gjoa Heaven and Sachs Harbor are also close to 70° N in the Canadian Arctic. Steensby Inlet invertebrate communities are unique, with many abundant taxa

that were found nowhere else, e.g. high densities of Ostracoda and Foraminifera, which may be related to low human disturbance and flow edge depositions (Ruiz et al. 2005, Seidenkrantz 2013). Steensby Inlet was also characterized by the highest macroalgal cover of all regions, although it had more low-lying, resistant, cold-adapted taxa, including Desmarestiales, Fucales, and *Laminaria solidungula* (Wiencke & Amsler 2012). Within Desmarestiales, *Desmarestia viridis*, a common species in Arctic waters, is recognized for its influential role in shaping benthic communities. It has been documented to enhance macrobenthic diversity compared to barren areas (Bégin et al. 2004), support distinct epiphytic communities compared to kelp beds (Blain & Gagnon, 2014), and deter adjacent macroalgal grazing by green urchins (Molis et al. 2009). Images of Steensby Inlet fauna are presented as Fig. S10 in the Supplement.

Iqaluit and Deception Bay display intermediate environmental conditions relative to those observed in Churchill and Steensby Inlet. PAR, sea-ice cover, and turbidity are in a range likely advantageous for the growth of tall kelp forests, although access to light is slightly better in Deception Bay, with consequent higher kelp abundance. In Deception Bay, high spring values of POC did not seem to impact water clarity, while in Iqaluit turbidity co-occurred with high POC, potentially indicating additional inputs of nutrients. Invertebrate taxa richness differed drastically between the 2 regions; Deception Bay had the highest taxa richness and Iqaluit the lowest. A part of this disparity may be explained by the fact that 3 fewer stations were sampled in Iqaluit, but taxa accumulation curves and Chao 1 estimates suggest that Iqaluit still exhibited a lower taxa richness even when accounting for comparable sampling efforts across regions. Interestingly, our findings diverge from those of Gianasi et al. (2022b), who reported Iqaluit as hosting the highest macroinvertebrate richness among Eastern Canadian Arctic regions, based mainly on trawl surveys targeting larger epifauna. This discrepancy could suggest potential differences in the processes influencing small versus large invertebrates. Koojessee Inlet, where Iqaluit is located, has a very large tidal range and is impacted by human activities, including ships and smaller vessels, coastal infrastructure including a sewage lagoon, and a growing population, relative to Deception Bay and Steensby Inlet (Dale et al. 2002). Some of these disturbances could be affecting the richness of the smaller fauna (Samuelson 2001), while promoting high densities in deposit-feeding nematodes which are also attracted by algal depositions (Gianasi et al.

2022a). Altogether, in this study, conditions at Deception Bay sustained the highest kelp abundance as well as the highest diversity and densities of invertebrates.

4.1.2. Substratum

Substratum type is well demonstrated as a fundamental driver of benthic assemblages for both algae and invertebrates. Usually, substratum heterogeneity increases taxa richness, with different substratum size categories leading to the establishment of different communities (Buhl-Mortensen et al. 2012, Lacharité & Metaxas 2017, Gallucci et al. 2020). In this study, except for a small group of stations in Deception Bay having more cobbles, the visual sorting of the substratum did not reveal many variations among stations, hence the lack of a major substratum effect. Most frequently, substrata at the stations were flat and composed of fine sediment, layered with scattered pebbles or cobbles. This homogeneity in the shallow subtidal substratum type has also been reported in previous studies based in the Eastern Canadian Arctic (Thomson 1982, Dale & Leontowich 2006). This type of substratum and more generally this type of seascape is common in the coastal Arctic and has previously been described as 'glacial till' or a covering glacial clay plain (Conlan et al. 1998). Around the world, kelps are found predominantly on hard substrata, and their associated diversity is most often sampled using quadrats rather than sediment cores (Dayton 1985, Wernberg et al. 2019, but see Brown et al. 2011 for *S. latissima*). Such extensive presence of kelp in Arctic coastal areas, which primarily consist of soft substrates, may be linked to sea-ice cover. Sea ice prevents direct wind and wave mixing (Rainville et al. 2011), dampens water velocity (Newbury 1983), and reduces the turbulence associated with tides (Prinsenberg 1986b, St-Laurent et al. 2008), all of which could reduce the entrainment of kelp attached to small pebbles and cobbles (Thomsen et al. 2006).

4.2. Effects of kelp cover (and other macroalgae) on benthic invertebrate diversity, community assemblages, and functional trait variability

Our results support the hypothesis that benthic species along the coasts of the 4 regions were influenced by the presence of kelp, albeit to various degrees. The main detected effect was an increase in taxa richness, and, to some extent, shifts in benthic community assemblages and functional traits along gradients in kelp cover. Our results also led to a pre-

liminary list of taxa according to their level of selectivity for kelp forests as habitats, which can be used to better predict the consequences of climate-driven changes in kelp cover on benthic communities.

