

Benthic trophic sensitivity to on-going changes in Pacific Arctic seasonal sea ice cover – insights from the nitrogen isotopic composition of amino acids

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ABSTRACT

We studied trophic relations among benthic species collected in the northern Bering and Chukchi seas, specifically in biologically productive “hotspots” within the Distributed Biological Observatory (DBO) program. The stable nitrogen isotope composition of compound-specific amino acids ($\delta^{15}\text{N}_{\text{AA}}$) was used as an approach to assess how several benthic species in this Arctic ecosystem are responding to the earlier timing of sea-ice melt and associated shifts to the onset of the annual production season. The trophic level of 16 common benthic taxa with different feeding behaviors were collected along a south-to-north latitudinal gradient extending

from the northern Bering Sea, south of St. Lawrence Island, to the northern Chukchi Sea, including the Barrow Canyon undersea feature, and examined with respect to the available food sources. The $\delta^{15}\text{N}_{\text{AA}}$ values of source and trophic amino acids varied among studied regions and among species. $\delta^{15}\text{N}_{\text{AA}}$ -based trophic level estimations, using $\delta^{15}\text{N}$ values in both source and trophic amino acids and the ΣV index, provided new insights on trophic levels and feeding behaviors of different taxonomic groups that were not apparent from more commonly used isotopic measurements of bulk tissues. The compound-specific amino acid isotope compositions varied geographically, but not necessarily by latitude. This indicates that a simple time for space replacement perspective extending from south to north over the study area and reflecting variable persistence of seasonal sea ice, is inadequate to explain food web complexity. Highest bulk $\delta^{15}\text{N}$ and $\delta^{15}\text{N}_{\text{AA}}$ values were observed in depositional zones (near and within the St. Lawrence Island Winter-Spring Polynya, in particular). The $\delta^{15}\text{N}_{\text{AA}}$ values also suggested high feeding plasticity in benthic species in the northern Bering and Chukchi seas hotspots. Benthic consumers most likely can change feeding behavior (e.g. suspension versus deposit feeding) in response to different environmental conditions and resulting changes in the quality of organic matter reaching the sea floor. We conclude that the sensitivity of productive arctic benthic ecosystems to climate related change, i.e. earlier sea-ice melt and related onset of primary production, might be mitigated by robust capabilities to adapt to changes in food quality and supply.

Key words: Food webs, Trophic relationships, Pacific Arctic, Sea-ice retreat, Benthos, Stable isotopes, Amino-acids, Distributed Biological Observatory (DBO)

1. Introduction

48

49 Arctic marine benthic food webs are known to play an important role in overall ecosystem
50 functioning including production, turnover rates, and remineralization (Iken et al., 2010; Renaud
51 et al., 2008). Yet, predicting and estimating trophic relations in complex food webs remains a
52 continuous challenge, particularly in seasonally ice-covered ecosystems where sampling is often
53 limited. The Arctic shallow shelves, and the northern Bering and Chukchi seas are among the
54 most productive soft bottom ecosystems. With high primary production (PP) and tight pelagic-
55 benthic coupling, the Pacific Arctic benthic communities reach high diversity and biomass
56 (Grebmeier et al., 2006a). These communities constitute an important food source for higher
57 trophic level seabirds and marine mammals, and thus play a crucial role in carbon and energy
58 transfer (Grebmeier et al., 2006a, 2015a).

59 Rapid changes in seasonal sea-ice cover patterns and persistence are particularly
60 prominent in the Pacific Arctic (Frey, et al., 2014, 2015; Overland and Wang, 2018).
61 Modifications in temperature and sea-ice coverage are expected to affect resource-consumer
62 interactions due to changes in the quantity and timing of resource supply to consumers (Hoegh-
63 Guldberg and Bruno, 2010; Kędra et al., 2015). Although overall primary production (PP) on
64 shallow Arctic shelves is predicted to increase along with sea-ice retreat (Arrigo and van Dijken,
65 2011, 2015; Arrigo, et al., 2014; Assmy, et al., 2017; Mundy, et al., 2014), the volume of early
66 spring ice-associated PP reaching the sea floor will likely be reduced (Arrigo et al. 2008).
67 Changes in the quality and quantity of organic matter (OM) fluxes are expected to influence
68 benthic communities, including species composition, abundances and functioning (Ambrose and
69 Renaud, 1997; Kędra et al., 2015; Morata, et al., 2015). As the abundance of the OM resources
70 may influence the level of trophic specialization (Pyke et al., 1997), changes in the food supply
71 may also affect benthic feeding preferences, and thus their trophic levels (TLs). Therefore,

assessing TLs among benthic organisms on the Arctic shelves is poised to be even more important.

One of the widely-used methods for determining food web structure in various Arctic locations involves the use of naturally occurring stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) (e.g. Divine et al., 2016; Feder et al., 2011; Iken et al., 2005, 2010; Kędra et al., 2012). The $\delta^{15}\text{N}$ value in bulk material (whole organic tissue; $\delta^{15}\text{N}_{\text{bulk}}$) is particularly useful for delineating TL and food web structure, and reflects a longer-term diet over weeks to month-long intervals (reviewed by Hobson and Welch, 1992; Kaufman et al., 2008; Layman et al., 2012). However, this method suffers from some important disadvantages. First, the $\delta^{15}\text{N}_{\text{bulk}}$ values of primary producers representing the base of the food web (TL=1) are needed to calculate associated TLs of organisms (Iken et al., 2010). This may be challenging since the $\delta^{15}\text{N}_{\text{bulk}}$ values of primary producers, like phytoplankton, can vary greatly in the marine ecosystems in space and time due to various biotic and abiotic factors, such as community composition, nutrient utilization, spatial and seasonal differences in nutrient sources and subsequent biological transformation of these nutrients (Martinez del Rio et al., 2009; Tamelander et al., 2009; Vanderklift and Ponsard, 2003). Establishing food web baseline information is particularly difficult in the Arctic Ocean, where co-occurring mixtures of sea ice algae and phytoplankton often have dissimilar isotopic values. With respect to the benthos, consumers can prey on a number of potential food sources, including regularly reworked organic matter (OM) such as detritus for which stable isotope ratios may change during decomposition (Currin et al., 1995). Consequently, variability in $\delta^{15}\text{N}_{\text{bulk}}$ values of primary producers can be three times greater than the assumed average ^{15}N -trophic enrichment factor of ~ 3.4 (Hannides et al., 2009). This variability introduces potential errors in TL assignment that are further propagated to higher TLs, where more errors may arise due to different enrichments factors varying among different species, feeding behaviors, diet quality, or

physiological stress (Martinez del Rio et al., 2009; McCutchan et al., 2003; Vander Zanden and Rasmussen, 2001).

One possible solution is the application of compound-specific stable isotope analysis of amino acids (CSI-AA). This approach has provided some potential improvements that reduce the uncertainties associated with bulk isotopic analyses of food webs (Chikaraishi et al., 2009, 2014; Hannides et al., 2013; McClelland and Montoya, 2002; Mompean et al., 2016; Nielsen et al., 2015). The success of this approach is based on studies that show that $\delta^{15}\text{N}$ values of specific individual amino acids (AAs) vary predictably with trophic transfer. Some AAs - termed 'trophic' - show large ^{15}N enrichments ($\sim 7\text{‰}$) while others - 'source' - show little change at each TL (McClelland and Montoya, 2002). An important advantage of the CSI-AA approach is that, unlike bulk analysis, it does not require the characterization of the $\delta^{15}\text{N}$ values of the primary producers to estimate the TL. CSI-AA has recently been applied to estimate the TLs of marine organisms from spatially and temporally variable environments (e.g. Hannides et al., 2009; McCarthy et al. 2007; McMahon et al., 2015; Pakhomov et al., 2004; Schmidt et al., 2006), including paleoapplications (McMahon et al., 2018; Sherwood et al., 2011) and polar locations (Lorrain et al., 2009); however, studies on benthic organisms remain scarce.

