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DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of *Pandalus borealis*, a keystone species in the Arctic

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Abstract

Information about the dietary composition of a species is crucial to understanding their position and role in the food web. Increasingly, molecular approaches such as DNA metabarcoding are used in studying trophic relationships, not least because they may alleviate problems such as low taxonomic resolution or underestimation of digestible taxa in the diet. Here, we used DNA metabarcoding with universal primers for cytochrome *c* oxidase I (COI) to study the diet composition of the northern shrimp (*Pandalus borealis*), an Arctic keystone species with large socio-economic importance. Across locations, jellyfish and chaetognaths were the most important components in the diet of *P. borealis*, jointly accounting for 40%–60% of the total read abundance. This dietary importance of gelatinous zooplankton contrasts sharply with published results based on stomach content analysis. At the same time, diet composition differed between fjord and shelf locations, pointing to different food webs supporting *P. borealis* in these two systems. Our study underlines the potential of molecular approaches to provide new insights into the diet of marine invertebrates that are difficult to obtain with traditional methods, and calls for a revision of the role of gelatinous zooplankton in the diet of the key Arctic species *P. borealis*, and in extension, Arctic food webs.

KEYWORDS
Barents Sea, cytochrome c oxidase I (COI), jellyfish, metabarcoding, *Pandalus borealis*, pelagic, trophic ecology

1 | INTRODUCTION

The Arctic Ocean is one of the most vulnerable biomes on Earth (Post et al., 2013; Serreze & Barry, 2011). Perturbations linked to human-induced climate change and mounting anthropogenic pressures (Griffith et al., 2018; Klanderud, 2005; Schweiger et al., 2010) alter the biological communities (Frederiksen, 2017), leading to changes in food webs and, ultimately, the entire ecosystem (Post et al., 2013; Serreze & Barry, 2011). To characterize food webs, knowledge of predator–prey interactions is essential and can be studied using various methods (Nielsen et al., 2018). Stomach content analysis (SCA) is one of the most commonly applied (Hyslop, 1980). SCA follows a visual, taxonomic identification of the prey items. Thus it provides overall information on predator–prey interactions (e.g., prey

size, weight, stages, and consequently parameters such as predator size selection or gape size effects), stomach fullness and consumption rates important for process-based studies (Garcia et al., 2018; Nielsen et al., 2019; Riaz et al., 2019). At the same time, the method also has limitations. The taxonomic identification of diet items can be time-consuming and introduce bias due to varying experience of the investigating expert as well as the state of digestion of the prey (Nielsen et al., 2018; Sheppard & Harwood, 2005; Wangensteen et al., 2011). Moreover, the dietary contribution of soft-bodied prey items such as jellyfish and other gelatinous zooplankton can be strongly underestimated with SCA (Brodeur et al., 2021; Hays et al., 2018; McInnes et al., 2017; Sheppard & Harwood, 2005) because they are more rapidly digested than hard-bodied prey (Hays et al., 2018). Consequently, dietary regime shifts in an ecosystem may remain undetected (McInnes et al., 2017). Another method used for the identification of predator–prey interactions is stable isotope analysis (SIA). In SIA, ecological information is gained through analysis of the isotopic composition of the tissues of a species (e.g., consumer) of interest (Nielsen et al., 2018; Peterson & Fry, 1987). Based on the principle "you are what you eat", the comparison of isotopic values of a consumer and its possible prey then holds information about dietary composition, trophic position and foraging habitat (Peterson & Fry, 1987). At the same time, the method usually cannot resolve taxonomically diverse diets (Nielsen et al., 2018). Recently, molecular methods applied to the stomach, gut contents or faeces of species represent new possibilities to characterize consumer diets (Asahida et al., 1997; Blankenship & Yayanos, 2005; Boyer et al., 2015; Ray et al., 2016; van der Reis et al., 2018; Symondson, 2002).

DNA metabarcoding is one of the methods that is gaining momentum in trophic ecology studies (Berry et al., 2015; Jensen et al., 2018; McInnes et al., 2017; van der Reis et al., 2018; Siegenthaler et al., 2019). The method combines DNA barcoding with high-throughput sequencing (HTS), allowing the identification of species based on the presence of their DNA in the samples. By amplifying DNA from the stomach content, the method reduces the bias introduced in visual prey identification (Berry et al., 2015; Boyer et al., 2015; McInnes et al., 2017). HTS also allows processing of a large number of samples at a time and reduces the per-sample cost of trophic assessments (Binladen et al., 2007). Given an extensive reference sequence database, DNA metabarcoding can provide highly reliable identification of prey items (Nielsen et al., 2018), and the use of high-resolution markers can even retrieve intraspecific taxonomic information (Turon, Angulo-Preckleret al., 2020; Turon, Antich et al., 2020). Recent studies indicate the usefulness of DNA metabarcoding in the detectability of elusive prey, such as soft-bodied organisms (Boyer et al., 2015; McInnes et al., 2017), which often were believed to be dead ends of food chains (Hays et al., 2018). Consequently, these studies can help to close the knowledge gap regarding the fate of, for example, gelatinous zooplankton in marine food webs (McInnes et al., 2017). Nevertheless, DNA metabarcoding has its own possible limitations; for example PCR (polymerase chain reaction) amplification can lead to the overestimation of abundant DNA fragments (Pompanon et al., 2012; Vestheim & Jarman, 2008). It is particularly problematic when excrement or the digestive tract of organisms are analysed as these sources of dietary components contain large amounts of the consumer's DNA (Vestheim & Jarman, 2008).

The northern shrimp, *Pandalus borealis* Krøyer 1838 is an important component of the sub-Arctic and Arctic food webs, but our understanding of its diet remains incomplete (Berenboim, 1981; Wienberg, 1980). *P. borealis* is of both socio-economic (Garcia, 2007) and ecological importance (Shumway et al., 1985). It plays a central role in food chains, being an influential scavenger and predator as well as an important prey for marine fish, mammals and invertebrates throughout the North Atlantic (Parsons, 2005), and it is frequently referred to as a keystone species in the Arctic ecosystem (e.g. Arnberg et al., 2018; Dupont et al., 2014; Olsen et al., 2012; Shumway et al., 1985). Scavengers play key ecological roles promoting the recycling of nutrients and energy-rich matter in the ecosystem (Britton & Morton, 1994; Jeffreys et al., 2011; Sweetman et al., 2014). Trophic ecology studies so far have determined the diet of *P. borealis* based on SCA and SIA. Using SIA, McGovern et al. (2018) and Søreide et al. (2013) found that *P. borealis* occupies a relatively high trophic level compared to other benthic species and feeds opportunistically. The most extensive trophic ecological studies based on SCA of *P. borealis* to our knowledge date back to the 1980s (Berenboim, 1981; Wienberg, 1980). Comparing the two studies based on SCA, it becomes apparent that *P. borealis*' diet varies over large geographical ranges. In the North Sea, *P. borealis* was reported to feed on a wide range of prey, including foraminifera, nematodes, molluscs and echinoderms (Wienberg, 1980) while in the Barents Sea it was reported to feed mainly on polychaetes and euphausiids as well as molluscs, and echinoderms (Berenboim, 1981). Thus far, molecular methods such as DNA metabarcoding have not been applied to extensively study the trophic ecology of *P. borealis*.

