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Detecting community change in Arctic marine ecosystems using the temporal dynamics of environmental DNA

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Abstract

Large-scale biomonitoring of Arctic coastal marine communities is essential to track temporal changes in ecosystems. Despite the potential of environmental DNA (eDNA) as an innovative coastal biomonitoring tool, important questions remain pertaining to its temporal and spatial variation and how this may affect the evaluation of ecosystem changes over time in hydrodynamic ecosystems. In this study, we used eDNA metabarcoding of coastal water samples in two Canadian Arctic ports to evaluate the potential of eDNA to detect temporal transition in marine coastal communities. We sequenced eDNA from approximately 20 surface water samples collected each month ($N \approx 150$ samples) covering the transition period between summer and late fall using four different universal primer pairs (two pairs of COI mitochondrial genes and two pairs of 18S rRNA genes). Our results from both primer pairs highlighted a significant transition from the summer to the fall marine community. We also observed a putative link between eDNA peaks of read abundance and timing for different life stages (e.g., spawning and larvae) of several species with the most abundant sequence reads. As such, our results show that temporal variation must be considered in ensuring comprehensive coastal biomonitoring with eDNA. Although much remains to be investigated about the ecology of eDNA, our results contribute to fundamental knowledge on the origin of eDNA and highlight the importance of considering temporal variation in developing guidance for coastal biomonitoring with this approach.

KEYWORDS

Arctic, coastal marine community, eDNA, invertebrates, metabarcoding, metazoan, temporal variation

1 | INTRODUCTION

The Arctic is home to a diversity of uniquely adapted plants and animals with many species most likely still to be discovered (Walczyńska et al., 2018). At the same time, this region is experiencing unprecedented global change, with the fastest warming rates in the world causing substantial changes to this fragile environment especially within aquatic ecosystems (Post et al., 2009). At the global scale, between the years 1970 and 2012, freshwater and marine populations declined in abundance by 81% and 36%, respectively (Senapati et al., 2018). In the Arctic, warmer ocean temperatures and reduced sea ice coverage are leading to a poleward movement of boreal marine species (Fossheim et al., 2015). Furthermore, greater shipping traffic in the Arctic Ocean is increasing the risk for the introduction of chemical pollution and nonindigenous species (NIS) (ACIA, 2004; Chan et al., 2013; Goldsmit et al., 2018; Niimi, 2004). Mitigating the impacts of human stressors and consequences on Arctic marine communities requires the establishment of monitoring strategies, using standardized protocols that can be implemented across large spatial and temporal scales.

One of the greatest challenges to coastal monitoring in the Arctic is the limited access/infrastructure and the associated high costs and logistic complexity of sampling using standard methods. As a consequence, the few large-scale ongoing coastal monitoring programs and surveys are typically conducted during the short window without ice cover. Analysis of environmental DNA (eDNA), the DNA released into the environment by living organisms (small whole organisms, feces, urine, skin secretions, skin cells, gametes, and body putrefaction), is receiving increasing attention due to its potential as a biomonitoring tool integrating a broad array of taxa (Deiner et al., 2017). Moreover, metabarcoding analysis of eDNA may offer a revolutionary approach to improve spatially and temporally extensive monitoring of marine taxa (Haile et al., 2009; Lydolph et al., 2005; Thomsen et al., 2012). Although research on evaluating the power of eDNA metabarcoding for biomonitoring is steadily increasing, drivers of environmental eDNA variation remain poorly understood (Deiner et al., 2017; Senapati et al., 2018), which limits our capacity to contrast samples over time and space to evaluate biodiversity changes.

Few studies to date have focused on investigating the spatiotemporal dynamics of eDNA variation in aquatic environments (Sigsgaard et al., 2017; Stoeckle et al., 2017) which is also complicated by the fact that the detection rate is a function of the complex equilibrium between eDNA production, degradation, and flushing rate (Lacoursière-Roussel & Deiner, 2019; Senapati et al., 2018). Whereas the rate of eDNA production depends on the abundance of organisms, and ecology of species (physiology, metabolism, and behavior), the eDNA degradation rate depends on environmental factors such as microbial activity, extracellular enzymes, temperature, UV, and chemical reactions (de Souza et al., 2016). In the Arctic, Lacoursière-Roussel et al. (2018) found greater eDNA species richness in water samples collected under ice cover than summer in Arctic marine waters. This highlights a potentially lower eDNA degradation under ice cover which could be expected due to the limited UV exposure, colder water temperatures, and lower velocity of water displacement (Barnes et al., 2014; Jeunen et al., 2019). However findings were based on only two sampling periods; thus, further studies are needed to differentiate relative effects of species and eDNA ecologies between seasons in the Arctic.

The abundance of eDNA may reflect important demographic characteristics of communities such as population abundance (Lacoursière-Roussel et al., 2016), migration (Stoeckle et al., 2017), and potentially reproduction period of different species (Laramie et al., 2015). In the Arctic, little is known about the species ecology due to the challenge of surveying coastal biodiversity under ice cover with traditional methods (Laidre et al., 2008; Wassmann et al., 2010). Despite these sampling difficulties, Darnis et al. (2012) highlighted winter activity in major food web components and found evidence of under ice reproduction by several Arctic invertebrates. Here, we hypothesize that this type of winter activity in the Arctic marine environment could be detected through eDNA metabarcoding. For instance, several studies in freshwater environments have detected peaks of eDNA corresponding to breeding or larval hatching (Buxton et al., 2018; Erickson et al., 2016; Laramie et al., 2015; Spear et al., 2015; Tillotson et al., 2018; Xu et al., 2018).

A better understanding on how the ecology of different species will affect the eDNA patterns in the Arctic coastal environment is essential to develop efficient, standardized eDNA-based biomonitoring surveys for evaluating ecosystems changes. Knowledge of consistent temporal eDNA patterns driven by putative species' life cycles (e.g., reproduction period) or putative stochastic hydrodynamic and environmental processes is crucial for interpreting eDNA shifts over time and ensuring that these sources of variability do not mask the detection of biological changes resulting from processes such as climate change over time.

In this study, we investigated the temporal transition in eDNA of coastal marine communities between open-water and ice-covered periods to test the hypothesis that ecological processes are the main drivers of eDNA changes overtime, despite the influence of environmental factors on spatiotemporal eDNA distribution. We characterized the diversity of taxa and the metazoan coastal community structure obtained from eDNA metabarcoding of water samples collected at different temporal scales in two Arctic ports, Churchill and Pond Inlet. We further hypothesized that events in the annual life cycle of Arctic species can be inferred from eDNA read abundance. This was tested based on biological knowledge from the literature for those species that showed strong temporal changes in read abundance over the time frame of our study. To our knowledge, this study is the first to document temporal variation of coastal metazoan communities in the Arctic based on eDNA metabarcoding and, as such, represents a step forward in understanding how this approach could contribute to improving knowledge of ecological processes (i.e., life stage transitions and migration).

2 | METHODS

2.1 | Sample collection

Two Arctic ports were selected for collection of eDNA from water samples: Churchill (Manitoba, Canada, Hudson Bay) and Pond Inlet (Nunavut, Canada, Baffin Island) located at the southern and northern extremes of the eastern Arctic, respectively (Figure 1). Pond Inlet is marine, while Churchill is estuarine and thus may contain a mixture of eDNA from marine and freshwater species as demonstrated by Lacoursière-Roussel et al. (2018).

Based on previous eDNA studies in Arctic ports (Grey et al., 2018; Lacoursière-Roussel et al., 2018), twenty 250 ml shore-based surface water samples were collected once a month over 4 months spanning late summer to late fall (September to December for Churchill port and August to November for Pond Inlet port) to ensure adequate representation of coastal diversity within a given sampling period. Filtration of each sample was performed within <1 hr using a syringe (BD 60 ml) equipped with a filter head containing a 0.7-µm glass microfiber filter (Whatman GF/F, 25 mm). Field negative controls (i.e., 250 ml distilled water) were filtered for every 10 samples. Filters were preserved at 4°C in 700 µl of Longmire's lysis preservation buffer within a 2-ml tube for less than a month (Wegleitner et al., 2015) and then frozen at −20°C until DNA extraction. Meticulous care was taken to reduce the risk of cross-contamination in the field by using individual sampling kits for each sample (bottles and filter housing sterilized with a 10% bleach solution and new sterilized gloves, syringes, and tweezers). Moreover, each bagged and sealed sampling kit was exposed to UV for 30 min.

