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The Sinking Dead—Arctic Deep-Sea Scavengers' Diet Suggests Nekton as Vector in Benthopelagic Coupling

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ABSTRACT

Many benthic deep-sea animals rely on carcasses from the overlying water column that sink to the seafloor and form local organic enrichments known as food falls. This flux of organic carbon from the shallow pelagic to the deep sea is part of the biological carbon pump (BCP) and as such contributes to carbon sequestration. For a complete understanding of local carbon budgets, it is crucial to identify the diversity and distribution of sinking carcasses which are difficult to detect by observational methods. Here, we analyzed the diet of the abundant amphipod scavenger, *Eurythenes gryllus*, by DNA metabarcoding to assess their potential to identify food falls in the Fram Strait, a gateway to the Arctic. *E. gryllus* scavenges on nekton but so far it was not certain whether this represents their main diet. We detected dietary taxa (26 in total) in 20 out of 101 analyzed amphipods. We found that amphipods primarily fed on larger nekton including fish, cephalopods, and mammals, with bony fish being the most targeted food source in terms of diversity and abundance. Only one amphipod had fed on a gelatinous organism. These results support the hypothesis that *E. gryllus* targets mostly nekton food falls. The diversity of dietary taxa differed between the Eastern and Western Fram Strait, which suggests regional variability in food falls availability. We also detected, for the first time in *E. gryllus*, infections with the parasitic dinoflagellate *Hematodinium*. This detection demonstrates the potential of metabarcoding for revealing both food web dynamics and host–parasite interactions in the deep sea. *E. gryllus* seems a promising "natural sampler" to monitor the diversity of deep-sea food falls which will help to investigate the importance of medium-sized food falls in local vertical carbon export in a rapidly changing Arctic Ocean.

1 | Introduction

The deep-sea floor (> 200 m of depth) comprises an enormous part of the ocean, where organism numbers and biomass may be high, yet, food can be scarce. Primary producers in the epipelagic zone are responsible for generating the basis for the oceanic biomass that is divided over multiple trophic levels. Demersal deep-sea organisms (except chemosynthetic communities) rely on organic matter, which settles on the seafloor from the water column. This vertical flux of particulate

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organic matter is part of the biological carbon pump (BCP) and consists of marine aggregates comprising dead phytoplankton cells, fecal pellets, crustacean molts, and mucus, but also carcasses of zooplankton and larger nekton (Siegel et al. 2023). The flux of organic carbon to the ocean interior may be enhanced by the vertical migration of pelagic organisms, which feed in the upper layers at night and subsequently migrate down to mesopelagic depths where they digest and defecate during the day (Hays 2003). Ultimately, the BCP contributes to carbon sequestration, a crucial ecosystem service of the deep sea (Thurber et al. 2014). Identifying and quantifying the vectors of the coupling between the water column and the seafloor is essential to close carbon budgets and enhance our understanding of the capacity of the deep ocean for long-term carbon storage (Nowicki, DeVries, and Siegel 2022; Stukel, Décima, and Landry 2022). However, the magnitude and pace of the BCP varies regionally and still remains unidentified for many ocean regions. One of the vectors in the BCP, which nature and quantity remain poorly studied, are the sinking of carcasses of nekton and large zooplankton to the seafloor (Pinti et al. 2023).

When pelagic fauna die, their corpses sink to the seafloor where they form food falls, patches of organic enrichment that may attract high numbers of scavenging fauna (Stockton and DeLaca 1982). The consumption of food falls occurs in successional stages that differ in the taxonomic composition of the scavenging fauna. The regional ecology of food falls (i.e., the taxonomic diversity of food falls and scavenging communities, and scavenging successional stages and rates), has to date been mostly studied with in situ observations obtained via towed cameras, camera landers, or remotely operated vehicles. Observations of food falls are still rare. This is due to the relatively low number of deep-sea expeditions, which are complex and expensive, to detect food falls. The scattered occurrence and the rapid consumption of food falls complicates their detection. The best studied natural food falls are probably whale falls, which may be visible on the seafloor for years and may occur at a higher likelihood along migration routes (Smith et al. 2015). Nevertheless, observations are few and only recently the first whale fall was documented in the southern Atlantic (Sumida et al. 2016), and the third whale fall in the Antarctic (Stauffer et al. 2022). Other documented megafaunal food falls include a whale shark, mobiliid rays (Higgs, Gates, and Jones 2014), and a penguin (Stauffer et al. 2022). It is hypothesized that medium-sized food falls (1–100 cm) such as fishes, crustaceans, cephalopods and large zooplankton contribute significantly to local carbon budgets (Hoving et al. 2017; Smith 1985). Indeed, observations and quantification show that such food fall pulses may locally be similar or even exceed the carbon flux of particulate organic matter, and can supply the seafloor with organic matter over extended regions (Hoving et al. 2017, 2023; Simon-Lledó et al. 2023; Sweetman and Chapman 2015). Medium-sized carcasses are rapidly scavenged, typically within hours (Sweetman et al. 2014; Scheer et al. 2022). Therefore, observations are rare and typically few individual carcasses are documented (Smith 1985; Soltwedel et al. 2003). As a result, knowledge gaps related to food fall ecology that were highlighted decades ago still remain, including the regional frequency and nature of food falls (Stockton and DeLaca 1982). Investigating the diet of scavengers that consume medium-sized food falls may therefore be an efficient way to investigate the diversity and distribution of carcasses, in particular in remote regions such as polar deep seas.

Artificial and natural food falls in the Arctic deep sea show that amphipods are dominant scavengers, in particular the lysianassoid genus *Eurythenes* (S.I. Smith in Scudder, 1882) (Premke, Klages, and Arntz 2006; Rohlfer et al. 2022; Soltwedel et al. 2003). The genus *Eurythenes* occurs globally in marine systems from coastal waters to the deepest regions of our ocean, including hadal trenches (D'Udekem D'Acoz and Havermans 2015). The genus now consists of 10 described species (Horton et al. 2023), after a high number of species complexes were identified through molecular methods (Havermans 2016; Havermans et al. 2013). Regionally, *Eurythenes* species show a vertical population structure, with larger individuals occurring deeper and closer to the seafloor (Christiansen, Pfannkuche, and Thiel 1990; Christiansen and Diel-Christiansen 1993). The few publications on the diet of these abundant amphipods present conflicting information. *Eurythenes* amphipods seem to specialize in large food parcels and typically arrive first and within minutes at artificial food falls at depths from 1000–2500 m (Premke, Klages, and Arntz 2006; Scheer et al. 2022). Morphologically, *Eurythenes* seems to be adapted to carrion consumption due to the enlargement of the storage capacity of the midgut (Havermans and Smetacek 2018). Stable isotope analysis place Arctic *E. gryllus* as a consumer at higher trophic levels (Bergmann et al. 2009), indeed suggesting the consumption of nekton food falls. Diet studies using lipid and fatty acids analysis also support the consumption of carrion (Bühring and Christiansen 2001) while visual examination of stomach contents of individuals from the South Atlantic revealed sediment and suggested detritivory (Barnard 1962). Diet studies on hadal *Eurythenes* in trenches suggest they do not fully rely on nekton carrion, but instead can switch between necrophagy, predatory and detritivory (Blankenship and Levin 2007). Overall, the diet of this abundant deep-sea scavenger is shrouded in mystery hampering our understanding of the Arctic deep-sea food web. Here, we aim to test the hypothesis that Arctic *Eurythenes* consumes mostly nekton food falls.

