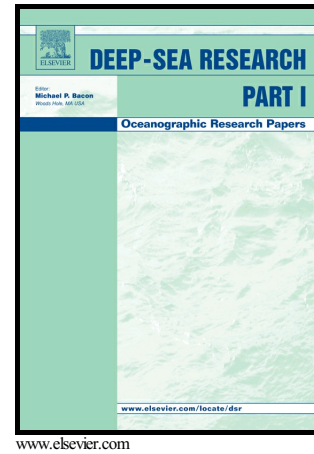


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Relationships between depth and $\delta^{15}\text{N}$ of Arctic benthos vary among regions and trophic functional groups

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ABSTRACT

Stable isotope ratios of nitrogen ($\delta^{15}\text{N}$) of benthic primary consumers are often significantly related to water depth. This relationship is commonly attributed to preferential uptake of ^{14}N from sinking particulate organic matter (POM) by microbes, and suggests that relationships between $\delta^{15}\text{N}$ and water depth may be affected by local POM sources and flux dynamics. We examined the relationships between $\delta^{15}\text{N}$ and water depth (20 to 500 m) for six trophic functional groups using a mixed effects modelling approach, and compared relationships

between two contiguous Arctic marine ecosystems with different POM sources and sinking export dynamics: the Canadian Beaufort Sea and Amundsen Gulf. We demonstrate for the first time in the Arctic that $\delta^{15}\text{N}$ values of mobile epifaunal carnivores increased as a function of depth when considered separately from benthopelagic and infaunal carnivores, which contrarily did not exhibit increasing $\delta^{15}\text{N}$ with depth. The $\delta^{15}\text{N}$ of suspension/filter feeders, infaunal deposit feeders and bulk sediment also increased with water depth, and the slopes of the relationships were steeper in the Amundsen Gulf than in the Beaufort Sea. We propose that regional differences in slopes reflect differences in POM sources exported to the benthos. In the Beaufort Sea, terrestrial POM discharged from the Mackenzie River quantitatively dominates the sedimentary organic matter across the continental shelf and slope, dampening change in $\delta^{15}\text{N}$ of benthic POM with depth. In the Amundsen Gulf, we attribute a faster rate of change in $\delta^{15}\text{N}$ of POM with increasing depth to larger contributions of marine-derived POM to the benthic sedimentary pool, which had likely undergone extensive biological transformation in the productive offshore pelagic zone. Differences in POM input regimes among regions should be considered when comparing food webs using stable isotopes, as such differences may impact the rate at which consumer $\delta^{15}\text{N}$ changes with depth.

Keywords: marine fish; benthic invertebrates; stable isotopes; water depth; Arctic; functional groups

1.0 INTRODUCTION

Deep-sea food webs at high latitudes are often characterized by two interlinked trophic pathways (e.g., Iken et al., 2001). 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 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, many studies in marine systems have documented that the $\delta^{15}\text{N}$ values of benthic suspension/filter feeders tend to increase as a function of water depth, 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). Together, these variable relationships between $\delta^{15}\text{N}$ and depth confound comparative analyses 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 al. 2007). Many benthic suspension feeders consume small particles (2 - 200 μm ; Riisgård and Larsen, 2010) that may include a mix of newly-arrived pelagic POM and re-suspended sedimentary POM. Longer residence times for small, slowly sinking particles in the water

column or in the bulk sediment pool result in generally higher $\delta^{15}\text{N}$ values than those of larger POM fractions (Mintenbeck et al. 2007). Indeed, organisms that consume larger ranges of particle sizes tend to exhibit weak $\delta^{15}\text{N}$ -depth relationships, presumably because their food has more intact biochemical compositions, consisting of faster-sinking POM (e.g. aggregates, zooplankton fecal pellets, algal mats) and/or benthic or benthopelagic prey (Mintenbeck et al., 2007; Bergmann et al., 2009; Roy et al., 2015). If particle characteristics drive $\delta^{15}\text{N}$ -depth relationships in benthic consumers, regional variation in water column processes that govern particle source, size, sinking flux, cross-shelf transport and transformation should underlie variation in the strength of the relationships observed among marine regions. To date, regional comparisons that link the strength of consumer $\delta^{15}\text{N}$ depth-relationships to POM source inputs and flux dynamics are lacking.

Identifying heterogeneity in $\delta^{15}\text{N}$ -depth relationships among trophic functional groups and/or species is important for benthic food web studies, because such differences may necessitate group- or taxon-specific isotopic baselines to be established prior to comparative studies of trophic enrichment (Papiol et al., 2013; Roy et al., 2015). Most studies that have quantified $\delta^{15}\text{N}$ -depth relationships at the functional group level have used linear regression (Mintenbeck et al., 2007; Bergmann et al., 2009; Roy et al., 2015), which is not ideal given the inherent non-independence of multi-species groups (Pinheiro and Bates, 2000; Zuur et al., 2009). A modelling approach that accounts for taxon-level variation can provide a more robust analysis of whether $\delta^{15}\text{N}$ -depth relationships may be considered characteristic of a trophic functional group. Further, primary feeding habitats may be important to consider within a given trophic functional group. Demersal carnivores are often treated as a single group in $\delta^{15}\text{N}$ -depth analyses (e.g., Bergmann et al., 2009; Roy et al., 2015) despite the fact that some taxa regularly consume

benthopelagic prey in addition to benthos. Since their primary consumer prey often exhibit significant $\delta^{15}\text{N}$ -depth relationships themselves, benthic predators may have increasing $\delta^{15}\text{N}$ with depth if they are considered separately from their benthopelagic counterparts.

