Description and Spatial Modelling of Benthic Communities Distribution in the Canadian Arctic Archipelago

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In the Arctic, sea ice loss has already transformed the dominant sources and periodicity of primary production in some areas, raising concerns over climate change impacts on benthic communities. Considered to be excellent indicators of environmental changes, benthic invertebrates play important roles in nutrient cycling, sediment oxygenation and decomposition. However, this biological component of the Canadian Arctic Archipelago (CAA) is still somewhat poorly studied compared to other Arctic regions. To partly fill this need, this study aims to evaluate benthic community composition and its relationship to significant environmental drivers and to develop spatial predictive explanatory models of these communities to expand coverage between sampled stations across the Kitikmeot Sea region and Parry Channel. Results from previously collected samples suggest that biodiversity is higher in this region compared to the Beaufort and Baffin Seas, two adjacent regions to the West and East, respectively. This finding leads to the main hypothesis that (1) benthic communities are succeeding one another, forming an ecotone (transition area) between the Beaufort Sea and the Baffin Sea. Other hypotheses are that (2) Pacific Ocean water influence through the CAA can explain part of this gradient, and that (3) terrigenous inputs affect the distribution of species. Overall, results tend to confirm hypotheses. Generalized Linear Models (GLMs) (with R^2 up to 0.80) clearly displayed a succession in community distribution from Queen-Maud Gulf (Southwest) to Lancaster Sound (Northeast). Such models can be useful in identifying potential biodiversity hotspots and as a baseline for marine spatial planning purposes. Further, Pacific origin water (traced with concentrations of nitrate relative to phosphate) and terrigenous inputs (traced with silicate concentrations) were related to species and community distribution. Given that these two inputs/factors are generally increasing in the Canadian Arctic, their influence on benthic communities may also be seen to increase in the upcoming years.

Keywords: benthos, modelling, Canadian archipelago, environmental drivers, epifauna, infauna

INTRODUCTION

Quantitatively, marine invertebrates are the most taxon rich group of the animal kingdom in the Arctic (Payer et al., 2013) and 90% of these are benthic species (Meltofte et al., 2013). Because of their high abundance, they play an important role in Arctic food webs and overall biodiversity, and are linked to higher trophic levels that feed on the seafloor (Bluhm and Gradinger, 2008; Darnis et al., 2012). Benthic species can often be used as indicators of environmental conditions and changes in an environment. Moreover, species' distribution variability can inform of previous events/impacts in the marine environment and whether current ecological states tend to improve or decline (Borja et al., 2000; Niemi and McDonald, 2004).

Among several environmental factors shown to influence Arctic marine invertebrates in their abundance, distribution and assemblage characteristics, river inflow is of mention. In fact, the Arctic Ocean receives more than 10% of global river discharges (Opsahl et al., 1999), and river runoff contributes significantly to the freshwater budget (Carmack, 2000; Prowse et al., 2015) and has increased in the past decades (Déry et al., 2009; Holmes et al., 2012; AMAP, 2017). Freshwater inputs reduce salinity in the marine environment with negative impacts on benthic diversity (Cusson et al., 2007; Witman et al., 2008) and the benthic community structures (Pierrejean et al., 2020). River water flowing into the Arctic marine environment may also contain terrigenous components such as terrestrial organic matter, inorganic carbon, nutrients and ions such as silicate (McClelland et al., 2006). Because silicate concentrations are higher in Arctic rivers than the marine environment, this parameter can be used to trace terrigenous inputs (Ekwurzel et al., 2001). Freshwater river inputs are also associated to increases in CO_2 concentrations, which decreases water pH (Cooper et al., 2008; Vallières et al., 2008). This can have an negative impact on benthos calcification abilities (Fabry et al., 2008).

The Canadian Arctic Archipelago (CAA) receives substantial volumes of Pacific Ocean origin water, which enters through Bering Strait and generally flows eastwards towards Baffin Bay (Carmack et al., 1997; Kliem and Greenberg, 2003). Compared to Atlantic Ocean water, Pacific Ocean water has a lower density because it is of lower salinity (more freshwater). The effects of a lower density in Pacific Water is that it migrates to the upper ocean layer while Atlantic Water is below (Granger et al., 2018). Pacific Ocean influence is so strong in the CAA that even in areas far from the inflow like Lancaster Sound (at the entry of Baffin Bay), most of the surface water is of Pacific origin (Jones et al., 2003). Because of its location at the entry of Baffin Bay, this area is, however, the most influenced by the Atlantic Ocean (McLaughlin et al., 2006). In addition to its low salinity, Pacific Water that enters the Canadian Arctic is nitrate depleted, resulting in lower nitrate:phosphate ratios than Atlantic Ocean water (Yamamoto-Kawai et al., 2006; McLaughlin et al., 2009). Because of climate-related increases in sea surface temperatures and closely related decrease in ice cover, Pacific water inputs are currently increasing in the Arctic through Bering Strait (Shimada et al., 2006; Woodgate et al., 2010) and are projected to substantially increase in the upcoming years (Woodgate, 2018). Furthermore, the Canadian Arctic is quite shallow in many of the areas of interest, e.g. Queen-Maud Gulf (QMG) is no deeper than 75 meters (Carmack and McLaughlin, 2011).

There is a particularly large knowledge gap for benthic biodiversity in the Canadian Arctic and especially the Kitikmeot Sea region (Wassmann et al., 2004; Archambault et al., 2010; Piepenburg et al., 2011; Roy et al., 2015a). In general, the number of species found increases with the number of sampled stations (Jones et al., 2007; Bluhm et al., 2011; Piepenburg et al., 2011; Roy et al., 2014) but this can be difficult when describing such a large region. To efficiently fill spatial gaps, species/community distributions must be predicted. One way of predicting distributions is through species distribution modelling (SDM), based on identified relevant environmental drivers (Moritz et al., 2013). Since some of these drivers (e.g. temperature, salinity, ice cover) can be observed by satellite imagery, it is possible to model community assemblages on large spatial scales and for difficult to access locations. SDM is widely used in ecology and can somewhat compensate the lack of data in a changing environment (Brown et al., 2016; Brodie et al., 2020). Since regional (≥1 km2) community variability is mostly influenced by environmental gradients (Levin et al., 2001), understanding how abiotic drivers influence species distributions may be useful for filling spatial gaps of biodiversity hotspots and valuable habitats (McArthur et al., 2010; McHenry et al., 2017; Saeedi et al., 2017; Pierrejean et al., 2020). Results from these SDMs can be used for conservation purposes and hopefully contribute to efforts in reducing biodiversity loss.

Few research projects have been conducted on the subtidal benthic communities of the Kitikmeot Region and Parry Channel, CAA, but some information is available. Foremost, Roy et al. (2015a) and Balsom et al. (2003) found that epifauna collected in the southwestern portion of the Archipelago (essentially matching the Kitikmeot Region) have a higher Shannon-Wiener diversity index compared to neighboring areas. Another study [Roy et al. (2015a)] shows that benthic biomass is higher in the deeper Eastern Archipelago, from Barrow strait to Lancaster Sound in the Parry Channel segment, than in the shallower Kitikmeot Western Archipelago study area.

The main objective of this study is to increase knowledge of the macrobenthic infauna and epifauna composition and predict their distribution across much of the Kitikmeot sea region and Parry Channel. Specifically, we first evaluated benthic composition and its relationship to relevant environmental factors. Second, we created models to predict spatially different benthic communities across the studied area. The prediction tested is that benthic fauna spatial distribution and benthic communities are succeeding one another in the CAA, forming a transitional area (ecotone) between Baffin Bay and Beaufort Sea, where diversity is higher. The second prediction is that the decreasing Pacific Ocean water influence through the CAA can explain part of this succession. The third prediction is that

terrigenous inputs transported into the region by numerous rivers also play an important role in the Kitikmeot Region's benthic community composition.

