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Relationships between depth and $\delta^{15}\text{N}$ of Arctic benthos vary among
regions and trophic functional groups

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31 ABSTRACT

32 Significant relationships between the stable isotope ratios of nitrogen ($\delta^{15}\text{N}$) of benthic
33 primary consumers and water depth are commonly attributed to the preferential uptake of ^{14}N
34 from sinking particulate organic matter (POM) by microbes. Such a mechanism suggests the
35 relationships may be affected by local POM sources and flux dynamics. We examined the
36 relationships between $\delta^{15}\text{N}$ and water depth (20 to 500 m) for six trophic functional groups using
37 a mixed effects modelling approach, and compared relationships between two contiguous Arctic
38 marine ecosystems with different POM sources and sinking export dynamics, the Canadian
39 Beaufort Sea and Amundsen Gulf. We demonstrate for the first time in the Arctic that $\delta^{15}\text{N}$
40 values of mobile epifaunal carnivores increased as a function of depth when considered apart
41 from benthopelagic and infaunal carnivores. The $\delta^{15}\text{N}$ of suspension/filter feeders, infaunal
42 deposit feeders and bulk sediment also increased with water depth, and the slopes of the
43 relationships were steeper in the Amundsen Gulf than in the Beaufort Sea. We propose regional
44 differences in slopes reflect the prevalent POM sources exported to the benthos. In the Beaufort
45 Sea, terrestrial POM discharged from the Mackenzie River quantitatively dominates the
46 sedimentary organic matter across the continental shelf and slope, dampening change in $\delta^{15}\text{N}$ of
47 benthic POM with depth. In the Amundsen Gulf, a faster rate of change in benthic POM $\delta^{15}\text{N}$
48 with depth was linked to increasing contributions of marine-derived POM to the benthic
49 sedimentary pool, which had likely undergone extensive biological transformation in the
50 productive offshore pelagic zone. Differences in POM input regimes among regions should be
51 considered when comparing food webs using stable isotopes, as such differences may impact the
52 rate at which consumer $\delta^{15}\text{N}$ changes with depth.

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1.0 INTRODUCTION

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Deep-sea food webs at high latitudes are often characterized by two interlinked trophic pathways (e.g., Iken et al., 2001; Trueman et al., 2014). These include a benthic pathway in which organic matter available at the seafloor forms the base of the food web for obligate benthic animals, and a benthopelagic pathway in which mobile species subsidize their benthic diets with prey from the upper water column (e.g., Iken et al., 2001; Trueman et al., 2014; Stasko et al., 2016). Multiple trophic pathways can complicate interpretation of trophic structure in deep-sea food webs, especially when inferences are derived from stable isotope ratios of nitrogen ($\delta^{15}\text{N}$; e.g., Roy et al., 2015). Consumers are generally enriched in ^{15}N relative to their food, so that higher values of $\delta^{15}\text{N}$ are taken to indicate higher relative trophic positions (Minagawa and Wada, 1984). However, the $\delta^{15}\text{N}$ values of benthic suspension/filter feeders commonly increase as a function of water depth in various marine systems, whereas those of mobile demersal predators/scavengers usually do not (e.g., Catalan Sea, Polunin et al., 2001; Weddell Sea, Mintenbeck et al., 2007; Fram Strait, Bergmann et al., 2009; San Juan Archipelago, Galloway et al., 2013; Canadian Arctic Archipelago, Roy et al., 2015). Reported $\delta^{15}\text{N}$ -depth relationships for other benthic consumer groups are variable, and can be negative for some deposit feeders (Bergmann et al., 2009; Roy et al., 2015; Bell et al., 2016), confounding the comparison of trophic levels across depth gradients.

Mintenbeck et al. (2007) were the first to provide a detailed explanation of the depth-dependence of suspension feeder $\delta^{15}\text{N}$, linking the relationship to the preferential uptake of ^{14}N from sinking particulate organic matter (POM) by microorganisms in the water column (Macko and Estep, 1984; Kellogg et al., 2011). Deeper water depths allow more time for microbial consumption, and thus greater ^{15}N enrichment of the sinking POM (Kiørboe 2001; Mintenbeck et

77 al. 2007). Many benthic suspension feeders consume small particles (2 - 200 μm ; Riisgård and
78 Larsen, 2010) that may include a mix of newly-arrived pelagic POM and re-suspended
79 sedimentary POM. Longer residence times of such small, slowly sinking particles in the water
80 column or in the bulk sediment pool result in generally higher $\delta^{15}\text{N}$ values than those of larger
81 POM fractions (Mintenbeck et al. 2007). Organisms that consume larger ranges of particle sizes
82 tend to exhibit weak $\delta^{15}\text{N}$ -depth relationships, presumably because their food has more intact
83 biochemical compositions, consisting of faster-sinking POM (e.g, aggregates, zooplankton fecal
84 pellets, algal mats) and/or benthic or benthopelagic animals (Mintenbeck et al., 2007; Bergmann
85 et al., 2009; Roy et al., 2015). If particle characteristics drive $\delta^{15}\text{N}$ -depth relationships in benthic
86 consumers, regional variation in water column processes that govern particle source, size,
87 sinking flux, cross-shelf transport and transformation should underlie variation in the strength of
88 the relationships observed among marine regions. To date, regional comparisons that link the
89 strength of consumer $\delta^{15}\text{N}$ depth-relationships to POM source inputs and flux dynamics are
90 lacking.

91 Identifying heterogeneity in $\delta^{15}\text{N}$ -depth relationships among trophic functional groups
92 and/or species is important for benthic food web studies because such differences may
93 necessitate group- or taxon-specific isotopic baselines for calculating and comparing trophic
94 enrichment (Papiol et al., 2013; Roy et al., 2015). Most studies quantifying $\delta^{15}\text{N}$ -depth
95 relationships at the functional group level have used linear regression (Mintenbeck et al., 2007;
96 Bergmann et al., 2009; Roy et al., 2015), which is not ideal given the inherent non-independence
97 of multi-species groups (Pinheiro and Bates, 2000; Zuur et al., 2009). A modelling approach that
98 accounts for taxon-level variation can provide a more robust analysis of whether $\delta^{15}\text{N}$ -depth
99 relationships may be considered characteristic of a trophic functional group. Further, primary

100 feeding habitats may be important to consider within a given trophic functional group. Demersal
101 carnivores are often treated as a single group in $\delta^{15}\text{N}$ -depth analyses (e.g., Bergmann et al., 2009;
102 Roy et al., 2015) despite the fact that some regularly consume benthopelagic prey in addition to
103 benthos. Since their primary consumer prey often exhibit significant $\delta^{15}\text{N}$ -depth relationships
104 themselves, benthic predators may have increasing $\delta^{15}\text{N}$ with depth if they are considered
105 separately from their benthopelagic counterparts.

