
Interspecific differences in feeding selectivity shape isotopic niche structure of three ophiuroids in the Arctic Ocean

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Abstract :

Understanding the mechanisms that support feeding interactions and species co-occurrence in regions subject to rapid environmental changes is becoming increasingly important to predict future trends in population dynamics. However, there is still little information available on the trophic ecology for many benthic species to help us better understand trophic interactions and individual trophic roles. Here, we used stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in conjunction with the Bayesian ellipses approach to explore spatial trends in isotopic niche width and overlap of 3 syntopic arctic brittle stars (Echinodermata: Ophiuroidea; *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis*) in Baffin Bay (BB), the Canadian Arctic Archipelago (CAA), and the North Water Polynya (NOW). These 3 coexisting ophiuroids displayed great interspecific plasticity in foraging behaviors and showed a high degree of inter-individual dietary flexibility. However, differences in surface carbon composition drove the variability of resource utilization at the individual level across stations, which in turn affected trophic interactions, niche overlaps, and isotopic niche breadth of ophiuroids. Greater niche overlap was found in the highly productive region of the NOW, where consumers exhibited similar food selectivity, whereas an increase in niche segregation occurred in regions with greater sea-ice concentration. These results suggest that isotopic niche size reflects individual responses to fluctuations in food availability and possibly past competition, both induced by local oceanographic features. Our study indicates that niche parameters of ophiuroids can respond quickly to ecological and environmental gradients, which suggests an important adaptability of these species facing multiple stressors.

Keywords : Benthic community, Ophiuroidea, Trophic ecology, Isotopic niche, Canadian Arctic Ocean

15 **1. INTRODUCTION**

16

17 Arctic marine offshore ecosystems are mainly sustained by seasonal organic carbon pulses from
18 phytoplankton (i.e., open water algae) and sympagic (i.e., ice-associated algae) communities (Tamelander
19 et al., 2009). When light conditions and inorganic nutrient supplies are favorable during spring, the
20 beginning of a limited period of sea-ice algal production begins, followed by a phytoplankton bloom
21 (Hegseth 1998, Leu et al. 2011, 2015). The duration of phytoplankton and ice algal production is
22 comparable, but in terms of biomass, phytoplankton generally exceeds sea-ice algae (Leu et al. 2011). Once
23 the organic matter is produced, the vertical export of particulate organic matter (POM) varies considerably
24 during seasons and among regions according to biological and physical processes (e.g. zooplankton grazing

1 pressure, microbial processes), which ultimately control the final amount and quality of POM that reaches
2 the benthos (Herndl & Reinthaler 2013).

3 The Arctic is warming faster than any other region on Earth (AMAP 2017). As a result, the Arctic
4 seascape changes abruptly, exhibiting accelerated reductions in the thickness and extent of sea ice, with
5 predictions estimating a seasonally ice-free Arctic Ocean by 2040 (Comiso et al. 2008, Kędra et al. 2015).
6 Sea ice plays a vital role in the Arctic Ocean ecosystem by mediating physical and biological processes
7 such as the primary production (Hunt et al. 2002, Gradinger 2009, Ramírez et al. 2017), but also by serving
8 as a habitat for a large number of organisms (e.g. from bacteria to marine mammals) and as a base substrate
9 for ice algae (Garrison, 1991; Werner, 2006). Consequently, sea ice loss may affect the magnitude of the
10 set of interactions between habitats (i.e., sympagic–pelagic and sympagic–benthic coupling) in which
11 exchanges of energy, mass, or nutrients occur (Wassmann & Reigstad 2011). Benthic fauna depends largely
12 upon the supply of organic carbon from primary producers (pelagic and sympagic); thus, benthic consumers
13 and food web structure are sensitive to changes in the timing, nature, quality, or abundance of nutrients
14 (Kędra et al. 2012). Therefore, the knowledge of the ecological and biological mechanisms that drive
15 trophic ecology and support species co-occurrence is important to predict how environmental changes may
16 affect trophic interactions, species coexistence, and food web dynamics.

17 In the Arctic Ocean, the benthic community structure varies significantly due to ecological (e.g. species
18 interactions, resource availability, seasonality) and environmental gradients (e.g. temperature, salinity,
19 depth, currents, sediment type, bottom topography) (Kędra et al. 2013, Roy et al. 2014). Ecological drivers
20 that include niche complexity coupled with species interactions shape benthic composition and influence
21 the transfer of energy through trophic levels (Collin et al. 2011, Roy et al. 2014). Stable isotope analysis
22 (SIA; carbon and nitrogen), which provides time- and space-integrated insight on diet and habitat use by
23 consumers, has emerged as a common approach to examine the structure and dynamics of ecological
24 communities and carbon flow in food webs (Post 2002, Layman et al. 2007, Jackson et al. 2011). In turn,
25 the use of the isotopic niche, a low-dimensional specification of the “Hutchinsonian niche” (Hutchinson
26 1957), which consists of the area occupied by individuals in the isotopic niche space, has served to analyze

1 patterns of interactions in various ecological resolutions (Shipley & Matich 2020), and to interpret levels
2 of dietary specialization of individuals (Araújo et al. 2007, Karlson et al. 2015). The characteristics of the
3 niche vary according to intrinsic (e.g. intra- and interspecific competition) and extrinsic factors (e.g. sea-
4 ice cover, resource availability, seasonality) that influence the dimensions of the niche (Costa-Pereira et al.,
5 2017; Shipley & Matich, 2020). Furthermore, individual levels of dietary specialization within a population
6 may drive the variability of the niches (Araújo et al. 2009, Semmens et al. 2009).

7 The high densities of ophiuroids, often observed in dense aggregations, make them the most common
8 components of benthic assemblages in the Arctic Ocean (e.g. Piepenburg & Schmid, 1996; Starmans *et al.*,
9 1999; Sejr *et al.*, 2000; Brooks *et al.*, 2007). With approximately 73 species recorded, brittle stars
10 (Echinodermata: Ophiuroidea) are present in a wide geographic and bathymetric distribution (Stöhr et al.
11 2012, Ravelo et al. 2017). Among the brittle stars studied, *Ophiacantha bidentata* is a widespread arctic–
12 boreal ophiuroid with a circumpolar distribution that can switch from deposit to suspension feeding
13 depending on food availability (Brooks et al. 2007). The ophiuroids *Ophiocten sericeum*, and *Ophiopleura*
14 *borealis* have been described as endemic Arctic species, and they are considered mobile deposit or
15 predator–scavenger feeders (Paterson et al. 1982, Piepenburg & Schmid 1996, Gallagher et al. 1998). Due
16 to the high densities that ophiuroids can reach, it is believed that this group plays a fundamental role in the
17 functioning of the ecosystem by increasing the number of trophic links and maintaining trophic cascades
18 in food webs (Pearson & Gage 1984). In general, brittle stars have been suggested to be opportunistic
19 facultative deposit or suspension feeders (Jangoux 1982). However, according to changes in the availability
20 of resources, ophiuroids display wide-ranging trophic flexibility, using more than one feeding mode
21 (Pearson & Gage 1984, Brooks et al. 2007).

22 Even though we have expanded our knowledge about the diet of brittle stars in the Arctic (e.g. Graeve
23 *et al.*, 1997; Gallagher *et al.*, 1998), there are still many knowledge gaps in the trophic ecology of most
24 ophiuroids and how they coexist using the same resources while avoiding interspecific competition. In the
25 present study, we examined changes in the isotopic niche structure of ophiuroids in response to variation

1 in sea-ice conditions, local productivity, and individual-level differences in feeding behavior. Three species
2 of coexisting ophiuroids were chosen as models to test the following hypotheses: (1) depending on sea-ice
3 concentration (SIC), patterns in species niche structure (i.e., segregation and overlap of niches) will change
4 across regions, where a higher overlap of niches will be linked to regions with more SIC due to brittle stars
5 exploiting more similar food items; (2) changes in the isotopic niche width of ophiuroids will be closely
6 related to sediment $\delta^{13}\text{C}$ carbon composition and individual feeding behaviors, in which niche width
7 reduction will be linked to regions with higher abundance of resources where consumers ingest the more
8 abundant sources; and (3) a decrease in niche overlap will be associated with regions with higher
9 heterogeneity of resources in which brittle stars can use a higher spectrum of resources.