METHODS

Study Area

The study area can be divided into two main parts. The first, Parry Channel, is situated in the middle of the CAA and the considered portion extends from Lancaster Sound to Viscount Melville Sound (**Figure 1**). The second is the Kitikmeot marine region, located in the Northern part of Nunavut and in the southern part of the CAA. Compared to Kitikmeot, Parry Channel is quite deep, extending from 500 m to 700 m, except around Barrow Strait which is closer to 200 m to 400 m in depth. The Kitikmeot region includes the Queen-Maud Gulf southward, M'Clintock Channel and Peel Sound northward, Coronation Gulf to the west and Chantry Inlet to the east. Our area of interest for this study is especially Queen-Maud Gulf (where most of our samples were taken), which is 20-75 meters deep, but also Victoria Strait and M'Clintock Channel. Queen-Maud Gulf is connected to Coronation Gulf by the shallow Dease Strait (~40 meters deep) (Carmack and McLaughlin, 2011) and many rivers are discharging into it. Queen-Maud Gulf receives inflows from the Simpson, Perry and Pitok rivers and a few others (Brown et al., 2020).

In total, 55 different locations were sampled across this area (**Figure 1**). Generally, infauna and epifauna were both sampled at the same location but a few stations have either only infauna or epifauna. For each station, benthic organisms and environmental data (detailed in section 2.3) were sampled/measured.
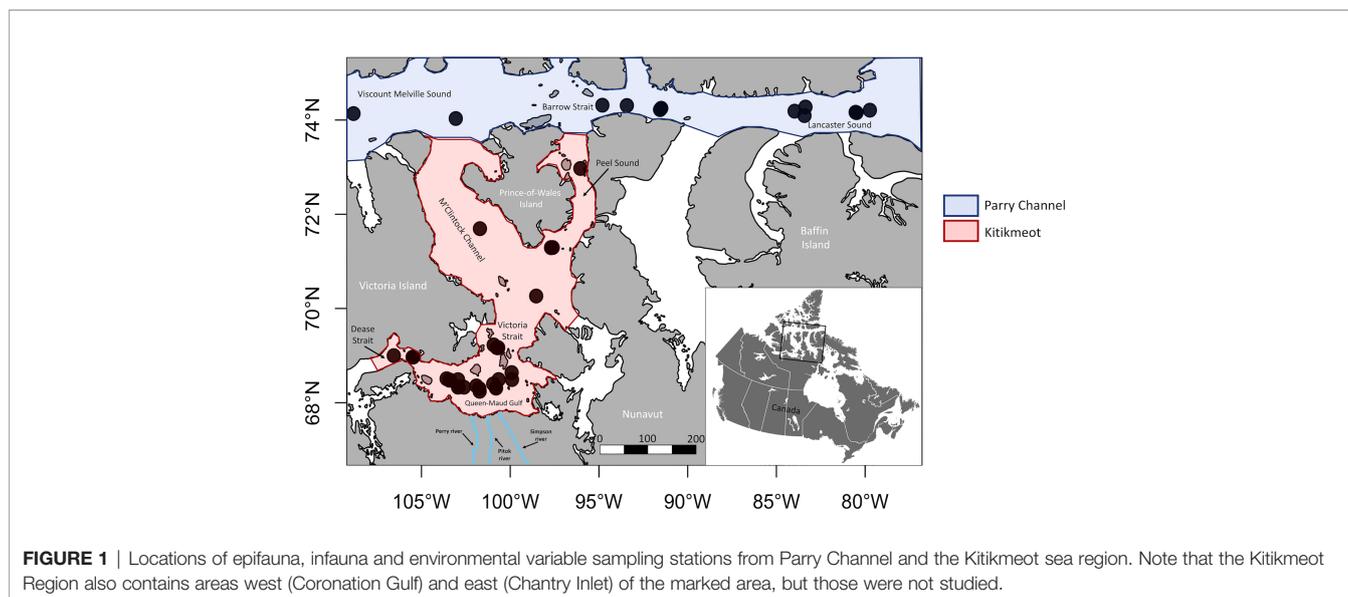
Sampling Procedures

Throughout this work, infauna and epifauna samples are treated separately. Samples were collected between August and September, from 2009 to 2018, onboard the Canadian research ice breaker CCGS Amundsen (ArcticNet, 2009; ArcticNet, 2010; ArcticNet, 2011; ArcticNet, 2013; ArcticNet, 2014; ArcticNet, 2015; ArcticNet, 2017; ArcticNet, 2020). Moreover, this study focuses only on subtidal macrobenthic (> 500μm) invertebrate communities living deeper than 30 meters.

Infauna was sampled with a Reineck box corer (50 cm x 50 cm), where sediments from half of the box surface (25 cm x 50 cm) and contained within the upper 10 cm were considered. Sediments were sieved on a 0.5 cm mesh size to sample organisms greater size than 0.5 x 0.5 cm. These sieved sediments containing organisms were preserved in a seawater and formaldehyde solution (4%), buffered with sodium tetraethylborate.

Epifauna was sampled using a single haul of an Agassiz trawl per station, the unit measuring 1.5 m in width, with a 1.5 cm net mesh size and 5 mm cod end. After having reached the sea bottom, the trawl was dragged for 3 minutes at an approximate forward speed of 1.5 knots. Since this trawl method is semi-quantitative (Eleftheriou and McIntyre, 2005), taxa count may contain minor biases. Trawl contents were thereafter sieved on a 2 mm mesh size and then sorted to taxon. In samples where trawl content was considerably higher than average, the contents were subsampled if the estimated sorting time was considered excessive. The subsampled fraction depended on the size of the catch and was noted to adjust abundance and biomass measures. Larger specimens were identified, counted and weighted on the ship and the others preserved as for the infauna.

Preserved infauna and epifauna samples were washed of the formaldehyde solution before sorting. After, infauna samples were sieved on a 500 μm sieve while epifauna samples were sieved on a 2 mm sieve in the lab. Washed and sieved organisms were then sorted under a dissecting microscope. Specimens were identified and counted to the lowest possible taxonomic level based on morphological criteria. Experienced taxonomists validated the identifications of less common specimens. However, nematodes were kept at phylum level, and foraminifera were not considered.

FIGURE 1 | Locations of epifauna, infauna and environmental variable sampling stations from Parry Channel and the Kitikmeot sea region. Note that the Kitikmeot Region also contains areas west (Coronation Gulf) and east (Chantry Inlet) of the marked area, but those were not studied.

Afterwards, specimen biomass was measured on a ± 0.0001g precision scale. Taxonomic identification names were verified on the World Register of Marine Species (WORMS) database.

A total of 19 environmental parameters were used in the analyses (**Table 1**). Bottom-water temperature, salinity and oxygen were obtained with a Seabird Scientific CTD profiler (SBE911 Plus). Water for nutrient analysis was taken simultaneously with a Niskin bottle attached to the Rosette sampler and filtered through GF/F filters. The concentrations of nitrite (NO_2^-) , nitrate+nitrite ($NO_3^- + NO_2^-$) , phosphate (PO_4^{3-}) and silicate ($Si(OH)_4$) were determined on board with a Bran +Luebbe autoanalyzer 3, following the methods of Grasshoff (2009). Analytical detection limits for these were 0.02, 0.03, 0.03 and 0.05 µM, respectively. Nitrate concentrations were obtained by difference of "nitrate+nitrite" – "nitrite". Silicate concentrations was used to trace terrigenous inputs. The N/P ratio used to trace back Pacific origin water that is nitrate depleted (Yamamoto-Kawai et al., 2006; Tremblay et al., 2015) is the ratio of nitrate concentration to phosphate concentration. As samples were collected during the summer and since nitrate concentrations are often very low or null after the spring bloom, the N* index was also used in parallel. The latter was calculated based on Gruber and Sarmiento (1997) and Deutsch et al. (2001) as:

$$N^* = [DIN] - (16 \quad x \left[PO_4^{3-}\right]) \qquad \text{Eq.1}$$

where [DIN] is the sum of nitrite and nitrate concentrations.

The bottom water current velocity was obtained using the updated version of Ocean-Navigator (Hernandez, 2007) and annual mean sea ice thickness was extracted from Bio-Oracle and estimated from 2000 to 2016 (Tyberghein et al., 2012; Assis et al., 2018). For the last 7 parameters in **Table 1**, the box core-collected sediments were analyzed in the laboratory. The grain size proportions were determined by laser diffraction (Horiba LA-960 particle size analyzer), and grain dimensions classified using the Gradistat classification (Blott and Pye, 2001). We burned the sediment at 450°C to obtain the dry mass

proportion of organic content (Byers et al., 1978). Pigment concentrations in sediments were obtained using acetone extraction followed by fluorometric analysis (Riaux-Gobin and Klein, 1993).

