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Comparing eDNA metabarcoding and species collection for documenting Arctic metazoan biodiversity

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Abstract

Background: Arctic biodiversity has long been poorly documented and is now facing rapid transformations due to ongoing climate change and other impacts, including shipping activities. These changes are placing marine coastal invertebrate communities at greater risk, especially in sensitive areas such as commercial ports. Preserving biodiversity is a significant challenge, going far beyond the protection of charismatic species and involving suitable knowledge of the spatiotemporal organization of species. Therefore, knowledge of alpha, beta, and gamma biodiversity is of great importance to achieve this objective, particularly when partnered with new cost-effective approaches to monitor biodiversity.

Method and results: This study compares metabarcoding of COI mitochondrial and 18S rRNA genes from environmental DNA (eDNA) water samples with standard invertebrate species collection methods to document community patterns at multiple spatial scales. Water samples (250 ml) were collected at three different depths within three Canadian Arctic ports: Churchill, MB; Iqaluit, NU; and Deception Bay, QC. From these samples, 202 genera distributed across more than 15 phyla were detected using eDNA metabarcoding, of which only 9%–15% were also identified through species collection at the same sites. Significant differences in taxonomic richness and community composition were observed between eDNA and species collections at both local and regional scales. This study shows that eDNA dispersion in the Arctic Ocean reduces beta diversity in comparison with species collections while emphasizing the importance of pelagic life stages for eDNA detection.

Conclusion: The study also highlights the potential of eDNA metabarcoding to assess large-scale Arctic marine invertebrate diversity while emphasizing that eDNA and species collection should be considered as complementary tools to provide a more holistic picture of coastal marine invertebrate communities.

KEYWORDS
Arctic, beta diversity, biodiversity, eDNA, marine invertebrates, metabarcoding

1 | INTRODUCTION

The Arctic Ocean has been poorly surveyed and thus likely harbors a great undetected biodiversity (Archambault et al., 2010; Darnis et al., 2012). Recent estimates suggest that there are more than 4,000 species of invertebrates that inhabit the Arctic Ocean (Gradinger et al., 2010; Jørgensen, Archambault, Piepenburg, & Rice, 2016; Piepenburg et al., 2011) with greater than 90% being benthic organisms (CAFF International Secretariat, 2013). The general pattern of biodiversity decline with increasing latitude may not apply to marine invertebrates (Kendall, 1996), suggesting that a great diversity and many species await discovery (Archambault et al., 2010; Piepenburg et al., 2011). Archambault et al. (2010) showed that benthic infaunal diversity in the Canadian Arctic was almost similar than in Canadian Atlantic waters, even with three times less sampling effort. Previously, considered as the second most pristine oceans on earth (UNESCO, 2010), this ecosystem has experienced extensive environmental change since the 1950s (IPCC, 2018). In addition to warmer temperatures, increased acidification, and greater freshwater inputs (Arctic Climate Impact Assessment [ACIA], 2004), other activities such as marine shipping (ACIA, 2004; Chan et al.,) and the associated risk of introducing nonindigenous species (NIS) are increasing (Casas-Monroy et al., 2014; Chan, Bailey, Wiley, & MacIsaac, 2013; Goldsmit et al., 2018; Goldsmit, McKindsey, Archambault, & Howland, 2019). The number of invasive species has more than tripled since the beginning of the century in North America and in northern environments (Millennium Ecosystem Assessment, 2005; UNEP, 2006). Comprehensive baseline surveys and ongoing monitoring are thus essential in the Arctic, especially due to the large number of cryptic and cryptogenic species (Carlton, 1996; Goldsmit, Archambault, & Howland, 2014; Knowlton, 1993). However, gaining a better understanding of Arctic invertebrate community structure and how it may vary over time is challenging due to the heterogeneous distribution of species, uncertain taxonomy, and limitations due to sampling under ice cover (Jarosław, Mioduchowska, & Petković, 2016; Ministry of Environment, 2006).

The design of a robust monitoring approach to evaluate biodiversity changes, including species losses and processes that maintain species diversity over longer time frames, must take into account the spatial and temporal organization of biodiversity. Biodiversity can be measured using different taxonomy-based metrics and at various scales by evaluating alpha, beta, and gamma diversity. Alpha diversity represents the species assemblage of a relatively small area, termed "within-habitat diversity" (sensu MacArthur, 1965), and is the most commonly studied biodiversity scale. Beta diversity, often referred to as "turnover diversity," is the variation in species composition (i.e., species abundances and identities) among local species assemblages. It is the net outcome of regional biotic and abiotic processes, such as disturbance, the study of which may provide a mechanistic understanding of the processes that produce observed patterns and provide conservation-relevant insights on the maintenance of diversity over large spatial scales (McGill, Dornelas, Gotelli, & Magurran, 2015; Mori, Isbell, & Seidl, 2018; Socolar, Gilroy, Kunin, & Edwards, 2015). Lastly, gamma diversity refers to the species assemblage of large areas, for example, regional diversity (Socolar et al., 2015), and is expressed in the same units as alpha diversity (Laurila-Pant, Lehikoinen, Uusitalo, & Venesjärvi, 2015). Large-scale biodiversity monitoring is essential for understanding more extensive changes in coastal community composition, but this is logistically challenging and costly in remote areas such as the Arctic. Coastal metazoan collection methods are generally intrusive (e.g., trawling, grab sampling), selective, and frequently limited to the summer open water period and rely on some degree of subjectivity with respect to taxonomic expertise (Jones, 1992; Jørgensen et al., 2016).

Ten years after the pioneering study of Ficetola, Miaud, Pompanon, and Taberlet (2008), the environmental DNA (eDNA) approach offers major advantages over conventional monitoring methods and is perceived as a game-changer for ecological research (Creer et al., 2016). This approach involves the collection and detection of DNA that has been released by organisms into the surrounding environment through metabolic waste products, gametes, or decomposition (Hansen, Bekkevold, Clausen, & Nielsen, 2018; Taberlet, Bonin, Zinger, & Coissac, 2018). Analysis of eDNA with metabarcoding is a rapid method of biodiversity assessment that links taxonomy with high-throughput DNA sequencing (Ji et al., 2013) to provide a snapshot of local species composition without the need for sampling individual organisms. Recent studies in coastal marine ecosystems have demonstrated the feasibility of eDNA metabarcoding to document marine metazoan biodiversity in the Arctic (Grey et al., 2018; Lacoursière-Roussel et al., 2018). Despite limited knowledge of eDNA ecology (i.e., origin, fate, state, and transport; Barnes & Turner, 2016; Lacoursière-Roussel & Deiner, in press), eDNA is increasingly being incorporated within monitoring toolboxes for a large variety of aquatic organisms and ecosystems (Deiner et al., 2017; Roussel, Paillisson, Tréguier, & Petit, 2015).

However, like any sampling approach, eDNA metabarcoding also has its weaknesses which must be considered to avoid misinterpretation of results. Although the tool allows rapid assessment of biodiversity, database gaps hamper the use of eDNA as sequence assignments are highly dependent on their availability in public databases (Elbrecht, Vamos, Meissner, Aroviita, & Leese, 2017; Kwong, Srivathsan, & Meier, 2012). Organism detection is also restricted by the primers used and their respective biases (Elbrecht & Leese, 2015). Furthermore, unlike direct species collection, eDNA does not provide any physiological or health information for the detected organisms (Thomsen & Willerslev, 2015).

In the aquatic realm, while many studies have compared species composition measured by eDNA with conventional methods for fish (Thomsen et al., 2012; Yamamoto et al., 2017), few such comparative studies have been performed on invertebrates, and even less have considered the spatial scales of observation. Among marine invertebrate species, meroplankton (organisms having planktonic larval life stages) and holoplankton (organisms spending their entire life as plankton) represent key components of the food web and ecosystem stability (Gajbhiye, 2002; Marcus & Boero, 1998). A better

understanding of how complex planktonic life stages of invertebrates affect the origin and transport of eDNA in coastal environments is essential to develop genomics-based biodiversity indices to inform conservation plans.