11 2. MATERIAL AND METHODS

13 2.1. *Study area*

14 Baffin Bay (BB; Fig. 1) is a semi-enclosed ocean basin located between Baffin Island and western
15 Greenland that connects the Arctic Ocean and the northwest Atlantic Ocean (Dunlap & Tang 2006,
16 Hamilton & Wu 2013). Annual sea-ice development in BB begins in late autumn and reaches its maximum
17 extent around March (Stern & Heide-Jørgensen 2003). Excluding the ice-free months between August and
18 September, BB is partially covered by sea ice (Tang et al. 2004). The Canadian Arctic Archipelago (CAA)
19 to the north-west of BB extends over an area of $3.3 \times 10^6 \text{ km}^2$, and comprises a large number of islands and
20 channels between Banks Island in the west and Baffin and Ellesmere Islands in the east (Melling 2002). In
21 this region, the sea-ice component is a mixture of both first-year and multi-year ice (MYI; Kwok, 2006).
22 The perennial multi-year ice, located almost entirely on Queen Elizabeth Islands, Western Parry Channel,
23 and M'Clintock Channel, can represent more than 50% of the total area covered by ice before the melt
24 season (Howell et al. 2013). The North Water Polynya (NOW) is located between Greenland and Canada
25 on the northern end of BB. This region is characterized by low SIC and exhibits one of the highest levels

1 of primary productivity recorded for the Arctic Ocean (Barber et al. 2001). Polynyas are areas of open water
2 or with minimal sea-ice coverage surrounded by a contiguous ice pack (Barber & Massom 2007).

3

4 **2.2. Sample collection**

5 On board the Canadian research icebreaker CCGS ‘Amundsen’ fifteen stations were visited from 19
6 August to 1 September 2018 and from 20 July to 23 August 2019 to collect sediment and brittle stars (i.e.,
7 *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis*) in 3 different Canadian Arctic
8 regions (Fig. 1). Brittle stars were found and collected at 9 of the 15 stations (Table S1) for subsequent SIA
9 using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm. In addition, surface sediment
10 samples were collected from 13 stations (Table 1), from the upper 1 cm of a box core (0.125 m²). From
11 each box core, sediments were collected for SIA (one sample per station) using 60 ml truncated syringes
12 and for pigment content analysis (three samples per station) using 10 ml truncated syringes. Since carbon
13 isotope ratios ($\delta^{13}\text{C}$) vary substantially among primary producers, but changes little between each trophic
14 level (0–1‰; Peterson & Fry 1987, Post 2002, Layman et al. 2007), the carbon isotopic composition of
15 surface sediment was used in the present study as a proxy to determine the relative contribution of primary
16 carbon food sources in the diet of ophiuroids. In addition, sediment surface chlorophyll *a* (chl *a*)
17 concentration, a short-term proxy of productivity, was carried out at Laval University, Quebec, Canada,
18 following the modified protocols of Riaux-Gobin & Klein (1993) and Link et al. (2011). After collection,
19 all samples were frozen for subsequent SIA and pigment analyses.

20

21 **2.3. Stable isotope analyses**

22 Sediment and brittle stars samples were freeze-dried at –50°C and ground to a fine powder with a mortar
23 and pestle. For sediments, carbonates were removed using 1 N HCl until bubbling ceased. For brittle stars,
24 a total of 92 individuals were used for SIA (Table S1). Lipid extraction was carried out in brittle stars using
25 a solution of dichloromethane:methanol (2:1). Brittle stars samples were then decarbonated by exposing

1 them to HCl vapors for 48 h in an airtight container. After acidification, to verify the total removal of
 2 carbonate in the samples, drops of acid were applied to dried material (champagne test) to check that no
 3 more bubbles (i.e., CO₂ that would be produced by the chemical dissociation of the carbonates) formed.

4 Stable nitrogen and carbon isotope ratios were measured using a continuous-flow isotope ratio mass
 5 spectrometer (Thermo Electron Delta Advantage) in the continuous-flow mode (Thermo Electron ConFlo
 6 III) with an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies) in
 7 the oceanography laboratory at Laval University. Replicate measurements of international standards
 8 (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental
 9 Microanalysis) established measurement errors of ≤0.2 ‰ for δ¹³C and δ¹⁵N. Stable isotope ratios were
 10 expressed in delta (δ) units (δ¹³C, δ¹⁵N) as the per mil (‰) difference with respect to standards: δX (‰) =
 11 [(R_{Sample} - R_{Standard})/R_{Standard}] × 10³, where X is ¹³C or ¹⁵N of the sample and R is the corresponding ratio
 12 ¹³C/¹²C or ¹⁵N/¹⁴N. Standards were calibrated against the international references Vienna PeeDee Belemnite
 13 for carbon and atmospheric air for nitrogen.

14

15 **2.4. Trophic positions**

16 The estimation of trophic positions (TPs) was used to characterize the functional role of individuals in
 17 brittle star species. The TP of ophiuroids was estimated using the ‘OneBaseline’ model in the Bayesian
 18 ‘tRophicPosition’ package (Quezada-Romegialli et al. 2018) using the following equation:

$$19 \quad \delta^{15}\text{N}_c = \delta^{15}\text{N}_b + \Delta\text{N}(\text{TP} - \lambda)$$

20 Where δ¹⁵N_c corresponds to the nitrogen stable isotope value of the consumer for which the TP is estimated,
 21 δ¹⁵N_b represents the nitrogen isotope ratio of surface sediment bulk organic matter for each region studied;
 22 ΔN corresponds to the trophic discrimination factor (TDF) for nitrogen, and λ is the TP of baseline sources.
 23 TP of basal primary producers was set to 1.0, meaning that TP ≤2 (low trophic level) represents primary
 24 consumers, >2 TP <3 (intermediate trophic level) represents secondary consumers (e.g. omnivores), and
 25 TP ≥3 (high trophic level) represents top consumers and scavengers.

1 **2.5. *Sea-ice concentration data***

2 Average SIC was derived from satellite Nimbus-7 SMMR and DMSP SSM / I-SSMIS passive
3 microwave at a grid cell size of 25×25 km (Cavalieri et al. 1996). The dataset was downloaded from the
4 National Snow and Ice Data Center (<https://nsidc.org/data/NSIDC-0051/versions/1>). For each station, we
5 calculated the average SIC (%) of 2 months: the month before the sampling and the month of the sampling
6 date. This average was considered relevant in this study because the isotopic turnover rate in tissues of
7 some marine invertebrates with Arctic distributions (e.g. *Onisimus litoralis*, *Mytilus edulis*, and *Macoma*
8 *calcareo*) can vary between 1 and 3 months, affecting dynamics in the isotopic composition of consumers
9 (e.g. McMahon et al. 2006, Kaufman et al. 2008). In addition, the isotopic composition of consumers may
10 vary over time due to environmental conditions such as seasonal sea-ice cover dynamics (Kaufman et al.,
11 2008).

13 **2.6. *Statistical analyses***

14 All statistical analyses were performed using R Studio version 1.4.1106 (R Core Team, 2019) and
15 graphical procedures with Ocean Data View version 5.1.7 (<https://odv.awi.de>). Homogeneity of variance
16 and normality of residuals were verified using the Shapiro-Wilk test on residuals. Linear models were
17 employed to simultaneously evaluate the effect of environmental variables (i.e., depth and SIC) and their
18 interactions on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values found in sediment and the ophiuroids' samples. A Kruskal-Wallis test
19 was conducted to examine the differences in stable isotope ratios of carbon and nitrogen in brittle stars
20 among species, stations, and regions. Significant effects implicating categorical factors (SIC, depth,
21 regions, and species) were further analyzed with Tukey post-hoc test using the 'emmeans' package (v2.27-
22 61) (Lenth & Lenth 2018). The core isotopic niche space occupied by brittle stars was calculated using the
23 standard ellipse area in the 'SIBER' package in R (Jackson et al. 2011). Furthermore, the probabilistic
24 method of Jackson et al. (2011) was used to estimate the mode and the credible interval of the Bayesian-
25 simulated standard ellipse areas. Specifically, we used the sample size-corrected standard ellipse area

1 (SEAc), which is a more robust approach that encompasses the core (around 40 %) of the isotopic
2 observations within each species group and is therefore less sensitive to sample size and isotopic outliers
3 (Jackson et al. 2011). SEAc's credibility intervals were based on 1000000 iterations and a burn-in of
4 100000.

