Opportunistic consumption of marine pelagic, terrestrial, and chemosynthetic organic matter by macrofauna on the Arctic shelf: A stable isotope approach

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Macrofauna can contribute substantially to the organic matter cycling on the seafloor, yet the role of terrestrial and chemosynthetic organic matter in the diets of microphagous (deposit and suspension) feeders is poorly understood. In the present study, we used stable isotopes of carbon and nitrogen to test the hypothesis that the terrestrial organic matter supplied with river runoff and local chemosynthetic production at methane seeps might be important organic matter sources for macrofaunal consumers on the Laptev Sea shelf. We sampled locations from three habitats with the presumed differences in organic matter supply: "Delta" with terrestrial inputs from the Lena River, "Background" on the northern part of the shelf with pelagic production as the main organic matter source, and "Seep" in the areas with detected methane seepage where chemosynthetic production might be available. Macrobenthic communities inhabiting each of the habitats were characterized by a distinct isotopic niche, mostly in terms of $\delta^{13}C$ values, directly reflecting differences in the origin of organic matter supply, while $\delta^{15}N$ values mostly reflected the feeding group (surface deposit/suspension feeders, subsurface deposit feeders, and carnivores). We conclude that both terrestrial and chemosynthetic organic matter sources might be substitutes for pelagic primary production in the benthic food webs on the largely oligotrophic Laptev Sea shelf. Furthermore, species-specific differences in the isotopic niches of species belonging to the same feeding group are discussed, as well as the isotopic niches of the symbiotrophic tubeworm *Oligobrachia* sp. and the rissoid gastropod *Frigidoalvania* sp., which are exclusively associated with methane seeps.

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Abstract

Macrofauna can contribute substantially to the organic matter cycling on the seafloor, yet the role of terrestrial and chemosynthetic organic matter in the diets of microphagous (deposit and suspension) feeders is poorly understood. In the present study, we used stable isotopes of carbon and nitrogen to test the hypothesis that the terrestrial organic matter supplied with river runoff and local chemosynthetic production at methane seeps might be important organic matter sources for macrofaunal consumers on the Laptev Sea shelf. We sampled locations from three habitats with the presumed differences in organic matter supply: "Delta" with terrestrial inputs from the Lena River, "Background" on the northern part of the shelf with pelagic production as the main organic matter source, and "Seep" in the areas with detected methane seepage where chemosynthetic production might be available. Macrobenthic communities inhabiting each of the habitats were characterized by a distinct isotopic niche, mostly in terms of $\delta^{13}C$ values, directly reflecting differences in the origin of organic matter supply, while $\delta^{15}N$ values mostly reflected the feeding group (surface deposit/suspension feeders, subsurface deposit feeders, and carnivores). We conclude that both terrestrial and chemosynthetic organic matter sources might be substitutes for pelagic primary production in the benthic food webs on the largely oligotrophic Laptev Sea shelf. Furthermore, species-specific differences in the isotopic niches of species belonging to the same feeding group are discussed, as well as the isotopic niches of the symbiotrophic tubeworm *Oligobrachia* sp. and the rissoid gastropod *Frigidoalvania* sp., which are exclusively associated with methane seeps.

1. Introduction

It is a widely accepted paradigm that environment and biodiversity jointly drive ecosystem functioning (van der Plas, 2019). Specifically, accounting for the functional diversity of benthic biota might improve understanding of various ecosystem functions on the seafloor including organic matter cycling (Snelgrove et al., 2018). Within marine sediments, organic matter mineralization in part depends on the processing of organic matter by macrofauna (Woulds et al., 2016; Middelburg. 2018). Different macrobenthic communities respond differently to inputs of organic matter depending on species and functional composition (Josefson et al., 2002; Norling et al., 2007; Karlson et al., 2010; Belley and Snelgrove, 2017). Moreover, organic matter differs in its bioavailability for macrobenthic consumers as well as its nutritional value depending on its origin and quality (Mayor et al., 2012; Hunter et al., 2013; Campanyà-Llovet et al., 2017). Therefore, identifying the organic matter sources for benthic food webs and functional differences within macrobenthic consumers are prerequisites for an improved understanding of benthic organic matter cycling.

There are several major sources of organic matter on the Arctic shelf: phytoplankton and ice algae are the main sources of marine primary production (Sakshaug, 2004; Søreide et al., 2006), while river runoff and coastal erosion supply organic matter of terrestrial origin (Goñi et al., 2000; Knies and Martinez, 2009; Vonk et al., 2012; Xiao et al., 2013). Macrobenthic communities mainly rely on the export flux of organic matter from the euphotic zone, both of sympagic (ice algae) and pelagic (phytoplankton) origin (Søreide et al., 2013; Mäkelä et al., 2017). There is also evidence of terrestrial organic matter being incorporated into benthic food webs, although it is considered more refractory compared to organic matter of marine origin (Dunton et al., 2012; Bell et al., 2016; Harris et al., 2018). The exact quality and quantity of organic matter reaching the seafloor might depend on many factors and processes, both biotic and abiotic, including depth, water mass properties and currents, overall primary production, terrestrial inputs, grazing by zooplankton, and microbial degradation of sinking organic matter (Iken et al., 2005; Roy et al., 2015; Stasko et al., 2018). Locally, benthic primary production is important for benthic food webs, including microphytobenthos and macroalgae in the coastal habitats (Woelfel et al., 2010, Renaud et al., 2015) and chemosynthetic production in the areas with seabed emission of reduced compounds, such as methane and hydrogen sulfide, also known as "methane seeps" and "hydrothermal vents" (Sweetman et al., 2013; Åström et al., 2022). Consequently, regional and local ecosystem features might drive differences in organic matter availability and consumption by macrofauna. In this respect, the Laptev Sea appears to be among the least studied Arctic seas (Kędra et al., 2015). This part of the Arctic is considered a region of high biogeochemical activity due to considerable river runoff, coastal erosion, and methane seepage (Dittmar and Kattner, 2003, Vonk et al., 2012, Savvichev et al., 2018, Baranov et al., 2020).

Macrofauna can be generally divided into microphages (e.g., deposit and suspension feeders) and macrophages (e.g., carnivores and herbivores), but some taxa, such as siboglinid tubeworms, are

85   symbiotrophic and host chemosynthetic bacteria (Jumars et al., 2015; Åström et al., 2020). Soft-
86   bottom macrobenthic communities are typically dominated by deposit and suspension feeding
87   fauna (Kokarev et al., 2017; Kokarev et al., 2021a). The food items consumed by microphages
88   include suspended and freshly deposited plankton, such as diatoms and flagellates, but also
89   organic matter of various origins in the form of particulate matter, or detritus, and associated
90   microorganisms (Levinton, 1972; North et al., 2014; Kędra et al., 2021). Since the visual analysis
91   of food resources utilized by microphagous feeders can be problematic due to the small size of
92   food items and high amount of consumed inorganic particles, indirect methods, such as stable
93   isotopes of carbon and nitrogen, proved to be useful in identifying sources of organic matter
94   consumed by macrofauna (Yokoyama and Ishihi, 2007; North et al., 2014). The ratio of ^{15}N to
95   ^{14}N ($\delta^{15}N$) is reflective of trophic level due to enrichment at each trophic level by 2.5-5‰ while
96   the ratio of $^{13}C/$ ^{12}C ($\delta^{13}C$) changes little in the food chains and is therefore used to trace carbon
97   sources within food webs (Bearhop et al., 2004). Stable isotopes can be used both for comparing
98   resource use between species (i.e., isotopic niche overlap) or community-wide aspects of trophic
99   structure or resource use (Karlson et al., 2015; Swanson et al., 2015; Jackson et al., 2011;
100   Włodarska-Kowalczuk et al., 2019). However, in order to differentiate the consumption of
101   different carbon sources, these carbon sources must differ in their isotopic signature. For
102   instance, on the Laptev Sea shelf, macrobenthic consumers can be expected to exploit terrestrial,
103   marine, and chemosynthetic organic matter (Kokarev et al., 2017; Vedenin et al., 2020). Carbon
104   isotopic values of terrestrial organic matter are in the range of -28 to -26‰, while phytoplankton-
105   derived organic matter is typically in the range of -22 to -20‰, although marine signatures can
106   be more variable in the Arctic, especially when ice algae are considered -15 to -8‰ (Stein and
107   Macdonald, 2004). However, there are seasonal and geographic variation in the baseline of
108   marine and terrestrial organic matter (Tamelander et al., 2009; Søreide et al., 2013; Bell et al.,
109   2016; McClelland et al., 2016). In the areas of methane seepage, distinct microbial communities
110   in the sediments are formed that include chemosynthetic microorganisms capable of utilizing
111   either methane (methanotrophs) or hydrogen sulfide (thiotrophs) as an energy source (Åström et
112   al., 2020). Carbon in the biomass sulfur-oxidizing bacteria and methanotrophic microorganisms
113   is usually characterized by very low $\delta^{13}C$ values (< -30‰) (Levin and Michener, 2002; Decker
114   and Olu, 2012; Åström et al., 2022).