Here, we provide the first trophic assessment of *P. borealis* in the Barents Sea based on DNA metabarcoding of stomach contents. Our objective was to gain high taxonomic resolution of prey and to provide an up-to-date detailed taxonomic characterization of the diet of this Arctic keystone scavenger, including the possible presence of easily digestible prey taxa not observed in previous SCA studies. Second, we investigated changes in *P. borealis* diet composition on a small geographical scale, between fjord and shelf habitats. By placing the results on *P. borealis* feeding provided here in the light of SCA results, we then provide a reassessment of the possible food web connections provided by this species in Arctic marine ecosystems. Finally, we discuss the considerations of these results for the application of *P. borealis* as a natural sampler to monitor biodiversity in the Arctic region.

2 | MATERIAL AND METHODS

2.1 | Sampling

Sampling of *Pandalus borealis* adults was conducted during two scientific surveys aimed at testing new trawl gears designed for bycatch reduction. Sampling took place in Kvænangenfjord (Troms and

Finnmark, northern Norway), October 28–30, 2018 (one fjord locality), and around Svalbard (northern Barents Sea), January 2–21, 2019 (two fjord localities and four shelf localities), using the Research Vessel *Helmer Hanssen* (UiT the Arctic University of Norway) (Figure 1; Table 1). Campelen-type bottom trawls, equipped with a Nordmøre grid, were used for sampling (Isaksen et al., 1992). The gear was towed along the bottom (depth range: 165–498 m) with an average speed of 3.1 knots (≈5.7 km/h) and door spread of 48–60 m (Table 1). At each location, a random subsample of 12 males and 12 females (*n* total =24) of *P. borealis* specimens was taken (Table 1). After removal of macroscopic external contaminants by a short immersion in freshwater, individuals were preserved in 96% EtOH and stored at −20°C until DNA extraction in the laboratory.

2.2 | DNA extraction

All work on *P. borealis* was performed under a laminar flow hood, decontaminated by UV light before and after stomach content preparation. We followed strict decontamination routines consisting of soaking dissection tools in bleach (70%) for at least 5 min prior to usage, then rinsing them in Mili-Q water and EtOH (96%), and lastly flame sterilizing them to avoid cross-contamination between *P. borealis* individuals (contamination of individuals coming from different locations) and within *P. borealis* (contaminations arising from dissecting the specimen). Separate dissection tools were used for dissection of *P. borealis* (for exposing the inner parts of the cephalothorax) and later stomach content preparation. Before dissection of *P. borealis*, the length of each specimen was measured to the nearest 0.01 mm with a caliper (Rasmussen, 1953) and weight was determined to the nearest 1 mg. DNA was extracted from 15–30 mg of the stomach content from each specimen using the DNeasy Blood & Tissue Kit (Qiagen). Extraction followed the manufacturer's protocol for "Purification of Total DNA from Animal Tissue (Spin-Column Protocol)" for rodent tails with adjustment made to the incubation time (>12 h, e.g., overnight) and centrifugation (20 000 *g* in most steps). DNA was eluted using 100 µl of heated elution buffer EA.

2.3 | PCR amplification and HTS

The genetic marker used in this study targets the 313-bp-long "Leray fragment" of mitochondrial cytochrome *c* oxidase I (hereafter COI) (Leray et al., 2013). We used the forward primer (5′-GGWACWRG WTGRACWITITAYCCYCC-3′) developed by Wangensteen et al. (2018), called Leray-XT, which is a modified version of the mlCOIintF primer (Leray et al., 2013) that contains two additional degenerate bases and two iosine nucleotides. The reverse primer used was jgHCO2198 (5′-TAIACYTCIGGRTGICCRAARAAYCA-3′) (Geller et al., 2013). This primer set has been succesfully used in previous trophic studies of marine broad-diet predators (Rodríguez-Barreras et al., 2020; Siegenthaler, Wangensteen, Benvenuto, et al., 2019).

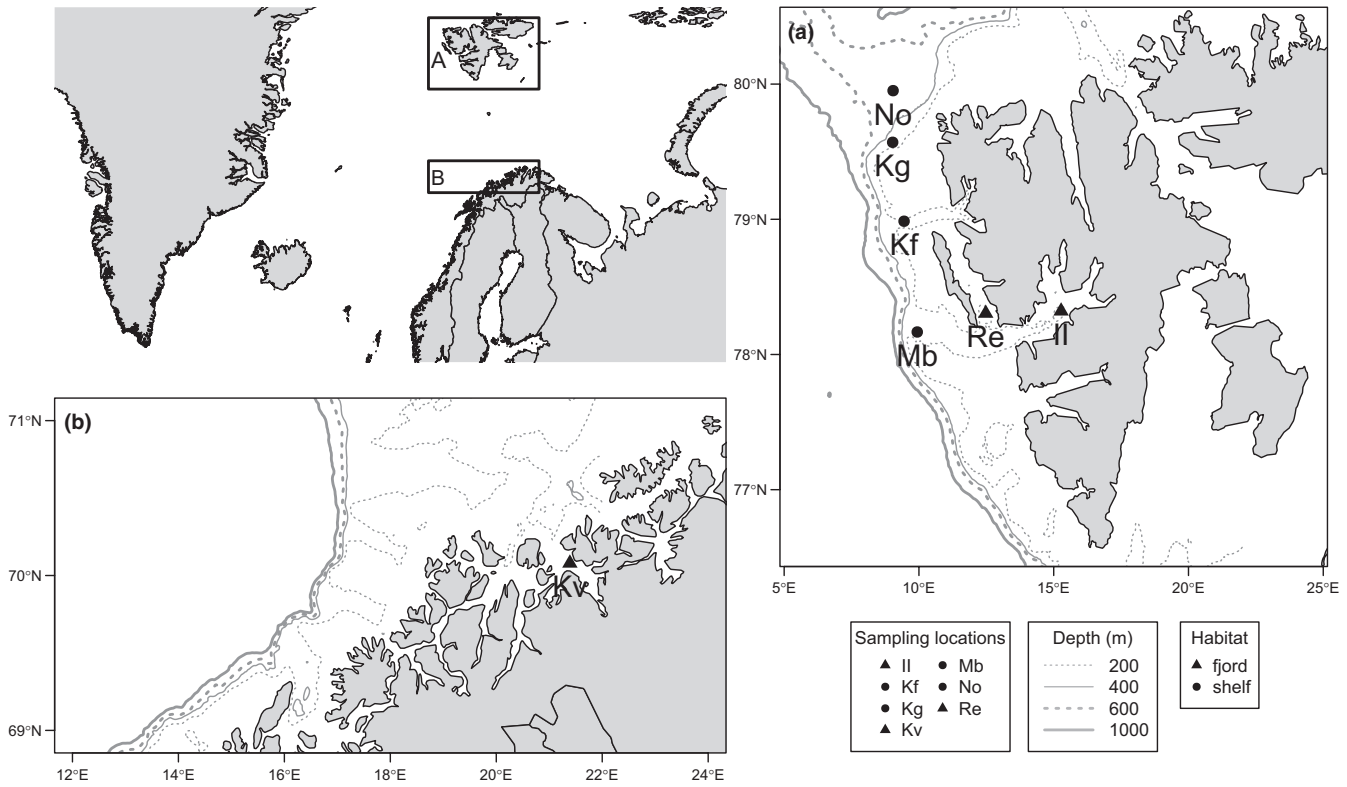

FIGURE 1 Map of the sampling locations used for collection of *Pandalus borealis* specimens. *P. borealis* were caught at seven sampling locations in bottom trawls equipped with Nordmøre grid. (a) Close-up of the sampling locations around Svalbard; (b) the Kvænangenfjord location, the only location along the Norwegian coastline

