

Regional Variability of Megabenthic Community Structure across the Canadian Arctic

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ABSTRACT. Major climate changes are underway in the Canadian Arctic, but our ability to monitor and predict their impact on faunal community structure is hindered by the lack of baseline diversity data. This study combined megabenthic community data sampled at 78 stations from 2007 to 2011 across the Western and Eastern Canadian Arctic biogeographic units. These large biogeographic units were divided into five geographical regions to provide regional estimates of observed and predicted taxon richness. We did not detect a strong regional difference in benthic community characteristics, observing only a lower richness in the Amundsen Gulf region than in the neighboring Beaufort Sea region. The Amundsen Gulf region had the highest turnover (beta) diversity, coincident with high environmental heterogeneity. The strong and distinctive presence in the Beaufort Sea region of *Saduria* spp., a euryhaline isopod, demonstrated the particular influence of the Mackenzie River on the community composition of that region. Our analysis showed that in various regions, about 34% to 59% of megabenthic taxa in Canadian Arctic waters are still to be documented. This study provides useful baseline data for both national and pan-Arctic evaluations of benthic diversity in the Arctic Ocean.

Key words: Canadian Arctic; benthos; megafauna; richness; community; Beaufort Sea; Amundsen Gulf; Canadian Arctic Archipelago; Baffin Bay

RÉSUMÉ. Des changements climatiques majeurs sont en cours dans l'Arctique canadien, mais notre capacité à surveiller et à prévoir leurs impacts sur la structure des communautés est entravée par le manque de données de référence sur la diversité. Cette étude combine des données sur les communautés mégabenthiques échantillonnées à 78 stations de 2007 à 2011 à l'intérieur des unités biogéographiques de l'ouest et de l'est de l'Arctique canadien. Ces grandes unités biogéographiques ont été divisées en cinq régions géographiques afin de fournir des estimations régionales de richesse taxonomique observée et prédite. Nous n'avons pas détecté de fortes différences régionales dans les caractéristiques des communautés benthiques. Seule la richesse observée est inférieure dans le golfe d'Amundsen par rapport à la région voisine de la mer de Beaufort. La région du golfe d'Amundsen a la diversité bêta la plus élevée, ce qui coïncide avec une grande hétérogénéité de conditions environnementales. La composition taxonomique de la mer de Beaufort est différente de celle des autres régions. La présence distinctive et forte de *Saduria* spp., un isopode euryhalin, dans la région de la mer de Beaufort illustre l'influence du fleuve Mackenzie sur la composition taxonomique de cette région. Notre analyse démontre que régionalement, environ 34 % à 59 % des taxa mégabenthiques restent à être répertoriés dans les eaux arctiques canadiennes. Cette étude fournit des données de référence utiles pour les évaluations nationales et panarctiques de la diversité benthique de l'océan Arctique.

Mots clés : Arctique canadien; benthos; mégafaune; richesse; communautés; mer de Beaufort; golfe d'Amundsen; archipel canadien; baie de Baffin

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INTRODUCTION

In the Arctic, major changes (e.g., warming sea surface temperatures, coastal erosion) are already underway and are projected to continue as a result of global climate change (ACIA, 2004). Arctic sea ice retreat during the summer is fueling interest in the Canadian Arctic for shipping in the Northwest Passage and for oil exploration (Melling, 2002; Rogers et al., 2013). Possible impacts of climate change and anthropogenic activities on the Arctic benthic

marine environment may be acute, but these effects are difficult to assess and predict because extensive baseline data documenting present marine benthic ecosystem conditions are lacking (Wassmann et al., 2011). Research programs in the Canadian Arctic have increased in the last two decades; examples are the International North Water Polynya Study, the Canadian Arctic Shelf Exchange Study, the International Polar Year-Circumpolar Flaw Lead System Study (IPY-CFL), and the CCGS *Nahidik* and ArcticNet-CCGS *Amundsen* programs. Yet despite these programs, little is

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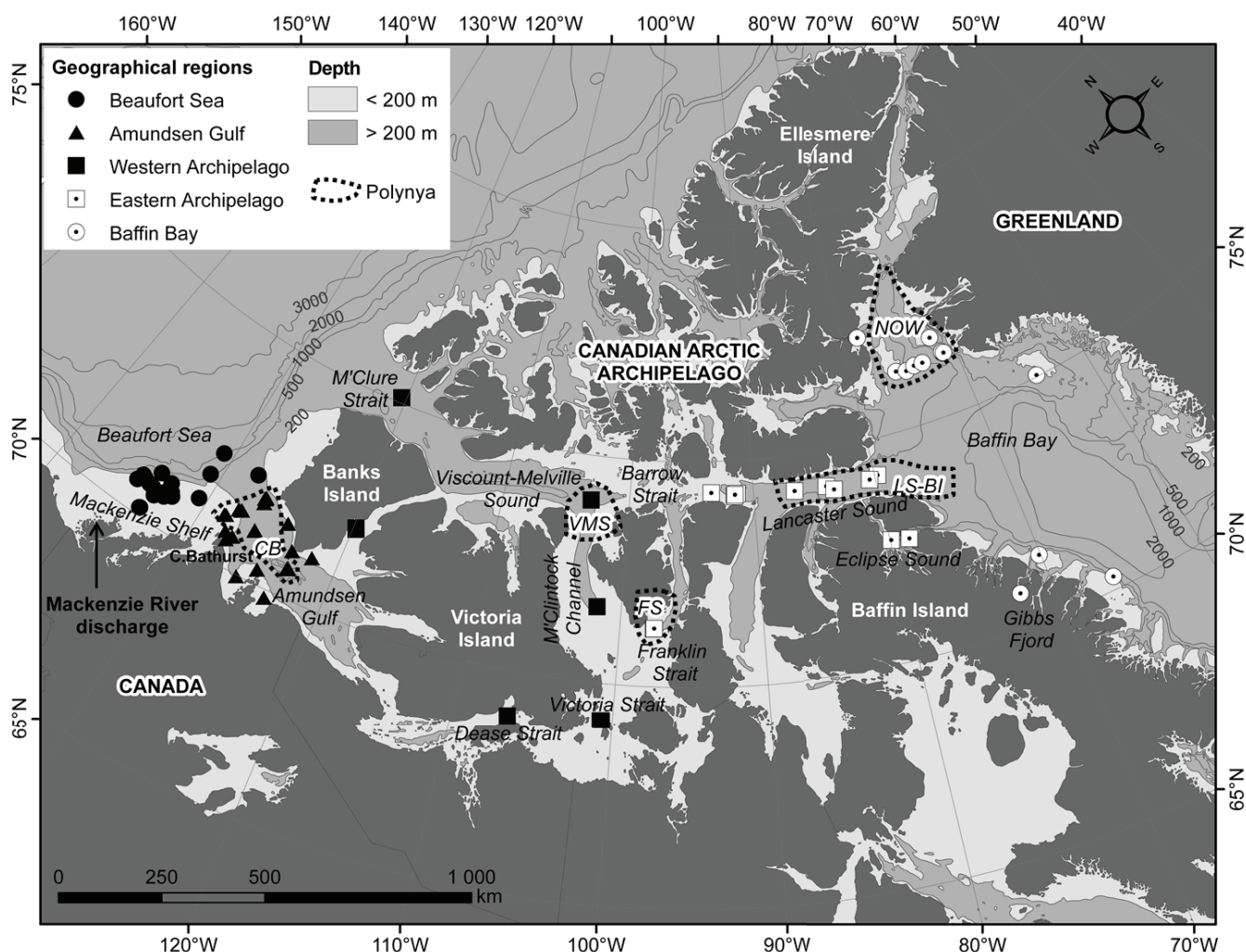