In this study, we aimed to assess the elasticity of trophic variability of several common Arctic benthic species found along a latitudinal gradient, as part of the international Distributed Biological Observatory (DBO) network. Our initial expectations were that the latitudinal gradient would reflect the varying persistence of seasonal sea ice in the Pacific Arctic (Frey et al., 2015; Grebmeier et al., 2018). In other words, we expected to see evidence of a south-to-north gradient in the apparent importance of sea-ice algae deposited directly to the sea floor relative to OM processed in the water column (mainly phytoplankton) before deposition to the benthos (Cooper et al., 2002). Our objective was to examine the potential implications of changes in sea-ice cover

for benthic organisms, particularly their TLs, along a south-to-north latitudinal gradient extending from the northern Bering Sea, south of St. Lawrence Island, to the northern Chukchi Sea, including the Barrow Canyon subsea feature. We sampled selected key benthic species found throughout this latitudinal range to detect changes in their TLs with respect to available food sources. We also collected species that are less common but represent different feeding behavior to assess response to local organic matter (OM) input. Finally, we compared results of CSI-AA analyses with $\delta^{15}\text{N}$ values obtained for bulk organic material.

2. Material and Methods

2.1. Study area

The northern Bering and Chukchi seas are seasonally ice-covered, very productive shallow shelf systems. These shelves are influenced by Pacific water masses flowing northward into the deep Arctic Ocean basins. During the summer, the Alaska Coastal Water flowing along the Alaskan coast is surface-intensified, nutrient-poor, warm and fresher (<31.8) than the Anadyr Water near the Siberian coast, which is more nutrient-rich and saline (>32.5) while the Bering Shelf Water flowing through the central Chukchi Sea is moderately warm, and has an intermediate salinity (31.8–32.5) (Coachman et al., 1975; Grebmeier et al., 2006a; Weingartner et al., 2005; Woodgate et al., 2005a, b; Fig. 1). The advection of OM from the south and local production associated with different water masses are important drivers of dynamic benthic food-web structure in the northeast Chukchi Sea (Grebmeier et al., 2015). The hydrography of these water masses strongly influences the intensity of primary and secondary production in the region, since currents redistribute nutrients, algal production, organic carbon and zooplankton organisms,

along with heat and salt from the Bering slope and the central Bering shelf into the northern Bering and Chukchi seas (Grebmeier et al., 2015a; Lowry et al., 2015; Walsh et al., 1989; Weingartner et al., 2005, 2017; Woodgate et al., 2012). The hydrological regime is locally modified and altered by increasing temperatures that result from climate warming, changes in water circulation patterns (Nghiem et al., 2007; Woodgate et al., 2010, 2012) and increased light availability for PP (Arrigo et al., 2014; Arrigo and van Dijken, 2015).

The Chirikov Basin (between St. Lawrence Island and Bering Strait) and the southern Chukchi shelf north of Bering Strait are considered the most productive areas (Hill et al., 2018) with PP estimated to be $570 - 840 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Springer et al., 1996; Springer and McRoy, 1993). Over recent years a decline in PP has been reported in the northern Bering Sea (Lee et al., 2012), and an increase has been noted in the Chukchi Sea coastal waters (Hirawake et al., 2012; Petrenko et al., 2013). Some of these changes appear to be linked to the earlier timing of sea-ice retreat (Hill et al., 2018). Almost 70% of OM that is formed in surface shelf waters is exported unconsumed to the seafloor and fuels productive benthic communities (Grebmeier, 2012; Grebmeier et al., 2006a, 2015a; Walsh et al., 1989). Due to tight pelagic-benthic coupling, the biomass of benthic fauna is high and provides predictable feeding resources for specialized marine mammals and sea birds that forage on the seafloor (Grebmeier, 2012; Grebmeier and Barry, 2007; Grebmeier et al., 2006a; Sheffield and Grebmeier, 2009). The total organic carbon content in the surface sediments is positively correlated with silt and clay content, and is high in deposition areas (Grebmeier and Cooper, 1995, 2014). Offshore sediments are dominated by muds and muddy sand sediments, while gravel, pebbles, rocks, and sand dominate close to St. Lawrence Island, in nearshore regions of the Chirikov Basin, Bering Strait, and near the Alaskan coast (Grebmeier and Cooper, 2014; Grebmeier et al., 2006a; Pisareva et al., 2015).

2.2. Sampling

Sampling was based upon the latitudinal design of the Distributed Biological Observatory (DBO). The DBO was established as a change detection array for the identification and consistent seasonal and interannual monitoring of biophysical responses to the on-going climate related changes in the Pacific Arctic Region (DBO; <http://www.pmel.noaa.gov/dbo/>; Fig. 1). Each DBO area was previously identified as biologically important with significant biodiversity and biomass, and these locations have been characterized as “hotspots” with enhanced deposition of OM to the benthos (Grebmeier, 2012; Grebmeier et al., 2015a, b; Moore and Grebmeier, 2018). Each area has distinctive dominant benthic species and diversity characteristics and is exposed to different sea-ice cover duration and physical forcing. Our study focuses on these DBO areas, which have relatively well understood physical mechanisms driving high benthic community abundance and productivity (Grebmeier et al., 2015a). In particular, DBO1-3 have recently undergone changes in benthic macrofaunal populations in response to changes in seasonal sea-ice persistence (Grebmeier et al., 2018).

Samples were collected during a cruise of the Canadian Coast Guard Service (CCGS) Sir Wilfrid Laurier in July 2015, at five DBO areas (Fig. 1, Table 1) chosen to reflect changes in possible food sources to the benthos along the latitudinal gradient in addition to sea-ice persistence. The studied areas include: the St. Lawrence Island Polynya region (DBO1), the Chirikov Basin between St. Lawrence Island and Bering Strait (DBO2), the Southern Chukchi Sea (DBO3), the Northeast Chukchi Sea (DBO4), and Barrow Canyon (DBO5). Biological samples were collected using a 0.1 m² van Veen grab and sieved through 1 mm screen. Benthic animals were sorted, and kept cool until taxonomic identification under a stereomicroscope shipboard. All samples were subsequently frozen and returned to the Chesapeake Biological

Laboratory in Solomons, Maryland, USA, where they were stored in a -20°C freezer prior to processing for compound specific isotope analyses. Benthic invertebrates selected for the CSI-AA analyses included 16 species (48 specimens) commonly occurring along the latitudinal gradient in the northern Bering and Chukchi seas (Table 1, 2).

2.3. Compound-specific stable isotope analysis

CSI-AA is based on the observation that some AAs show large ^{15}N enrichments (~7-10‰) while others show little change at each TL (McClelland and Montoya, 2002). Trophic AAs (Tr-AAs): alanine (Ala), aspartic acid (Asp), glutamic acid (Glu), isoleucine (Ile), leucine (Leu), proline (Pro), and valine (Val) become enriched in ^{15}N as a result of isotopic fractionation during metabolic transamination (e.g. $\delta^{15}\text{N}_{\text{Glu}}$ increases up to 8-10‰ for each step in TL between consumer and producer (Chikaraishi et al., 2009; Popp et al., 2007). These AAs are rapidly transaminated during reactions that cleave carbon-nitrogen bonds, and therefore trophic AAs are isotopically closely linked to an organism's central N pool (McCarthy et al., 2013). In contrast, source AAs: glycine (Gly), lysine (Lys), methionine (Met), phenylalanine (Phe), serine (Ser), and tyrosine (Tyr), show little change in $\delta^{15}\text{N}$ values along food chains (owing to no formation nor cleavage of nitrogen containing bonds) and thus, retain their source isotopic ratio (Chikaraishi et al., 2009). $\delta^{15}\text{N}$ values of Phe and Met, have been shown to remain essentially unchanged through multiple trophic transfers, e.g., $\delta^{15}\text{N}_{\text{Phe}}$ increases by only 0.4‰ per trophic level (Chikaraishi et al., 2009; Germain et al., 2013; McClelland and Montoya, 2002). In addition, Threonine (Thr), which was originally classified as a source AA (McClelland and Montoya, 2002), may vary isotopically in response to specific metabolic processing. It has been reported to display unique, “inverse” $\delta^{15}\text{N}$ fractionation behavior with trophic transfer and can be used as a

separate indicator of TL (Bradley et al., 2014; Germain et al., 2013; McMahon et al., 2015) and as a metabolic indicator for physiological stresses such as starvation (Hare et al., 1991).