115   In the present study, we hypothesized that macrofauna on the Laptev Sea shelf might utilize
116   organic matter of three origins: marine pelagic, terrestrial, and chemosynthetic. To test this
117   hypothesis, we have obtained data on the carbon and nitrogen stable isotope composition of
118   macrofauna from three soft-bottom habitats with the presumed differences in organic matter
119   sources. The "Background" habitat on the northern part of the shelf was chosen to represent the
120   baseline for the consumption of pelagic primary production. In the "Delta" habitat reliance on
121   the terrestrial organic matter supplied with Lena River runoff was expected in addition to the
122   marine primary production. Finally, the "Seep" habitat in the areas with detected methane
123   seepage where additional bacterial chemosynthetic production might be available for
124   consumption, which is absent in the "Background" and "Delta". Specifically, we aimed to

125 answer the following questions: (1) how different are the isotopic niches of the studied
126 communities, and (2) whether pronounced isotopic differences exist between species with similar
127 feeding habits?

2. Materials and methods

2.1. Study area and definition of habitats

130 The Laptev Sea is a Siberian epicontinental sea with an average water depth of around 50 meters
131 (Fig. 1). Prolonged ice coverage and considerable freshwater runoff, mainly supplied by the Lena
132 River, largely shape ecological patterns on the eastern part of the Laptev Sea shelf (Schmid et al.,
133 2006). The primary production and the fluxes of phytoplankton-derived organic matter to the
134 seafloor generally decrease with increasing latitude (Stein and Fahl, 2004; Demidov et al., 2020).
135 The highest organic carbon content in the sediments is recorded east of the Lena Delta and is the
136 consequence of the accumulation of terrestrial organic supplied with the river runoff (Stein and
137 Fahl, 2004; Xiao et al., 2013). There is a pronounced latitudinal gradient in the composition of
138 macrobenthic communities associated with the riverine discharge and regime of sedimentation
139 (Kokarev et al., 2017). Close to the Lena Delta, species-poor communities are mainly dominated
140 by the bivalve *Portlandia arctica,* while on the northern part of the shelf, the number of species
141 increases, and tube-dwelling annelid worms are abundant, including *Myriochele heeri*, *Owenia*
142 *polaris,* and *Maldane sarsi.* In addition, on the northern part of the shelf, specific benthic habitats
143 are associated with the methane seeps (Baranov et al., 2020; Vedenin et al., 2020). These habitats
144 are characterized by the presence of carbonate crusts and white microbial mats on the sediment
145 surface. Few species are found exclusively at methane seeps, most notably the siboglinid
146 tubeworm *Oligobrachia* sp. and the rissoid gastropod *Frigidoalvania* sp.

147 For this study, sampling stations, nine in total, were divided into three types of soft-bottom
148 benthic habitats based on the presumed differences in organic matter supply to the sediments
149 (Fig. 1): the habitat in the vicinity of the Lena Delta with high sedimentation rates of riverine
150 organic matter ("Delta"), the northern shelf habitat in the area with no detected methane seepage
151 ("Background") and methane seeps ("Seep"). Two stations from the "Delta" habitat, 6976 and
152 6977, were treated as one location as these stations are located close to each other (<500m) and
153 no small-scale heterogeneity was expected in this habitat based in terms of organic matter
154 sources based on prior knowledge (Kokarev et al., 2017). Contrary, small-scale heterogeneity
155 was expected at the "Seep" habitat (stations 5625, 6939, 6947, 6952, 6953, 6992) as there is
156 evidence that chemosynthetic production is distributed very locally, e.g., patches of white
157 microbial mats (Baranov et al., 2020; Vedenin et al., 2020). The "Background station (6950) was
158 located outside of the influence of Lena Delta but close to "Seep" so that they would be similar
159 in terms of bentho-pelagic coupling and fluxes of organic matter to the seafloor but differ in the
160 sediment biogeochemical processes associated with microbial activities (Savvichev et al., 2018;
161 Savvichev et al., 2023). Although the "Background" and "Delta" had only one location sampled,
162 we consider the number of animals sampled from each of these habitats to be sufficient to
163 represent the isotopic niche of respective communities (Table 1; Supplemental Table S1).

2.2. Collection and processing of macrofauna

For the present study, most of the material was collected during the 82nd cruise of the R/V "Akademik Mstislav Keldysh" in October 2020 (data on the sampling stations are available in the Supplemental Table S2). The sediment samples were obtained at eight stations using a grab sampler "Okean" (0.25 m²). Sediments from the grab samples were sieved on the 0.5 mm mesh, and the residues were sorted under a stereomicroscope onboard. Specimens were cleared of debris (and polychaetes removed from their tubes), identified to the species level wherever possible, and frozen at -20 °C before further processing. In addition, the gastropods *Frigidoalvania* sp., collected in September 2017 during the 69th cruise of the R/V "Akademik Mstislav Keldysh" with a Sigsbee trawl and kept frozen at -20 °C, were used in this study (station 5625, for more details on 69th cruise see Vedenin et al., 2020 and Baranov et al., 2020). These gastropods were not found during the 82d cruise, most probably due to a very patchy distribution based on grab samples (Vedenin et al., 2020). Overall, 24 taxa were sampled in this study (Table 1; Fig. 2; Fig. 3). In the lab, the shells of mollusks were removed with a razorblade and tweezers, and for larger specimens the foot muscle was dissected for stable isotope analyses. For the smaller bivalves, annelids, and *Frigidoalvania* sp. all the soft tissues were used. For *Thyasira* cf. *gouldii, Parathyasira dunbari*, *Yoldiella lenticula*, *Yoldiella solidula,* and one sample of *Ennucula tenuis*, several individuals of the same species were pooled in one sample due to the very low amount of soft tissues in a single specimen. Subsequently, samples were dried at 60 °C and homogenized with mortar and pestle. Field samplings and experiments were approved by the Ministry of Education and Science of the Russian Federation (the field study approval number DN-09-54/52).

2.3. Collection and processing of sediments

In addition to animal samples, at each station during the 82nd cruise (except for 6976) surface sediments were sampled from the grab prior to sieving with a spoon and immediately frozen at -20 °C. Subsequently, sediment samples were dried at 60°C. For the stable isotope analyses, dried samples were divided into 2 replicates. One replicate was acidified with 2M HCl to remove inorganic carbon and was used to determine the $\delta^{13}C$ value. Since acidification alters the $\delta^{15}N$ value, non-acidified samples were used to determine $\delta^{15}N$ (Silberberger et al., 2021).

2.4. Stable isotope analyses

Dried samples (200-500 μg for animal tissues and 3 to 10 mg for sediment samples) were wrapped into tin capsules and analyzed for stable carbon and nitrogen isotope composition using Flash 1112 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA, USA) and a Thermo Delta V Plus isotope ratio mass spectrometer connected via a Conflo IV peripheral at the A.N. Severtsov Institute of Ecology and Evolution RAS. Results are reported in permille (‰) using the delta (δ) notation and were normalized to VPDB and air N_2 using USGS40 and USGS41 reference materials (US Geological Survey, Reston, VA, USA). The drift was corrected using an internal laboratory standard (casein). The standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values in the laboratory standard (n = 8) was < 0.2 ‰. Although C:N ratios appeared to be variable,

203 particularly between foot vs. whole clam samples, which is clearly a consequence of differences
204 in lipid content (Weems et al., 2012), the data were not corrected for lipids using mathematical
205 corrections as available equations might not be suitable for benthic invertebrates such as bivalves
206 and polychaetes (Silberberger et al., 2021). All the measured $\delta^{13}C$, $\delta^{15}N$, and C:N values for each
207 animal sample are available in the Supplemental Table S1. The values in the text are presented as
208 mean ± SD.

2.5.   Classification of the macrofauna based on feeding habits

210 Prior to the data analyses, species were assigned to trophic groups based on Jumars et al. (2015)
211 and Kokarev et al. (2017) (Table 1). Surface deposit feeders and suspension feeders were
212 combined for two reasons: (1) some species can switch from deposit feeding to suspension
213 feeding, e.g. *Owenia*, *Spiochaetopterus*, *Macoma* (Jumars et al., 2015; Reid and Reid, 1969) and
214 (2) both groups utilize similar food sources: fresh phytoplankton material, food resources
215 deposited in the upper layer of the sediments, which are available to suspension feeders through
216 resuspension (Christensen and Kanneworff, 1985; Sokołowski et al., 2014). Moreover, only two
217 species could be classified as strict suspension feeders: *Thracia myopsis* and *Periploma*
218 *aleuticum* (Sartori and Domaneschi, 2005; Morton, 1981). Subsurface deposit feeders are
219 represented by annelids that feed in the deeper layers of the sediment and rely on more
220 microbially degraded organic matter, which is reflected in higher $\delta^{15}N$ values (North et al., 2014;
221 Jumars et al., 2015). The symbiotrophic tubeworm *Oligobrachia* sp. and carnivores nephtyid
222 polychaetes were the only taxa in their respective feeding group. In the section "Seep-associated
223 fauna" we used additional data on *Oligobrachia* and $\delta^{13}C$ values of methane from North Atlantic
224 and Arctic seeps for comparison on a larger scale (Gebruk et al., 2003; Decker and Olu, 2012;
225 Lee et al., 2019a; Åström et al., 2022; Kravchishina et al., 2021). Several taxa were not assigned
226 to a particular feeding habit: the gastropod *Frigidoalvania* sp., the bivalve *Montacuta*
227 *spitzbergensis,* and thyasirid bivalves. *Frigidoalvania* sp. is currently known only from the seeps
228 in the Laptev Sea, and little is known about its feeding habits (Nekhaev and Krol, 2020). *M.*
229 *spitzbergensis* belongs to the family Montacutidae, which comprises commensal bivalves, but its
230 host is unknown with all the specimens (including this study) found freely in sediments
231 (Kamenev, 2008). Feeding strategies in the thyasirid bivalves are diverse, particularly in the
232 cryptic *Thyasira* cf. *gouldii,* which might derive its nutrition from sulfide-oxidizing bacteria in
233 the gills, subsurface pedal feeding, and suspension feeding (Zanzerl and Dufour, 2017; Zanzerl et
234 al., 2019).