4.2.1. Diversity

Several mechanisms, either direct or indirect, may explain the increased diversity found along kelp cover gradients. One of the most accepted direct mechanisms is that kelp adds extra dimensionality to the seascape and creates new habitat by increasing the surfaces for invertebrates to cling to and new interstices to colonize (Norderhaug et al. 2002, Teagle et al. 2017, Pessarrodona et al. 2021). Here, it is plausible that low-lying kelp blades or deposited kelp material may also enhance spatial heterogeneity both at the sediment—water interface and within the sediment, potentially generating important effects at the scale of smaller-sized fauna (Christie et al. 2009, Gallucci et al. 2020). Similarly, kelp canopies could offer more protection against pelagic predation, creating refuge spaces in the understory that support higher diversity (Watanabe 1984, Gotceitas et al. 1995). Other, more indirect, mechanisms could involve the enhanced complexity of the local food web (Graham 2004), either by attracting predators of kelp-associated fauna such as Nemertea or through the availability of new food sources like kelp fragments or kelp-derived POC/DOC (Duggins et al. 1989, Kaehler et al. 2000). The latter mechanism is supported by the higher number of grazers, filter feeders, and surface/subsurface detritus feeders in kelp forests in our study. Finally, kelp-mediated flow alterations could help entrain a part of the meroplankton, thereby increasing food availability to the seafloor and supporting additional filter feeders or detritivores (Eckman et al. 1989, Duggins et al. 1990, Paar et al. 2019).

4.2.2. Community assemblages and feeding traits

Patterns in feeding traits along the kelp cover gradient primarily involved increased diversity and abundance in grazers, filter feeders, subsurface deposit feeders, and certain predators with an increasing kelp cover. These patterns likely stemmed from factors contributing to enhanced taxa diversity, such as the creation of new living or feeding niches, with additional support from a wealth of unique and rarer taxa. Higher taxa diversity within feeding categories also implies an increase in functional redundancy, a factor proven to enhance ecological resilience and stability in local benthic communities (Ellingsen et al. 2007, Biggs et al. 2020). Findings related to the increase in subsurface deposit feeders with the rise in kelp cover were particularly surprising. Kelps are typically associated with rocky bottoms and have specific communities attached to holdfasts, stipes, and fronds and fewer opportunities or spatial niches for substrate dwellers or even for local organic material accumulations (Włodarska-Kowalczuk et al. 2009, Krause-Jensen & Duarte 2016, Teagle et al. 2017). However, Arctic conditions with ice-protected coasts may offer a different scenario. Here, erect kelp forests dominated by *S. latissima* over soft substrate result in ecosystems analogous to terrestrial forests, influencing the fauna on the substrate immediately below, similar to forest litter. For example, the total abundance and biomass of oligochaetes increased significantly under kelp canopies, indicating the potential availability of organic matter, i.e. decaying plant material, living plant cells, and microorganisms attached to the sediment, that they could use as food, similar to stranded kelp on beaches (Giere 1975, Stenton-Dozey 1983). Nematodes, which are selective feeders on bacteria or diatoms in soft substrata, were slightly bigger under kelp, indicating the potential accumulation of organic matter and associated bacterial degradation (Benwell 1980, Trotter & Webster 1984). Furthermore, while the feeding categories employed to define functional groups in this study may not fully capture the diverse diets of the encountered species, and despite limited knowledge about many species in this system, our review of feeding traits revealed that a significant proportion of the surface and subsurface deposit-feeding taxa identified tend to consume macroalgal detritus. Sediment enrichment with kelp and macroalgal micro fragments could therefore partially explain the high level of invertebrate activity underneath, aligning with recent conclusions drawn from kelp farming studies, reporting increases in endobenthic densities and diversity under farms (Visch et al. 2020). Furthermore, a wealth of research on isotopic tracing and fatty acid analyses has reported kelp-derived carbon in the fauna surrounding kelp forests. While grazing activities can be significant, it should represent only ~10% of the kelp productivity, leaving the greatest part to enter food webs as detritus or POC depositions (Dunton & Schell 1987, Duggins et al. 1989, Simenstad et al. 1993, von Biela et al. 2016, Paar et al. 2019). Our findings provide further evidence of the importance of this resource subsidy pathway in structuring coastal communities.

4.2.3. Gains vs. losses

Structurally complex habitats are declining in both tropical and temperate marine areas of the world, and usually shifts from complex to less complex habitats lead to declines in abundances and species richness and eventually ecosystem functions (Airoldi et al. 2008). Our results suggest that kelp forests are a major structural component of the Arctic subtidal zone that not only support higher densities and diversity in most taxonomical and functional groups but also host rare and/or intimately associated taxa. Many species which are part of the infauna and small epifauna are important prey for fish, mobile invertebrates, and some marine mammals, and changes in their abundance could therefore have broader impacts across the coastal food web (McMeans et al. 2013). While our results are fragmentary, as they encompass only small invertebrates, they still offer a glimpse into the potential consequences of increased or decreased kelp abundance in the Canadian Arctic. Current models suggest 20−40% gains in kelp area in the Canadian Arctic, and conditions that could largely benefit the kelp *S. latissima* (Krause-Jensen et al. 2020, Goldsmit et al. 2021, Assis et al. 2022). However, these predictions are highly uncertain, and no long-term time series exist (Krause-Jensen et al. 2020). Increased kelp cover, especially in *S. latissima*, should lead to altered and potentially enhanced benthic diversity, possibly increasing available habitat and the abundance of distinct taxa closely related to kelp forests, as found in this study.