The main objective of this study is to compare patterns of biodiversity at different spatial scales revealed by eDNA metabarcoding and conventional species collection within and among three ports in the Canadian Arctic Ocean. More specifically, gamma biodiversity (species richness between ports) was compared based on results from eDNA and conventional collecting methods, namely benthic trawl, Van Veen grab, cores, and plankton net tows. Secondly, alpha (species richness within ports) and beta (similarity of species between sites within ports) biodiversity indices were contrasted for results based on eDNA and species collections, to better understand how eDNA may inform species distributions and ecological processes such as dispersion and biotic heterogenization or homogenization. Finally, the life histories of organisms were considered to interpret how this basic biological parameter may affect eDNA detections from coastal invertebrates and contribute to discrepancies between eDNA detection and conventional species collections.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Individual specimens from traditional sampling methods and eDNA were collected at 13 subtidal stations (≤20 m at low tide) in three commercial harbors of the Canadian Arctic in summer (Figure 1). Churchill was surveyed 11–14 August 2015, Iqaluit between 17–22 August 2015 and 24–26 July 2016, and Deception Bay between 19 and 27 August 2016. These three Arctic ports were selected because of their risk to potential changes in their local marine invertebrate communities due to climate change and the relatively high levels of shipping activity in each, which places them at greater risk for introduction of nonindigenous species (Chan et al., 2013; Chan et al., ; Goldsmit et al., 2019).

2.1.1 | Species collection

Throughout the paper, we use *specimens collected* and *species collection* to refer to the following collecting methods: benthic trawls, Van Veen grabs, sediment cores, and plankton tows. We use the term benthic communities to refer to organisms collected through benthic trawls, Van Veen grabs, and sediment cores, while we use the term zooplankton to refer to organisms collected using net tows. Benthic invertebrates living on the sea floor substrate (epifauna) were collected using a benthic trawl with a 500-µm-mesh net, while benthic invertebrates living in soft sea bottoms (infauna) were collected using a Van Veen grab (0.1 m^2 sample area; Deception Bay and Iqaluit) with the contents sieved on a 500-µm mesh. Zooplankton was collected using 0.5-m-diameter net tows: one vertical 80 µm and one oblique 250 µm. Zooplankton samples were taken at 10 of the 13 stations where eDNA was sampled, whereas benthic trawl and Van Veen grab samples were taken at all 13 stations. Trawling and oblique net tows were carried out for 3 min at a speed of 1–2 knots. Due to logistical constraints, Iqaluit Van Veen and trawl samples were collected in 2015 and 2016, respectively. Infauna samples in Churchill were collected by divers using corers (15 cm high × 10 cm diameter) from the same areas used by Goldsmit (2016). Since the sediment volume accumulated by these subtidal sediment cores was less than that of the Van Veen grab, the replicates of a given site for the sediment cores were combined together such that the final volume included for analyses was similar to the volume of site-specific Van Veen grab samples from the other ports. With the exception of common easily identifiable macroinvertebrates, which were enumerated, recorded, and released, all specimens were preserved in 95% ethanol and later identified by trained taxonomists to the lowest taxonomic level possible.

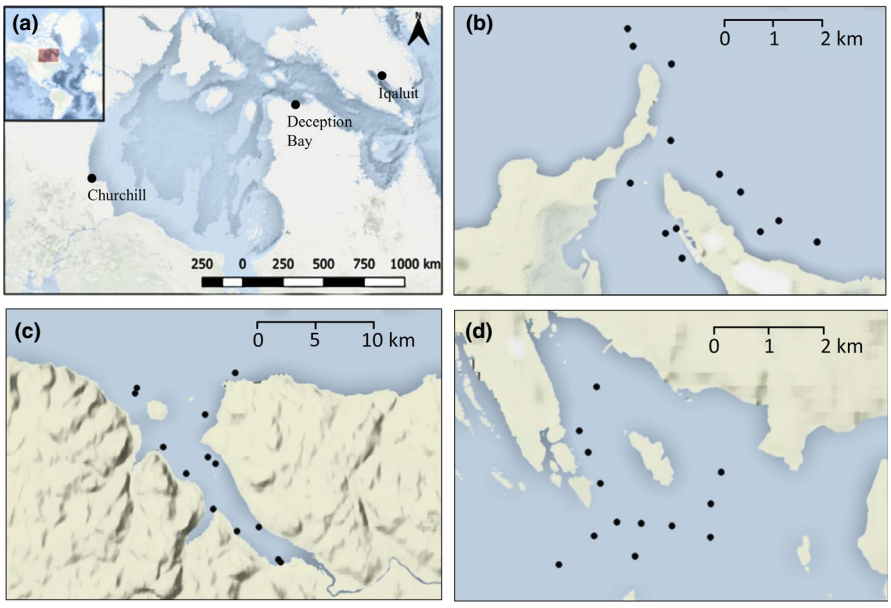

FIGURE 1 Geographic location of Churchill, Deception Bay, and Iqaluit harbors in the Canadian Arctic (a) and distribution of stations within Churchill (b), Deception Bay (c), and Iqaluit (d)

2.1.2 | Environmental DNA samples

A total of 117 water samples were collected and filtered following the methods outlined in Lacoursière-Roussel et al. (2018). A 250-ml water sample was taken at each of the three depths (surface, mid-depth, and deep water [i.e., 50 cm from the bottom]) for each station and port using 5-L Niskin bottles. The surface water was collected within the first meter, whereas mid-depth samples were collected at an average depth of 7.2 m (*SD* = 1.9), 6.8 m (*SD* = 2.8), and 9.8 m (*SD* = 3.5) for Churchill, Deception Bay, and Iqaluit, respectively, while deep-water samples were collected at an average depth of 12.7 m (*SD* = 2.7) and 15.5 m (*SD* = 4.6) for the same port, respectively. Each sample was filtered in the field using a 0.7-µm glass microfiber filter (Whatman GF/F, 25 mm) and syringes (BD 60 ml, Franklin Lakes, NJ, USA). Negative field controls were made by filtering 250 ml of autoclaved distilled water for every 10 collected samples. All filters were preserved in 2-ml microtubes containing 700 µl of Longmire's lysis/preservation buffer, kept at 4°C until the end of a sampling campaign, and then frozen at −20°C until extraction (at most 4 months). Risks of cross-contamination during the field sampling process were reduced by using a separate sterile kit for each sample. Sampling kits included bottles and a filter housing sterilized with a 10% bleach solution and new sterilized gloves, syringes, and tweezers sealed in a transparent plastic bag. Each sampling kit was exposed to UV light for 30 min following assembly.

2.2 | Metabarcoding

2.2.1 | Environmental DNA extraction, amplification, and sequencing

To avoid risk of laboratory cross-contamination, eDNA extraction, PCR preparation, and post-PCR steps were done in three separate rooms. All PCR manipulations were done in a decontaminated UV hood. All laboratory bench surfaces were cleaned with DNA AWAY®, and all laboratory tools were sterilized with a 10% bleach solution and exposed to UV light for 30 min before any manipulations were carried out. DNA was extracted from filters following a QIA shredder and phenol/chloroform protocol (Lacoursière-Roussel et al., 2018). Negative control extractions (950 µl distilled water) were done for each sample batch (i.e., one for every 23 samples) and were treated as normal samples for the remaining manipulations until sequencing. No positive controls were done in the context of this study since the efficiency of the selected primers used was previously tested on 104 zooplankton species and was validated on mock metazoan communities collected in Canadian ports by Zhang (2017). Furthermore, the primer sequences were also previously evaluated in silico with sequence databases for their ability to detect native and potential non-indigenous Arctic metazoans by Lacoursière-Roussel et al. (2018).

To maximize biodiversity detection and reduce the bias of eDNA dominance among species groups, two pairs of primers from two different genes (COI and 18S) were used. These have been shown to work well for detecting a wide variety of taxa including invertebrates and have reasonably comprehensive databases of reference sequences. Following Lacoursière-Roussel et al. (2018), we used the forward mlCOIintF (Leray et al., 2013) and reverse jgHCO2198 (Geller, Meyer, Parker, & Hawk, 2013) (hereafter called COI1) and the forward LCO1490 (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994) and reverse ill_C_R (Shokralla et al., 2015) (hereafter called COI2). Two additional universal 18S primer pairs were also used, the forward F-574 and reverse R-952 (Hadziavdic et al., 2014) (hereafter called 18S1) and the forward TAReuk454FWD1 and reverse TAReukREV3 (Stoeck et al., 2010) (hereafter called 18S2). Three PCR replicates were done for each sample of each primer set and were then pooled following amplification and purification (see Data S1 for more details). Sequencing was carried out using an Illumina MiSeq (Illumina) with a paired-end MiSeq Reagent Kit V3 (Illumina) at the Plateforme d'Analyses Génomiques (IBIS, Université Laval, Québec, Canada). Each port was analyzed on a separate run to ensure independence, but the samples within a port were pooled within a single Illumina MiSeq run to ensure the equality of sequencing depth among samples. Raw sequence reads were deposited in NCBI's Sequence Read Archive (SRA, http://www.ncbi.nlm.nih.gov/sra) under Bioprojects PRJNA388333 and PRJNA521343.