FIG. 1. Locations of the 78 stations sampled from 2007 to 2011 across the Canadian Arctic. Symbols represent five geographical regions within the Western Canadian Arctic biogeographic area (black symbols) and Eastern Canadian Arctic biogeographic area (white symbols) (DFO, 2009, 2011). Dotted-line polygons indicate the main polynyas (CB: Cape Bathurst polynya, FS: Franklin Strait polynya, LS-BI: Lancaster Sound-Bylot Island polynya, NOW: North Water polynya, VMS: Viscount-Melville Sound polynya). The black arrow indicates the Mackenzie River discharge area.

known today about megabenthic taxon richness across the large spatial extent of the Canadian Arctic.

The main objectives of this study were therefore to assess the number of megabenthic taxa observed and predict the total number of taxa expected to occur in five geographical regions located within the Western and Eastern Canadian Arctic biogeographic units (DFO, 2009, 2011): the Beaufort Sea, Amundsen Gulf, the Western Archipelago, the Eastern Archipelago, and Baffin Bay. These five geographical regions largely correspond to discrete annual segments (legs) of the CCGS *Amundsen* sampling program as well, so the results can inform national programs, such as the Fisheries and Oceans Canada (DFO) conservation assessments, and the planning of future field campaigns aimed at increasing megabenthic species records in the Canadian Arctic. This study also increases our knowledge of marine diversity on a pan-Arctic level and will serve as a benchmark against which changes in megabenthic diversity deriving from species range shifts or new invasions can be tracked (e.g., Węśławski et al., 2011).

MATERIALS AND METHODS

Study Area

This study was conducted across the Canadian Arctic from the Mackenzie Shelf in the southeastern Beaufort Sea in the west (135°W) to northern Baffin Bay in the east (65°W) (Fig. 1). The two main water masses flowing through the Canadian Arctic originate mainly from the Pacific and Atlantic Oceans. The colder, fresher, waters from the Pacific (average depth < 200 m) lie above the warmer, saline, Atlantic-origin waters (average depth > 200 m) (McLaughlin et al., 2004). The transition between these water masses across the study area generally coincides with the 200 m isobath along the shelf break (O'Brien et al., 2006; Spalding et al., 2007). The Beaufort Sea and Amundsen Gulf regions are highly influenced by the Mackenzie River, which drains a watershed of 1.7 million km² and discharges approximately 340 km³ of freshwater (McLaughlin et al., 2004) and 127 million tons of sediment

load (Macdonald et al., 1998) into the Beaufort Sea each year. The complex topography of the Canadian Arctic Archipelago, with its numerous islands and channels, has a profound influence on sea-ice circulation and marine biological productivity regimes (Michel et al., 2006). During winter, the study area is ice-covered, and sea ice can be found throughout the summer as landfast ice or first-year and multiyear pack ice (Howell et al., 2009; Environment Canada, 2010). Summer sea-ice distribution exhibits large interannual variation, as do ice breakup and freeze-up dates (Howell et al., 2009; Environment Canada, 2010). As a general trend, ice remains longer into the summer in the central part of the Archipelago than in areas where large and latent heat polynyas open in spring. These polynyas include the North Water (NOW), Lancaster Sound-Bylot Island (LS-BI), and the Cape Bathurst (CB) polynyas (Michel et al., 2006; Howell et al., 2008) (Fig. 1). Polynyas located in the northeastern Canadian Arctic (i.e., NOW and LS-BI) exhibit intense marine biological productivity and tight pelagic-benthic coupling, as revealed by field observations of diatom-based phytoplankton communities (Ardyna et al., 2011), satellite-derived high annual primary production estimates (Bélanger et al., 2013), high concentrations of chlorophyll *a* in sediment, and benthic boundary fluxes (Grant et al., 2002; Kenchington et al., 2011; Link et al., 2013). In the CB polynya, in contrast, highly variable intensity, timing, and duration of phytoplankton blooms (Arrigo and van Dijken, 2004) and strong grazing pressure by zooplankton lead to weak pelagic-benthic coupling (Conlan et al., 2008; Darnis et al., 2012; Link et al., 2013). The central Archipelago has been defined as an oligotrophic system (Ardyna et al., 2011).

Faunal Data Collection

Benthic megafauna were sampled at 78 stations from onboard the Canadian research icebreaker CCGS *Amundsen* from June to October in 2007 to 2011 (Fig. 1). Station depths ranged from 34 to 1024 m, mostly below the most intense ice-scouring zone of 8–35 m (Blasco et al., 1998; Carmack and MacDonald, 2002). One trawl deployment was conducted at each station. All faunal samples were collected with an Agassiz trawl (effective opening of 1.5 m and a 40 mm net mesh size, with a 5 mm cod end liner) with average trawl time of 5 min and speed of 1.5 knots. In order to compare community characteristics among stations (by m²), bottom trawling time and vessel speed at each station were used to calculate towed area (trawl opening of 1.5 m × distance towed; average trawled area of 372 ± 161 m²). This trawl design is very effective at collecting both epibenthic and larger burrowing invertebrates. Following the method of Piepenburg et al. (1996), invertebrates larger than 2 cm were sorted from the trawl catches directly after capture and classified as megabenthos. In addition, the sediment contained in the catches was washed through a 2 mm sieve under running seawater onboard (Piepenburg et al., 1996). Fish and planktonic invertebrates that were accidentally

collected by the trawl (e.g., Chaetognatha, Euphausiacea, Scyphozoa) were removed so that only benthic invertebrates were included in the sample analysis. Members of the class Ascidiacea were not considered in this study because this taxon was excluded during the first years of sampling. Only large echinoderm taxa that could be reliably identified to species level were counted and wet-weighted in the field because on-board mass measurements had low precision (detection limit of 5 g). All other taxa were preserved in a 4% formaldehyde-seawater solution buffered with sodium tetraethylborate or frozen for later identification in the lab, and their biomass was determined as formaldehyde wet mass or wet mass (after thawing) at 0.001 g precision. Possible biases in total biomass calculations introduced by different preservation methods were considered minor since all specimens within a phylum were processed the same way (Wetzel et al., 2005) and trawl catches were considered semi-quantitative estimates (Eleftheriou and McIntyre, 2005). Specimens were identified to the lowest possible taxonomic level. However, some taxa (e.g., Brachiopoda, Nemertea, Platyhelminthes, and Porifera) were identified only to phylum level because no thorough identification keys exist for Canadian Arctic waters; we acknowledge that this study has probably underestimated the richness of these taxa. Taxonomic names were verified using the World Register of Marine Species (WoRMS Editorial Board, 2014). Four species of the phylum Bryozoa (*Cellepora smitti*, *Escharopsis rosacea*, *E. sarsi*, and *Porella sacata*) and one from the phylum Hydrozoa (*Obelia loveni*) were not listed in WoRMS, but were verified using the Integrated Taxonomic Information System (ITIS, www.itis.gov).