TABLE 1 Overview of sampling locations with their names, abbreviations used in the text and the figures, and average physical measures of *Pandalus borealis* specimens caught

Cruise	Location	Abbr.	Habitat	Latitude	Longitude	Depth (m)	Speed (knots)	Door spread (m)	Time (start of trawling)	*P. borealis* total	*P. borealis* ♂	*P. borealis* ♀	Mean length(mm) ♂ ± SD	Mean length(mm) ♀ ± SD
October 2018	Kvænangenfjord	Kv	Fjord	70°04.773	21°23.388	360	3.1		2:47:07	24	12	12	19.9 ± 1.0	24.7 ± 1.9
January 2019	Inner Isfjorden	Il	Fjord	78°19.260	15°16.465	194	3.14	49.5	14:58:51	24	12	12	19.3 ± 1.4	21.8 ± 1.3
January 2019	Rekesøyla	Re	Fjord	78°18.269	12°28.712	244	3.05	51.1	20:11:21	24	12	12	20.3± 1.4	23.6 ± 1.8
January 2019	Kongsfjordrenna	Kf	Shelf	78°59.138	09°26.922	222			9:44:16	24	12	12	17.4 ± 1.9	22.3± 1.6
January 2019	Kongsgrunnen	Kg	Shelf	79°34.169	09°01.532	411	3.05	49.3	19:45:45	24	12	12	20.2 ± 1.2	24.5 ± 1.3
January 2019	Minkebanken	Mb	Shelf	78°09.982	09°56.255	242	3.06	49.7	16:06:52	24	12	12	17.5 ± 1.2	22.7 ± 1.3
January 2019	North	No	Shelf	79°57.086	0902.478	477	2.94	50.9	2:40:23	24	12	12	20.6 ± 1.7	23.9 ± 1.2

For PCR amplification, we prepared a master mix consisting of 10 µl AmpliTaq gold 360 Master mix (Applied Biosystems), 0.16 µl bovine serum albumin (Thermo Scientific), 2 µl of each of the 5 µM forward and reverse tagged Leray-XT primers (with attached 2–4 leading Ns and 8-bp oligo-tags), 5.64 µl ultrapure H_2O, to which we added 2 µl of the DNA extract. Single-step PCR followed an initial denaturing step at 95°C for 10 min, 35 cycles of 94°C for 1 min, 45°C for 1 min and 72°C for 1 min, and a final extension step of 72°C for 5 min. PCR products (including one negative control) with twin sample tags attached at both ends were pooled and purified using MinElute columns (Qiagen). Up to 90 samples and controls were multiplexed in each library. In total, six extraction controls and one PCR-negative control were demultiplexed and sequenced along with the samples. Two libraries were prepared using the NextFlex PCR-free library preparation kit (BIOO Scientific) and quantified using the NEBNext qPCR quantification kit (New England Biolabs). Leray-XT libraries were sequenced in equimolar concentrations (final molarity of 21 pM) along with 1% PhiX on the Illumina MiSeq platform in the UiT The Arctic University of Norway, using V3 chemistry (2 × 250-bp paired-ends).

2.4 | Bioinformatics analysis

For the DNA metabarcoding pipeline the OBITOOLS version 1.01.22 software suite (Boyer et al., 2016), VSEARCH version 1.10.1 (Rognes et al., 2016) and SWARM version 2 algorithm (Mahé et al., 2015) were used. The length of the raw reads was trimmed to a median Phred quality score >30, after which paired-reads were aligned using illuminapairedend from the OBITOOLS version 1.01.22 software suite (Boyer et al., 2016). Those reads with paired-end alignment quality scores >40 were demultiplexed using ngsfilter (also a function of OBITOOLS version 1.01.22; Boyer et al., 2016), which additionally removes the primer sequences. Using obigrep, from OBITOOLS version 1.01.22 software (Boyer et al., 2016), a length filter of 300–320 bp was applied to the demultiplexed reads. Chimeric sequences were detected and removed using uchime_denovo implemented in VSEARCH version 1.10.1 (Edgar et al., 2011; Rognes et al., 2016), followed by dereplication of nonchimeric reads (using obiuniq, from OBITOOLS version 1.01.22 software (Boyer et al., 2016)). Sequences were clustered using the Swarm version 2 algorithm (Mahé et al., 2015) with a clustering distance of $d = 13$. This algorithm results in variable thresholds for delimiting MOTUs (molecular operational taxonomic units) across different branches of the taxonomic tree, following the natural intraspecies variability of the clusters. The taxonomic assignment was performed using ecotag from OBITOOLS version 1.01.22 software (Boyer et al., 2016), and a custom local reference database, publicly available from github.com/metabarpark/Reference-databases. Sequences with <1 best identity score were searched again using the public reference database BOLD (Ratnasingham & Hebert, 2007), and corrected if a better match with higher identity score was found. After taxonomic assignment, the LULU algorithm (Frøslev et al., 2017) was used to remove spurious

MOTUs arising from pseudogenes and NUMTs (nuclear mitochondrial DNA sequences) (Bakker et al., 2019). Final refinement was made to remove false positives, which consisted of blank correction (removal of MOTUs with a ratio of read abundance in the blanks to total abundance in all samples >5%), removal of MOTUs occurring in fewer than two samples, and removal of contaminations of terrestrial origin (e.g., human, cow, pig, booklice) (Wangensteen & Turon, 2017). The threshold for blank correction was chosen to ensure a robust data set, since it follows a stricter method for removing contamination than previously recommended: Wangensteen and Turon (2017) proposed a proportion of 10% of total reads in the blanks. As a result, the number of specimens used for the analyses might deviate from 24 (Table S2).

2.5 | Statistical analysis

Statistical analyses and visualizations were performed in R 3.6.0 (R Core Team, 2015). The packages used for the statistical analyses were vegan (version 2.5-4) and BiodiversityR (version 2.11-1) (Kindt & Coe, 2005; Oksanen et al., 2015). For rarefaction curves the package iNEXT (Hsieh et al., 2016) was used, whereas for the accumulation curves the function *rarecurve* was applied. Using the adonis function we performed PERMANOVA (permutational multivariate analysis of variance; Anderson et al., 2008) to assess differences in the diet of *P. borealis* based on the geographical location and the type of habitat (fjord or shelf). The assumption of equal dispersion within groups was tested using the *betadisper* function. Bray–Curtis and Jaccard dissimilarity matrices were calculated using the function *vegdist* and used to generate nonmetric multidimensional scaling (nMDS) ordinations.

2.6 | Diet analysis

The composition of the diet was assessed using both a qualitative (presence/absence) and a semiquantitative approach. The qualitative approach, also referred to as species list or occurrence, determines MOTU richness in the diet (Deagle et al., 2019). The semiquantitative approach has been previously used to assess the abundances of MOTUs in community DNA (Wangensteen et al., 2018). Thereby, each MOTU is classified into one of five categories depending on the percentile in which the MOTU falls after ranking all MOTUs in each sample by their read abundances, according to the following thresholds (0: absent, 1: <50th percentile, 2: 50–75th percentile, 3: 75–90th percentile, 4: >90th percentile).