Traditional visual investigations of the diet from small organisms such as crustaceans can be challenging. Typically, only small parts of the ingested food remain which may already be at an advanced state of digestion. Instead, DNA metabarcoding identifies organisms based on short and variable DNA fragments flanked by more conservative regions (Leray and Knowlton 2015). This molecular method uses universal polymerase chain reaction (PCR) primers to amplify and sequence DNA from environmental or bulk samples to identify communities. When applied to gut contents this approach can be an efficient tool to investigate the qualitative composition of a species' diet, also for the marine realm (De Sousa et al. 2019). Here, we performed DNA metabarcoding on gut contents of Arctic *Eurythenes gryllus* to investigate (1) their diet spectrum and their place in the food web, (2) the diversity of food falls in the Arctic deep sea, and (3) if the diet of these amphipods can be used to identify nekton carcass fluxes in the Arctic deep sea.

2 | Materials and Methods

2.1 | Sampling

Sampling of *E. gryllus* was conducted during the R/V *Polarstern* expedition PS126 to the Fram Strait in May to June 2021 (Figure 1). Sampling took place at two locations between Greenland and the Svalbard archipelago: station 21-1 (EG-I) at 1100 m depth close to the Eastern Greenland shelf and station 10-1 (SV-I) at 980 m depth off the Western Svalbard archipelago shelf (Table 1). At both locations, a free-fall lander (sensu Scheer et al. 2022) equipped with four steel baited trap boxes was deployed to lure and catch benthopelagic scavenging amphipods. Amphipods attracted by the bait (mackerel *Scomber scombrus*) could enter the traps via funnel shaped openings with a diameter of 1–4 cm. The funnel shape of the opening prevented the amphipods from leaving the box. Inside the box, the bait was wrapped in mesh and hence not accessible to feed on for the amphipods. At station 10-1, the lander was deployed on the seafloor for approx. 18 h, and at station 21-1 for approx. 8 h. Collected amphipods were immediately frozen at −80°C, killing them instantly and preventing further digestion of dietary items. Amphipods from the two sampling sites (station 10-1 and station 21-1) did not significantly differ in average weight (Welch *t*-test, *p*-value = 0.3118) and size (*p*-value = 0.04359) (Table 1).

2.2 | DNA Extraction

In total, 101 *E. gryllus* individuals were dissected, (*n* = 50 for station 10-1 and *n* = 51 for station 21-1, Table S1) at GEOMAR Helmholtz Centre for Ocean Research Kiel. Length (rostrum to telson tip) and weight were determined for each individual amphipod. The complete digestive tract was dissected from thawing animals and frozen at −20°C until DNA extraction. To prevent cross-contamination between samples, dissection instruments and surfaces were sterilized with Ethanol and RNaseAWAY (Thermo Scientific) between individuals. DNA extractions were performed with the Blood and Tissue Kit (Qiagen). Extraction followed the manufacturer's protocol for "Purification of Total DNA from Animal Tissue (Spin-Column Protocol)" using 25 mg tissue per extraction and with adjustment made to the incubation time (> 12 h, i.e., overnight). DNA was eluted in 60 μL elution buffer. DNA extracts with concentrations > 300 ng/μL were diluted 1:1 with elution buffer. For each set of extractions (23 samples), one "lab blank" was simultaneously extracted as a contamination control, which was treated as a sample but no amphipod digestive system content was added.

2.3 | Library Preparation and Sequencing

Two universal genetic markers were used in this study to identify metazoan dietary taxa in amphipod digestive tracts. The first marker targeted the 313-bp-long "Leray fragment" of metazoan mitochondrial cytochrome *c* oxidase I (hereafter COI), and the second targeted the 356-bp-long 18S-V1V2 region of the 18S ribosomal RNA gene (hereafter 18S). For COI, the forward Primer mlCOIintF (5′GGWACWGGWTGAACWGTWTAYCCYCC3′) (Leray et al. 2013) and the reverse Primer jgHCO2198 (5′TANACYTCNGGRTGNCCRAARAAYCA3′) (Geller et al. 2013) were used. For 18S, the forward Primer SSUF04 (5′GCTTGTCTCAAAGATTAAGCC3′) (Blaxter et al. 1998) and the reverse Primer SSURmod (5′CCTGCTGCCTTCCTTRGA3′) (Sinniger et al. 2016) were used.

For each primer pair, two-step library preparation was performed. Each sample was run in triplicates for the first PCR, and
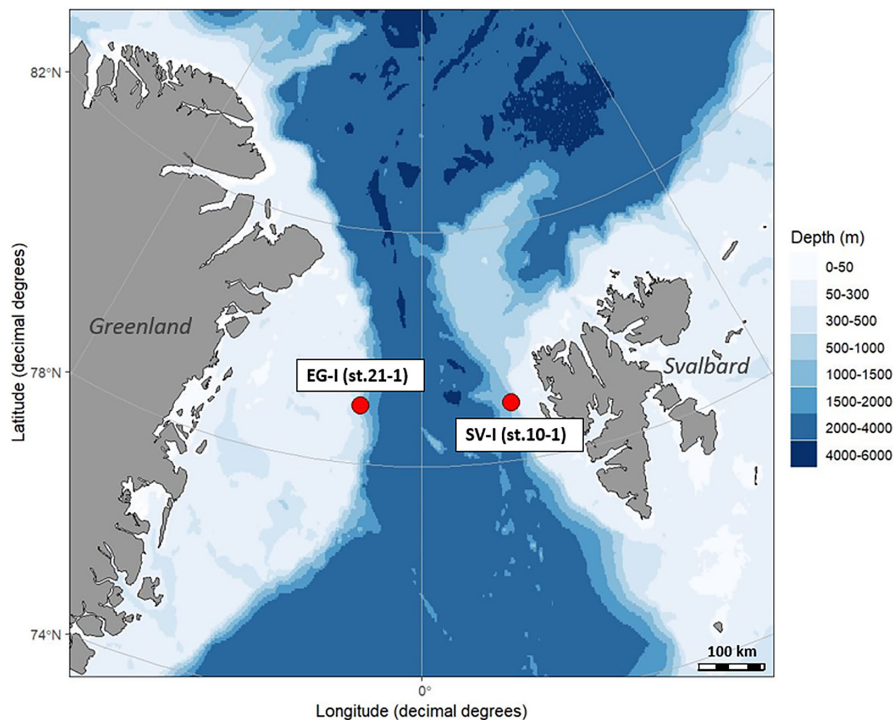

FIGURE 1 | Map of Fram Strait bathymetry with locations of the two sampling sites SV-I (1099.9 m) and EG-I (983.7 m) (79°01.85′ N 001°65.26′ E and 79°00.74′ N 005°37.35′ W, respectively).

TABLE 1 | Overview of sampled station locations during PS126 and physical measures of *Eurythenes gryllus* samples caught.