2.6.   Data analysis

236 Stable isotope data were visualized as biplots using R version 4.2.2 (R Core Team, 2022) and
237 package ggplot2 version 3.4.1 (Wickham, 2016). Since the data partially were not normally
238 distributed in bivariate isotopic space (tested with Shapiro-Wilk multivariate normality test in the
239 package RVAideMemoire version 0.9-81-2 (Hervé, 2022)), the data analysis was performed with
240 non-parametric approaches that do not assume normal distribution or homogeneity of variance.
241 Differences between pre-defined groups ("Habitat" , "Feeding habit" and "Station") were tested

242 with a two-way non-parametric Scheirer Ray Hare test in the package rcompanion version 2.4.21
243 (Mangiafico, 2023) or one-way Kruskall-Wallis test and subsequent pairwise Dunn's test with
244 Holm's procedure to adjust p-value for multiple comparisons in the package dunn.test version
245 1.3.5. (Dinno, 2017). The multivariate differences on the species level were investigated using
246 non-parametric rank-based Wilks' Lambda type statistic, for which p-value was calculated using
247 *F* approximation, and the empirical nonparametric relative treatment effects for each variable in
248 the package npmv version 2.4.0 (Ellis et al., 2017). The relative effects quantify probability that
249 a randomly chosen individual from one species exhibits a higher value for the variable (δ^{13}C or
250 δ^{15}N) than a randomly chosen individual across all species.

3. Results

3.1.   Habitat-associated patterns

253 The sediment stable isotope data showed some differences between "Background", "Seep" and
254 "Delta" habitats: lower δ^{13}C values were observed for the "Seep" and the "Delta" as well as a
255 considerably lower δ^{15}N value for "Delta" sediments. (Table 2)."Background" and "Seep"
256 habitats had similar δ^{15}N values.

257 The patterns within macrobenthic consumers were more prominent. There was a considerable
258 difference between the symbiotrophic annelid *Oligobrachia* sp. from"Seep" stations and all the
259 other macrobenthic taxa due to non-overlapping δ^{13}C values (-48.4 ± 3.1‰ for *Oligobrachia* sp.
260 and -24.3 ± 2.7‰ for all the other taxa). The dispersion of the *Oligobrachia* sp. samples in the
261 isotopic space was of comparable magnitude to all the other taxa (Supplementary Figure S1).
262 Therefore, subsequent comparisons of different habitats were performed excluding *Oligobrachia*
263 sp.

264 Exclusion of *Oligobrachia* sp. revealed the significant differences between macrobenthic
265 consumers from the three habitats (Fig. 4A). The "Delta" community was characterized by lower
266 values of δ^{13}C (-27.9 ± 1.6‰) compared to the "Background" community (-22.7 ± 1.2‰). The
267 "Seep" community (-24.0 ± 2.6‰) with the widest isotopic niche overlapped both with the
268 "Delta" and "Background" communities. The two-way Scheirer Ray Hare test (excluding taxa
269 unassigned to feeding group and carnivores due to their low representation (n < 5) in the "Delta"
270 and "Background") revealed that the effect of interaction of "Habitat" and "Feeding habit" on the
271 δ^{13}C is not significant (H = 5.2, df = 2, p = 0.075), as well as the main effect of "Feeding habit"
272 (H = 3.6, df = 1, p = 0.056), while the main effect of "Habitat" was significant (H = 31.7, df = 2,
273 p < 0.001). Further, differences in the range of δ^{13}C values were revealed between different
274 "Seep" stations (Fig. 5): while station 6939 and 6992 were completely within the "Background"
275 range, considerably lower δ^{13}C values were recorded for the stations 6952, 6953, and 6947, with
276 stations 6953 and 6947 being significantly different from "Background" (results of Kruskal-
277 Wallis test and subsequent Dunn's test are presented in the Supplementary Table S3).

278 Macrobenthic consumers with different feeding habits could be differentiated based on their δ^{15}N
279 values (Fig. 4B): surface deposit feeders and suspension feeders had the lowest and carnivores

280   the highest $\delta^{15}N$ values (7.1 ± 0.9‰ and 11.6 ± 0.6‰, respectively) with subsurface deposit
281   feeders in between (10.3 ± 1.2‰). In addition, centroid of the "Delta" community was clearly
282   skewed towards lower $\delta^{15}N$ (7.1 ± 2.2‰) compared to "Background" (8.6 ± 2.3‰) and "Seep"
283   (8.5 ± 2.0‰). The two-way Scheirer Ray Hare test (excluding taxa unassigned to feeding group
284   and carnivores due to their low representation (n < 5) in the "Delta" and "Background") revealed
285   that the effect of interaction of "Habitat" and "Feeding habit" on the $\delta^{15}N$ is not significant (H =
286   1.4, df = 2, p = 0.500), while the main effects of "Habitat" (H = 13.5, df = 2, p = 0.001) and
287   "Feeding habit" (H = 93.7, df = 1, p < 0.001) are significant. Among taxa with unassigned
288   feeding habits, thyasirid bivalves and the gastropod *Frigidoalvania* sp. clearly grouped with
289   surface deposit and suspension feeders (Fig. 4B). The single sample of the bivalve *Montacuta*
290   *spitzbergensis* grouped with a few outliers from the "Seep" community with the lowest $\delta^{13}C$
291   values.

292   In the following section "Background" and "Seep" samples for surface deposit/suspension
293   feeders and subsurface deposit feeders are discussed together since there samples clearly overlap
294   (Fig. 4 and Fig. 5).

295   3.2.   Species isotopic niches

296   *3.2.1. Surface deposit/suspension feeders*

297   "Delta" surface deposit/suspension feeders were represented only by *Portlandia arctica* ($\delta^{13}C$ = -
298   29.0 ± 1.0‰; $\delta^{15}N$ = 5.6 ± 0.2‰) and *Macoma* spp. ($\delta^{13}C$ = -29.0 ± 0.4‰; $\delta^{15}N$ = 6.0 ± 0.3 ‰).
299   This group occupied a narrow and distinct isotopic niche that did not overlap with the isotopic
300   niches of the same taxa from "Seep" and "Background" (*P. arctica*: $\delta^{13}C$ = -22.5 ± 1.7‰; $\delta^{15}N$ =
301   6.5 ± 0.4 ‰; *Macoma* spp.: $\delta^{13}C$ = -23.5 ± 1.4‰; $\delta^{15}N$ = 6.9 ± 0.4‰).

302   Surface deposit/suspension feeders from "Background" and "Seep" habitats were represented by
303   12 taxa, and there was a general trend in lower $\delta^{13}C$ values being associated with lower $\delta^{15}N$
304   values (Fig. 6). Two "Seep" samples of the bivalve *Thracia myopsis* had the lowest $\delta^{13}C$ values
305   (≈-30‰). Oweniid annelids *Myriochele heeri* and *Owenia polaris* along with annelid
306   *Spiochaetopterus typicus* and bivalve *Periploma aleuticum* had the values of the $\delta^{13}C$ higher than
307   -24‰. Contrary, the majority of the other bivalve species (*Yoldiella lenticula*, *Nuculana pernula*,
308   *Portlandia arctica*, *Macoma* spp.) showed a wide range of $\delta^{13}C$ values with some of the "Seep"
309   samples depleted in ^{13}C. The bivalve *Y. solidula* had higher $\delta^{15}N$ values compared to *Y. lenticula*,
310   *N. pernula*, *P. arctica,* and *Macoma* spp. The lowest $\delta^{13}C$ value (-25.3‰) from the
311   "Background" was observed for the bivalve *Ennucula tenuis,* which appeared to be an outlier
312   compared to the rest of the background species, but a similar value for this species was recorded
313   from the "Seep" habitat. However, the samples of *E. tenuis* had a high C:N ratio (> 6), which
314   might have resulted in decreased $\delta^{13}C$ values due to high lipid content.

315   The multivariate differences among surface deposit and suspension feeding species from
316   "Background" and "Seep" habitats- with sample size ≥ 7 were significant (Wilks Lambda = 10.3,
317   df1 = 10, df2 = 140, p < 0.001). The relative effects revealed that these differences were mainly

318   due to the difference between surface deposit feeding bivalves and oweniid polychaetes, both in
319   terms of δ¹³C and δ¹⁵N (Table 3). Moreover, *O. polaris* appeared to have the most distinct niche.

