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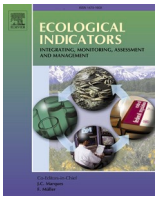

Meiofauna as a valuable bioindicator of climate change in the polar regions

Francesca Leasi [a,*], Joseph L. Sevigny [b], Brandon T. Hassett [c]

[a] Department of Biology, Geology and Environmental Science. University of Tennessee at Chattanooga. 615 McCallie Ave, Chattanooga, TN 37403, United States
[b] Hubbard Center for Genome Studies, University of New Hampshire, 35 Colovos Rd, Gregg Hall, Durham, NH 03824, United States
[c] Department of Arctic and Marine Biology, UiT – The Arctic University of Norway. Framstredet 6, 9019 Tromsø, Norway

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ABSTRACT

Establishing robust estimates of polar marine biodiversity is important for interpreting future changes in the Arctic; however, despite a recent increase in scientific expeditions, this region remains relatively underexplored. Particularly overlooked in biodiversity assessments are small species, such as protists, fungi, and many small invertebrates that are collectively known as meiofauna. These species contribute to the foundation of food webs and are crucial for the survival of larger species that are economically and socially important. The application of high-throughput sequencing methodologies has proven effective for biomonitoring small metazoan species but has sparingly been applied in the Arctic. We used a metabarcoding approach to assess the diversity of sea ice and sediment-associated metazoans from Utqiaġvik (Barrow), Alaska. Sea ice and sediment samples were collected six times over eight months (January through August) encompassing three seasons (winter, spring, and summer) from polar night to ice-out in August. Biodiversity was assessed as both richness and community composition by incorporating incidence data and phylogenetic distance. Environmental conditions associated with ice, sediment, water, and snow were measured and tested for possible correlations with biodiversity estimates. We found a high number of taxa distributed locally, suggesting that metabarcoding can be effectively applied to Arctic biomonitoring programs. In addition, these results show that season and habitat are significant predictors of meiofaunal biodiversity, supporting hypotheses that meiofauna can be used as a valuable indicator of climate change.

1. Introduction

The Arctic Ocean is a semi-enclosed ocean covered by approximately seven million square kilometers of ice in summer and 15 million square kilometers of ice in winter. Arctic sea ice plays a fundamental role in governing the extent of the photic zone by attenuating light transmission in covered areas. Sea ice governs and supports the life history strategies of many Arctic organisms, including polar cod nursing (Huserbråten et al., 2019) and benthic polychaeta larval development (Carey and Montagna, 1982) while providing habitat for copepod larvae (Bluhm et al., 2018) and sea ice endemic species (Arrigo, 2014; Kiko et al., 2017). Sadly, the rise in atmospheric temperatures, coupled with elevated heat flux into the Arctic Ocean from warming Atlantic and Pacific waters, is reducing sea ice extent, concentration, and thickness with consequences associated with snow and rain precipitation regimes (Granskog et al., 2016; Hezel et al., 2014; 2012;; Webster et al., 2014). Snow coverage regulates photosynthetic ice algal growth by significantly changing light attenuation (Perovich, 2006; Yun et al., 2019). The decrease of snow coverage due to climate change is driving ice-covered ecosystems towards tipping points, with an associated loss of biodiversity and shifting equilibrium states (Duarte et al., 2012; Nelson et al., 2014; Yurkowski et al., 2018).

The survival of species in the Arctic, including humans, strongly depends on seasonal ice formation (Baztan et al., 2017; Bromaghin et al., 2015; Grainger, 1991; Granskog et al., 2016; Lebrun et al., 2019; Massonnet et al., 2018). Seasonality plays a fundamental role in the Arctic due to fluctuations between extreme winter conditions (<−40 °C) and warming summers, with large temperature gradients within seasons. During ice formation, hypersaline liquid (brine) forms a reticulate network of channels, whose volume and salinity are governed by temperature. The large gradient of temperature across the vertical ice plane, extending from the ice-air interface (close to atmospheric temperatures) to the ice-water interface (~−1.8 °C), allows for the formation of a variety of microhabitats, which are inhabited by small organisms, such as bacteria, protists, and meiofauna (Ewert and Deming, 2013; Hassett and Gradinger, 2016; Hunt et al., 2016).

* Corresponding author.
E-mail address: francesca-leasi@utc.edu (F. Leasi).

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Investigating the effects of ice melting due to climate change on Arctic biodiversity is an urgent issue (Bluhm et al., 2011). Despite a recent increase in scientific exploration of the area, the region remains relatively underexplored, and its biodiversity is largely unknown (Gill et al., 2008), as thousands of Arctic marine species remain undescribed (Bluhm et al., 2011). As a result, many species might be lost or regionally displaced before being observed, classified, and appreciated. It is difficult to discern which taxonomic group is most undercharacterized, relative to its ecological impact, as the diversity of major biological lineages is still being described for the first time in the Arctic (Hassett et al., 2019). However, the diversity of microbes and small invertebrates appear to be a consensus gap in Arctic science's knowledge (Bluhm et al., 2018; Gradinger and Bluhm, 2020; Hassett and Gradinger, 2016; Marquardt et al., 2011; Nozais et al., 2001; Poulin et al., 2011; Zeppilli et al., 2017). These lower-trophic organisms comprise the majority of biomass in the ocean, are the base of complex food webs (Gradinger and Bluhm, 2020), and are consequently crucial for the survival of larger species that are economically and socially important (Schmid-Araya and Schmid, 2000). Small species, such as meiofauna, are also important bioindicators for environmental and climate change (Leasi et al., 2016; Zeppilli et al., 2015), and because of their short generation time and fast response to changing conditions, they can be used as a model to understand the effect of ice melting on biodiversity.