Location	Latitude	Longitude	Depth [m]	Date	Samples total	Mean length [cm]	Mean weight [g]	Bait
SV1 (st.10–1)	78.99995	7.99810	1099.9	2021/06/07	50	4.47 ± 2.11	3.82 ± 1.57	Mackerel
EG1 (st.21–1)	79.00096	−5.49112	983.7	2021/06/15	51	4.79 ± 0.76	4.47 ± 2.11	Mackerel

technical replicates pooled prior to the second PCR. Per PCR plate, two positive controls (*Danio rerio*, *Halichondria panicea* (COI_FR1)/*Pareledone felix* (COI_FR2)), one mock control (mix of both positive controls) and one negative control were added in duplicates. For PCR plates, all samples and technical replicates were randomized.

For the first PCR amplification, a master mix was prepared, consisting of 15 µL Phusion High Fidelity PCR 2X Master Mix with GC (Thermo Scientific), 0.5 µL of each of the 10 µM forward and reverse primers, 0.6 µL of 2.5 mM $MgCl_2$ (only for COI) and PCR grade water. For each reaction, 4 µL DNA extract was used (total PCR volume 30 µL). The PCR for both COI and 18S followed an initial denaturing step at 98°C for 30 s, 40 cycles of 98°C for 10 s, annealing for 45 s and 72°C for 1 min, and a final extension step of 72°C for 10 min (annealing temperature 48°C and 50°C for COI and 18S, respectively). All controls and 5–10 random samples per plate were checked for amplification after each PCR with gel electrophoresis. Plates were stored at 4°C if further processed within 2 days, or stored at −20°C.

Prior to the second PCR, technical replicates were pooled and diluted 1:10 with PCR grade water. For the second PCR amplification of COI and 18S, a master mix was prepared consisting of 2 µL 5× KAPA High Fidelity Fid Buffer (Roche), 0.2 µL KAPA High Fidelity DNA polymerase (5 U/µL, Roche), 0.3 µL dNTPs (10 mM, Roche), 0.2 µL DMSO (Roche), 0.5 µL of each forward and reverse index primers (10 µM), and 1.3 µL PCR grade water. To each reaction, 5 µL of the pooled 1:10 DNA extract was added (total PCR volume 10 µL). The PCR for both COI and 18S followed an initial denaturing step at 95°C for 5 min, 10 cycles of 98°C for 20 s, 55°C for 15 s and 72°C for 1 min, and a final extension step of 72°C for 10 min. PCR products were quantified with the Qubit high sensitivity kit (Invitrogen) and diluted to equimolar concentration (25 ng/µL). Samples were then pooled and purified with a gel electrophoresis for each library and subsequent DNA recovery was performed using the Zymoclean Gel DNA Recovery Kit (Zymo Research) following manufacturers protocol on a 2% agarose gel. The final eluted DNA extract was quantified by Qubit and stored at −20°C prior to sequencing. Sequencing was performed at the Institute of Clinical Molecular Biology (IKMB) Kiel on a MiSeq platform with the MiSeq Reagent Kit v3 (2 × 300 bp, MiSeq FGx; Illumina, San Diego, USA).

After sequencing the COI library (referred to as first full run, COI_FR1, 101 samples), we found that there was a high variability in read number per sample (several below 100 reads, while others had > 10,000). We experienced PCR inhibition from amphipod (host) DNA extractions during standard barcoding also using other primers, and tested dilution of DNA extracts prior to library preparation as a method to minimize

inhibitory effects and achieve more even sequencing results (MiSeq Reagent Kit v2 Nano 2 × 250 bp; COI_NR, 32 samples). After detecting new potential dietary taxa in this test sequencing run, a second full run with all samples was performed on 1:10 diluted extracts (MiSeq Reagent Kit v3 2 × 300 bp; COI_FR2, 101 samples). For the 18S gene amplification, one full sequencing run was conducted (MiSeq Reagent Kit v3 2 × 300 bp; 18_FR, 101 samples). It is important to note that the reverse sequences for 18S had low quality but we decided to analyze the high-quality forward sequences. These results are marked (18S_f) and are implemented to give a full picture of our efforts and findings. The focus in this research article is on the results and not method comparison and we therefore present results from all runs in the results section while providing information on the respective sequencing run.

2.4 | Bioinformatic Analysis

Following sequencing, the generated reads underwent demultiplexing by the sequencing center. PCR primer and adapter sequences were removed using cutadapt (version 1.18; Martin 2011). Only sequences containing both the forward and reverse primers were utilized for subsequent analysis using the Diverse Amplicon Denoising Algorithm (DADA2, version 1.16.0; Callahan et al. 2016; run in R version 4.2.3; R Core Team 2021; RStudio Team 2019). Paired reads were merged (for COI) and subjected to quality trimming with a threshold of ≤ 2. Potential chimeras were removed, and an amplicon sequence variant (ASV) table created. SINTAX was used for taxonomic classification of unique reads (Edgar 2016) based on the databases MIDORI2 and BOLD (Leray, Knowlton, and Machida 2022; Ratnasingham and Hebert 2007). Taxonomic assignments identified in negative controls and blanks were eliminated from the respective plates or batches of samples. After the initial taxonomic assignments, sequences were further verified using the naive Bayesian classifier method akin to BLAST (megablast, accessed October 2023) in GenBank (Altschul et al. 1990). A hit from megaBLAST was considered a species-level match if it exhibited a percent identity and query cover of at least 99% and had no closer or equal match to another species. If species-level could not be assigned due to no match in the database, matches on genus (> 96%), family (> 95%), etc. level were assessed.

Nonmarine taxa were excluded from the complete dataset. Also, taxa with a solely tropical Atlantic distribution and Pacific distribution were excluded from the final taxa list. In the following, the presence of taxa was marked as dubious in case the respective taxon has not been reported in the North Atlantic or could stem from contamination during sample processing. To account for extraction controls, we subtracted the maximum number of reads found for any ASV from the corresponding ASV read count

in all samples connected to that respective control. Remaining sequences with less than 10 reads were discarded. Taxonomic assignments were performed to lowest possible level. It should be regarded that the species diversity in the Arctic is under-sampled and could lead to assignments belonging to cryptic or unknown species.

2.5 | Statistical and Further Analyses

Statistical analyses were conducted in RStudio (R version 4.2.1; R Core Team 2021; RStudio Team 2019). Beta diversity was analyzed with the *vegan* package (version 2.6-4; Oksanen et al. 2022) by calculating a Jaccard dissimilarity matrix (*vegdist* function) on dietary taxa excluding dubious taxa. For this, we combined the results from all sequencing runs and counted the number of detections of each taxon per station (if a taxon was detected in the same sample by several sequencing runs, it was considered only as one detection). A principal coordinate analysis was conducted using the Jaccard dissimilarity matrix to visualize differences in dietary taxa diversity between stations. Differences were statistically tested with a permutational multivariate analysis of variance (*adonis2* function) after the assumption of equal dispersion within groups was tested (*betadisper* function). Differences in amphipod size and weight between stations were tested with a Welch *t*-test from the R *stats* package (version 4.2.1).

To assess the contribution of different organism groups (e.g., fish, mammals) to the diet of *E. gryllus*, the frequency of occurrence (FOO) and the relative read abundance (RRA) were calculated. The FOO was calculated as the number of samples that included a particular dietary group divided by the total number of samples with dietary taxa detections (Table S7). The RRA was calculated as the number of sequence reads (combined from all sequencing runs) divided by the number of total dietary taxa reads (Table S8).