3.2.2. Subsurface deposit feeders

321   The polychaetes *Sternapsis* sp. and *Pectinaria hyperborea* from the "Delta" habitat had very
322   different δ¹⁵N values (6.8-7.3‰ for *Sternapsis* sp. and 9.7-10.7‰ for *P. hyperborea*), and
323   therefore their isotopic niches did not overlap. Within "Background" and "Seep" habitats three
324   sampled species had three overlapping but significantly different isotopic niches (Fig. 7; Wilks
325   Lambda = 10.2, df1 = 4, df2 = 88, p < 0.001). The relative effects revealed that *M.sarsi* had
326   generally higher δ¹⁵N, while *Sternapsis* sp. had the highest δ¹³C value (Table 4).

3.2.3. Carnivores

328   Represented by the single taxon (Nephtyid polychaetes), this group showed the highest δ¹⁵N
329   (11.6 ± 0.6‰) values but had a similar δ¹³C (24.0 ± 2.7‰) range to the surface
330   deposit/suspension feeders and subsurface deposit feeders (Fig. 4B).

3.2.4. Thyasiridae

332   Thyasirid bivalves grouped with suspension/surface deposit feeders (Fig. 4B). However, two
333   samples of *Parathyasira dunbari* could be distinguished from *Thyasira* cf. *gouldii* on the
334   northern part of the shelf by lower δ¹⁵N values (4.9‰ and 5.9‰ versus 7.5 ± 0.5‰). Moreover,
335   *P. dunbari* had the lowest recorded δ¹⁵N value for "Background" and "Seep" habitats among all
336   the sampled taxa, excluding *Oligobrachia* sp.

3.2.5. Seep-associated fauna

338   Two species were associated exclusively with the "Seep" sites: the rissoid gastropod
339   *Frigidoalvania* sp. and the tubeworm *Oligobrachia* sp. *Frigidoalvania* sp. had relatively low
340   values of δ¹³C (-27.2 ± 0.5‰) and a distinct niche among surface deposit/suspension feeders
341   from the seep sites (Fig. 4B).

342   The samples of *Oligobrachia* sp. had a very wide dispersion in the isotopic space and had the
343   lowest values both for δ¹³C and δ¹⁵N (down to -53.9‰ and to -4.0‰, respectively; Supplemental
344   Figure S1). The analysis of *Oligobrachia* isotopic signatures from different seep locations in the
345   North Atlantic and the Arctic revealed no clear relationship between δ¹³C of methane and δ¹³C of
346   *Oligobrachia* (Supplemental Figure S2).

4. Discussion

4.1.   Habitat-associated patterns

349   Macrobenthic communities from the three studied habitats differed in terms of the δ¹³C range,
350   reflecting variability in organic matter sources for macrobenthic communities. However, there
351   were no differences in the δ¹³C range between different feeding groups, including primary
352   consumers (deposit and suspension feeders) and secondary consumers (carnivores). The
353   differences in the δ¹³C range between habitats were much more pronounced for macrofauna than

354 for sediments, thus, the isotopic signatures of the sediments cannot be used as a food source
355 baseline. "Background" macrofaunal samples had δ^{13}C values larger than -24‰ (except for two
356 samples with values ≈ -25‰), indicating the predominant reliance of the community on marine
357 organic matter (Vonk et al, 2012; Bell et al., 2016). However, the role of marine organic matter
358 decreased for "Delta" and partially for "Seep" habitats.

4.1.1. "Delta"

360 On the eastern Laptev Sea and East Siberian Sea shelf macrobenthic communities are influenced
361 by riverine input and regime of sedimentation, which results in low species and functional
362 diversity close to the deltas due to environmental filtering (Kokarev et al., 2017; Kokarev et al.,
363 2021a). The species found close to the Lena Delta, are wide-spread shelf species, which can
364 successfully establish a population in waters with warmer temperatures, fluctuating salinity, and
365 enhanced sedimentation (e.g., *Portlandia arctica*, *Macoma* spp., *Thyasira* cf. *gouldii*, *Sternapsis*
366 sp., *Pectinaria hyperborea*, nephtyid annelid *Aglaophamus malmgreni*). In the present study, we
367 showed that these species might consume organic matter of different origins depending on
368 availability as inferred from their variable δ^{13}C signatures. Macrofauna from the "Delta" habitat,
369 especially surface deposit feeding bivalves, was considerably depleted in ^{13}C and slightly
370 depleted in ^{15}N relative to "Background" (down to -30.5‰ and 5.3‰, respectively) directly
371 reflecting the isotopic signature of Lena River particulate organic matter (δ^{13}C = -31.1 ± 0.8‰;
372 McClelland et al., 2016) and terrestrial end-member values used for the Arctic shelf (δ^{13}C =
373 −28.8 ± 3.2‰, δ^{15}N = 0.8 ± 1.0‰; Bell et al., 2016). This fact suggests that terrestrial organic
374 matter is a primary food source for the "Delta" community at least during the season the samples
375 were taken. Such low values for δ^{13}C and δ^{15}N were not previously recorded for the Arctic
376 macrofauna in the areas influenced by river runoff (Dunton et al., 2012; Bell et al., 2016; Harris
377 et al., 2018; Stasko et al., 2018), which either reflects the higher contribution of terrestrial
378 organic matter to the benthic food web close to Lena Delta, or seasonal/geographical variations
379 in the isotopic signatures of fluvial particulate organic matter (McClelland et al., 2016).

4.1.2. "Seep"

381 Little is known about the nutrition of macrobenthos, particularly deposit feeders, from the arctic
382 cold seeps (Åström et al., 2020). Our data revealed a wider δ^{13}C range for the "Seep"
383 community relative to "Background" indicating that carbon of chemosynthetic origin is actively
384 consumed by the non-symbiotrophic deposit feeding macrofauna in addition to photosynthetic
385 carbon. Individuals of many species were more depleted in ^{13}C at seep sites compared to
386 "Background", which is consistent with patterns observed at some other methane seeps, usually
387 located below shelf depths (Levin and Michener, 2002; Levin, 2005; Thurber et al., 2010;
388 Sellanes et al., 2011), and indicates partial reliance on chemosynthetic production which is ^{13}C-
389 depleted (δ^{13}C ≈ -35‰ for sulfur-oxidising bacteria from white microbial mats at high-latitude
390 seeps, Åström et al., 2020). It should be noted, however, that for many species from "Seep" sites
391 along with more depleted isotopic signatures, isotopic signatures within the "Background" range
392 were observed. Moreover, samples from stations 6939 ang 6992 were completely within

393 "Background" $\delta^{13}C$ range. Both of these facts suggest the patchy distribution of chemosynthetic
394 organic matter and its opportunistic consumption. Indeed, video observations from the seeps in
395 the Laptev Sea documented patchy distributions of white microbial mats at scales < 1m (Baranov
396 et al., 2020). However, these results differ from the shelf of the Barents Sea, where differences
397 between isotopic niches of seep and non-seep communities were less pronounced with no
398 apparent consumption of chemosynthetic organic matter at shallow (< 200m) seeps (Åström et
399 al., 2022). This supports the previous hypothesis that in the less productive Laptev Sea
400 chemosynthetic organic matter is more readily consumed by macrofauna supporting higher
401 abundances at the seep sites (Vedenin et al., 2020), which likely makes the Laptev Sea seeps
402 more of an exception among the shallow-water seeps (Dando, 2010).

403 4.2. Species isotopic niches

404 4.2.1. Surface deposit and suspension feeders

405 Surface deposit feeders from the "Delta" habitat, represented by bivalves *Macoma* spp. and
406 *Portlandia arctica,* had very similar isotopic signatures. On the northern part of the shelf at
407 "Seep" and "Background", similarly, deposit feeding bivalves *Macoma* spp. *P. arctica*, *Yoldiella*
408 *lenticula,* and *Nuculana pernula* had high niche overlap and appeared to have a contribution
409 from chemosynthetic carbon to their diet at "Seep" sites. This result corroborates previous results
410 that different species of surface deposit feeding bivalves generally consume similar food sources
411 from the sediment pool (North et al., 2014; Oxtoby et al., 2016). Interestingly, *Yoldiella solidula*
412 had slightly higher $\delta^{15}N$ values compared to the above-mentioned bivalves, possibly indicating a
413 different resource use pattern for this species.