For a better overview of the diet, a cumulative value of detected MOTUs was calculated pooling all individuals of *P. borealis* per prey category and per location. The cumulative value was calculated using the occurrence and the semiquantitative data (Figure S3). A large cumulative value indicates that many individuals fed upon many different MOTUs of that category in that location. DNA metabarcoding can reveal information about both primary and secondary predation (Sousa et al., 2019). The former refers to the targeted prey of *P. borealis*, whereas the latter refers to the prey items of *P. borealis*' prey (i.e., "the prey of the prey"). We differentiated between the MOTUs that belong to either primary or secondary predation mainly through a literature research (i.e., phytoplankton and other microeukaryotic species were considered secondary predation). For MOTUs that could not be classified to either primary or secondary predation based on their taxonomic assignment, we defined an abundance threshold for MOTUs belonging to primary predation (≥500 read counts in the entire data set). Primary predation of *P. borealis* was then assigned to one of six ecological categories: gelatinous zooplankton, chaetognaths, holoplanktonic, meroplanktonic and holobenthic invertebrates, and vertebrates. To determine whether differences in the diet of *P. borealis* can be explained by different habitats (fjord and shelf locations) and are due to primary or secondary predation, we performed separated PERMANOVAs (Anderson et al., 2008) using locations and habitats as independent variables. We also used a machine learning algorithm based on a random forest approach implemented in the R package randomForest (Liaw & Wiener, 2002) to test the ability to assign samples to their habitat of origin (shelf or fjord) based on MOTU composition. RandomForest evaluates an ensemble of decision trees to perform the classification and regression task, where each decision tree is constructed using a different set of samples from the training data. Two-thirds of data were used to determine the association between the MOTUs and habitat of samples collected and one-third of data were used to evaluate the predictive power of the MOTU sets ("out of bag" error rate, OOB) to correctly classify the samples into the habitat of origin. We removed MOTUs that were present in less than 5% of the total number of samples (166) (i.e., all rare MOTUs that could bias the analysis). The remaining MOTUs (43) were used to run the classification model in randomForest. Each random forest was created with 5001 trees, using the importance and proximities options, and iterated three times with different initial seeds. The importance of MOTUs as indicators of the habitat was measured as "mean decrease in accuracy (MDA)" and the MOTUs with the lowest MDA were removed from the next round of the analysis. We reiterated this procedure until we observed an increase in OOB values (i.e., lowest point in the elbow curve). Model performance was further cross-validated using leave-one-out cross-validation (LOOCV) from the R package caret (Kuhn et al., 2020). We performed this analysis for both occurrence and semiquantitative data (overview of analyses in Table S6).

3 | RESULTS

In total, 19,226,459 sequence reads of the COI fragment were recovered. After bioinformatic filtering the number of sequence reads dropped to 14,888,950. After taxonomic assignment, final refinement and removing reads assigned to *PAndalus borealis*, the COI data set was composed of 304 MOTUs with 625,615 reads. Of these, 83 MOTUs were assigned to the species level. The proportion of reads used for the different steps and analyses is summarized in

Table 2. Overall, a total of 25 different phyla were detected in the stomachs of *P. borealis*. Seventy-four MOTUs belonging to 12 phyla and accounting for 95.08% of the total reads (excluding the predator reads) were classified as primary prey of *P. borealis*, and were assigned to one of the six ecological prey categories, indicating a diverse diet. The remaining 230 MOTUs were considered secondary predation (Table S7).

3.1 | Diet composition of *P. borealis*

The total number of MOTUs detected per location ranged from 24 to 41 (Table 3; Tables S4 and S5). Overall, the category of meroplanktonic species had the highest MOTU richness (33 MOTUs). Gelatinous zooplankton and chaetognaths had the lowest MOTU richness (six and seven MOTUs respectively). Four of the seven chaetognatha MOTUs were consistently present at all locations. For the meroplanktonic prey MOTUs, 14 of 33 MOTUs were present at all locations. MOTU richness of holobenthic species varied greatly between locations, with zero to seven of nine MOTUs present per location (Table 3).

Chaetognaths occured very frequently in the stomach content of *P. borealis* (Figure 2). Specifically, at four of seven locations assessed (Isfjorden, Kongsfjordrenna, Kvænangenfjord and Rekesøyla) the median chaetognath richness per stomach exceeded one MOTU. In contrast, holobenthic and vertebrate species occurred at low frequencies (Figure 2). Often, their detections were driven by outliers. For example, at the North location, the median of vertebrate MOTUs detected was zero, with three outliers indicated (one specimen with three MOTUs, another with two MOTUs, and another with one vertebrate MOTU detected).

Figure 3 shows the cumulative value in percentage of MOTUs assigned to the different ecological categories for each location. Chaetognaths dominated *P. borealis* diet in all analysed locations. Gelatinous zooplankton, and holoplanktonic and meroplanktonic prey showed consistent contributions to the diet across all sampled locations. The contribution of holobenthic species to the diet varied distinctively between locations, which was also apparent from Table 3 and Figure 2. The overall pattern in foraging (i.e., the contributions of prey categories to the diet) of *P. borealis* remained remarkably consistent across all locations (Figure 3). Analyses based on semiquantitative data supported these results from occurrence data (Figure S3).

3.2 | Habitat-related differences in the diet composition of *P. borealis*

The composition of stomach contents (all 304 MOTUs) differed significantly between locations according to PERMANOVA ($F = 1.96$, $p < .0001$). Pairwise PERMANOVAs showed that locations inside fjords (Isfjorden, Kvænangenfjord and Rekesøyla), together with the shelf location Kongsfjordrenna, each differed significantly from Kongsgrunnen, Minkebanke, and North, all located on the shelf (Table 4a). PERMANOVA using the type of habitat as a factor also found significant differences between fjord and shelf localities ($F = 2.38$, $p < .0001$). These results suggest that habitat is a main driver of the feeding patterns of *P. borealis*. In addition, we performed the PERMANOVA using only primary prey items (74 MOTUs). The differences between localities ($F = 2.09$, $p < .0001$) and the effect of type of habitat ($F = 1.86$, $p = .014$) remained significant (Table 4b).

The whole data set and the primary predation data set were further analysed as semiquantitative abundance data using PERMANOVA. For the whole data set, the semiquantitative data gave the same results as the occurrence data (locality: $F = 2.51$, $p < .0001$; habitat: $F = 3.26$, $p < .0001$), and all three fjord locations were significantly different from the three shelf locations. In the primary predation data set, the PERMANOVA based on semiquantitative data remained significant ($F = 2.70$, $p < .0001$), but showed a reduced ability to detect significant differences between locations, with only four pairwise comparisons remaining significant, all involving the North location (Table 4b). Again, the difference between fjord and shelf habitats remained significant ($F = 2.51$, $p = .003$).