The meiofauna community inhabiting the Arctic has been investigated across various geographic locations (e.g., Svalbard, Greenland, Canada, Alaska, and the deep sea) and habitats, such as the sediment (benthic meiofauna), water column (pelagic meiofauna), and sea ice (sympagic meiofauna) (Aswathy et al., 2017; Hoste et al., 2007; Kendall et al., 1997; Michel et al., 2002; Nozais et al., 2001; Rysgaard et al., 2000; Urban-Malinga et al., 2004; Włodarska-Kowalczuk et al., 2016; Krishnapriya et al., 2019). At a spatial scale, studies have revealed a broad Arctic distribution of phyla, which is primarily dominated by rotifers and nematodes, and strong variability in community composition driven primarily by location (Bluhm et al., 2011; Gradinger and Bluhm, 2005). At a temporal scale, meiofauna occurrence may be affected by the presence of primary producers, such as algae, which depend on light. Sympagic meiofauna feed on the seasonally abundant and highly concentrated ice algae (Bluhm et al., 2018; Gradinger and Bluhm, 2020; Grainger and Hsiao, 1990). This foraging allows high meiofaunal growth rates early in the season while the phytoplankton bloom develops (McConnell et al., 2012). Yet, other meiofaunal taxa, such as some nematodes, exhibit an alternative feeding modality by directly absorbing dissolved organic matter (Tchesunov and Riemann, 1995). Sympagic meiofaunal predators are rare, likely due to space limitations in the sea ice habitat (Bluhm et al., 2017). Regardless of the feeding strategy, it is clear that sea ice not only provides a feeding substrate for meiofauna but also acts as shelter and a safe nursery grounds for those organisms that live in such an extreme environment (Schnack-Schiel, 2003). However, it is not clear if and how the loss of ice would affect the meiofaunal biodiversity and community composition in the Arctic.

This work contributes to filling biodiversity knowledge gaps of meiofauna in the Arctic by investigating if meiofauna are informative bioindicator for climate change, specifically ice melting, in the polar regions. The main novelty of this work is that, for the first time, the biodiversity of meiofauna from both ice and surrounding sediment is simultaneously investigated in order to examine potential shifts in meiofaunal taxa between the two habitats and across seasons. Moreover, although meiofaunal ecology has been explored throughout the Arctic, few sympagic meiofaunal taxa have been identified using molecular techniques (Marquardt et al., 2018). We use a metabarcoding approach to molecularly assess the sympagic and under-ice sediment metazoans and the relationship of this diversity to environmental factors. Both ice and sediment samples were collected from Utqiaġvik (Barrow), Alaska, between January and August 2014. In this area, ice starts to freeze in October or November and breaks up between June and July (Mahoney et al., 2007). Environmental conditions related to snow cover, ice thickness, brine volume, water temperature, and salinity were measured and tested for possible correlations with biodiversity estimates.

2. Material and methods

2.1. Sampling and measurement of environmental parameters

The sampling procedure followed the same protocol described in Hassett and Gradinger (2016). Ice cores and seafloor sediment samples