Statistical Analysis

Statistical analyses presented below were performed separately on infaunal and epifaunal data, using R Software, version 3.6. (R Core Team, 2020). Except for functions from the base package, most of the statistical functions used are from the Vegan package (Oksanen et al., 2018).

A cluster tree analysis based on a Bray-Curtis dissimilarity matrix was performed on biomass data which was initially transformed using the Hellinger method (Legendre and Gallagher, 2001). Afterwards, the most representative species in each community were identified using the indicator value index (IndVal) (Dufrêne and Legendre, 1997). Values of IndVal range between from 0 to 100%. A value of 100% for a particular species would indicate that it is encountered exclusively in a given group and at every station.

Subsequently, a redundancy analysis (RDA) was done to determine which environmental parameters are related to the differences between communities. Again, Hellinger transformed faunal biomass data was used and environmental data was transformed with the *standardize* method of the vegan package (Oksanen et al., 2018). Such transformations are used to reduce the effect of outlier values in analyses. In the first iteration, a best fit selection of variables was performed to obtain an RDA with the highest adjusted-R^2. Then, to answer the second and third hypotheses, selection of environmental variables that are significantly related to the biomass was performed *via* a two-step process with forward selection. The alpha value was set at 0.05. Only significantly influential variables were used to build a graphical representation (i.e. x-y graph), where the distance between each community represents the Euclidian distance and each influential driver is represented by an arrow, for which communities are influenced and positioned in relation to each other by these drivers. The length of the arrow is related to the strength of influence. The p-value of the model was obtained with a permutation test for RDA under a reduced model and 9999 permutations.

Generalized linear models (GLMs) were used to predict spatial community likelihood of occurrence (on a scale from 0 to 1). The family type of the GLMs in this case is binomial because the presence of communities was expressed by either 1 (presence) or 0 (absence). To obtain the highest R^2 possible, we used a best fit approach, where every combination of environmental variables possible was tested in a GLM. The combination with the highest R^2 and lowest Bayesian Information Criterion (BIC) was selected. The McFadden pseudo-R^2 (McFadden, 1973) was used along with the GLMs statistics. Using GIS rasters of chosen environmental data and the GLM, we predicted the probability of occurrence of the community for every cell in the study area. Rasters for every parameter used were extracted from Bio-Oracle (Assis et al., 2018), for which resolution is 0.083° of latitude by 0.083° of longitude, and cells are approximately 3 km of longitude by

TABLE 1 | Environmental parameters considered for the statistical analysis.

Environmental parameter	Unit	Abbreviation
Bottom water temperature	°C	T
Bottom water salinity	PSU	S
Water Depth	m	D
Bottom water Oxygen concentration	mL·L^{-1}	O
Bottom and Surface water N/P ratio	–	b.N/P and s.N/P
Bottom and Surface water N* index	–	b.N* and s.N*
Bottom and Surface Nitrate	µmol·L^{-1}	b.N and s.N
Bottom and Surface Nitrite	µmol·L^{-1}	b.NO$_2$ and s.NO$_2$
Bottom and Surface Phosphate	µmol·L^{-1}	b.PO$_4$ and s.PO$_4$
Bottom and Surface Silicate	µmol·L^{-1}	SiB and SiS
Bottom water velocity	m·s^{-1}	WV
Annual Mean Ice Thickness	m	Ice
Gravel	%	Gravel
Sand	%	Sand
Mud	%	Mud
Sediment Organic Matter	%	OM
Sediment Chlorophyll *a*	µg·g^{-1}	C.*a*
Sediment Phaeopigments	µg·g^{-1}	Pha
Total sediment pigments	µg·g^{-1}	P

9.3 km of latitude in our study area, hence every cell has an area of 27.9 km². It is important to note that some areas were blanked due to the lack of data, which was useful in preventing false identification of unexplored benthic regions. Because sediment content of pigments (phaeopigments and chlorophyll *a*) is not available on Bio-Oracle as raster, this variable was replaced by bottom water chlorophyll concentration (mg·m⁻³) for the GLMs only. Upon analysis, field data was found to be quite similar to GIS data. In the stations that differed, slightly different values could be observed at times, and some outliers were also observed but mean values were very similar. Nevertheless we used extracted environmental data from the rasters to perform GLMs. Due to the unavailability of Bio-Oracle data relating to sediment types (sand, mud and gravel), these were not considered in the process of modelling communities.

Taxonomic richness was the chosen unit to measure diversity (Supplemental 5, 6, 7 and 8). We applied the same method as for the community models except using the Poisson family type of GLMs because the number of taxa is discrete, and predictor environmental variables are continuous.

Epifauna community distribution models were partly validated using seafloor images from Lancaster Sound by Bouchard Marmen et al. (2017). This was done to validate if indicator species of the communities were in fact present or not at a predicted location. These images are from a North-South transect photographed in Lancaster Sound around 83° W of longitude with a Digital Benthic Camera, but acquired in different sites than the ones in this study. The photos cover an average of 0.692 m² (0.675 m x 1.025 m).

RESULTS

Infauna

A total of 40 stations were sampled and 407 taxa were identified in the infauna. The most dominant taxon was Annelida (38%), followed by Arthropoda (25%). Most of the Annelida found were polychaetes (99,8%) and Arthropoda were mainly composed of Amphipoda (42%) and Cumacea (27%). Based on the Bray-Curtis dissimilarity, stations clearly clustered into 4 spatially contiguous station groups (**Figure 2** , **Figure 3**). Which are used in all subsequent species assemblage related analyses.

The first community of the cluster analysis (**Figure 2**) is composed of the shallowest stations, located around Victoria Strait and in the northern portion of Queen-Maud Gulf. They also display the lowest salinity values and the highest sediment chlorophyll *a* concentration (**Figure 4**). The second community encompasses some northern stations of Kitikmeot, in the M'Clintock Channel and at the entry of Peel Sound in Franklin Strait. According to the RDA, this is the community with the highest bottom N/P ratio and bottom nitrate concentration (**Figure 4**). Moreover, two locations within this community show the lowest concentrations of chlorophyll *a* in the sediment and mean sediment organic matter content between all communities. This second community also has some stations which are overlapping with some of the third

community, although the average depth (100 meters) a little deeper than for the third community (85 meters). The main indicator species in this second community is the bivalve *Astarte crenata/montagui* (**Table 2**).

The third community has some stations in Queen-Maud Gulf. This community is different from the second by, 1) the absence of stations in the Northern Kitikmeot, 2) the presence of stations in Dease Strait (**Figure 3**), and 3) the lowest mean surface N* value, according to the RDA (**Figure 4**). Indicator species are represented by bivalves in 3 out of 5 total species and are characterized by very low mobility. Along with the brittle star *Ophiocten sericeum* (IndVal of 39%), 4 of the 5 indicator taxa are calcified organisms. The genus *Yoldiella* is strongly representative of the community with the two species, *Y. intermedia* and *Y. solidula*, as main indicators. The fourth community is composed of stations located almost exclusively within the Parry Channel region, and is the closest of four to the Atlantic Ocean and also furthest from the Pacific Ocean (**Figure 3**). Stations here are characterized by the lowest ocean depth measurements as well as highest mean bottom water temperatures (**Supplemental 2**). As observed on the RDA (**Figure 4**), these stations share some similarities with the first and third communities. The taxon that best distinguishes this community is the gastropod family Philinidae (Indval of 83%) (**Table 2**).

In a best-fit RDA with the selected environmental variables, 19 parameters (D, s.N*, P, b.N/P, S, WV, SiS, Sand, T, Pha, s.PO₄, Mud, SiB, Gravel, s.N/P, b.N, b.N*, Ice and C.*a*) explained 63% of the variation among stations (adj-R² = 0.28) (**Supplemental 1**). Nine of these were statistically significant and explained 40% of the variation among stations (adj-R² = 0.22) (**Figure 4**). Sediment chlorophyll *a* concentration, annual mean ice thickness and surface silicate had the strongest influence on the species composition. Additionnally, an interesting observation among studied regions was that annual mean ice thickness and surface silicate were inversely correlated. Chlorophyll *a* concentration is also inversely correlated with depth and salinity. However, depth and salinity generally tend to be vary proportionally (**Figure 4**).