5

6 **3. RESULTS**

7

8 **3.1. Isotopic composition of sediments**

9 Sediment organic matter $\delta^{13}\text{C}$ values covered a wide range in the CAA region (from -16.5 to -23.9‰ ;
10 mean \pm SD = $-22.0 \pm 2.7\text{‰}$, $n = 6$), compared with a narrower range observed in the NOW (-22.2 to $-$
11 22.8‰ ; mean = $-22.4 \pm 0.3\text{‰}$, $n = 4$) and BB region (-21.0 to -22.8‰ ; mean = $-21.6 \pm 0.8\text{‰}$, $n = 4$). At
12 stations on the west of the CAA region (i.e., Stns QMG3, QMG4, and QMGM; see Fig. 1), $\delta^{13}\text{C}$ values of
13 surface sediments were slightly depleted in carbon isotopes ($\leq -23\text{‰}$). The $\delta^{13}\text{C}$ values of surface sediments
14 found in this study overlapped partially with those determined in previous studies. For instance, $\delta^{13}\text{C}$ values
15 ranged from -24.2 to -20.4‰ in the CAA (Goñi et al. 2013), from -22.7 to -18.8‰ in BB (Yunda-Guarin
16 et al. 2020), and from -22.9 to -22.1‰ in the NOW (Friscourt 2016, unpublished data). $\delta^{15}\text{N}$ sediment
17 values covered a wide range among stations ranging from 5.6 to 8.6‰ (Table 1). The most ^{15}N -enriched
18 values in sediments occurred at the deepest BB stations, whereas the most ^{15}N -depleted values were found
19 in the NOW (Table 1, Fig. 3). Significant differences were found in $\delta^{15}\text{N}$ values of sediments among regions
20 (ANOVA, $F = 7.29$, $df = 2$, $p = 0.001$). Linear models revealed a significant effect of depth on sediment
21 $\delta^{15}\text{N}$ values ($F = 28.59$, $p < 0.001$).

22

23 **3.2. Trophic position and isotopic composition of brittle stars**

24 TPs of brittle stars ranged between the second and the fifth trophic level. *Ophiacantha bidentata* had
25 the highest modal TP (mean TP = 4.33), while *Ophiocten sericeum* showed the lowest modal TP (mean TP

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1 = 2.63) in the CAA region (Fig. 2). The greatest modal TP of *O. sericeum* (mean = 3.99) was evidenced
2 mainly in the NOW, where all brittle stars predominantly occupied high TPs compared to BB. The greatest
3 modal TP of *Ophiopleura borealis* (mean = 4.05) was found in the CAA region. The greatest ranges of TPs
4 were observed for all 3 species of brittle stars in BB (Fig. 2).

5 Brittle stars displayed a wide range of isotopic compositions among stations and regions (Table 2, Fig.
6 3). Linear models revealed a significant effect of SIC and depth on $\delta^{13}\text{C}$ values of brittle stars species among
7 regions ($p < 0.001$; Table S2) and also an interactive effect of SIC and depth on $\delta^{13}\text{C}$ values of ophiuroids
8 ($p = 0.03$; Table S2). In addition, linear models showed an interactive effect of SIC and chl *a* concentration
9 on $\delta^{13}\text{C}$ values of ophiuroids ($p < 0.001$). However, chl *a* content alone was not shown to be an
10 environmental variable that significantly affected the $\delta^{13}\text{C}$ values of ophiuroids ($p = 0.33$). Significant
11 differences in $\delta^{13}\text{C}$ values across species (Kruskal-Wallis, chi-squared = 41.94, $df = 2$, $p < 0.001$) and
12 regions (Kruskal-Wallis, chi-squared = 21.36, $df = 2$, $p < 0.001$) were found in this study. Among species,
13 the most ^{13}C -enriched value ($\delta^{13}\text{C} = -18.2\text{‰}$) was found in *O. bidentata* in the NOW region, while the most
14 ^{13}C -depleted value ($\delta^{13}\text{C} = -24.9\text{‰}$) corresponded to the species *O. sericeum* in the CAA region (Table
15 S1). Average $\delta^{13}\text{C}$ values ranged from $-24.5 \pm 0.2\text{‰}$ (*O. sericeum*) to $-19.0 \pm 0.4\text{‰}$ (*O. bidentata*) in the
16 CAA region, from $-20.2 \pm 0.4\text{‰}$ (*O. sericeum*) to $-19.1 \pm 1.5\text{‰}$ (*O. bidentata*) in the NOW, and from –
17 $20.5 \pm 0.5\text{‰}$ (*O. sericeum*) to $-19.3 \pm 0.4\text{‰}$ (*O. bidentata*) in the BB (Table 2).

18 Linear models revealed an effect of depth on $\delta^{15}\text{N}$ values of brittle stars species among regions ($p <$
19 0.01) and an interaction effect of SIC and depth on $\delta^{15}\text{N}$ values of ophiuroids ($p < 0.001$; Table S3).
20 Likewise, significant differences in $\delta^{15}\text{N}$ values among stations were found (chi-squared = 24.15, $df = 8$, p
21 = 0.002). However, $\delta^{15}\text{N}$ values showed no significant differences across regions (chi-squared = 0.32, $df =$
22 2 , $p = 0.85$). $\delta^{15}\text{N}$ varied across species (chi-squared = 26.41, $df = 2$, $p < 0.001$). The most ^{15}N -depleted
23 values were found in *O. sericeum* (10.1‰) in the CAA, and the most ^{15}N -enriched value in *O. bidentata*
24 (15.2‰) in the BB region (Table S1). Average $\delta^{15}\text{N}$ values ranged from $10.2 \pm 0.1\text{‰}$ (*O. sericeum*) to 14.5

1 $\pm 0.4\%$ (*O. bidentata*) in the CAA, from $11.6 \pm 0.8\%$ to $13.8 \pm 1.3\%$ (*O. sericeum*) in the NOW, and from
2 $12.6 \pm 0.4\%$ (*O. borealis*) to $13.9 \pm 0.84\%$ (*O. bidentata*) in the BB (Table 2).

3

4 **3.3. Isotopic niche widths and niche overlap of brittle stars**

5 The isotopic niche width of brittle stars species, measured as the SEAc, differed by regions (see Figs. 4
6 and 5). SEAc ranged from 0.54 to 3.45 for *O. bidentata*, from 1.22 to 3.31 for *O. sericeum*, and from 0.52
7 to 1.21 for *O. borealis* (Fig. 4). Based on SEAc values, the largest isotopic niche width was found for *O.*
8 *bidentata* in the NOW region (SEAc = 3.45) and *O. sericeum* in the CAA region (SEAc = 3.31). In contrast,
9 the smallest niche width was found for *O. borealis* in the CAA region (SEAc = 0.52). The isotopic niche
10 area of the species *O. sericeum* in the CAA region pointed to 2 different sub-groups, one with ^{13}C -depleted
11 values to the west (Station QMG4; Table S1), another with more ^{13}C -enriched values to the east. Based on
12 posterior Bayesian estimates, the probability of an increase in the amplitude of the SEAc varied within
13 species and among regions. In the CAA, *O. sericeum* showed the highest probability (100%) of having a
14 greater isotopic niche width than *O. bidentata* and *O. borealis*. However, in the NOW, *O. bidentata* showed
15 the highest probability (99%) of having a wider isotopic niche width than the other 2 species. Finally, in
16 BB, *O. sericeum* had the highest probability of having a broader isotopic niche width than *O. borealis*
17 (96%) and *O. bidentata* (81%).