Data Analysis

Megabenthic community characteristics (univariate) and community composition (multivariate) regionally were compared among the five geographical regions (from west to east: the Beaufort Sea, Amundsen Gulf, Western Archipelago, Eastern Archipelago, and Baffin Bay; Fig. 1). Because sampling efforts differed in the five geographical regions, the observed number of taxa was compared to the rarefied number of taxa expected to be documented in each geographical region if only nine stations (the smallest number observed, in the Western Archipelago) had been sampled (RS_9) and to non-parametric Chao 2 estimates of the predicted number of taxa (Magurran, 2004). Station-based rarefaction curves (999 permutations), which are the equivalent of “randomized” or “smoothed” species accumulation curves (Gotelli and Colwell, 2001), were used to calculate RS_9 . Following the terminology of Whittaker (1972) and Gray (2000), taxon richness in each of the five geographical regions is referred to as γ diversity, and taxon richness at a given station is α diversity. The turnover (β) diversity, which relates to the extent of change in species composition among samples along a gradient, was assessed using Whittaker’s classical β_w diversity index ($\beta_w = \gamma/\text{mean}(\alpha)$; Whittaker, 1972; Magurran, 2004). In addition, we used a

multivariate measure based on the mean Bray-Curtis dissimilarity (%) between all combinations of stations from a given geographical region (β_{BC} ; Magurran, 2004). For both β diversity indices, higher values represent higher β diversity. Bray-Curtis dissimilarity was calculated from the biomass matrix so that colonial taxa could be included. The fourth-root transformation was chosen to balance the effects of high-biomass and low-biomass taxa (Clarke and Warwick, 2001), and the same was done for multivariate analyses discussed below.

For each of the five geographical regions, this study considered regional means of six benthic community characteristics: biomass (g m^{-2}), density (individuals m^{-2}), taxon richness (number of taxa station $^{-1}$), taxon richness density (number of taxa 1000 m^{-2}), Shannon-Wiener diversity (H' , using $\log_e$), and Pielou evenness (J'). Taxon richness density was included as a community characteristic since all stations were sampled following the same protocol. H' and J' were calculated from biomass data that included colonial taxa. Density was calculated after removal of colonial taxa (i.e., Bryozoa, Hydrozoa, Nephtheidae (soft corals), and Porifera) because the abundance of those taxa cannot be recorded. Analysis of variance (ANOVA) and Tukey post-hoc multiple comparison tests were carried out to test differences in benthic univariate community characteristics among geographical regions. Normality was tested using the Shapiro-Wilk test, and homogeneity of variances was determined using Bartlett's test. Logarithmic transformation was applied to biomass, taxon richness, taxon richness density, and density to satisfy those two assumptions.

For multivariate analyses, taxa identified at the species level were scaled at the genus level, and taxa found at only one station were discarded, leaving a total of 303 taxa found at two or more stations. Scaling at the genus level was done since identifications were patchy at the species level among stations (Brind'Amour et al., 2014). We chose to remove species found at only one station to allow better detection of the underlying community similarities (Clarke and Warwick, 2001). Analyses of similarity (ANOSIM) on the biomass-based Bray-Curtis similarity matrix were used to seek differences in community composition among the geographical regions. Also, a Similarity Percentages Test (SIMPER) was used to identify the top three taxa contributing most to the dissimilarity between significantly different regions, as shown by ANOSIM. SIMPER analysis was also used to identify the top three characteristic taxa of the five geographical regions.

Rarefaction curves, Chao 2 estimates, multidimensional scaling (MDS), ANOSIM, and SIMPER analyses were performed using PRIMER-E software version 6 (Clarke and Gorley, 2006). All other tests were performed using the statistical package R version 3.0 (R Development Core Team, 2013). Statistical significance was defined at $\alpha < 0.05$ for all statistical tests except for post-hoc multiple comparison tests (ANOVA, ANOSIM), where a statistical significance of $\alpha < 0.01$ was used to account for the increasing probability of Type I error in multiple testing (Quinn and Keough, 2002).

RESULTS

Faunal Inventory

A total of 527 taxa were identified at the lowest possible taxonomic level (430 at the species level) across 13 phyla (Appendix 1 online: Table S1). Arthropoda had the highest number of taxa (161 taxa; mostly Crustacea), followed by Annelida (122; mostly Polychaeta), Mollusca (114; mostly Bivalvia and Gastropoda), Bryozoa (50), Echinodermata (43), Cnidaria, both Anthozoa and Hydrozoa (27), and other phyla with one to three taxa (Brachiopoda, Cephalorhyncha, Entoprocta, Nemertea, Platyhelminthes, Porifera, Sipuncula). Arthropoda and Annelida represented on average 25% and 18% respectively of all megabenthic taxa across the Canadian Arctic (Fig. 2), while Echinodermata represented on average 44% of the biomass (Fig. 3). Across the Canadian Arctic, the five most common taxa were the ophiuroids *Ophiocten sericeum* (found at 55% of stations), *Ophiacantha bidentata* (at 48%) and *Ophiopleura borealis* (at 33%); the soft corals Nephtheidae (at 48%); and the onuphid polychaete *Nothria conchylega* (at 39%).

Observed regional taxon richness (S_{obs}), or γ diversity, was higher in the Beaufort Sea and Amundsen Gulf regions, where sampling effort was highest, than in Western and Eastern Archipelago regions and in Baffin Bay (Table 1, Fig. 4). Rarefied number of taxa expected for each geographical region (RS_e) was highest in the Western Archipelago region and lowest in the Amundsen Gulf region (Figs. 4 and 5). Station-based rarefaction curves for each of the five geographical regions did not reach a plateau (Fig. 5). Chao 2 estimates were highest for the Amundsen Gulf region and the two Archipelago regions, followed by the Beaufort Sea and Baffin Bay regions (Table 1, Fig. 4). Between 41% and 50% of expected taxa were documented in the Amundsen Gulf and the two Archipelago regions, while almost 60% of expected taxa were documented in the Baffin Bay region and 70% in the Beaufort Sea region (Table 1). Turnover (β) diversity was relatively similar in all regions, but considerably higher in the Amundsen Gulf region, where both β_W and β_{BC} were the highest (Fig. 4).