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

2.0 METHODS

2.1 Study Area

Samples were collected in the southern Canadian Beaufort Sea and Amundsen Gulf (herein collectively referred to as the Canadian Beaufort region; Fig. 1) aboard the stern trawler FV *Frosti* as part of the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada, www.beaufortrea.ca). Despite being contiguous marine regions,

the Beaufort Sea and Amundsen Gulf exhibit significant differences in sediment characteristics (Morata et al., 2008), primary production regimes (Ardyna et al., 2013), and vertical flux of POM (O'Brien et al., 2006; Forest et al., 2010). Primary production is higher in the Amundsen Gulf than in the Beaufort Sea (Ardyna et al., 2013; Sallon et al., 2011), but export to the benthos is lower (O'Brien et al., 2006; Sallon et al., 2011). An estimated 70 to 95 % of autochthonous particulate organic carbon in the Amundsen Gulf is retained in the upper 100 m of the water column by the pelagic community, except in the vicinity of Cape Bathurst (Forest et al., 2010; Sampei et al., 2011). The Beaufort Sea shelf is strongly influenced by the Mackenzie River, which discharges $> 130 \times 10^6$ t of terrestrial sediment annually (Macdonald et al., 1998; Doxaran et al., 2015), exceeding that of any other Arctic River (Rachold et al., 2004). Consequently, > 70 % of the bulk organic matter pool in the Amundsen Gulf is comprised of marine-derived organic carbon, whereas that in the Beaufort Sea is comprised of > 50 % terrigenous organic carbon (Magen et al., 2010).

2.2 Sampling and Stable Isotope Analysis

Sampling took place from early August to late September of 2012 and 2013 along 8 transects that spanned the continental shelf and associated slope. Each sampling transect had five to eight pre-defined sampling stations at depths ranging from 20 to 500 m (Fig. 1). Demersal fish and epifaunal invertebrates were collected with a combination of two bottom trawl nets: a modified Atlantic Western IIA benthic otter trawl (12.7 mm cod end liner) and a 3 m High-Rise Benthic Beam Trawl (6.3 mm cod end liner) towed for 20 and 10 minutes bottom-contact time, respectively. Trawling was targeted at a speed-over-ground of 2.0 knots (1.81 to 2.35 acceptable range), and was monitored with a Scanmar CGM-05/TE40-2 trawleye sensor (Scanmar,

Åsgårdstrand, Norway). Sediments were collected with a 0.5 m² USNEL box core and the upper 25 cm were sieved through a 1 mm stainless steel mesh to retain infaunal invertebrates. A sample of bulk sediment from the top 1 cm was retained for stable isotope analysis and used as a reference for the composition of the bulk sedimentary organic matter pool. Biota were sorted to the lowest possible taxonomic resolution onboard with the help of taxonomists (L. De Montety, Université du Québec à Rimouski; W. Walkusz, Fisheries and Oceans Canada), rinsed with seawater, and frozen immediately along with the sediment samples at -50 °C. Taxonomy was standardized to the currently accepted names in the World Register of Marine Species (WoRMS Editorial Board 2016). Fish and macroinvertebrates were selected for stable isotope analysis across the observed range of body sizes to capture potential covariation between $\delta^{15}\text{N}$ and size (e.g., Stasko et al., 2016).

Bulk sediment and tissue samples dissected for stable isotope analysis were dehydrated in a standard laboratory convection oven at 50 °C (fish) or a FreeZone 18 freeze-drier (Labconco; invertebrates, sediment), then ground to homogenous powder and analysed for N isotopic composition using a Delta Plus continuous flow isotope spectrometer (Thermo-Finnigan) coupled to a 4010 Elemental Analyzer (Costech Instruments) at the University of Waterloo Environmental Isotopes laboratory (Waterloo, Canada). C isotopic composition was additionally analysed in samples of bulk sediment and invertebrates tissues that including exoskeleton following acidification with 10 % HCl to remove inorganic carbon (Jacob et al., 2005). Slow-turnover tissues were targeted for analysis, consistent with the literature and dissection constraints: dorsal muscle for fish, tail muscle for large decapods, and whole body for invertebrates that could not be reliably separated from exoskeleton (e.g., Dunton 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 notation as parts per

mil (‰) relative to the international standards atmospheric N_2 for nitrogen and Vienna Pee Dee Belemnite for carbon (Craig, 1957; Mariotti, 1983). Analytical error for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ never exceeded 0.3 and 0.2 ‰, respectively, based on repeated measurements of working laboratory standard materials cross-calibrated to the international standards. Repeatability of duplicate measurements of sample material was 0.3 ‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Stable isotope values for all taxa and sediments, averaged by region and depth, are available in Stasko et al. (2017; open access).

2.3 Statistical Analyses

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

Taxa were delineated into six trophic functional groups based on published trophic marker data and feeding observations (Stasko et al. *unpublished*). We defined trophic functional groups as taxa that employ similar feeding strategies and may utilize similar food types. Trophic group classification followed systems proposed by Macdonald et al. (2010) and Jumars et al. (2015) using trophic traits, and included: (1) benthopelagic carnivores that are highly mobile and feed both at and above the seafloor as predators, scavengers, or both; (2) epifaunal carnivores that are mostly mobile and feed at the sediment surface as predators, scavengers, or both; (3)

infaunal carnivores that prey on fauna below the sediment surface (in this study, all are predatory marine worms); (4) suspension/filter feeders that live on the seafloor and feed omnivorously on fresh or resuspended POM filtered from the water; (5) epifaunal deposit feeders that feed omnivorously at the sediment surface on deposited material that can include decomposed carcasses and zooplankton molts, phytodetritus, recycled organic matter, bacteria, or bacterial products; and, (6) infaunal deposit feeders that feed omnivorously below the sediment surface on detritus and/or bacteria and bacterial products. (e.g., Coad and Reist, 2004; Macdonald et al., 2010; Weśławski et al., 2010; Jumars et al., 2015). Facultative suspension/deposit feeders that switch between feeding modes were excluded to avoid unquantified variation.