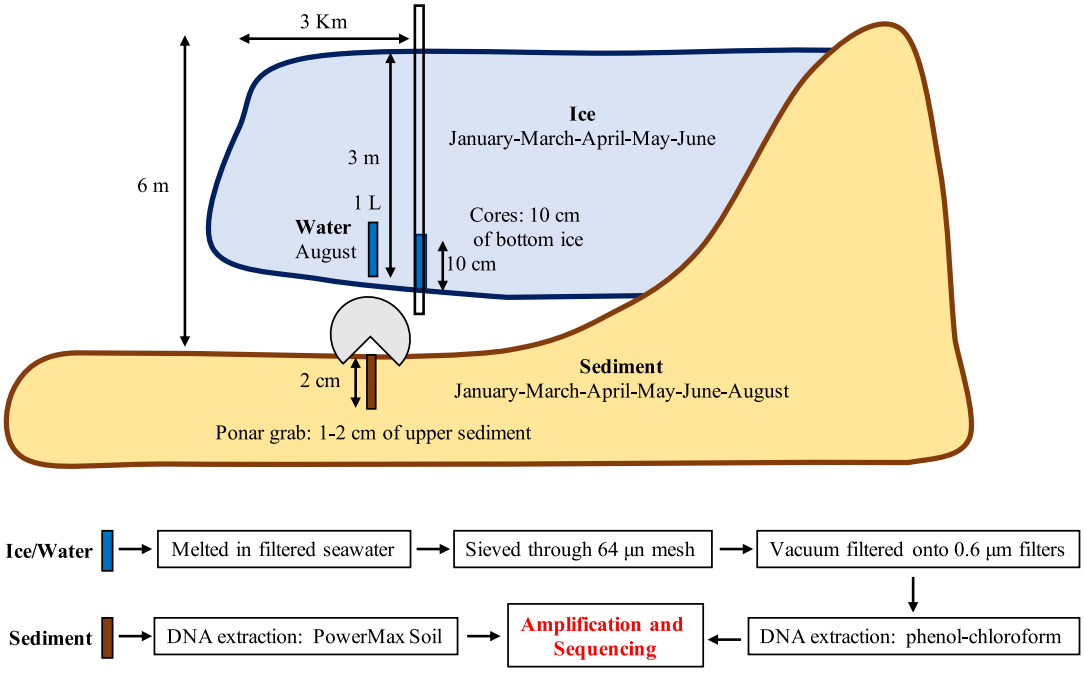

Fig. 1. Schematic view showing the procedure for ice, sediment, and water sampling (top) and the procedure for sample processing (bottom). The figure is not drawn to scale.

Table 1
Sampling habitat, date of sample, and environmental parameters measured for this study. The number of phyla and the number of genetic reads assessed with metabarcoding are indicated for each sample activity. BrSal, brine salinity in ‰; BrVol, brine volume fraction as a %; IceTh, ice thickness measured in meters; Reads, number of genetic reads; SflSal, seafloor salinity in ‰; SnDpt; snow depth measured in meters; T Ice/Water, temperature of ice or water measured in °C.; NA, not applicable; NM, not measured.

Habitat	mm/dd/2014	BrSal	BrVol	IceTh	Phyla	Reads	SflSal	SnDpt	T Ice/Water
Ice	01/13	65.6	9.7	78	9	34,254	NA	23.5	−3.8
Ice	03/10	68.8	8.8	102	9	1619	NA	12.5	−4
Ice	04/09	45.8	16.7	134	7	66,460	NA	12.8	−2.6
Ice	05/28	32.2	13.6	139	6	172	NA	5.6	−1.8
Ice	06/15	0.1	52.3	129.5	7	266	NA	6	−0.01
Water	08/13	NA	NA	NA	10	2396	NA	NA	0.5
Sediment	01/13	NA	NA	NA	7	32,955	NM	NA	NA
Sediment	03/10	NA	NA	NA	8	41,313	31.1	NA	NA
Sediment	04/09	NA	NA	NA	8	10,237	24.8	NA	NA
Sediment	05/28	NA	NA	NA	8	21,972	NM	NA	NA
Sediment	06/15	NA	NA	NA	11	35,634	31.7	NA	NA
Sediment	08/13	NA	NA	NA	9	25,893	27.5	NA	NA

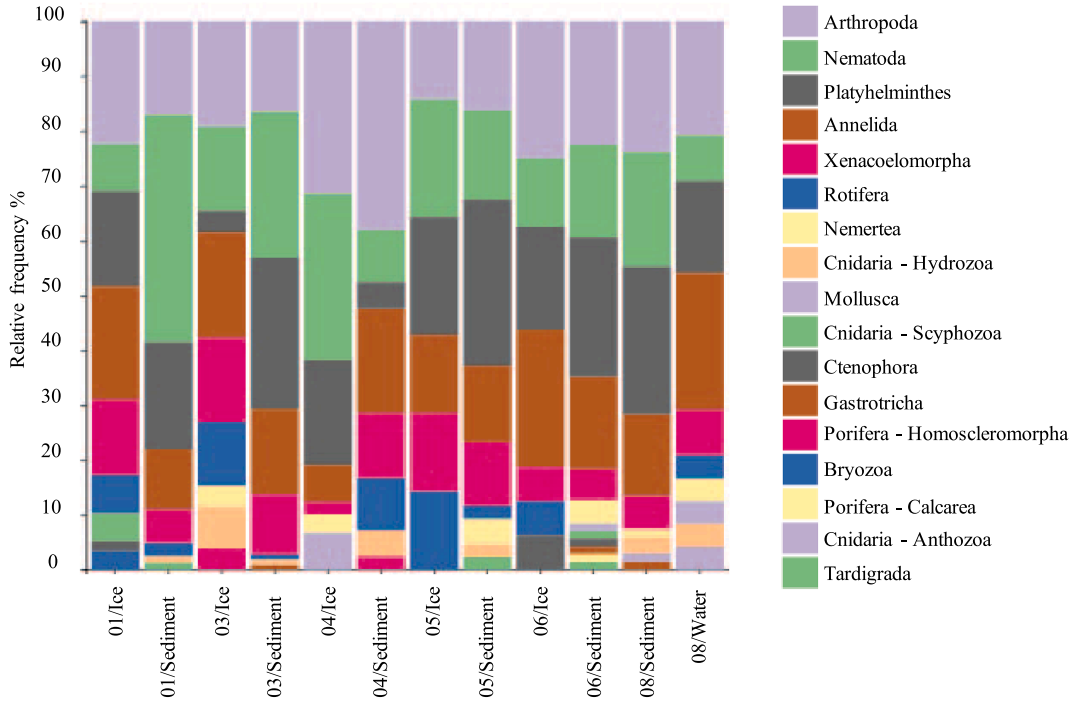

Fig. 2. BarPlots showing the frequency of the *major taxa* in each sample. The frequency is based on incidence data (number of ASVs); taxa are listed in order of descending frequency. The complete list of taxa at lower taxonomic levels is available in Table S1. Samples are indicated as "sampling month/habitat."