2.2 | DNA extraction, amplification, and sequencing

In the laboratory, cross-contamination risk was reduced by using the following steps: (a) eDNA extraction, PCR preparation, and post-PCR steps performed in different rooms; (b) PCR manipulations performed in a decontaminated UV hood; (c) samples within a specific port treated all together but processed in a randomized order; and (d) the bench space and laboratory tools were bleached (10% solution) and exposed to UV for 30 min prior to processing the next port. DNA was extracted using a QIAshredder and phenol/chloroform protocol as described in Lacoursière-Roussel et al. (2018). Negative control extractions (950 µl distilled water) were done for each sample batch (i.e., one for each 23 samples).

Four different universal primer pairs were used to amplify eDNA. These included two pairs of mitochondrial cytochrome c oxidase subunit I (COI) primers: the forward mlCOIintF and reverse jgHCO2198 amplifying 313 bp (hereafter called COI1) and the primer LCO1490and ill_C_R amplifying 325 bp (COI2) (Folmer et al., 1994; Geller et al., 2013; Leray et al., 2013; Shokralla et al., 2015). Additionally, two primer pairs of ribosomal gene 18S were also used to amplify eDNA in the V4 region: the primers F-574 and R-952 (18S1) and the primers TAReuk454FWD1 and TAReukREV3 (18S2) which amplify a region of 378 and 399 bp, respectively (Hadziavdic et al., 2014; Stoeck et al., 2010). Details of eDNA amplification are provided in Lacoursière-Roussel et al. (2018). In brief, DNA amplifications were performed using a one-step dual-indexed PCR approach with Illumina barcoded adapters. Each PCR was composed of 6 µl Qiagen Multiplex Master Mix, 4 µl diH_2O, 1 µl of each primer (10 µM), and 3 µl of DNA. The PCR program consisted of an initial denaturation step at 95°C for 15 min, followed by 35 cycles at 94°C for 30 s, 54°C for 90 s (except for primers LCO1490/ill_C_R which was at 52°C for 90 s), and 72°C for 60 s, and a final elongation at 72°C for 10 min. Because barcodes were different for each sample, a negative PCR control was done for each sample and primer pair. PCR negative controls had the same barcode and were then not sequenced, but DNA extraction negative controls were treated as regular samples and sequenced. To reduce potential PCR biases, the same number of cycles for all the primer pairs at a limit of 35 cycles was performed

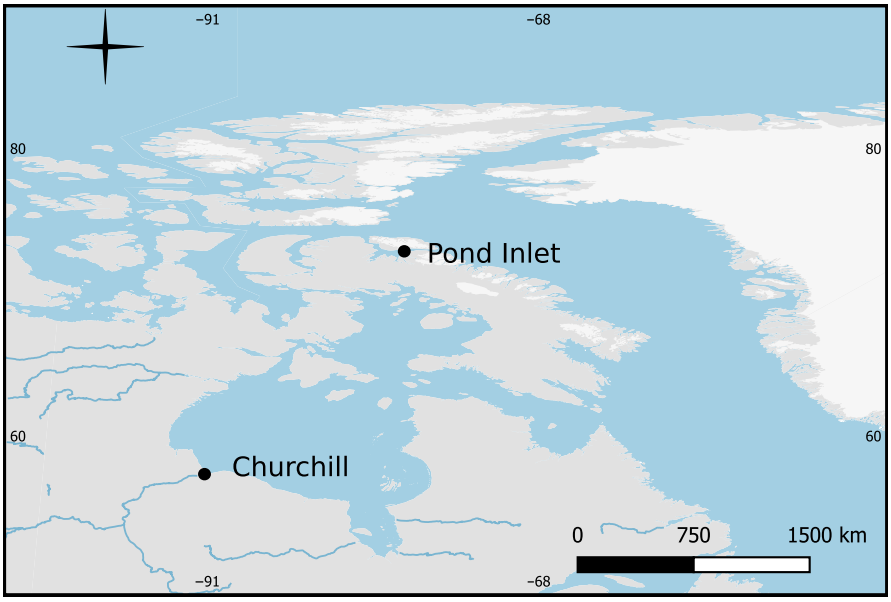


FIGURE 1 Map of the study area in the Canadian Arctic. eDNA samples were collected from two ports: Churchill and Pond Inlet

as advised in Kelly et al. (2019). Moreover, three PCR replicates were done for each sample with the four primer pairs allowing to obtain 12 PCR replicates per sample which were then pooled together. The PCRs were also done in triplicate and pooled together to reduce potential bias through stochastic variation (Elbrecht & Leese, 2015; Mauvisseau et al., 2019). The sample products (12 PCR replicates) were purified using Ultra AMPure beads, quantified by PicoGreen, and then pooled in equal molar concentrations. Sequencing was carried out using an Illumina MiSeq (Illumina, San Diego, CA, USA) at the Plateforme d'Analyses Génomiques (IBIS, Université Laval, Québec, Canada, http://www.ibis.ulaval.ca/). Each port samples were analyzed on a separate Illumina MiSeq run to ensure independency, but the PCR replicates of each sample within a port were pooled within a single run to ensure the equality of sequencing depth among samples.

2.3 | Cleaning of the raw data

Raw forward and reverse reads were trimmed, merged, and classified using the Barque pipeline version v1.5.2, an eDNA metabarcoding pipeline (www.github.com/enormandeau/barque). More precisely, forward and reverse sequences were trimmed and filtered using Trimmomatic v 0.30 with the following parameters: (TrimmomaticPE, -phred33, ILLUMINACLIP:"$ADAPTERFILE":3:30:6, LEADING:20, TRAILING:20, SLIDINGWINDOW:20:20, MINLEN:200 2) (Bolger et al., 2014). Read pairs were merged with FLASH v1.2.11 (Fast Length Adjustment of Short reads) with the following options: (-t 1 -z -O -m 30 -M 280) (Magoč & Salzberg, 2011). The contigs were split following their primers pairs (COI1, COI2, 18S1, and 18S2), and reads with lengths outside the expected range were removed (see https://github.com/enormandeau/barque/blob/master/02_info/primers.csv). Chimeric sequences were removed using VSEARCH v 2.8.4 (uchime_denovo command and the default parameters) (Rognes et al., 2016). Finally, BOLD (http://v3.boldsystems.org/) and SILVA (https://www.arb-silva.de/), two reference sequence databases for COI and 18S, respectively, were used to annotate the most likely species of the sequences with a threshold of 97% similarity. In order to analyze the marine community only, endogenous sequences from the dataset which were identified as nonmarine species or insect species were removed and those that could not be taxonomically assigned. More details about the removal of species and the management of multiple hits are described in Lacoursière-Roussel et al. (2018). In this study, sequences with multiple hit assignments were annotated to the genus and the species was left as "sp.". Likewise, a percentage threshold was established for the sequences from taxa deemed to be associated with sample contamination. This threshold was established considering that the removal of some genera or species with a very low contamination would have led to an erroneous representation of the dataset. Therefore, to limit this potential bias, the following criteria developed by Leduc et al. (2019) were used: Taxa were removed if the total number of sequences detected in negative controls (field and PCR; $N = 24$) was greater than 2% of the total number of sequences detected across all samples for a given genus or species. Conversely, taxa were remained if the threshold was lower than 2%. Finally, after the cleaning of the four datasets generated by the four primer pairs COI1, COI2, 18S1, and 18S2, the sequences from the COI1 and COI2 and from 18S1 and 18S2 datasets were added within each sample, respectively, allowing for the analysis of the two combined datasets.

2.4 | Statistical analyses

Matrices, generated by the Barque pipeline and containing eDNA sequences for each sample at the species and the genus level, were used in statistical analyses. These eDNA sequences are not absolute abundance but proportional read abundance which is referred to as "read abundance" in this study. The read abundance of eDNA samples from a same library sequencing may be compared (Quinn et al., 2018).

To document variation within and among primer sets (combined 18S and COI genes), ports and temporal transition (i.e., months), two bar plots were generated with Rstudio v3.3.1 (RStudio Team, 2015) from presence/absence and from the read abundance of the genus taxonomy matrix where genera from the same phylum were combined. A PERMANOVA analysis (number of permutations = 10,000) was also performed using the vegan package (Oksanen et al., 2006) in R to test for gene primer, port, and temporal transition effects. This analysis was performed on the genus matrix with two kinds of statistical transformations: the Hellinger transformation (read abundance score) and presence–absence transformation (presence/absence score). Finally, in order to build the PCoAs, a Bray–Curtis distance matrix was made from the genus matrix after Hellinger transformation or presence–absence transformation using the vegan package in R.