Given evidence of non-independence as suggested by clustering within taxonomic groups (see *Supplementary Material*), linear mixed effects were used to investigate relationships between $\delta^{15}\text{N}$ and the fixed factor water depth for all individuals within each trophic functional group. The approach directly considers taxon-level variation within a functional group by allowing the intercept and/or slope to vary randomly by taxon to account for non-independence (Pinheiro and Bates, 2000). To assess whether relationships between $\delta^{15}\text{N}$ and water depth differed between the Beaufort Sea and Amundsen Gulf, an interaction term between depth and region was included in the models. Model selection between random effect structures (slope, intercept, or both) was conducted using likelihood ratio tests after model fitting with a maximum likelihood procedure (Zuur et al., 2009; Bates et al. 2015). Likelihood ratio tests were then used to assess whether the interaction between water depth and region improved fit, and if not the interaction term was dropped from the model. To more closely examine regional differences, models were fit individually for the Beaufort Sea and Amundsen Gulf for those trophic functional groups that displayed both a strong relationship between $\delta^{15}\text{N}$ and water depth, and a

significant interaction between water depth and region. Finally, the best model in all cases was refit using a restricted maximum likelihood procedure for parameter reporting (Zuur et al., 2009). Goodness-of-fit was evaluated using the marginal and conditional coefficients of determination (R_m^2 and R_c^2), which, respectively, describe the proportion of variance explained by the fixed effects alone, and the fixed and random effects combined (Nakagawa and Schielzeth, 2013). Following Sullivan and Feinn (2012), an $R_c^2 \geq 0.63$ was considered strong and indicative of a well-fit model. Effect size for well-fit models was considered the average change in $\delta^{15}\text{N}$ (Δ) estimated for the trophic functional group across the entire depth gradient. Relationships between sediment $\delta^{15}\text{N}$ and water depth were assessed with least squares linear regression. In all cases, assumptions of homogeneity of variance and normality of errors were assessed with a series of residual plots, and depth was log-transformed where it improved linearity (Zuur et al., 2009). Where residual variance increased as a function of depth (epifaunal and infaunal deposit feeders), linear mixed effects models included a fixed variance structure (Zuur et al., 2009; Pinheiro et al., 2016). Linear regression and likelihood ratio tests were considered significant at $\alpha = 0.05$.

We estimated the error introduced to trophic level calculations when a common baseline is applied across depths despite increasing consumer $\delta^{15}\text{N}$. Error was evaluated for a change in consumer $\delta^{15}\text{N}$ of up to 2 ‰, reflecting the maximum average within-group change across depth observed in this study. Trophic levels were calculated using the average $\delta^{15}\text{N}$ of sedimentary POM from sites < 40 m deep in the Beaufort Sea as a baseline (3.42 ‰), according to Hussey et al. (2014; although we caution the model was created primarily with fish data).

The isotopic composition of sedimentary organic matter in the Canadian Beaufort region is influenced by three primary sources: terrestrial, fresh marine, and refractory marine organic

matter (Magen et al., 2010). To verify that the composition of sedimentary POM differed between the Beaufort Sea and Amundsen Gulf, as previously reported (Morata et al., 2008; 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of representative terrestrial, fresh marine, and refractory marine source data taken from the literature. The terrestrial source data were based on organic material recovered from the Mackenzie and Colville River Deltas ($\delta^{15}\text{N} = 1.0 \text{ ‰}$, $\delta^{13}\text{C} = -27.0 \text{ ‰}$; as estimated by Magen et al., 2010 from various studies). The refractory marine source data were taken from Amundsen Gulf sediments, where pigment analyses indicated the presence of highly degraded marine POM ($\delta^{15}\text{N} = 6.7 \text{ ‰}$, $\delta^{13}\text{C} = -21.1 \text{ ‰}$; Morata et al., 2008). For fresh marine sources we averaged $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measured in pelagic POM collected from the chlorophyll maximum depth at our sampling sites in the Amundsen Gulf in 2013 (C. Michel, unpublished data), combined with pelagic POM values from the eastern Beaufort Sea and Amundsen Gulf slope reported by Roy et al. (2015). The resulting values ($\delta^{15}\text{N} = 5.6 \text{ ‰}$, $\delta^{13}\text{C} = -26.5 \text{ ‰}$) fall within the range reported for summer across the Canadian Beaufort region by Morata et al. (2008). Some sites in the Amundsen Gulf were excluded as outliers due to anomalous $\delta^{13}\text{C}$ ($> \text{median} + \text{interquartile range}$).

All statistical and graphical procedures were performed in R (ver. 3.3.1, R Core Team, 2016) using the packages lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2016), peicewiseSEM (Lefcheck, 2015), ggplot2 (Wickham, 2009), ggtern (Hamilton, 2016) and plyr (Wickham, 2011).

3.0 RESULTS

Linear mixed effects models indicated $\delta^{15}\text{N}$ was strongly related to depth for epifaunal carnivores, suspension/filter feeders, epifaunal deposit feeders and infaunal deposit feeders, but not for benthopelagic or infaunal carnivores (Table 2). The slope of the relationship was positive and steepest for suspension/filter feeders and infaunal deposit feeders, followed by epifaunal carnivores (Fig. 2, Table 2). The estimated increase in $\delta^{15}\text{N}$ for these groups between 20 and 500 m depths ranged between 0.82 and 1.44 ‰ (Table 2). Epifaunal deposit feeder $\delta^{15}\text{N}$ was strongly negatively related to depth, but had the shallowest slope of all trophic functional groups when both regions were considered together (Table 2). There were no strong associations between $\delta^{15}\text{N}$ and water depth for benthopelagic and infaunal carnivores (Table 2). Plots of $\delta^{15}\text{N}$ versus water depth are available in the Supplementary Material for all trophic functional groups and taxa.