106 Here, we examined relationships between $\delta^{15}\text{N}$ and water depth for six trophic functional
107 groups along a depth gradient from 20 to 500 m in two contiguous Arctic marine regions, the
108 Canadian Beaufort Sea and Amundsen Gulf. POM sources and flux dynamics differ significantly
109 between regions; the majority of organic matter inputs are derived from terrestrial sources in the
110 Canadian Beaufort Sea, and from marine sources in the Amundsen Gulf (see further description
111 in *Methods*; Morata et al., 2008; Sallon et al., 2011). Our primary objective was to identify
112 which trophic functional groups display increasing $\delta^{15}\text{N}$ as a function of water depth in each
113 region using a linear mixed-modelling approach that allows for taxon-level variation within a
114 functional group (Pinheiro and Bates, 2000). Secondly, we assessed whether consumer $\delta^{15}\text{N}$ -
115 depth relationships differed between regions, given known differences in their particle sources
116 and flux dynamics. We predicted that (1) in addition to suspension feeders, $\delta^{15}\text{N}$ –depth
117 relationships would be significant for benthic carnivores when analysed separately from other
118 carnivorous groups, and (2) the slope and/or strength of relationships for all trophic functional
119 groups would differ between the two adjacent marine regions.

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2.0 METHODS

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2.1 Study Area

123 Samples were collected in the southern Canadian Beaufort Sea and Amundsen Gulf
124 (herein collectively referred to as the Canadian Beaufort region; Fig. 1) aboard the stern trawler
125 FV *Frosti* as part of the Beaufort Regional Environmental Assessment Marine Fishes Project
126 (Fisheries and Oceans Canada, www.beaufortrea.ca). Despite being contiguous marine regions,
127 the Beaufort Sea and Amundsen Gulf exhibit significant differences in sediment characteristics
128 (Morata et al., 2008), primary production regimes (Ardyna et al., 2013), and vertical flux of
129 POM (O'Brien et al., 2006; Forest et al., 2010). Primary production is higher in the Amundsen
130 Gulf than in the Beaufort Sea (Ardyna et al., 2013; Sallon et al., 2011), but export to the benthos
131 is lower (O'Brien et al., 2006; Sallon et al., 2011). An estimated 70 to 95 % of autochthonous
132 particulate organic carbon in the Amundsen Gulf is retained in the upper 100 m of the water
133 column by the pelagic community, except in the vicinity of Cape Bathurst (Forest et al., 2010;
134 Sampei et al., 2011). The Beaufort Sea shelf is strongly influenced by the Mackenzie River,
135 which discharges $> 130 \times 10^6$ t of terrestrial sediment annually (Macdonald et al., 1998;
136 Doxaran et al., 2015), exceeding that of any other Arctic River (Rachold et al., 2004).
137 Consequently, > 70 % of the bulk organic matter pool in the Amundsen Gulf is comprised of
138 marine-derived organic carbon, whereas that in the Beaufort Sea is comprised of > 50 %
139 terrigenous organic carbon (Magen et al., 2010).

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141 *2.2 Sampling and Stable Isotope Analysis*

142 Sampling took place from early August to late September of 2012 and 2013 along 8
143 transects that spanned the continental shelf and associated slope. Each sampling transect had five
144 to eight pre-defined sampling stations at depths ranging from 20 to 500 m (Fig. 1). Demersal fish
145 and epifaunal invertebrates were collected with a combination of two bottom trawl nets: a

146 modified Atlantic Western IIA benthic otter trawl towed for 20 minutes (12.7 mm cod end liner)
147 and a 3 m High-Rise Benthic Beam Trawl towed for 10 minutes (6.3 mm cod end liner) towed
148 for 20 and 10 minutes bottom-contact time, respectively. Trawling was targeted at a speed-over-
149 ground of 2.0 knots (1.81 to 2.35 acceptable range), and was monitored with a Scanmar CGM-
150 05/TE40-2 trawleye sensor (Scanmar, Åsgårdstrand, Norway). Sediments were collected with a
151 0.5 m² USNEL box core and the upper 25 cm were sieved through a 1 mm stainless steel mesh to
152 retain infaunal invertebrates. A sample of bulk sediment from the top 1 cm was retained for
153 stable isotope analysis and used as a reference for the composition of the bulk sedimentary
154 organic matter pool. Biota were sorted to the lowest possible taxonomic resolution onboard with
155 the help of taxonomists (L. De Montety, Université du Québec à Rimouski; W. Walkusz,
156 Fisheries and Oceans Canada), rinsed with seawater, and frozen immediately along with the
157 sediment samples at -50 °C. Taxonomy was standardized to the currently accepted names in the
158 World Register of Marine Species (WoRMS Editorial Board 2016). Fish and macroinvertebrates
159 were selected for stable isotope analysis across the observed range of body sizes to capture
160 potential covariation between $\delta^{15}\text{N}$ and size (e.g., Stasko et al., 2016).