18 Among regions, the isotopic niches ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ biplots) revealed differences in overlap of consumers
19 (Fig. 5). Niche analysis showed that the NOW was the only region where the 3 brittle stars shared the
20 isotopic niche space. However, in other regions, our results showed marked differences in isotopic
21 composition, and brittle stars either did not share niche space (i.e., CAA), or niche overlap only occurred
22 between 2 species (i.e., BB; Fig. 5). The area of overlap comprised between 13 and 54% of the total isotopic
23 niche area among all regions. The greatest niche overlaps occurred between the species *O. sericeum* and *O.*
24 *borealis*, which shared at least 54 and 29% of the isotopic niche area in the NOW and BB regions,
25 respectively (Fig. 5B,C). Moreover, biplots showed differences in resource use among species on a local

1 and regional scale, revealing greater variability in resource use by ophiuroids in the CAA region than in the
2 other 2 regions. Finally, isotopic niche and TP models indicated that *O. sericeum* encompassed a greater
3 degree of isotopic variability in its prey, feeding lower in the food chain than the other ophiuroids, whereas
4 individuals of the species *O. bidentata* fed high in the food chain.

5

6 **4. DISCUSSION**

7

8 **4.1. Isotopic composition and carbon use by consumers**

9 Previous studies denoted a pattern in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of benthic fauna in both the Arctic and
10 Antarctic Oceans with respect to fluctuations in local oceanographic conditions such as SIC (e.g. Michel et
11 al., 2019; Norkko et al., 2007; Yunda-Guarin et al., 2020) and depth (Stasko et al. 2018b). Together, these
12 studies highlighted the key indirect control of environmental conditions (e.g. SIC and depth) in the isotopic
13 composition and availability of food resources, which ultimately induced benthic food web structure shifts.
14 For instance, seasonal changes in oceanographic conditions (e.g. depth, SIC, water temperature) and
15 variability in the composition of food items proved to be 2 important factors altering the isotopic
16 composition of Arctic amphipods by inducing changes in nitrogen and carbon turnover rates (Kaufman et
17 al. 2008). Isotopic values may also reflect a range of varying proportions of food items assimilated by
18 individuals over time (Bearhop et al. 2004) or similar food items with different $\delta^{13}\text{C}$ isotopic compositions.
19 In our study, SIA did not provide high resolution of dietary information of brittle stars according to
20 oceanographic conditions or food availability. However, $\delta^{13}\text{C}$ values of surface sediment organic matter in
21 this study were a useful indicator of the relative contribution of primary organic carbon sources to
22 ophiuroids. Considering that $\delta^{13}\text{C}$ values in surface sediments in the Arctic Ocean typically range between
23 -22 and -30‰ (average -26.8‰) for terrestrial sources and between -17 and -22‰ for marine sources
24 (average -20.6‰) (Koziorowska et al. 2016, Kumar et al. 2016, Włodarska-Kowalczyk et al. 2019), $\delta^{13}\text{C}$
25 values found in surface sediments in this study suggested a mix of carbon sources available for benthic

1 consumption (Table 1). In addition, the $\delta^{13}\text{C}$ values of primary sources calculated in previous studies ranged
2 from -13.4 to -20.7‰ in the BB, from -7.1 to -25.3‰ in the CAA, and from -8.9 to -14.1‰ in the NOW
3 for sympagic algae, and from -20.1 to -26.3‰ in the BB, from -23.2 to -27.4‰ in the CAA, and from $-$
4 22.1 to -27.6‰ in the NOW for suspension POM (SPOM) (Roy 2014, Friscourt 2016, Yunda-Guarin et al.
5 2020, Gosselin, unpublished data). Hence, $\delta^{13}\text{C}$ values of surface sediments found in this study implied that
6 ophiuroids diet was influenced by carbon items from different origins. On the one hand, depleted
7 $\delta^{13}\text{C}$ values in ophiuroids ($<-23\text{‰}$) suggested that brittle stars could use a mix of mostly marine-derived
8 carbon sources of benthic or pelagic origin such as SPOM. On the other hand, in the NOW, the BB regions,
9 and the east part of the CAA, $\delta^{13}\text{C}$ values suggested that brittle stars could rely on at least 2 food sources:
10 marine-derived carbon and detritus enriched by microbial activity.

11

12 **4.2. Niche structure under local oceanographic conditions and food supply**

13 Bayesian estimation of the standard ellipse area (SEAc) showed differences in the isotopic niche width
14 of brittle stars across species and regions. In this study, linear models revealed a significant effect of SIC
15 on $\delta^{13}\text{C}$ values of ophiuroids among regions, suggesting that feeding habits may differ according to changes
16 in environmental conditions. However, a clear pattern of the influence of sea-ice condition on niche
17 dynamics and structure could not be established, in part due to a great inter- and intraspecific variability in
18 patterns of resource use by consumers. For example, results showed that the isotopic niche area of
19 *Ophiecten sericeum* within the CAA region was made up of 2 different sub-groups of individuals, in which
20 individuals had marked differences in $\delta^{13}\text{C}$ values between western and eastern stations. In addition, our
21 results highlighted differences in patterns of overlap and segregation of niches according to SIC, but
22 contrary to what we expected, an increase in the segregation of the niches was linked to regions with more
23 SIC. In contrast, a higher overlap of niches was associated with open water regions. In other words, niches
24 were less similar when the SIC was greater.

1 Lesser et al. (2020) examined the connection between niche size and ecosystem productivity outside of
2 the environmental influence in niche structure and found a correlation between increases in primary
3 productivity and reductions in trophic niche size. Here, it was not possible to distinguish a clear trend of
4 niche size reduction of brittle star species according to sediment chl *a* concentration, a proxy of the amount
5 of local primary production (Table 1), suggesting that production intensity alone is not the principal driver
6 of isotopic variability in organisms and therefore niche characteristics. For example, our findings
7 highlighted a greater isotopic niche width for *O. sericeum* and *Ophiacantha bidentata* associated with the
8 CAA and NOW regions, where the highest concentrations of chl *a* were recorded (Table 1). Meanwhile,
9 *Ophiopleura borealis* displayed the narrowest niche width in the CAA region, suggesting reliance upon a
10 narrower range of food items or changes in dietary preferences over time (Bearhop et al. 2004). However,
11 since sediment pigments are often considered an extremely short-term proxy of productivity due to rapid
12 degradation processes, they are less appropriate descriptors for long-term benthic responses (Ming-Yi et al.
13 1993). In contrast, isotope values integrate a measure of carbon and nitrogen over longer temporal scales
14 (Bearhop et al. 2004).

15 Based on $\delta^{13}\text{C}$ values of individuals, the niche width of brittle stars could be influenced by differences
16 in individual-spatial patterns of food selectivity driven by local variation in carbon items and ecological
17 interactions (Bolnick et al. 2010). In this sense, trends towards broader niches suggest that regions with
18 more heterogeneity of resources could support greater dietary variation among consumers, allowing the
19 exploitation of preferred or more nutritive food items (Costa-Pereira et al. 2017). In contrast, a reduction of
20 the niche size among ophiuroids could be associated with regions with more homogeneous resources due
21 to a reduction in the number of specialist individuals. Taken together, these results suggest that the spatial
22 variability in niche structures (niche breadth) could reflect the degrees of exposure of consumers to multiple
23 resource pools over time and individual spatial patterns of dietary selectivity (see Section 4.3). However,
24 given that our results correspond to a seasonal timeframe (summer), it is difficult to infer trends in niche
25 dynamics across all seasons accurately. Therefore, further studies that monitor benthic niche dynamics in

1 relation to environmental changes, including global warming, over a long timescale (multiyear) are
2 necessary to more accurately predict food web variations in areas exposed to rapid environmental changes.