Figures were generated in RStudio with the *ggplot* package (version 3.4.1; Wickham et al. 2019; R version 4.2.1) and the *ggOcean-Maps* package (version 2.1.1; Vihtakari 2021; R Version 3.6.3) and Figures 2 and 3 arranged in Microsoft PowerPoint (2019).
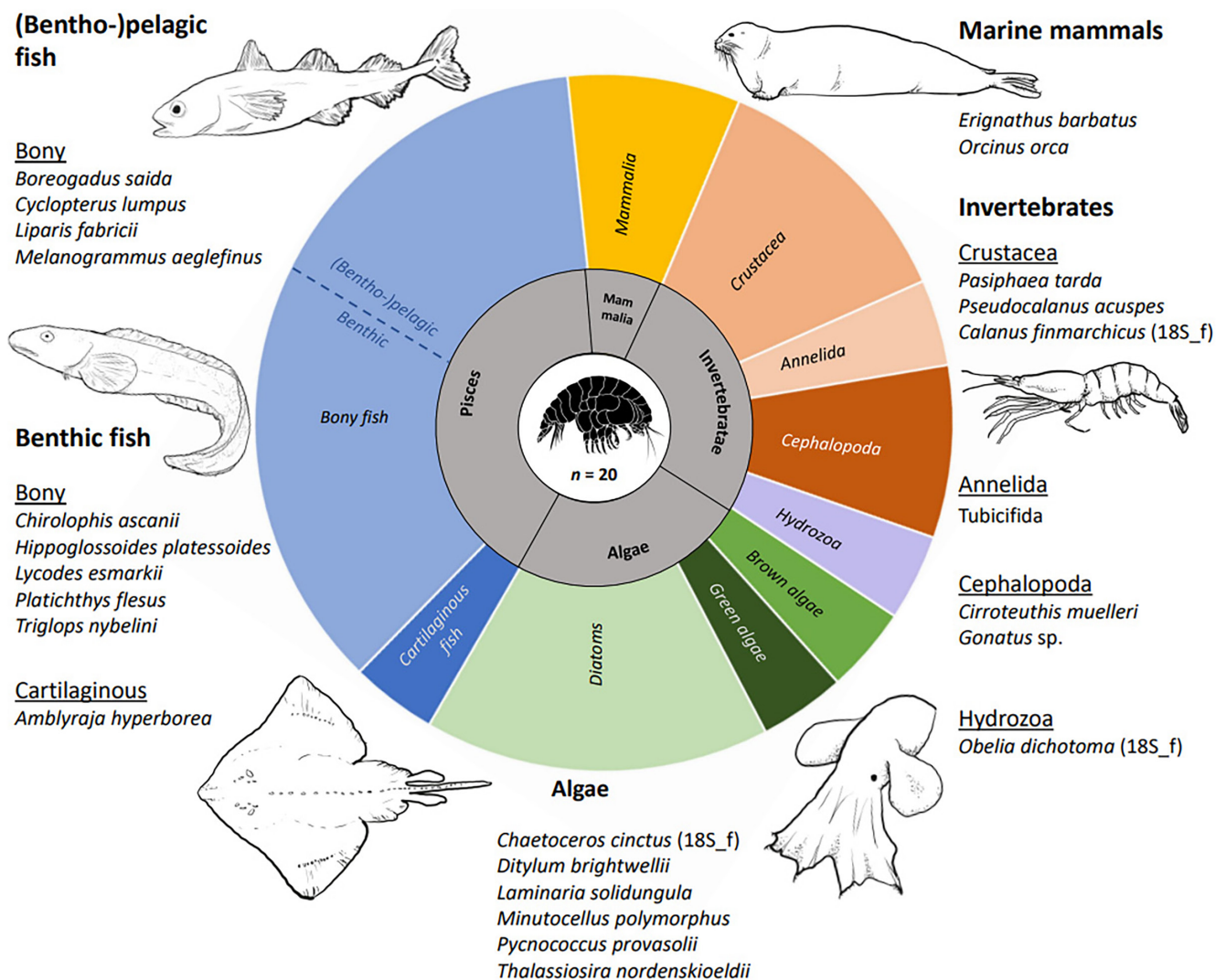

FIGURE 2 | The diversity of dietary taxa detected with metabarcoding in the stomachs of 20 *E. gryllus* individuals. Each colored section in the pie chart represents the relative contribution of a taxonomic group to all taxon assignments (*n* = 25). Taxonomic groups included fish (bony and cartilaginous fish classified into their typical habitat "benthic" vs. "(bentho-)pelagic" after Mecklenburg et al. 2018), algae (diatoms (Bacillophyaceae), green algae (Chlorophyta), brown algae (Phaeophyceae), invertebrates (Hydrozoa, Cephalopoda, Annelida, Crustacea) and mammals).
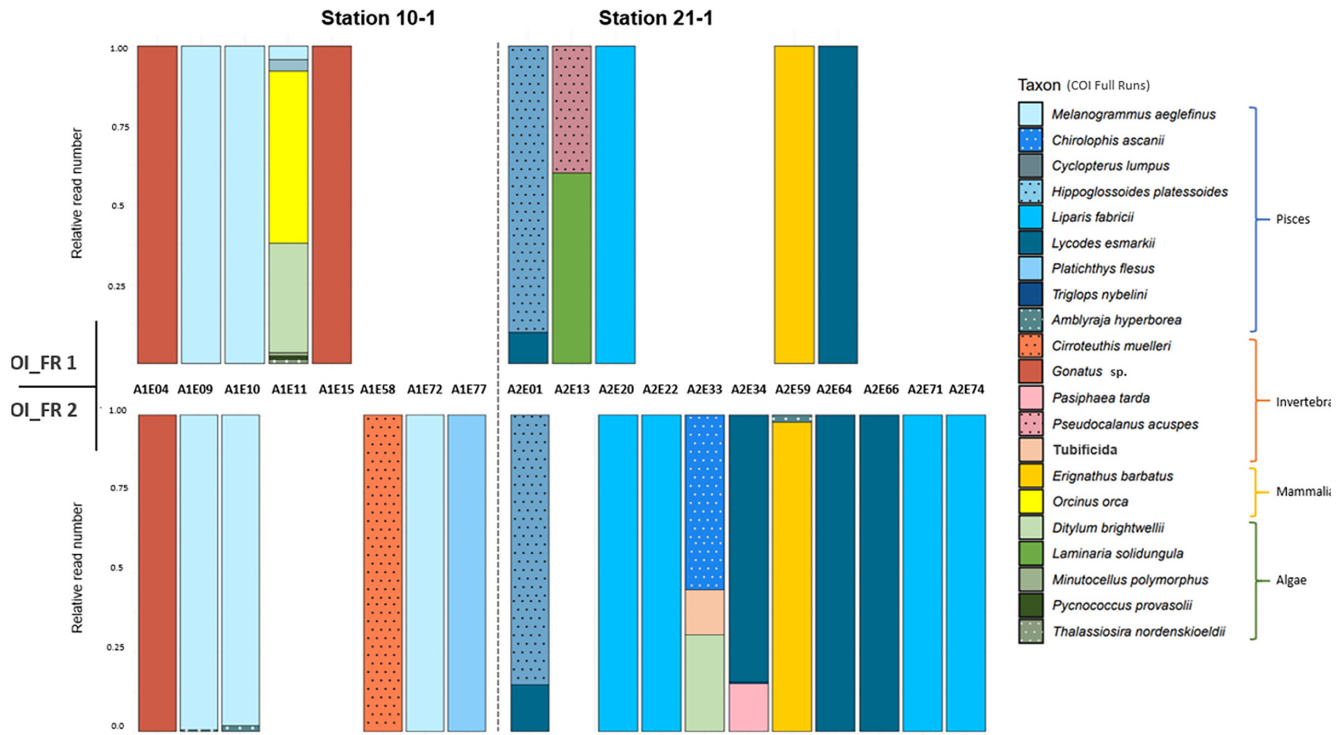
FIGURE 3 | Dietary taxa composition represented in the relative read numbers of each taxon within 19 samples of COI_FR1 (top) and COI_FR2 (bottom).