Sample preparation for CSI-AA generally followed the methods outlined in Macko and Uhle (1997) and Silfer et al. (1991). Specifically, 5-10 mg of dried animal tissue was homogenized, weighed, and acid hydrolyzed in 0.5mL of 6N HCl in vials flushed with nitrogen gas at 110°C for 20 hours to extract AAs from proteinaceous components. The remaining acid was evaporated at 55°C under an N₂ stream and the residue was then re-dissolved by adding 1 mL of 0.01N HCl and purified by cation exchange. After drying under a stream of N₂ gas, the total free AAs were derivatized by esterification with acidified isopropanol followed by acetylation with trifluoroacetic anhydride (Silfer et al., 1991). The final product was dissolved in 1 mL methylene chloride and stored in a freezer (-20°C).

Derivatized AAs standards and samples were analyzed using a Thermo Trace GC Ultra gas chromatograph interfaced with a Thermo Delta V Plus isotope ratio mass spectrometer (GC-IRMS). One mL of derivatized material was equally divided into two parts, one for carbon isotope analysis (to be reported elsewhere) and the other for nitrogen isotope analysis. A 5 µL AA solution was injected onto a BPX5 capillary column (60m × 0.32mm × 1.0µm film thickness) at an injection temperature of 180°C using a split/splitless injector (in splitless mode) with a constant helium flow rate of 2.0 mL min⁻¹. The column was held at an initial temperature of 75°C for 2 min; ramped up to 90°C at 4 °C min⁻¹, held for 4 min; ramped up to 185°C at 4°C min⁻¹, held for 5 min; ramped up to 250°C at 10°C min⁻¹, held for 2 min; and finally ramped up to 300°C at 20°C min⁻¹, and held for 8 min.

The separated AAs were combusted in a GC Isolink at 980°C, passed through a Thermo Conflo IV continuous flow interface, and the isotopic composition was then measured on the

isotope ratio mass spectrometer. The sample peaks generated were larger than 1V for all nitrogen isotope analyses. Thirteen individual AAs identified had sufficient baseline separation to allow isotopic ratio determinations. To correct for derivatization, and to assess analytical precision, all CSI-AA samples were analyzed simultaneously with AA standards of known isotopic composition (source, Indiana University) (<http://pages.iu.edu/~aschimme/compounds.html>) that were derivitized in batches with the samples. Individual samples were analyzed two to three times.

2.4. Data analysis

For $\delta^{15}\text{N}_{\text{AA}}$, we assumed: (1) that Phe is a source AA that is not isotopically fractionated between TL (i.e. it was assumed to be a source AA), (2) that Glu is a trophic AA that demonstrates a step-wise trophic enrichment (i.e. a trophic AA) from one TL to the next above the primary producers, and therefore (3) the difference between Glu and Phe ($\Delta\delta^{15}\text{N}_{\text{glu-phe}} = \delta^{15}\text{N}_{\text{glu}} - \delta^{15}\text{N}_{\text{phe}}$) can be considered as an index of TL for each species (see Schmidt et al., 2004; Hannides et al., 2009). TL for each benthic species was estimated according to the formula:

$$\frac{(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{species}} + (\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}}{\text{TEF}} + 1$$

The value of $(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}$ represents the isotopic difference between $\delta^{15}\text{N}_{\text{Glu}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ in primary producers (-3.4‰ for aquatic cyanobacteria and algae; Chikaraishi et al., 2009). The trophic enrichment factor (TEF) has been determined directly and indirectly to be 7.6‰ at each shift of TL (Chikaraishi et al., 2009). Thus, the TLs presented here were calculated according to the following formula:

$$\text{TL}_{\text{Glu-Phe}} = \frac{(\Delta\delta^{15}\text{N}_{\text{Glu-Phe}}) - 3.4}{7.6} + 1$$

Since determination of TL relying on only two AAs can be susceptible to diagenetic alteration or error in any single value additionally we used the formula based on the difference in the averages of trophic (TrAA: Asp, Glu, Ala, Ile, Leu, Val, and Pro) and source AAs (SrAA: Gly, Lys, Phe; Hannides et al., 2013; Hannides et al., 2009; McCarthy et al., 2007; Sherwood et al., 2011):

$$TL_{TrAA-SrAA} = \frac{(\Delta\delta^{15}N_{TrAA-SrAA}) - 3.4}{7.6} + 1$$

Additionally, the degradation index ΣV (McCarthy et al., 2007) was calculated as a measure of the relative re-synthesis of the original autotrophic AA pool in each benthic taxon as the mean deviation of $\delta^{15}N$ of each individual trophic AAs, from their average:

$$\Sigma V = \frac{\sum |AA_i - Avg_{trp}|}{n}$$

where AA_i - individual trophic $\delta^{15}N_{AA}$ values, Avg_{trp} – the average value of all trophic $\delta^{15}N_{AA}$ (Ala, Asp, Glu, Ile, Leu, Pro, and Val), and n - the total number of Tr-AA used in the calculation. Ser and Tyr were not included in the analysis due to missing or limited measurements to keep the results comparable among samples.

Results are given as means with standard deviations where replicates were available. To explore patterns in the dataset, we performed principal component analysis (PCA, PRIMER7; Clarke and Godley, 2015) on the nitrogen isotopic composition of each individual AAs ($\delta^{15}N_{AA}$) values. For the PCA procedure, data were normalized to their respective sample means. Two outliers, both collected in DBO1 (*Axiiothella catenata* and *Anonyx* spp.), with $\delta^{15}N_{AA}$ values significantly different from all other samples analyzed, were removed from the analysis to avoid unnecessary bias.

3. Results

We quantified $\delta^{15}\text{N}_{\text{AA}}$ values of 5 source AAs (Gly, Phe, Lys, Ser, Tyr), 1 metabolic AA (Thr), and 7 trophic AAs (Ala, Pro, Asp, Glu, Val, Leu, Iso). In general, all measured trophic AAs were ^{15}N -enriched (mean: 14.1 ± 5.3 SD) relative to all source AAs (mean: 6.1 ± 3.0 SD) and Thr (mean: 2.4 ± 5.0 SD). The $\delta^{15}\text{N}_{\text{AA}}$ values were more ^{15}N -enriched to the south (Fig. 2, 3, Table 2).

The first principal component of PCA accounted for 68.4% of the variation, and separated samples by feeding type and taxonomic group (Fig. 4). The second principal component of PCA accounted for 16.6% of the variation and separated samples by latitude and feeding type. Animal samples were grouped according to their feeding types. However, bivalves grouped separately, regardless of their primary feeding behavior. Also, ampeliscid amphipods, which can both suspension feed and surface deposit feed, formed a separate group and did not group with other suspension feeders (Fig. 4).

When compared among feeding types, one of the striking patterns was that suspension feeders had lower $\delta^{15}\text{N}_{\text{bulk}}$, source and trophic $\delta^{15}\text{N}_{\text{AA}}$ values compared to other feeding groups (Fig 2., Table 2). However, there was some region-to-region and taxonomic variation. For example, suspension feeding bivalves (*Mya arenaria*, *Serripes groenlandicus*) collected in DBO3 had higher source $\delta^{15}\text{N}_{\text{AA}}$ values than suspension feeding amphipods (*Ampelisca macrocephala*, *Byblis* sp.) collected in the same area. *Byblis* sp. had higher values of source and trophic $\delta^{15}\text{N}_{\text{AA}}$ in the depositional sediments of DBO4 compared to DBO2, which has strong currents. The $\delta^{15}\text{N}_{\text{bulk}}$, source and trophic $\delta^{15}\text{N}_{\text{AA}}$ values of surface deposit feeding species also varied among species and areas (Fig. 2, Table 2). For example, the surface deposit feeding bivalve, *Macoma calcaria* had higher source and trophic $\delta^{15}\text{N}_{\text{AA}}$ values towards the south (Fig. 3, Table 2). $\delta^{15}\text{N}_{\text{bulk}}$

values of *Macoma* spp. collected in DBO2, DBO3 and DBO5 were lower than in DBO1 and DBO4. Another surface deposit feeding bivalve, *Yoldia hyperborea*, had similar $\delta^{15}\text{N}_{\text{AA}}$ values to the *Macoma* species collected, and higher in ^{15}N source and trophic $\delta^{15}\text{N}_{\text{AA}}$ values in DBO5 compared to DBO3 (Table 2). The subsurface deposit feeders had similar values of source $\delta^{15}\text{N}_{\text{AA}}$ compared to surface deposit feeders but higher trophic $\delta^{15}\text{N}_{\text{AA}}$ values (Fig. 2, Table 2).