161 Bulk sediment and tissue samples dissected for stable isotope analysis were dehydrated in
162 a standard laboratory convection oven at 50 °C (fish) or a FreeZone 18 freeze-drier (Labconco;
163 invertebrates, sediment), then ground to a homogenous powder and analysed for N isotopic
164 composition using a Delta Plus continuous flow isotope spectrometer (Thermo-Finnigan)
165 coupled to a 4010 Elemental Analyzer (Costech Instruments) at the University of Waterloo
166 Environmental Isotopes laboratory (Waterloo, Canada). C isotopic composition was additionally
167 analysed in bulk sediment samples following acidification with 10 % HCl to remove inorganic
168 carbon (Jacob et al., 2005). Slow-turnover tissues were targeted for analysis, consistent with the

169 literature and dissection constraints: dorsal muscle for fish, tail muscle for large decapods, and
170 whole body for invertebrates that could not be reliably separated from exoskeleton (e.g., Dunton
171 et al., 2006; see Stasko et al., 2017). Isotope ratios ($^{15}\text{N}:^{14}\text{N}$, $^{13}\text{C}:^{12}\text{C}$) were expressed in δ
172 notation as parts per thousand (‰) relative to the international standards atmospheric N_2 for
173 nitrogen and Vienna Pee Dee Belemnite for carbon (Craig, 1957; Mariotti, 1983). Analytical
174 error for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ never exceeded 0.3 and 0.2 ‰, respectively, based on repeated
175 measurements of working laboratory standard materials cross-calibrated to the international
176 standards. Repeatability of duplicate measurements of sample material was 0.3 ‰ for both $\delta^{15}\text{N}$
177 and $\delta^{13}\text{C}$. Stable isotope values for all taxa and sediments, averaged by region and depth, are
178 available, open access, in Stasko et al. (2017).

179

180 *2.3 Statistical Analyses*

181 To account for potential bias caused by differences in species composition, statistical
182 analyses were restricted to those taxa that were sampled in both the Beaufort Sea and the
183 Amundsen Gulf across the same depth range (20 to 500 m). A total of 2239 biological samples
184 representing 38 taxa across 6 phyla, and 56 samples of marine sediment were included in
185 analyses (Table 1). Analyses were repeated with the full set of taxa sampled (74 total) to ensure
186 excluded species did not change the conclusions drawn from results (i.e., taxa lists in both
187 regions were not identical in the secondary analyses).

188 Taxa were delineated into six trophic functional groups based on published trophic
189 marker data and feeding observations (Stasko et al. *unpublished*). We defined trophic functional
190 groups as taxa that employ similar feeding strategies and may utilize similar food types, but may
191 not necessarily compete with one another. Trophic group classification followed systems

192 proposed by Macdonald et al. (2010) and Jumars et al. (2015) using trophic traits, and included:
193 (1) benthopelagic carnivores that are highly mobile and feed both at and above the seafloor as
194 predators, scavengers, or both; (2) epifaunal carnivores that are mostly mobile and feed at the
195 sediment surface as predators, scavengers, or both; (3) infaunal carnivores that prey on fauna
196 below the sediment surface (in this study, all are predatory marine worms); (4) suspension/filter
197 feeders that live on the seafloor and feed omnivorously on fresh or resuspended POM filtered
198 from the water; (5) epifaunal deposit feeders that feed omnivorously at the sediment surface on
199 deposited material that can include decomposed carcasses and zooplankton molts, phytodetritus,
200 recycled organic matter, bacteria, or bacterial products; and (6) infaunal deposit feeders that feed
201 omnivorously below the sediment surface on detritus and/or bacteria and bacterial products (e.g.,
202 Coad and Reist, 2004; Macdonald et al., 2010; Węśławski et al., 2010; Jumars et al., 2015).
203 Facultative suspension/deposit feeders that switch between feeding modes were excluded to
204 avoid unquantified variation.

205 Some taxa formed clear groups with conspecifics in preliminary plots of $\delta^{15}\text{N}$ versus
206 depth, suggesting non-independence (see Supplementary Material). Linear mixed effects models
207 were thus used to investigate relationships between $\delta^{15}\text{N}$ and the fixed factor water depth for
208 each trophic functional group, allowing the intercept and/or slope to vary randomly by taxon to
209 account for non-independence (Pinheiro and Bates, 2000). To assess whether relationships
210 between $\delta^{15}\text{N}$ and water depth differed between the Beaufort Sea and Amundsen Gulf, an
211 interaction term between depth and region was included in the models. Model selection between
212 random effect structures (slope, intercept, or both) was conducted using likelihood ratio tests
213 after model fitting with a maximum likelihood procedure (Zuur et al., 2009; Bates et al. 2015).
214 Likelihood ratio tests were then used to assess whether the interaction between water depth and

215 region improved fit, and if not the interaction term was dropped from the model. To more closely
216 examine regional differences, models were fit individually for the Beaufort Sea and Amundsen
217 Gulf for those trophic functional groups that displayed both a strong relationship between $\delta^{15}\text{N}$
218 and water depth, and a significant interaction between water depth and region. Finally, the best
219 model in all cases was refit using a restricted maximum likelihood procedure for parameter
220 reporting (Zuur et al., 2009). Goodness-of-fit was evaluated using the marginal and conditional
221 coefficients of determination (R_m^2 and R_c^2), which, respectively, describe the proportion of
222 variance explained by the fixed effects alone, and the fixed and random effects combined
223 (Nakagawa and Schielzeth, 2013). Following Sullivan and Feinn (2012), an $R_c^2 \geq 0.63$ was
224 considered strong and indicative of a well-fit model. Effect size for well-fit models was
225 considered the average change in $\delta^{15}\text{N}$ (Δ) estimated for the trophic functional group across the
226 entire depth gradient. Relationships between sediment $\delta^{15}\text{N}$ and water depth were assessed with
227 least squares linear regression. In all cases, assumptions of homogeneity of variance and
228 normality of errors were assessed with a series of residual plots, and depth was log-transformed
229 where it improved linearity (Zuur et al., 2009). Where residual variance increased as a function
230 of depth (epifaunal and infaunal deposit feeders), linear mixed effects models included a fixed
231 variance structure (Zuur et al., 2009; Pinheiro et al., 2016). Linear regression and likelihood ratio
232 tests were considered significant at $\alpha = 0.05$. We estimated the error introduced to trophic level
233 calculations when a common baseline is applied across a change in consumer $\delta^{15}\text{N}$ of up to 2 ‰,
234 as observed in this study. Trophic levels were calculated using the average $\delta^{15}\text{N}$ of sedimentary
235 POM from sites < 40 m deep in the Beaufort Sea as a baseline (3.42 ‰), according to Hussey et
236 al. (2014; although we caution the model was created primarily with fish data).