2.2.2 | Bioinformatics

Adaptor and primer sequences were removed and raw sequencing reads demultiplexed into individual samples files using the MiSeq Control software v2.3. Raw reads were analyzed using Barque version 1.5.1, an eDNA metabarcoding pipeline (www.github.com/enormandeau/barque). Forward and reverse sequences were trimmed and filtered using Trimmomatic v 0.30 with the following parameters: TrimmomaticPE, -phred33, LEADING: 20, TRAILING: 20, SLIDINGWINDOW: 20:20, and MINLEN: 200 (Bolger, Lohse, & Usadel, 2014). Pairs of reads were merged with FLASh v1.2.11 (Fast Length Adjustment of Short reads) with the following options: -t 1 -z -m 30 -M 280 (Magoč & Salzberg, 2011). The amplicons were split using their primer pairs (COI1, COI2, 18S1 and 18S2), and sequences that were either too short or too long were removed. Chimeric sequences were removed using VSEARCH v 2.5.1 (uchime_denovo command with default parameters) (Rognes, Flouri, Nichols, Quince, & Mahé, 2016). COI sequences were blasted on the BOLD database and 18S sequences against the SILVA database. Sequences from most terrestrial species (insects, human, birds, and mammals) and sequences that had no taxonomic match were also removed from the reference databases. Finally, following these steps, chordates others than tunicates (Table S1) were removed from the results since they were not targeted in this study and would therefore blur the analyses and subsequent interpretations regarding invertebrate communities. The Barque pipeline (https://github.com/enormandeau/barque) was then used to create operational taxonomic units (OTU). The OTUs were generated using VSEARCH 2.5.1 (id 0.97) (https://github.com/torognes/vsearch) using only reads present more than 20 times in the full dataset due to its meaningful size. For each station, sequences

collected at different depths and for all primers were pooled to obtain an overall representation of potential biodiversity.

2.3 | Data analysis

All analyses were performed at the genus level to facilitate comparisons between the approaches since only ~60% and 80% of the invertebrate taxa could be identified to species level with species collections and the eDNA approach, respectively. All analyses were done using R version 3.4.3 (R Core team, 2017) except for the SIMPER analyses which were done using PRIMER 6 and PERMANOVA+ (Clarke and Gorley, 2006).

In order to determine the effect of sampling effort on overall detected richness, genus-level rarefaction curves were created for each port and data collection type using the "specaccum" function in the R *vegan* package (Oksanen et al., 2016). Variation in taxonomic composition detected with eDNA and species collection within ports was depicted using a barplot generated in R from the raw relative abundance of genus taxonomy matrices assigned to a corresponding phylum. PERMANOVAs (number of permutations = 10,000) were performed using the *vegan* package to test the effect of port and sampling method on taxonomic composition, while nonmetric multidimensional scaling (nMDS) was used to visualize differences in taxonomic composition among ports and sampling methods.

Using an integrative approach based on the data at hand, alpha diversity indices (richness, Shannon diversity H', and Pielou evenness J) were calculated using the R *vegan* package (Oksanen et al., 2016) following the Hellinger standardization. Variations in diversity indices between ports and sampling methods were evaluated using two-way ANOVAs followed by the Tukey honestly significant difference (Tukey HSD) tests. When standard ANOVA assumptions of normality were not met, PERMANOVAs were done based on Euclidean distances, thereby ensuring approximate multivariate normality (Clarke & Warwick, 2001), followed by pairwise comparisons using the "pairwise.adonis" function in R to evaluate variation in diversity due to sampling approaches among ports.

Beta diversity was estimated from the Sorensen distance using the "vegdist" function in the *vegan* package (Oksanen et al., 2016) computed based on presence–absence data. Geographic distance matrices between stations within ports were calculated using the "spDistsN1" function in the R *sp* package (Bivand, Pebesma, & Gomez-Rubio, 2008) for Deception Bay and Iqaluit, while distance between Churchill stations was determined using ArcGIS version 10.4 due to some peculiarities of the geographic layout of this port (this port has a large peninsula separating some sample stations; Figure 1b, and as *sp* simply calculates the straight-line distance between two points, the distances between stations on either side of this peninsula are underestimated using *sp*, whereas ArcGIS allows for calculation of the true distance by water). The dispersion of eDNA within ports was evaluated from correlations between beta diversity and spatial distance matrices using Mantel tests in the R *ade4* package (Dray & Dufour, 2007) except for Churchill for which the correlation was calculated using the "cor.test" function (method = Spearman) in the R stats package as ArcGIS does not provide a suitable distance matrix format for the Mantel test.

Finally, we investigated the probability of detecting different marine invertebrate taxa according to their life cycle, paying particular attention to those including pelagic stages (holoplankton and meroplankton) due to their potential presence in the water column. To contrast the proportion of species with an entirely pelagic (i.e., holoplankton) versus benthic–pelagic (i.e., meroplankton) life cycles, a barplot was constructed in R from a presence/absence data list with the lowest taxonomic resolution for each organism and the associated life cycle category. Variation in taxonomic composition among ports within each life history type (holoplankton vs. taxa with meroplanktonic life stages) was assessed using PERMANOVA using the *vegan* package. Similarity percentage analysis (SIMPER) in PRIMER 6 and PERMANOVA+ was used to determine which taxa contributed the most to explaining differences among groups.

3 | RESULTS

3.1 | Sequencing quality

A total of 478,046 aquatic metazoan reads were obtained in Churchill, 95,658 in Deception Bay, and 203,245 in Iqaluit (see Table S2 for further details on pipeline processes). The 18S markers generally generated more sequences than did COI markers, except for Iqaluit where the opposite trend was observed (Table 1). Genus-level taxonomic resolution provided a satisfactory description of biodiversity given that less than 20% were not assigned at this taxonomic level in all locations (Figure S1). Thus, a total of 2,682, 1,413, and 1,056 operational taxonomic units (OTUs) were identified at the genus level in the ports of Churchill, Deception Bay, and Iqaluit, respectively.

No amplification was observed on agarose gels for the negative PCR controls, but a small number of sequences were present in our laboratory and field negative controls (Table S3). Two correction factors were applied to ensure the reliability of the data and quality of the resulting analyses. First, the few sequences present in the laboratory negative controls were subtracted from the samples from the same extraction batch. These sequences represent 0.003%, 0.1%, and 0.06% of Churchill, Deception Bay, and Iqaluit total number of sequences, respectively. Second, for the negative field controls, a genus was removed if its abundance in all the field controls was greater than 2% of the total number of sequences for all field samples combined for that genus. This percentage threshold was established considering that the removal of genera with a contamination between 0% and 2% would have led to an erroneous representation of marine invertebrates detected by eDNA. Following application of correction factors for background contamination, 0.1% and 1.4% of all COI and 18S sequences, respectively, were removed (Table S4). An exception to applying correction was made in the case of 18S *Pseudocalanus* sequences for which 96% of all the field contamination occurred in only one field negative control. Given that *Pseudocalanus* in real samples represented nearly half of all 18S sequences and this genus is known to be a dominant part of the Arctic

TABLE 1 Summary of the numbers of reads, the proportion of species and genera present in the historic (i.e., previously described from) Arctic database, and the mean number of OTUs for the COI primer set and the 18S primer set that are assigned and nonassigned on BOLD and SILVA for each harbor

	Number of reads		Proportion of species known in Arctic (%)		Proportion of genera known in Arctic (%)		Mean no. of assigned OTUs (genus)		Mean no. of nonassigned OTUs (genus)	
Harbor	COI	18S	COI	18S	COI	18S	COI	18S	COI	18S
Churchill	52,749	425,297	52.3	18.7	61.7	45.9	633	708	39	100
Deception Bay	30,214	65,454	62.9	18.3	74.3	52.6	348	359	16	105
Iqaluit	125,104	78,141	69.4	15.4	77.6	46.3	238	291	4	92

Note: The list of described species in the Arctic was obtained by pooling various species databases (N = 1,054 species; K.L. Howland, P. Archambault, N. Simard and R. Young, unpublished data) and published information (Cusson, Archambault, & Aitken, 2007; Goldsmit et al., 2014; Link, Chaillou, Forest, Piepenburg, & Archambault, 2013; López et al., 2016; Olivier, San Martín, & Archambault, 2013; Piepenburg et al., 2011; Roy, Iken, & Archambault, 2015; Young, McCauley, Galetti, & Dirzo, 2016).

zooplankton community (Dispas, 2019), removing it would significantly bias the analyses. When read abundance of a given genus in field controls was lower than 2% of the total number of sequences for that genus, it was retained because contamination was considered low enough that it would not lead to false interpretations. In contrast, discarding those genera could bias analyses due to their high number of sequences in real samples.