Regional differences in feeding were suggested by the data from the subsurface deposit feeding bivalve, *Ennucula tenuis*, which had trophic $\delta^{15}\text{N}_{\text{AA}}$ compositions that were the most ^{15}N -enriched in DBO3, but the least ^{15}N -enriched in the DBO4 and DBO5 areas. At the same time source $\delta^{15}\text{N}_{\text{AA}}$ values were the highest in DBO1 where other deposit feeders also tended to be enriched in ^{15}N . *E. tenuis* $\delta^{15}\text{N}_{\text{bulk}}$ values were the lowest in DBO2 (Fig 3, Table 2). *Nuculana pernula* also had more enriched source and trophic $\delta^{15}\text{N}_{\text{AA}}$ compositions in DBO1 compared to DBO3 (Table 2). The subsurface deposit feeding polychaete, *Maldane sarsi*, had source $\delta^{15}\text{N}_{\text{AA}}$ compositions that were most ^{15}N -enriched in DBO1, and the least ^{15}N -enriched in DBO5 (Fig. 3, Table 2) but this trend was not seen in other subsurface deposit feeding polychaetes (*Axiiothella catenata*, *Praxillella praetermissa*, *Pectinaria granulata*). *P. praetermissa* source $\delta^{15}\text{N}_{\text{AA}}$ values increased northwards while the amphipod *Pontoporeia femorata* had higher source $\delta^{15}\text{N}_{\text{AA}}$ values in DBO1 compared to DBO3 but the opposite for trophic $\delta^{15}\text{N}_{\text{AA}}$. Finally, the only scavenger collected, the amphipod *Anonyx* sp. had the most enriched source and trophic $\delta^{15}\text{N}_{\text{AA}}$ compositions of all species collected and had higher source and trophic $\delta^{15}\text{N}_{\text{AA}}$ values in DBO1 compared to DBO4 (Fig. 2, Table 2).

$\delta^{15}\text{N}_{\text{bulk}}$ values were lower than $\delta^{15}\text{N}_{\text{AA}}$ values of Glu but higher than $\delta^{15}\text{N}_{\text{AA}}$ values of Phe, as might be expected based upon the mixture of trophic AAs (isotopically fractionating) and source AAs (not isotopically fractionating) present in bulk OM. As expected, $\delta^{15}\text{N}$ values of Phe were lower than those of Glu in all trophic groups (Fig. 5, Table 2). These patterns remained

consistent over the latitudinal gradient and consistent with results obtained from the averages of source and trophic AAs, with an exception of one *M. calcarea* collected in DBO3, which had similar Phe $\delta^{15}\text{N}_{\text{AA}}$ values compared to $\delta^{15}\text{N}_{\text{bulk}}$. The TL calculations yielded similar values regardless of the method used ($\text{TL}_{\text{Glu-Phe}}$ versus $\text{TL}_{\text{TrAA-SrAA}}$) for all species at the second TL. However, species in which $\text{TL}_{\text{Glu-Phe}}$ was estimated to >3 show some discrepancies with $\text{TL}_{\text{TrAA-SrAA}}$ that can give lower estimates (Fig. 6, Table 3). Differences of one TL between $\text{TL}_{\text{Glu-Phe}}$ and $\text{TL}_{\text{TrAA-SrAA}}$ methods were indicated for the ampeliscid *Byblis* spp. and the polychaete *P. granulata* collected in DBO4 (Table 3). In general, the lowest estimated TL=2 was occupied by bivalves, including suspension feeders and species that feed on both surface and subsurface deposits. Subsurface deposit feeding polychaetes occupied the third and fourth TL, while scavenging crustaceans were in the fourth TL. Suspension feeding ampeliscid amphipods were classified as occupying TL 2 or higher (Fig. 6, Table 3). The ΣV parameter was the lowest (≤ 1.3) for the bivalves of all feeding types, and the highest (>2) for scavengers and suspension feeding ampeliscid amphipods, and subsurface deposit feeding *Pectinaria* polychaetes and *Pontoporeia* amphipod species (Fig. 7, Table 3).

4. Discussion

4.1. CSI-AA parameters in Arctic benthos: latitudinal and taxonomic variability

The $\delta^{15}\text{N}_{\text{AA}}$ values of source AAs directly reflect source $\delta^{15}\text{N}$ values of primary producers due to minimal isotopic fractionation during trophic transfers. This feature of the CSI-AA method is particularly valuable when working in complex or dynamic ecosystems where multiple,

distinct baseline end-members are present (e.g. Hannides et al., 2013; Ruiz-Cooley et al., 2014; Sherwood et al., 2011). The northern Bering and Chukchi seas are such systems, with strong water mass variation, shifting seasonal sea-ice cover affecting the timing and type of PP, and strong currents that either deposit or resuspend OM to the sea floor, resulting in the production of high and variable baseline isotopic end-members. Moreover, most of the benthic invertebrates, that are particularly abundant in these ecosystems, feed on OM that has been reworked to different degrees and stored on and in the sediments. Thus, $\delta^{15}\text{N}_{\text{AA}}$ values are potentially useful for examination of Arctic sea floor communities dominated by organisms feeding on phytodetritus.

Among the source AAs, Phe shows the lowest trophic isotopic fractionation across diverse consumer-resource relationships (Chikaraishi et al., 2009; McMahon and McCarthy, 2016). In our study, higher values of Phe $\delta^{15}\text{N}_{\text{AA}}$ were found in the DBO1, where deposition processes prevail, while the least ^{15}N -enriched organisms were observed in the DBO2 and the southern part of the DBO3 just north of Bering Strait, where currents are stronger (Grebmeier et al., 2015a). Similar trends were obtained for other source AAs like Gly and Lys. Since the source $\delta^{15}\text{N}_{\text{AA}}$ values closely reflect the values of the resources, this suggests that different species in this study were utilizing OM of various isotopic composition and, thus, from various sources. Species that register a narrow range of the $\delta^{15}\text{N}$ value of Phe are likely highly specialized consumers while species with a wide range can exploit various resources and are likely omnivorous (Chikaraishi et al., 2014). In our study, the range of Phe $\delta^{15}\text{N}_{\text{AA}}$ values of individual species was in most cases $< 3\text{‰}$, however, *M. calcarea* and *P. granulata* registered ranges of 6‰ and 9‰ respectively. This suggests that most sampled species were mainly feeding on the local food sources with a high level of selectiveness, while *Macoma* and *Pectinaria* were utilizing OM of various sources, possibly both produced *in situ* and advected.

The general patterns of lower values of individual source $\delta^{15}\text{N}_{\text{AA}}$ (and $\delta^{15}\text{N}_{\text{bulk}}$) in suspension and surface deposit feeders, which prefer fresh phytodetritus and/or fresh OM, and higher values in subsurface deposit feeders, which utilize highly reworked OM and possibly ingest bacteria and their metabolic products, reflect our expectations. Heavy isotope enriched Phe $\delta^{15}\text{N}_{\text{AA}}$ compositions in subsurface deposit feeders are also consistent with isotopic fractionation of the fresh OM pool due to heterotrophic degradation of the OM used. For example, surface sediment Chl *a* inventories result from seasonal accumulation of OM to the sea floor (Cooper et al., 2013; Pirtle-Levy et al., 2009) and provide food with different isotopic compositions, depending on the season. Deposit-feeders are likely to utilize a large fraction of bacteria and their products rather than detritus or living algal cells (Lopez and Levinton, 1987; Lovvorn et al., 2005). They appear to select a consistent microbially reworked fraction from the pool of sediment OM favoring OM that was stored longer in the sediment (North et al., 2014). Microbial biomass has also been reported to increase with the supply of labile OM to the sea floor (Boetius and Damm, 1998). Even small bacterial components in benthic invertebrate diets would result in ^{15}N -enrichment in observed $\delta^{15}\text{N}_{\text{AA}}$ values (McCarthy et al., 2007; Calleja et al., 2013), particularly in species that are subsurface deposit feeders and use more refractory material. At the same time, the $\delta^{15}\text{N}_{\text{AA}}$ values of Gly and Ser are known to show large variability in trophic enrichment from the baseline (McMahon and McCarthy, 2016). Particularly, Gly is strongly affected by microbial degradation (Calleja et al., 2013; McCarthy et al., 2007). Therefore, it should be used with caution as a source AA in ecosystems where microbial degradation or direct contributions are significant, as is the case with our study.