were collected at about 3 km from the ice edge near Utqiaġvik (Barrow), Alaska (N 71.3647; W 156.5242). Three ice cores were extracted in January, March, April, May, and June 2014, using a 9-cm diameter Kovacs ice corer (Fig. 1). The bottom 10 cm of sea ice contains the majority of meiofaunal taxa and biomass (Bluhm et al., 2018; Schünemann and Werner, 2005). Therefore, we sampled the bottom 10 cm of each core by sectioning ice with an ethanol-sterilized handsaw. Ice core sections were melted into 1 L of 0.22-µm filtered seawater. In August, triplicate 1 L water samples were collected in a Kemmerer water sampler at 3 m depth (the total depth at that site was about 6 m). Melted ice cores/water were sterilely sieved (64 µm mesh) and vacuum filtered onto 0.6 µm DTTP filters (Millipore). Three independent sediment samples were collected along with the ice or water using a Ponar grab and stored in sterile polypropylene tubes (Fig. 1). The top ~2 cm of sediment was considered for this work; lower layers were represented by permafrost. Samples were stored at −80 °C until DNA extraction.

The temperature was measured by extracting a separate ice core and rapidly measuring internal core temperature with a handheld temperature probe. Bulk salinity was measured after melting ice core sections with a handheld YSI salinity probe. Brine salinity and brine volume fraction were calculated according to the equations of Cox and Weeks (1986).

2.2. DNA amplification and sequencing

DNA amplification and sequencing protocols followed Hassett and Gradinger (2016). DNA from the sediment was extracted using the PowerMax Soil DNA isolation kit (MO-BIO). Sea ice filter extractions were conducted by bead beating for 1 min in phosphate buffer, followed by phenol–chloroform extraction. Replicates were pooled before performing the polymerase chain reaction (PCR). Target amplicons were generated using the eukaryote-specific primers 18S-82F (5′-GAAACTGCGAATGGCTC-3′) and Ek-516R (5′-ACCAGACTTGCCCTCC-3′) (López-García et al., 2003). Sequencing libraries were prepared using the Illumina TruSeq DNA Library Preparation Kit LT at Michigan State University following the manufacturer's protocol with six samples per run. High-throughput sequencing was conducted on a MISEQ v2 flow cell using 2 × 250 paired-end reads. Base-calling was performed by

Table 2
List of phyla and number of respective ASVs assessed for each sample and their total. Sampling habitat and month of sampling are indicated. Phyla are listed in alphabetic order.

Habitat	Sampling Month	Annelida	Arthropoda	Bryozoa	Cnidaria	Ctenophora	Gastrotricha	Mollusca	Nematoda	Nemertea	Platyhelminthes	Porifera	Rotifera	Tardigrada	Xenacoelomorpha	Total
Ice	January	12	13	2	3	1	0	0	5	0	10	0	4	0	8	58
Ice	March	5	5	0	2	0	0	0	4	1	1	1	3	0	4	26
Ice	April	6	28	0	0	0	0	6	27	3	17	0	0	0	2	89
Ice	May	2	2	0	0	0	0	0	3	0	3	0	2	0	2	14
Ice	June	4	4	0	0	1	0	0	2	0	3	0	1	0	1	16
Water	August	6	5	0	1	1	0	1	2	1	4	0	1	0	2	24
Sediment	January	9	14	0	2	0	0	0	34	0	16	0	2	0	5	82
Sediment	March	17	18	0	1	0	1	0	29	0	30	0	1	0	12	109
Sediment	April	8	16	0	2	0	0	0	4	0	2	1	4	0	5	42
Sediment	May	6	7	0	2	0	0	0	7	2	13	0	1	0	5	43
Sediment	June	12	16	0	1	1	1	1	12	3	18	0	0	1	4	71
Sediment	Aug	10	16	0	2	0	1	1	14	1	18	0	0	0	4	67
Total		48	75	2	13	2	3	8	65	6	73	1	9	1	23	329

Illumina Real-Time Analysis v1.18.54 and was de-multiplexed and converted to FASTQ format with Illumina BCL2FASTQ v1.8.4.

2.3. Computational analyses

Initial sequence analyses and processing were conducted using the QIIME2 platform (version 2019.10.0) (Bolyen et al., 2019). Within the QIIME2 platform, Cutadapt (Martin, 2011) with a default setting was used to remove sequencing adapters. Further sequence quality control and generation of amplicon sequence variants (ASVs) were completed using the DADA2 V1.4 pipeline (Callahan et al., 2016) with default settings. Primer sequences were trimmed from the sequences by removing the first seventeen base pairs of each read, and the reads were truncated at the first instance of a quality score less than two. All reads were then truncated to 238 base-pairs (bps) based on their quality profiles. Any remaining sequencing read that was less than 238 bps in length or was flagged with an expected number of errors greater than two was discarded. The output of DADA2 analysis is available in Table S1.