414 Oweniids *Myriochele heeri* and *Owenia polaris* had niches distinct from each other and limited
415 overlap with most abundant deposit feeding bivalves. Oweniids might selectively consume algal
416 material recently deposited on the seafloor or from the near-bottom suspension (Jumars et al.,
417 2015). The high densities of oweniid polychaetes are also sometimes linked to the input of fresh
418 pelagic organic matter to the seafloor (Fiege et al., 2000; Kokarev et al., 2021b). In our study, *M.*
419 *heeri* and *O. polaris* had $\delta^{13}C$ > -24‰, indicative of phytoplankton consumption (Vonk et al,
420 2012; Bell et al., 2016). Probably, dense populations of these species on the northern Laptev Sea
421 shelf (Kokarev et al., 2017) rely less on bacterially reworked sediment pool of organic matter
422 compared to deposit feeding bivalves and selectively feed on fresh phytodetritus, avoiding
423 consumption of bacterially derived chemosynthetic organic matter at seep sites. The differences
424 in the isotopic niches between *M. heeri* and *O. polaris* are most probably related to morpho-
425 functional differences between the two genera: *Owenia* uses a tentacular crown to feed, while
426 *Myriochele* lacks any anterior appendages (Fig. 3; Jumars et al., 2015).

427 Consumption of chemosynthetic carbon was not evident also for the polychaete
428 *Spiochaetopterus typicus* and the bivalves *Periploma aleuticum, Yoldiella solidula,* and
429 *Ennucula tenuis,* but only a few samples of these species were analyzed. However, two samples
430 of the bivalve *Thracia myopsis* and a single sample of the bivalve *Montacuta spitzbergensis* were
431 depleted in ^{13}C characteristic of chemosynthetic carbon consumption. *T. myopsis* is a strict

432   suspension feeder and has common for the genus mucous lining of the siphon passage in the

433   sediment that restricts the deposited sediment from entering the inhalant siphon aperture (Sartori

434   and Domaneschi, 2005). Thus, *T. myopsis* feeds on suspended organic matter, which was shown

435   to be depleted in ^{13}C at the seep sites (δ^{13}C = 34.8-35.9‰; Savvichev et al., 2018).

4.2.2. Subsurface deposit feeders

437   Subsurface deposit feeders, e.g., the polychaete *Pectinaria hyperborea*, consume mainly

438   bacterially reworked detritus and are characterized by higher δ^{15}N relative to surface deposit

439   feeding bivalves (North et al., 2014). In the present study, we observed a similar pattern.

440   However, three of the studied species had distinct isotopic niches. In the "Delta" community,

441   *Sternapsis* sp. and *P. hyperborea* consumed different resources, while on the northern part of the

442   shelf, at "Background" and "Seep" sites, their isotopic niches partially overlapped with each

443   other and *Maldane sarsi*. It is not clear how these species partition resources, but possible

444   mechanisms include feeding at different sediment levels or selection for different particle sizes

445   (Hughes, 1977; Whitlatch, 1980). For all three species consumption of chemosynthetic organic

446   matter was evident at the seep sites.

4.2.3. Thyasiridae

448   Thyasirid bivalves grouped with surface deposit feeders, although they form pedal tracts that

449   penetrate deep into the sediment (Zanzerl and Dufour, 2017), while specimens identified as

450   *Thyasira* cf. *gouldii* can be also symbiotrophic (Batstone et al., 2014). Isotopic signatures of *T.*

451   cf. *gouldii* in the present study varied widely among habitats suggesting direct consumption of

452   deposited organic matter in the surface sediment layer rather than symbiont-based nutrition.

453   Interestingly, samples of *Parathyasira dunbari* with similar δ^{13}C values to *T.* cf. *gouldii* had

454   lower δ^{15}N values. Such a pattern was also observed in Bonne Bay, Newfoundland, where

455   symbiotic *T.* cf. *gouldii,* asymbiotic *T.* cf. *gouldii,* and *Parathyasira* sp. could be distinguished

456   by δ^{15}N but not δ^{13}C values, and in conjunction with fatty acid analysis it was hypothesized that

457   *Parathyasira* sp. might rely on free-living sulfur-oxidizing bacteria in the sediment (Zanzerl et

458   al., 2019). We observed numerous bacteria on the inner fold of the mantle margin for

459   *Parathyasira dunbari* during SEM investigation of this species, but not for *T.* cf. *gouldii,*

460   supporting this hypothesis (Kokarev et al., in prep.).

4.2.4. Seep-associated fauna

462   Rissoid gastropods are characteristic of seep and vent fauna in the Arctic and North Atlantic,

463   where they are associated with bacterial mats of sulfur-oxidizing bacteria, particularly of the

464   genus *Sulfurovum* (Gebruk et al., 2003, Decker and Olu, 2012; Sweetman et al., 2013; Sen et al.,

465   2019). *Sulfurovum* is abundant also in seep bacterial communities in the Laptev Sea (Savvichev

466   et al., 2018). Although in our study rissoid gastropod *Frigidoalvania* sp. showed quite low δ^{13}C

467   values (mean -27.2 ± 0.5‰) relative to the "Background" surface deposit feeders, these values

468   were quite high relative to the one measured for *Alvania* sp. from the North Atlantic (Decker and

469   Olu, 2012). This indicates either a feeding habit on a mixture of different bacteria (Sweetman et

470 al., 2013) or probably a mixed diet with significant contributions of photosynthetic organic
471 matter.

472 The siboglinid worm *Oligobrachia* sp. showed very variable isotopic signatures in the Laptev
473 Sea and across a wider geographical range, which is not directly related to the isotopic signature
474 of methane (Supplemental Figure S2). Although there are several cryptic *Oligobrachia* species in
475 the Arctic and North Atlantic, similar symbiotic sulfide-oxidizing bacteria were detected in all
476 the species (Lösekann et al., 2008; Sen et al., 2018; Lee et al., 2019b; Karaseva et al., 2021). A
477 variable pattern in the isotopic signatures might be a result of autotrophic fixation of inorganic
478 carbon from a mixture of sources: the inorganic carbon from the overlaying seawater and a more
479 ^{13}C-depleted pore-water inorganic carbon resulting from anaerobic oxidation of methane in the
480 sediment (Lösekann et al., 2008; Lee et al., 2019a). This contrasts with the pattern observed for
481 the siboglinid *Siboglinum poseidoni* hosting methanotrophic bacteria, which carbon isotopic
482 signature directly reflects the isotopic signature of methane (Schmaljohann et al., 1990). High
483 variation in δ^{15}N values might also indicate a wide spectrum of nitrogen sources available for
484 *Oligobrachia*, possibly including local assimilation of inorganic nitrogen (Levin, 2005) or amino
485 acids from dissolved organic matter (Southward and Southward, 1981). Therefore, *Oligobrachia*
486 might benefit from a wide spectrum of carbon and nitrogen sources available for the worm
487 simultaneously, resulting in high variability of isotopic signatures even on small scales. More
488 studies are needed on the biology of this species and its symbiotic bacteria in order to assess its
489 role in carbon and nutrient cycling at methane seeps.

5. Conclusion

491 Our study revealed that the terrestrial and chemosynthetic organic matter might be more
492 substantial food sources for macrofauna than previously demonstrated for the Arctic shelf.
493 Distribution of many species, e.g. surface deposit feeding bivalves and subsurface deposit
494 feeding polychaetes found in all three habitats, is not constrained by the origin of organic matter
495 as demonstrated by the high variability of their isotopic signatures and suggests opportunistic
496 consumption of available resources. However, differences in resource use among some species
497 with the same feeding habits were observed, particularly between oweniid polychaetes and
498 bivalves, suggesting that species-specific traits might be important for ecosystem functioning
499 (Norling et al., 2007; Godbold et al., 2009). These findings might have important implications
500 for assessing macrobenthic carbon demand and the carbon budget of the Arctic shelf ecosystem
501 (Schmid et al., 2006; Zaborska et al., 2018).

502 It must be noted, however, that both consumption of terrestrial and chemosynthetic organic
503 matter results in lower δ^{13}C values of macrofaunal consumers, making the interpretation of data
504 contextual. Therefore, a combination of a stable isotope approach with supplementary methods,
505 such as fatty acid analysis, might be a more beneficial yet more time-consuming and less cost-
506 effective strategy to further assess the consumption of terrestrial/chemosynthetic organic matter
507 by macrofauna.