237 The isotopic composition of sedimentary organic matter in the Canadian Beaufort region
238 is influenced by three primary sources: terrestrial, fresh marine, and refractory marine organic
239 matter (Magen et al., 2010). To verify that the composition of sedimentary POM differed
240 between the Beaufort Sea and Amundsen Gulf, as previously reported (Morata et al., 2008;
241 Magen et al., 2010), the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of bulk sediments at each site were plotted relative to the
242 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of representative terrestrial, fresh marine, and refractory marine source data taken
243 from the literature. The terrestrial source data were based on organic material recovered from the
244 Mackenzie and Colville River Deltas ($\delta^{15}\text{N} = 1.0 \text{ ‰}$, $\delta^{13}\text{C} = -27.0 \text{ ‰}$; estimated from various
245 studies by Magen et al., 2010). The refractory marine source data were taken from Amundsen
246 Gulf sediments, where pigment analyses indicated the presence of highly degraded marine POM
247 ($\delta^{15}\text{N} = 6.7 \text{ ‰}$, $\delta^{13}\text{C} = -21.1 \text{ ‰}$; Morata et al., 2008). Source values for fresh marine organic
248 matter were more difficult to assign due to high spatial and seasonal variation in the isotopic
249 composition of primary producers (Morata et al., 2008). Consequently, we averaged $\delta^{15}\text{N}$ and
250 $\delta^{13}\text{C}$ measured in pelagic POM collected from the chlorophyll maximum depth at our sampling
251 sites in the Amundsen Gulf in 2013 (C. Michel, unpublished data), combined with pelagic POM
252 values from the eastern Beaufort Sea and Amundsen Gulf slope reported by Roy et al. (2015).
253 The resulting fresh marine source values ($\delta^{15}\text{N} = 5.6 \text{ ‰}$, $\delta^{13}\text{C} = -26.5 \text{ ‰}$) fall within the range
254 reported for summer across the Canadian Beaufort region by Morata et al. (2008; $\delta^{15}\text{N} = 1.0$ to
255 7.0 ‰ , $\delta^{13}\text{C} = -27.0$ to -21.0 ‰). Some sites in the Amundsen Gulf were excluded as outliers due
256 to anomalous $\delta^{13}\text{C}$ ($>$ median + interquartile range).

257 All statistical and graphical procedures were performed in R (ver. 3.3.1, R Core Team,
258 2016) using the packages lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2016), peicewiseSEM

259 (Lefcheck, 2015), ggplot2 (Wickham, 2009), ggtern (Hamilton, 2016) and plyr (Wickham,
260 2011).

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3.0 RESULTS

264 Linear mixed effects models indicated $\delta^{15}\text{N}$ was strongly related to depth for epifaunal
265 carnivores, suspension/filter feeders, epifaunal deposit feeders and infaunal deposit feeders, but
266 not for benthopelagic or infaunal carnivores (Table 2). The slope of the relationship was positive
267 and steepest for suspension/filter feeders and infaunal deposit feeders, followed by epifaunal
268 carnivores (Fig. 2, Table 2). The estimated increase in $\delta^{15}\text{N}$ for these groups between 20 and 500
269 m depths ranged between 0.82 and 1.44 ‰ (Table 2). Epifaunal deposit feeder $\delta^{15}\text{N}$ was strongly
270 negatively related to depth, but had the shallowest slope of all trophic functional groups when
271 both regions were considered together (Table 2). There were no strong associations between
272 $\delta^{15}\text{N}$ and water depth for benthopelagic and infaunal carnivores (Table 2). Plots of $\delta^{15}\text{N}$ versus
273 water depth are available in the Supplementary Material for all trophic functional groups and
274 taxa. Applying a common baseline to calculate trophic levels resulted in over-estimations of
275 almost an entire trophic level when the $\delta^{15}\text{N}$ of hypothetical organisms at trophic level 5 changed
276 by 2 ‰. Error in trophic level estimations decreased with decreasing trophic level (Fig. 3).

277 For those trophic functional groups that displayed a strong relationship between $\delta^{15}\text{N}$ and
278 depth (Table 2), a model that included an interaction term between water depth and region
279 (Beaufort Sea vs. Amundsen Gulf) fit the data significantly better than a model with no
280 interaction (likelihood ratio tests; $p < 0.01$ for epifaunal carnivores, suspension/filter feeders,
281 epifaunal deposit feeders, and infaunal deposit feeders). In other words, the slopes of the $\delta^{15}\text{N}$ -
282 depth relationships were significantly different between the Beaufort Sea and Amundsen Gulf.

283 Slopes were steeper in the Amundsen Gulf for suspension/filter feeders and infaunal deposit
284 feeders, whereas slopes were steeper in the Beaufort Sea for epifaunal carnivores and epifaunal
285 deposit feeders (Table 3, Fig. 2). When fit for individual regions, infaunal deposit feeders
286 displayed the largest increase in $\delta^{15}\text{N}$ of any group, albeit based on two taxa (Table 3). Including
287 taxon as a random variable (R_c^2) explained an additional >40 % of the variance relative to depth
288 alone (R_m^2) for all groups except infaunal deposit feeders (Table 2, Table 3). Including all
289 available taxa in analyses (i.e., not restricting taxa assemblages to be identical in both regions)
290 did not reveal any differences between which trophic functional groups displayed strong $\delta^{15}\text{N}$ -
291 depth relationships, but did increase the strength of fit (data not shown).

292 Bulk sediment $\delta^{15}\text{N}$ was weakly, but significantly positively related to water depth in
293 both the Beaufort Sea ($p < 0.01$, $R^2 = 0.30$, $F_{1,31} = 13.12$) and Amundsen Gulf ($p = 0.03$, $R^2 =$
294 0.20 , $F_{1,21} = 5.19$). The slope of the relationship between $\delta^{15}\text{N}$ and water depth was significantly
295 steeper in the Amundsen Gulf relative to the Beaufort Sea (ANCOVA, $p = 0.03$, $F_{3,34} = 5.94$;
296 Fig. 4). Sediment isotopic composition was clearly more influenced by terrestrial sources in the
297 Beaufort Sea than in the Amundsen Gulf, where sediment $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at most sampling sites
298 were well constrained between fresh and refractory marine end-members (with the exception of a
299 few terrestrially-dominated nearshore sites; Fig. 5).