Applying a common baseline to calculate trophic levels resulted in over-estimations of almost an entire trophic level when the $\delta^{15}\text{N}$ of hypothetical organisms at trophic level 5 changed by 2 ‰. Error in trophic level estimations decreased with decreasing trophic level (Fig. 3).

For those trophic functional groups that displayed a strong relationship between $\delta^{15}\text{N}$ and depth (Table 2), a model that included an interaction term between water depth and region (Beaufort Sea vs. Amundsen Gulf) fit the data significantly better than a model with no interaction (likelihood ratio tests; $p < 0.01$ for epifaunal carnivores, suspension/filter feeders, epifaunal deposit feeders, and infaunal deposit feeders). In other words, the slopes of the $\delta^{15}\text{N}$ -depth relationships were significantly different between the Beaufort Sea and Amundsen Gulf. Slopes were steeper in the Amundsen Gulf for suspension/filter feeders and infaunal deposit feeders, whereas slopes were steeper in the Beaufort Sea for epifaunal carnivores and epifaunal deposit feeders (Table 3, Fig. 2). When fit for individual regions, infaunal deposit feeders

displayed the largest increase in $\delta^{15}\text{N}$ of any group, albeit based on two taxa (Table 3). Including taxon as a random variable (R_c^2) explained an additional >40 % of the variance relative to depth alone (R_m^2) for all groups except infaunal deposit feeders (Table 2, Table 3). Including all available taxa in analyses (i.e., not restricting taxa assemblages to be identical in both regions) did not reveal any differences between which trophic functional groups displayed strong $\delta^{15}\text{N}$ -depth relationships, but did increase the strength of fit (data not shown).

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

4.0 DISCUSSION

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 epifaunal carnivores can also increase as a function of depth. The rate of change in consumer $\delta^{15}\text{N}$ with depth differed between two contiguous Arctic marine regions as predicted. Below, we discuss potential mechanisms underlying $\delta^{15}\text{N}$ -depth relationships for all trophic functional

groups studied, and propose that regional differences in $\delta^{15}\text{N}$ -depth relationships may be linked to heterogeneity in POM input and vertical flux properties.

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

The significant, positive effect of water depth on the $\delta^{15}\text{N}$ values of suspension/filter feeders, infaunal deposit feeders, and sediment is likely linked to the transformation of POM during sinking, as suggested by others (Mintenbeck et al., 2007; Galloway et al., 2013). Summer maximum chlorophyll *a* concentrations in the Canadian Beaufort Sea and Amundsen Gulf occur deeper than in other oceans, between ~ 40 to 60 m depths (Carmack et al., 2004; Ardyna et al., 2013). As a result, fresh, relatively untransformed phytodetritus is more accessible to benthos in shallow habitats than in deep habitats. Marine-derived POM received by benthos in deeper habitats is subject to longer periods of dissolution, physical disaggregation, and microbial consumption in the water column (Smith et al., 1992; Kiørboe et al., 2001). There appear to be two vertical zones of elevated biological activity in the Beaufort Sea and Amundsen Gulf that would promote the degradation, remineralization, and recycling of POM (Kiørboe et al., 2001). The primary zone is the euphotic layer, as with most oceans, where the majority of POM synthesized during the spring bloom is consumed by heterotrophic zooplankton and bacteria (Sampei et al., 2011). The second is the transition from nutrient-rich Pacific-origin water to warmer Atlantic-origin water around 200 to 350 m depths near the upper continental slope (McLaughlin et al., 1996). Here, the hyperbenthic habitat appears to be a hotspot for organic matter transformation and interception via large aggregations of zooplankton and predatory benthopelagic fish (Crawford et al., 2012; Majewski et al., 2017), which may be linked to low POM export below 200 m (Forest et al., 2015). With little fresh marine-derived POM reaching

the seafloor along the upper slope, benthic primary consumers would be limited to ^{15}N -enriched POM that has either been recycled among the benthos and sedimentary bacteria (e.g., North et al., 2014; Bell et al., 2016), or resuspended and advected downslope by upwelling/downwelling events characteristic of the Beaufort Sea shelf-break (Forest et al., 2007).

In contrast to suspension and infaunal deposit feeders, epifaunal deposit feeder $\delta^{15}\text{N}$ did not change strongly with depth. Differing trends in the $\delta^{15}\text{N}$ -depth relationships between epifaunal and infaunal deposit feeding groups is unintuitive, but may be explained by differences in trophic flexibility. Epifaunal taxa that feed omnivorously at the sediment surface can be more trophically flexible than infaunal taxa, both in terms of food source and particle size (e.g., North et al. 2014). Such trophic flexibility was supported by the increasing variance of $\delta^{15}\text{N}$ within individual epifaunal deposit-feeding taxa with water depth, especially for the asteroid *Pontaster tenuispinus* (see Suppl. Material). Although epifaunal deposit feeders primarily rely on accumulated sedimentary organic matter (e.g., Minks et al. 2005), they can respond quickly to the availability of other foods, including sunken algal mats released from sea ice, seasonal pulses of sedimented phytoplankton, sedimentary bacterial abundances, or even occasional predation (e.g., McMahon et al., 2006; Renaud et al., 2007; Bergmann et al., 2009; Gale et al., 2013). Conversely, the two infaunal deposit feeding taxa examined here extract nutrition directly from ingested sediment at deeper layers (MacDonald et al., 2010). Infauna with similar feeding habits have been observed to exploit more consistent fractions of bulk sedimentary organic matter than their epifaunal counterparts (North et al., 2014), perhaps partly because epifauna consume some of the more variable fractions of organic matter before it is bioturbated to deeper sediment layers. Infaunal deposit feeder $\delta^{15}\text{N}$ values would therefore be expected to reflect the of bulk sedimentary organic matter more closely than those of epifaunal deposit feeders.