3 | Results

Both primer sets amplified host DNA which contributed between 78% and 89% of total reads per sample. All specimens were genetically assigned to *E. gryllus* with 100% similarity based on both the BOLD and the Genbank database.

The three combined COI sequencing run efforts (two full runs COI_FR1, COI_FR2, and one nano run COI_NR, Tables S2–S4) yielded a total of 22 possible dietary taxa which were assigned to 20 *E. gryllus* individuals. For 15 samples that were included in all three sequencing runs, the same taxa were identified, indicating robust detection. Dietary taxa reads (10–68,378 reads) accounted on average to 5.01% in COI_FR1, to 6.15% in COI_FR2, and to 15.23% in COI_NR of total reads per sample.

Merging the forward and reverse sequences of the 18S sequencing run resulted in low quality sequences allowing only one taxonomic assignment (*Amblyraja* sp., 53 reads) that met the quality thresholds. We also analyzed the 18S forward sequences without merging which resulted in 5.7 million sequence reads (Table 2, Table S5). Along with *Amblyraja* sp., another three unique dietary taxa (*Obelia dichotoma*, *Calanus finmarchicus*, and *Chaetoceros sinctus*) were identified and included in the final taxa list (marked with an '18S_f' in Figure 2). *Amblyraja* sp. was detected in the amphipod same sample that had a 100% match for *Amblyraja hyperborea* with the COI primers, and *A. hyperborea* is used for the figures and analyses. In 18S forward sequences, dietary taxa reads (17–2025 reads) accounted on average to 0.97% of total reads per sample.

Except for ASVs of *Gonatus* sp. and Tubificida, all ASVs defined as dietary taxa were assigned to species level. Potential dietary taxa were removed from the analysis if they were classified as "dubious" based on potential contamination during field and lab work (*Scomber scombrus* (bait), *Gadus morhua*, and *Discoteuthis laciniosa*) and/or absence from boreal and Arctic waters (*D. laciniosa*, *Mastigopsis hjorti*, and *Halofilum ramosum*).

3.1 | Potential Dietary Taxa Found in Eurythenes

After combining the results from all sequencing efforts, a total of seven different phyla, including 25 species, were detected in 20 of 101 *E. gryllus* specimens (Figure 2, Table S6). Vertebrate dietary taxa included 10 fish species and two mammal species. Invertebrate dietary taxa consisted of three crustacean, two cephalopod, one hydrozoan, and one annelid species. Also, six eukaryotic algae (probably secondary "prey") were detected as dietary taxa consisting of four diatom species, two green and one brown algae species. In the stomachs of 8 *E. gryllus* specimens from both stations the parasite *Hematodinium* sp. was detected. Only one of these specimens had dietary items in its stomach (*Chirolophis ascanii*, Tubificida, *Ditylum brightwelli*).

A total of 164,402 reads of dietary taxa were obtained from all sequencing runs. We assessed the RRA of dietary taxa groups as the number of sequence reads divided by the number of total dietary taxa reads. Fish taxa accounted for 90.8% of total dietary reads (bony 90.6%, cartilaginous 0.2%), followed by 7% invertebrate taxa reads (mainly cephalopods with 6.4%), 1.7% mammal taxa reads, and 0.3% algal taxa reads (Table S7). We also assessed

TABLE 2 | Summary of data processing of sequencing runs for analyzed COI and 18S sequencing runs. Total numbers of reads (# reads) with mean and standard deviation. ASVs number after DADA2 merging. Taxa consists of marine eukaryotic taxa with suitable distribution patterns. FR = full run, NR = nano run.

Sequencing run	# Total amphipod samples	# Reads after sequencing (mean + − SD)	# Reads after cleaning (mean + − SD)	# Reads of *Eurythenes* sp. ASVs	# Reads of dietary taxa	# ASVs after cleaning	# Dietary taxa	# Samples with dietary taxa detection
COI_FR1	101	5,538,696 (109,672)	5,185,188 (103,955)	4,065,945	81,461	17	14	10
COI_FR2	101	3,993,621 (65,788)	3,673,496 (60,922)	3,195,637	55,918	16	14	16
COI_NR	36	416,904 (10,677)	399,999 (10,288)	358,254	24,775	8	8	6
18S_FR (forward)	101	7,310,204 (89,817)	5,627,775 (81,316)	4,900,716	2248	8	8	4

FOO as the number of samples that included a particular dietary taxon divided by the total number of samples with dietary taxa detections. Across the 20 samples with dietary taxa detections, the most frequently detected taxonomic group was fish with 75% (bony 65%, cartilaginous 10%), followed by invertebrates with 35% (cephalopods 15%). Mammals and algae were present in 10% of all samples with dietary taxa (Table S8).

The composition of dietary taxa differed between *E. gryllus* samples (Figure 3). The two full sequencing runs targeting the COI gene were similar in the diversity of detected dietary items, while some were only detected in the second run using diluted template DNA (mostly detections of *Amblyraja hyperborea*) (Figure 3). In the majority of samples, only a single dietary taxon was detected. In most cases, these taxa belonged to bony fishes (e.g., COI_FR2 has eight samples with a single fish taxon detected). Three of the five algal taxa were found in one sample. Mammals were present in two samples.

3.2 | Dietary Taxa Diversity at Sampling Stations

The beta diversity (Jaccard index) of potential dietary taxa differed between the two sampling stations 10-1 and 21-1. The first and second principal component axes explain 19.76% and 13.63% of the total variance, respectively (Figure 4A). Permutational multivariate analysis of variance suggests that ~10% of the variance are explained by differences between the stations (adonis, $F(1,19) = 2.07$, p-value = 0.013). Of the 25 dietary taxa, 16 taxa were detected in amphipods from station 10-1 and 15 taxa were found in amphipods from station 21-1 (Figure 4B). Five taxa were found at both stations. Most dietary taxa were only detected in a single amphipod individual, while four fish species and one cephalopod were detected in more than one. Two of these were only detected at station 21-1. The diversity of fish taxa was higher at station 21-1 (8 species compared to 5 at 10-1), while cephalopods were only detected at station 10-1.