The number of species by month was graphed for each port and gene primer using R. The monthly diversity was evaluated for each gene primer and port based on the inverse Simpson index generated from the genus matrix after a Hellinger transformation (read abundance score) using the vegan package in R. We then used a generalized linear model (GLM) with a Gaussian distribution followed by ANOVA to test the month, port, and gene primer effects as well as their interactions. To finish, a box plot with the inverse Simpson index for each month was generated using R.

To improve our knowledge on temporal transition in ecological processes, the species characterized by the highest read abundances were further investigated with a heat map using the d3heatmap package in R (Cheng et al., 2015) to observe the read abundance variation among months; this analysis was restricted to the COI primers which provide much greater resolution at the species level (Hebert et al., 2003). Among the species investigated within the heat map, approximately 20 species were plotted by months using R to illustrate peaks in eDNA (i.e., an elevated read abundance only present for one month). A Kruskal–Wallis test was performed using R

to evaluate the statistical significance of any visually observed read abundance differences.

3 | RESULTS

3.1 | Sequencing quality

In Pond Inlet, after trimming for the entire dataset, a total of 360,657 and 133,226 sequences were obtained with the combined 18S and COI gene primers, respectively. In Churchill, fewer sequences were obtained after trimming with a total of 64,198 and 45,503 sequences, respectively. There were differences between the number of raw sequences and final sequences due to the cleaning steps described in Table S1 and the sequence assignment and filtration steps. Overall (both ports combined), 454 and 645 different operational taxonomic units (OTUs) were identified at the 97% identity threshold for the gene primers 18S and COI, respectively. At the species level, 186 and 259 species were matched for the 18S and COI gene primers, respectively (Table S1).

Although all the eDNA samples had raw reads before the dataset trimming, six (18S primers) and three (COI primers) samples from Churchill had no final sequence after trimming. Therefore, these samples were removed from the dataset, leaving 152 and 155 samples in total that were analyzed for the 18S and COI gene primers, respectively. The accumulation curves for both ports (Churchill and Pond Inlet) and gene primers (18S and COI) reached a plateau suggesting a sufficient sampling effort over the collective sampling periods in each port (Figure S1 and S2).

Although there were no visible bands after PCR amplification and despite meticulous care in the field and within the laboratory to avoid contamination, contaminant sequences were observed in our 24 field and laboratory negative controls, albeit in very small proportions (Tables S2 and S3). Based on two approaches to eliminate the contamination and limit potential bias in interpreting our results (see methods for detailed removal criteria; Tables S2 and S3), ten (18S) and 15 (COI) genera and eight (18S) and 14 (COI) species were removed from analyses for both ports. However, several genera and species with very weak contamination levels were retained (Tables S2 and S3) because they were below thresholds deemed to influence the main interpretations of our results. All remaining genera and species were typically associated with Arctic coastal or freshwater communities.

Detected phyla significantly differed between 18S and COI gene primers (Figure 2, Figure S3). Although the major groups such as *Annelida* and *Arthropoda* were similar between the gene primers, other phyla were mainly detected by a single gene primer set. Therefore, subsequent community analyses were performed separately for each primer set.

3.2 | Temporal eDNA-based transition in marine coastal structure community

Results showed a strong temporal transition in eDNA with a distinct structure per month. Indeed, high variability in the community structure was detected among months based both on presence/absence and read abundance (PERMANOVA, $p < .001$; Table 1, Table S4). Strong temporal transition in eDNA was also evident based on PCoA at the genus level (Figure 3, Figure S4). In Churchill, clusters followed a trend of continuity from September to December suggesting a transition from the summer to the late fall marine communities (Figure 3a,b). This trend of continuity from August to November was less obvious in Pond Inlet due

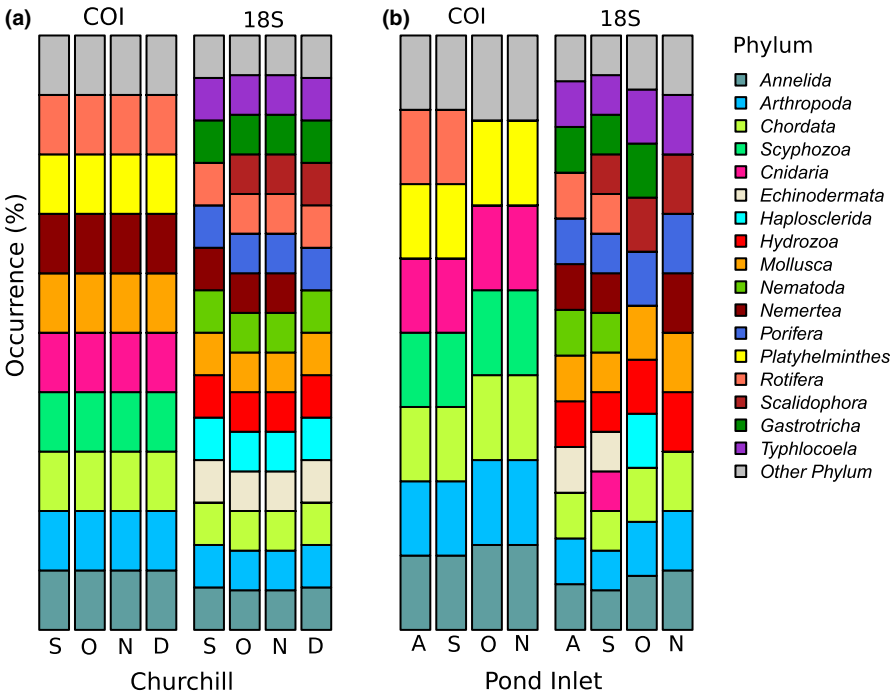


FIGURE 2 Temporal transition in taxonomic composition of marine metazoan eDNA at the phylum level for Arctic ports based on presence/absence scores. (a) Churchill port. (b) Pond Inlet port. Two combined gene primers were used in this study: 18S (F-574/ R-952 and TAReuk454FWD1/TAReukREV3) and COI (mlCOIintF/jgHCO2198 and LCO1490/ ill_C_R). Each bar plot represents a month; A: August, S: September, O: October, N: November, and D: December

TABLE 1 Summary of PERMANOVA test statistics for marine metazoan eDNA detected in Arctic ports based on presence/absence scores with the two combined gene primers (see legend Figure 1)

Primer	Source of variation	PERMANOVA		
		F value	R^2	Pr(>*F*)
Churchill				
18S	Month	15.172	.40453	<.001
COI		8.2736	.27032	<.001
18S	Sept vs. Oct	9.618	.237	.001
	Oct vs. Nov	10.277	.222	.001
	Nov vs. Dec	22.422	.384	.001
COI	Sept vs. Oct	4.861	.135	.001
	Oct vs. Nov	5.842	.139	.001
	Nov vs. Dec	10.999	.234	.001
Pond Inlet				
18S	Month	37.576	.59731	<.001
COI		25.348	.50014	<.001
18S	Aug vs. Sept	31.860	.456	.001
	Sept vs. Oct	29.580	.438	.001
	Oct vs. Nov	17.124	.311	.001
COI	Aug vs. Sept	23.718	.384	.001
	Sept vs. Oct	27.834	.423	.001
	Oct vs. Nov	13.528	.262	.001
Churchill and Pond Inlet				
18S	Month	17.275	.32125	<.001
COI		13.522	.27032	<.001

Note: These statistic tests were performed with a presence–absence transformation on read abundance matrix. Comparison of the 4 months and side-by-side comparison between months was done for each gene primer, each port, and both ports combined.

to the October group falling outside of the continuum formed by the other three months (Figure 3c,d). Community structure also differed between ports (PERMANOVA, $p < .001$; Table 1); although the same phyla were generally present within both ports, their read abundances were different (PERMANOVA, $p < .001$; Table S4). Despite the observed differences between ports, the trend of monthly continuity persisted when ports were combined for the PCoA results (Figure 3e,f).

The number of species detected showed similar monthly patterns between COI and 18S gene primers but was different between ports (Figure 4). In Churchill, the numbers of detected species considerably increased from September to October and then stabilized, whereas in Pond Inlet, they increased from August to September and October to November, but decreased from September to October.