Water depth is thought to have a weaker effect on the $\delta^{15}\text{N}$ of mobile carnivorous predators and scavengers than on primary consumers because the former can feed on both benthic and benthopelagic prey (Bergmann et al., 2009; Roy et al., 2015). Our findings suggest the relationships between $\delta^{15}\text{N}$ and depth differ when carnivores are analysed separately by their primary feeding habitat. The positive trend between epifaunal carnivore $\delta^{15}\text{N}$ and water depth might be a consequence of feeding on ^{15}N -enriched benthic prey at depth. For example, suspension feeders are an important prey for many of the taxa in this trophic group (e.g., Birkely and Gulliksen, 2003; Coad and Reist, 2004). Epifaunal predators may be more reliant on benthic prey on the continental slope of the Beaufort Sea region because vertically migrating pelagic prey, such as zooplankton, are intercepted by large aggregations of benthopelagic predators (e.g., Arctic Cod *Boreogadus saida*; Crawford et al., 2012; Majewski et al., 2017). Notably, infaunal carnivore $\delta^{15}\text{N}$ values did not reflect those of the infaunal deposit feeders that may comprise an important part of their prey base. The infauna are the most data-poor trophic groups in this study (2 and 4 taxa for infaunal deposit and carnivore groups, respectively; $n < 100$ individuals for each group). Without additional dietary information it is difficult to estimate the importance of infaunal deposit feeders to the diets of infaunal carnivores examined in this study. Regardless of the cause, the different $\delta^{15}\text{N}$ -depth relationships among the three carnivore groups highlight variation in the use of benthic and pelagic trophic pathways. Benthopelagic carnivores subsidize their diets with pelagic prey (e.g., Bjelland et al., 2000; Cui et al., 2012) and are not restricted to benthic resources that have undergone depth-related ^{15}N enrichment. Consequently, we recommend considering carnivorous trophic groups separately in food web analyses rather than pooling them as one group.

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

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

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

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

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

Epifaunal carnivores were the only trophic group with a positive $\delta^{15}\text{N}$ -depth relationship that was slightly steeper in the Beaufort Sea than in the Amundsen Gulf. The difference appeared to be most influenced by a few taxa, including the generalist-feeding fishes Atlantic Poacher (*Leptagonus decagonus*), Gelatinous Eelpout (*Liparis fabricii*), and Canadian Eelpout (*Lycodes polaris*; Coad and Reist, 2004; Giraldo et al., 2016). Some generalist benthic fishes can switch feeding strategies to take advantage of benthopelagic prey when benthic resources are scarce (e.g., Carrassón and Cartes, 2002), which could explain the flatter $\delta^{15}\text{N}$ -depth relationships observed in the Amundsen Gulf for these fishes. However, there is little evidence for such a shift according to $\delta^{13}\text{C}$ (see data in Stasko et al., 2017). Without further diet information, the flatter $\delta^{15}\text{N}$ -depth relationships of these fish species in the Amundsen Gulf remain difficult to explain.

Conclusions and considerations

Results presented here are relevant to studies that take a functional group approach to marine food web analyses, but must be interpreted in light of data limitations. Our dataset is comprehensive, but many taxa occurred across a limited depth range, and some occurred along a limited number of transects (Table 1). Any trophic functional group is, therefore, influenced by the taxa included in the analysis. The importance of taxon-level variation was underscored by the fact that including taxon as a random variable in the models consistently explained an additional > 40 % of variance ($R^2_c > R^2_m$).

Despite the limitations, we confirm previously documented positive relationships between benthic consumer $\delta^{15}\text{N}$ and water depth. In the Beaufort Sea and Amundsen Gulf, the relationships were characteristic of three benthic trophic functional groups: epifaunal carnivores, suspension/filter feeders, and infaunal deposit feeders. We agree with other authors that a depth-

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

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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 (m)		Transects
			Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
Benthopelagic carnivore							
Arthropoda	<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

Phylum	Taxon	Plot ID #	Sample size		Depth range (m)		Transects
			Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
Chordata	<i>Gymnocanthus tricuspis</i>	6	49	16	20 - 200	40 - 75	dar, ulu a1, dal, kug, gry, tbs, dar a1, kug, gry, tbs, cbh,
Chordata	<i>Icelus bicornis</i>	7	64	44	40 - 200	40 - 275	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 kug, cbh,
Chordata	<i>Lycodes pallidus</i>	10	4	21	40 - 500	200 - 350	dar, ulu dal, kug, gry, dal, kug, gry gry, dal
Chordata	<i>Lycodes polaris</i>	11	23	11	20 - 200	40 - 75	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 a1, tbs, gry, cbh, dar, ulu
Echinodermata	<i>Heliometra glacialis</i>	14	47	45	40-350	75-350	dal, 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</i>	17	39	10	40 - 75	75	gry, tbs,

Phylum	Taxon	Plot ID #	Sample size		Depth range (m)		Transects
			Beaufort Sea	Amundsen Gulf	Beaufort Sea	Amundsen Gulf	
	<i>greenlandicus</i>						dar
Mollusca	Thyasiridae*	18	13	9	75 - 500	200 - 500	dal, kug, gry, cbh , dar , ulu
Epifaunal deposit feeder							
Annelida	Ampharetidae	19	11	11	350 - 500	200 - 500	dal, kug, gry, tbs, cbh , dar , ulu
Arthropoda	<i>Synidotea</i> spp.	20	17	23	40 - 75	40 - 300	tbs, cbh
Echinodermata	<i>Ctenodiscus crispatus</i>	21	6	25	200	75 - 350	dal, cbh , dar , ulu
Echinodermata	<i>Pontaster tenuispinus</i>	22	63	21	75 - 500	200 - 500	a1, dal, kug, gry, tbs, cbh , dar
Infaunal deposit feeder							
Annelida	<i>Maldane</i> spp.	23	34	24	75 - 500	40 - 500	dal, kug, gry, tbs, cbh , dar , ulu
Echinodermata	<i>Molpadia</i> sp.	24	19	19	350 - 500	350 - 500	dal, kug, gry, tbs, dar , ulu

*Thyasiridae can derive nutrition from chemosynthetic sulfur-oxidizing bacteria in addition to suspended POM (Dando and Spiro, 1993). The $\delta^{13}\text{C}$ values of Thyasiridae individuals included in this study indicated, however, that they were heterotrophic. See *Supplementary Material, Appendix B*.

