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

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ABSTRACT

Significant relationships between the stable isotope ratios of nitrogen (δ¹⁵N) of benthic primary consumers and water depth are commonly attributed to the preferential uptake of ¹⁴N from sinking particulate organic matter (POM) by microbes. Such a mechanism suggests the relationships may be affected by local POM sources and flux dynamics. We examined the relationships between δ¹⁵N 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 δ¹⁵N values of mobile epifaunal carnivores increased as a function of depth when considered apart from benthopelagic and infaunal carnivores. The δ¹⁵N 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 regional differences in slopes reflect the prevalent 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 δ¹⁵N of benthic POM with depth. In the Amundsen Gulf, a faster rate of change in benthic POM δ¹⁵N with depth was linked to increasing 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 δ¹⁵N changes with depth.
1.0 INTRODUCTION

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 ($\delta^{15}$N; e.g., Roy et al., 2015). Consumers are generally enriched in $^{15}$N relative to their food, so that higher values of $\delta^{15}$N are taken to indicate higher relative trophic positions (Minagawa and Wada, 1984). However, the $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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
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 of such small, slowly sinking particles in the water column or in the bulk sediment pool result in generally higher δ¹⁵N values than those of larger POM fractions (Mintenbeck et al. 2007). Organisms that consume larger ranges of particle sizes tend to exhibit weak δ¹⁵N-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 animals (Mintenbeck et al., 2007; Bergmann et al., 2009; Roy et al., 2015). If particle characteristics drive δ¹⁵N-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 δ¹⁵N-depth-relationships to POM source inputs and flux dynamics are lacking.

Identifying heterogeneity in δ¹⁵N-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 for calculating and comparing trophic enrichment (Papiol et al., 2013; Roy et al., 2015). Most studies quantifying δ¹⁵N-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 δ¹⁵N-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 δ\textsuperscript{15}N-depth analyses (e.g., Bergmann et al., 2009;
Roy et al., 2015) despite the fact that some regularly consume benthopelagic prey in addition to
benthos. Since their primary consumer prey often exhibit significant δ\textsuperscript{15}N-depth relationships
themselves, benthic predators may have increasing δ\textsuperscript{15}N with depth if they are considered
separately from their benthopelagic counterparts.

Here, we examined relationships between δ\textsuperscript{15}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. POM sources and flux dynamics differ significantly
between 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 δ\textsuperscript{15}N as a function of water depth in each
region using a linear mixed-modelling approach that allows for taxon-level variation within a
functional group (Pinheiro and Bates, 2000). Secondarily, we assessed whether consumer δ\textsuperscript{15}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, δ\textsuperscript{15}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 x 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 towed for 20 minutes (12.7 mm cod end liner) and a 3 m High-Rise Benthic Beam Trawl towed for 10 minutes (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 δ¹⁵N 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 a 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 bulk sediment samples 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 ($^{15}$N:$^{14}$N, $^{13}$C:$^{12}$C) were expressed in δ notation as parts per thousand (‰) relative to the international standards atmospheric N$_2$ for nitrogen and Vienna Pee Dee Belemnite for carbon (Craig, 1957; Mariotti, 1983). Analytical error for δ$^{15}$N and δ$^{13}$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 δ$^{15}$N and δ$^{13}$C. Stable isotope values for all taxa and sediments, averaged by region and depth, are available, open access, in Stasko et al. (2017).

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 the secondary 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, but may not necessarily compete with one another. 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; Węsławski et al., 2010; Jumars et al., 2015).

Facultative suspension/deposit feeders that switch between feeding modes were excluded to avoid unquantified variation.