Regional Comparisons

Relative taxonomic composition (%) did not vary greatly between the geographical regions (Fig. 2). However, relative faunal composition of biomass varied among the geographical regions (Fig. 3). The biomass proportions of Arthropoda, Bivalvia, and Gastropoda were greatest in the Western Canadian Arctic regions (Beaufort Sea, Amundsen Gulf, Western Archipelago) compared with in the Eastern Canadian Arctic regions (Eastern Archipelago, Baffin Bay) (Fig. 3). Cnidaria and Porifera were proportionally greatest, in terms of biomass, in the Eastern Canadian Arctic regions (Eastern Archipelago, Baffin Bay) (Fig. 3). Among the benthic community characteristics tested, only richness and richness density were significantly lower in the Amundsen

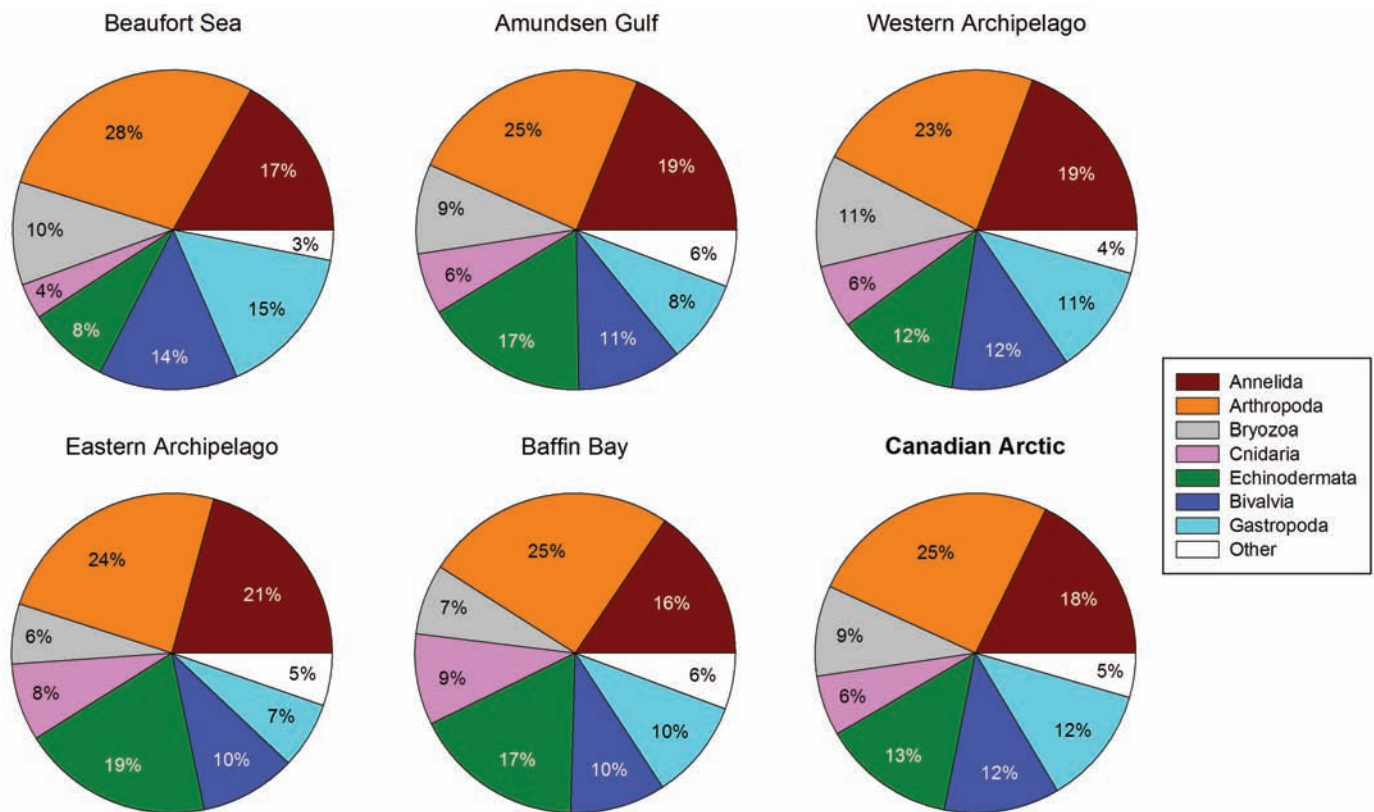


FIG. 2. Comparison of megafaunal taxonomic composition (mean percentages of the main phyla and classes sampled) in the five geographical regions and in the Canadian Arctic as a whole.