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4.0 DISCUSSION

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Enrichment of ^{15}N in consumer tissues with increasing water depth is a commonly
observed phenomenon among benthic marine organisms at high latitudes and elsewhere,
particularly in deposit and suspension feeders (e.g., Mintenbeck et al., 2007; Bergmann et al.,
2009; Roy et al., 2015). Here, we demonstrated for the first time in the Arctic that the $\delta^{15}\text{N}$ of

306 epifaunal carnivores can also increase as a function of depth. The rate of change in consumer
307 $\delta^{15}\text{N}$ with depth differed between two contiguous Arctic marine regions as predicted. Below, we
308 discuss potential mechanisms underlying $\delta^{15}\text{N}$ -depth relationships for all trophic functional
309 groups studied, and propose that regional differences in $\delta^{15}\text{N}$ -depth relationships may be linked
310 to heterogeneity in POM input and vertical flux properties.

311

312 *Differences in $\delta^{15}\text{N}$ -depth relationships among trophic functional groups*

313 The significant, positive effect of water depth on the $\delta^{15}\text{N}$ values of suspension/filter
314 feeders, infaunal deposit feeders, and sediment is likely linked to the transformation of POM
315 during sinking, as suggested by others (Mintenbeck et al., 2007; Galloway et al., 2013). Summer
316 maximum chlorophyll *a* concentrations in the Canadian Beaufort Sea and Amundsen Gulf occur
317 deeper than in other oceans, between ~ 40 to 60 m depths (Carmack et al., 2004; Ardyna et al.,
318 2013). As a result, fresh, relatively untransformed phytodetritus is more accessible to benthos in
319 shallow habitats than in deep habitats. Marine-derived POM received by benthos in deeper
320 habitats is subject to longer periods of dissolution, physical disaggregation, and microbial
321 consumption in the water column (Smith et al., 1992; Kiørboe et al., 2001). There appear to be
322 two vertical zones of elevated biological activity in the Beaufort Sea and Amundsen Gulf that
323 would promote the degradation, remineralization, and recycling of POM (Kiørboe et al., 2001).
324 The primary zone is the euphotic layer, as with most oceans, where the majority of POM
325 synthesized during the spring bloom is consumed by heterotrophic zooplankton and bacteria
326 (Sampei et al., 2011). The second is the transition from nutrient-rich Pacific-origin water to
327 warmer Atlantic-origin water around 200 to 350 m depths near the upper continental slope
328 (McLaughlin et al., 1996). Here, the hyperbenthic habitat appears to be a hotspot for organic

329 matter transformation and interception via large aggregations of zooplankton and predatory
330 benthopelagic fish (Crawford et al., 2012; Majewski et al., 2017), which may be linked to low
331 POM export below 200 m (Forest et al., 2015). With little fresh marine-derived POM reaching
332 the seafloor along the upper slope, benthic primary consumers would be limited to ^{15}N -enriched
333 POM that has either been recycled among the benthos and sedimentary bacteria (e.g., North et
334 al., 2014; Bell et al., 2016), or resuspended and advected downslope by upwelling/downwelling
335 events characteristic of the Beaufort Sea shelf-break (Forest et al., 2007).

336 In contrast to suspension and infaunal deposit feeders, epifaunal deposit feeder $\delta^{15}\text{N}$
337 decreased slightly with depth. Opposing $\delta^{15}\text{N}$ -depth relationships between epifaunal and infaunal
338 deposit feeding groups is unintuitive, but may be explained by differences in trophic flexibility.
339 Epifaunal taxa that feed omnivorously at the sediment surface are more trophically flexible than
340 infaunal taxa, both in terms of food source and particle size. Such trophic flexibility was
341 supported by the increasing variance of $\delta^{15}\text{N}$ within individual epifaunal deposit-feeding taxa
342 with water depth, especially for the asteroid *Pontaster tenuispinus* (see Suppl. Material).
343 Although epifaunal deposit feeders primarily rely on accumulated sedimentary organic matter
344 (e.g., Minks et al. 2005), they can respond quickly to the availability of other foods, including
345 sunken algal mats released from sea ice, seasonal pulses of sedimented phytoplankton,
346 sedimentary bacterial abundances, or even occasional predation (e.g., McMahon et al., 2006;
347 Renaud et al., 2007; Bergmann et al., 2009; Gale et al., 2013). Conversely, the two infaunal
348 deposit feeding taxa examined here extract nutrition directly from ingested sediment at deeper
349 layers (MacDonald et al., 2010). Infauna with similar feeding habits have been observed to
350 exploit more consistent fractions of bulk sedimentary organic matter than their epifaunal
351 counterparts (North et al., 2014). Infaunal deposit feeder $\delta^{15}\text{N}$ values would therefore be

352 expected to reflect the of bulk sedimentary organic matter more closely than those of epifaunal
353 deposit feeders.

354 Water depth is thought to have a weaker effect on the $\delta^{15}\text{N}$ of mobile carnivorous
355 predators and scavengers than on primary consumers because the former can feed on both
356 benthic and benthopelagic prey (Bergmann et al., 2009; Roy et al., 2015). Our findings suggest
357 the relationships between $\delta^{15}\text{N}$ and depth differ when carnivores are analysed separately by their
358 primary feeding habitat. The positive trend between epifaunal carnivore $\delta^{15}\text{N}$ and water depth
359 might be a consequence of feeding on ^{15}N -enriched prey at depth. Suspension feeders are an
360 important prey for many of the taxa in this trophic group (e.g., Birkely and Gulliksen, 2003;
361 Coad and Reist, 2004). Access to vertically migrating pelagic prey, such as zooplankton, is likely
362 limited for benthic predators on the continental slope because those prey are intercepted by large
363 aggregations of benthopelagic predators (Crawford et al., 2012; Majewski et al., 2017).
364 Curiously, infaunal carnivore $\delta^{15}\text{N}$ values did not reflect those of the infaunal deposit feeders that
365 may comprise an important prey base. The infauna are the most data-poor trophic groups in this
366 study ($n < 100$ individuals for each group), and without additional dietary information it is
367 difficult to estimate the importance of infaunal deposit feeders to the diets of infaunal carnivores
368 examined in this study. Regardless, the different $\delta^{15}\text{N}$ -depth relationships among carnivore
369 groups highlight variation in their use of benthic and pelagic trophic pathways. Benthopelagic
370 carnivores subsidize their diets with pelagic prey (e.g., Bjelland et al., 2000; Cui et al., 2012) and
371 are not restricted to trophic pathways beginning in benthic resources that have undergone depth-
372 related ^{15}N enrichment. We recommend considering carnivorous trophic groups separately in
373 food web analyses rather than pooling them as one group.