3.2 | Arctic coastal gamma diversity

With the exception of benthos communities sampled using trawls, grabs, and cores, genera rarefaction curves of marine invertebrates were close to saturation for both zooplankton and eDNA (Figure S2). A total of 634 marine invertebrate genera from 23 phyla were identified when eDNA and species collection datasets were combined. Gamma richness was consistently higher for species collections methods (432 genera identified) than for eDNA (202 genera detected), and there was variation between sampling approaches among ports. eDNA gamma richness was higher for Churchill and Deception Bay but lower for Iqaluit, whereas the opposite pattern was observed for the gamma richness of communities detected with species collection (Figure 2a). Although a substantial collective number of organisms were detected, few genera were shared between eDNA and species collections (Churchill 15%, Deception Bay 15%, and Iqaluit 9%). Of the organisms found with both approaches, annelids accounted for almost half (42.7%), followed by arthropods and mollusks with 20.2% and 11.2%, respectively, of the common genera obtained within all ports (Figure 2b).

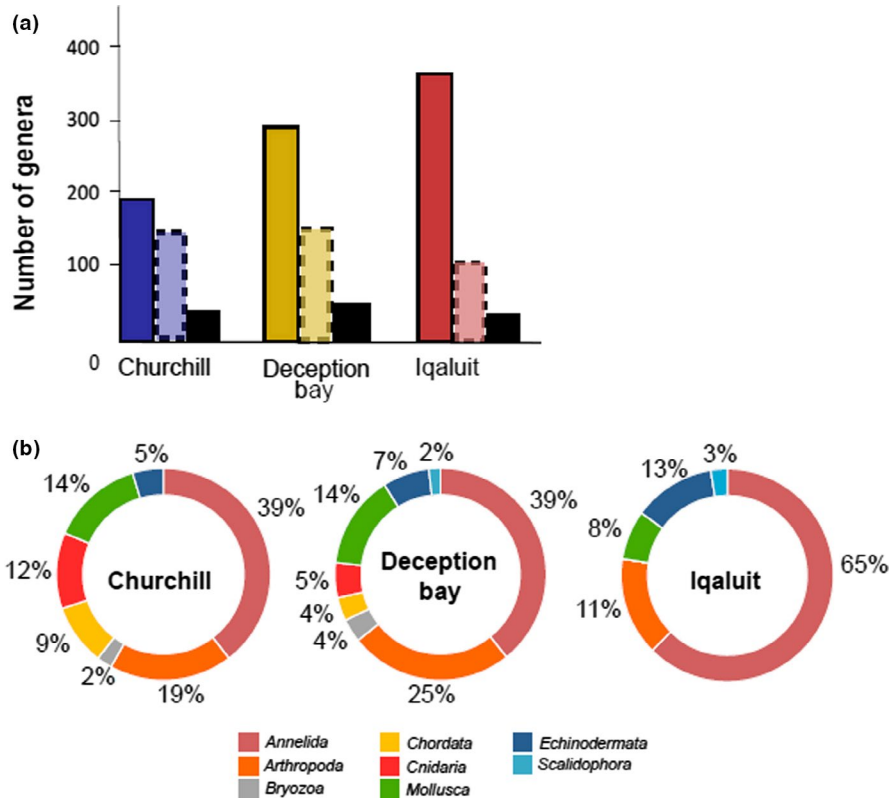

FIGURE 2 (a) Barplots of gamma richness (the total number of genera found) in Churchill (blue), Deception Bay (yellow), and Iqaluit (red). Darker bars represent species collection methods, whereas pale bars with dashed outlines represent eDNA and black bands represent the number of genera in common between the two collection methods. (b) Relative proportion of common genera identified by eDNA and species collection methods by phylum. Data represent pooled COI and 18S primer and traditional collection methods datasets for both (a) and (b)

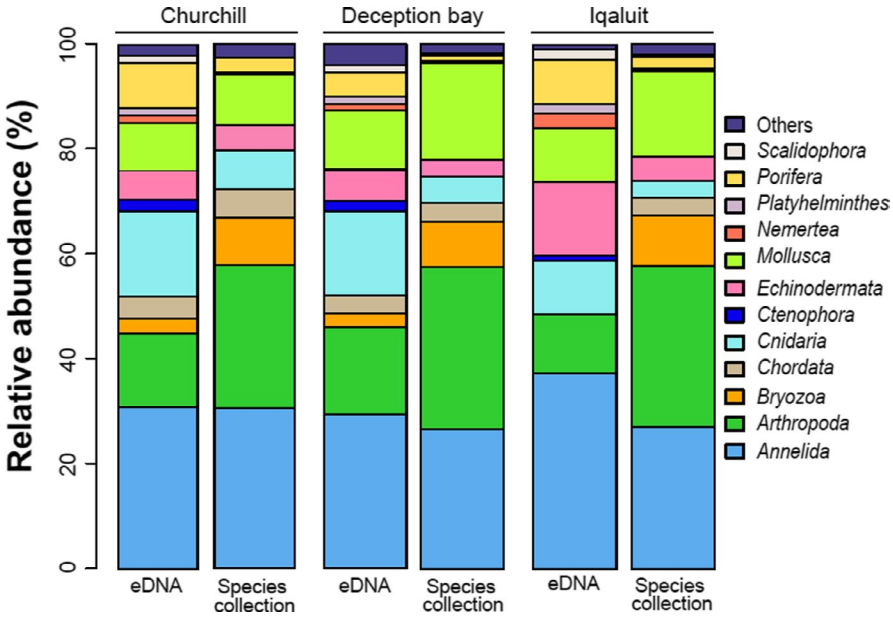

FIGURE 3 Marine invertebrate taxonomic composition at the phylum level for eDNA and species collection methods, respectively, for the ports of Churchill, Deception Bay, and Iqaluit ports. The COI and 18S datasets and benthic trawl, core, Van Veen grab, and net tow datasets are pooled for the eDNA and species collection barplots, respectively

The same phyla were generally present among the three ports, with *Annelida* and *Arthropoda* consistently being the most abundant phyla for both eDNA and species collections. However, the relative abundance of most taxa differed significantly between eDNA and species collections (PERMANOVA, $p < .001$; Table S5; Figure 3). Community composition of eDNA clearly differed among ports (PERMANOVA, $p < .001$; Table S5; Figure 4a) as did, although less clear visually, that for species collections (PERMANOVA, $p < .001$; Table S5; Figure 4b). Differences in community structure with eDNA versus species collection were mainly driven by *Annelid* and *Arthropod* genera (SIMPER analysis; 30% and 23%, respectively), followed by mollusks, echinoderms, cnidarians, and bryozoans (SIMPER analysis; 11%, 6%, 5%, and 4%, respectively). The remaining differences between eDNA and species collection community compositions may be partly driven by taxon-specific differences in detectability by these approaches. For example, some taxa such as *Brachiopoda*, *Foraminifera*, *Cephalorhyncha*, and *Chaetognatha* (grouped in the *Others* category with additional phyla of low relative abundance) were only found using species collection, while others such as *Bryozoa* were only rarely detected using eDNA. In contrast, taxa such as *Porifera*, *Nemertea*, *Cnidaria*, and *Echinodermata* were more frequently detected with higher read abundances in eDNA samples than in species collections.