The main observation from the infauna GLMs models is the succession of habitat suitability between the communities (**Figure 5**). Starting from the Southwest, habitat suitability in Dease Strait and towards Coronation Gulf was highest for the third community. Environmental conditions also appeared favorable for this same community in the middle of Queen-Maud Gulf and in Northern Peel Sound, albeit the species' group characteristic of this community were not found within these two locations. This could mean that more sampling may have revealed this community or perhaps a similar one, given that the environmental conditions were favorable.

The second community was predicted to be present in suitable habitat within coastal areas and especially in Queen-Maud Gulf, surrounding the third community. Suitable habitat for the first community was predicted to occur a little northward of the second community. Habitat suitability for the first community was higher around Victoria Strait and inside
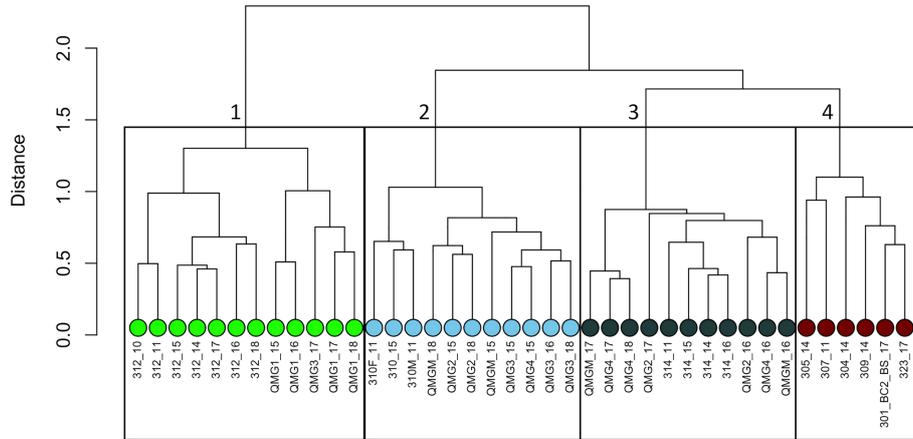
FIGURE 2 | Infauna cluster tree (Bray-Curtis Distance) based on Bray-Curtis dissimilarity matrix with transformed species biomass data. Green dots are the stations from the first community, pale blue dots are community 2, dark gray dots are community 3 and red dots are community 4.

Ommanney Bay near Prince-Of-Wales Island, with a patch around Barrow Strait which is a shallower portion of Parry Channel. Completing the niche succession northeastwards, the fourth community found high predicted habitat suitability for Viscount Melville Sound and Lancaster Sound. In summary, communities 3, 2, 1 and 4 seem to be largely succeeding one another from the Southwest, near Beaufort Sea, to the Northeast and nearer to Baffin Bay.

When considering the environmental variables retained for creating the GLM models (**Supplemental 2**), silicate

concentration is present in all four models. Also, annual mean ice thickness explains the presence/absence of 3 out of 4 communities. The first community seems to thrive where explaining variable values are intermediate. Furthermore, shallow depths, low annual mean ice thickness and high surface silicate concentration explaining the second community is consistent with its nearshore location inside Queen-Maud Gulf. The third community is explained by the lowest annual mean ice thickness, low bottom nitrate and moderate bottom silicate concentration. The fourth community is not explained by
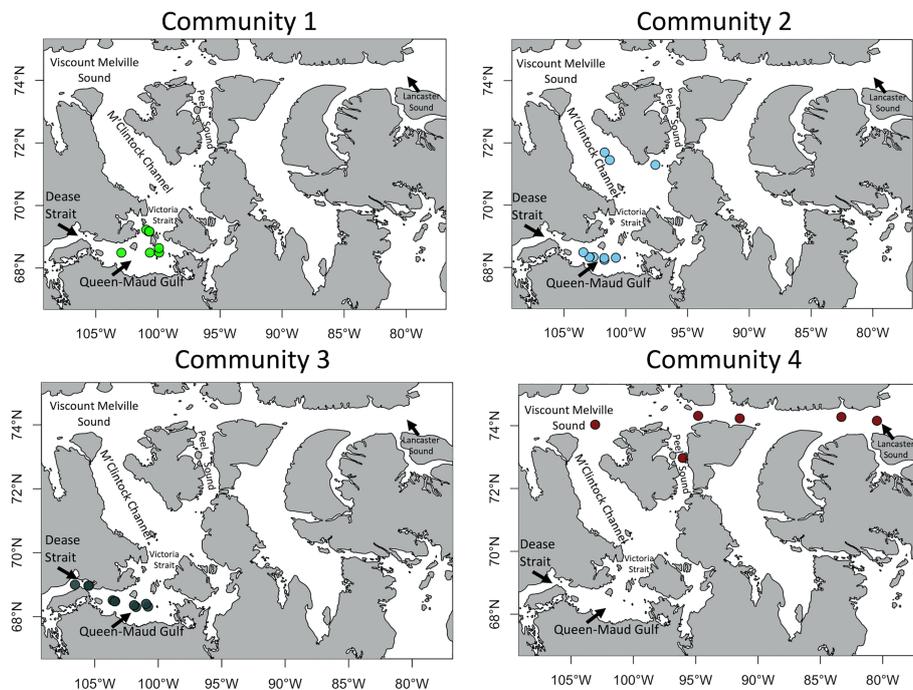

FIGURE 3 | Location of the 4 infaunal communities across the Kitikmeot Sea region and Parry Channel. Colors represent the communities assigned in **Figure 2**.
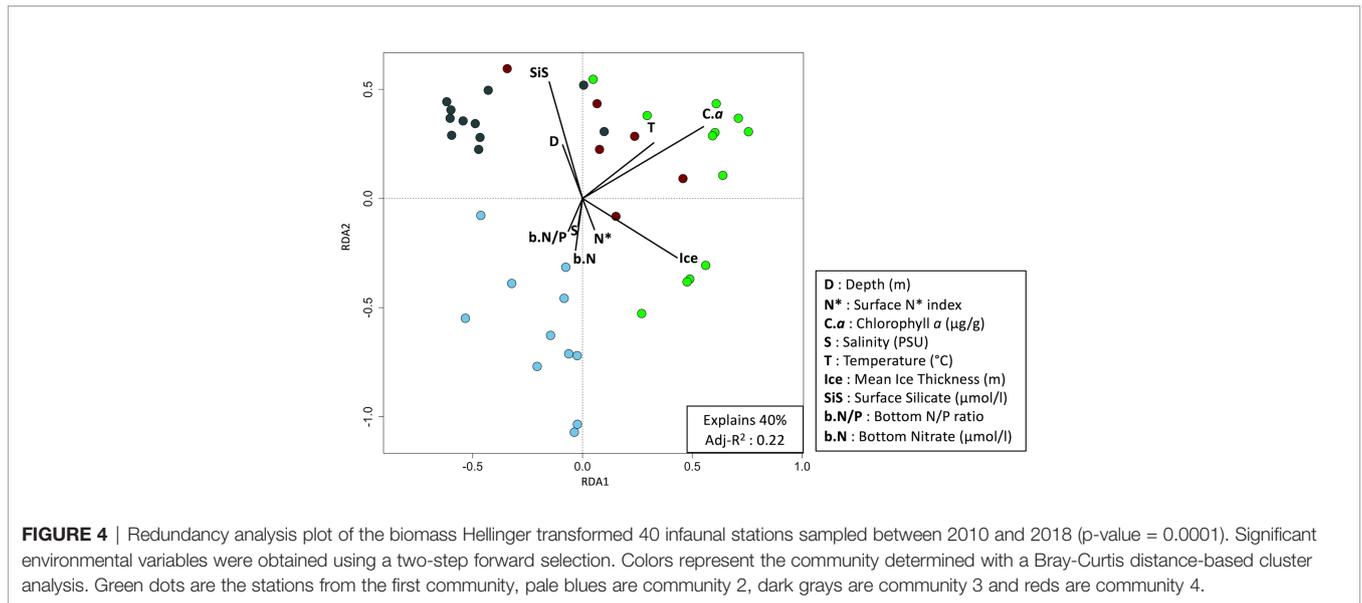
FIGURE 4 | Redundancy analysis plot of the biomass Hellinger transformed 40 infaunal stations sampled between 2010 and 2018 (p-value = 0.0001). Significant environmental variables were obtained using a two-step forward selection. Colors represent the community determined with a Bray-Curtis distance-based cluster analysis. Green dots are the stations from the first community, pale blues are community 2, dark grays are community 3 and reds are community 4.

depth, but its distribution pattern clearly fits the deepest regions of the studied area. The variable with the strongest influence on this community is the bottom current velocity, which is clearly higher compared to the other groups even though it is in deeper water.