Some taxa formed clear groups with conspecifics in preliminary plots of $\delta^{15}$N versus depth, suggesting non-independence (see Supplementary Material). Linear mixed effects models were thus used to investigate relationships between $\delta^{15}$N and the fixed factor water depth for each trophic functional group, 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 $\delta^{15}$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 δ¹⁵N
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 (R²ₘ and R²ₑ), 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 R²ₑ ≥ 0.63 was
considered strong and indicative of a well-fit model. Effect size for well-fit models was
considered the average change in δ¹⁵N (Δ) estimated for the trophic functional group across the
entire depth gradient. Relationships between sediment δ¹⁵N 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 α = 0.05. We estimated the error introduced to trophic level
calculations when a common baseline is applied across a change in consumer δ¹⁵N of up to 2 ‰,
as observed in this study. Trophic levels were calculated using the average δ¹⁵N 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 $\delta^{15}$N and $\delta^{13}$C of bulk sediments at each site were plotted relative to the $\delta^{15}$N and $\delta^{13}$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 ($\delta^{15}$N = 1.0 ‰, $\delta^{13}$C = -27.0 ‰; estimated from various studies by Magen et al., 2010). The refractory marine source data were taken from Amundsen Gulf sediments, where pigment analyses indicated the presence of highly degraded marine POM ($\delta^{15}$N = 6.7 ‰, $\delta^{13}$C = -21.1 ‰; Morata et al., 2008). Source values for fresh marine organic matter were more difficult to assign due to high spatial and seasonal variation in the isotopic composition of primary producers (Morata et al., 2008). Consequently, we averaged $\delta^{15}$N and $\delta^{13}$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 fresh marine source values ($\delta^{15}$N = 5.6 ‰, $\delta^{13}$C = -26.5 ‰) fall within the range reported for summer across the Canadian Beaufort region by Morata et al. (2008; $\delta^{15}$N = 1.0 to 7.0 ‰, $\delta^{13}$C = -27.0 to -21.0 ‰). Some sites in the Amundsen Gulf were excluded as outliers due to anomalous $\delta^{13}$C (> median + 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
Linear mixed effects models indicated $\delta^{15}$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 $\delta^{15}$N for these groups between 20 and 500 m depths ranged between 0.82 and 1.44 ‰ (Table 2). Epifaunal deposit feeder $\delta^{15}$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 $\delta^{15}$N and water depth for benthopelagic and infaunal carnivores (Table 2). Plots of $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$N of any group, albeit based on two taxa (Table 3). Including taxon as a random variable ($R^2_c$) explained an additional >40% of the variance relative to depth alone ($R^2_m$) 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 $\delta^{15}$N-depth relationships, but did increase the strength of fit (data not shown).

Bulk sediment $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$N and $\delta^{13}$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 $\delta^{15}$N of
epifaunal carnivores can also increase as a function of depth. The rate of change in consumer
δ¹⁵N with depth differed between two contiguous Arctic marine regions as predicted. Below, we
discuss potential mechanisms underlying δ¹⁵N-depth relationships for all trophic functional
groups studied, and propose that regional differences in δ¹⁵N-depth relationships may be linked
to heterogeneity in POM input and vertical flux properties.

Differences in δ¹⁵N-depth relationships among trophic functional groups

The significant, positive effect of water depth on the δ¹⁵N 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 $^{15}$N decreased slightly with depth. Opposing $^{15}$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 are more trophically flexible than infaunal taxa, both in terms of food source and particle size. Such trophic flexibility was supported by the increasing variance of $^{15}$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). Infaunal deposit feeder $^{15}$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 $\delta^{15}$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 $\delta^{15}$N and depth differ when carnivores are analysed separately by their
primary feeding habitat. The positive trend between epifaunal carnivore $\delta^{15}$N and water depth
might be a consequence of feeding on $^{15}$N-enriched prey at depth. 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). Access to vertically migrating pelagic prey, such as zooplankton, is likely
limited for benthic predators on the continental slope because those prey are intercepted by large
aggregations of benthopelagic predators (Crawford et al., 2012; Majewski et al., 2017).