4 | Discussion

Metabarcoding of gut contents of the Arctic deep-sea amphipod *E. gryllus* from ~1000 m depth revealed a diet consisting primarily of larger nekton including fishes, cephalopods, and mammals. Therefore, it seems that *E. gryllus* falls. Fish clearly dominated the dietary taxa in terms of diversity, RRA, and FOO. Potential dietary items were detected in about one fifth of analyzed amphipod individuals and the majority of individuals had DNA of a single taxon in their stomach, suggesting consumption and filling the stomach with a single species, likely a carcass. One amphipod had fed on a gelatinous hydrozoan. A significant difference in beta diversity between diet components of amphipods from the Eastern and Western Fram Strait suggests regional variability in food-fall diversity. Metabarcoding of the stomach contents also detected parasite infections, highlighting the potential dual use of this method for revealing food web and parasite–host interactions in the deep sea. *Eurythenes gryllus* belongs to a globally distributed genus and is a promising "natural sampler" to study the diversity of deep-sea nekton food falls, which are extremely difficult
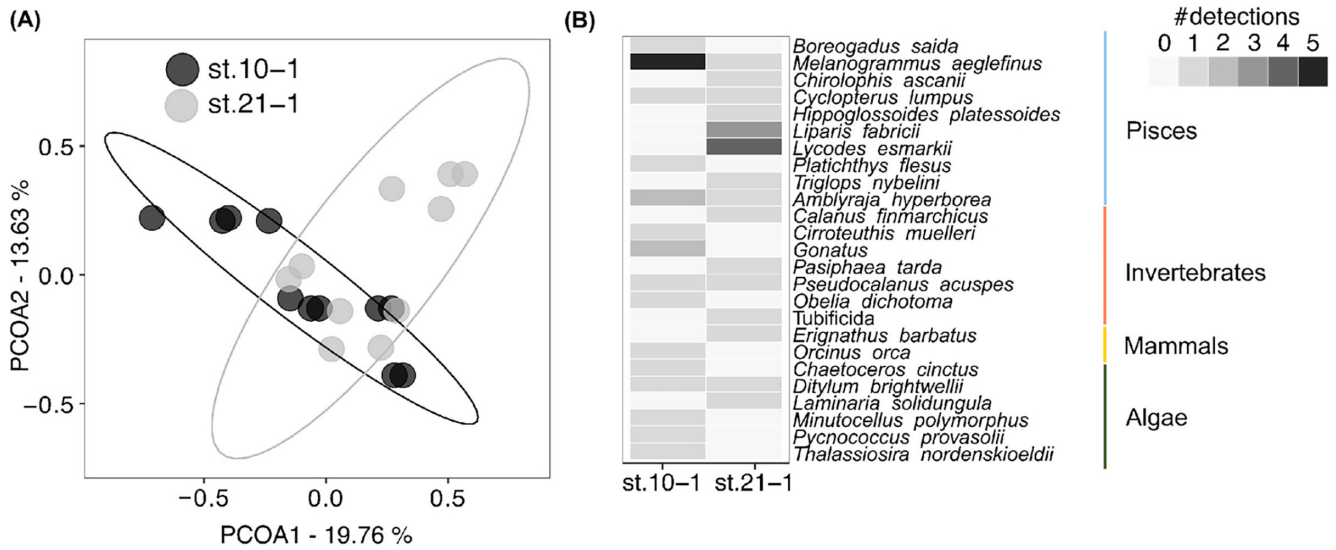
FIGURE 4 | Diversity of potential diet at station 21-1 (East Greenland) and station 10-1 (West Svalbard) (A) Principal component analysis of beta diversity (Jaccard index) of potential dietary taxa at the two sampling stations 10-1 and 21-1. (B) Heatmap visualizing the number of detections of potential dietary taxa at each of the two sampling stations.

to detect by observational methods. Such results can help identify sources that contribute to local carbon fluxes into the deep sea and aid in closing gaps in our understanding of the BCP.

4.1 | Diversity and Distribution of Dietary Taxa

Metabarcoding of *E. gryllus* stomach contents revealed 25 possible dietary taxa that are known to occur in the Arctic Ocean and adjacent Arctic waters (Jensen et al. 2023; Mecklenburg et al. 2018; Xavier et al. 2018). Around 60% of the dietary taxa (algae excluded) typically occur shallower than 500 m and most have a benthic or benthopelagic lifestyle (Mecklenburg, Møller, and Steinke 2011). The majority of detected fauna typically live close to the coast, indicating that *E. gryllus* scavenges on carcasses that traveled a significant horizontal and vertical distance. Dispersal with ocean currents can lead to the deposition of sinking carcasses on the seafloor hundreds of kilometers away from where the animals died (Simon-Lledó et al. 2023; Wiese 2003). Physical oceanographical tools such as hydrodynamic modeling and Lagrangian particle tracking, can help increase our understanding on carcass dispersal distances and the trophic linkage between the pelagic ocean and deep-sea floor (Jones et al. 2019; Nero et al. 2013).

Below we review the distribution, habitat, and ecology of each dietary group and discuss if and how these taxa may be food for *E. gryllus*.

4.1.1 | Vertebrates (Fish and Mammals)

All 10 detected fish species occur in the Arctic Ocean and adjacent waters (Mecklenburg, Møller, and Steinke 2011; Mecklenburg et al. 2018). *Cyclopterus lumpus*, *Hippoglossoides platessoides*, and *Triglops nybelini* are endemic, bentho/cryo-pelagic fish taxa from the Fram Strait (Gjøsæter et al. 2023). Except *Platichthys flesus* and *Chirolophis ascanii*, all other fish taxa have ranges

in adjacent waters of Eastern Greenland and Western Svalbard (Mecklenburg et al. 2018; Yershov, Fuks, and Khaitov 2022).

The most frequently detected fish (and allover most detected taxon) was the boreal haddock *Melanogrammus aeglefinus*. This species has expanded its range to the northern Svalbard shelf break and was recently detected in the Fram Strait by environmental DNA (eDNA) metabarcoding (Merten et al. 2023). *Melanogrammus aeglefinus* is also a diet component of pelagic crustaceans including the amphipod *Themisto* and the Arctic shrimp *Pandalus*, implying that it may serve as food source for a diversity of Arctic crustaceans with different habitats and foraging styles (Dischereit et al. 2022; Urban et al. 2022). Interestingly, the crustaceans *Themisto* (Dischereit et al. 2022), *Pandalus* (Urban et al. 2022) and *E. gryllus* (this study), which all occur in the Fram Strait, all consume the fishes: *Boreogadus saida*, *Liparis fabricii*, *Hippoglossoides platessoides*, *Triglops nybelini*, *Amblyraja hyperborea*, and members of the genus *Lycodes*. Lysianassoid species from shallow Arctic waters (Svalbard fjords) were also found to predominantly feed on fish, together with a high variety of other taxa (crustaceans, macroalgae) (Dischereit et al. 2024). In general, it should be noted that presence of fish DNA could also reflect feeding on fish eggs, larvae or feces, or secondary prey.