Epifauna

A total 50 stations were considered and 436 taxa were identified. The most dominant phylum was Arthropoda (28%), which was dominated by the order Amphipoda (48%), followed by Annelida (13%) (mostly Polychaeta at 99%) and by Bivalvia (12%).

TABLE 2 | Indicator species (5 most important species are presented) of each benthic infaunal community in the Kitikmeot sea region and Parry Channel based on the IndVal Index.

Community	Mean depth (m)	Taxa (Phylum)	IndVal (%)
1	55	*Haploops laevis* (Arthropoda)	83
		Ennucula tenuis (Mollusca)	81
		Nuculana pernula (Mollusca)	72
		Maldane sarsi (Annelida)	67
		Micronephthys minuta (Annelida)	62
2	99	*Astarte crenata/montagui* (Mollusca)	58
		Alcyonidium sp. (Bryozoa)	41
		Abyssoninoe abyssorum (Annelida)	36
3	85	*Bathyarca glacialis* (Mollusca)	67
		Yoldiella intermedia (Mollusca)	64
		Yoldiella solidula (Mollusca)	42
		Diastylis oxyrhyncha (Arthropoda)	39
		Ophiocten sericeum (Echinodermata)	39
4	445	Philinidae (Mollusca)	83
		Diplocirrus hirsutus (Annelida)	66
		Prionospio sp. (Annelida)	56
		Thyasira sp. (Mollusca)	52
		Chirimia biceps (Annelida)	50

Based on a Bray-Curtis dissimilarity matrix, epifauna stations clustered into 3 different groups (**Figure 6**). Almost half of all stations represent the first community which occurs at the highest mean depth, mostly in Parry Channel (**Figure 7**) and with a few stations in Queen-Maud Gulf. The latter stations from 2018 are more similar to deeper area communities in Parry Channel than to stations sampled in previous years a few kilometers away. The first community has the highest N* index values, is furthest from Pacific Ocean sources and has the low mean surface silicate concentrations. Two indicator species of that group are echinoderms of the class ophiuroids (brittle stars) (**Table 3**). The second and third share few similarities in taxonomic composition (**Table 3**), though both are found mainly in Queen-Maud Gulf, Victoria Strait and Dease Strait (**Figure 7**). However, locations in which the second community is present have lower salinity and higher surface silicate values, which are indicative of terrigenous water inputs. The five indicator species of this group are quite taxonomically diverse (**Table 3**). Most of third community stations were in Kitikmeot area, although, some are in Barrow Strait where the sea is shallower compared to the rest of Parry Channel. Overall, Community 3 stations are found deeper than the ones from the second community. In terms of silicate concentrations and salinity, this group is between the first and second community. The N* index value is the lowest, therefore indicative of strong Pacific Ocean water influence.

In a best-fit RDA, 11 parameters (S, D, b.N*, O, b.N/P, SiS, WV, Sand, OM, C.*a* and P*)* explain 32% of the variation among stations (adj-R^2 = 0.13) (**Supplemental 3**). The forward selection indicate that 6 environmental parameters are significantly influential (depth, N* index, pigment, salinity, organic matter, and surface silicate) and when combined, explain 22% of the differences between the 50 stations (adj-R^2 = 0.12) (**Figure 8**). Overall, high surface silicate and organic matter concentrations are inversely proportional to high salinity concentration, N* index (used to trace Pacific Ocean water), and depth values. High
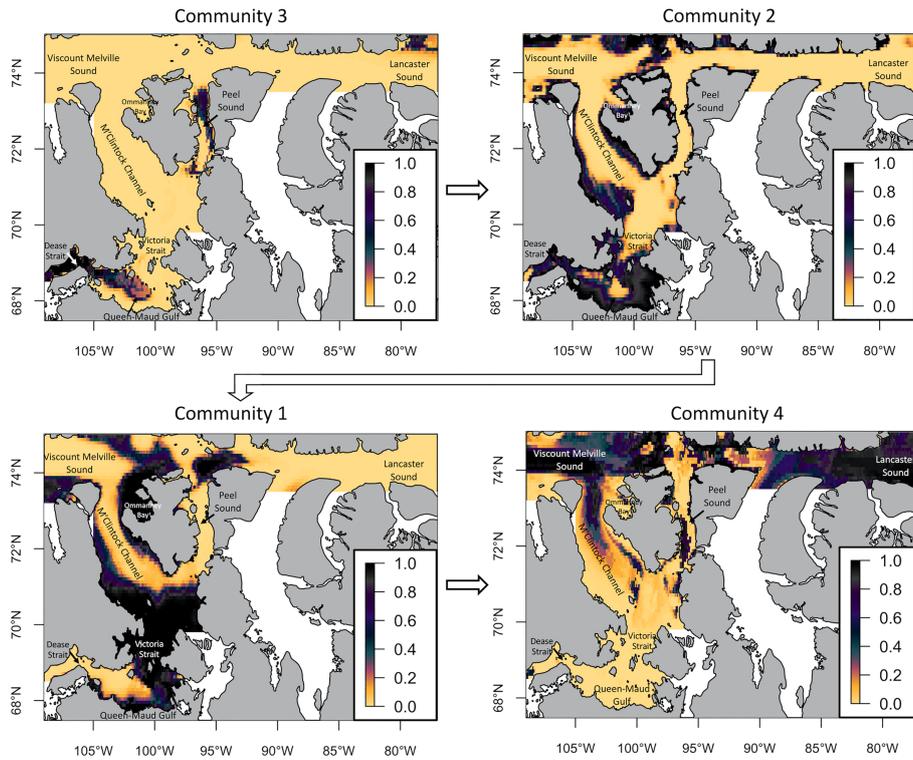
FIGURE 5 | Habitat suitability of 4 infaunal groups in the Kitikmeot sea region and Parry Channel regions obtained with GLMs. The scale from 0 to 1 represents the probability of occurrence of each community. The arrows show the gradient of species community distribution from Dease Strait to Lancaster Sound.

values of the latter five parameters are mainly associated to stations of the first community (**Figure 8**, displayed in red). High concentrations of surface silicate and organic matter are associated with stations from the second and third community.

In the GLMs models, habitat suitability for the three communities shows a somewhat obvious spatial succession from Southwest to Northeast, albeit not as clear as with the infauna (**Figure 9**). The second community is mostly present in southern Kitikmeot. The third community has high habitat suitability inside most of Kitikmeot sea region and is located just beyond coastal areas. There are also high habitat suitability

values North of Prince-of-Wales Island and Barrow Strait. Hence, this can be interpreted as an intermediate community between the communities of Lancaster Sound (1) and Queen-Maud Gulf (2). Finally, community 1 has high habitat suitability values in North M'Clintock, Viscount Melville Sound, Peel Sound and especially Lancaster Sound with a tendency to expand East towards Baffin Bay. Overall, the 3 epifaunal communities are succeeding one another inside the study area. For Community 1, the coefficient with the highest value is associated with depth (**Supplemental 4**). Indeed, high habitat suitability values for this community are found mostly for deeper
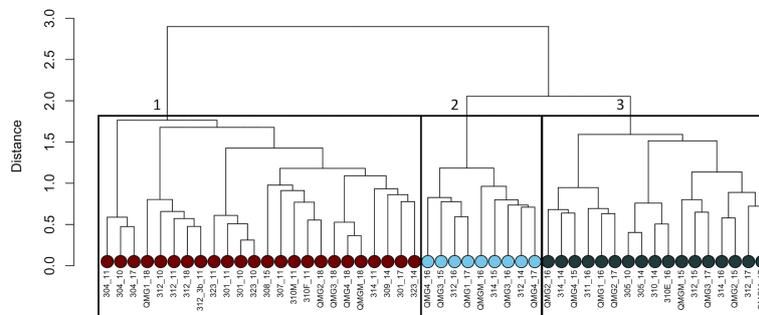