3

4 **4.3. Species-specific dietary selectivity and niche dynamics**

5 In general, brittle stars are considered generalist species and employ a large variety of foraging behaviors
6 to access a wide diversity of resources (Pearson & Gage 1984). These feeding attributes have led different
7 ophiuroid species to be recognized as ecologically equivalent species that share habitat and food sources
8 (Pearson & Gage 1984). Nevertheless, foraging behaviors in consumers are dynamic and tend to vary over
9 time as a response to multiple variables including prey availability, seasonality, competition, and even the
10 physiological state of the consumer (Yeakel et al. 2016). Since tendencies in generalist species towards a
11 particular diet only exist on a short time scale, it is difficult to establish with precision the fluctuations in
12 the isotopic composition of these individuals, especially when their isotopic composition probably reflects
13 an average of different food items ingested over time (Bearhop et al. 2004). As expected, our results showed
14 high variability in resource-use patterns (i.e., changes in the dietary niche width) among brittle star species
15 and differences in species-specific feeding selectivity, which ultimately led to significant changes in niche
16 width of these ophiuroids. Based on the isotopic composition of brittle stars, changes in the relative
17 contribution of primary sources seem to have affected the interspecific characteristics of the feeding mode
18 of ophiuroids. Interestingly and contrary to what is specified in most of the literature (see Section 1), brittle
19 stars showed high inter-individual variability in feeding behavior across stations in which each individual
20 showed its own pattern of feeding. Accordingly, the species niche width varied significantly due to
21 intraspecific variability in foraging behaviors and individual species trends in dietary selectivity linked to
22 ecological processes such as productivity (Semmens et al. 2009, Araújo et al. 2011). For instance,
23 consumers exhibited greater differences in resource use in the less productive regions of the CAA and BB,
24 increasing the segregation of the niches (Robinson & Strauss 2020). Notably, in the CAA region, a broad
25 isotopic niche (SEAc) occurred in *O. sericeum*, which suggested variation in its feeding selectivity at the
26 individual level across stations, leading to an expansion of its trophic diversity. In contrast, in the same

1 region, a reduction of the isotopic niche width (i.e., low trophic diversity) in *O. bidentata* and *O. borealis*
2 suggested high feeding selectivity or low dietary evenness over time (Bearhop et al. 2004). This is also
3 supported by the field experiment conducted by Mäkelä et al. (2017a) with benthic macrofauna, showing
4 that differences in food utilization by polychaetes, bivalves, and crustaceans were site-specific, with no taxa
5 exclusively exhibiting higher rates of ice algal uptake, suggesting high feeding plasticity.

6 Variations in niche width could also be largely driven by the range of trophic levels at which individuals
7 obtained their prey (Bearhop et al. 2004). In connection with this assumption, an increase in brittle star
8 isotopic niche could also be associated with the use of a greater spectrum of trophic levels at which
9 individuals obtained their prey. On this basis, the wide difference in $\delta^{15}\text{N}$ values among ophiuroids was
10 interpreted as a reflection of the considerable feeding flexibility of these invertebrates. Among these, *O.*
11 *sericeum* seemed to consume the widest spectrum of prey items, as shown by the important variability in
12 both isotopic dimensions.

13 Trophic position estimates showed that brittle stars fed at various trophic levels. In most regions,
14 ophiuroids occupied intermediate to high trophic levels, suggesting that ophiuroids were predominantly
15 mobile deposit feeders and omnivores (including carnivores/scavengers). However, brittle stars did not
16 always show a similar range of TPs within the same region. For example, in the CAA region, *O. sericeum*
17 had the most ^{15}N -depleted values of the 3 study species, which suggested that individuals predominantly
18 fed on lower trophic levels than the other species. In contrast, in other regions, such as the NOW, ophiuroids
19 shared higher mean trophic levels, implying that consumers relied primarily on heterotrophic prey or
20 reworked organic matter typically ^{15}N -enriched by microbial activity (Mäkelä et al. 2017a). Finally, brittle
21 stars in the BB region showed the broadest range in TPs, indicating that individuals adopted a
22 predominantly omnivorous behavior to exploit a broad spectrum of trophic resources (i.e., trophic
23 generalists or intermediate feeding specialists). Based on our results, it seems likely that individuals within
24 each species do not always share similar diets and have varied preferences towards different food items.
25 The inter-individual dietary flexibility observed in brittle stars would suggest that ophiuroids play an
26 important role in benthic food webs from the point of view of increasing the number of trophic links and

1 energy flow pathways from one trophic level to the next. Considering the high densities that ophiuroids
2 represent in benthic ecosystems of the Arctic, for example >400 ind. m^{-2} in Young Sound, Greenland and
3 the Barents Sea (Piepenburg & Schmid 1996, Blicher & Sejr 2011), brittle stars could be critical ecological
4 species driving dynamics, functioning, and stability of benthic food webs.

5

6 **4.4. Niche overlap and brittle stars co-occurrence**

7 The co-occurrence of ecologically similar species is founded on the partitioning of their ecological
8 niches or in exploiting different niches driven in some part by diet shifts (Lush et al. 2017, English et al.
9 2020). Some studies have been conducted in the Arctic Ocean based on approaches using multiple
10 biomarkers to assess how benthic species co-occur using common resources (Stasko et al. 2018a, Yunda-
11 Guarin et al. 2020). However, only a few studies have been carried out to study ecological interactions of
12 ecologically similar species, including trophic relationships and niche partitioning using the isotopic niche
13 concept. In resource-limited environments, competition for food sources among sympatric species is likely
14 to increase during periods of low primary production (Chase & Leibold 2003). Therefore, seasonality and
15 availability of resources may be the main variables driving competition and restricting species co-
16 occurrence in space and time (MacArthur 1969). Furthermore, species co-occurrence may also depend on
17 changes in the diversity of the resources (Costa-Pereira et al. 2019). According to our analysis, fluctuations
18 in spatial patterns of sediment organic matter composition and variations in species-specific food selectivity
19 in response to prey availability and/or competition could have influenced niche partitioning. In this instance,
20 a greater resource heterogeneity, including the availability of a high range of sources, for example in the
21 CAA (Fig. 3), could induce a high degree of inter-individual dietary variation among individuals avoiding
22 isotopic niche overlap between species in our study. Costa-Pereira et al. (2019) pointed out that an increase
23 in niche overlaps may suggest a low degree of inter-individual diet variation promoted by resource
24 homogeneity and omnivorous feeding behaviors. Therefore, without considering possible competition with
25 other species, our results suggest that reductions in niche overlap between the 3 species studied were more
26 closely related to inter-individual dietary flexibility to exploit different resources.

1 The greatest niche overlap among brittle stars occurred between *O. sericeum* and *O. borealis* in the
2 NOW region, highlighting moderate levels of resource partitioning between both species. However, given
3 that the isotopic niche overlap between these species was moderate (54%), their co-occurrence could be
4 viable in natural conditions when species delimited their foraging niche using flexible feeding
5 strategies. Conversely, *O. bidentata* exhibited little niche overlap with the other 2 species in the NOW and
6 complete segregation of their niches in the CAA and BB regions, suggesting limited potential competition
7 with co-occurring species. In this case, some individuals of *O. bidentata* showed food preferences for a ¹³C-
8 enriched food source, increasing plasticity at the species level in foraging behavior. Our results suggest that
9 isotopic niche aspects might result from past competition, environmental conditions, or changes in organic
10 carbon composition that shape individuals into adopting a specific feeding strategy to satisfy their energy
11 requirements. Finally, based on Tinker et al. (2008) and our results, food limitation could lead to behavioral
12 diversification and dietary specialization of benthic species, including ophiuroids. Therefore, an increase in
13 the individual level of diet specialization could be a factor driving the structure and dynamics of benthic
14 food webs.

15

16 **Concluding remarks**

17 Climate change is expected to lead to shifts in the availability and abundance of food sources for benthic
18 consumption in the future Arctic Ocean that are not yet identified and may affect the dynamics and stability
19 of food webs (Kędra et al. 2015). Despite the ecological importance of ophiuroids as key species in benthic
20 assemblages and trophic cascades in the Arctic Ocean (Pearson & Gage 1984), only a few studies have
21 been carried out to date to better understand better the mechanisms that drive feeding ecology and trophic
22 niches of Arctic brittle star species. Here, ecological niche analyses of 3 syntopic brittle star species using
23 the isotopic niche approach provided insight into the mechanisms driving niche dynamics, feeding behavior,
24 and co-occurrence of ophiuroids. We found some evidence that SIC is an important driver of niche structure
25 in ophiuroids. Greater interspecific niche segregation was indeed associated with regions with greater SIC.