The taxonomy of each ASV was determined by comparing the top five hits identified with BLAST against the SILVA 128 database and assigning them with the best consensus taxonomy. BLAST hits were only considered if the percent identity of the match fell within 0.5% identity of the top hit and if the alignment of the hit spans was >120 bp. Taxonomic identifications were made for species, family, and phylum level if the percent identity of the best hit was >97, 93, and 90, respectively. These threshold values were arbitrarily chosen in line with diverse literature sources and investigations that were mostly based on mock communities of selected taxa (Brown et al., 2015; Holovachov, 2016; Leasi et al., 2018). Sequences classified within Chordata, Insecta, and Fungi were removed and, therefore, excluded from subsequent analyses. After removing such sequences, a rarefaction sampling depth of 2000 was applied using the tool rarefy in QIIME2 to ensure even sampling (Bolyen et al., 2019; Heck et al., 1975).

2.4. Statistical analyses

Our goal was to assess differences in biodiversity across the samples and how possible differences affected the correlation with the environmental parameters measured across three seasons. The samples collected in January and March were grouped as winter samples, those collected in April and May as spring, and those in June and August as summer. The measured environmental variables were snow depth, brine volume, brine salinity, seafloor salinity, ice/water temperature, and ice thickness.

Biodiversity was assessed by (i) richness (namely the number of observed unique ASVs), (ii) community composition, and (iii) UniFrac, namely community composition considering the phylogenetic distance among features (Lozupone et al., 2006) as assessed in QIIME2 (Caporaso et al., 2010). A rooted tree of the ASVs was constructed using MAFFT (Katoh and Standley, 2013) for sequence alignment and FastTree (Price et al., 2010) for the phylogenetic inference; default settings within QIIME2 were applied to both. Diversity metrics, including richness and composition, were calculated using the QIIME2 core-metrics-phylogenetic method.

To test whether the explanatory variables (measured environmental parameters and seasons) were significant predictors of richness (response variable), we used analysis of variance (ANOVA) implemented in R (RCoreTeam, 2019). To test whether explanatory variables (measured environmental parameters and seasons) were significant predictors of community composition and UniFrac (response variables), we used a permutational multivariate analysis of variance (PERMANOVA) applied on distance matrices (adonis2 function in R package vegan 2.4–5; Legendre and Anderson, 1999; Oksanen et al., 2013) using a *Jaccard* dissimilarity index. Pairwise comparisons between group levels were performed with the function pairwise.perm.manova

(package RVAideMemoire 0.9–72; Hervé and Hervé, 2020). Further, we performed in R a two-dimensional non-metric multidimensional scaling (nMDS) ordination to investigate community dissimilarities. The *Jaccard* dissimilarity index was used to generate a rank dissimilarity matrix, which was converted into an nMDS (Faith et al., 1987; Oksanen et al., 2013).

3. Results

3.1. Taxonomic observations

The environmental parameters and the number of phyla assessed for each sample are summarized in Table 1. Genetic sequences are submitted to NCBI (https://www.ncbi.nlm.nih.gov/sra?term=SRP059698). Overall, the collected samples revealed the DNA signature of 14 invertebrate phyla distributed across 329 unique ASVs. Six of the 14 phyla detected are exclusively meiofaunal. Specifically, the identified phyla were Annelida, represented by 48 ASVs, Arthropoda (75 ASVs), Bryozoa (2 ASVs), Cnidaria (9 ASVs), Ctenophora (2 ASVs), Gastrotricha (3 ASVs), Mollusca (6 ASVs), Nematoda (65 ASVs), Nemertea (6 ASVs), Platyhelminthes (73 ASVs), Porifera (1 ASV), Rotifera (9 ASVs), Tardigrada (1 ASV), and Xenacoelomorpha (23 ASVs) (Tables 2 and S2; Fig. 2 obtained in QIIME2). Annelids, arthropods, nematodes, platyhelminthes, and xenacoelomorphs were present in all samples collected. The DNA of bryozoans, gastrotrichs, and tardigrades were detected sporadically in one or two samples either of ice (bryozoans) or sediment (gastrotrichs and tardigrades). The other phyla, namely Mollusca (8 ASVs), Cnidaria (13 ASVs), Ctenophora (2 ASVs), and Porifera (1 ASV), were found in ice and/or sediment at different times of the year (Tables 2 and S2).

Among the 329 ASVs, 76 were detected in at least three samples, of which 26 were ubiquitously present in different habitats, regardless of the month of sampling. Of the remaining 50 ASVs, eight were present only in the sediment, whereas 42 taxa alternated the type of habitat, according to the sampling time. For example, three copepod taxa, two nematodes, and four xenacoelomorphs occupy the sea ice in winter and the sediment in spring and summer (Table 2). The sample containing the highest number of phyla was the sediment collected in June (11 phyla), whereas the lowest number of phyla (6) was found in the ice cores collected in May (Table 2). The sample with the highest number of ASVs was the sediment collected in late winter (March; 109 ASVs), whereas the fewest ASVs were found in the ice collected in late spring (May; 14 ASVs; Table 2).

Among arthropods, the most frequent taxa detected were copepod harpacticoids followed by copepod cyclopoids, ostracods, and copepod calanoids. Copepods comprised a maximum of almost 40% of the entire metazoan community (i.e., sediment collected in April: 14% harpacticoids, 14% cyclopoids, and 10% calanoids; Table S2). The water sample did not include any harpacticoids, whereas both ice and sediment samples include all three copepod orders (Table S2).