Trophic AAs generally exhibit large positive increases in $\delta^{15}\text{N}$ values with trophic transfers, and this was also observed in our study. Glu, used here and elsewhere to determine the TL, is one of the most abundant AAs in consumer tissues and displays the highest trophic

isotopic fractionation across diverse consumer-resource relationships (McMahon and McCarthy, 2016). The range of Glu $\delta^{15}\text{N}$ values in our study was 26‰, with the highest values for scavengers and subsurface deposit feeding polychetes, while the smallest Glu $\delta^{15}\text{N}$ range was observed in suspension and surface deposit feeders. Glu $\delta^{15}\text{N}$ values were higher in DBO1, but relatively less so in DBO2. Similar trends were observed for other trophic AAs that are expected to undergo similar biochemical transformations leading to heavy isotopic fractionation enrichment in $\delta^{15}\text{N}_{\text{AA}}$ values. The only exception was Ala, which had highly variable $\delta^{15}\text{N}$ values over the geographical distribution studied.

4.2. Export production and OM sources

The particulate organic carbon export fluxes on the Chukchi continental shelf are mostly composed of freshly produced labile material in the productive season (Lalande et al., 2007). Arctic OM export fluxes vary spatially and temporally peaking shortly after sea-ice cover retreats (Cooper et al., 2002). However, in highly productive areas of the Chukchi Shelf, the difference between fluxes in the presence and in the absence of sea-ice cover may be small reflecting higher biological productivity and more labile organic carbon reaching the seafloor throughout the productive season (Lalande et al., 2007; Cooper et al., 2009). This means, that even though the spring bloom was largely over by the time of our July sampling, in highly productive waters, such as the southern Chukchi Sea hotspot sampling site, benthic organisms with preferences for fresh OM are likely to have access to significant organic inventories to feed on throughout the open water season.

This scenario, however, may not apply to the most southern of our sampling locations, in the northern Bering Sea. The source $\delta^{15}\text{N}_{\text{AA}}$ values provide a robust proxy for $\delta^{15}\text{N}$ baseline in the

ecosystem (McMahon and McCarthy, 2016), and both $\delta^{15}\text{N}_{\text{bulk}}$ and source $\delta^{15}\text{N}_{\text{AA}}$ values, and consequently, the trophic $\delta^{15}\text{N}_{\text{AA}}$ compositions were consistently enriched in deposition areas, and the DBO1 in particular. This biological benthic hotspot, to the southwest of the location of the winter polynya of St. Lawrence Island, is a region where high PP rapidly settles to the seafloor in a quiescent setting while the more northern locations (Chirikov Basin (DBO2), southern Chukchi Sea (DBO3) and the Barrow Canyon (DBO5) have high production facilitated by stronger currents (Cooper et al., 2013; Dunton et al., 1989; Grebmeier et al., 2006, 2015a; Lovvorn et al., 2005). Compared to other sampling areas in this study, where deposition processes are also dominant (e.g. most northern stations at DBO3, and northeast Chukchi Sea (DBO4), the spring bloom would first occur in the DBO1 area, due to earlier ice break-up than in the more northern locations (Grebmeier et al., 2015a). This means that the OM inventories in the DBO1 were likely more reworked due to longer exposure to bacterial activity than in the northern part of DBO3 or northeastern Chukchi Sea (DBO4). Also, high quality sea-ice algal OM produced in the spring would be proportionally less significant compared to the larger open water phytoplankton bloom that occurs following sea-ice retreat. OM inventories at different stages of degradation are also present in the sediments in the DBO1 (Cooper et al., 2012; Pirtle-Levy et al., 2009). This implies that species feeding in the DBO1 use more refractory material and more bacterially metabolized OM than do species elsewhere in our study area, which is reflected by higher ΣV of some species and heavy-isotope enriched $\delta^{15}\text{N}_{\text{AA}}$ compositions. Furthermore, the $\delta^{15}\text{N}_{\text{AA}}$ values in DBO1 may be affected by sedimentary ammonia. Early spring releases of ammonia from the sediments were particularly notable southeast of St. Lawrence Island, leading to increased bottom-water ammonium concentrations (Cooper et al., 2013). The influence of ammonia on AAs and subsequent enrichment of their ^{15}N have been reported by McMahon et al. (2016) for higher TL organisms. Enriched $\delta^{15}\text{N}_{\text{AA}}$ values in DBO1 and DBO4 are also consistent

with the expected influence of ^{15}N -enriched nitrate in this region that originates from sedimentary releases of ammonium, leading to elevated values of $\delta^{15}\text{N}$ of NO_3^- available in the northern Bering and some parts of Chukchi Seas (Brown et al. 2015).

4.3. Trophic levels and diet of sampled benthic species

TLs determination based on the Glu and Phe CSI-AA model (Chikaraishi et al., 2009) has been applied to lower trophic level animals like marine zooplankton (e.g. Hannides et al., 2013; Mompean et al., 2016), but less often to benthic invertebrate fauna (e.g. McMahon et al., 2018; Sherwood et al., 2011). TEF may change across TLs, with a tendency to decrease in higher-level consumers (Bradley et al., 2014; Chikaraishi et al., 2015; Germain et al., 2013; McMahon et al., 2015; Nielsen et al., 2015; Popp et al., 2007). However, for lower trophic organisms like zooplankton (at <3 TL), the $+7.6\%$ increase per TL gives reasonable results (Batista et al., 2014; McCarthy et al., 2007; Mompean et al., 2016). McMahon and McCarthy (2016) showed that variability in $\text{TEF}_{\text{Glu-Phe}}$ values, ranging from 0% to $>10\%$ depends on diet quality and mode of nitrogen excretion. Consumers feeding on high-quality diets, defined as the relative match of AAs between diet and consumer (e.g. fish feeding on fish), tend to have significantly lower $\text{TEF}_{\text{Glu-Phe}}$ values than consumers feeding on low-quality diets (e.g. re-worked detritus). Benthic invertebrates mainly feed on detritus and rely on a presumably lower quality diet since it is compositionally different from their own tissues. Thus, we assume that the use of $\text{TL}_{\text{Glu-Phe}}$ with a $+7.6\%$ increase with each trophic step for benthic invertebrates is appropriate, and our results yielded reasonable TL estimates. Another method, based on the pooled values of trophic and source $\delta^{15}\text{N}_{\text{AA}}$ values, was reported to provide better TL estimates for benthic invertebrate fauna (Sherwood et al., 2011). Our results obtained with $\text{TL}_{\text{TrAA-SrAA}}$ method also seemed to better

reflect TL of species feeding on highly reworked material and occupying higher TLs. Both the $TL_{Glu-Phe}$ and TP_{Tr-Sr} produced apparently better TL estimates than more commonly used $\delta^{15}N_{bulk}$ values.

For example, maldanid polychaetes are generally comparatively large, slow growing and relatively sedentary head-down, conveyor-belt type deposit feeders (Levin et al., 1997; Dufour et al., 2008). This would qualify them as secondary consumers, but they are reported to occupy a higher (3.9-4) TL in $\delta^{15}N_{bulk}$ studies in case of *Maldane* (Kędra et al. 2012) and 3.1 TL in case of *P. praeterrissa* (Iken et al. 2010). Our TL estimations give lower, more reasonable results (second $TL_{Glu-Phe}$ and TP_{Tr-Sr} for *P. praeterrissa* and third $TL_{Glu-Phe}$ and TP_{Tr-Sr} for *M. sarsi*), indicating that the sampled organisms were feeding on both fresh detritus, possibly from the surface, and highly reworked OM. Also, our TL estimates for the deposit feeding bivalve, *Y. hyperborea* (~1.5 for $TL_{Glu-Phe}$ and TP_{Tr-Sr}), is consistent with its dependence on the input of fresh algal material even if sedimentary OM is available (Stead and Thompson, 2003) suggesting that CSI-AA approach likely produces a better indicator for this species. By comparison, $\delta^{15}N_{bulk}$ studies usually classify this bivalve family at third (Iken et al., 2005; Kędra et al., 2012) or second TL (Iken et al., 2010), but in other cases very close to primary producers in the Beaufort Sea (Bell et al., 2016).