508 **Acknowledgments**

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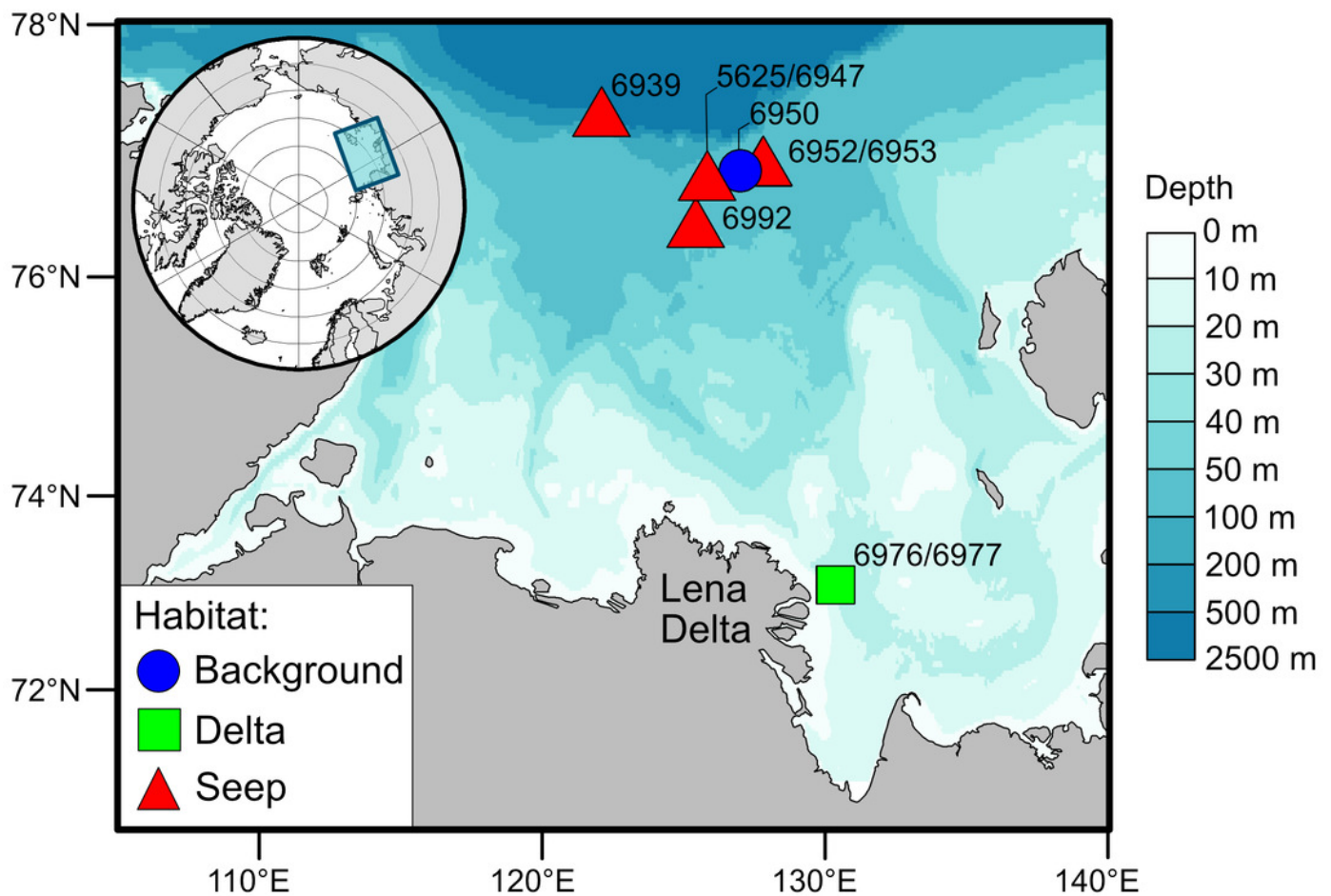
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Figure 1

Map of the study area.

Figure 2

Macrophotographs of the mollusk species studied.

(A) *Macoma calcarea*, (B) *Ennucula tenuis*, (C) *Yoldia hyperborea*, (D) *Thyasira cf. gouldii*, (E) *Periploma aleuticum*, (F) *Portlandia arctica*, (G) *Yoldiella lenticula*, (H) *Nuculana pernula*, (I) *Montacuta spitzbergensis*, (G) *Frigidoalvania* sp., (K) *Thracia myopsis*, (L) *Yoldiella solidula*, (M) *Parathyasira dunbari*. All scale bars equal 1 mm. Photo credit: Valentin Kokarev.

Figure 3

Macrophotographs of the studied annelids.

All alive except (A) and (G). (A) *Owenia polaris*, (B) *Sternapsis* sp., (C) *Aglaophamus malmgreni* (Nephtyidae), (D) *Spiochaetopterus typicus*, (E) *Pectinaria hyperborea*, (F) *Oligobrachia* sp. (with metatrochophore larvae), (G) *Maldane sarsi*, (H) *Myriochele heeri*. All scale bars equal 1 mm. Photo credit: (A, G) Valentin Kokarev, (B, D, E, F, H) Petr Kuznetsov, (C) Tina Molodtsova.

Figure 4

Stable isotope biplot of $\delta^{13}C$ and $\delta^{15}N$ values for the macrobenthic taxa excluding *Oligobrachia* sp.

Habitats are locations on the Laptev Sea shelf with the presumed differences in organic matter sources for macrofauna (marine vs. terrestrial vs. chemosynthetic). Group centroids (calculated as mean $\delta^{13}C$ and $\delta^{15}N$ values) are shown. (A) and (B) are the same plot but differently color-coded. Abbreviations: Surface Deposit Feeders (SDF), Suspension Feeders (SF), Subsurface Deposit Feeders (SSDF). Asterisk (*) indicates taxa unassigned to a particular feeding habit. Thyasridae was represented by two species: *Thyasira gouldi* and *Parathyasira dunbari*.
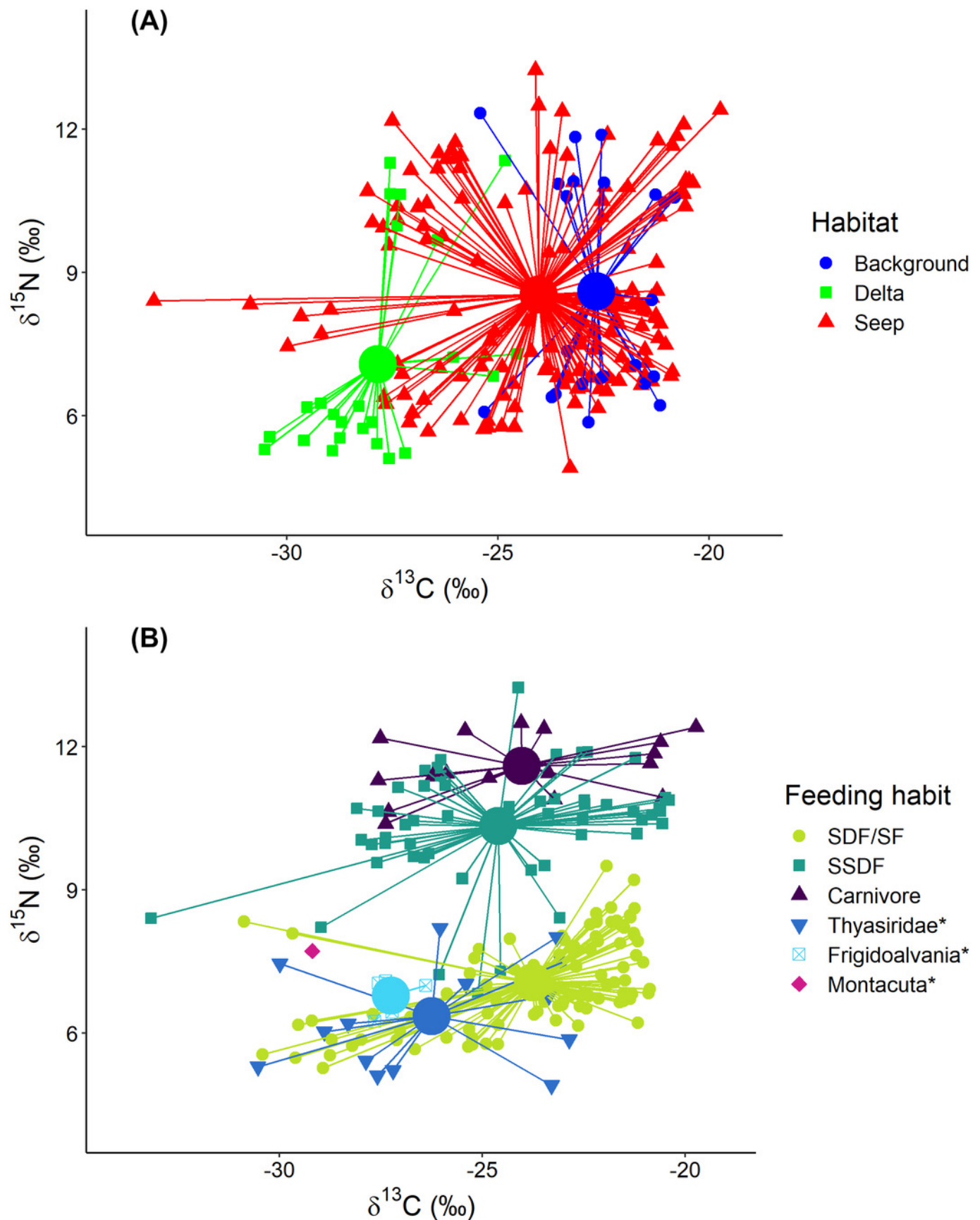
Figure 5

Boxplot of δ^{13}C values for the macrobenthic taxa (excluding *Oligobrachia* sp) grouped by sampling station