374 The question remains of how large a change in $\delta^{15}\text{N}$ ($\Delta^{15}\text{N}$) is ecologically significant. A
375 $\Delta^{15}\text{N}$ of ~ 3 to 4 ‰ is often assumed to represent a trophic level when averaged across the food
376 web (Post, 2002). The specific $\Delta^{15}\text{N}$ between any two successive trophic levels, however, can
377 become smaller up the food chain in marine systems (Hussey et al., 2014). We estimated that the
378 error in trophic level calculations associated with a $\Delta^{15}\text{N}$ of up to 2 ‰, as observed in this study,
379 can approach one trophic level for upper-trophic animals, but may be minimal for lower-trophic
380 animals (Fig. 3). The potential error in food web interpretations due to variation in $\delta^{15}\text{N}$ -depth
381 relationships among trophic functional groups may thus depend on the scope of the food web
382 being considered, and certainly depends on the depth range (e.g., $\Delta^{15}\text{N} < 0.69$ ‰ observed for
383 epifaunal deposit feeders between 20 and 500 m depths in this study, compared to $\Delta^{15}\text{N} > -4.5$ ‰
384 from 1000 to 5000 m depths in Fram Strait; Bergmann et al., 2009).

385

386 *Differences in $\delta^{15}\text{N}$ -depth relationships between regions*

387 Remineralization of organic matter by the pelagic food web, and its link to POM sources
388 and flux dynamics (Sallon et al., 2011; Kellogg et al., 2011), may be key to steeper $\delta^{15}\text{N}$ -depth
389 relationships for suspension/filter feeders, infaunal deposit feeders, and sediments in the
390 Amundsen Gulf than in the Beaufort Sea. Primary production is generally higher in the offshore
391 Amundsen Gulf than in the Beaufort Sea (Ardyna et al., 2013; Sallon et al., 2011), but up to 95
392 % of that autochthonous organic carbon is retained and recycled by the pelagic community
393 (Sampei et al., 2011). Proxies of primary production in the Amundsen Gulf and elsewhere have
394 been positively correlated to microbial enzymatic activity (Kellogg et al., 2011), which is likely
395 linked to correspondingly greater proportions of algal cells and exopolymeric substances
396 observed in sinking POM (Sallon et al., 2011). Sallon et al. (2011) suggested that the presence of

397 exopolymeric coatings on sinking particles in regions of high primary production likely
398 intensified microbial activity by facilitating bacterial attachment. The small volume of marine-
399 derived POM that is exported below 100 m in the offshore Amundsen Gulf thus has a
400 substantially altered biochemical composition (Kellogg et al. 2011). Our sediment data indicated
401 such ^{15}N -enriched marine POM comprised increasing proportions of the bulk sedimentary pool in
402 the Amundsen Gulf with increasing depth, leading to relatively steeper $\delta^{15}\text{N}$ -depth relationships
403 for sediment and benthic consumers that rely on sinking POM compared to the Beaufort Sea.

404 In contrast, the bulk sedimentary organic matter pool in the Beaufort Sea is quantitatively
405 dominated by terrigenous material from the Mackenzie River plume (Magen et al., 2010).
406 Terrestrial organic matter from the Mackenzie River can become entrained in upper water
407 masses upon entry into the Beaufort Sea or via frequent resuspension events on the shelf
408 (Carmack and Macdonald, 2002; Forest et al., 2007). Once suspended, terrestrial POM is
409 typically directed eastwards and offshore by winds and the Coriolis force at the surface
410 (Carmack and Macdonald, 2002), and by eddies and the prevailing eastward-flowing Beaufort
411 Undercurrent in deeper waters (O'Brien et al., 2006; Forest et al., 2007). Consequently,
412 terrestrial POM can comprise > 50 % of the bulk sediment pool as far as the eastern tip of
413 Tuktoyaktuk Peninsula and as deep as 1000 m (Magen et al., 2010). The quantitative dominance
414 of terrestrial POM in the benthic POM pool, even at great depths, may explain why the $\delta^{15}\text{N}$
415 measured in sediment, suspension/filter feeders and infaunal deposit feeders changes at a slower
416 rate with depth in the Beaufort Sea than in the Amundsen Gulf.

417 Epifaunal carnivores were the only trophic group with a positive $\delta^{15}\text{N}$ -depth relationship
418 that was slightly steeper in the Beaufort Sea than in the Amundsen Gulf. This finding appeared
419 to be most influenced by a few taxa, including the generalist-feeding fishes Atlantic Poacher

420 (*Leptagonus decagonus*), Gelatinous Eelpout (*Liparis fabricii*), and Canadian Eelpout (*Lycodes*
421 *polaris*; Coad and Reist, 2004; Giraldo et al., 2016). Some generalist benthic fishes can switch
422 feeding strategies to take advantage of benthopelagic prey when benthic resources are scarce
423 (e.g., Carrassón and Cartes, 2002), which could explain the flatter $\delta^{15}\text{N}$ -depth relationships
424 observed in the Amundsen Gulf for these fishes. However, there is little evidence for such a shift
425 according to $\delta^{13}\text{C}$ (see data in Stasko et al., 2017). Without further diet information, the flatter
426 $\delta^{15}\text{N}$ -depth relationships of these fish species in the Amundsen Gulf remain difficult to explain.