FIGURE 6 | Epifauna cluster tree based on Bray-Curtis dissimilarity matrix with Hellinger transformed species biomass data. Red dots are the stations from group 1, pale blue dots are group 2 and dark grey dots are group 3.
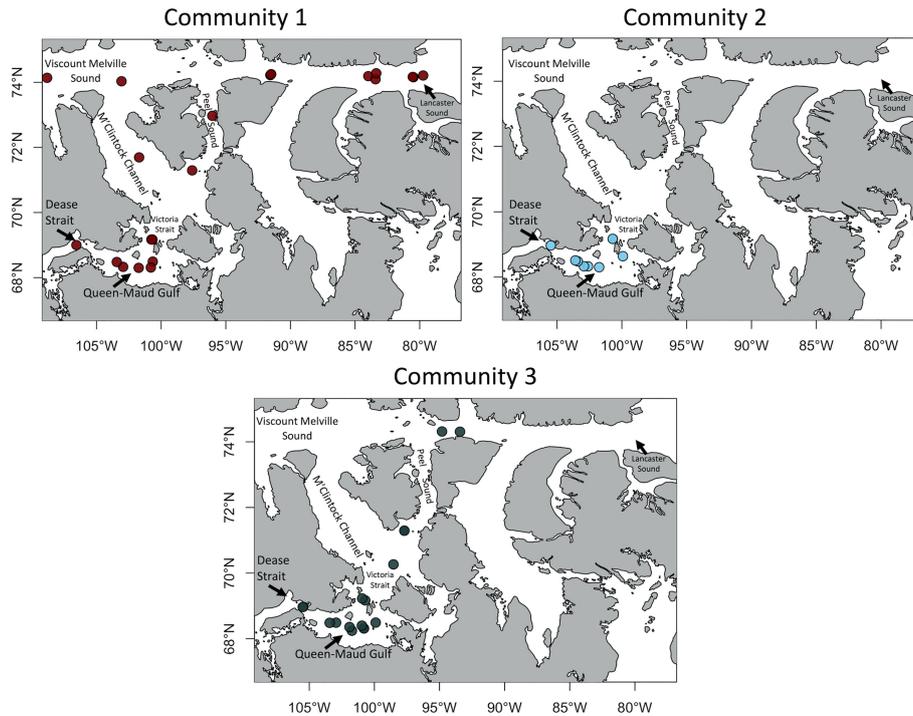
FIGURE 7 | Location of the 3 epifaunal communities across the Kitikmeot sea region and Parry Channel. Colors represent the communities determined at **Figure 6**.

areas such as Parry Channel while the community has 'near zero' habitat suitability values in shallow regions like Queen-Maud Gulf. Regarding the second community, the highest absolute value of coefficients is associated with high bottom current velocities, which are mainly observed within channels. Moreover, this community has higher suitability values when

dissolved oxygen increases. Finally, the third community is present in areas with the highest mean current velocities, whereas the first community is found mainly in areas of medium mean current and the second community, the lowest mean current velocities.

TABLE 3 | Indicator species (5 first if available) of each benthic epifauna community in the Kitikmeot sea region and Parry Channel based on the IndVal Index.

Community	Mean Depth (m)	Indicator Species	IndVal (%)
1	318	*Ophiocten sericeum* (Echinodermata)	75
		Ophiopleura borealis (Echinodermata)	57
		Alcyonidium gelatinosum (Bryozoa)	40
		Phascolion sp. (Sipuncula)	37
		Cuspidaria glacialis (Mollusca)	33
2	68	*Yodiella intermedia* (Mollusca)	77
		Anonyx sp. (Arthropoda)	74
		Eurycyde hispida (Arthropoda)	72
		Arcturus baffini (Arthropoda)	69
		Bathypolypus arcticus (Mollusca)	68
3	97	*Ophiacantha bidentata* (Echinodermata)	88
		Grammaria abietina (Cnidaria)	82
		Nothria conchylega (Annelida)	76
		Nototropis smitti (Arthropoda)	76
		Lophaster furcifer (Echinodermata)	76

DISCUSSION

This study demonstrates that benthic communities in the southern and central CAA are succeeding one another from Southwest to Northeast, with 4 infaunal and 3 epifaunal communities that are mostly contiguous and partly overlapping. Pacific Ocean water flowing through the CAA, from Bering Strait to Baffin Bay, is an influential environmental parameter for the community composition. Moreover, we observed that benthic assemblages are potentially influenced by terrigenous inputs in the marine environment. This is the first time that benthic communities and diversity are modelled in the Kitikmeot sea region.

Indicator Taxa

All characteristic species are well known from Arctic shelf areas. In the epifauna, indicator species of 2 out of 4 communities are both ophiuroids, or brittle stars, which are often observed in the Arctic. A potential explanation suggested by Piepenburg (2003) for their omnipresence in Arctic regions is that they are exposed to very low predation pressure. In Community 1, *Ophiocten*
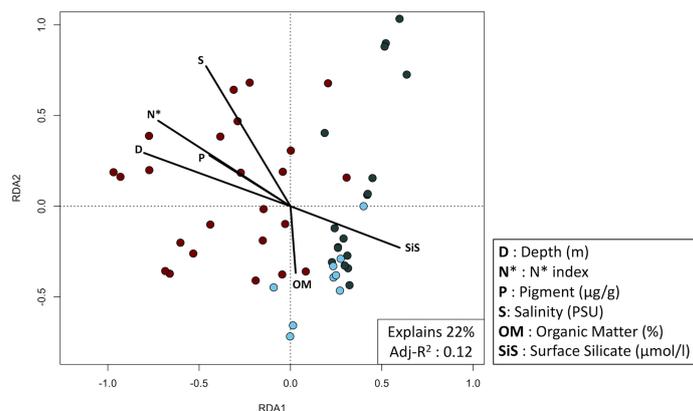
FIGURE 8 | Redundancy analysis plot of the biomass Hellinger transformed 50 epifaunal stations sampled between 2010 and 2018 (p-value = 0.0001). Significant environmental variables were obtained using a two-step forward selection. Colors represent the community determined with a Bray-Curtis distance-based cluster analysis. Red dots are the stations from community 1, pale blues are community 2 and dark grays are community 3.