Table 2. Results of linear mixed effects models describing the relationship between $\delta^{15}\text{N}$ and water depth for six trophic functional groups in the Canadian Beaufort region. Random effect structures allowed either intercept (b), 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 variation, which respectively describe the 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 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 well-fit models.

Trophic functional group	n individuals	n taxa	Intercept (b)	Slope (m)	t	Goodness of fit		Random effects	Depth range (m)	Δ (‰)
						R_m^2	R_c^2			

Infaunal deposit feeders	Beaufort			$8.13 \pm$	$1.04 \pm$	4.1	0.6	0.6		75 -	1.4
	Sea	53	2	1.49	0.25	4	1	1	b	500	5
	Amundsen			$7.12 \pm$	$1.37 \pm$	6.1	0.8	0.8		40 -	2.0
	Gulf	43	2	1.24	0.22	9	0	1	b	500	8

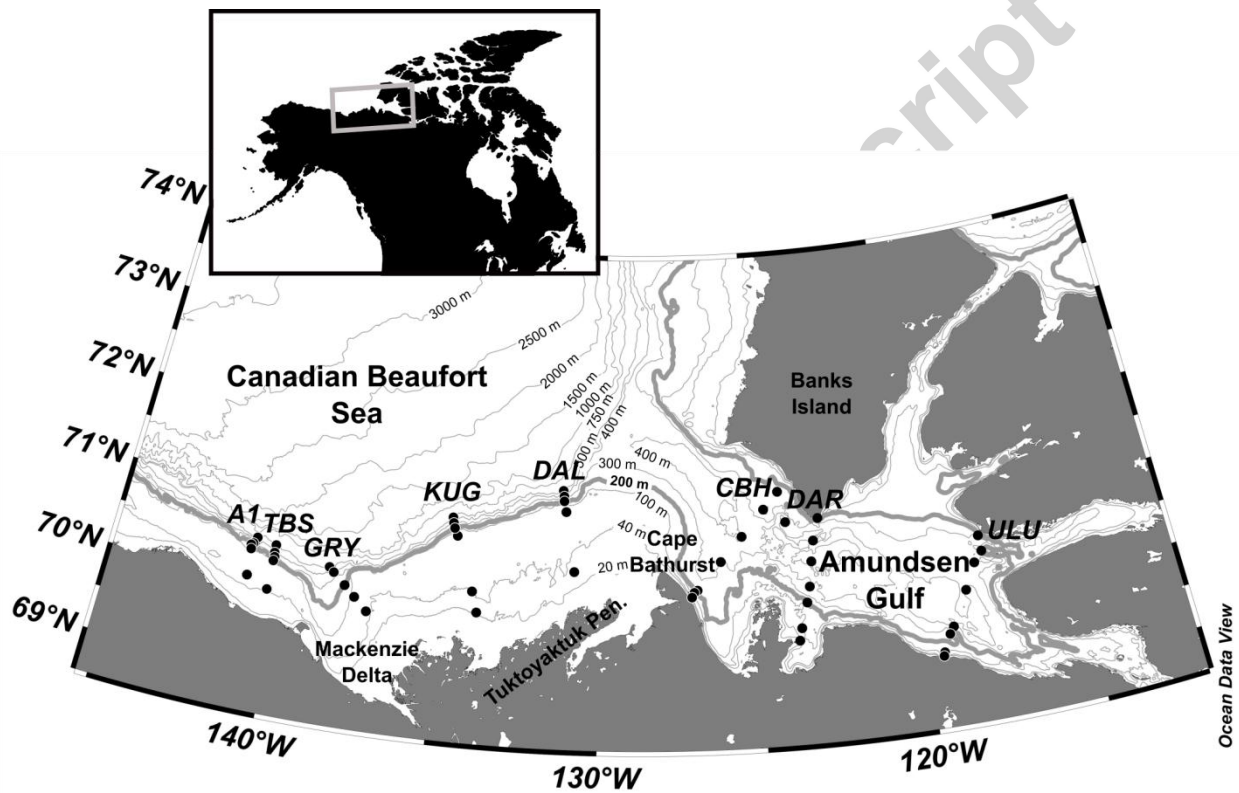


Fig. 1. Map of sampling station locations (black circles) along 8 transects in the Canadian Beaufort Sea (A1, TBS, GRY, KUG, DAL) and Amundsen Gulf (CBH, DAR, ULU). The 200 m isobath that defines the continental shelf break is shown bolder than other isobaths. Map was created using Ocean Data View 4.