4. Statistical analyses

Among the investigated response variables, significant predictors of biodiversity are as follows: (i) variation in the season, which resulted a significant predictor of UniFrac ($p = 0.037$), and (ii) the interaction between the type of habitat and season, which resulted a significant predictor of both community composition ($p = 0.023$) and UniFrac ($p = 0.047$; Table 3). Pairwise comparisons between community compositions grouped by season showed a significant difference between the communities sampled in winter versus summer ($p = 0.05$). Other measured parameters listed in Table 1 did not yield significant predictors of meiofaunal biodiversity ($p > 0.1$).

The non-metric multidimensional scaling (nMDS) analysis supports a pattern of diversity linked to the season and habitat (Table 3; Fig. 3). According to the nMDS plot, communities are more similar when collected from the same habitat (ice/water or sediment) and during a particular season, such as winter or summer. In spring, communities do not show any similarity pattern (Fig. 3). Interestingly, metazoan communities collected from the sea ice in winter show similarities with the communities collected from the sediment in spring, whereas communities collected from the sea ice in spring show similarities with the communities collected from the sediment in winter.

5. Discussion

This work applied a metabarcoding approach to investigate changes in small metazoan communities occupying diverse Arctic ecosystems (sympagic, benthic, and partially water) across three seasons (winter, spring, and summer). The main outcome of this research is that the meiofaunal community composition differs according to the habitat (ice vs. sediment) and season (winter vs. summer), regardless of the close distance between sea ice and under-ice sediment (less than 5 m). The effects of habitat and season were not independent of each other, as their interaction was a predictor of community composition.

Seasonal variation of meiofauna has been previously assessed in the Arctic (Bluhm et al., 2018; Gradinger et al., 2009; Granskog et al., 2016; Włodarska-Kowalczuk et al., 2016), but the communities investigated were from samples collected exclusively from sea ice, water (Gradinger et al., 2009; Gradinger and Bluhm, 2005), or sediment (Włodarska-Kowalczuk et al., 2016). To our knowledge, this is the first work that comparatively analyzes interstitial sympagic and benthic communities in the Arctic. Although we intentionally used a relatively small sample size, limited to one location to reduce biogeographic variability, investigated over eight months, the results suggest shifts in meiofaunal taxa across habitats with the change of season. Winter ice communities show taxonomic similarities with spring benthic community, and winter benthic communities show taxonomic similarities with spring ice communities. This is likely due to those taxa that were alternatively occupying one specific habitat at different sampling times (e.g., species of copepods, nematodes, and xenacoelomorphs occupy sea ice in the winter and sediment in the spring and summer). These communities may segregate according to a combination of strong environmental selection and a seasonal preference for respective environments, which is driven by unique life-history strategies (Zeppilli et al., 2017). Not surprisingly, the exchange of taxa between sea ice and sediment occurs around April, near the peak of the algal bloom. This suggests that seasonality in the Arctic affects many meiofaunal species that inhabit not only the sea ice but also the surrounding sediment. Therefore, meiofaunal species can be used as valuable indicators of biodiversity shift due to ice melting and global warming in general, regardless of the investigated habitat.

Global warming has resulted in a considerable decline in the extent of Arctic summer sea ice during the last decade (Serreze and Meier, 2019; Smedsrud et al., 2017; Stroeve et al., 2012), occurring throughout all months of the year (Ono et al., 2019). With the continued predicted ice melt, there is an associated risk of losing ice-dependent species. As there are close relationships between habitat and recovered taxa, we surmise that the loss of sea ice would impact the occurrence and life history strategies for many of these organisms. The physical parameters of sea ice were expected to influence metazoan community diversity and composition, as it has been observed in other organisms. For example, reduced snow cover has been seen to negatively affect diatoms also due to increase disease susceptibility due to parasitic chytrids fungi (Hassett and Gradinger, 2016). Snow cover is a major factor affecting light modulation and has proved to be responsible for biological variables, including not only disease susceptibility but also occurrence of phototactic larval species reproducing in sea ice (Gradinger et al., 2009). Likewise, variations in brine salinity and snow thickness largely affect algal biomass, a primary producer in sympagic ecosystems (Palmisano and Garrison, 1993; Smith et al., 1998). However, the measured parameters (e.g., snow cover, brine salinity, and snow thickness) did not prove to be a significant predictor of meiofaunal communities. This lack

Table 3
Results of the statistical analyses of variance (ANOVA) show the effect of seasonality, the type of habitat, and the interaction of the two variables on the overall richness; permutational multivariate analysis of variance (PERMANOVA) was applied on distance matrices to show the effect of seasonality, the type of habitat, and the interaction of the two variables on both the community composition and community composition when the phylogenetic relationships between features were considered (UniFrac). * = statistically significant. Df, degrees of freedom; F, F-test test statistics; MeanSq, mean square; Pr(>F), p value; R^2, coefficient of determination; SumOfSqs, sum of squares.