Random forest analysis on the occurrence data of 43 MOTUs predicted the habitat of capture with an initial OBB rate of 31.33%. After subsequent backwards purging by removing the least important MOTUs at each random forest run (based on importance score) we

TABLE 2 Overview of the data curation steps after sequencing of the cytochrome *c* oxidase I (COI) marker. Information of the number of reads and MOTUs retained is shown for each treatment step

Data treatment	COI
Total read no.	19,226,459 reads
Quality control and demultiplexing	15,033,109 reads
Nonchimeras	14,888,950 reads
Dereplicate sequences	1,859,104 seqs.
Clustering and taxonomic assignment	1,408 MOTU
Pandalus borealis	13,943,505 reads (93.6%)
Final refinement	657 MOTUs; 631,149 reads
MOTU filtering	304 MOTUs; 625,615 reads
Primary predation	74 MOTUs; 163 *P. borealis*
Proportion of reads used for PERMANOVA	100%
Proportion of reads used for random forest	14.14%

TABLE 3 Composition of the diet presented as MOTU richness for each ecological category per sampled location. The MOTU richness for each category in the total data set is given in parentheses after the category names

Location	Gelatinous zooplankton (6 MOTUs)	Chaetognaths (7 MOTUs)	Holoplanktonic (11 MOTUs)	Meroplanktonic (33 MOTUs)	Holobenthic (9 MOTUs)	Vertebrates (8 MOTUs)	Total no. of MOTUs	Sum of all prey occurrences
Il	6	5	6	13	7	4	41	131
Kf	4	7	4	12	0	4	31	121
Kg	1	6	4	8	2	3	24	84
Kv	3	6	6	10	1	4	30	115
Mb	3	4	9	9	4	6	35	80
No	2	5	3	14	1	4	29	61
Re	4	7	4	14	4	4	37	131

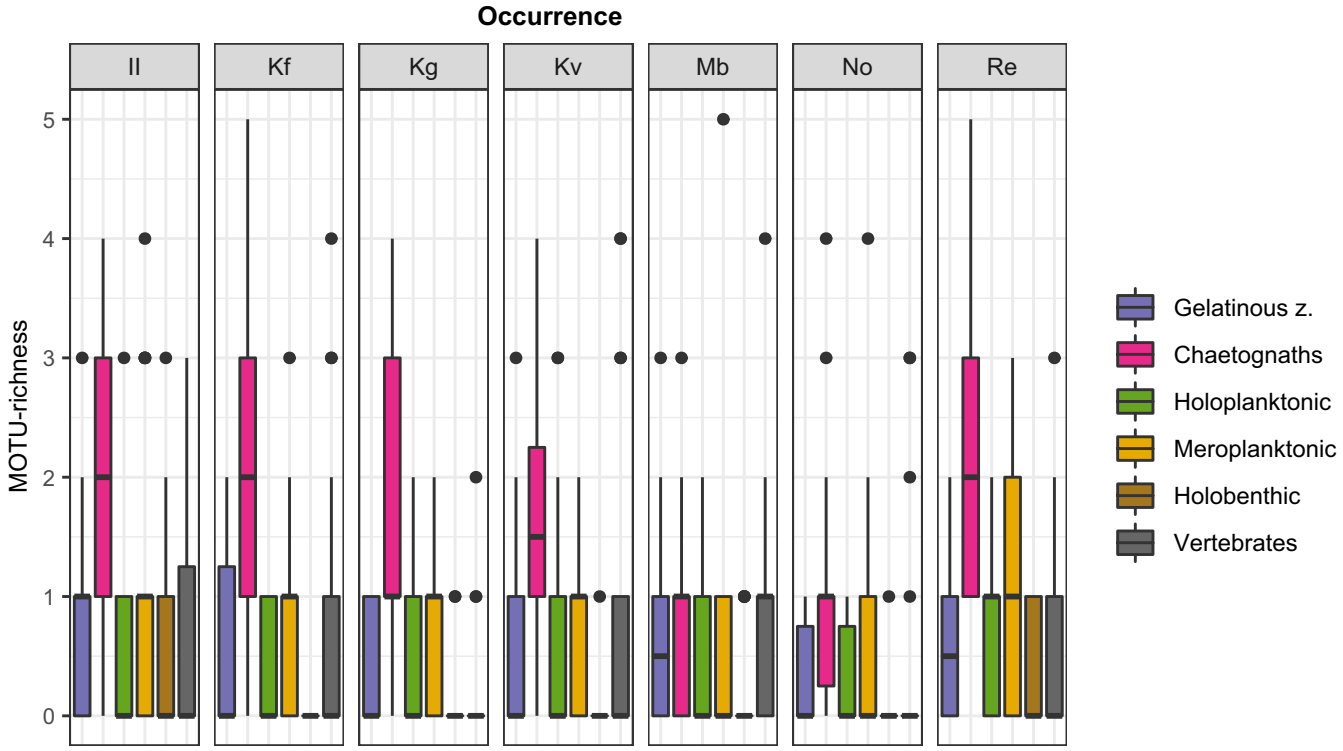

FIGURE 2 Distributions of MOTU richness per individual of different prey categories within location. Chaetognaths were the most frequently detected group in the stomach content of *Pandalus borealis*. Numbers of *P. borealis* specimens analysed per location are: Isfjorden =24, Kongsfjordrenna =24, Kongsgrunnen =23, Kvænangenfjord =24, Minkebanken =22, North =22, Rekesøyla =24

achieved a final OOB rate of 21.11%, with a total number of 21 MOTUs (Table S3) using occurrence data and OOB rate of 26.51% (after retaining 21 MOTUs) for semiquantitative data. This means that the occurrence of these 21 MOTUs correctly predicted *P. borealis* habitat of capture in 78.89% of cases. Shelf specimens were most likely to be correctly classified during cross-validation (84.21%, with 80 out of 95 shelf specimens correctly assigned) than fjord specimens (57.75%, with only 41 out of 71 fjord specimens being correctly assigned). Fourteen of the 21 MOTUs (66.6%) selected as important by the random forest analysis belonged to secondary prey of *P. borealis*. Similar results were obtained after analysing the semiquantitative data using random forest.

nMDS of the occurrence (Figure 4) and semiquantitative data (Figure S4) showed a high degree of dispersion among individuals, leading to considerable overlapping of inertia ellipses. However, the position of the centroids revealed differences between fjord and shelf locations. These differences are more evident when analysing the whole data set (Figure 4a) than the primary predation data (Figure 4b), in agreement with the *p*-values detected by PERMANOVA, and supported by the results of the random forest analysis.

4 | DISCUSSION

With accelerating environmental changes in Arctic ecosystems, understanding the consequential changes in biological networks has become a research priority. To do so, characterization of the trophic