1 Additionally, changes in organic carbon composition highlighted a strong influence of species-specific
2 degrees of dietary selectivity shaping niche structure and overlap. Since the Arctic Ocean ecosystem is
3 experiencing strong changes in abiotic conditions due to climate change that could affect ecosystem
4 functioning, more studies of this type are needed to better understand the role of individual species in the
5 functioning and stability of benthic food webs. Finally, our results revealed the great ability of some
6 individuals to adjust their dietary behaviors according to fluctuations in resource composition, highlighting
7 the difficulty of generalizing feeding modes of benthic consumers and the lack of information about trophic
8 interactions, diets, and habitat use by benthic species.

9

10 **Data accessibility statement**

11 The species datasets generated and/or analyzed during the present study are included in this article
12 (Tables S1–S3 in the Supplement). Additional datasets, including all scripts, are available in GitHub
13 (<https://doi.org/10.5281/zenodo.5584830>).

14

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3

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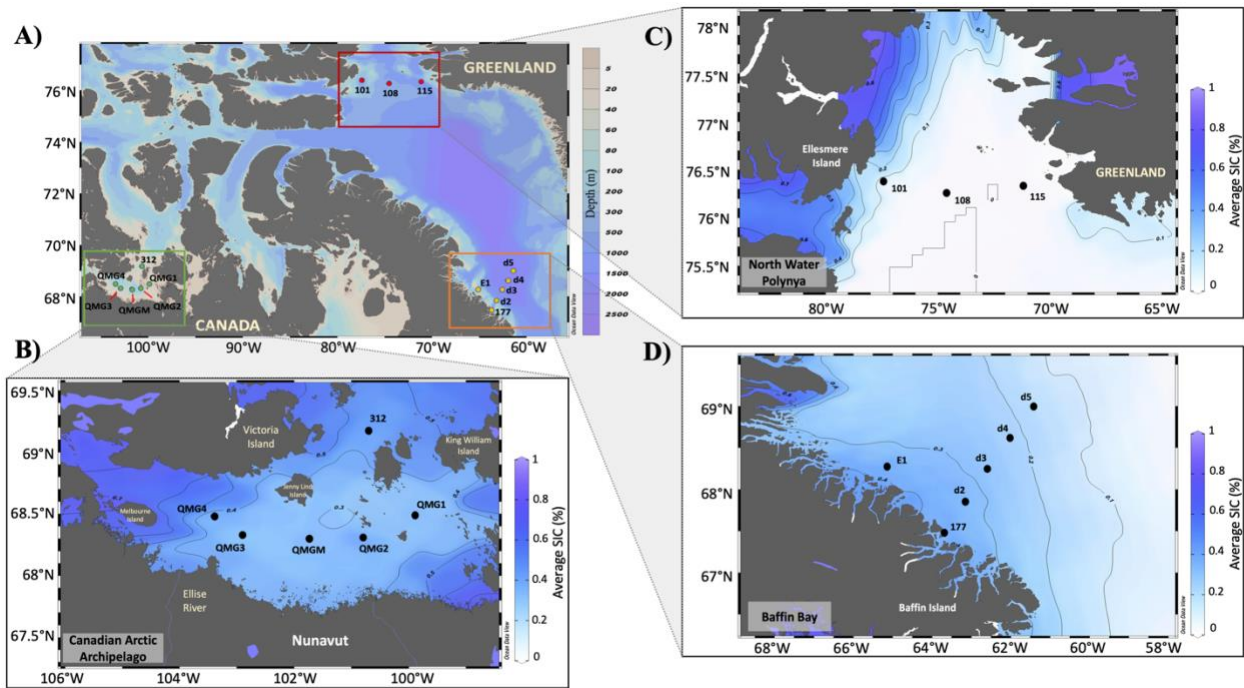
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- 20

1 **Figures**

2

3 **Fig. 1. Location of sampling stations with bathymetric gradients.** (A) Red dots represent the stations in

4 the North Water Polynya, green dots in the Canadian Arctic Archipelago, and orange dots in Baffin Bay.

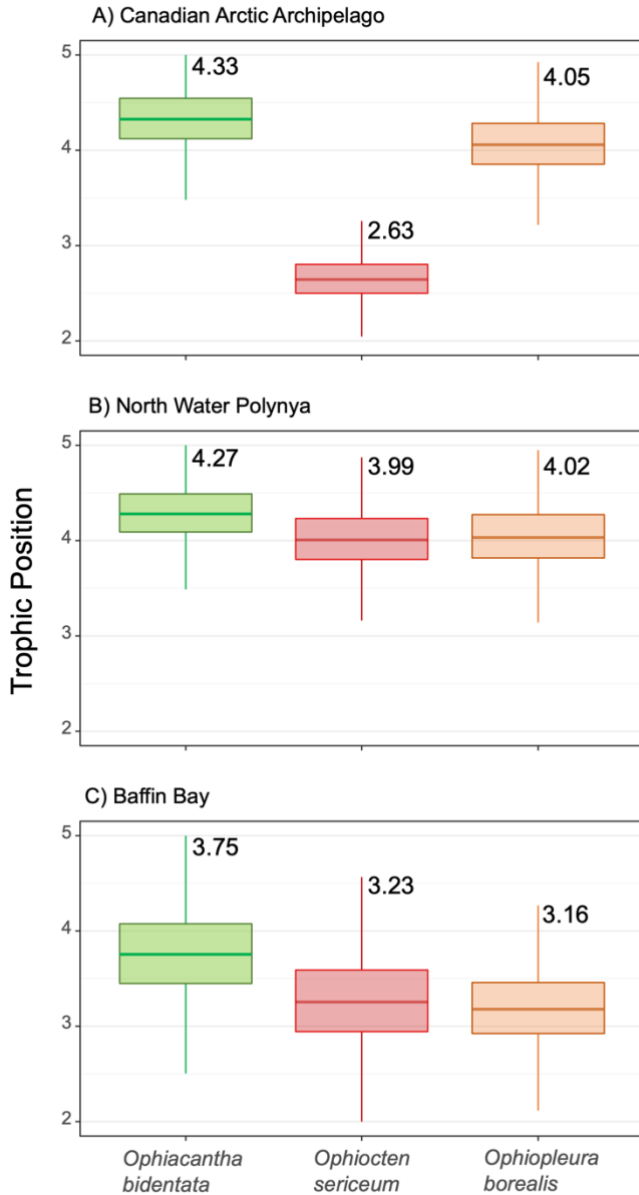
5 (B–D) Average sea-ice concentrations (SIC) for the regions studied, ranging from 0 to 100% (expressed

6 here between 0 and 1; gray lines), in the summer (June to August, between 2018 and 2019) were derived

7 from the National Snow and Ice Data Center (<https://nsidc.org/data/nsidc-0051>).

8

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1

2 **Fig. 2. Estimated trophic position (TP) of brittle stars.** Horizontal lines represent the modal TP occupied

3 by different brittle star species (mean TP values given above the boxes; black numbers). The middle part