Both the bearded seal *Erignathus barbatus* and the killer whale *Orcinus orca*, occur in the Fram Strait (Davis et al. 2008; Dietz et al. 2020; Jensen et al. 2023). However, so far, there is no visual record of a whale fall nor a seal food fall in the Arctic Ocean (Li et al. 2022). *Erignathus barbatus* forages on benthos and usually dives to depths not greater than 100 m off the Svalbard archipelago. *Orcinus orca* populations off eastern Greenland and the Barents Sea tend to stay in shallower waters close to the continental shelf edge (Cameron et al. 2010; Dietz et al. 2020; Gjertz et al. 2000). Their presence in *E. gryllus'* diet may imply direct consumption of their carcasses, or ingestion of their eDNA, e.g., shed via feces. For example, in one *E. gryllus* individual, DNA of the killer whale *O. orca* was detected but to a lower proportion

also that of the fish taxa *Cyclopterus lumpus*, *Scomber scombrus*, and *M. aeglefinus*. All these fish taxa are also prey of Norwegian killer whale populations (Jourdain et al. 2020) and therefore may have been ingested by the orca. The amphipods may have consumed both the orca carcass and the fishes in the stomach, or the amphipod may have fed on the feces of the orca. We cannot differentiate between scavenging and ingestion of feces at this point.

4.1.2 | Invertebrates (Cephalopods, Crustaceans, and Annelids)

Two cephalopod species were detected in *E. gryllus'* diet. The cirrate octopus *Cirroteuthis muelleri* was identified to species level and is native to high-latitude Arctic waters. It follows a benthopelagic lifestyle and feeds on the seafloor and moves up in to the upper water column (Golikov et al. 2023). It appears to be part of a distinct deepwater faunal community on the Yermark plateau off Western Svalbard where it makes up a large biomass (Jørgensen et al. 2022). So far, *Cirroteuthis* has not been detected in stomach contents of scavengers. The abundant genus of armhook squids *Gonatus* sp. was also detected in the amphipod stomach contents. There are two species, *G. fabricii* (Nesis 1987; Golikov et al. 2013), which is the most abundant cephalopod in the Arctic, and the sub-arctic *Gonatus steenstrupi*, which is distributed in the North Atlantic up to 63°N (Kristensen 1981). Detection of the latter could potentially be the result of a range expansion as suggested earlier (Golikov et al. 2013, 2014; Xavier et al. 2018).

All three decapod crustaceans found in *E. gryllus'* stomachs occur in and around the Fram Strait (Klages et al. 2001; Østvedt 1955). The copepod *Calanus finmarchicus* is a native key copepod species that dominates the zooplankton biomass of the Fram Strait. It is a food source of numerous crustaceans, fish, and mammals (Hop et al. 2006). The other detected copepod species, *Pseudocalanus acuspes*, is documented from Western Svalbard fjords. Hence, it was most likely secondary prey or was transported by ocean currents to deeper regions of the Fram Strait (Hop et al. 2006). Copepods and other crustaceans were also detected in stomach contents of Arctic lysianassoid scavenging amphipods of the genus *Onisimus*, *Orchomenella* (Legezyńska 2001; Dischereit et al. 2024), and *Anonyx* (Sainte-Marie 1992; Dischereit et al. 2024), and in the diet of two other crustaceans from the Fram Strait, *Pandalus* und *Themisto* (Dischereit et al. 2022; Urban et al. 2022). The bathypelagic Caridean shrimp *Pasiphaea tarda*, which was detected once, is also consumed by the scavenging lysianassid amphipod *Uristes* sp. in the abyssal Fram Strait (Klages et al. 2001; Rodrigues and Cardoso 2019).

The order Tubificida was the single representation of annelid worms in the diet of *E. gryllus*. These oligochaetes occur worldwide in fresh and brackish waters as well as marine habitats from coasts to the deep sea (Erséus 1980).

4.1.3 | Algae

Diet metabarcoding of *E. gryllus* also revealed the presence of seven algae species of which only *Halofilum ramosum* is not known from the Arctic Ocean (Gasulla et al. 2019). Amphipods were sampled during late spring which coincides with peak POC

fluxes at the Fram Strait seafloor (> 2000 m) and with bloom episodes of some of the herein identified algae (van Oevelen et al. 2011; Nöthig et al. 2015; Bachy et al. 2022). The here identified *Chaetoceros* is one of the dominant diatom taxa during summer blooms in the Fram Strait and seems to be food for taxa in deeper water layers (Bachy et al. 2022; Cardozo-Mino et al. 2021). The presence of algae could indicate detrivory and feeding on marine snow aggregates which was previously suggested for *E. gryllus* (Barnard 1962; Blankenship and Levin 2007). Visual gut analyses of other Arctic scavenging, lysianassoid amphipods show feeding on algae and detritus (Legezyńska 2001; Sainte-Marie 1992). However, in our study, algal taxa were always detected alongside higher trophic dietary taxa such as fish or crustaceans, which could indicate that they may be ingested as secondary dietary items. The presence of algae in diets of other larger crustaceans from the Fram Strait was also attributed to secondary ingestion (Urban et al. 2022).

4.1.4 | Absence of Gelatinous Taxa

The sequencing of the COI gene did not result in detections of gelatinous dietary taxa. Sequencing of the 18S rRNA gene resulted in one detection of the hydrozoan, *Obelia dichotoma*. It is a common and almost cosmopolitan hydrozoan that indeed occurs in Svalbard fjords (Orejas et al. 2013) which is close to the eastern station st.10-1 where *O. dichotoma* was detected in this study. The absence of gelatinous zooplankton in *E. gryllus'* diet is supported by scavenger observations on experimental food falls in Fram Strait. *E. gryllus* was present in high abundance on fish and cephalopod carcasses, but absent on jellyfish carcasses (*Periphylla periphylla*) (Scheer et al. 2022). This is not the case for shallow-water Arctic lysianassoids, which feed occasionally on jellyfish carcasses (Dischereit et al. 2024). Scavenging on gelatinous plankton is commonly difficult to identify because of the high consumption rates and fast digestion of these soft-bodied and mostly small organisms (Hays, Doyle, and Houghton 2018). Therefore, the relevance of gelatinous plankton for higher trophic levels was long underestimated (Hays, Doyle, and Houghton 2018). Molecular methods such as DNA metabarcoding have improved the detection of gelatinous species in the diet of consumers (Hays, Doyle, and Houghton 2018). To investigate the diet of *E. gryllus*, we chose to apply two genetic markers to increase the chances of detecting gelatinous plankton. 18S rRNA gene primers have been discussed to detect gelatinous taxa more reliably compared to COI primers, particularly for ctenophores and pelagic tunicates (Günther et al. 2021; Ruiz et al. 2024). However, COI has been efficient in detecting a diversity of gelatinous zooplankton, including cnidarians (Dischereit et al. 2022, 2024; Urban et al. 2022), with the same COI fragment as used in the present study. There, also other invertebrate groups, (chaetognaths, mollusks, and echinoderms) were detected, which we did not find in *E. gryllus*. The absence of these groups including gelatinous taxa in our results is therefore most likely a realistic reflection of the diet of *E. gryllus* and not a bias of markers or methodology. However, the quality of the 18S rRNA gene sequencing was limited and overall few dietary taxa were detected. We therefore cannot exclude the possibility that some gelatinous taxa were overlooked due to limited sequencing output also caused by the dominance of host reads.