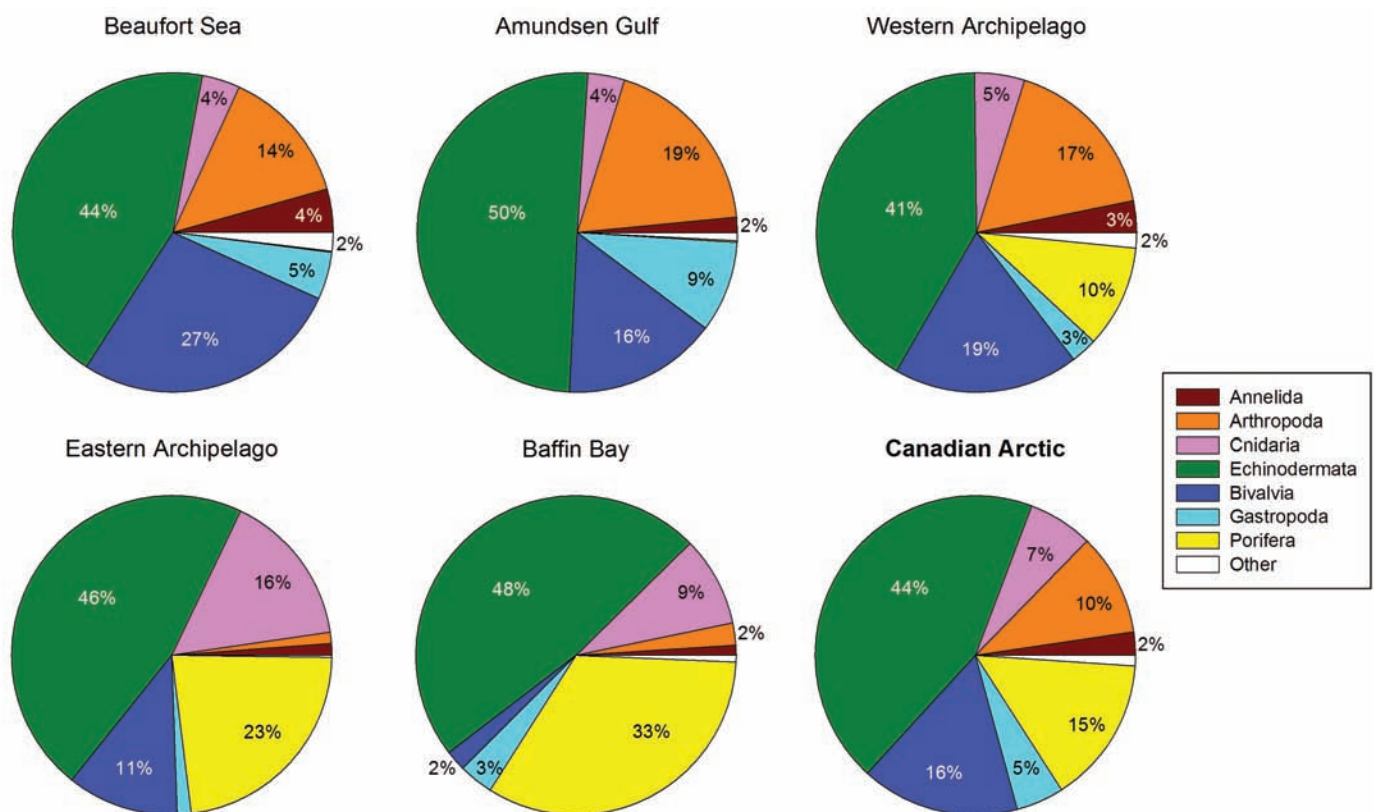


FIG. 3. Comparison of megafaunal biomass composition (mean percentages of the main phyla and classes sampled; only $\geq 2\%$ shown) in the five geographical regions and in the Canadian Arctic as a whole.

TABLE 1. Richness estimates and turnover (β) diversity for the five geographical regions. Number of taxa includes the rarefied number of taxa expected to be documented in each geographical region from nine stations (RS_9), based on the Western Archipelago (the least sampled region); the observed number of taxa (S_{obs} or regional (γ) diversity); and Chao 2 estimates of predicted number of taxa. Also shown are the predicted proportions of documented ($S_{obs}/\text{Chao 2}$) and undocumented taxa ($100\% - \% \text{ documented taxa}$). β diversity indices include Whittaker's index (β_W), based on the number of taxa, and mean Bray-Curtis dissimilarity (β_{BC}), based on distribution of biomass among the taxa. Mean ($\pm$ SD) RS_9 and Chao 2 estimates are based on 999 permutations.

Geographical region	No. of stations	Depth range (m)	Number of taxa			Predicted proportion of documented taxa (%)	Predicted proportion of undocumented taxa (%)	Turnover (β) diversity	
			RS_9 (mean $\pm$ SD)	S_{obs} or γ diversity	Chao 2 estimate (mean $\pm$ SD)			β_W	β_{BC}
Beaufort Sea	20	34–1024	234 $\pm$ 17	335	507 $\pm$ 39	66	34	5.9	79.1
Amundsen Gulf	23	35–619	164 $\pm$ 27	300	599 $\pm$ 63	50	50	10.9	86.4
Western Archipelago	9	55–424	255	255	556 $\pm$ 69	46	54	5.0	82.5
Eastern Archipelago	13	130–789	198 $\pm$ 13	250	617 $\pm$ 88	41	59	6.6	78.5
Baffin Bay	13	247–759	196 $\pm$ 18	243	416 $\pm$ 40	58	42	6.5	82.2

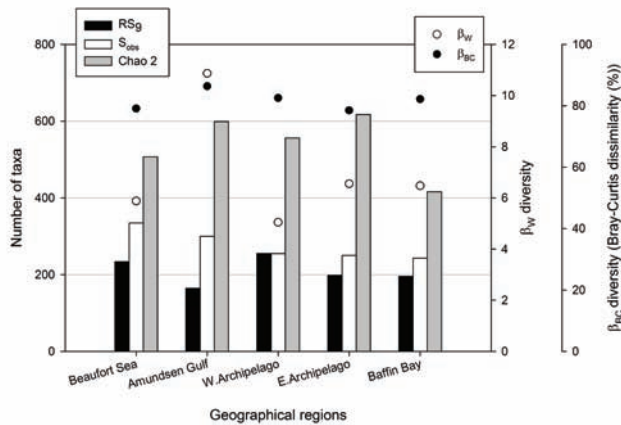


FIG. 4. Richness and turnover (β) diversity in the five geographical regions. Rarefied number of taxa expected to be documented in each geographical region based on nine stations (RS_9), observed number of taxa (S_{obs} or regional (γ) diversity), as well as Chao 2 estimates of predicted number of taxa, and β diversity using Whittaker's index (β_W ; white circles) and mean Bray-Curtis dissimilarity (β_{BC} ; black circles).

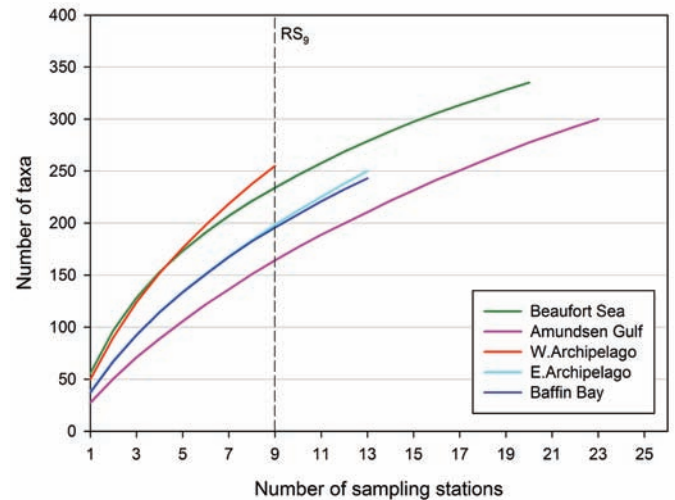


FIG. 5. Station-based rarefaction curves for the five geographical regions. RS_9 represents the rarefied number of taxa expected to be documented in each geographical region based on nine stations (999 permutations).

Gulf region than in the neighboring Beaufort Sea region (Table 2, Fig. 6).