Curiously, infaunal carnivore $\delta^{15}$N values did not reflect those of the infaunal deposit feeders that
may comprise an important prey base. The infauna are the most data-poor trophic groups in this
study ($n < 100$ individuals for each group), and 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, the different $\delta^{15}$N-depth relationships among carnivore
groups highlight variation in their 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 trophic pathways beginning in benthic resources that have undergone depth-
related $^{15}$N enrichment. 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). The specific $\Delta^{15}\text{N}$ between any two successive trophic levels, however, can become smaller up the food chain in marine systems (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 variation in $\delta^{15}\text{N}$-depth relationships among trophic functional groups may thus depend on the scope of the food web being considered, and certainly depends on the depth range (e.g., $\Delta^{15}\text{N} < 0.69$ ‰ observed for epifaunal deposit feeders between 20 and 500 m depths in this study, compared 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 steeper $\delta^{15}\text{N}$-depth relationships for suspension/filter feeders, infaunal deposit feeders, and sediments in the Amundsen Gulf than in the Beaufort Sea. Primary production is generally higher in the offshore Amundsen Gulf than in the Beaufort Sea (Ardyna et al., 2013; Sallon et al., 2011), 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 microbial enzymatic activity (Kellogg et al., 2011), which is likely linked to correspondingly greater proportions of algal cells and exopolymeric substances observed in sinking POM (Sallon et al., 2011). Sallon et al. (2011) suggested that the presence of
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exopolymeric coatings on sinking particles in regions of high primary production likely
intensified microbial activity by facilitating bacterial attachment. The small volume of marine-
derived POM that is exported below 100 m in the offshore Amundsen Gulf thus has a
substantially altered biochemical composition (Kellogg et al. 2011). Our sediment data indicated
such $^{15}$N-enriched marine POM comprised increasing proportions of the bulk sedimentary pool in
the Amundsen Gulf with increasing depth, leading to relatively steeper $\delta^{15}$N-depth relationships
for sediment and benthic consumers that rely on sinking POM compared to the Beaufort Sea.

In contrast, 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 quantitative dominance
of terrestrial POM in the benthic POM pool, even at great depths, may explain why the $\delta^{15}$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 $\delta^{15}$N-depth relationship
that was slightly steeper in the Beaufort Sea than in the Amundsen Gulf. This finding 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 δ^{15}N-depth relationships observed in the Amundsen Gulf for these fishes. However, there is little evidence for such a shift according to δ^{13}C (see data in Stasko et al., 2017). Without further diet information, the flatter δ^{15}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 applied with caution. Our dataset is limited by taxon occurrences and distributions, as well as sample availability. Many taxa occurred across a limited depth range, and some occurred along a limited number of transects (Table 1). Any trophic functional group, including suspension feeders, can include taxa that feed at substantially different trophic levels from each other (e.g., Bergmann et al. 2009), affecting how closely linked their δ^{15}N values are to POM. 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). Confidence that the results can be applied more generally to other studies should be evaluated in light of the limitations in taxa richness and distributions available in this dataset.

In conclusion, we used a linear mixed effects modelling approach to confirm that positive δ^{15}N-depth relationships in the Beaufort Sea and Amundsen Gulf 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 making conclusions about consumer trophic levels from δ¹⁵N 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 δ¹⁵N changes with depth.
5.0 ACKNOWLEDGEMENTS

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6.0 REFERENCES


Doxaran, D., Devred, E., Babin, M., 2015. A 50 % increase in the mass of terrestrial particles delivered by the Mackenzie River into the Beaufort Sea (Canadian Arctic Ocean) over the last 10 years. Biogeosciences 12, 3551–3565. doi:10.5194/bg-12-3551-2015