Benthic organisms on Arctic shelves are highly dependent on the pulsed nature of OM fluxes to the sea floor (e.g. Grebmeier et al., 2006a), and therefore commonly exhibit a high degree of omnivory, multiple feeding behaviors, and can change their diet temporally (Iken et al., 2010; Kędra et al., 2012; 2015). High plasticity of feeding behaviors allows benthic organisms to adapt to the accessibility of the OM by switching the sources of OM and/or the feeding behavior (Morata et al., 2015; Stead and Thompson, 2006). Most benthic consumers are considered temporal couplers of resources that utilize PP but switch to a detritus based diet when no fresh PP

is available later in the season (McMeans et al., 2013). For example, ampeliscid amphipods can undertake both suspension and surface deposit feeding on both particulate OM, and benthic diatoms and foraminifera (Coyle and Highsmith, 1994; Iken et al., 2010; Legeżyńska et al., 2012). Some studies, including ours, classified this family higher than the second TL (third TL_{Glu-Phe} and second TP_{Tr-Sr}), clearly indicating utilization of reworked OM sourced detritus. In areas with fast currents, like the DBO2 region, where fresh OM settling to the sea floor is often resuspended from the bottom, reworked OM might be the main source of food for ampeliscids. These tube dwellers collect particles both from sediment surfaces and the water column. They mainly rely on pelagic production that sinks through the water column or is transported laterally from other locations, and/or on settled and phytodetritus on bottom surfaces (Dauby et al., 2001; Legeżyńska et al., 2012). The balance between the two feeding behaviors depends upon local/seasonal availability of fresh phytoplankton in the water column and resuspended OM (Mills, 1971) and it varies depending on the properties of overlying water currents (Iken et al., 2010). This suggests that TL estimations may be highly dependent on the local conditions and seasonality.

Other taxa known to switch feeding behavior depending on the quality of the OM available are surface deposit feeding bivalves, specifically *Macoma* spp. and *Y. hyperborea* (Rossi et al., 2004; Stead and Thompson, 2006). These organisms prefer phytodetritus as soon as it is available but throughout the year they either depend on the annual cycle of phytoplankton production or high organic content of sediment (Legeżyńska et al., 2014; Levinton, 1991; Stead and Thompson, 2003). Lovvorn et al. (2005) showed that in the northern Bering Sea, *Macoma* spp. mainly selectively fed on bacteria and non-selectively on bacterially reworked detritus. However, our samples collected in the DBO1 indicate that *M. calcarea* feeds close to the first TL, i.e., at the food base. In our study, *Macoma* spp. and *Y. hyperborea* occupied the second TL, and

both $TL_{Glu-Phe}$ and $TL_{TrAA-SrAA}$ methods suggest that they consume fresher OM than primarily suspension feeding bivalves and primary consumers such as *M. arenaria* and *S. groenlandicus* (Khim, 2001, 2002), and the subsurface deposit feeding bivalves *Nuculana* spp. and *E. tenuis*. Despite different feeding strategies and niches, these bivalve species seem to feed on near-surface sediments and on relatively fresh PP when available. By comparison, it is expected that the diet of *Nuculana* spp., a bivalve with very short siphons and no access to the surface of sediments when buried, includes a larger mix of subsurface sediments, thus more reworked material than another subsurface feeder studied here, *E. tenuis* (Lovvorn et al., 2005). Yet, this result was apparently not the case in this study where both bivalves were classified as having similar TLs. The apparent low TL of subsurface feeding bivalves suggests that they also preferentially utilize relatively fresh OM. Similar results were obtained in the southern Chukchi Sea (DBO3) with use of $\delta^{15}N_{bulk}$ values (TL ~2) (Iken et al., 2010). This also implies that relatively fresh OM is available for organisms during the summer in subsurface sediments.

Deposit feeders, the predominant macrobenthos on the Arctic shelves (Grebmeier et al., 2006a; Pisareva et al., 2015), can use either OM as it arrives at the sediment surface or, as soft bottom benthos worldwide, the fraction that has been buried through bioturbation (Middelburg et al., 2000). Feeding depth is one of the main niche axes differentiating habitat use by deposit feeders (Lopez and Elmgren, 1989). Animals feeding at different sediment depths are likely to ingest OM of different quality, which decreases in the underlying sediment layers due to organismal respiration and bacterial reworking (Lopez and Elmgren, 1989). The degree to which OM is reworked affects the TL of animals that utilize it. In general, subsurface deposit feeders rely on more reworked OM due to feeding at greater depths in the sediment, and thus can be expected to occupy higher TLs. In our study, the subsurface feeding crustacean *P. femorata*, malidanid polychaetes and the polychaete *Pectinaria* (but not bivalves) were evaluated to be at

second to fourth $TL_{Glu-Phe}$, and second and third $TP_{TrAA-SrAA}$. *P. femorata*, occupied the third TL, although it is a near-subsurface feeder. This species is a very active burrower that mainly feeds on near-surface phytodetritus with preferences for diatoms (Byrén et al., 2002; Legeżyńska et al., 2014), but it can also utilize microbial aggregations or prey upon meiofaunal organisms (Hill and Elmgren, 1987). Other studies suggest that the main food item for *P. femorata* is highly reworked algal-derived detritus with negligible amounts of directly deposited fresh diatoms (Bund et al., 2001; Lovvorn et al., 2005). The latter is consistent with our results that show TL decreases in the DBO1 region compared to DBO3 where muddier sediments are present (compared to DBO1), indicating a higher level of OM deposition (Grebmeier and Cooper, 2014).

Even higher TL estimates (third and fourth $TL_{Glu-Phe}$ and third TP_{Tr-Sr}) were obtained for *P. granulata*, a head-down polychaete that ingests sediments mainly from below the sediment surface (Fauchald and Jumars 1979). *Pectinaria* spp. responds slowly to the influx of fresh algae, with increased consumption of ice algae during later stages in blooms (Lovvorn et al., 2005; North et al., 2014). Earlier, it mainly consumes phytoplankton deposited during previous seasons, which may be months after being buried in the sediments by bioturbation (Hansen and Josefson, 2003; Pirtle-Levy et al., 2009). It also feeds deeper in the sediments on larger particles (including meiofauna and fecal pellets). *Pectinaria*'s TL increased by one from DBO1 to the northeastern Chukchi Sea, where more reworked OM was present (Grebmeier and Cooper, 2014).

4.4. ΣV parameter and metabolic AA

The ΣV parameter increased in general with TL, with the highest values occurring for scavengers, suspension/deposit feeding ampeliscid amphipods and subsurface deposit feeding malidanids (Table 3). The ΣV parameter increases from algae through mixed plankton and into

detrital POM, for example, through *de novo* heterotrophic reprocessing. Thus, this parameter has been used as a proxy for total heterotrophic re-synthesis (McCarthy et al., 2007). Heterotrophic reworking of proteinaceous material encompasses a range of metabolic processes promoted by heterotrophic organisms such as bacteria and zooplankton, including hydrolysis, uptake and *de novo* synthesis, incorporation of existing AA into new protein, and strict catabolism. The ΣV parameter values below 1.5 are typical for fresh algal biomass, and generally its values increase in detrital POM with an increasing proportion of degrading algae and zooplankton (McCarthy et al., 2007). This prior study suggested that the ΣV parameter reflects that autotrophs have more homogenous trophic AA distributions than heterotrophs or detrital materials and that the increasing values derive from progressive AA re-synthesis in both animal and microbial consumers. Our results are consistent with this model because the organisms that occupied higher TL reflected more heterotrophic processes than the primary consumers. However, there were subsurface deposit feeding species, e.g. *P. praetermissa* that had very low (<1) ΣV values. The most reasonable explanation is that this species can possibly switch to fresh OM if suitable food was available. Specific feeding preferences largely explain the ΣV values, but there was no obvious geographical pattern.