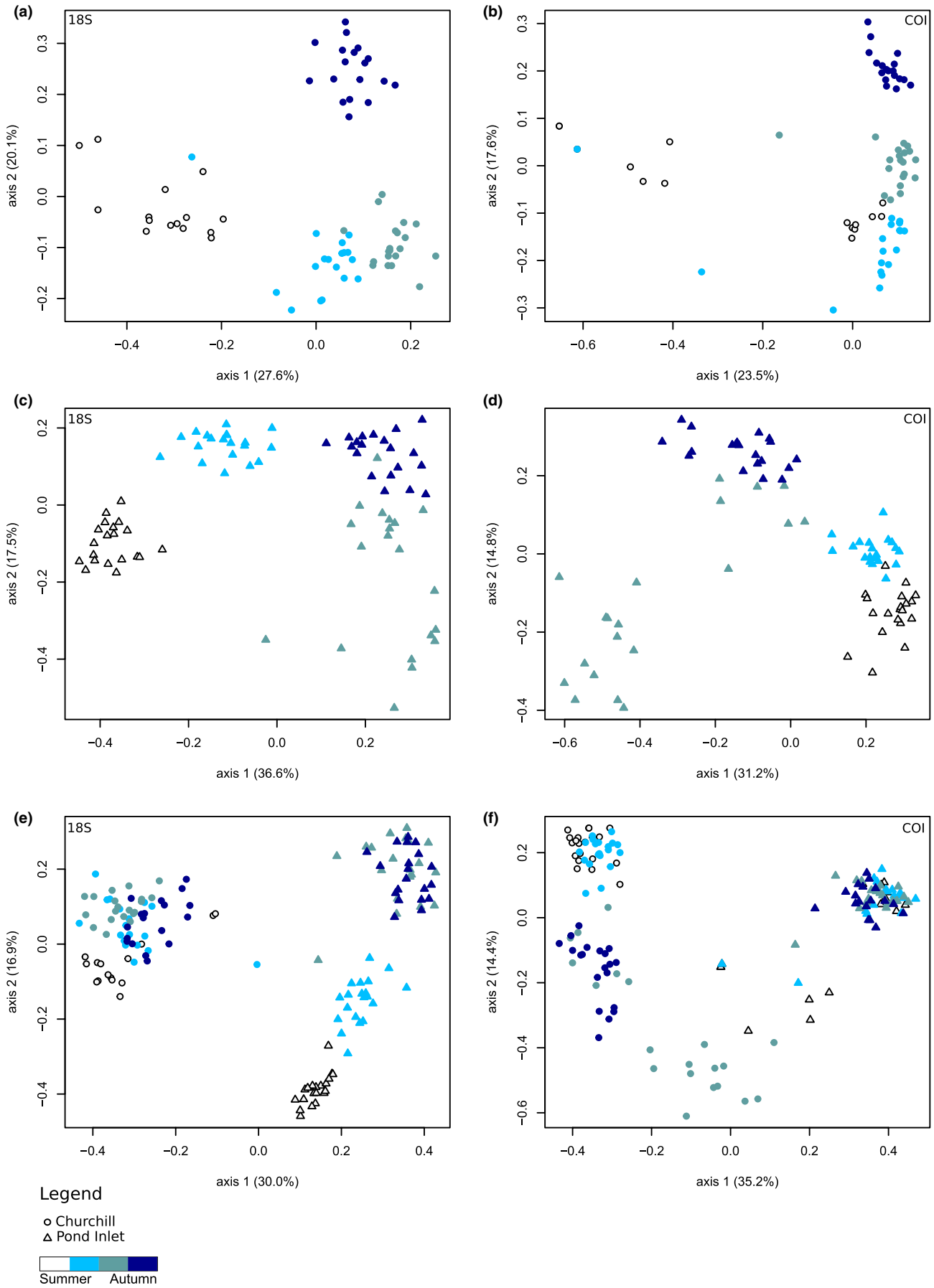
There was also evidence of a temporal transition in biodiversity based on the inverse Simpson index (Table 2). Significant differences among months were found with the inverse Simpson index for the both primers in Pond Inlet and for the COI primers in Churchill (Table 2). Moreover, a similar trend was observed with 18S primers in Churchill (GLM + ANOVA, $p = .006$; Table 2). Furthermore, the diversity variation among months represented by the inverse Simpson index was similar to the number of species detected per month (Figure 4). In Churchill, the diversity tended to increase from September to October and then slightly decreased until December. In Pond Inlet, the diversity in August and October was lower than September and November, respectively.

3.3 | Species variation by month

The temporal transition in eDNA was also evaluated using the read abundance of the top 30 species for both ports, which included a diverse array of taxa such as fish, various marine invertebrates (e.g., annelids, echinoderms, gastropods, and crustaceans), and marine mammals (e.g., polar bear, narwhal, and ringed seal) (Table 3; full list of species detected by eDNA in each port provided in Table S5 and S6). Among these, only six were common to Pond Inlet and Churchill corroborating the PERMANOVA results indicating divergent marine community structure between the two ports. This difference was partly due to the higher number of freshwater species in Churchill (13 species) compared with Pond Inlet (only two freshwater species) (Table 3).

Several trends in read abundance were observed among months with the 30 most abundant species (Figure S5). Significant peaks of read abundance were observed within a single month for a 17 species in both Arctic ports (Kruskal–Wallis test, all $p < .05$; Table S7 and Figure 5); a greater number of species were characterized by eDNA peaks in Pond Inlet than Churchill; 14 species showed an eDNA read abundance peak in Pond Inlet compared with only four in Churchill. Similarly, the read abundance of eDNA increased significantly during the last month for three species in Churchill and Pond Inlet respectively, suggesting the beginning of peak in eDNA (Figure 6 and Table S7). A trend in increased read abundance among the four months was revealed for 11 species in both ports combined (Figure S5A,B). The opposite trend with a steady decrease in the read abundance was observed for eight species in both ports (Figure S5A,B). Finally, trends of fluctuating decrease/increase in read abundance over time were observed for 15 species in both ports combined (Figure S5).

FIGURE 3 Principal coordinate analyses (PCoA) of time-series survey performed of marine metazoans detected with eDNA at the genus level for two Arctic ports based on presence/absence scores. (a) PCoA for Churchill with 18S primers, (b) PCoA for Churchill with COI primers, (c) PCoA for Pond Inlet with 18S primers, (d) PCoA for Pond Inlet with COI primers, (e) PCoA for both Arctic ports with 18S primers, (f) PCoA for both Arctic ports with COI primers. These PCoAs were performed using R (*vegan* package) with a presence–absence transformation on the read abundance matrix


(a)
18S
axis 2 (20.1%)
axis 1 (27.6%)
(b)
COI
axis 2 (17.6%)
axis 1 (23.5%)
(c)
18S
axis 2 (17.5%)
axis 1 (36.6%)
(d)
COI
axis 2 (14.8%)
axis 1 (31.2%)
(e)
18S
axis 2 (16.9%)
axis 1 (30.0%)
(f)
COI
axis 2 (14.4%)
axis 1 (35.2%)
Legend
Churchill
Pond Inlet
Summer
Autumn