Megabenthic community composition was not strongly different among geographical regions, with poor segregation of the geographical regions in the MDS (relatively high stress level, > 0.2), except for a greater separation of the Beaufort Sea (Fig. 7). ANOSIM analysis revealed that community composition of the Beaufort Sea region was significantly different from that of all other regions, and that community composition in the Western Archipelago was different from that in Baffin Bay (Table 2). However, ANOSIM R values overall were small ($R < 0.5$). SIMPER analysis of those regions that differ significantly in community composition as determined by ANOSIM analysis showed between-region dissimilarity to be high on average, varying from 82% to 87% (Table 3). Among the top three megabenthic taxa contributing most to this dissimilarity, the isopod *Saduria* spp. always appeared as a significant discriminant taxon between the Beaufort Sea region and the other four regions (Table 3). The cumulative

percentage of dissimilarity explained by the top three megabenthic taxa was on average low (7.5%), since up to 82 taxa were needed on average to reach a cumulative percentage of dissimilarity of 75% (list of these taxa not shown). SIMPER analysis showed within-region similarity to be low on average (23%), varying from 18% to 28% (Table 4). Some of the top three characteristic taxa of within-region similarity (e.g., the bivalve *Astarte* spp. and the ophiuroids *Ophiacantha* sp., *Ophiocten* sp., and *Ophiopleura* sp.) were found in more than one geographical region (Table 4). The bivalves *Macoma* spp. were a characteristic taxon of the Beaufort Sea region, while the soft corals Nephtheidae were a characteristic taxon of the Eastern Archipelago region (Table 4).

DISCUSSION

In this study, we compare megabenthic community characteristics and composition across five geographical regions

TABLE 2. Regional comparisons of benthic univariate community characteristics (ANOVA analysis) and of multivariate (biomass-based) community composition (ANOSIM analysis).

Community characteristic	Geographical regions (post-hoc significant differences are shown if $p < 0.01$)
Univariate	
ln(biomass)	ns ¹
ln(taxon richness)	Amundsen Gulf < Beaufort Sea ($p = 0.0004$)
ln(taxon richness density)	Amundsen Gulf < Beaufort Sea ($p = 0.0008$)
ln(density)	ns
H'	ns
J'	ns
Multivariate	
Community composition (4th-root transformed)	Global test ($R = 0.229$; $p = 0.001$) Beaufort Sea vs. Amundsen Gulf ($R = 0.252$; $p = 0.001$) Beaufort Sea vs. W. Archipelago ($R = 0.299$; $p = 0.007$) Beaufort Sea vs. E. Archipelago ($R = 0.445$; $p = 0.001$) Beaufort Sea vs. Baffin Bay ($R = 0.495$; $p = 0.001$) W. Archipelago vs. Baffin Bay ($R = 0.317$; $p = 0.001$)

¹ ns = non-significant.

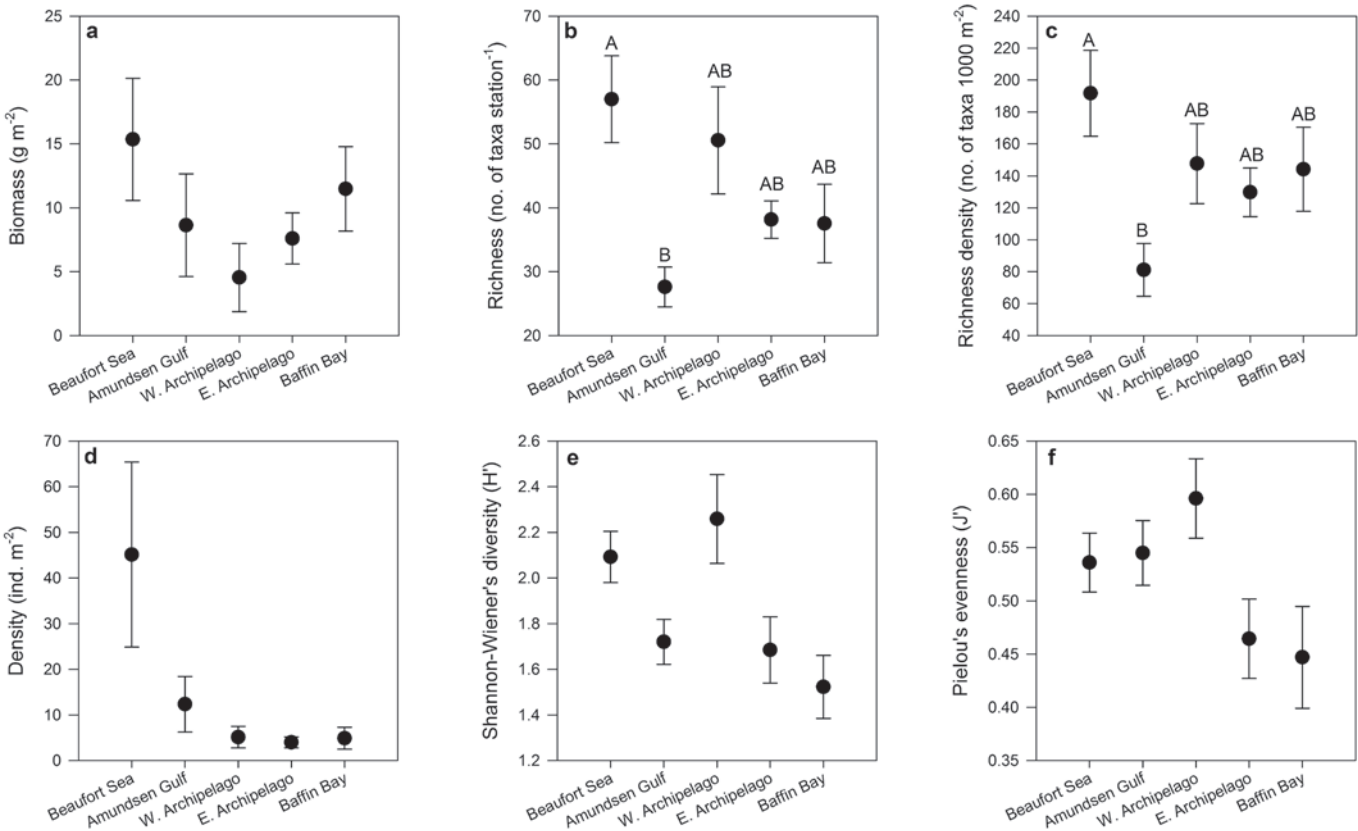


FIG. 6. Mean ($\pm$ SE) benthic community characteristics for the five geographical regions. (a) biomass (g m^{-2}); (b) taxon richness (no. of taxa station⁻¹); (c) taxon richness density (no. of taxa 1000 m⁻²); (d) density (individuals m⁻²); (e) Shannon-Wiener's diversity index (H'); (f) Pielou's evenness index (J'). Different letters (A, B) above points indicate significant differences ($p < 0.01$) based on post-hoc ANOVA tests (after data transformation; see Table 2).

of the Canadian Arctic. Our results show overall high similarity in megabenthic community characteristics among the study regions, with significant differences observed only between the Beaufort Sea and Amundsen Gulf regions. In terms of community composition, the Beaufort Sea region was slightly, but significantly, different from all other geographical regions. We discuss the weak influence of

geographical divisions on benthic patterns compared to the influence of environmental gradients.