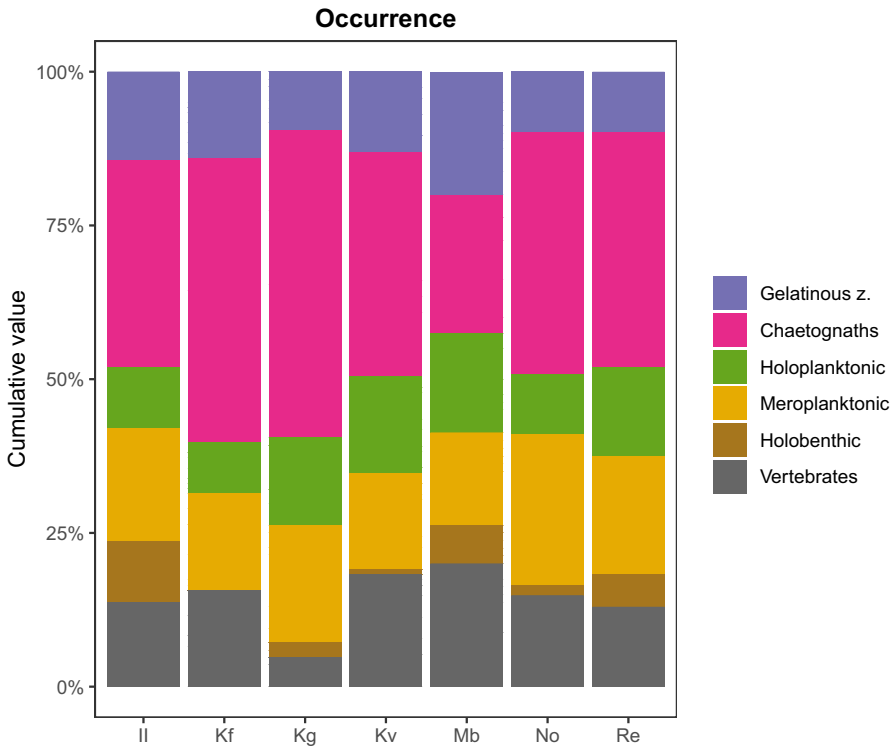

FIGURE 3 Contribution of different ecological categories to the stomach content of *Pandalus borealis* based on COI DNA metabarcoding, expressed as percentage of cumulative MOTUs present in sampled locations for each prey category. Out of all MOTUs found in the stomach of *P. borealis*, 74 were identified as primary predation items and assigned to one of the categories: Gelatinous z. (Gelatinous zooplankton), Chaetognaths, Holoplanktonic, Meroplanktonic, Holobenthic and Vertebrates. Total number of MOTUs at locations: Isfjorden =131, Kongsfjordrenna =121, Kongsgrunnen =84, Kvænangenfjord =115, Minkebanken =80, North =61, Rekesøyla =131

ecology and position of keystone species in Arctic food webs is essential. The scavenging species *Pandalus borealis* represents such a keystone species, but its dietary ecology has not been assessed in such detail. Here, we provided the first high-resolution taxonomic characterization of the diet of this species based on DNA metabarcoding, with a particular focus on the possible role of easily digestible prey species that may have been overlooked in previous SCA studies. Based on our new results and existing reports, we reassess the food web connections and the ecological role of *P. borealis* in Arctic systems.

4.1 | Diet composition dominated by gelatinous zooplankton in *P. borealis*

Based on the results of our molecular assessment, soft-bodied prey, consisting of gelatinous zooplankton and chaetognaths, was the main component of the diet of *P. borealis*. The gelatinous zooplankton identified consisted of taxa from three classes (Hydrozoa, Scyphozoa, Tentaculata). This diet composition contrasts sharply with previous reports of *P. borealis* diet composition based on SCA that did not identify any Scyphozoa (i.e., true jellyfishes) or Ctenophora, and provided limited information about the presence of hydrozoans (such as *Thuiaria articulata*) (Table S1) (Berenboim, 1981; Wienberg, 1980). It seems likely that the fast disintegration of soft gelatinous plankton during digestion and potential limited detectability of this group with SCA (Hays et al., 2018) underlies this contrast. Prey items that have chitin or calcareous skeletons (e.g., some hydrozoan species) are easier to identify based on their hard parts. Moreover, the digestion of these hard parts takes time so the probability of their detection is higher (Arai et al., 2003). The relevance of gelatinous zooplankton as prey of *P. borealis* reported here is in line with an ongoing paradigm shift regarding the role of gelatinous prey in marine systems (e.g. Ates, 2017; Hays et al., 2018; Lebrato et al., 2019; Sweetman & Chapman, 2015). While this group has been long considered irrelevant as a prey item, and thus not a source of energy to higher trophic levels (Sweetman et al., 2014), it is now increasingly recognized as an important prey item of many other groups, including fish (Brodeur et al., 2021; Clarke et al., 2018; Eriksen et al., 2020), seabirds (Jarman et al., 2013; McInnes et al., 2017) and cephalopods (Hoving & Haddock, 2017). The use of molecular-based methods, such as DNA metabarcoding, among others, has played a central role in these efforts (Hays et al., 2018).

The changed perspective regarding the prey preference of *P. borealis* gained from this study can have implications for our understanding of carbon cycling in the Arctic Ocean. In the Arctic Ocean, pelagic and benthic communities are tightly coupled (Wassmann & Reigstad, 2011). On the shelves, most of the surface production sinks to the bottom and supports benthic communities (Bluhm et al., 2015; Wassmann & Reigstad, 2011). Sinking jellyfish contribute to the biological carbon pump (i.e., storing carbon at great depths) (Lebrato et al., 2019; Luo et al., 2020). However, our study shows that routing of jellyfish production through the food web can be more direct, by fuelling *P. borealis* growth. This implicates *P. borealis* as a mediator of benthic–pelagic coupling, which should be considered in assessments of energy transfer and recycling between these two system components.

Similarly, the important contribution of chaetognaths, another soft-bodied prey, to the diet at all locations observed here contrasted with the much lower importance reported in previous

TABLE 4 Results of PERMANOVAs to test differences in diet composition between different locations and habitats. (a) PERMANOVA performed on the whole data set (304 MOTUs, 166 *Pandalus borealis* individuals). (b) PERMANOVA performed only on primary predation (74 MOTUs, 163 *P. borealis* individuals). Pairwise differences between locations were assessed using the pairwise.adonis function, and *p*-values were corrected for multiple comparisons using the Benjamini–Hochberg correction

Factor	Presence/absence data set	Semiquantitative data set
(a) PERMANOVA on whole data set		
Location (7 levels)	***($F = 1.96$, $p < .0001$) *Betadisper significant, $p = .027$ Post-hoc pairwise significances: II vs. Kg II vs. No II vs. Mb Kv vs. No Kv vs. Mb Re vs. Kg Re vs. No Re vs. Mb Kf vs. No Kf vs. Mb	***($F = 2.51$, $p < .0001$) *Betadisper significant, $p < .0001$ Post-hoc pairwise significances: II vs. Kg II vs. No II vs. Mb Kv vs. No Kv vs. Mb Re vs. Kg Re vs. No Re vs. Mb No vs. Kf Mb vs. Kf
Habitat (Fjord vs. Shelf)	***($F = 2.38$, $p < .0001$) Betadisper not significant	***($F = 3.26$, $p < .0001$) *Betadisper significant, $p = .0008$
(b) PERMANOVA on primary predation		
Location (7 levels)	***($F = 2.09$, $p < .0001$) Betadisper not significant Post-hoc pairwise significances: II vs. No II vs. Mb Kv vs. No Kv vs. Mb Re vs. Kg Re vs. No Re vs. Mb Kf vs. Kg Kf vs. No Kf vs. Mb	***($F = 2.70$, $p < .0001$) *Betadisper significant, $p = .0002$ Post-hoc pairwise significances: II vs. No Kv vs. No Re vs. No Kf vs. No
Habitat (Fjord vs. Shelf)	*($F = 1.86$, $p = .014$) Betadisper not significant	**($F = 2.51$, $p = .003$) *Betadisper significant, $p = .025$

Note: The significance of *, **, *** are visual expressions.