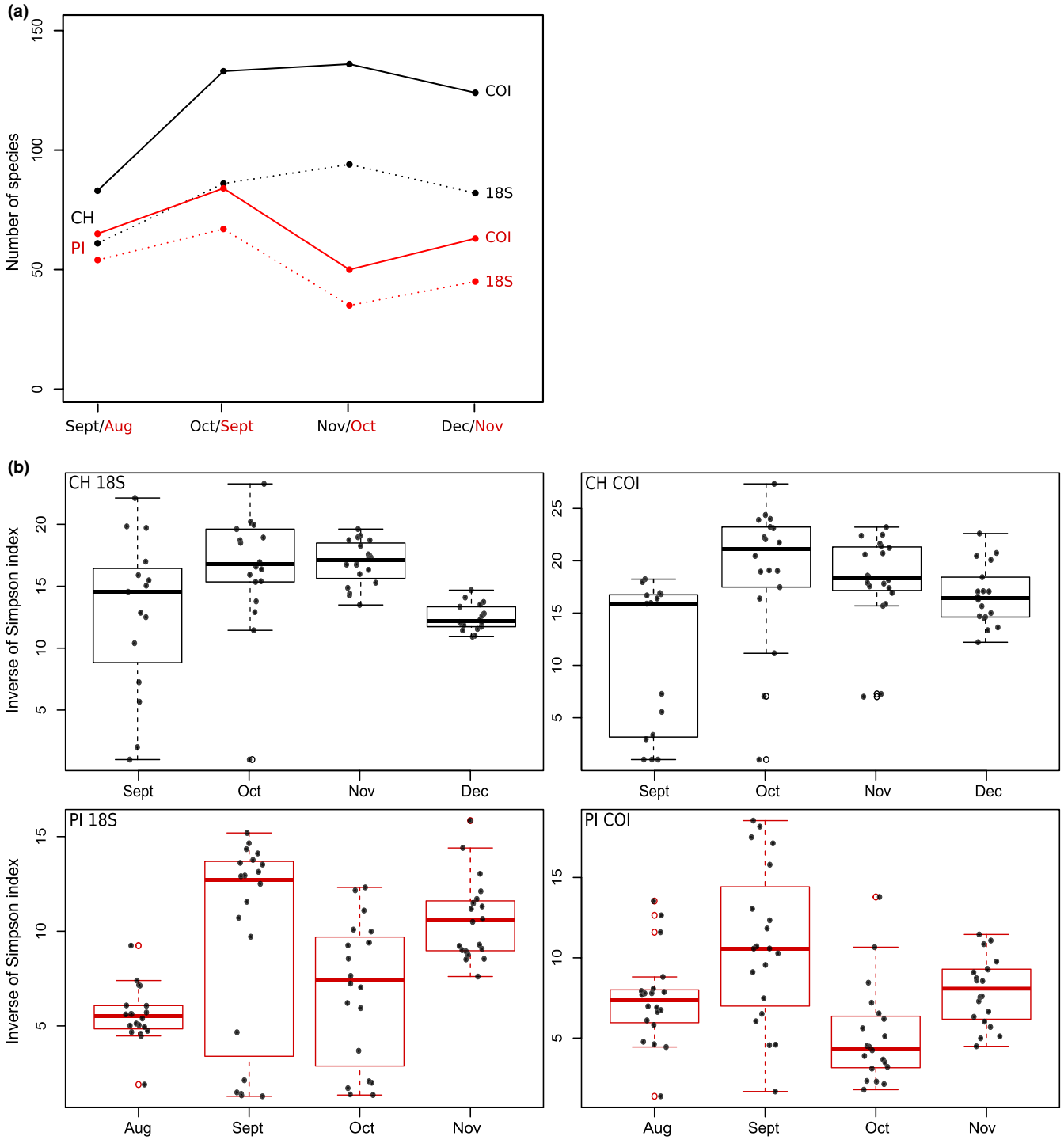


FIGURE 4 Time-series survey of detected species' number and marine metazoans diversity in both Arctic ports with combined gene primers. (a) Number of detected species. The ports Churchill and Pond Inlet are represented by black and red colors, respectively, while the 18S and COI primers are represented by dotted and continuous lines, respectively. (b) Box plot of diversity performed with the inverse of Simpson's index. The black points represented the sample for each month

4 | DISCUSSION

In this study, we investigated temporal transition in eDNA structure with the ultimate goal of providing guidelines to optimize and improve the standardization of Arctic coastal biodiversity monitoring. Our results characterize the temporal dynamics of eDNA in the coastal Arctic environment and highlight a strong transition from the summer to late fall Arctic marine community with the eDNA metabarcoding approach. Furthermore, we observed an eDNA peak of read abundance may coincide with a life cycle step of some marine species. Below, we discuss several aspects pertaining to the eDNA marine community change in response to the temporal transition

TABLE 2 Summary of GLM and ANOVA test statistics on the diversity (inverse of Simpson index) of marine metazoan eDNA in both Arctic ports (Churchill and Pond Inlet) with combined gene primers (18S and COI)

Ports	Primers	Effect	*Z* value	*F* value	*p* value
Churchill	*GLM + ANOVA*				
	18S	Month	–	4.479	.006
	COI		–	7.754	<.001
	GLM				
	18S	Sept vs. Oct	−2.389	–	.079
		Oct vs. Nov	−0.650	–	.915
		Nov vs. Dec	2.677	–	.037
	COI	Sept vs. Oct	−4.199	–	<.001
		Oct vs. Nov	0.112	–	.999
		Nov vs. Dec	0.520	–	.954
Pond Inlet	*GLM + ANOVA*				
	18S	Month	–	6.674	<.001
	COI		–	9.631	<.001
	GLM				
	18S	Aug vs. Sept	2.664	–	.038
		Sept vs. Oct	1.907	–	.225
		Oct vs. Nov	−3.268	–	.006
	COI	Aug vs. Sept	2.732	–	.032
		Sept vs. Oct	5.255	–	<.001
		Oct vs. Nov	−3.159	–	.008
	GLM + ANOVA				
Both	18S	Month	–	69.084	<.001
	COI		–	76.746	<.001

Note: The comparison of the four months and pairwise comparisons between months were done for each gene primer and port as well as both ports combined.

and the potential of eDNA to test hypotheses about marine life stages in the Arctic.

4.1 | Quality control and primers difference taxonomy

Although substantial progress has been made toward standardizing metagenomic eDNA studies, this approach has still limitations with variation due to different eDNA collection methods (filter types, volume of filtered water) and analyses in different laboratories (extraction, sequencing, and bioinformatics pipeline) (Deiner et al., 2017). Admittedly another aspect of the eDNA limitations was data analysis based on the read abundance which could be affected by some biases detailed below. Nevertheless, an increasing number of studies have recently shown that useful information about relative abundance can be extracted and interpreted from eDNA metabarcoding data (Bylemans et al., 2019; Evans et al., 2015).

In this study, thousands of sequences were removed, especially during the sequence assignment and filtration steps. Many sequences could not be assigned because, despite considerable barcoding effort, a high proportion of Arctic species have not yet been sequenced (Hardy et al., 2011). Among the assigned sequences, many were associated with insect taxa which were removed from the analyses as explained in the methods section.

Despite meticulous care in the field and within the laboratory to avoid contamination, contaminant sequences were observed in our 24 field and laboratory negative controls, albeit in very small proportions (Table S2 and S3). Among previous studies that sequenced PCR negative controls, many found contamination without bands following PCR amplification (Andruszkiewicz et al., 2017; Klymus et al., 2017; Macher & Leese, 2017) similar to our study. Contamination may often occur especially during the amplification step through volatile short PCR amplicons or "universal" primer bias (Axtner et al., 2018). Thus, in order to estimate the risk of contamination, sequencing of PCR negative controls must be applied systematically.

To improve species detection and reduce primer bias effects (e.g., Li et al., 2018), two set of primers of cytochrome c oxidase subunit I gene (COI) and two set of primers of the ribosomal gene 18S were used in this study. By combining two COI primer pairs or two 18S primers, the biodiversity accuracy may improve (Deagle et al., 2014). The COI gene is the most common primer used for metazoan detection and generally provides good species-level

TABLE 3 Species with the highest eDNA read abundances in Churchill (CH) and Pond Inlet (PI) ports as detected with the combined COI primers (see legend Figure 1). The table is divided into two parts: referenced Arctic species (i.e., those previously reported from the region; represented by the symbol √) and those not referenced (i.e., not previously reported from the region; represented by the symbol ×). The abbreviation Fresh designates freshwater species