Some negative effects of higher kelp cover could still be debated in terms of losses to distinct High-Arctic coastal habitats (>75° N). On Svalbard's rocky seafloors, transitions from naturally low abundances (<8%) of species with higher light and temperature requirements (including *Phycodrys rubens*, *Saccho-riza dermatodea*, and *Desmarestia* spp.) to a sudden full kelp cover, led to a rapid increase in overall invertebrate diversity, but also to substratum competition with encrusting algae and larger filter feeders, resulting in the subsequent loss of 80% of sea anemones originally present at the studied sites (Kortsch et al. 2012). Similar scenarios could be underway in the Canadian High Arctic, but growth conditions there still need further assessment. Recent studies have proposed a limited capacity for temperate or cryotolerant species (like *S. latissima*) to perform at higher latitudes, and for cryophilic species (like *S. solidungula*) not to have a northern range limit (Scheschonk et al. 2019, Bringloe et al. 2022), suggesting only modest gains for these species. The impacts of global warming in the Arctic will vary from one region to another, but processes that increase turbidity (e.g. in the vicinity of fjords, glaciers, rivers, and permafrost coasts) may lead to the replacement of kelp forests with barren habitats like turf reefs or sand, which in turn could result in a significant reduction of resident species, food resources, and possibly ecosystem functions. Shifts of this scale have already been noticed in certain areas of the Arctic, mainly due to increases in turbidity. Sediment resuspension due to heightened water movements in the Beaufort Sea has led to sparser and shallower *L. solidungula* beds (Bonsell & Dunton 2018). Similarly, extensive glacier melts and adjacent turbid waters in northern Svalbard have been shown to be detrimental to the kelps, leading to shallower *S. latissima* forests (Bartsch et al. 2016, Niedzwiedz & Bischof 2023). Another threat that warrants further investigation in the Canadian Arctic is the presence of over-grazed areas by green sea urchins in the adjacent sub-arctic, along the coasts of Labrador (Filbee-Dexter et al. 2022, A. Savoie pers. obs.), and the possibility that these barrens could extend poleward as environmental conditions change (Hart & Scheibling 1988, Blicher et al. 2007).

Our results suggest that shifts in kelp forest cover in the Arctic could have potential cascading effects on coastal food webs, with implications for Inuit communities that rely on these resources. These changes may also be influenced by new benthic species (macroalgae and invertebrates) introduced into the system by shipping transportation (Goldsmit et al. 2020). However, ecosystem functions and trophic interactions are more likely to endure through interspecies competition, contrary to potential impacts of habitat loss (Goldsmit et al. 2024). A deeper understanding of these ecological changes will require additional research on the drivers of kelp loss and the use of these habitats by macroinvertebrates, fish, and marine mammals.

4.3. Conclusions

This study provides insights into how local environmental parameters and seascapes shape benthic diversity in the Canadian Arctic. We demonstrate that turbidity and excess nutrients may be detrimental to overall taxa richness, kelp, and macroalgal coverage, while seasonal sea-ice regimes play a crucial role in shaping unique Arctic benthic communities. Conditions of intermediate open-water duration and good water clarity are ideal for the growth of tall kelp forests, serving as important drivers of local soft-bottom

diversity and enhanced ecosystem processes. These forest-forming kelps share similarities with terrestrial forests, as they provide habitat at different scales and heights, and associated fauna can be found on their holdfasts, stipes, blades, and canopies, but also below-ground, with higher abundances and diversity of sediment dwellers occurring under kelp forests. Further research on other components of these habitats, such as macrofauna and fish communities, will shed light on the extent of their supporting and provisioning roles for both local Inuit communities and Arctic marine ecosystems. While in the Arctic, and especially in the Canadian Arctic, kelp research is still in its infancy, many authors have concurred that coastal recovery processes are likely to be much slower than in temperate waters (Dunton et al. 1982, Conlan & Kvitek 2005, Keck Al-Habahbeh et al. 2020). Several experiments and measurements done in the Beaufort Sea Boulder Patch have revealed that, following a major disturbance, it could take more than a decade for the sessile community, including kelp, to fully recover (Konar 2013, Bonsell & Dunton 2021). Similarly, in temperate ecosystems, transitions into barrens dominated by either turf algae or by high densities of sea urchins have proven difficult to reverse (Chapman 1981, Filbee-Dexter & Scheibling 2014, Filbee-Dexter & Wernberg 2018). Given the rapidly changing environmental conditions in the Arctic and the long recovery trajectories for these species, kelp forests in the Arctic should be regarded as a valuable and sensitive resource. As such, we recommend pursuing efforts to integrate kelp forests into marine protected areas and to minimize, as much as possible, human-induced eutrophication, sedimentation and other damaging activities within or adjacent to these habitats.

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