studies of *P. borealis* based on SCA. Wienberg (1980) mentioned chaetognaths briefly as prey items and estimated their contribution to *P. borealis* diet to vary between 0.1% and 0.5%. In our data, chaetognaths contributed 12%–50% to the overall diet, which corresponds to a 40-fold contribution compared to previous findings using SCA. In marine systems, chaetognaths, after copepods, contribute to the highest portion of the zooplankton biomass (5%–30% of the planktonic food web; Feigenbaum, 1991; Reeve, 1970). Yet, only in a few cases have chaetognaths been mentioned as a food source for organisms (Feigenbaum, 1991; Sampey et al., 2007; Saunders et al., 2012; Wienberg, 1980). Similarly to jellyfish, chaetognaths are soft-bodied species that might swiftly disappear during the digestion process. DNA metabarcoding is a powerful method to identify these fragile, soft-bodied prey in the digestive tracts of organisms. Nevertheless, caution should be taken in the interpretation of DNA metabarcoding results, as long as the species-specific DNA decay rate during digestion is unknown, which could lead to under- or overestimation of certain species groups. A recent study found that environmental DNA (eDNA) from the soft-bodied organism *Ciona intestinalis* can be detected for a longer time in water samples than the eDNA from the crustacean *Monocorophium insidiosum* after removal of the organism (Holman et al., 2021). It is difficult to come to general conclusions about the DNA decay rate of soft-bodied and hard-bodied organisms based on only one study, and more research is needed to generalize on DNA decay rates in different organism groups, in order to be able to draw conclusions about species-specific differences

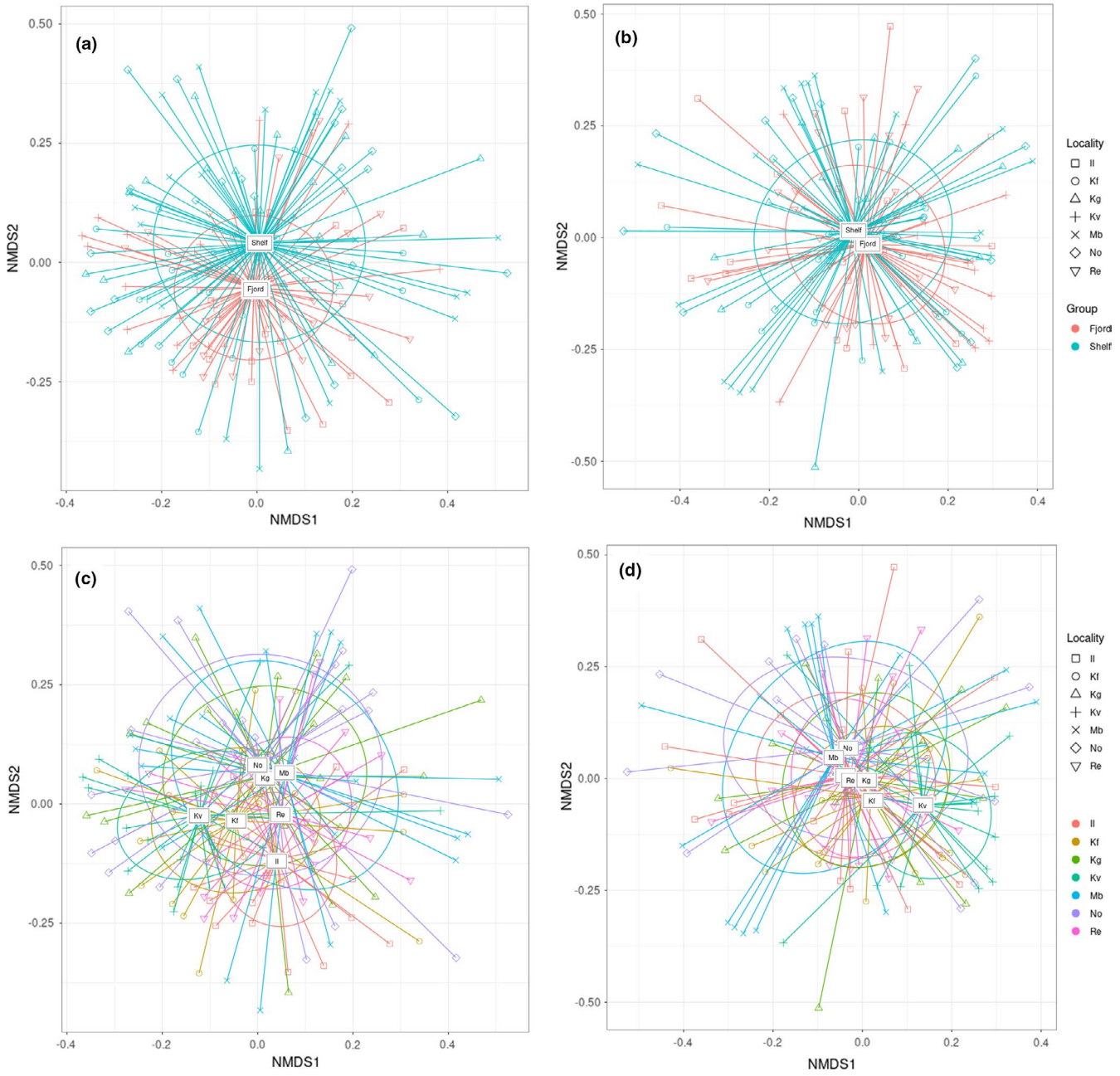

FIGURE 4 Nonmetric multidimensional scaling (nMDS) ordination of occurrence data in *Pandalus borealis* stomachs (using Jaccard distances). (a, c) Results from the whole data set of 304 MOTUs; (b, d) results from primary predation (74 MOTUs). Groupings by habitat (a and b) or by locality (c and d) are shown. Stress values are 0.297 for (a) and (c) and 0.288 for (b) and (d)

in detectability. In general, more research is needed to generalize on DNA decay rates in organism groups within stomachs of marine predators. The MOTU diversity in the diet of *P. borealis* in our study, although high (304 MOTUs), is probably still an underestimation, given the insufficient sequencing depth in samples (Figure S1), the relatively low sampling effort (Figure S2), and the dominance of *P. borealis* sequence reads in the output (>95% of the total reads), as this study did not use predator blocking primers.

Despite these potential limitations, the identification of previously unreported trophic links between the scavenger *P. borealis* and soft-bodied organisms calls for a reconsideration of the trophic networks established for the marine sub-Arctic and Arctic environment. An accurate description of the trophic relationships is needed, especially for vulnerable ecosystems, to create a baseline against which future changes can be measured.

4.2 | Habitat-induced differences in diet composition of *P. borealis*

DNA metabarcoding revealed differences in the prey composition of *P. borealis* collected in different habitats (i.e., fjords vs. Shelf),

probably corresponding to different food web structure. The shelf habitat on the west side of Svalbard is heavily influenced by Atlantic water (Svendsen et al., 2002), whereas the fjords are partly composed of Arctic water and Atlantic advected waters, and are additionally being affected by terrestrial input such as sediments and freshwater (Milner et al., 2017; Shiklomanov & Shiklomanov, 2003; Syvitski, 1989). These physical influences can lead to a higher species richness in the open ocean and shelf areas compared to the fjords (Włodarska-Kowalczuk et al., 2012), consequently modulating the species diversity of both (Węsławski et al., 2011).