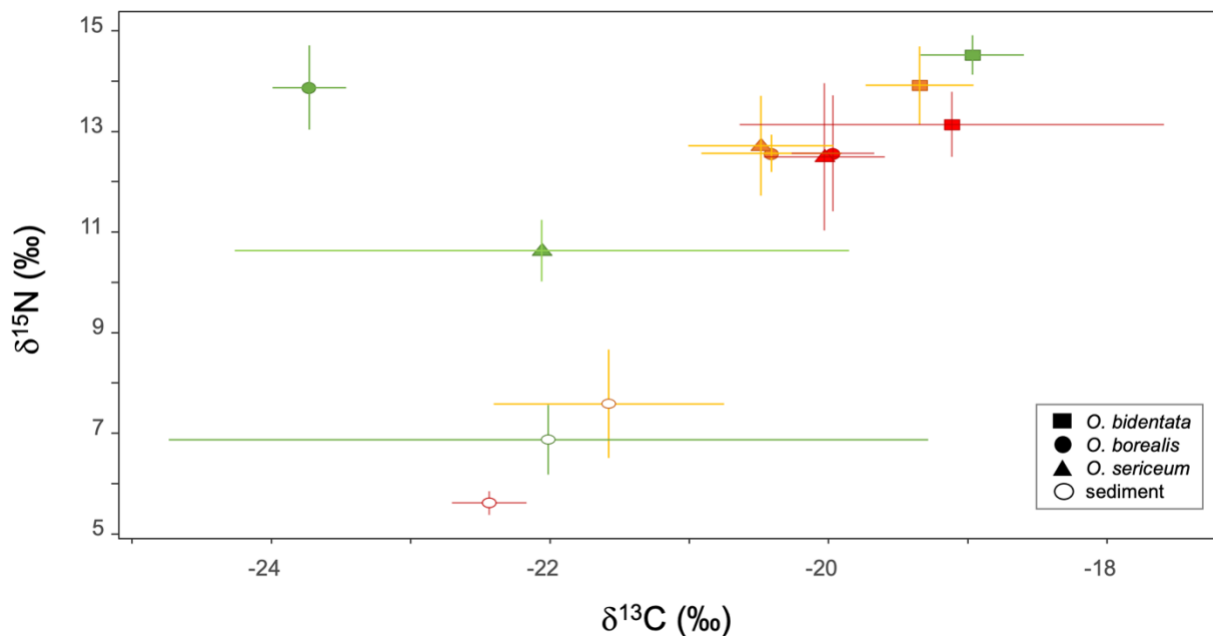
4 of the boxes represents the interquartile range, i.e., the middle quartiles (or the 75th minus the 25th

5 percentile). Estimates were made using the ‘tRophicPosition’ model across the Arctic regions: (A) the

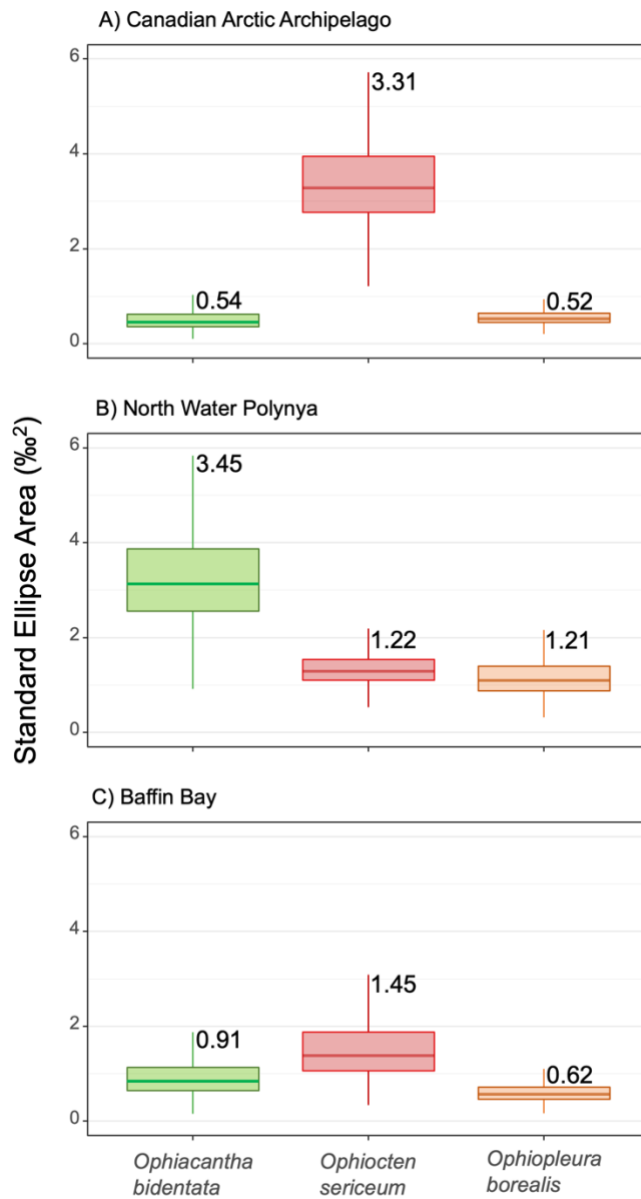
6 Canadian Arctic Archipelago, (B) the North Water Polynya, and (C) Baffin Bay.

7

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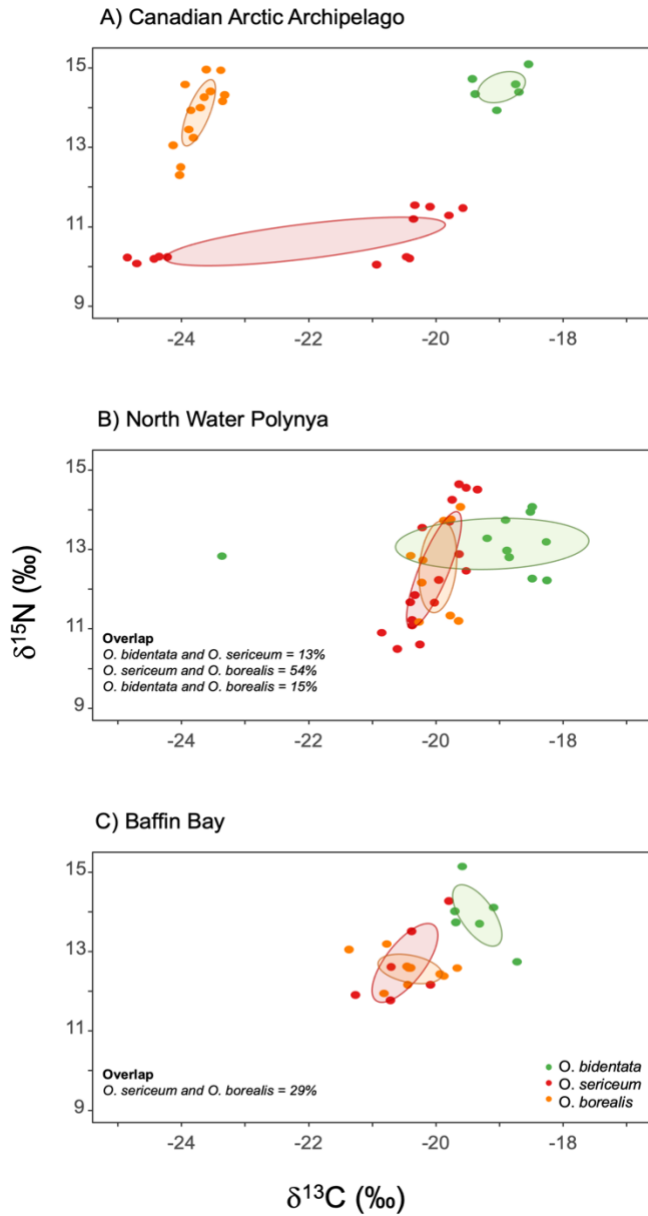
1
2 **Fig. 3. Carbon and nitrogen isotopic composition of sediment and ophiuroids.** Stable isotope bi-plots
3 illustrating the isotopic composition of the brittle star species *Ophiacantha bidentata*, *Ophiocten sericeum*,
4 and *Ophiopleura borealis* across the Arctic Ocean regions: the Canadian Arctic Archipelago (green), the
5 North Water Polynya (red), and Baffin Bay (yellow). The isotopic composition of sediments is represented
6 by a solid symbol (line). Ophiuroid data points are group means with error bars representing \pm SE. Sample
7 sizes are presented in Tables 1 & 2.



1
 2 **Fig. 4. Variation in standard ellipse areas for each brittle star species using SIBER.** The sample size-
 3 corrected standard ellipse area (SEAc; numerical value given above the boxes) of the 3 brittle stars:
 4 *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis* for 3 Canadian Arctic Ocean
 5 regions: (A) the Canadian Arctic Archipelago, (B) the North Water Polynya, and (C) Baffin Bay. Box plot
 6 parameters as in Fig. 2.

7

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1
2 **Fig. 5. Stable isotope bi-plots for each region, illustrating the isotopic niche and overlap of the 3**
3 **Ophiuroidea species.** Standard ellipses (solid lines) enclose the core isotopic niches of the brittle stars:
4 *Ophiacantha bidentata* (green), *Ophiocten sericeum* (red), and *Ophiopleura borealis* (yellow) across 3
5 Arctic regions: (A) the Canadian Arctic Archipelago, (B) the North Water Polynya, and (C) Baffin Bay.