4.1.5 | Detection of *Hematodinium*

The crustacean parasite *Hematodinium* was detected in eight *E. gryllus* individuals that were captured in both sample locations in the Fram Strait. It is a protist that is the causative agent of the 'bitter crab disease'. Our records are the first detection of these parasites in *E. gryllus* and perhaps the first evidence that these protists occur as deep as 1000 m (records from ~500 m depths exist, Eigemann, Burmeister, and Skovgaard 2010; Mullowney et al. 2011). *Hematodinium* is a parasitic dinoflagellate that is well known to infect over 40 crustacean species, including amphipods. It occurs globally and causes epidemics in the wild as well as in aquaculture (Li, Li, and Huang 2021). Infection with *Hematodinium* could be common in deep-sea *E. gryllus* amphipods since about 8% of the sampled individuals were carrying this parasite. This rate is similar to *Hematodinium* infection rates in other crustacean species (3%–23%, Hamilton, Shaw, and Morritt 2009). For the studied species, it is known that *Hematodinium* is localized in the haemolymph and causes metabolic dysfunction and tissue damage, which may ultimately lead to mortality at high infection levels (Li, Li, and Huang 2021). In the present study, ~12% of the amphipods with an infection had detectable prey reads, hence assumed to have recently eaten, while about 23% of the noninfected individuals had eaten. A higher sequencing output per individual, a larger sample size, and repeated sampling would be needed to investigate such a potential correlation between infection, feeding, and mortality.

4.2 | *E. gryllus* Ecology and Feeding Strategy

Observations on artificial and natural food falls show that amphipods are dominant scavengers in the Arctic deep sea, in particular the members of the genus *Eurythenes* (Premke, Klages, and Arntz 2006; Scheer et al. 2022). The deep sea potentially provides room for specialization of scavengers on different food sources, which contrasts the opportunistic lifestyle of many deep-sea taxa. However, for most amphipod species it is not yet fully understood whether they have a predominantly generalist and/or specialist feeding behavior. Food fall deployments confirm that different carcasses of different species attract specific scavenging communities at different time scales (Scheer et al. 2022). *Eurythenes* amphipods seem to prefer medium-size fish and cephalopods over jellyfish, and typically arrive at artificial food falls within minutes at 1000–2500 m depth (Premke, Klages, and Arntz 2006; Scheer et al. 2022). When different fish species are offered simultaneously, *Eurythenes* individuals show a preference for round fish over flat fish species (Premke, Klages, and Arntz 2006). The metabarcoding results from the present study confirm that *E. gryllus* feeds on medium sized nekton that do not include gelatinous organisms. Fish were the most represented taxa in terms of diversity, read abundance, and FOO. Hence, our results are in line with previous studies on the anatomy and foodweb position of Arctic *Eurythenes* which place this amphipod as consumer of carrion and at higher trophic levels (Bergmann et al. 2009; Bühring and Christiansen 2001; Havermans and Smetacek 2018). Although we cannot rule out that dietary taxa detections from metabarcoding might also stem from other sources than dead fauna (e.g., fish eggs,

whale feces), we would argue that cumulative experimental, morphological, molecular, and biochemical evidence strongly suggest that *E. gryllus* consumes dead fauna.

One fifth of our analyzed *Eurythenes* specimens had recently eaten. Therefore, the majority of individuals may have been starving when arriving at the baited traps. In most individuals that had fed, a single dietary taxon was detected. This suggests no sequential feeding on several food-falls within a short time, or a very rapid digestion. Sinking of larger nekton carrion is mostly unpredictable in space and time except for seasonal die offs after spawning events (Havermans and Smetacek 2018; Hoving et al. 2017). *Eurythenes* amphipods are indeed able to cope with periods of starvation of up to several months in between meals (Hargrave et al. 1994) due to both morphological (Dahl 1979; De Broyer, Nyssen, and Dauby 2004) and behavioral adaptations (Hargrave 1985; Hargrave et al. 1994). Although it is likely that at least a proportion of the specimens were starving, an overdominance of host reads may have masked further dietary reads. To improve the efficiency of future studies on *E. gryllus* as a natural sampler, we would therefore suggest to consider host DNA blocking primers if universal metazoan primer sets are used. While we were here interested in overall metazoan taxa, we mostly detected larger nekton. For future studies on *E. gryllus'* diet we suggest the use of specific primer sets that target nekton (e.g., fish, Miya et al. 2015, or cephalopods 18S cephalopods, De Jonge et al. 2021) in addition to universal primers. This approach would avoid host amplification and increases the chance of detecting relevant dietary taxa. Additionally, detection of dietary items could be improved by pooling gut content from several individuals per sample (5–10), and increasing sequencing depth by a more powerful sequencing method (e.g., NovaSeq).

4.3 | *Eurythenes gryllus* as a Natural Sampler to Monitor Changing Arctic Pelagic Communities

Different marine taxa have been used as "natural samplers" to monitor biodiversity. These taxa include sponges and other filter feeders that passively filter seawater (Jeunen et al. 2023; Mariani et al. 2019; Turon et al. 2019), and crustaceans such as *Crangon crangon* (Siegenthaler et al. 2019) or *Pandalus borealis* (Urban et al. 2022) that act as eDNA collectors. Scavenging species such as *E. gryllus* are efficient natural samplers that can aid in monitoring nekton food falls from the pelagic realm to the deep-sea floor. Indeed, we show that diet metabarcoding of *E. gryllus* amphipods from the Fram Strait allows detection of different metazoan species, including rare, mobile, and elusive taxa such as marine mammals and cephalopods. The relatively easy capture of *E. gryllus* amphipods in baited traps, the global distribution of the genus, and potential targeted scavenging on larger nekton species makes them a promising candidate as natural samplers in the context of benthic-pelagic coupling. Gut content analyses of scavengers can reveal a unique perspective on local biodiversity, in addition to species specific contributions to deep-sea food-web and the BCP.

The nature and efficiency of the BCP is changing locally as a result of climate change. This is particularly so in the Arctic Ocean, a hotspot of climate change, where warming, sea ice retreat, and

meltwater stratification are causing large scale changes in the eco-system and the BCP (Von Appen et al. 2021). As a result of increasing northward flow of Atlantic water (Atlantification) (Polyakov et al. 2023), the Arctic ecosystem is subject to an influx of Atlantic marine fauna and subsequent northward migration of Arctic species (borealization) (Fossheim et al. 2015). These changes in pelagic communities are expected to affect the BCP and deep sea through changes in food-falls, both their nature and quantity, but to which extent remains currently unknown. A time-series approach with annual sampling of *E. gryllus* as natural samplers, while increasing sequencing output and an improved knowledge on the species´ ecology would be a way forward to monitor the nature of food falls sinking to the deep sea in an Arctic Ocean that is changing fast under climate change.

Ethics Statement

The current study involved sampling of *c.* Handling of specimens followed ethical principles in the absence of formal approval processes as to minimize the distress of study animals. The sampling and utilization of samples took place in compliance with all relevant legislation of the provider countries Greenland and Norway. Norway is a party to the Nagoya Protocol but did not regulate access to genetic resources at the time of this study. Under section 9 of the Greenland Parliament Act no. 3 of 3 June 2016 the Greenland Government granted a NonExclusive License no. G21-007 for the Utilization of Greenland Genetic Resources.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Metabarcoding sequence data and sample metadata are available at the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under the BioProject number PRJNA1128413, accession numbers SAMN42050232- SAMN42050346. Bioinformatic analysis can be accessed at Zenodo under https://doi.org/10.5281/zenodo.12633102.

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Supporting Information

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