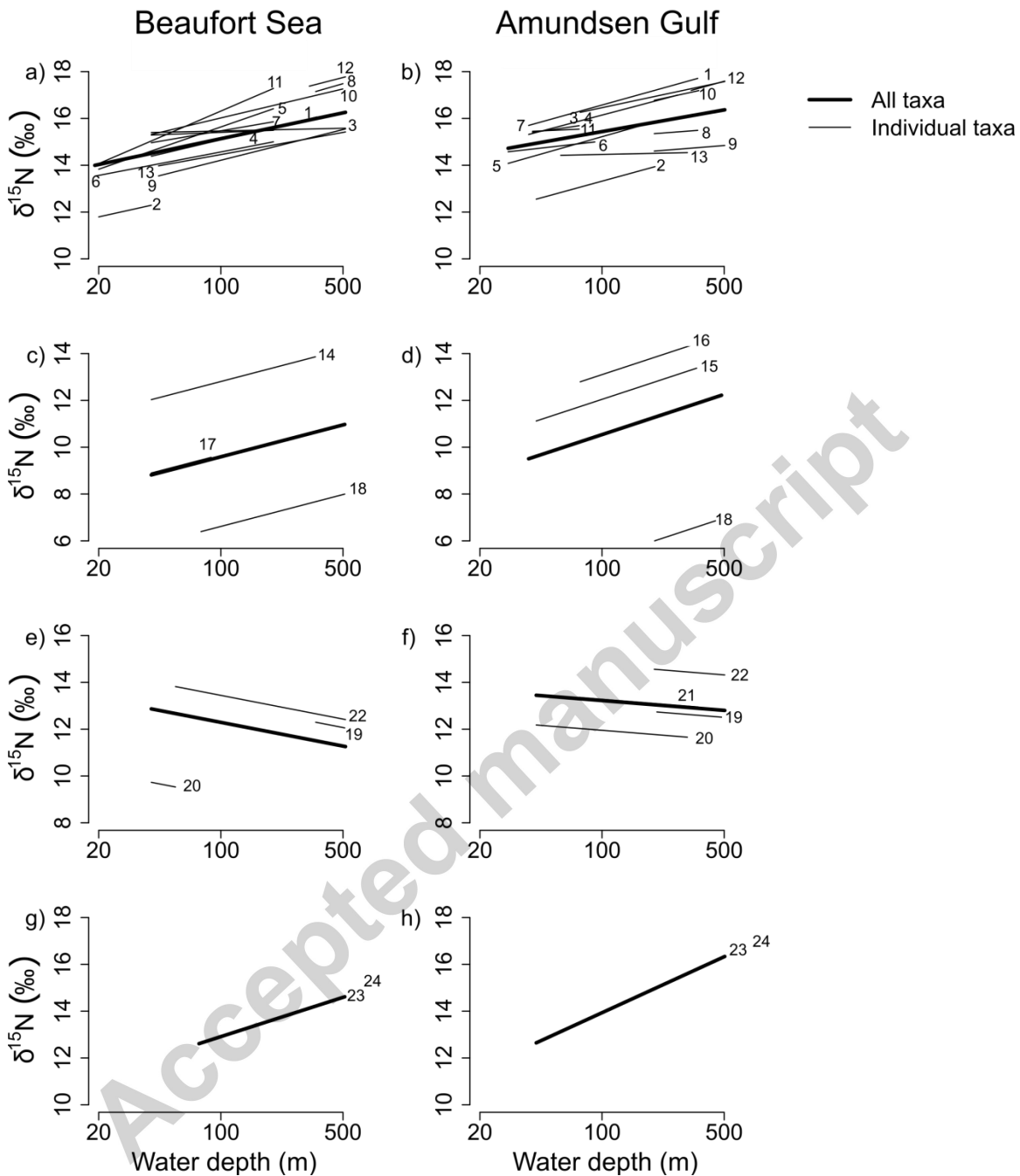


Fig. 2. Relationships between $\delta^{15}\text{N}$ (‰) and log water depth (m) for epifaunal carnivores (a, b), suspension/filter feeders (c, d), epifaunal deposit feeders (e, f) and infaunal deposit feeders (g, h) in the Beaufort Sea and Amundsen Gulf. Relationships estimated from linear mixed effects models for the entire functional group are shown in bold lines, whereas those for individual taxa are shown in thin lines. Separate intercepts were estimated for each taxon in all cases, but were almost identical for the two infaunal deposit feeders (g, h). Separate slopes were estimated for epifaunal carnivore taxa (a, b). Taxa are numbered according to Table 1 on either the leftmost or rightmost extent of the regression line, whichever provided more visual clarity.

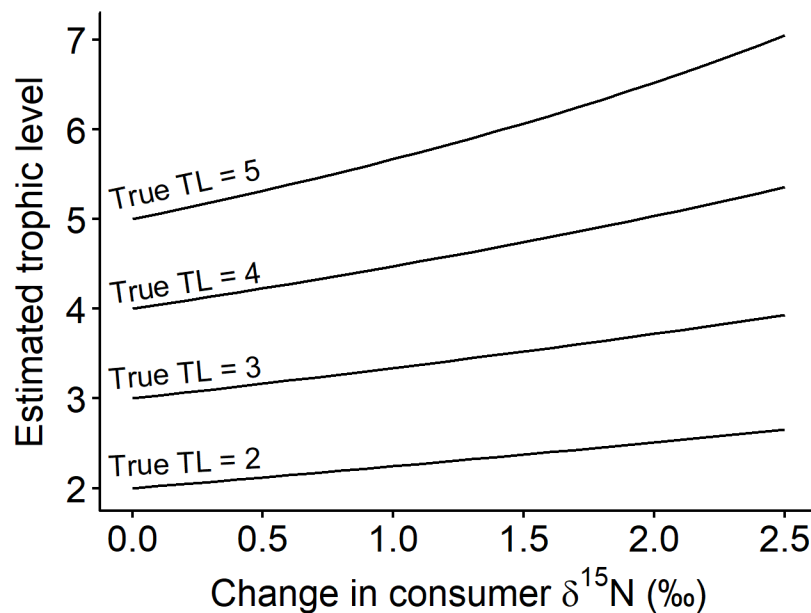


Fig. 3. Error in the trophic levels estimated for hypothetical animals that exhibit increasing $\delta^{15}\text{N}$ values, if a common baseline is used to make trophic level calculations. Trophic levels were calculated using the average $\delta^{15}\text{N}$ of sedimentary POM from sites < 40 m deep in the Beaufort Sea as a baseline (3.42 ‰), according to a scaled model that accounts for narrowing stepwise ^{15}N enrichment with increasing trophic level (Hussey et al., 2014). The error introduced to trophic level calculations is larger for upper-trophic animals than for lower-trophic animals.