3.3 | Arctic coastal alpha biodiversity

As for gamma diversity, alpha richness for eDNA samples was significantly higher in Churchill and Deception Bay than in Iqaluit (Tukey HSD, $p < .01$), with the number of genera per station ranging from 49 to 75 (mean = 63 ± 2) in Churchill, 45 to 93 (mean = 70 ± 4) in Deception Bay, and 34 to 53 (mean = 41 ± 2) in Iqaluit (Figure 5a). In contrast, Churchill had the lowest alpha richness for species collection samples (Tukey HSD, $p < .01$; Figure 5b) with only 8–58 genera per station (mean = 27 ± 3) as compared to 30–142 (mean = 78 ± 9) and 59–151 (mean = 100 ± 8) genera per station in Deception Bay and Iqaluit, respectively. Overall differences between sampling approaches varied between ports, with eDNA-based alpha richness being higher than species collection sample-based richness in Churchill (PERMANOVA, $p < .001$; Table S5), similar in Deception Bay (PERMANOVA, $p = .4$; Table S5), and lower in Iqaluit (PERMANOVA,

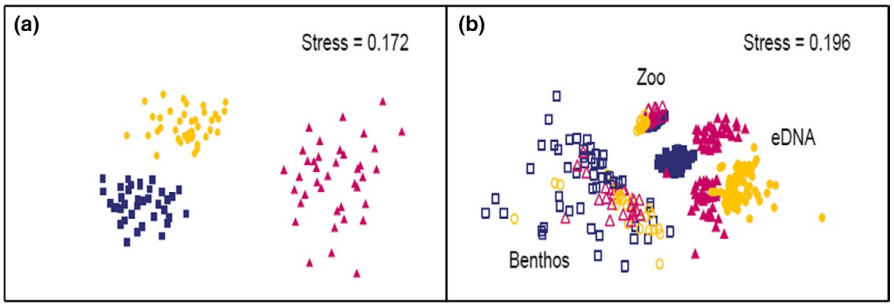

FIGURE 4 Variation in biodiversity (a) among ports based on eDNA and (b) among sampling methods within ports. Ordination of taxonomic composition (genera) calculated using the Sorensen index (incidence based) with each data point representing a sample. Blue squares represent Churchill, yellow circles Deception Bay, and magenta triangles Iqaluit. Filled and hollow symbols represent eDNA and species collection samples, respectively

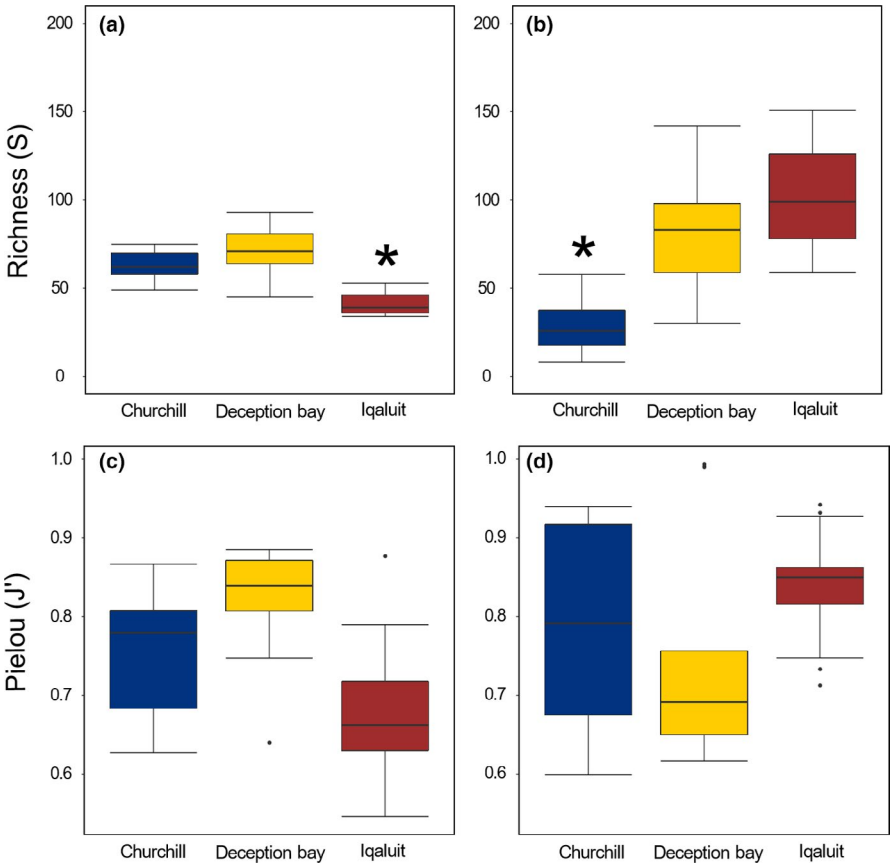

FIGURE 5 Boxplots of alpha diversity for genus-level richness and Pielou evenness index in Churchill, Deception Bay, and Iqaluit harbors for eDNA (a, c) and species collection (b, d). The COI and 18S datasets and benthic trawl, core, Van Veen grab, and net tow datasets are pooled for the eDNA and species collection boxplots, respectively. Significantly different richness are marked with an *

$p < .001$; Table S5). A similar pattern was observed for the Shannon biodiversity index (Figure S3).

Despite the contrasting alpha richness between sampling approaches within each port, the generally high values of Pielou's evenness indices revealed a pronounced taxonomic evenness with little indication of particular genera being overrepresented in communities detected by eDNA or species collection methods within the studied ecosystems (Table 2). Community evenness evaluated with eDNA was similar across ports except between Deception Bay and Iqaluit, where a lower or greater dominance by some taxa was observed in Iqaluit (PERMANOVA, $p < .05$; Table S5; Figure 5c). This is consistent with the SIMPER analyses where, for Iqaluit, 19 genera explained 90% of the similarity among stations in contrast to 30 and 42 genera for Churchill and Deception Bay, respectively. There were no differences in community evenness detected in species collections among the three ports (PERMANOVA, $p = .2$; Table S5; Figure 5d).

3.4 | Arctic coastal beta diversity

Community structure between stations within ports differed significantly for both eDNA and species collection but was greater for species collections than eDNA (Table 2). For eDNA, highest dissimilarity among stations was found in Iqaluit (0.37 ± 0.005), followed by Deception Bay (0.33 ± 0.005) and Churchill (0.31 ± 0.004), while the opposite trend was observed for species collections (Churchill: 0.84 ± 0.008; Deception Bay: 0.62 ± 0.01; Iqaluit: 0.58 ± 0.007).

TABLE 2 Summary of richness and alpha and beta biodiversity indices for eDNA and species collection of marine invertebrate communities on abundance data following Hellinger (Shannon and Pielou indices) and presence/absence (beta index) transformations, respectively. The COI and 18S datasets and benthic trawl, core, Van Veen grab, and net tow datasets are pooled for the eDNA and species collection datasets, respectively

Method	Harbor	Gamma richness (S_γ)	Mean alpha richness (S_α) ± *SE*	Mean Pielou (*J*) ± *SE*	Mean Shannon (*H'*) ± *SE*	Beta index ± *SE*
eDNA	Churchill	138	63 ± 2	0.75 ± 0.02	3.12 ± 0.1	0.31 ± 0.004
	Deception Bay	145	70 ± 4	0.82 ± 0.02	3.48 ± 0.1	0.33 ± 0.005
	Iqaluit	101	41 ± 2	0.67 ± 0.03	2.50 ± 0.1	0.37 ± 0.005
Species collection	Churchill	193	27 ± 3	0.79 ± 0.02	2.50 ± 0.1	0.84 ± 0.008
	Deception Bay	292	78 ± 9	0.75 ± 0.04	3.17 ± 0.1	0.62 ± 0.01
	Iqaluit	365	100 ± 8	0.84 ± 0.02	3.84 ± 0.1	0.58 ± 0.007

Positive correlations between beta diversity and geographic distance between stations were observed for most eDNA and species collections across all ports. Positive correlations between distance and eDNA beta diversity were significant and strongest in Churchill and Deception Bay (R^2 = .13 and .23, respectively; p < .05; Figure 6; Table S6), whereas a significant, albeit weaker, correlation was found in Iqaluit (R^2 = .09; p = .02; Table S6; Figure 6). For species collections, the correlation between beta diversity and geographic distance varied by port and collection method (zooplankton tow nets vs. benthos sampling methods). In Churchill, none of the correlations were significant (zooplankton R^2 = .014; p = .2, benthos R^2 = .004; p = .5; Table S6; Figure 6). For Deception Bay, a lower positive and significant correlation was found for the benthos (R^2 = .12, p = .02; Table S6; Figure 6) than for eDNA (R^2 = .23; p = .01; Table S6; Figure 6), while a stronger and significant positive correlation was found for zooplankton (R^2 = .26; p = .01; Table S6; Figure 6). For Iqaluit, a stronger and significant positive correlation was observed for the benthos (R^2 = .14, p = .01; Table S6; Figure 6) than for eDNA (R^2 = .09; p = .02; Table S6; Figure 6), while a negative and nonsignificant correlation was found for the zooplankton (R^2 = −.16; p > .05; Table S6; Figure 6).