sericeum is the most indicative species most likely because of its large depth range (Piepenburg, 2003). The best indicators of Community 2 are the bivalve *Yoldiella intermedia*, the amphipod *Anonyx* sp. and the pycnogonid *Eurycyde hispida*, all of which have been observed in shallow and low salinity areas such as in fjords (Arnaud and Bamber, 1988; Shea and Percy, 1990; Różycki, 1992; Bryazgin, 1997). The exception among indicator species for that community would be *Bathypolypus arcticus*, a cosmopolitan deep-water octopus, though its variable distribution may include shallow areas (Wood, 2000; Gardiner and Dick, 2010). For Community 3, the first indicator species is *Ophiacantha bidentata*, a shallow water brittle star species (Martynov and Litvinova, 2008). The second indicator species, *Grammaria abietina*, is a sessile hydroid while the third is the shallow water polychaete *Nothria conchylega*. These two latter species are present despite a mostly fine sediment structure, although they do need coarser sediment for attachment and to build a dwelling, respectively (La Porta et al., 2011).
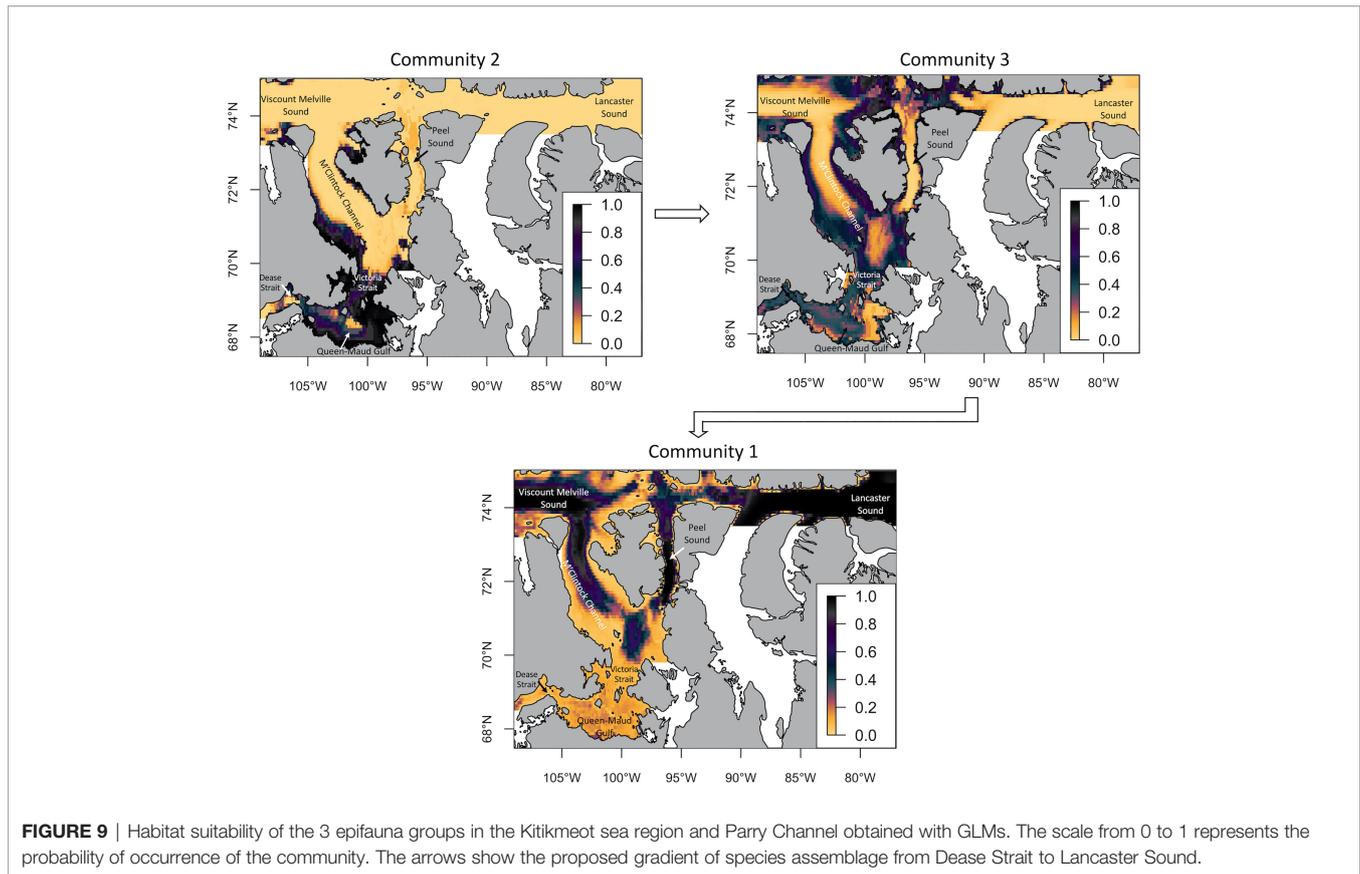
For infauna, Bivalvia and Polychaeta were the main indicator taxa, which are often dominant within the sediment in the Arctic and globally (Dale et al., 1989; Olsen et al., 2007; Schonberg et al., 2014). The main indicator for Community 1 is a common shallow water amphipod, *Haploops laevis* (Bryazgin, 1997). In Community 2, the most important species is *Astarte crenata/montagui*, which is also omnipresent in the Arctic, followed by the bryozoan genus *Alcyonidium*. The latter species can be an indicator of the presence of at least sparse, coarse substratum enabling attachment of these organisms. The third indicator species of this community is the Polychaeta *Abyssoninoe abyssorum*. Unlike its name may suggest, it can be found in shallow water (Bakken et al., 2010). In addition, the burrowing bivalve genus (Kokarev et al., 2017) *Yoldiella* is common in the community, also found worldwide and often in the Arctic (Bernard, 1979). Finally, Philinidae is the main indicator species of Community 4, being a family of small carnivorous gastropods that mainly feed on foraminifera (Ohnheiser and Malaquias, 2013). Except for this family, the other indicator taxa are all deposit feeders, which suggests low predation from other species in that environment. Among these, the bivalve genus *Thyasira* may tolerate hypoxia conditions due to chemoautotrophic abilities (Dando and Spiro, 1993).

Environmental Influence on Assemblages

The most notable results are that N* index and surface silicate concentrations significantly explain the differences between benthic assemblages within stations. This means that Pacific Ocean origin water and terrigenous input have an influence on benthic communities in the CAA. Pacific waters that enter by the Bering Strait are nitrate depleted (Yamamoto-Kawai et al., 2006) and fresher than the Atlantic water. In the Arctic, nitrogen in the form of nitrate is a limiting element for marine primary productivity (Gray and Elliott, 2009). Because of its lower density, water of Pacific origin is mostly found within the upper 200 meters (Woodgate, 2013). More than 3 stations out of 4 were sampled no deeper than 200 meters. This means that most of our stations are literally in the depth zone of these lesser dense waters. Moreover, other depth zones may also be influenced by it, for instance by receiving organic matter from the euphotic zone. Not only is the influence of the Pacific observable in the study area, but as mentioned before, Pacific water input is currently increasing in the Arctic (Woodgate, 2018).

The modelling of the distributions of epifauna and infauna communities suggests that they largely succeed one another across the study area. The distribution of habitat suitability values for every community suggests that every community occupies a distinct niche and geographic area. However it is possible to observe that communities occupy succeeding geographic locations. This succession is mainly from South to North with a slight tendency of West to East. This West-East tendency is more obvious for the infauna where the first community of the succession (Community 3) has very high suitability values in the West in Dease Strait and the last community (Community 4) has very high habitat suitability values in Lancaster Sound at the entrance of Baffin Bay.

FIGURE 9 | Habitat suitability of the 3 epifauna groups in the Kitikmeot sea region and Parry Channel obtained with GLMs. The scale from 0 to 1 represents the probability of occurrence of the community. The arrows show the proposed gradient of species assemblage from Dease Strait to Lancaster Sound.

The community turnover occurs along the same gradient as the strength of influence of Pacific Ocean origin water (a significantly influential parameter) (Yamamoto-Kawai et al., 2006) that flows through the CAA. Moreover, an increasing volume of higher temperature seawater (Woodgate, 2018) may promote Pacific Ocean water inflow in the Arctic and hence allow for the northward movement of sub-polar species *via* Bering Strait (Waga et al., 2020). Based on these insights, we suggest that the community succession observed in the models could potentially move North and/or Eastwards towards Baffin Bay in the future, depending on the original location of the community. Furthermore, this could also include exotic species in the near as suggested by the change in future conditions (Goldsmit et al., 2018; Goldsmit et al., 2020).

Another significant observation is that surface silicate and salinity are correlated. This is especially the case where rivers are present because silicate concentrations are higher in Arctic rivers than in the Pacific Ocean (Ekwurzel et al., 2001). This is the case here as there are a significant number of terrestrial sources in the studied area (in particular QMG). When looking at redundancy analysis and group averages for each environmental variable, Kitikmeot stations have higher surface silicate concentrations, which was used to trace terrigenous inputs. However this will need to be explored further. For instance, $\delta^{13}C$ could be a better tool to evaluate organic matter origin and its impact on benthic communities (Naidu et al., 1993; Bell et al., 2016). Moreover, $\delta^{18}O$ can be used to trace more precisely the presence and

movement of freshwater masses and indicate if water is from marine sources, such as sea ice melting or of terrigenous origin (Yamamoto-Kawai et al., 2008; Lansard et al., 2012).