Species	Ports	Environment	Phylum/type of animal	Repertories in Arctic database or literature	Authors, year
Cephalothrix spiralis	PI	Marine	Nemertea (Worm)	×	Coe, 1930
Chaetogaster diastrophus	Both	Fresh	Annelida (Worm)	×	Gruithuisen, 1828
Eunapius sp.	CH	Fresh	Porifera (Sponge)	×	Gray, 1867
Gyraulus circumstriatus	PI	Fresh	Mollusca (Gastropod)	×	Tryon, 1866
Motobdella montezuma	CH	Fresh	Annelida (Leech)	×	Davies et al., 1985
Physella ancillaria	CH	Fresh	Mollusca (Gastropod)	×	Say, 1825
Pseudosuberites nudus	CH	Marine	Porifera (Sponge)	×	Koltun, 1964
Slavina appendiculata	CH	Fresh	Annelida (Worm)	×	Udekem, 1855
Specaria josinae	CH	Fresh	Annelida (Worm)	×	Vejdovský, 1884
Spongilla sp.	CH	Fresh	Porifera (Sponge)	×	Lamarck, 1816
Stagnicola elodes	CH	Fresh	Mollusca (Gastropod)	×	Baker, 1911
Stylaria lacustris	CH	Fresh	Annelida (Worm)	×	Linnaeus, 1767
Aeginopsis laurentii	PI	Marine	Cnidaria (Hydrozoan)	√	Brandt, 1838
Arcteonais lomondi	CH	Fresh	Annelida (Worm)	√	Martin, 1907
Aurelia aurita	CH	Marine	Cnidaria (Jellyfish)	√	Linnaeus, 1758
Aurelia sp.	PI	Marine	Cnidaria (Jellyfish)	√	Lamarck, 1816
Balanus sp.	PI	Marine	Arthropoda (Barnacle)	√	Costa, 1778
Boreogadus saida	PI	Marine	Chordata (Fish)	√	Lepechin, 1774
Candona candida	CH	Fresh	Arthropoda (Crustacea)	√	Müller, 1776
Calanus glacialis	PI	Marine	Arthropoda (Crustacea)	√	Jaschnov, 1955
Cephalothrix linearis	PI	Marine	Nemertea (Worm)	√	Rathke, 1799
Clione limacina	PI	Marine	Mollusca (Gastropod)	√	Phipps, 1774
Coregonus clupeaformis	CH	Marine/fresh	Chordata (Fish)	√	Mitchill, 1818
Daphnia magna	CH	Fresh	Arthropoda (Crustacea)	√	Straus, 1820
Delphinapterus leucas	CH	Marine/Fresh	Chordata (Beluga whale)	√	Pallas, 1776
Gonothyraea loveni	PI	Marine	Cnidaria (Hydroid)	√	Allman, 1859
Halichondria panicea	CH	Marine	Porifera (Sponge)	√	Pallas, 1766
Harmothoe imbricata	Both	Marine	Annelida (Worm)	√	Linnaeus, 1767
Limacina helicina	PI	Marine	Mollusca (Gastropod)	√	Phipps, 1774
Lota lota	CH	Fresh	Chordata (Fish)	√	Linnaeus, 1758
Macoma balthica	CH	Marine	Mollusca (Mollusk)	√	Linnaeus, 1758
Monodon monoceros	PI	Marine	Chordata (Narwhal)	√	Linnaeus, 1758
Nais bretscheri	Both	Marine/Fresh	Annelida (Worm)	√	Michaelsen, 1898
Nais elinguis	CH	Marine/Fresh	Annelida (Worm)	√	Müller, 1774
Nereimyra aphroditoides	PI	Marine	Annelida (Worm)	√	Fabricius, 1780
Oithona similis	PI	Marine	Arthropoda (Crustacea)	√	Claus, 1866
Ophelia limacina	PI	Marine	Annelida (Worm)	√	Rathke, 1843
Paranais litoralis	CH	Fresh	Annelida (Worm)	√	Müller, 1780
Pectinaria granulata	Both	Marine	Annelida (Worm)	√	Linnaeus, 1767
Pista maculata	CH	Marine	Annelida (Worm)	√	Dalyell, 1853
Polyarthra dolichoptera	CH	Fresh	Rotifera (Worm)	√	Idelson, 1925
Polycirrus medusa	CH	Marine	Annelida (Worm)	√	Grube, 1850

(Continues)

TABLE 3 (Continued)

Species	Ports	Environment	Phylum/type of animal	Repertories in Arctic database or literature	Authors, year
Praxillella praetermissa	Both	Marine	Annelida (Worm)	√	Malmgren, 1865
Pseudocalanus acuspes	Both	Marine	Arthropoda (Crustacea)	√	Giesbrecht, 1881
Pseudocalanus minutus	PI	Marine	Arthropoda (Crustacea)	√	Krøyer, 1845
Pseudocalanus newmani	CH	Marine	Arthropoda (Crustacea)	√	Frost, 1989
Pseudoscalibregma parvum	PI	Marine	Annelida (Worm)	√	Hansen, 1879
Pusa hispida	PI	Marine	Chordata (Ringed seal)	√	Schreber, 1775
Scalibregma inflatum	PI	Marine	Annelida (Worm)	√	Rathke, 1843
Spio filicornis	PI	Marine	Annelida (Worm)	√	Müller, 1776
Strongylocentrotus droebachiensis	PI	Marine	Echinodermata (Sea urchin)	√	Müller, 1776
Terebellides stroemii	PI	Marine	Annelida (Worm)	√	Sars, 1835
Tisbe furcata	PI	Marine	Arthropoda (Crustacea)	√	Baird, 1837
Ursus maritimus	PI	Marine	Chordata (Polar bear)	√	Phipps, 1774

identification (Hebert et al., 2003). However, several studies have revealed poor amplification quality for some aquatic taxa such as crustaceans or nematodes (Bhadury et al., 2006; Elias, 2008; Jeffery, 2011; Zhan et al., 2014). As shown here, the 18S primers recovered a broader range of taxa than COI and amplified complex communities of taxa such as nematodes and zooplankton, suggesting that the 18S primers were a good complement to COI (Zhan et al., 2014). The species detected using these two gene primers were very different due to the dominance of some taxa and the distinct sequences available in reference databases (BOLD and Silva) for one primer set versus the other. In sum, the same significant findings with COI and 18S primers provide support for the reliability of these eDNA results in reflecting the transition of the marine community from summer to late fall.

4.2 | The temporal transition of the eDNA Arctic marine community

The lack of knowledge pertaining to the spatiotemporal variation of eDNA in vast and complex ecosystems has limited its use for detecting community shifts over time and application to coastal biomonitoring and management (Deiner et al., 2017). Notwithstanding stochastic factors that may influence the eDNA detected from metazoan marine coastal communities, our results highlight a transition from the summer marine community to the late fall marine community detected through eDNA in the Arctic, indicating that eDNA offers the potential to provide information about changes in Arctic coastal ecosystems. Previous studies have reported temporal eDNA transition in coastal populations. For example, Stoeckle et al. (2017) and Sigsgaard et al. (2017) observed a consistent trend between eDNA of various fish species and corresponding migrations. The seasonal movement (fish migration or plankton vertical migration) and activities (physiology, metabolism, or behavior) of species may reflect observed transitions of marine communities detected through eDNA analysis. Under ice surveys are often difficult, and therefore, little is known about the winter ecology of Arctic marine species, including reproduction periods (Wassmann et al., 2011). Here, the observed changes in transitional ecosystem of eDNA communities suggest that eDNA metabarcoding could be a useful alternative to traditional species surveys for providing information about the reproduction periods and movements of Arctic species.

4.3 | Putative relationship between peaks in eDNA read abundance and the species ecology

A better understanding of eDNA temporal changes is essential for providing guidelines on the best periods to monitor for improved species detections (e.g., optimizing invasive and/or endangered species detection). In this study, peaks in eDNA read abundance were observed for 19 species among the 60 most abundant species for both ports. Although uncertainty exists about the relationship between eDNA abundance and species ecology, several studies observed peaks of read abundance corresponding to breeding or larval hatch in the freshwater environment (Buxton et al., 2018; Erickson et al., 2016; Laramie et al., 2015; Spear et al., 2015; Tillotson et al., 2018; Xu et al., 2018). Peaks in eDNA were also observed in Chinook Salmon (*Oncorhynchus tshawytscha*), Sockeye Salmon (*Oncorhynchus nerka*), and Bighead Carps (*Hypophthalmichthys* spp.) during spawning periods (Erickson et al., 2016; Laramie et al., 2015; Tillotson et al., 2018). Buxton et al. (2018) also highlighted two peaks in eDNA corresponding to breeding and larval hatch, respectively, in the Crested Newt (*Triturus cristatus*).

In this study, the eDNA peak of seven species occurs in the same range of time as one of their life cycle steps, as reported in the literature (Table 4). For invertebrates, *Pseudocalanus acuspes* and