High Richness across the Canadian Arctic

The overall high taxon richness observed for all geographical regions in this study advances our understanding

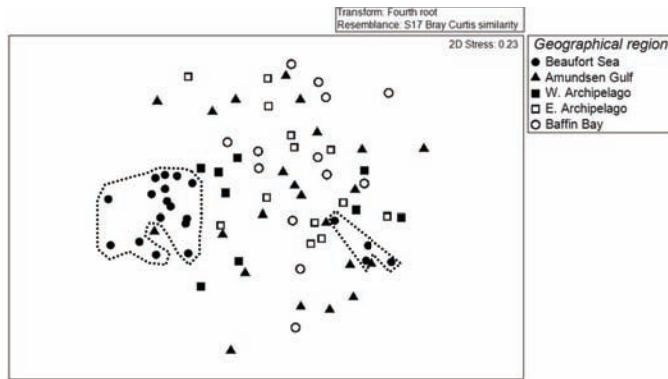


FIG. 7. Non-metric multidimensional scaling (MDS) ordination of megabenthic community composition of the five geographical regions (from Bray-Curtis similarity biomass-based matrix after fourth-root transformation). The greater separation of the Beaufort Sea region is highlighted by polygons enclosed in dotted lines.

of marine diversity in the Canadian Arctic, a severely undersampled region of the Arctic Ocean (Archambault et al., 2010; Piepenburg et al., 2011). None of the rarefaction curves reached a plateau, and in fact, only about 40% to 70% of predicted taxa per region were documented, indicating that about one-third to one-half of the expected species pool is still unrecorded. Predicted richness estimates for the study regions are in the range of estimates (using Chao 2 estimator) predicted for other Canadian Arctic regions, such as Northern Labrador (591 taxa) and the Hudson Bay Complex (483 taxa), and for other Arctic shelves close to

the Canadian Arctic, such as West and North Greenland (432–478 taxa) and the Chukchi Sea (443 taxa) (Piepenburg et al., 2011). Lower predicted richness estimates have been reported for the Siberian seas (161–311 taxa) and a higher one for the Barents Sea (712 taxa) (Piepenburg et al., 2011). The large rivers draining into the Siberian seas likely explain the lower richness of these Arctic shelves, but pronounced differences in sampling effort among regions may also generate these dissimilarities (Piepenburg et al., 2011). For instance, the Barents Sea is one of the most thoroughly studied Arctic regions, and this fact coincides with high species records.

Comparison of observed richness (as opposed to predicted richness estimates) among Arctic megabenthos studies is hampered by methodological constraints. First, the few Arctic studies that have employed trawls to sample megafauna (Piepenburg et al., 1996; Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014; this study) have used different types of trawls, and different trawl designs are known to differ in their sediment penetration and their ability to catch some large infaunal specimens (Eleftheriou and McIntyre, 2005). In addition, studies using trawls do not generally cover the same depth range and spatial extent, hindering direct comparisons of absolute species numbers. Lastly, most Arctic megabenthic research has used videos and images, thus producing generally less in-depth taxonomic determination (e.g., Piepenburg and Schmid, 1997; Bluhm et al., 2005; Soltwedel et al., 2009). Regardless of method, additional sampling in the Canadian Arctic, and

TABLE 3. Top three megabenthic taxa contributing most to dissimilarity between those regions that significantly differ in community composition based on biomass, as determined by ANOSIM analysis in Table 2. Contrib.: % contribution, Cum.: % cumulative.

Regional comparisons/Taxa	Average biomass (g m ⁻²)		Average dissimilarity (%)	SD of dissimilarity (%)	Contrib. (%)	Cum. (%)
Beaufort Sea vs. Amundsen Gulf; average dissimilarity = 85%	Beaufort Sea	Amundsen Gulf				
<i>Saduria</i> spp.	1.57	0.06	2.42	1.40	2.86	2.86
<i>Astarte</i> spp.	1.96	0.20	1.93	1.19	2.28	5.14
<i>Icasterias</i> sp.	2.10	0.05	1.90	1.04	2.25	7.39
Beaufort Sea vs. W. Archipelago; average dissimilarity = 82%	Beaufort Sea	W. Archipelago				
<i>Saduria</i> spp.	1.57	0.07	2.12	1.28	2.59	2.59
<i>Ophiocten</i> sp.	1.30	0.38	1.69	1.43	2.06	4.64
<i>Astarte</i> spp.	1.96	0.13	1.57	1.13	1.91	6.56
Beaufort Sea vs. E. Archipelago; average dissimilarity = 85%	Beaufort Sea	E. Archipelago				
<i>Saduria</i> spp.	1.57	0.00	2.27	1.53	2.67	2.67
<i>Gorgonocephalus</i> sp.	1.55	2.66	2.18	0.77	2.55	5.22
<i>Astarte</i> spp.	1.96	0.48	1.89	1.22	2.22	7.44
Beaufort Sea vs. Baffin Bay; average dissimilarity = 87%	Beaufort Sea	Baffin Bay				
<i>Ophiura</i> sp.	0.31	0.62	2.35	1.37	2.70	2.70
<i>Saduria</i> spp.	1.57	0.00	2.29	1.42	2.62	5.32
<i>Ophiopleura</i> sp.	0.09	1.64	2.25	0.87	2.59	7.91
W. Archipelago vs. Baffin Bay; average dissimilarity = 83%	W. Archipelago	Baffin Bay				
<i>Ophiura</i> sp.	< 0.01	0.62	2.66	1.38	3.18	3.18
<i>Ophiopleura</i> sp.	0.06	1.64	2.54	0.94	3.05	6.23
<i>Ophiacantha</i> sp.	0.28	0.13	1.67	1.28	2.00	8.23

TABLE 4. Top three megabenthic characteristic taxa contributing most to similarity within each of the five geographical regions. Contrib.: % contribution, Cum.: % cumulative.

Region/Taxa	Average biomass (g m ⁻²)	Average similarity (%)	SD of similarity(%)	Contrib. (%)	Cum. (%)
Beaufort Sea; average similarity = 28%					
<i>Saduria</i> spp.	1.57	2.22	1.13	7.99	7.99
<i>Ophiecten</i> sp.	1.30	1.21	0.89	4.34	12.33
<i>Macoma</i> spp.	0.30	1.19	0.91	4.27	16.61
Amundsen Gulf; average similarity = 18%					
<i>Ophiecten</i> sp.	0.16	2.05	0.98	11.30	11.30
<i>Astarte</i> spp.	0.20	1.90	0.76	10.46	21.76
<i>Ophiacantha</i> sp.	0.13	1.81	0.80	9.96	31.72
W. Archipelago; average similarity = 22%					
<i>Ophiacantha</i> sp.	0.28	2.86	1.35	13.24	13.24
<i>Ophiecten</i> sp.	0.38	2.02	1.00	9.36	22.60
<i>Astarte</i> spp.	0.13	1.28	0.70	5.89	28.49
E. Archipelago; average similarity = 26%					
Nephtheidae	0.44	2.30	1.32	8.93	8.93
<i>Ophiopleura</i> sp.	0.21	1.99	0.87	7.72	16.65
<i>Astarte</i> spp.	0.48	1.73	0.67	6.73	23.38
Baffin Bay; average similarity = 22%					
<i>Ophiura</i> sp.	0.62	3.35	1.23	14.90	14.90
<i>Ophiopleura</i> sp.	1.64	1.76	0.52	7.81	22.71
<i>Astarte</i> spp.	0.21	1.58	0.75	7.02	29.73

the Arctic in general, will certainly improve assessments of pan-Arctic megabenthic richness. There is growing evidence that nearly all Arctic shelf regions host rich and diverse benthic communities (Piepenburg et al., 2011).