The station 5625, where only *Frigidoalvania* sp. was sampled, is not shown. Blue dashed lines correspond to δ^{13}C range (min-max) of the "Background" habitat. Red dashed line corresponds to carbon isotopic signature (-35) of sulphur-oxidizing bacteria at high-latitude seeps (Åström et al., 2022). Green dashed line corresponds to the isotopic signature of Lena River (-31.1) particulate organic matter (McClelland et al., 2016).
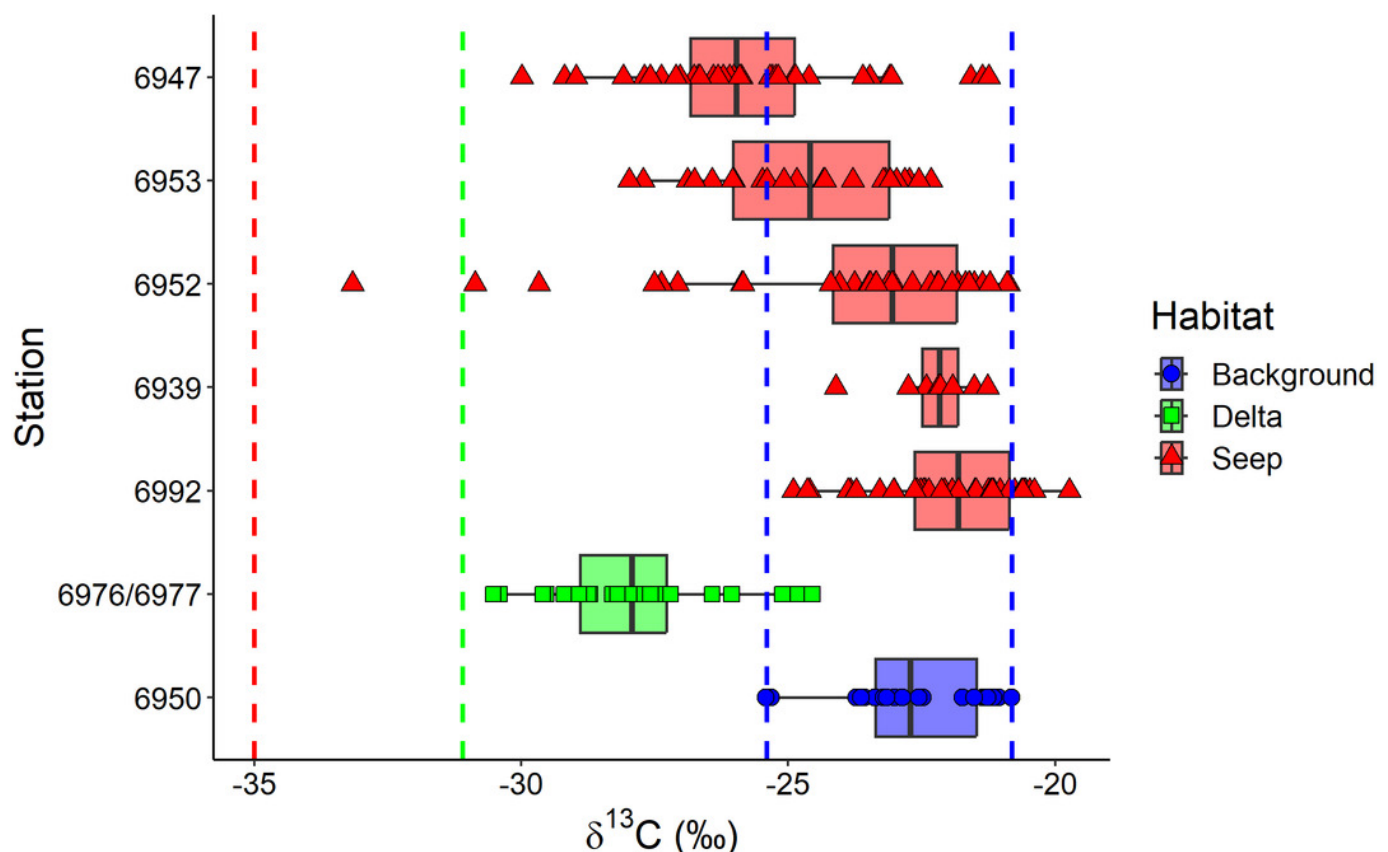
Figure 6

Stable isotope biplot of δ^{13}C and δ^{15}N values for surface deposit and suspension feeders from the northern part of the Laptev Sea shelf.

Group centroids (calculated as mean δ^{13}C and δ^{15}N values) are shown for groups with 7 or more samples.The following samples are not shown to improve readability: "Background" *E. tenuis* (δ^{13}C = -25.3‰, δ^{15}N = 6.1‰) , "Seep" *E. tenuis* (δ^{13}C = -25.2‰, δ^{15}N = 5.8‰) , "Background" *P. aleuticum* (δ^{13}C = -22.6‰, δ^{15}N = 6.8‰), "Seep" *P. aleuticum* (δ^{13}C = -21.9‰, δ^{15}N = 6.5‰), "Seep" *S. typicus* (δ^{13}C = -22.8‰, δ^{15}N = 7.7‰ and δ^{13}C = -21.3‰, δ^{15}N = 8.1‰), "Seep" *Y. hyperborea* (δ^{13}C = -24.9‰, δ^{15}N = 6.4‰).
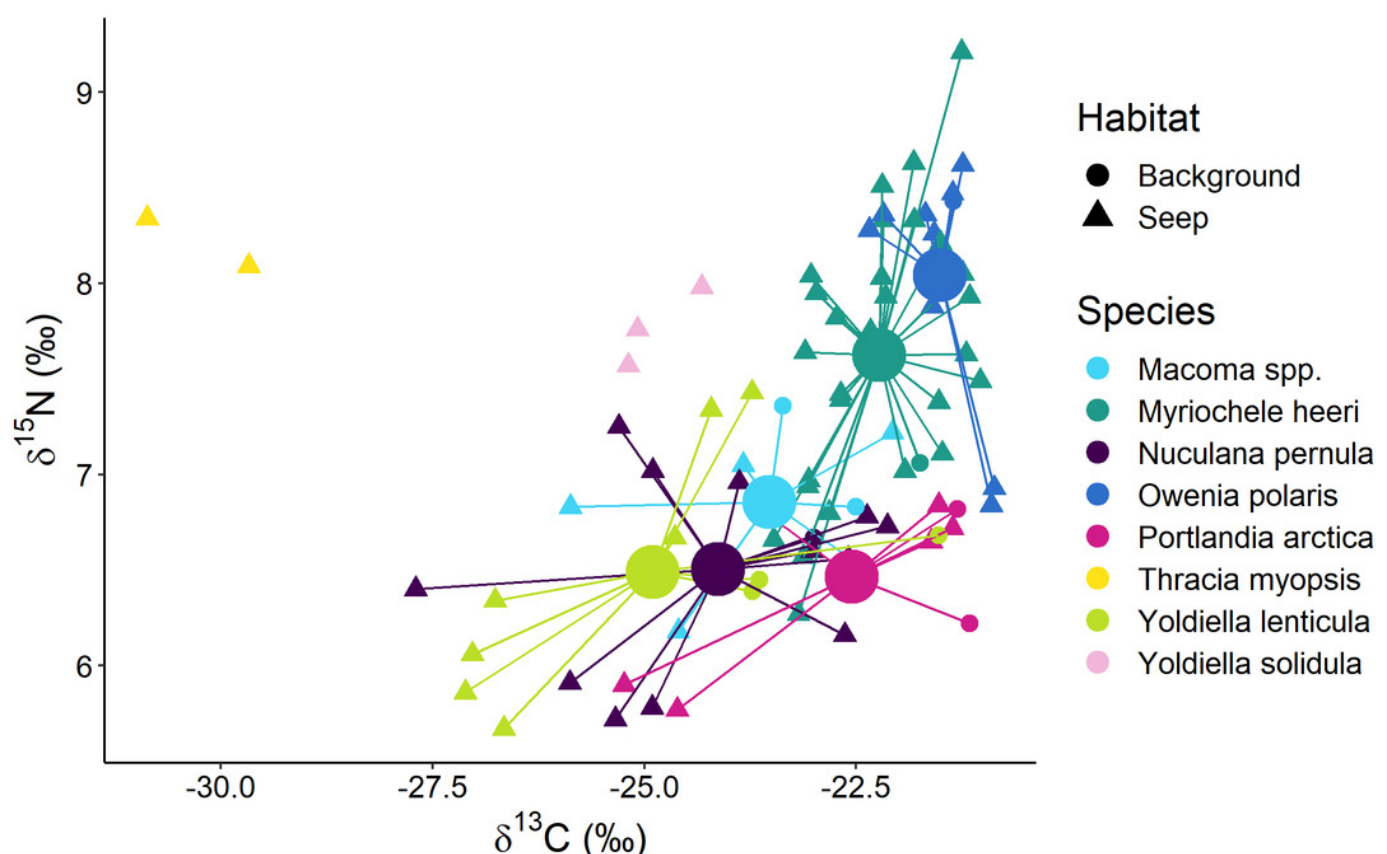
Figure 7

Stable isotope biplot of $\delta^{13}C$ and $\delta^{15}N$ values for subsurface deposit feeders from the northern part of the Laptev Sea shelf.