3.5 | Origin of coastal eDNA

Taxa with the meroplanktonic life histories were the most commonly observed group based on eDNA sampling across ports (≥70% of observed taxa; Figure 7). Although the relative abundance of taxa by life history type varied among ports (PERMANOVA, p < .001), the proportions of taxa with meroplanktonic or holoplanktonic (taxa with only pelagic stage) life history types detected by eDNA were similar (Churchill: 69% meroplankton, 14% holoplankton; Deception Bay: 72% meroplankton, 17% holoplankton; Iqaluit: 80% meroplankton, 12% holoplankton; Figure 7). *Annelida* was the most dominant phylum detected with a meroplankton life history type, followed by *Mollusca* and *Echinodermata* (SIMPER analysis; 45.8% and 15.7% for both latter two species, respectively), whereas *Arthropoda* (copepods) was the dominant phylum in the holoplankton across the three ports (SIMPER analysis; 81.1%). Interestingly, similar dominant taxa were identified for the meroplankton component of communities detected via eDNA and species collection approaches, with the exception of *Echinodermata* for eDNA, which was replaced by *Arthropoda* (mostly amphipods) in species collection samples (SIMPER analysis; *Annelida* 45.6%, *Arthropoda* 24.0%, and *Mollusca* 16.5%). For holoplankton, *Arthropoda* (copepods) was the dominant phylum for both eDNA and zooplankton tows (SIMPER analysis; 81.1% and 96.1%, respectively).

4 | DISCUSSION

Arctic coastal regions are subject to harsh conditions, a wide range of temperatures and photoperiods, and support various forms of life over long periods of sea ice cover (PAME, 2016; Payne, Reusser, & Lee, 2012). Despite this, the Arctic Ocean is home to a great diversity of organisms, one which deserves increased attention, especially

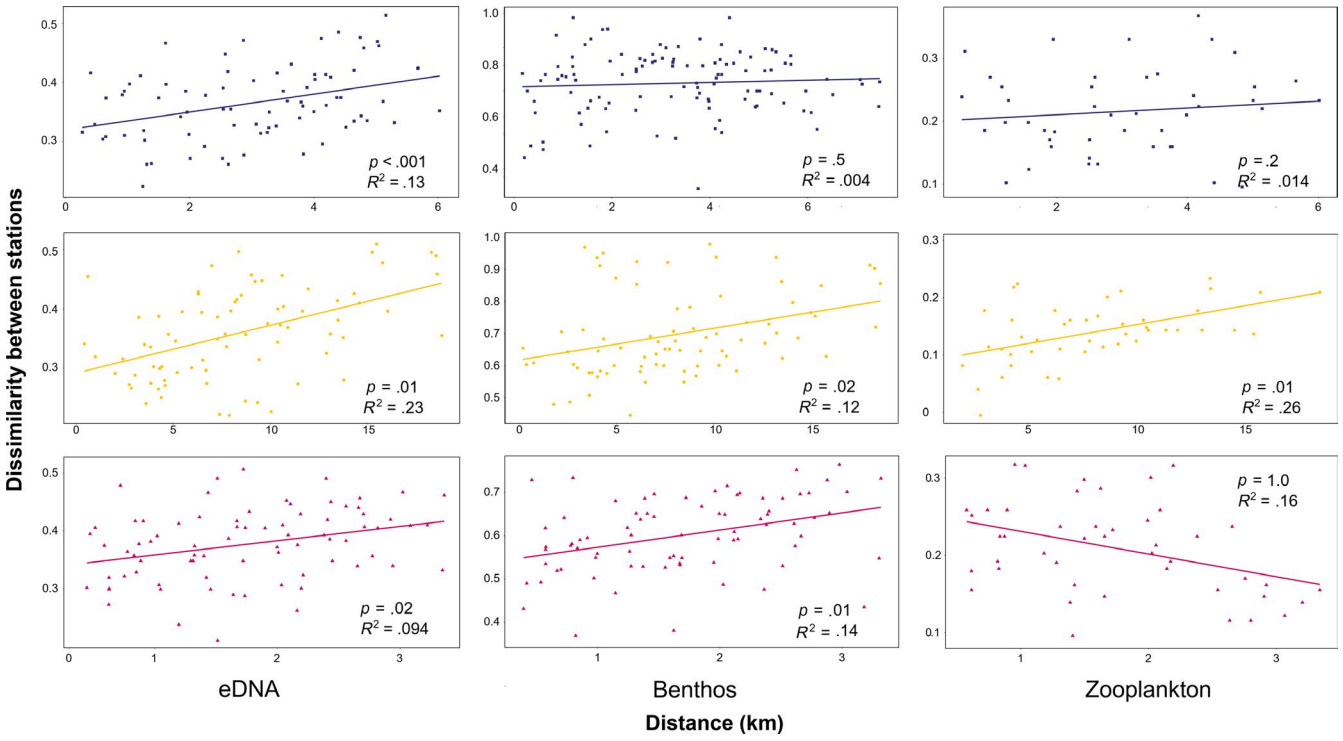

FIGURE 6 The Sorensen dissimilarity index between pairs of stations as a function of distance between the stations based on incidence data (presence/absence transformation on abundance) for different sampling methods (eDNA and species collections of benthos and zooplankton) in Churchill (blue), Deception Bay (yellow), and Iqaluit (magenta)

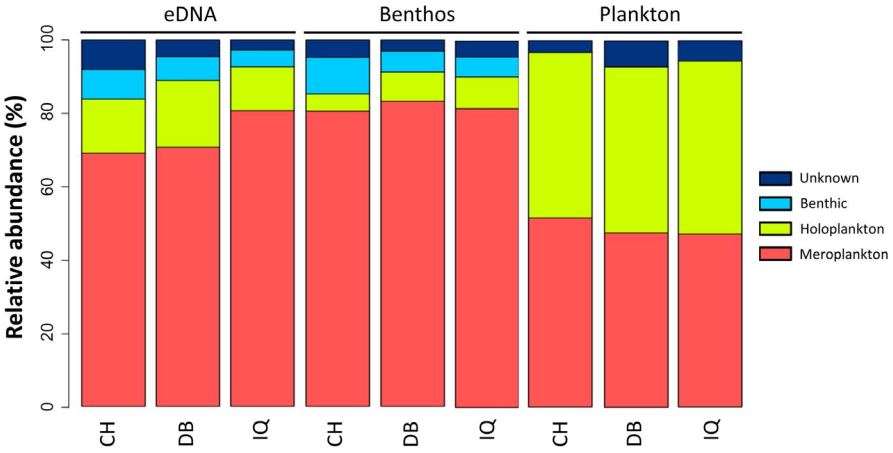

FIGURE 7 Relative abundance of organisms obtained with eDNA and species collection within Churchill, Deception Bay, and Iqaluit ports by life history type. Species collection for *benthos* includes benthic trawls, Van Veen grabs, and cores; *plankton* includes vertical and oblique pelagic plankton net tows. The sum of the detections for each genus (i.e., presence/absence) has been combined for all primer sets

lower trophic taxa, including invertebrates, which make up the base of ecosystem (Archambault et al., 2010; Piepenburg et al., 2011). The presence of marine invertebrates in the diets of Arctic fishes, birds, and mammals highlights their trophic importance (Bluhm & Gradinger, 2008; CAFF International Secretariat, 2010; Gajbhiye, 2002). Significant changes in their communities could thus affect ecosystem stability and impact the availability of food resources for coastal human communities (Guyot, Dickson, Paci, Furgal, & Chan, 2006; Ruiz, Carlton, Grosholz, & Hines, 1997). Marine biodiversity conservation is progressively becoming a crucial aim of environmental management (Spalding et al., 2007) but requires sufficient spatial data on biodiversity (Laurila-Pant et al., 2015). Despite substantial research efforts in recent years (Goldsmit et al., 2014; Piepenburg et al., 2011), there is limited knowledge about the diversity of many invertebrate groups (Archambault et al., 2010), including spatial distributions and how they are influenced by life stage transitions. Indeed, many species unknown to science await discovery (Jabr, Archambault, & Cameron, 2018; López, Olivier, Grant, & Archambault, 2016).