Three of the five most widely distributed taxa in the present study area, the ophiuroids *Ophiecten sericeum* and *Ophiacantha bidentata* and the onuphid polychaete *Nothria conchylega*, are common throughout the Arctic shelves (Piepenburg et al., 2011). Ophiuroids are generally present in high numbers throughout the Arctic, presumably because predation pressure on these taxa is low (Piepenburg, 2000). The high respiration rates of ophiuroids make them important ecological players in carbon remineralization on Arctic shelves, although their importance is often neglected in carbon cycling models (Ambrose et al., 2001). The broad diet spectrum of ophiuroids (they are commonly omnivorous surface deposit feeders; Piepenburg, 2000) and of onuphids (predator/scavengers; Fauchald and Jumars, 1979) may also contribute to their widespread occurrence.

Regional Comparisons

The highest β diversity was observed in the Amundsen Gulf, reflecting a high degree of difference in community composition among the stations sampled in this region. This difference is likely attributable to the environmental heterogeneity found in this region. The Amundsen Gulf region is composed of coastlines subjected to intense

erosion, narrow shelves, and steep continental slopes, along with deep-water habitats (> 200 m) exhibiting low particulate organic carbon fluxes (O'Brien et al., 2006; Forest et al., 2010). The Amundsen Gulf region also is influenced to the west by the sediment load discharge from the Mackenzie River and a strong upwelling current near Cape Bathurst (O'Brien et al., 2006; Williams and Carmack, 2008). However, despite its environmental heterogeneity, this region had significantly lower mean taxon richness than the Beaufort Sea region. The higher number of stations sampled at great water depths (> 200 m) in the central Amundsen Gulf region than in the Beaufort Sea region may be an important factor explaining this difference in richness, because species richness usually decreases with depth (Levin et al., 2001). Except in taxon richness, the geographical regions did not differ significantly in their mean benthic community characteristics, revealing a high similarity in community structure among regions. Contrary to our results, Cusson et al. (2007) reported on the basis of historical macrobenthic data from the 1950s to 1970s that the Beaufort Sea region had moderate species richness and low H' diversity compared to eastern regions of the Canadian Arctic. Our study did not include nearshore stations, which are often under severe seasonal disturbances such as variable salinity and ice scouring, which were suggested to drive some of the observed difference in macrofaunal diversity patterns (Cusson et al., 2007). The distinctiveness of the Beaufort Sea region was rather revealed in our study on megafauna by

community composition of this region, which was slightly different from that of all the other regions. For instance, the isopod *Saduria* spp. is euryhaline (Percy, 1983; Hagerman and Szaniawska, 1988), and its high average biomass in the Beaufort Sea region compared with the other regions presumably reflected the strong influence of the Mackenzie River on the Beaufort Sea community composition.

The overall high similarity among geographical regions, in terms of both community characteristics and community composition, reflects the weak effect of regional divisions on megabenthic diversity patterns. Across the study area, Roy et al. (2014) defined six megabenthic community clusters, according to their biomass-based community composition. Community patterns were spatially organized according to large-scale environmental gradients (e.g., depth and water masses) and meso-scale gradients (e.g., substrate type, food supply proxies). Except for one community cluster spatially restricted to the Mackenzie Shelf in the Beaufort Sea region, all the other community clusters were found in more than one of the regions considered in the present study. The widespread occurrence of many of the megabenthic community clusters defined by Roy et al. (2014) across the Canadian Arctic is likely explained by the fact that each of the geographical regions covered similar depth gradients and contained distinct water masses (Pacific vs. Atlantic) and substrate (hard vs. soft) gradients, which are more important in driving benthic spatial patterns than are geographical divisions. Benthic geographical differences are well defined only in regions that have specific environmental conditions, such as the western Canadian Arctic regions (Beaufort Sea and Amundsen Gulf regions), where the Mackenzie River has a profound influence on the oceanographic setting. The high terrestrial carbon and freshwater influxes from the Mackenzie River (Carmack and MacDonald, 2002; Macdonald et al., 2004) exert a particular abiotic pressure on the benthos in these western regions, especially on the shelf (Conlan et al., 2008, 2013). Our results suggest that any assessment-based or management-based approaches that consider megabenthic spatial variability across the Canadian Arctic regions should focus primarily on the influence of environmental gradients on benthic patterns and less on the weak influence of geographical divisions.

CONCLUSION

Marine ecosystems of the Arctic will experience numerous changes with the expected loss of summer sea ice in the near future (Post et al., 2013). Extensive baseline data documenting present ecosystem condition (e.g., biodiversity) are crucial to monitor and predict impacts of climate changes on these ecosystems. This study and subsequent efforts across the Canadian Arctic contribute to pan-Arctic initiatives, such as the Circumpolar Biodiversity Monitoring Program (CBMP; Gill et al., 2011), that harmonize and integrate efforts toward global monitoring of Arctic marine

biota and the effects of climate change. Recent research initiatives have considerably increased our understanding of Arctic marine biodiversity (e.g., Bluhm et al., 2011), but few Arctic studies have investigated megabenthic diversity across continental scales. The present study represents a significant advancement in our knowledge of marine diversity in the Canadian Arctic and provides a baseline against which future changes can be tracked. However, while we have demonstrated that observed megabenthic richness was relatively high in all regions, future sampling is needed to increase actual species records across the Canadian Arctic and to support our conclusions. Additional sampling is especially important in the Western and Eastern Archipelago regions, where we estimated that 54% and 59% of taxa, respectively, have yet to be documented. In addition, future studies should include more extensive sampling of shallow and nearshore areas of the Canadian Arctic, where several biological communities in different habitats may have been largely or completely missed by the present study. Finally, the overall weak influence of geographic divisions on megabenthic community patterns in this study strongly suggests that interpretation of benthic spatial patterns across the Canadian Arctic should focus on environmental factors.

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APPENDIX 1.

The following table is available as a supplementary file to the online version of this article at: <http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic/issue/view/282>

TABLE S1. Faunal inventory of all megabenthic taxa identified at the lowest possible taxonomic level across five geographical regions of the Canadian Arctic.

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