Group centroids (calculated as mean $\delta^{13}C$ and $\delta^{15}N$ values) are shown.
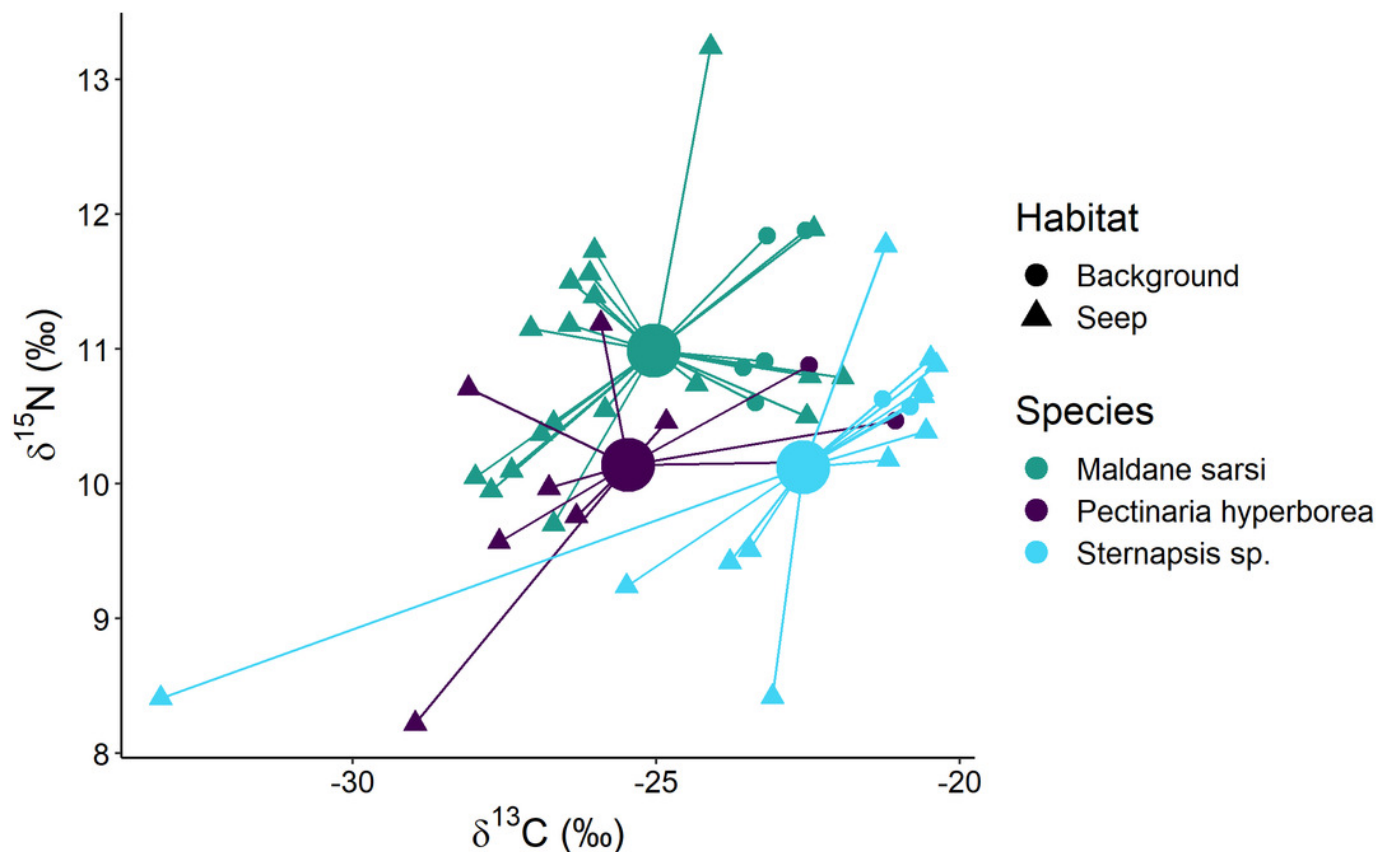
Table 1(on next page)

List of the macrobenthic taxa sampled.

Numbers indicate the number of samples used for stable isotope analyses. Abbreviations: Surface Deposit Feeders (SDF), Suspension Feeders (SF), Subsurface Deposit Feeders (SSDF) (for details see section "Classification of the macrofauna based on feeding habits"). Asterisk (*) indicates taxa unassigned to a particular feeding habit, and a double asterisk. Station-wise data and all the measured δ^{13}C, δ^{15}N, and C:N values for each sample are available in the Supplemental Table S1.

1 **Table 1. List of the macrobenthic taxa sampled.** Numbers indicate the number of samples
2 used for stable isotope analyses. Abbreviations: Surface Deposit Feeders (SDF), Suspension
3 Feeders (SF), Subsurface Deposit Feeders (SSDF) (for details see section "Classification of the
4 macrofauna based on feeding habits"). Asterisk (*) indicates taxa unassigned to a particular
5 feeding habit, and a double asterisk. Station-wise data and all the measured δ^{13}C, δ^{15}N, and C:N
6 values for each sample are available in the Supplemental Table S1.

Taxonomic group	Species	Feeding habit	Habitat		
			Background	Delta	Seep
Bivalvia	*Ennucula tenuis* (Montagu, 1808)	SDF/SF	1		1
Bivalvia	*Macoma calcarea* (Gmelin, 1791)	SDF/SF		2	2
Bivalvia	*Macoma moesta* (Deshayes, 1855)	SDF/SF	1	2	
Bivalvia	*Macoma* sp.	SDF/SF	1		2
Bivalvia	*Macoma torelli* (A. S. Jensen, 1905)	SDF/SF			1
Bivalvia	*Nuculana pernula* (O. F. Müller, 1779)	SDF/SF	1		12
Bivalvia	*Periploma aleuticum* (A. Krause, 1885)	SDF/SF	1		1
Bivalvia	*Portlandia arctica* (Gray, 1824)	SDF/SF	2	5	6
Bivalvia	*Thracia myopsis* Møller, 1842	SDF/SF			2
Bivalvia	*Yoldia hyperborea* (A. Gould, 1841)	SDF/SF			1
Bivalvia	*Yoldiella lenticula* (Møller, 1842)	SDF/SF	3		7
Bivalvia	*Yoldiella solidula* Warén, 1989	SDF/SF			3
Bivalvia	*Parathyasira dunbari* (Lubinsky, 1976) *	n/a	1		1
Bivalvia	*Thyasira* cf. *gouldii**	n/a	1	6	5
Bivalvia	*Montacuta spitzbergensis* Knipowitsch, 1901	n/a			1

	*				
Gastropoda	*Frigidoalvania* sp.*	n/a			6
Annelida	Nephtyidae	Carnivore	1	3	14
Annelida	*Maldane sarsi* Malmgren, 1865	SSDF	5		19
Annelida	*Pectinaria (Cistenides) hyperborea (Malmgren, 1866)*	SSDF	2	3	8
Annelida	*Sternapsis* sp.	SSDF	2	3	12
Annelida	*Myriochele heeri* Malmgren, 1867	SDF/SF	1		28
Annelida	*Owenia polaris* Koh, Bhaud & Jirkov, 2003	SDF/SF	1		9
Annelida	*Spiochaetopterus typicus* M Sars, 1856	SDF/SF			2
Annelida	*Oligobrachia* sp.	Symbiotroph			27

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Table 2(on next page)

$\delta^{13}C$ and $\delta^{15}N$ measured for the sediment samples.

(*) average values for two samples.

1 **Table 2. δ^{13}C and δ^{15}N measured for the sediment samples.** (*) average values for two
2 samples.

	Background	Delta			Seep		
	6950	6977	6939	6947*	6952	6953	6992
δ^{13}C, ‰	-23.5	-25.8	-26.0	-24.2	-24.4	-24.4	-23.6
δ^{15}N, ‰	5.9	3.0	5.3	5.6	6.0	5.9	5.7

3

Table 3(on next page)

Nonparametric relative effects for surface deposit and suspension feeders.

The relative effects quantify probability that a randomly chosen individual from one species

exhibits a higher value for the variable (δ^{13}C or δ^{15}N) than a randomly chosen individual

across all species.

1 **Table 4. Nonparametric relative effects for surface deposit and suspension feeders**. The
2 relative effects quantify probability that a randomly chosen individual from one species exhibits
3 a higher value for the variable (δ^{13}C or δ^{15}N) than a randomly chosen individual across all
4 species.

Species	δ^{13}C	δ^{15}N
Macoma spp.	0.35714	0.41466
Myriochele heeri	0.60099	0.66906
Nuculana pernula	0.28921	0.27123
Owenia polaris	0.79805	0.80195
Portlandia arctica	0.59578	0.25731
Yoldiella lenticula	0.20649	0.25909

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Table 4(on next page)

Nonparametric relative effects for subsurface deposit.

The relative effects quantify probability that a randomly chosen individual from one species exhibits a higher value for the variable (δ^{13}C or δ^{15}N) than a randomly chosen individual across all species.

1 **Table 5. Nonparametric relative effects for subsurface deposit**. The relative effects quantify
2 probability that a randomly chosen individual from one species exhibits a higher value for the
3 variable ($\delta^{13}C$ or $\delta^{15}N$) than a randomly chosen individual across all species.

Species	$\delta^{13}C$	$\delta^{15}N$
Maldane sarsi	0.41667	0.62153
Pectinaria hyperborea	0.37708	0.36771
Sternapsis sp.	0.73065	0.38616

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