To our knowledge, this study is the first to compare eDNA, benthos, and zooplankton community patterns in the Arctic. Our use of eDNA sampling in parallel with species collection at Arctic ports provides insight into the ecological properties of eDNA in relation to the distribution and life stages of coastal marine invertebrates. While differing from observations made using species collection approaches, eDNA metabarcoding of Arctic coastal zone taxa provided relevant, complementary biodiversity information at various spatial scales using alpha, beta, and gamma indices.

4.1 | Overall biodiversity and community structure

Despite limited sample volumes (only 30 L water in total) and sequencing depth, eDNA metabarcoding identified 202 marine genera, covering 15 phyla and complementing biodiversity information obtained from species collection using traditional benthic trawls, cores, grabs, and net tows, representing a combined total of 634 genera, covering 23 phyla for eDNA and species collection. Following the qualitative results obtained by Thomsen et al. (2016) when comparing fish biodiversity detected by eDNA and species caught by trawl offshore Greenland, a greater similarity between sampling methods was expected. Instead, we observed important differences between phylum whereby *Bryozoa*, *Arthropoda*, and *Mollusca* were more commonly encountered with species collections of coastal marine communities while *Echinodermata*, *Porifera*, *Nemertea*, and *Cnidaria* were more frequently detected in eDNA samples. Several physical and biological factors might explain the differences in detectability of taxa between approaches. For example, echinoderms and sponges (*Porifera*) are often attached to large boulders in the seabed (Bell & Barnes, 2003; Chapman, 2003) and are difficult to collect using trawls or grabs, which may negatively bias their detectability in species-based collections. Identification issues, directly or in combination with biases in detectability, may also explain differences in community assemblages identified through eDNA and species collections. For instance, ribbon worms often lack easily diagnosable external body features making identification challenging and are frequently found under rocks, making them difficult to access (Thiel & Norenburg, 2009). eDNA metabarcoding may thus be particularly useful in such cases where taxa are more difficult to sample or identify morphologically. It is also important to note the considerable phylum-specific variation in previous sequencing efforts which impacts the chance of eDNA from a given group of being matched to sequences of morphologically identified organisms. For example, 54.5%–56.3% of the *Arthropods*, *Cnidarians*, and *Mollusks* identified by our traditional collection sampling methods were present in the sequence databases, while only 28.6% of the bryozoans had been previously sequenced for the barcoding regions used in this study (Table S7). This clearly limits the ability of eDNA metabarcoding to fully document community composition in the Arctic and highlights the importance of improving sequencing effort for particular taxa to fill the taxonomic gaps in available databases.

Another salient observation of this study is that detected community structure differed substantially between sampling methods with benthic communities being more variable within and between harbors and zooplankton communities being more similar within and between harbors. The broader range of biodiversity dissimilarities observed among benthic communities may be explained by highly

variable seabed characteristics, which play an important role in distribution of megafauna as they impact several factors, including larval settlement, anchorages, and shelter (Kedra, Renaud, Andrade, Goszczko, & Ambrose, 2013; Preez, Curtis, & Clarke, 2016). In contrast, zooplankton experience less variation in their habitat, due to the greater homogeneity of the water column relative to benthic substrates (Angel, 1993; Gray, 1997). Variation in eDNA community structure was intermediate between the variation observed using the two different species collection approaches. Thus, eDNA community structure represented greater community dissimilarity than what was observed for plankton communities but less dissimilarity than what was observed for benthic communities (trawl, grabs, and cores). This pattern could be due to the origin of eDNA, transport, and degradation processes. The high prevalence of meroplanktonic organisms (reflective of benthic communities) detected within eDNA communities may explain why they display greater dissimilarity than do plankton communities as depicted by species collections. On the other hand, eDNA communities likely display less dissimilarity than do benthic communities as depicted by species collections due to the homogenization and degradation of eDNA particle in the water column, whereas living specimens remain in/on seafloor and are less affected by water movement. In the future, it would be relevant to characterize habitats from which the samples originate to see if the eDNA approach could have detected differences in microhabitats, for instance, as reported by Port et al. (2016). Similarly, as the biological substrate sampled for eDNA is a critical factor influencing the biotic composition (Hermans, Buckley, & Lear, 2018; Koziol et al., 2019), the use of eDNA sediment substrates in addition to the eDNA water samples might have revealed dissimilarity patterns closer to the benthic communities. Our observations of distinct patterns of community structure depicted using either COI and 18S primer sets are consistent with several studies that have shown an effect of markers on the detection rate of marine invertebrates (Djurhuus et al., 2018; Drummond et al., 2015; Elbrecht et al., 2017; Kelly et al., 2017; Shaw et al., 2016). This highlights the importance of using a combination of different primer sets covering different genomic regions until a more universal primer set is available. Here, our results suggested a greater affinity of COI primers for *Annelids*, *Arthropods*, and *Echinoderms* relative to 18S primers, as previously reported by Drummond et al. (2015). These affinities could potentially explain why the observed Iqaluit community composition based on COI and 18S clearly differed from Churchill and Deception Bay communities as more *Annelids* and *Echinoderms* and less *Arthropods* taxa were detected in Iqaluit relative to the other two locations.

Despite the large number of taxa observed in this study, many marine invertebrates were likely missed, as suggested by the rarefaction curves. This is especially true for benthic communities, for which the rarefaction curves showed little indication that species increases were slowing. Coastal areas present complex mosaics of benthic habitat which, in addition to creating diverse epi- and infaunal communities, increases the possibility of missing taxa when sampling (Gray, 1997). For eDNA sampling, the number of genera detected may be influenced by a number of factors, including sample size and their vertical and horizontal distributions (Lacoursière-Roussel et al., 2018), filter types, volume of filtered water, extraction method (Deiner et al., 2018), sequencing depth, and bioinformatics pipeline. Thus, a larger volume of filtered seawater for each sample (Shaw et al., 2016) and a greater sequencing depth would likely have improved the detection rate (Mächler, Deiner, Spahn, & Altermatt, 2016) and increased the observed generic richness. Similarly, a greater detection rate could have been achieved by sampling a greater number of stations within each port. Although eDNA rarefaction curves were very similar between Churchill and Deception Bay harbors, Iqaluit grew less rapidly at first and appeared closer to reaching a plateau than did Churchill and Deception Bay due to the lower alpha and gamma biodiversity measured with this harbor. Further, alpha biodiversity and gamma biodiversity were greater within Iqaluit for species collections. This suggests that the opposing trends observed for the two approaches might reflect decreased previous monitoring effort in more northern regions which would logically result in more incomplete sequence reference databases rather than a true lower biodiversity. Sequence reference databases are estimated to contain only 13% of marine species inhabiting the Arctic Ocean (Hardy et al., 2011), and a latitudinal gradient of sequencing effort might exist within the Arctic itself. Indeed, we observed an increasing fraction of unknown OTUs from Churchill north to Iqaluit.

4.2 | Transport and homogenization of eDNA

Knowledge on the spatial arrangement of biodiversity is crucial for protecting regional diversity and supporting conservation planning (Socolar et al., 2015). The complex mosaic of benthic habitats in Arctic coastal areas makes it difficult to obtain a comprehensive sampling of this component of biodiversity. Our results found much lower beta diversity for eDNA communities compared to species collection communities which, suggesting that species eDNA is more homogeneous in space than the associated species themselves in coastal zones, as has been observed in several studies of freshwater systems (Dejean et al., 2011; Ficetola et al., 2008; Li et al., 2018; Thomsen et al., 2012).