427

428 *Conclusions and considerations*

429 Results presented here are relevant to studies that take a functional group approach to
430 marine food web analyses, but must be applied with caution. Our dataset is limited by taxon
431 occurrences and distributions, as well as sample availability. Many taxa occurred across a limited
432 depth range, and some occurred along a limited number of transects (Table 1). Any trophic
433 functional group, including suspension feeders, can include taxa that feed at substantially
434 different trophic levels from each other (e.g., Bergmann et al. 2009), affecting how closely
435 linked their $\delta^{15}\text{N}$ values are to POM. The importance of taxon-level variation was underscored
436 by the fact that including taxon as a random variable in the models consistently explained an
437 additional > 40 % of variance ($R^2_c > R^2_m$). Confidence that the results can be applied more
438 generally to other studies should be evaluated in light of the limitations in taxa richness and
439 distributions available in this dataset.

440 In conclusion, we used a linear mixed effects modelling approach to confirm that positive
441 $\delta^{15}\text{N}$ -depth relationships in the Beaufort Sea and Amundsen Gulf were characteristic of three
442 benthic trophic functional groups: epifaunal carnivores, suspension/filter feeders, and infaunal

443 deposit feeders. We agree with other authors that a depth-stratified normalization approach may
444 be necessary when making conclusions about consumer trophic levels from $\delta^{15}\text{N}$ across depth
445 gradients in marine systems (e.g., Mintenbeck et al., 2007; Roy et al., 2015), and demonstrated
446 such an approach may also be necessary for benthic-feeding carnivores. This work additionally
447 highlights the need to be cognisant of differences in POM input and vertical flux regimes when
448 comparing food webs among distinct marine systems, as such differences may impact the rate at
449 which consumer $\delta^{15}\text{N}$ changes with depth.

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TABLES

Table 1. List of taxa used in the study, sorted by trophic functional group and Phylum. The sample sizes, depth ranges, and occurrences by transect for each taxon are given individually for the Beaufort Sea and Amundsen Gulf. Transects in the Amundsen Gulf are indicated in bold. Plot ID # is indicated for those taxa shown in Fig. 2. Dashes indicate those taxa missing from Fig. 2 because they were only sampled at one water depth.

Phylum	Taxon	Plot ID #	Sample size		Depth range		Transects
			Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
Benthopelagic carnivore							
AR	<i>Argis dentata</i>		49	21	40 - 200	40 - 200	a1, dal, kug, gry, tbs, cbh, dar
Arthropoda	<i>Eualus gaimardii</i>		92	49	20 - 500	40 - 350	a1, dal, kug, gry, tbs, cbh, dar, ulu
Arthropoda	<i>Lebbeus polaris</i>		6	55	500	75 - 500	tbs, cbh, dar, ulu
Chordata	<i>Boreogadus saida</i>		327	91	20 - 500	40 - 500	a1, dal, kug, gry, tbs, cbh, dar, ulu
Chordata	<i>Icelus spatula</i>		53	3	20 - 200	40 - 75	a1, dal, kug, gry, tbs, cbh, dar, ulu
Chordata	<i>Reinhardtius hippoglossoides</i>		67	10	350 - 500	300 - 350	a1, dal, kug, gry, tbs, cbh, ulu
Chordata	<i>Triglops pingelii</i>		54	14	20 - 350	40 - 200	a1, dal, kug, gry, tbs, dar
Epifaunal carnivore							
Arthropoda	<i>Sabinea septemcarinata</i>	1	25	23	40 - 350	40 - 350	kug, gry, tbs, dar, ulu
Arthropoda	<i>Saduria sabini</i>	2	9	15	20 - 40	40 - 200	kug, dal, cbh, dar
Arthropoda	<i>Sclerocrangon ferox</i>	3	73	70	40 - 500	75 - 500	a1, gry, tbs, cbh, dar, ulu
Chordata	<i>Anisarchus medius</i>	4	53	7	40 - 200	40 - 75	kug, gry, cbh, dar
Chordata	<i>Aspidophoroides olrikii</i>	5	118	40	20 - 200	40 - 200	a1, dal, kug, gry, tbs, cbh, dar, ulu
Chordata	<i>Gymnocanthus tricuspis</i>	6	49	16	20 - 200	40 - 75	a1, dal, kug, gry, tbs, dar
Chordata	<i>Icelus bicornis</i>	7	64	44	40 - 200	40 - 275	a1, kug, gry, tbs, cbh, dar, ulu
Chordata	<i>Leptagonus decagonus</i>	8	10	7	350 - 500	200 - 350	dal, dar
Chordata	<i>Liparis fabricii</i>	9	14	11	40 - 500	200 - 500	a1, kug, gry, tbs, dar, ulu
Chordata	<i>Lycodes pallidus</i>	10	4	21	40 - 500	200 - 350	kug, cbh, dar, ulu

Phylum	Taxon	Plot ID #	Sample size		Depth range		Transects
			Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
Chordata	<i>Lycodes polaris</i>	11	23	11	20 - 200	40 - 75	dal, kug, gry, dal, kug, gry
Chordata	<i>Lycodes sagittarius</i>	-	7	3	350	350	gry, dal
Chordata	<i>Lycodes seminudus</i>	12	39	7	350 - 500	350 - 500	a1, kug, gry, dar, ulu
Cnidaria	Actiniaria	-	13	4	500	200	tbs, dar
Echinodermata	<i>Gorgonocephalus</i> spp.	13	35	19	40 - 500	75 - 300	a1, gry, tbs, cbh, dar
Infaunal carnivore							
Annelida	<i>Abyssoninoe</i> sp.		2	5	350	75 - 350	kug, gry, cbh, ulu
Annelida	<i>Aglaophamus</i> sp.		5	3	350 - 500	350 - 500	kug, gry, tbs, cbh, dar, ulu
Annelida	<i>Eucranta</i> spp.		6	11	40 - 200	75 - 350	kug, gry, tbs, cbh, dar, ulu
Annelida	<i>Nephtys</i> spp.		4	3	40 - 75	40 - 75	dal, tbs, dar
Suspension/filter feeder							
Arthropoda	<i>Haploops laevis</i>	-	3	5	75	40	gry, ulu
Echinodermata	<i>Heliometra glacialis</i>	14	47	45	40-350	75-350	a1, tbs, gry, cbh, dar, ulu
Mollusca	<i>Astarte</i> spp.	15	4	15	75	40 - 350	dal, cbh, dar, ulu
Mollusca	<i>Batharca</i> spp.	16	8	4	75	300 - 500	gry, cbh, dar
Mollusca	<i>Similipecten greenlandicus</i>	17	39	10	40 - 75	75	gry, tbs, dar
Mollusca	Thyasiridae*	18	13	9	75 - 500	200 - 500	dal, kug, gry, cbh, dar, ulu
Epifaunal deposit feeder							
Annelida	Ampharetidae	18	11	11	350 - 500	200 - 500	dal, kug, gry, tbs, cbh, dar, ulu
Arthropoda	<i>Synidotea</i> spp.	19	17	23	40 - 75	40 - 300	tbs, cbh
Echinodermata	<i>Ctenodiscus crispatus</i>	20	6	25	200	75 - 350	dal, cbh, dar, ulu
Echinodermata	<i>Pontaster tenuispinus</i>	21	63	21	75 - 500	200 - 500	a1, dal, kug, gry, tbs, cbh, dar
Infaunal deposit feeder							
Annelida	<i>Maldane</i> spp.	22	34	24	75 - 500	40 - 500	dal, kug, gry, tbs, cbh, dar, ulu