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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.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Taxon</th>
<th>Sample size</th>
<th>Depth range</th>
<th>Transects</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Plot ID #</td>
<td>Beaufort Sea</td>
<td>Amundsen Gulf</td>
</tr>
<tr>
<td>Benthopelagic carnivore</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AR</td>
<td>Argis dentata</td>
<td>49</td>
<td>21</td>
<td>40 - 200</td>
</tr>
<tr>
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<td>Eualus gaimardii</td>
<td>92</td>
<td>49</td>
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<td>Icelus spatula</td>
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<td>Plot ID #</td>
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<td>Amundsen Gulf</td>
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<td>Amundsen Gulf</td>
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<td></td>
<td></td>
<td></td>
<td>Beaufort Sea</td>
<td>Amundsen Gulf</td>
</tr>
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<td><em>Lycodes polaris</em></td>
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<td>23</td>
<td>11</td>
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<tr>
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<td><em>Actinaria</em></td>
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<td>4</td>
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<td><em>Gorgonocephalus</em> spp.</td>
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<td><em>Astarte</em> spp.</td>
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<td>8</td>
<td>4</td>
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<td>Mollusca</td>
<td><em>Similipecten greenlandicus</em></td>
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<td>10</td>
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<tr>
<td>Mollusca</td>
<td><em>Thyasiridae</em></td>
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<td>13</td>
<td>9</td>
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<tr>
<td>Echinodermata</td>
<td><em>Ctenodiscus crispatus</em></td>
<td>20</td>
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<td>25</td>
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<td>Echinodermata</td>
<td><em>Pontaster tenuispinus</em></td>
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<td>Annelida</td>
<td><em>Ampharetidae</em></td>
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<td>11</td>
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<td><em>Synidotea</em> sp.</td>
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<td><em>Pontaster tenuispinus</em></td>
<td>21</td>
<td>63</td>
<td>21</td>
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<tr>
<td>Annelida</td>
<td><em>Maldane</em> spp.</td>
<td>22</td>
<td>34</td>
<td>24</td>
</tr>
</tbody>
</table>
*Thyasiridae can derive nutrition from chemosynthetic sulfur-oxidizing bacteria rather than from suspended POM. The $\delta^{13}$C values of Thyasiridae individuals included in this study indicated that they were heterotrophic. See Supplementary Material.
Table 2. Results of linear mixed effects models describing the relationship between $\delta^{15}$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 ($R^2_m$) and conditional ($R^2_c$) 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 $\delta^{15}$N ($\Delta$) across the observed water depth range is given for well-fit models.

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

*No model fit the infaunal carnivore data better than a null model with intercept as the only term (i.e., depth had little effect)
Table 3. Results of linear mixed effects models describing the relationship between δ¹⁵N and water depth for those trophic groups that exhibited significantly different slopes in the Beaufort Sea and Amundsen Gulf. Random effect structures allowed either intercept (b), slope (m), or both to vary by taxon. Goodness-of-fit was evaluated using the marginal (R²ₘ) and conditional (R²ₖ) coefficients of variation, which respectively describe the proportion of variance explained by depth alone and by depth and taxon together. An R² ≥ 0.63 was considered a strong fit and is indicated in bold (Sullivan and Feinn, 2012). The estimated change in δ¹⁵N (Δ) across the observed water depth range is given for well-fit models.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Region</th>
<th>n individuals</th>
<th>n taxa</th>
<th>Intercept (b)</th>
<th>Slope (m)</th>
<th>t</th>
<th>R²ₘ</th>
<th>R²ₖ</th>
<th>Random effects structure</th>
<th>Depth range (m)</th>
<th>Δ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epifaunal carnivores</td>
<td>Beaufort Sea</td>
<td>536</td>
<td>15</td>
<td>11.97 ± 0.71</td>
<td>0.69 ± 0.15</td>
<td>4.67</td>
<td>0.20</td>
<td>0.70</td>
<td>m, b</td>
<td>20 - 500</td>
<td>0.96</td>
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<tr>
<td></td>
<td>Amundsen Gulf</td>
<td>298</td>
<td>15</td>
<td>12.79 ± 0.79</td>
<td>0.58 ± 0.16</td>
<td>3.66</td>
<td>0.13</td>
<td>0.73</td>
<td>m, b</td>
<td>20 - 500</td>
<td>0.81</td>
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<tr>
<td>Suspension/filter feeders</td>
<td>Beaufort Sea</td>
<td>114</td>
<td>6</td>
<td>5.69 ± 1.11</td>
<td>0.84 ± 0.14</td>
<td>5.99</td>
<td>0.08</td>
<td>0.89</td>
<td>b</td>
<td>40 - 500</td>
<td>1.17</td>
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<tr>
<td></td>
<td>Amundsen Gulf</td>
<td>88</td>
<td>6</td>
<td>5.62 ± 2.21</td>
<td>1.07 ± 0.36</td>
<td>2.99</td>
<td>0.04</td>
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<tr>
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<td>4</td>
<td>15.19 ± 1.77</td>
<td>-0.63 ± 0.27</td>
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<td>0.06</td>
<td>0.93</td>
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<td>40 - 500</td>
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<tr>
<td></td>
<td>Amundsen Gulf</td>
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<td>14.42 ± 1.39</td>
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<td>0.02</td>
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<td>0.81</td>
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