The flexible diet of *P. borealis* confirms its role as a generalized scavenger using resources available in the system. DNA metabarcoding revealed differences in the composition of stomach contents between fjord and shelf specimens. When interpreting DNA metabarcoding data it is important to distinguish primary predation from secondary predation (Bowser et al., 2013; Sousa et al., 2019). Detection of changes in diet based on the analysis of solely primary predation items could hint at behavioural changes rather than changes in the surroundings. Thus, it is valuable to confirm the observed pattern in fjord–shelf diet composition using the fraction of the diet for which the predator probably had no direct influence on, namely secondary predation. Thereafter, secondary predation provides another dimension to the dietary analysis (Sousa et al., 2019). In the case of *P. borealis*, adding secondary predation to the analysis further confirmed habitat-driven diet composition in both PERMANOVA and random forest analysis. Fourteen out of the 21 most informative MOTUs (66.6%) identified by the random forest approach were classified as secondary predation, and just seven MOTUs of these informative MOTUs belonged to primary predation. The method chosen for defining primary and secondary predation combined previous knowledge on prey taxa reported in *P. borealis* diet with an abundance threshold for DNA reads detected in this study (used for previously unreported taxa). Thus, abundant detected diet items were considered primary predation, even if not previously reported from the stomachs of *P. borealis*. Accidental ingestions of nontargeted species (e.g., ingestion of abundant larva or eggs) or freshly eaten prey by *P. borealis*-targeted prey can lead to high DNA abundances in the stomach content and consequently lead to false positive assignments to primary prey (Tercel et al., 2021). Here we provide a way of investigating the secondary prey fraction in an ecologically meaningful context. However, more research is needed to develop methods for reliable prediction of primary and secondary species from trophic DNA metabarcoding data.

The locations at which *P. borealis* was collected were sampled at different time intervals (between 2:40 a.m. and 8:11 p.m.). *P. borealis*, similar to other demersal crustaceans, performs diel vertical migrations (DVMs) to avoid visual predators (Shumway et al., 1985). These migrations are coupled to specific daytimes and as such could influence the stomach composition. This study did not investigate the effect of sampling time on the stomach content, because of the lack of replication for different time intervals of DVMs for all sampled habitats. However, locations from different habitats sampled at the same time (i.e., Rekesøyla and Kongsgrunnen) show significant differences in species composition, which suggests that the possible effect of sampling time on prey composition would be less important than the effects of location and habitat. Moreover, crustacean digestion times are often longer than their diel migrations (McGaw & Curtis, 2013), and hence organic matter found in *P. borealis* stomachs probably integrates items taken along the whole diel cycle. More intensive studies focused on sampling individuals from the same location and habitat at different time intervals would be needed to study the effect of diel vertical migration on the stomach composition.

Habitat-related diet differences were revealed using PERMANOVA and random forest classification. PERMANOVA is widely applied in the analysis of multivariate data, but it is known to introduce bias when many variables are analysed. With increasing dimensions (number of variables), the chances of detecting differences using PERMANOVA increase too (Anderson et al., 2008; Anderson & Walsh, 2013; Schweiger et al., 2010). Up to 304 MOTUs were used as variables for our PERMANOVAs, exceeding the number of observations and thus increasing the chances of false positive detections. To additionally support the observed pattern in fjord–shelf diet distinction, nMDS and random forest classification were used. Ordinations using nMDS plots could not clearly reveal the pattern of dissimilarity between habitats, probably due to the high interindividual diet variability leading to high dispersion of the data. In contrast, random forest classification underpinned the pattern observed from PERMANOVA. Random forest classification is considered exceptionally robust and accurate in classifying observations from complex, multidimensional data (Breiman, 1996; Liaw & Wiener, 2002). Moreover, it is considered robust to missing data and uneven sampling of variables, both common in trophic DNA metabarcoding data sets (Waljee et al., 2013). The classification approach of random forest was more likely to correctly assign *P. borealis* from the shelf habitats than from fjords. Although successful, the false prediction rate (OOB rate) was still at 21.11%. There is no hard threshold that defines an acceptable OOB rate. As long as an improvement in sample classification using a reduced set of variables can be achieved, we assume that this is an acceptable outcome for a predictive model.

4.3 | Proposed future application of *P. borealis* as a natural sampler

We detected a wide range of different taxa, from primary producers to vertebrates, in the diet of *P. borealis* from both fjord and shelf systems, which confirms its role as a generalized scavenger in different Arctic food webs as stated by Shumway et al. (1985). We propose that this characteristic would make *P. borealis* an ideal "natural sampler" of sub-Arctic and Arctic ecosystems. In the marine realm, natural samplers (e.g., sponges or other generalist shrimp species such as *Crangon crangon*) have so far been proposed to monitor marine vertebrate communities (Mariani et al., 2019; Siegenthaler, Wangensteen, Soto, et al., 2019). The evidence of fish-remains from *Clupea harengus*, *Boreogadus saida*, *Benthosema glaciale* and many

more in *P. borealis* stomachs indicates that stomach content metabarcoding could provide valuable information for assessments of fish communities. Moreover, our results show that use of this natural sampler could be expanded even further, as universal markers applied on *P. borealis* stomach content could be useful for assessing not only vertebrate communities, but other key taxa such as primary producers, by using opportunistic sampling (e.g., from commercial fisheries). Understanding the seasonal variations in *P. borealis* trophic ecology would enable more solid conclusions about the foraging patterns and primary and secondary prey composition, which could be used for tracing multilevel seasonal changes in the food web of the Arctic Ocean.

5 | CONCLUSION

Our findings highlight the power of DNA metabarcoding to provide highly resolved taxonomic diet assessments, including gelatinous zooplankton that may be underestimated by traditional SCA. DNA-based methods should be used more systematically to increase our understanding of the role of gelatinous zooplankton in marine food webs. The new links between *Pandalus borealis* and gelatinous zooplankton, and the much higher contribution of other soft-bodied prey items than previously reported, highlights that the role of gelatinous zooplankton in Arctic food webs should be reassessed. Moreover, our study shows that separating information on primary and secondary predation of a species, available through DNA metabarcoding, can lead to valuable additional insights about the ecology of the species and the food webs that they occupy. Finally, based on our results, we propose *P. borealis* as a particularly suitable natural sampler of sub-Arctic and Arctic ecosystems, which could help to obtain occurrence baselines against which future changes can be measured.

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AUTHOR CONTRIBUTIONS

P.U. participated in study design, carried out fieldwork and molecular laboratory work, data analysis and statistical evaluation, and wrote the manuscript. K.P. conceived and designed the study, secured funding, participated in laboratory work and contributed to writing. S.B. carried out statistical analyses (random forest) and contributed to writing. J.D. contributed to study design and writing. O.S.W. conceived and designed the study, participated in molecular work, carried out bioinformatic analysis, helped in statistical data treatment and contributed to writing. All authors critically read, contributed, and approved the final version of the manuscript.

BENEFIT SHARING

Benefits from this research accrue from the sharing of our data and results on public databases as described above.

DATA AVAILABILITY STATEMENT

The DNA metabarcoding data set, including sequences, taxonomic assignment and abundances for all MOTUs in every sample, is deposited in Dryad (https://datadryad.org/stash/share/QsyiZ2yBYB5uNAotVlmii5T0aAEgJCnlvnAmw-IkoIg).

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