Thr, the AA that has recently been re-classified as a metabolic AA (Bradley et al., 2014; McMahon et al., 2015), displays inverse $\delta^{15}\text{N}$ fractionation behavior and has been reported to become less ^{15}N -enriched with increasing TL. However, the patterns of Thr $\delta^{15}\text{N}_{\text{AA}}$ values in our study are not clear. Low, negative values were observed for the scavenging amphipod *Anonyx*, but low Thr $\delta^{15}\text{N}_{\text{AA}}$ values were also observed for the suspension/deposit feeding ampeliscid amphipods and subsurface deposit feeding maldanid polychaetes. Thr has shown potential as a TL index for higher trophic level animals including mammals and fish (Bradley et al., 2014; Germain et al., 2013; McMahon et al., 2015), but also in some lower trophic level consumer

studies such as zooplankton (Germain et al., 2013; Mompean et al., 2016). Earlier isotopic studies on compound specific AA composition in zooplankton (McClelland and Montoya, 2002) did not report the inverse fractionation and classified Thr as a source AA. We did not find any clear relation between Thr and the apparent TL, so Thr $\delta^{15}\text{N}_{\text{AA}}$ values may not be a good estimator for the TL of benthic invertebrates, which largely feed on different forms of detritus and show large feeding plasticity. On the other hand, Sherwood et al. (2011) and McMahon et al. (2018), in their study on suspension feeding deep sea corals, observed that Thr was a consistent outlier relative to other AAs used for food web analysis. Obviously, more work is needed to clarify the use of Thr in TL estimates in benthic invertebrates.

5. Conclusions

Our study was conducted on a wide range of benthic organisms and provided new $\delta^{15}\text{N}_{\text{AA}}$ based TL estimations for benthic species on the productive shelves of the northern Bering and Chukchi seas. We showed that source and trophic AAs and their respective $\delta^{15}\text{N}$ values combined with the ΣV index indicate more complexities and probably a more precise estimation of TLs and feeding behavior of different groups than can bulk isotopic measurements of organic materials, but several complexities emerge, including the use of Thr. The AA isotope composition varied geographically (but not necessary latitudinally) with the highest $\delta^{15}\text{N}_{\text{AA}}$ values in depositional zones (DBO1 in particular), so it is inadequate to treat the DBO sampling array as a simple space for time experimental observation system for assessing the impacts of varying seasonal sea-ice persistence. A more nuanced view of each DBO sampling region as having other varying influences beyond sea-ice persistence, including water mass structure, granularity of sediments,

current flow, bloom development and phenology need to be considered. While not all causes of isotopic variability have been worked out, the isotopic composition of benthic species and calculated TLs in the northern Bering and Chukchi seas appear to reflect high feeding plasticity. These studied organisms, most likely, can change feeding behavior in response to different environmental conditions in different areas, with resulting changes in the quality of food sources. This is likely to have implications for understanding the implications of climate related changes. Our conclusions suggest the potential for high feeding adaptability of some common benthic species in the Arctic ecosystem where changes in the timing of the sea-ice melt, and, thus, earlier onset of the annual productive season, can be expected to affect the quality and quantity of food reaching the benthos.

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 1077

1078 **Table 1.** Location and depth of sampling stations grouped within each DBO region during CCGS Sir Wilfrid Laurier cruise in July
1079 2015.

Station group	Sampling Date	Latitude [°N]	Longitude [°W]	Depth [m]
DBO1	14 Jul	62.0–63.0	173.5 – 175.2	66 -76
DBO2	15-16 Jul	64.6 – 65.0	169.1 – 169.9	48
DBO3	17-18 Jul	67.0 – 67.7	168.7 – 168.9	46 - 51
DBO4	19-20 Jul	71.2 – 71.6	162.6 – 163.8	37 - 47
DBO5	20-21 Jul	71.2 – 71.4	157.1 – 157.4	47 – 125

1080

1081 **Table 2.** Mean with standard deviation $\delta^{15}\text{N}$ values of the bulk samples ($\delta^{15}\text{N}_{\text{Bulk}}$) and isolated amino acids (AA) $\delta^{15}\text{N}_{\text{AA}}$ of benthic
1082 species collected in the northern Bering and Chukchi seas. Source AAs are indicated by **bold** print. **Gly** – glycine, **Lys** – lysine, **Phe** –
1083 phenylalanine, **Thr*** – threonine, Ala – alanine, Asp – aspartic acid, Glu – glutamic acid, Ile – isoleucine, Leu – leucine, Pro – proline,
1084 Val – valine. * metabolic AA. Taxon type: A=amphipod, B=bivalve, P=polychaete. Location: Distributed Biological Observatory
1085 (DBO) regions.

Taxon/ Sampling site	$\delta^{15}\text{N}_{\text{bulk}}$ (‰)	$\delta^{15}\text{N}_{\text{AA}}$ values (‰, relative to air)												
		Gly	Lys	Phe	Ser	Tyr	Thr*	Ala	Asp	Glu	Ile	Leu	Pro	Val
<i>Suspension feeders</i>														
<i>Serripes groenlandicus</i> (B)														
DBO3	7.9 ± 0.1	4.5 ± 0.1	5.6 ± 0.3	2.9 ± 0.4	3.7 ± 0.4	4.4 ± 0.0	1.6 ± 0.7	12.0 ± 0.8	10.7 ± 0.2	12.4 ± 0.7	12.6 ± 0.5	11.2 ± 0.3	9.5 ± 1.2	12.9 ± 0.4
<i>Mya areanaria</i> (B)														
DBO3	5.9 ± 0.3	4.2 ± 0.2	5.5 ± 0.8	3.2 ± 0.4	2.4	3.6 ± 1.0	0.7 ± 0.7	10.3 ± 0.6	9.4 ± 0.4	10.7 ± 0.4	9.4 ± 0.2	8.9 ± 0.1	9.7 ± 0.9	11.9 ± 0.4
<i>Ampelisca macrocephala</i> (A)														

DBO2		4.1	-1.4	-2.3			-7.2	10.4	16.5	10.8	5.6	7.5	13.0	14.4
<i>Byblis</i> sp. (A)														
DBO2		1.0	-5.0	-8.3		-10.5	-15.0	4.8	2.9	6.2	-3.8	-0.6	0.7	3.1
DBO4		6.8	1.2			-5.2	-11.1	9.6	15.0	11.4	5.3	7.9	12.5	8.2
<i>Surface deposit feeders</i>														
<i>Macoma calcaria</i> (B)														
DBO1	9.6 ± 0.5	9.3 ± 0.4	8.2 ± 0.5	6.7 ± 0.7	6.7 ± 0.8		8.0 ± 1.9	11.3 ± 0.8	12.2 ± 0.4	12.9 ± 0.6	11.8 ± 0.6	10.6 ± 0.4	13.3 ± 0.9	14.1 ± 0.4
DBO2	7.4 ± 1.0	7.4 ± 1.0	5.6 ± 0.7	2.4 ± 1.6	5.5		3.7 ± 1.2	9.9 ± 2.4	10.2 ± 1.3	10.5 ± 2.2	11.0 ± 2.5	9.1 ± 2.8	11.6 ± 1.0	12.5 ± 2.1
DBO3	7.8 ± 0.7	7.4 ± 0.6	5.9 ± 0.6	4.9 ± 3.4	6.1		3.0 ± 0.2	11.4 ± 0.1	9.7 ± 0.4	10.8 ± 0.0	11.1 ± 0.0	9.1 ± 0.0	10.9 ± 0.3	12.5 ± 0.0
DBO4	9.3 ± 0.8	7.9 ± 2.5	6.5 ± 0.0	4.0 ± 0.6	6.0 ± 1.9		5.0 ± 3.4	9.6 ± 1.9	9.8 ± 0.4	11. ± 0.5	10.1 ± 1.7	8.7 ± 1.3	12.1 ± 1.8	11.7 ± 1.2
DBO5	7.9	7.0	6.7	4.9	4.8		4.4	8.7	9.8	10.9	9.3	7.0	10.9	12.2
<i>Macoma moesta</i> (B)														
DBO3	7.6	5.5	5.7	3.7	4.8		1.8	7.3	8.4	9.3	6.5	6.6	8.4	11.0
<i>Yoldia hyperborea</i> (B)														
DBO3	8.2	4.6	5.4	3.3	5.0	4.8	2.4	10.4	10.1	10.5	11.4	9.3	10.7	12.0
DBO5	9.6	6.7	6.8	4.9	7.1	-0.9	4.9	10.3	11.0	12.0	12.4	10.3	13.9	12.7
<i>Subsurface deposit feeders</i>														
<i>Ennucula tenuis</i> (B)														
DBO1	8.9 ± 0.4	7.0 ± 0.6	7.4 ± 0.3	6.1 ± 0.1			6.7 ± 0.5	11.7 ± 1.0	12.9 ± 0.5	12.8 ± 1.0	12. ± 0.9	10.9 ± 0.8	15.7 ± 0.5	14.4 ± 0.5
DBO2	7.6	5.8	4.7	4.3			3.8	12.3	12.0	12.6	11.2	8.5	12.0	13.2
DBO3	8.8	6.5	6.4	5.3			2.1	15.6	14.3	15.6	13.7	10.8	13.0	15.3
DBO4	9.4	5.3	6.4	4.2			4.9	11.1	12.1	12.9	10.6	10.0	14.5	13.1
DBO5		5.4	5.9	5.2			5.4	11.5	12.2	12.8	9.8	9.6	14.1	12.8
<i>Nuculana pernula</i> (B)														
DBO1	10.1	8.7	8.5	7.8				14.2	12.8	13.1	10.9	11.5	13.1	14.0
DBO3	7.5	5.1	6.7	5.4		1.9	-0.7	10.8	11.5	12.1	9.4	9.9	10.8	12.7
<i>Nuculana radiata</i> (B)														
DBO1		7.5 ±	6.6 ±	4.6 ±	7.8 ±	6.0 ±	4.1 ±	10.8 ±	11.2 ±	12.5 ±	11.7 ±	10.5 ±	10.6 ±	12.8 ±