Land inputs contribute meaningfully to the Arctic Ocean's organic carbon budget (Grebmeier and Barry, 1991; Wheeler et al., 1996) and freshwater budget, where the Arctic receives over 10% of global fluvial imports (Opsahl et al., 1999). All this freshwater entering marine ecosystems contains allochthonous organic matter, hence food for benthic invertebrates. Although it has a lower nutritional quality for benthos (Schell, 1983), this organic matter can be consumed by benthic organisms after microbial reworking and contributes in reducing the pelagic-benthic coupling (Bell et al., 2016). In some Arctic areas, it has been observed that autochthonous organic matter might not be enough for pelagic and benthic organisms. Hence, allochthonous sources are of importance for the carbon budget (Schmid et al., 2006). This connection is supported by our epifauna data, where the concentration of organic matter was correlated with the concentration of surface silicate. River discharge is expected to increase in the upcoming years, and this is especially the case around Queen-Maud Gulf, where predictions suggest the greatest increase along the Canadian Arctic coastline (Bring et al., 2017). Furthermore, Brown et al. (2020) demonstrated that smaller rivers may have a greater inorganic import potential in the future than previously anticipated. River discharge also favors species that are more tolerant than others to salinity variations (Remane and Schlieper, 1971). Precipitations in the

Arctic tend to increase and will continue to do so in the future (Bintanja and Selten, 2014), adding to the direct effect of river discharge and thus freshwater inputs in the marine environment (Peterson et al., 2002; Zhang et al., 2013).

In both infauna and epifauna, depth is a significant environmental driver, although depth *per se* does not necessarily have an influence on living organisms (Gage and Tyler, 1991; Gibson et al., 2005). Depth is especially linked to food availability by negatively affecting the benthic-pelagic coupling (Smith et al., 2008; Soltwedel et al., 2009; Roy et al., 2015b) and food quality (Grebmeier and Barry, 1991; Forest et al., 2011). This explains why depth and chlorophyll *a* are inversely correlated. In addition, the CAA has different and more heterogenous environmental conditions than Baffin Bay and the Beaufort Sea, located on either side. Additionally, to the Southwest-Northeast succession, the inter-regional heterogeneity could also explain why there is such a large-scale difference in species assemblages. This heterogeneity of habitat could be partly linked to depth fluctuations in the CAA where multiple sills are present (McLaughlin et al., 2006). For instance, Queen-Maud Gulf (shallower environment; maximum depth of 115 meters) communities are quite different from the ones in Lancaster Sound (deeper environment; maximum depth of 786 meters).

A prominent oceanographic phenomenon in the CAA, especially in the Kitikmeot sea region, is the local presence of strong tidal currents (Rotermund et al., 2021). These currents are fastest in narrow straits and contribute to reducing the ice cover during winter and are thought to increase pelagic-benthic coupling during summer (Williams et al., 2019). Even though current velocity is not an explanatory variable in the RDA, it was selected in GLMs of the three epifauna communities, suggesting it is a non-negligible factor for community distribution. In fact, Fredriksen et al. (2018) demonstrated that epifauna communities in areas with high current are dominated by suspension feeders, in agreement with Community 3, while lower current regions were dominated by deposit feeders.

As some environmental parameters are significantly influential, there is no key variable that can alone explain benthic communitiy distribution. It is more reasonable to assume that interactions between every variable influence the species assemblages, where some interactions can be antagonistic while others synergistic and very few variables act in isolation (Carrier-Belleau et al., 2021).

As observed on community location maps, stations that are geographically closer to each other tend to have similar community composition. There is one notable exception to this observation, and it is Community 1 of the epifauna. Indeed, Queen-Maud Gulf stations of 2018 are much more like those of Parry Channel than they are from stations of the same location from different years. However, Queen-Maud Gulf stations are in shallower depths and Parry Channel stations are within the deepest locations of our sampling effort. QMG stations of 2018 had less organic matter, less surface silicate (less terrigenous inputs), lower chlorophyll *a* concentration and less bottom oxygen concentration (which proposes a greater column water stratification) than observed in that region during other sampling periods. In 2018, there was a higher sea ice extent, lower temperatures and slightly lower precipitions (Smoliansky et al., 2018) than other years. All of which could have impacts on primary productivity and hence benthic communities (Gradinger, 1995; Arrigo et al., 2008; Wassmann and Reigstad, 2011; Link et al., 2013; Kędra et al., 2015). Another potential explanation of this unique result would be a greater increase in the nitrate depleted Pacific Ocean water inputs in the Arctic for that year. However, those stations do not exhibit different N* index value for that year. A sudden shift in benthic communities' composition driven by changes in the environmental conditions over only one year seems quite unlikely. Normally, shifts in benthic communities occur over more than a year given that many species are long-lived and slow growing (Grebmeier, 2012; Kortsch et al., 2012).

Modelling diversity is even more complex than doing so for presence/absence of communities, judging from the overall low R^2 values (**Supplemental 5, 6, 7, 8**). In the case of our data, the highest pseudo R^2 for these latter models was 0.28. For communities, they were at least higher than 0.30 and go up to 0.80. Despite some low R^2 values, diversity models are based on species level identifications, which brings more model strength since the species level is usually most impacted by the environment (Bertrand et al., 2006). Additionally, more parameters are selected to predict diversity and it is normally a combination of many parameters that affect diversity in marine ecosystems (Rosenzweig, 1995; McArthur et al., 2010). Many environmental variables are found to be significantly influential on the number of taxa for both epifauna and infauna. This is especially the case for surface silicate, salinity, bottom N/P and annual mean ice thickness.

Model Validity

The only possible validation of our model by external data was achieved with Lancaster Sound bottom pictures from Bouchard-Marmen et al. (2017), the latter having been taken exclusively in the area mostly occupied by epifauna of community 1 (Lancaster Sound). Our model shows that the two main indicator species for this community were *Ophiocten sericeum* and *Ophiopleura borealis*, which can be confirmed/validated by photographs showing their high abundance in that area. Comparatively, oher indicator species were not often observed in these pictures, probably due to the difficulty in detecting them by their smaller size. Therefore, a more detailed validation of these models would be warranted in the near future. Additionnaly, sampling effort should be increased in the whole area to have a maximal validation resolution. This was suggested by Wei et al. (2020), where future research activities must fill these knowledge gaps to improve the accuracy and resolution of pattern predictions. Furthermore, we must be careful with predictions of habitat suitability for communities around coastal areas, since we do not actually have any infauna or epifauna data shallower than 34 meters. Hence, models are not built to predict community presence or characteristics in such complex environments. Finally, models that were built are considered to be large-scale, where every cell measures 27 km². Consequently, community gradients may not be

observable everywhere since, on a local scale, it is interspecific relationships that impact community composition (Levin et al., 2001). This model does not consider these types of relationships.

SUMMARY AND CONCLUSION

Our research suggests that epifaunal and infaunal benthic communities are succeeding one another from Dease Strait, in the West of the CAA, to Lancaster Sound in the East, near Baffin Bay. This finding reinforces the hypothesis that the CAA is an ecotone, a transitional area, between the Beaufort Sea and Baffin Bay. Results also suggest that Pacific Ocean origin waters have significant influence on benthic communities in the CAA, further explaining the observed succession. A biogeographic analysis looking at gradients in Pacific affinity species could later support this finding. Unrelated to the transitional status, our results also suggest that river inputs have an important impact on benthic assemblages, particularly in Kitikmeot where many rivers are discharging in Queen-Maud Gulf. Many significantly influential parameters on benthic organism presence and community composition have already changed and will be subject to more important changes in the upcoming years (Polyakov et al., 2020). This is notably the case for the terrigenous imports, the Pacific Ocean water influence, the sea ice cover, sea temperature and the primary production (Stroeve and Notz, 2018; Woodgate, 2018; Brown et al., 2020; Lewis et al., 2020). Our study is also the first modelling of Kitikmeot and Parry Channel benthic communities. Moreover, such models could be useful for spatial planning applications or even for marine conservation purposes. However, further validations from external data sources are needed, especially in the Kitikmeot sea region. In the context of climate change, this region is a key area for the transition of Pacific Ocean water to the Baffin Bay areas, which will also experience an increase in human activities such as maritime transport.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because The few cephalopods caught on our bottom trawl were only identified and then released alive.

AUTHOR CONTRIBUTIONS

P-OD: Wrote most of this study. Performed every statistical analysis. Benthos taxonomy. CG: Provided benthic data and helped on statistical analysis. BB: Co-Principal Investigator. Supervised and commented during the whole process. LM: Benthos identification. LT: Benthos identification. J-ET: Provided Nitrate, Nitrite, Silicate and Phosphate data. PA: Principal investigator. Provided funding, laboratory space and feedback during the whole process. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.898852/full#supplementary-material

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