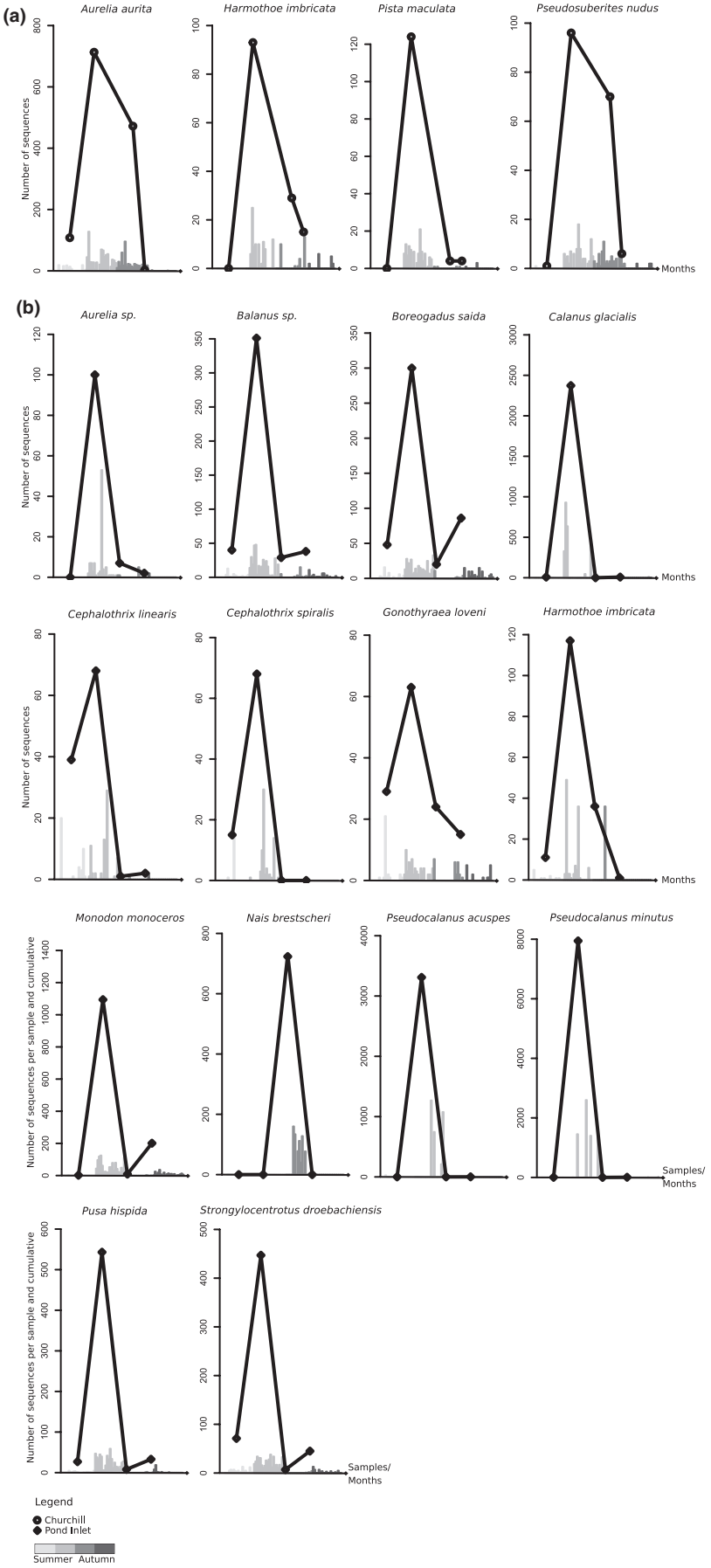


FIGURE 5 Peaks in eDNA observed in several Arctic species from both ports with the COI primers. (a) Arctic Species from Churchill with a peak in eDNA in October or November. (b) Arctic Species from Pond Inlet with a peak in eDNA in September or October. The black line represents the sum of the read abundance for all the samples by month; each month is characterized by a point. The grey bar plot illustrates the read abundance of the given taxon in each sample. There is a color gradient: from light grey representing the first month to dark grey characterizing the last month

Calanus glacialis have copepodite (larval stage) maturation phase in autumn suggesting the peak of eDNA might correspond to the time of molt for these species (McLaren et al., 1989; Søreide et al., 2010). The eDNA peak of the gastropod *Limacina helicina* may characterize a spawning period leading to the presence of numerous veligers (larval stage) and juveniles during late fall and winter (Gannefors et al., 2005). The peak of eDNA of the jellyfish *Aurelia aurita* may correspond with the peak in ephyrae (new jellyfish) abundance during October (Lucas, 2001). However, *Aurelia aurita* was not morphologically identified to species level in Pond Inlet. Further research is needed to verify presence of this species in the Arctic. For vertebrates, the Arctic Cod (*Boreogadus saida*) could spawn in September, and thus, the eDNA peak could reflect spawning or larval aggregations (Graham & Hop, 1995). Finally, the eDNA peak of the narwhal (*Monodon monoceros*) and the ringed seal (*Pusa hispida*) may correspond to their migration toward wintering areas in Baffin Bay (Harwood et al., 2015; Heide-Jørgensen et al., 2003; Smith et al., 1991).

More studies are needed to evaluate putative links between peaks in eDNA and specific segments of these species' life cycles. In this study, two species characterized by an eDNA peak (*Pseudocalanus minutus* and *Strongylocentrotus droebachiensis*) had no corresponding life cycle step from the literature occurring in the same range of time as eDNA peak (Himmelman, 1978; Lischka & Hagen, 2005; Table 4). Peaks in eDNA for another species, the scale worm *Harmothoe imbricata* could be associated with gametogenesis (oogenesis and spermatogenesis) which starts in September or October by the apparition and proliferation of gametic cells (Daly, 1972, 1974; Plyuscheva et al., 2004), although we cannot determine whether the gametogenesis may cause eDNA peaks. However, this species was characterized by a peak in eDNA during the second month of sampling in both ports (Table 4) suggesting that these peaks in eDNA were not random. Although the second month of eDNA collection was done at different times (September and October for Pond Inlet and Churchill, respectively), abiotic conditions (temperature, snow depth) were similar (Table S8). Finally, there are no published studies on the ecology of the remaining nine species that exhibited seasonal peaks in eDNA making it difficult to relate eDNA read abundance to their life histories (Table 4).

Monthly sampling throughout the year would be needed to determine the presence of other peaks in eDNA. Our result showed that seven species were characterized by an increased eDNA read abundance during the last month of sampling suggestive of a late fall peak in eDNA (Figure 6; *Oithona similis*, *Pseudocalanus newmani*, *Spongilla sp.*, *Eunapius sp.*, *Scalibregma inflatum*, and *Terebellides stroemii)*. For example, the putative peak in eDNA of *Oithona similis* may correspond with peak in the *Oithona similis* population abundance or to a reproduction period observed in November (Lischka & Hagen, 2005).

The warming of the Arctic accompanied by the potential invasion by new species will create unprecedented changes in this ecosystem (Goldsmit et al., 2018). Studies of ecosystem stability often refer to the equilibrium between reproduction period and food resources to ensure synchronization of hatch with peaks in food availability (Cushing, 1990; Moline et al., 2008). For example, the seasonal spawning of the copepod *Calanus finmarchicus* occurs just before lobster spawning (*Homarus americanus*) such that lobster larvae can feed on the copepod larvae; poor synchronization between reproduction in these two species may lead to a decline in recruitment of young lobsters (Carloni et al., 2018). The eDNA approach may have potential for improving our understanding of species ecology, for example, synchronism among the peaks in eDNA read abundance and reproduction period of various species. Such information is paramount in predicting ecosystem changes, including shifts in the reproduction period overtime. In the Arctic, species such as the copepod *Calanus glacialis* or its main consumer, the Arctic Cod, are key species for the transfer of energy through Arctic marine ecosystems (Darnis et al., 2012). A lack of synchronism in recruitment with prey availability could have a severe impact on the entire Arctic ecosystem (Carloni et al., 2018). Although more studies are needed to validate whether eDNA metabarcoding can successfully depict an increase in taxa abundance within a community as reproduction periods as well as species abundance and movement, our results support the idea that eDNA metabarcoding holds great potential for improving knowledge of life cycles for various taxa in complex coastal communities. In parallel, a better understanding of eDNA ecology will provide guidelines regarding the best periods for monitoring to improve species detections (e.g., optimizing invasive species detections).

4.4 | How the ice cover may affect the ecology of eDNA?

Ice cover may promote eDNA preservation and detection by slowing eDNA degradation due to a limited UV exposure and cold water temperature during the winter (Barnes et al., 2014; Lacoursière-Roussel et al., 2018). However, eDNA preservation is difficult to quantify because of the difference between levels of activity (metabolism, behavior) in different species during summer and winter. In fact, the decrease in metabolism due to cold water may lead to a decrease in eDNA release/detection (Lacoursière-Roussel et al., 2016). On the other hand, despite cold environmental conditions during winter, biological activity has been documented in the Arctic, for instance for bacterioplankton, zooplankton, and the Arctic Cod (Darnis et al., 2012). In Churchill port, the diversity (inverse of Simpson index) and the richness (number of species) decreased under ice-cover period, whereas the diversity and the richness increased in Pond Inlet. Our results suggest an improvement in species detection when water is collected under the ice-cover period within the marine environment (Pond Inlet). Further investigations are necessary to understand the eDNA ecology in estuarine environment (Churchill), especially the freshwater influence.