		0.4	0.3	0.5	0.6	0.2	0.4	0.2	0.2	0.3	0.7	0.2	0.5	0.3
<i>Axiiothella catenata</i> (P)														
DBO1		11.4	1.7	9.6	15.1	-1.5	6.9	24.0	22.9	25.3	26.3	26.1	20.4	27.6
<i>Maldane sarsi</i> (P)														
DBO1	14.5 ± 0.9	7.9 ± 0.4	8.5 ± 0.7	6.7 ± 0.7	8.9 ± 1.2	7.6 ± 1.8	0.1 ± 1.0	21.7 ± 1.6	17.9 ± 0.9	21.9 ± 1.1	21.2 ± 1.5	19.9 ± 1.0	18.5 ± 0.2	22.1 ± 1.0
DBO4	14.8	7.0	7.9	5.8		3.7	-1.1	24.2	17.9	21.6	19.1	20.4	17.6	21.1
DBO5		5.7	8.2	5.0		7.9		22.4	17.2	21.5	18.7	18.3	17.9	20.7
<i>Praxillella praetermissa</i> (P)														
DBO3	11.4	9.5	5.9	4.9	8.6	1.2	-1.1	19.4	14.7	17.4	19.5	17.3	12.7	17.9
DBO4		10.4	6.7	5.6		6.1	4.0	14.2	12.1	13.8	13.5	13.3	13.2	14.4
DBO5	12.6	11.2	7.5	7.2		1.1	-1.2	18.5	15.5	18.1	19.1	18.0	17.0	19.3
<i>Pectinaria granulata</i> (P)														
DBO1		10.6	3.4	10.5	11.9		4.4	17.6	21.5	24.1	23.1	22.3	15.3	22.1
DBO4		10.2	4.0	1.8		5.2	2.5	20.4	23.1	25.6	22.4	22.2	14.3	20.7
<i>Pontoporeia femorata</i> (A)														
DBO1		10.0	1.7	6.6	11.8		8.3	12.8	16.3	18.8	16.3	13.9	19.1	18.1
DBO3		8.9	0.6	4.6	12.3		2.5	15.2	18.7	21.2	16.6	14.2	21.6	18.8
Scavengers														
<i>Anonyx</i> sp. (A)														
DBO1		13.9	4.5	7.8	19.6		-7.1	26.1	27.0	32.2	33.8	29.6	23.2	30.2
DBO4		10.7	0.9					24.1	20.7	23.3	17.3	20.2	18.6	21.3

1086

1087 **Table 3.** Trophic level (TL; mean ± SD) of selected key species calculated from AA-specific isotope analysis: TL_{Glu-Phe} and TL_{TrAA-SrAA}. Basic information on species collected is included. Taxon type: B – bivalve, P – polychaete, A – amphipoda. Feeding type: Sus –
1088 suspension feeder, SD – surface deposit feeder, SSD – subsurface deposit feeder, SC – scavenger, f – facultative. Number of samples
1089 is given in brackets next to taxon name. ΣV parameter is also tabulated here.
1090

Family/taxon/ no of samples	Feeding type	Sampling site	TL _{Glu-Phe}	TL _{TrAA-SrAA}	ΣV
Cardiidae (B)	Sus	DBO3	1.8 ± 0.0	1.5 ± 0.0	1.0 ± 0.2
<i>Serripes groenlandicus</i> (2)					
Myidae (B)	Sus	DBO3	1.5 ± 0.0	1.3 ± 0.0	0.9 ± 0.1

<i>Mya areanaria</i> (2)					
Ampeliscidae (A)	Sus, SD	DBO2	2.3	2.0	3.0
<i>Ampelisca macrocephala</i> (1)					
Ampeliscidae (A)	Sus, SD	DBO2	2.5	1.3	2.7
<i>Byblis</i> sp. (2)		DBO4	-	1.3	2.6
Yoldiidae (B)	SD, SSD	DBO3	1.5	1.4	0.7
<i>Yoldia hyperborea</i> (2)		DBO5	1.5	1.3	1.1
Tellinidae (B)	SD, fSus	DBO1	1.4 ± 0.1	1.1 ± 0.1	1.0 ± 0.2
<i>Macoma calcarea</i> (12)		DBO2	1.6 ± 0.1	1.3 ± 0.1	0.9 ± 0.1
		DBO3	1.3 ± 0.3	1.2 ± 0.1	0.8 ± 0.0
		DBO4	1.5 ± 0.1	1.1 ± 0.1	1.0 ± 0.0
		DBO5	1.3	1.0	1.3
Tellinidae (B)	SD, fSus	DBO3	1.3	1.0	1.2
<i>Macoma moesta</i> (1)					
Nuculidae (B)	SSD	DBO1	1.4 ± 0.1	1.4 ± 0.1	1.3 ± 0.1
<i>Ennucula tenuis</i> (7)		DBO2	1.6	1.4	1.0
		DBO3	1.9	1.6	1.3
		DBO4	1.7	1.4	1.3
		DBO5	1.5	1.4	1.3
Nuculanidae (B)	SSD	DBO1	1.2	1.1	0.9
<i>Nuculana pernula</i> (2)		DBO3	1.4	1.3	0.9
Nuculanidae (B)	SSD	DBO1	1.6 ± 0.0	1.2 ± 0.1	0.8 ± 0.1
<i>Nuculana radiata</i> (6)		DBO5	1.5	1.6	1.1
Maldanidae (P)	SSD, fG	DBO1	2.6	2.8	1.9
<i>Axiiothella catenata</i> (1)					
Maldanidae (P)	SSD	DBO1	2.6 ± 0.2	2.2 ± 0.1	1.5 ± 0.3
<i>Maldane sarsi</i> (6)					

		DBO4	2.6	2.3	1.9
		DBO5	2.7	2.3	1.7
Maldanidae (P)	SSD	DBO3	2.2	1.9	1.9
<i>Praxillella praetermissa</i> (3)		DBO4	1.6	1.3	0.6
		DBO5	2.0	1.8	1.0
Pectinariidae (P)	SSD	DBO1	2.3	2.2	2.5
<i>Pectinaria granulata</i> (2)		DBO4	3.7	2.6	2.4
Pontoporeiidae (A)	SSD	DBO1	2.2	2.0	1.9
<i>Pontoporeia femorata</i> (2)		DBO3	2.7	2.3	2.3
Uristidae (A)	SC	DBO1	3.8	3.2	3.0
<i>Anonyx</i> sp. (2)		DBO4		2.5	1.8