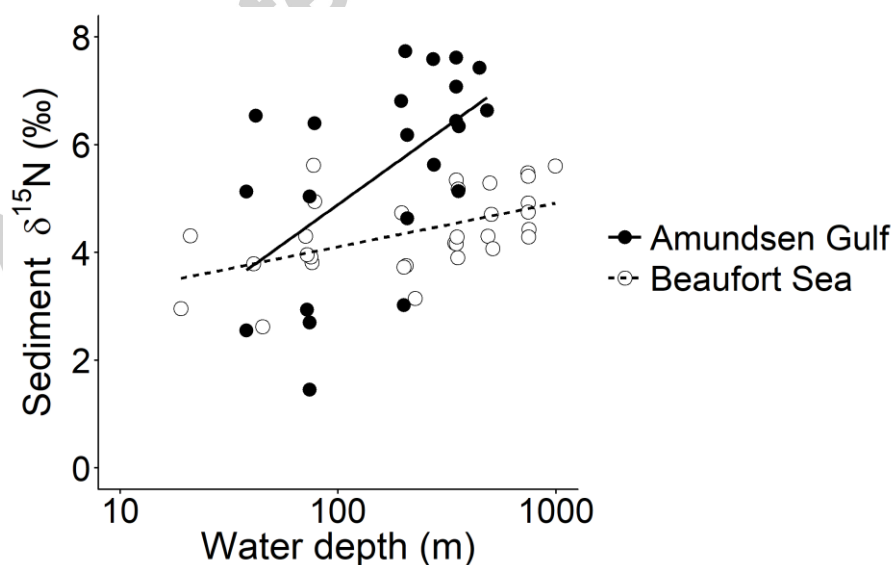


Fig. 4. Regressions of $\delta^{15}\text{N}$ (‰) against log water depth (m) from sediment sampled in the Beaufort Sea (white circles, dashed line; $\delta^{15}\text{N} = 2.5 + 0.35x$, $r^2 = 0.3$) and the Amundsen Gulf (black circles, solid line; $\delta^{15}\text{N} = -0.7 + 1.2x$, $r^2 = 0.2$). Sediment $\delta^{15}\text{N}$ was significantly positively related to depth in both regions, but the slope of the relationship was significantly greater in the Amundsen Gulf.

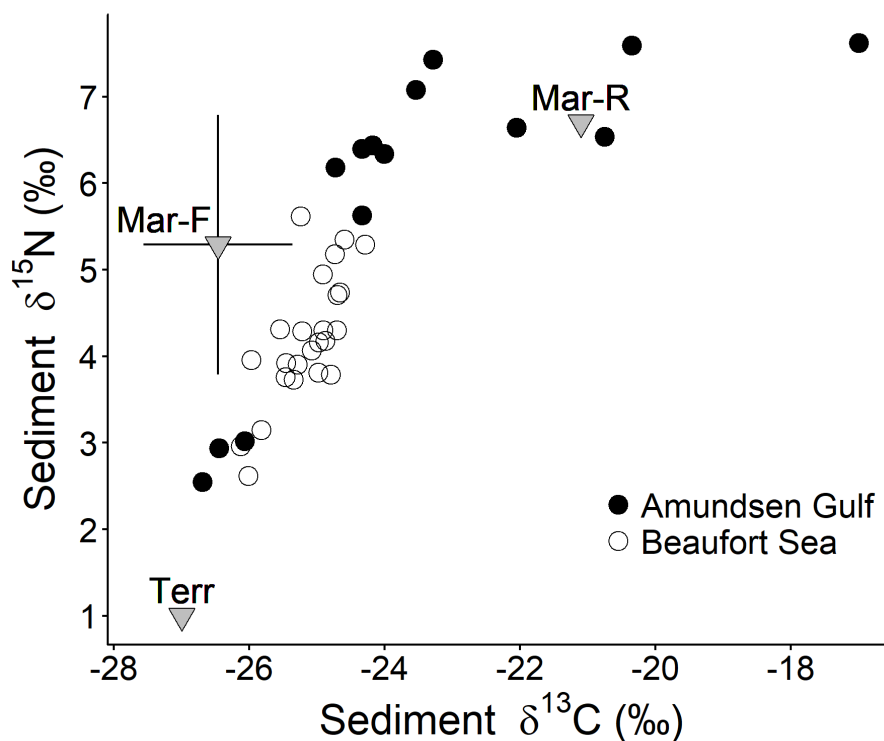


Fig. 5. Bulk sediment $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from the Beaufort Sea (filled black circles) and Amundsen Gulf (open circles), relative to terrestrial (Terr), fresh marine (Mar-F), and refractory marine (Mar-R) isotopic sources (grey triangles). Terrestrial source data were estimated by Magen et al. (2010) from samples from the Colville and Mackenzie River deltas. Refractory marine source data were taken from Amundsen Gulf sediments composed of highly degraded marine POM (Morata et al., 2008). Fresh marine source data were estimated from pelagic POM collected in the Amundsen Gulf and Beaufort Shelf from our sampling program (C. Michel, unpublished data) and from data reported by Roy et al. (2015). Error bars indicate standard deviation for the fresh marine source. Variation associated with terrestrial and refractory marine sources was not available. Sediments in the Beaufort Sea were more influenced by terrestrial organic matter inputs compared to those in Amundsen Gulf which were more influenced by fresh and refractory marine organic matter at deeper stations.

HIGHLIGHTS

- Arctic marine suspension and infaunal deposit feeder $\delta^{15}\text{N}$ increased with water depth
- Contrary to previous Arctic work, benthic carnivore $\delta^{15}\text{N}$ also increased with depth
- Slopes of $\delta^{15}\text{N}$ -depth relationships differed between two contiguous Arctic regions
- Regional differences are attributed to organic matter source and flux regimes
- Highlights variation in benthic/pelagic trophic pathway use among and within groups

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