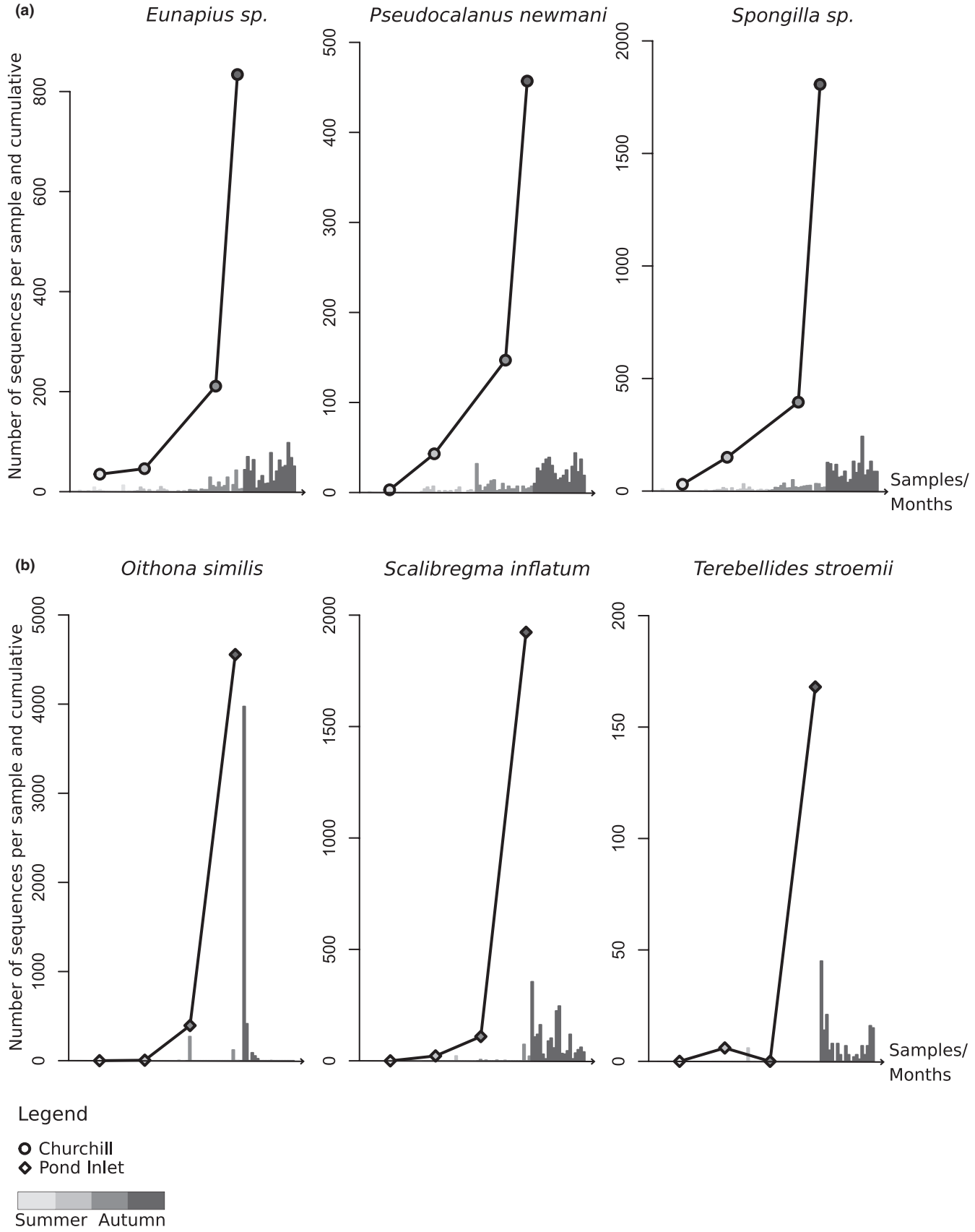


FIGURE 6 Putative peaks in eDNA observed in several Arctic species from both ports with the COI primers. (a) Arctic species from Churchill with a putative peak in eDNA in December. (b) Arctic species from Pond Inlet with a putative peak in eDNA in November. The black line represents the sum of the read abundance for all the samples by month; each month is characterized by a point. The grey bar plot illustrates the read abundance of the given taxon in each sample. There is a color gradient: from light grey representing the first month to dark grey characterizing the last month

TABLE 4 Comparison between peaks in eDNA observed in several metazoan marine species and related ecological studies. These species were detected with the combined COI primers (see legend Figure 1). The study sites of the references cited here were circumpolar except for McLaren et al. (1989) and Himmelman (1978) which were located in Nova Scotia and Newfoundland, Canada. CH and PI refer to Churchill and Pond Inlet, respectively. The abbreviations Sept and Oct designate months of September and October

Species	Taxonomic group	Port	Month of peak eDNA read abundance	Putative congruent life cycle	References
Aurelia aurita	Cnidaria (Jellyfish)	PI	Oct	Peak of ephyrae in October	Lucas (2001)
Calanus glacialis	Arthropoda (Crustacea)	PI	Sept	Peak of copepodites in September	Søreide et al. (2010)
Limacina helicina	Mollusca (Gastropod)	CH	Oct	Peak of veligers in Autumn	Gannefors et al. (2005)
Pseudocalanus acuspes	Arthropoda (Crustacea)	PI	Sept	Peak of copepodites in Autumn	McLaren et al. (1989)
Boreogadus saida	Chordata (Fish)	PI	Sept	Spawn in September	Graham and Hop (1995)
Monodon monoceros	Chordata (Narwhal)	PI	Sept	Migration in Autumn	Heide-Jørgensen et al. (2003)
Pusa hispida	Chordata (Ringed seal)	PI	Sept		Smith et al. (1991); Harwood et al. (2015)
Pseudocalanus minutus	Arthropoda (Crustacea)	PI	Sept	No temporal link between the eDNA peaks and the life cycle	Lischka and Hagen (2005)
Strongylocentrotus droebachiensis	Echinodermata (Sea urchin)	PI	Sept		Himmelman (1978)
Harmothoe imbricata	Annelida (Worm)	CH	Oct	Gametogenesis from September onwards	Daly (1972), Curtis (1977)
Harmothoe imbricata	Annelida (Worm)	PI	Sept		
Aurelia sp.	Cnidaria (Jellyfish)	PI	Sept	No study available	–
N Balananus sp.	Arthropoda (Barnacle)	PI	Sept		
Cephalothrix linearis	Nemertea (Worm)	PI	Sept		
Cephalothrix spiralis	Nemertea (Worm)	PI	Sept		
Gonothyraea loveni	Cnidaria (Hydroid)	PI	Sept		
Nais bretscheri	Annelida (Worm)	PI	Oct		
Pista maculata	Annelida (Worm)	CH	Oct		
Pseudocalanus acuspes	Arthropoda (Crustacea)	PI	Sept		
Pseudosuberites nudus	Porifera (Sponge)	CH	Oct		

5 | CONCLUSION

Understanding the temporal dynamics of eDNA in the environment is essential for interpreting long-term patterns of biodiversity based on this indirect, yet powerful approach. eDNA concentrations in water vary greatly within days, likely due to local oceanographic (e.g., tides) and ecological (e.g., planktonic daily migrations) processes. However, despite the incomplete understanding of factors impacting eDNA variation in the environment, the transitional changes in eDNA communities observed between months in this study suggest that eDNA metabarcoding could be a powerful biomonitoring tool to better understand complex marine communities change over a long-term duration.

Admittedly, limited understanding of how eDNA read abundance varies as a function of species behavior and life cycle could lead to misinterpretation of eDNA results. Here, we show that over a relatively short time period of four months, eDNA read abundance of some species display gradual monthly changes that appear to be linked to previously documented shifts in their life cycle, thus lending support to the biological meaning fullness of eDNA information for documenting demographic changes. This possible link deserves further investigation. Developing complementary bioindicators able to track ecosystem changes based on the sequence information obtained from eDNA, across time will help to pose new hypotheses and accelerate knowledge about human environmental impacts. Clearly, more research is needed toward evaluating whether there is a stable, recurrent, seasonal community structure across years and environmental conditions and whether community changes over longer time frames can be reliably detected using eDNA.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

ALR, KH, and LB conceived the study. ALR, KH, ES, and LB contributed resources. ALR, KH, AA, and LF contributed to field coordination/data collection. EN provided bioinformatics support (Barque). MS analyzed the data and wrote the manuscript, while ALR, KH, and LB helped to draft and improve the manuscript. All authors edited the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

The eDNA sequences are available in the Sequence Read Archive (SRA) database at NCBI under BioProject ID: PRJNA436081 and the SRA accession number: SRP133584.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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