Phylum	Taxon	Sample size			Depth range		Transects
		Plot ID #	Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
Echinodermata	<i>Molpadia</i> sp.	23	19	19	350 - 500	350 - 500	dal, kug, gry, tbs, dar, ulu

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649 *Thyasiridae can derive nutrition from chemosynthetic sulfur-oxidizing bacteria rather than from suspended POM. The $\delta^{13}\text{C}$ values of

650 Thyasiridae individuals included in this study indicated that they were heterotrophic. See *Supplementary Material*.

651 Table 2. Results of linear mixed effects models describing the relationship between $\delta^{15}\text{N}$ and water depth for six trophic functional
 652 groups in the Canadian Beaufort region. Random effect structures allowed either intercept (b), slope (m), or both to vary by taxon.
 653 Goodness-of-fit was evaluated using the marginal (R_m^2) and conditional (R_c^2) coefficients of variation, which respectively describe the
 654 proportion of variance explained by depth alone and by depth and taxon together. An $R^2 \geq 0.63$ was considered a strong fit and is
 655 indicated in bold (Sullivan and Feinn, 2012). The estimated change in $\delta^{15}\text{N}$ (Δ) across the observed water depth range is given for
 656 well-fit models.
 657

Trophic functional group	<i>n</i> individuals	<i>n</i> taxa	Intercept (b)	Slope (m)	t	Goodness of fit		Random effects structure	Depth range (m)	Δ (%)
						R_m^2	R_c^2			
Benthopelagic carnivores	891	7	11.50 ± 0.36	0.67 ± 0.04	16.24	0.25	0.60	b	20 - 500	
Epifaunal carnivores	834	15	12.37 ± 0.55	0.59 ± 0.11	5.42	0.24	0.67	m, b	20 - 500	0.82
Infaunal carnivores*	39	4	14.77 ± 0.51						40 - 500	
Suspension/filter feeders	202	6	3.79 ± 1.43	1.30 ± 0.20	6.64	0.12	0.83	b	40 - 500	1.43
Epifaunal deposit feeders	177	4	12.24 ± 1.22	-0.12 ± 0.20	-0.60	0.22	0.89	b	40 - 500	-0.13
Infaunal deposit feeders	96	2	8.12 ± 1.48	1.03 ± 0.25	4.16	0.84	0.84	m, b	20 - 500	1.44

658
 659 *No model fit the infaunal carnivore data better than a null model with intercept as the only term (i.e., depth had little effect)
 660
 661

662 Table 3. Results of linear mixed effects models describing the relationship between $\delta^{15}\text{N}$ and water depth for those trophic groups that
 663 exhibited significantly different slopes in the Beaufort Sea and Amundsen Gulf. Random effect structures allowed either intercept (b),
 664 slope (m), or both to vary by taxon. Goodness-of-fit was evaluated using the marginal (R_m^2) and conditional (R_c^2) coefficients of
 665 variation, which respectively describe the proportion of variance explained by depth alone and by depth and taxon together. An $R^2 \geq$
 666 0.63 was considered a strong fit and is indicated in bold (Sullivan and Feinn, 2012). The estimated change in $\delta^{15}\text{N}$ (Δ) across the
 667 observed water depth range is given for well-fit models.
 668
 669

Functional Group	Region	<i>n</i> individuals	<i>n</i> taxa	Intercept (b)	Slope (m)	<i>t</i>	Goodness of fit		Random effects structure	Depth range (m)	Δ (‰)
							R_m^2	R_c^2			
Epifaunal carnivores	Beaufort Sea	536	15	11.97 ± 0.71	0.69 ± 0.15	4.67	0.20	0.70	m, b	20 - 500	0.96
	Amundsen Gulf	298	15	12.79 ± 0.79	0.58 ± 0.16	3.66	0.13	0.73	m, b	20 - 500	0.81
Suspension/filter feeders	Beaufort Sea	114	6	5.69 ± 1.11	0.84 ± 0.14	5.99	0.08	0.89	b	40 - 500	1.17
	Amundsen Gulf	88	6	5.62 ± 2.21	1.07 ± 0.36	2.99	0.04	0.81	b	40 - 500	1.50
Epifaunal deposit feeders	Beaufort Sea	97	4	15.19 ± 1.77	-0.63 ± 0.27	-2.23	0.06	0.93	b	40 - 500	-0.69
	Amundsen Gulf	80	4	14.42 ± 1.39	-0.26 ± 0.24	-1.10	0.02	0.84	b	40 - 500	-0.29
Infaunal deposit feeders	Beaufort Sea	53	2	8.13 ± 1.49	1.04 ± 0.25	4.14	0.61	0.61	b	75 - 500	1.45
	Amundsen Gulf	43	2	7.12 ± 1.24	1.37 ± 0.22	6.19	0.80	0.81	b	40 - 500	2.08

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