Response Variable	Explanatory Variable	Df	SumOfSqs	MeanSq	F	Pr(>F)
Richness	Season	2	1423	711.6	0.96	0.443
	Habitat	2	2950	1475.2	1.99	0.231
	Season:Habitat	2	2426	1213	1.64	0.283
	Residual	5	3698	739.5		
		Df	**SumOfSqs**	**R^2**	**F**	**Pr(>F)**
Community Composition	Season	2	0.878	0.203	1.337	0.111
	Habitat	2	0.732	0.170	1.115	0.289
	Season:Habitat*	2	1.064	0.247	1.621	**0.023***
	Residual	5	1.641	0.380		
	Total	11	4.315	1.000		
UniFrac	**Season***	2	0.533	0.269	2.128	**0.037***
	Habitat	2	0.184	0.093	1.474	0.189
	Season:Habitat*	2	0.509	0.257	2.033	**0.047***
	Residuals	6	0.751	0.380		
	Total	11	1.977	1.000		

of correlation between metazoan biodiversity and the measured parameters was unexpected. Although meiofauna are known to feed on ice algae, meiofauna composition may not be affected by the differing quantities of algal biomass, supporting the conclusions obtained by Gradinger (1999). Yet, expanding the sample size and obtaining measurements of abundance will likely provide a better view of community assemblages responding to changes in snow cover, ice and snow thickness, and salinity.

Relationships between environmental DNA product and biomass, as well as environmental DNA product and regional abundances, have been established for metazoans, such as fish species (Pont et al., 2018; Salter et al., 2019; Takahara et al., 2012). However, these relationships have not been established or estimated for meiofauna. Consequently, the relationship between sequence abundance (confounded by body size, intragenomic variation, and rRNA copy numbers) and the number of individuals remains to be elucidated (Ambrose and Crease, 2011; Bista et al., 2018; Eagle and Crease, 2012; Pereira et al., 2020). In addition, aggregated high-throughput sequencing approaches are unable to discern the life stages of organisms. There is much room for more directed analyses (e.g. Ershova et al., 2019), which can serve as the basis for establishing relationships between population sizes, life-stages, and DNA sequence numbers. Molecular-based approaches, PCR amplifications, and bioinformatics pipelines can introduce biases and errors (Elbrecht and Leese, 2015; Leasi et al., 2018), which we attempted to minimize by utilizing established protocols. Even with known biases, our sequencing results do not disagree with previously published works of metazoan abundances in the Arctic. Nematodes are frequently reported as the numerically dominant interstitial group in the Arctic (Aswathy et al., 2017), which is consistent with many sites that we molecularly analyzed. In sea ice communities, the highest metazoan diversity was recorded in winter (January and March), whereas the highest number of genetic reads was recorded in early spring (April). These observations are concordant with previous studies that investigated the meiofaunal community using morphological data (Kiko et al., 2017). In fact, the highest diversity of sympagic meiofauna is expected to be seen in winter when the ice is growing (Kiko et al., 2017), whereas peak abundance was previously recorded in spring (Bluhm et al., 2018).

Analysis of environmental and community DNA (metabarcoding) is widely used for biomonitoring applications and conservation and is robustly applied; it often recovers more taxonomic richness than traditional morphological inventories in aquatic ecosystems (Bista et al., 2017; Elbrecht et al., 2017; Mächler et al., 2014). Yet metabarcoding has only been applied selectively to metazoans in the Arctic (e.g. Chain et al., 2016; Leduc et al., 2019; Peters et al., 2018). This approach, likely because it allowed us to detect traces of organisms that are difficult to identify morphologically (e.g., juveniles, eggs, or pieces of animals), recovered a substantially high proportion of local richness compared to what is so far known for the Arctic (Bluhm et al., 2011; Sirenko et al., 2010). Metabarcoding is very effective at recovering diversity, and there is likely a large fraction of uncharacterized metazoan species richness that remains to be described (Bluhm et al., 2011). Nevertheless, not only richness and abundance but also functional biodiversity would provide important insights to understand the role of organisms in the ecosystem (Májeková et al., 2016). Thus far, the only work that has investigated the functional biodiversity of meiofauna in the Arctic focused on nematodes (Aswathy et al., 2017). The authors investigated different morphological traits related to feeding behavior in relation to environmental parameters in sediment samples from Kongsfjord (Svalbard). A more recent work explored sea ice meiofauna food webs by measuring particulate organic carbon produced in sea ice, without disclosing taxonomic diversity (Gradinger and Bluhm, 2020). Molecular approaches, such as metagenomics and metatranscriptomics, are the next frontier to estimate functional diversity at the community level, but these techniques rely on genome references to properly map and annotate all the genes retrieved from such diverse environmental samples. Meiofauna are diverse, have different dispersal capacities, and have different capabilities to colonize newly formed ice (Kiko et al., 2017); therefore, they are an excellent model for biomonitoring the Arctic region and can provide significant evidence of functional biodiversity shifts in complex communities due to climate change. However, they are poorly represented in the genome reference database (Sevigny et al., 2021). To properly biomonitor climate change and understand its consequences on biodiversity, there is an urgent need to taxonomically and functionally elucidate the biodiversity of small metazoans as well as their biomass, especially in endangered regions, such as the Arctic.