Although Arctic coastal eDNA showed a more homogeneous community structure than do the composite species, this pattern was affected by spatial scale. Indeed, our results revealed a significant relationship between the dissimilarities within eDNA communities as a function of geographic distance, spanning distances from 4 to nearly 20 km. This is consistent with many spatial ecology processes whereby communities close to one another are more similar than are those that are further apart (Nekola & White, 1999), and in line with the observations of O'Donnell et al. (2017) of greater eDNA dispersion in nearshore marine habitats. Several studies have also revealed patterns of extensive eDNA dispersion over considerable distances within river systems (Deiner & Altermatt, 2014; Deiner, Fronhofer, Mächler, Walser, & Altermatt, 2016), which could influence community structure in estuarine settings such as the port of Churchill. In our study, the very cold Arctic waters may further contribute to reducing DNA degradation, thus

providing more time for dispersion over larger distances compared to what has been previously reported at more temperate latitudes (Jeunen et al., 2019). This raises the hypothesis that spatial eDNA homogenization should be more important in the Arctic Ocean than more southern regions. In contrast, given that sunlight is known to break down DNA in marine systems (El-Sayed, Van Dijken, & Gonzalez-Rodas, 1996), the prolonged daylight in the study sites at the time of sampling (up to 24 hr) may encourage DNA degradation (Mächler, Osathanunkul, & Altermatt, 2018). However, a study by Andruszkiewicz, Sassoubre, and Boehm (2017) concluded that sunlight may not be the primary factor causing degradation of the fish DNA in their experiment and that degradation of the latter would depend more on the time elapsed since its shedding in the water. As many chemical and biological processes influence eDNA production, transport, and degradation, it will be of interest in future studies to evaluate how latitude may influence patterns of eDNA biodiversity indices.

The weak correlation between dissimilarity and geographic distance in Iqaluit is in sharp contrast to the other two ports in this study. This may be explained by the greater tidal range in the region (7.5–11.7 m, as compared to 3.3–5.1 and 3.6–5.7 m for Churchill and Deception Bay, respectively) and associated currents occurring in this location (Fisheries & Oceans Canada, 2018). Interestingly, Churchill and Deception Bay ports showed significant distance differences between their stations (Churchill: 0.2–7 km; Deception Bay: 0.3–19 km), suggesting that the correlation between dissimilarity and distance might be consistent at various spatial scales for marine invertebrates in Arctic coastal environments with similar tidal conditions. In contrast to eDNA results, where dissimilarity increased as a function of geographic distance between stations, increased dissimilarity of communities with distance was not systematically observed in species collections, which again may reflect the fact that marine invertebrate communities are often characterized by a pronounced patchiness (Ministry of Environment, 2006). Thus, the homogeneity of eDNA distribution due to dispersion could potentially improve estimations of biodiversity at local spatial scales. On the other hand, the dispersion and persistence of eDNA in coastal environments also increase the risk of detecting organisms that are not actually present locally (Deiner & Altermatt, 2014; Jane et al., 2015). Further studies comparing the spatial distribution of eDNA communities and corresponding species collection communities (either benthos or plankton) in dynamic systems such as complex coastal areas are needed to improve our knowledge about how the multiple physical and biological factors influence eDNA distance decay. Such information will help to better inform eDNA sampling design for monitoring and management issues.

4.3 | Origins of eDNA

Benthic species with meroplanktonic life history type accounted for a greater proportion of the eDNA than did species with strict benthic or pelagic life history. This result suggests that coastal water eDNA is a mixture of organic material released to the environment (e.g., feces, skin, mucus) and plankton degradation and thus underlines the influence of variation in the life cycles on species detection probability. For instance, the fact that the discriminating taxa collected using eDNA and species collection approaches differed for holoplankton and meroplankton communities suggests that the different reproductive periods of the organisms, as well as the associated planktonic larval stages, may influence the detection of certain taxa. As a case in point, the daisy brittle star (*Ophiopholis aculeata*), the brittle star *Ophiura robusta*, and the green sea urchin (*Strongylocentrotus droebachiensis*) were discriminant echinoderm species detected by eDNA and not by benthic species collection (data not shown). Interestingly, these three species are known to synchronize their spawning periods with sharp increases in sea temperature (Himmelman, Dumont, Gaymer, Vallières, & Drolet, 2008), which typically occur during July within the sampled ports (Galbraith & Larouche, 2011; Prinsenberg, 1984), suggesting that the high number of sequences observed for those species could reflect the occurrence of these species in their pelagic phase.

The importance of planktonic stages to increasing eDNA detection is also supported by the absence of DNA from *Amphipods*, which were discriminant taxa in species collections for meroplankton. In general, studies on amphipod reproductive biology revealed that breeding occurs during the spring in most species (Węsławski & Legeżyńska, 2002). However, amphipods represent a complex case as some species are benthic while other species are planktonic and the two life history types coexist in the same environment. Sampling outside of breeding periods and the lack of a planktonic stage could explain the lower detectability of these organisms with eDNA. It is difficult to draw general patterns based on the life histories of organisms since species or genera differ substantially and there is a general lack of knowledge for life histories, including their reproduction periods, of many marine invertebrates inhabiting the Arctic. O'Donnell et al. (2017) also concluded that planktonic larval stages or released pelagic eggs may play an important role in the eDNA detection of some organisms. However, given that seasonal factors greatly influence the proportion of meroplanktonic and holoplanktonic organisms (Highfield et al., 2010; Lindeque, Parry, Harmer, Somerfield, & Atkinson, 2013) and eDNA ecology (e.g., water temperature, UV exposition), further studies on the detection of various marine invertebrate taxa at different times of the year would aid to determine how life histories of different organisms impact eDNA detection.

4.4 | Role of eDNA in Arctic conservation

Given the multiple environmental and anthropogenic factors that are currently threatening Arctic coastal biodiversity and the international objectives that many nations have agreed to, such as the protection of 10% of coastal and marine areas by 2020 (Secretariat of the Convention on Biological Diversity [SCBD], 2014), the development of rapid and efficient tools for monitoring biodiversity

changes is essential. eDNA metabarcoding provides valuable information toward a broader view of the taxonomic diversity that may help in developing more rigorous conservation plans, particularly in the Arctic. In addition, this approach provides numerous advantages due to its time-efficient and nonintrusive nature (Deiner et al., 2017). The simplicity of the sampling protocol for coastal water makes the method easy to learn, which constitutes a major asset for remote regions such as the Arctic, where it can be easily incorporated into existing sampling or community-based monitoring programs (Lacoursière-Roussel et al., 2018). By combining the study of invertebrate communities at different spatial scales detected by eDNA and species collection, this study highlights important features related to the ecology of eDNA biodiversity indices such as the origin of eDNA (i.e., planktonic phases of benthic taxa) and the effect of spatial homogenization. Together, our results suggest that eDNA diversity reflects complex interactions between the life cycles of organisms and their spatial distribution. As public sequence databases become more complete over time, species detection using eDNA metabarcoding will improve and is likely to increase understanding of a wide range of ecological processes (daily plankton migration, seasonal fish migration, food web interactions, etc.) where many elements remain undiscovered. Our results highlight that eDNA should be used as a complementary approach for improving characterization of coastal biodiversity from species collections as each method yielded distinct information on taxonomic composition of the invertebrates inhabiting coastal areas.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

AL-R, KLH, PA, and LB conceived the study. NL, AL-R, KLH, CWM, NS, and AD contributed to the data acquisition in the field. KLH, PA, CWM, and NS are specialized in the Arctic coastal surveillance and contributed to benthic component of the study dataset. GW and AD are specialized in Arctic zooplankton monitoring and contributed to the zooplankton component of the study dataset. EN developed the bioinformatics pipeline. NL, AL-R, MS, PA, and LB interpreted the data. NL wrote the manuscript, and all authors reviewed it.

DATA AVAILABILITY STATEMENT

Raw sequence reads were deposited in NCBI's Sequence Read Archive (SRA, http://www.ncbi.nlm.nih.gov/sra) under Bioprojects PRJNA388333 and PRJNA521343. The data that support the findings of this study are openly available in [repository name e.g., "figshare"] at http://doi.org/10.1002/edn3.35, reference number [16575833].

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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