Ongoing global warming will likely lead to further reduction of Arctic sea ice cover and the concomitant expansion of open-water areas (Barnhart et al., 2016). The consequences for biodiversity, if sea ice was no longer available or drastically reduced, are largely unknown. Would organisms just shift into the surrounding habitats, such as sediment and water, or disappear forever under the pressure of resource availability and/or predators? Increasing evidence is suggesting that while perhaps sea ice is advantageous, some sympagic organisms are capable of surviving in the absence of ice (Kunisch et al., 2020). Nonetheless, previous studies demonstrated that species with poor swimming ability and low dispersal capacities, such as harpacticoid copepods and endemic nematodes, are less successful in colonizing newly forming thin ice (Kiko et al., 2017). Therefore, further loss of multi-year ice, earlier melting, delayed freezing, and increased open-water areas in summer are expected to change the metazoan community composition, with an especially negative impact on poor swimming meiofauna, including early stages (e.g., eggs) of bigger species. After winter, the high biomass of meiofauna is expected to be released in the water during ice melt, providing food for pelagic and benthic macrofauna (Bluhm et al., 2017; Schnack-Schiel, 2003; Schnack-Schiel et al., 2001). As such, the loss of ice is leading to a drastic loss and shift of meiofaunal biodiversity and consequently of bigger species, with serious social and economic negative implications.

CRediT authorship contribution statement

Francesca Leasi: Conceptualization, Data curation, Formal analysis, Methodology, Resources, Writing - original draft, Writing - review & editing. **Joseph L. Sevigny:** Conceptualization, Data curation, Formal analysis, Methodology, Resources, Writing - review & editing. **Brandon T. Hassett:** Conceptualization, Data curation, Formal analysis, Funding

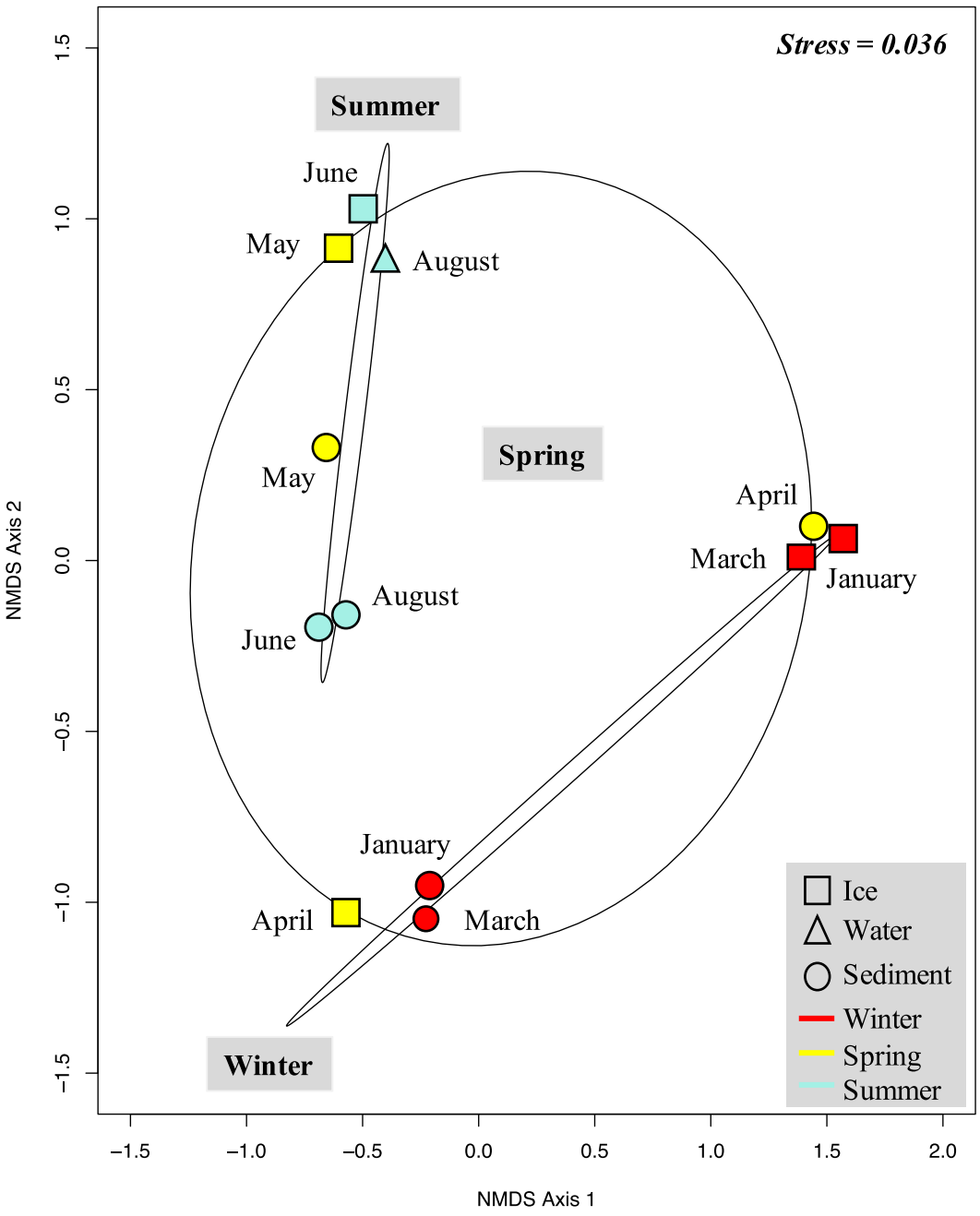

Fig. 3. Non-metric multidimensional scaling plot (MDS) of meiofauna communities collected as determined from incidence (presence/absence) data based on *Jaccard* dissimilarity index. Communities are highlighted by habitat and season and grouped by season.

acquisition, Methodology, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107133.

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