6
7

Tables

1 **Table 1.** Surface sediment dataset derived from sediment stations. Samples were collected in 3 regions in
 2 the Canadian Arctic Ocean: the Canadian Arctic Archipelago (CAA), the North Water Polynya (NOW),
 3 and Baffin Bay (BB). One replicate of sediments ($n\delta$) was used per station for the stable isotope analyses;
 4 $nChl$: number of replicates used for measurements of chlorophyll a ($chl\ a$) at each station; SIC: sea-ice
 5 concentration.

Stn	Depth (m)	Date (yyyy-mm-dd)	Latitude (°N)	Longitude (°W)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SIC (‰)	nChl	Chl a ($\pm SD$) ($\mu g\ g^{-1}$)
CAA									
312	67	2018-08-19	69.17	100.70	-16.5	7.3	45	3	0.07 \pm 0.0
QMG1	39	2018-08-21	68.49	99.89	-22.9	6.7	34	3	0.64 \pm 0.6
QMG2	73	2018-08-21	68.31	100.80	-22.7	6.2	43	1	0.05
QMG3	51	2018-08-22	68.33	102.94	-23.9	6.0	32	3	0.06 \pm 0.1
QMG4	70	2018-08-22	68.48	103.43	-23.0	7.9	36	2	0.02 \pm 0.0
QMGM	112	2018-08-22	68.30	101.74	-23.2	7.0	32	1	0.01
NOW									
101	373	2018-08-28	76.38	77.41	-22.8	5.6	0	2	0.16 \pm 0.1
108	447	2019-07-22	76.26	74.60	-22.3	5.9	1	10	0.48 \pm 0.3
115	663	2019-07-20	76.31	71.24	-22.3	5.5	0	3	0.19 \pm 0.1
BB									
d5	1838	2019-08-26	69.00	61.41	-21.0	8.6	0	3	0.01 \pm 0.0
d4	1809	2019-08-25	68.62	62.01	-21.0	7.8	1	4	0.02 \pm 0.0
d3	1570	2019-08-25	68.24	62.59	-21.5	7.9	1	3	0.02 \pm 0.0
d2	266	2019-08-25	67.86	63.15	-22.8	6.0	3	3	0.06 \pm 0.0

6
 7 **Table 2.** Sampling details and isotopic compositions in brittle stars. Samples were collected in 3 regions in
 8 the Canadian Arctic Ocean: the Canadian Arctic Archipelago (CAA), the North Water Polynya (NOW),
 9 and Baffin Bay (BB); SIC: sea-ice concentration.

Species	Station	Region	Depth (m)	Date (yyyy-mm-dd)	Latitude (N)	Longitude (W)	n	$\delta^{13}C$ ($\pm SD$) (‰)	$\delta^{15}N$ ($\pm SD$) (‰)	SIC (‰)
<i>Ophiacantha bidentata</i>	312	CAA	67	2018-08-19	69.17	-100.70	6	-19.0 \pm 0.4	14.5 \pm 0.4	45
	115	NOW	663	2018-08-29	76.33	-71.18	10	-19.1 \pm 1.5	13.1 \pm 0.6	0
	177	BB	694	2018-09-01	67.48	-63.68	6	-19.3 \pm 0.4	13.9 \pm 0.8	3
<i>Ophiocten sericeum</i>	312	CAA	67	2018-08-19	69.17	-100.70	5	-20.0 \pm 0.3	11.4 \pm 0.2	45
	QMG1	CAA	39	2018-08-21	68.49	-99.89	3	-20.6 \pm 0.3	10.2 \pm 0.1	34
	QMG4	CAA	70	2018-08-22	68.48	-103.43	6	-24.5 \pm 0.2	10.2 \pm 0.1	36
	101	NOW	373	2018-08-28	76.38	-77.41	10	-20.2 \pm 0.4	11.6 \pm 0.8	0
	115	NOW	662	2018-08-29	76.33	-71.18	7	-19.8 \pm 0.4	13.8 \pm 1.3	0
	177	BB	694	2018-09-01	67.48	-63.68	6	-20.5 \pm 0.5	12.7 \pm 1.0	3
<i>Ophiopleura borealis</i>	QMGM	CAA	112	2018-08-22	68.30	-101.74	8	-23.8 \pm 0.2	13.8 \pm 1.0	32
	QMG4	CAA	70	2018-08-22	68.48	-103.43	6	-23.6 \pm 0.3	14.0 \pm 0.6	36
	108	NOW	447	2019-07-22	76.26	-74.60	3	-20.0 \pm 0.3	13.5 \pm 0.5	1
	115	NOW	662	2018-08-29	76.33	-71.18	6	-20.0 \pm 0.3	12.1 \pm 1.1	0
	E1	BB	447	2019-08-23	68.28	-65.14	10	-20.4 \pm 0.5	12.6 \pm 0.4	3

Supplementary material

1
2
3 **Table S1.** Sampling details and isotopic compositions in brittle stars species. Samples were collected in
4 three regions in the Canadian Arctic Ocean: the Canadian Arctic Archipelago (CAA), the North Water
5 Polynya (NOW), and the Baffin Bay (BB).

Species	Station	Region	Depth (m)	Date (dd/mm/yyyy)	Latitude (N)	Longitude (W)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Ophiacantha</i>								
<i>bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-19.42	14.73
<i>O. bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-19.38	14.35
<i>O. bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-18.69	14.40
<i>O. bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-18.74	14.60
<i>O. bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-19.04	13.94
<i>O. bidentata</i>	312	CAA	67	19/08/2018	69.17	-100.70	-18.54	15.10
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.48	14.08
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.51	13.96
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-19.19	13.29
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.90	13.75
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.88	12.98
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.48	12.27
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.84	12.81
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.26	13.20
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-23.36	12.84
<i>O. bidentata</i>	115	NOW	663	29/08/2018	76.33	-71.18	-18.25	12.23
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.70	14.02
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.68	13.74
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.09	14.12
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.58	15.15
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.31	13.71
<i>O. bidentata</i>	177	BB	694	01/09/2018	67.48	-63.68	-18.72	12.75
<i>Ophiocten</i>								
<i>sericeum</i>	312	CAA	67	19/08/2018	69.17	-100.70	-20.33	11.55
<i>O. sericeum</i>	312	CAA	67	19/08/2018	69.17	-100.70	-19.57	11.48
<i>O. sericeum</i>	312	CAA	67	19/08/2018	69.17	-100.70	-19.79	11.29
<i>O. sericeum</i>	312	CAA	67	19/08/2018	69.17	-100.70	-20.35	11.20
<i>O. sericeum</i>	312	CAA	67	19/08/2018	69.17	-100.70	-20.09	11.51
<i>O. sericeum</i>	QMG1	CAA	39	21/08/2018	68.49	-99.89	-20.41	10.21
<i>O. sericeum</i>	QMG1	CAA	39	21/08/2018	68.49	-99.89	-20.93	10.05
<i>O. sericeum</i>	QMG1	CAA	39	21/08/2018	68.49	-99.89	-20.46	10.25
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.35	10.25
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.22	10.24
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.35	10.26
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.85	10.23
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.70	10.08
<i>O. sericeum</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-24.43	10.20
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.60	10.50
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.85	10.91
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.40	11.68
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.33	11.86
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-19.52	12.47
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-19.63	12.89
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.37	11.23
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.02	11.67
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-19.95	12.24
<i>O. sericeum</i>	101	NOW	373	28/08/2018	76.38	-77.41	-20.25	10.61

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<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.63	14.65
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.34	14.52
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.52	14.56
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-20.37	11.09
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.74	14.26
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.78	13.71
<i>O. sericeum</i>	115	NOW	662	29/08/2018	76.33	-71.18	-20.21	13.56
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-21.26	11.91
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-20.38	13.52
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-19.79	14.28
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-20.70	12.62
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-20.71	11.78
<i>O. sericeum</i>	177	BB	694	01/09/2018	67.48	-63.68	-20.08	12.17
<i>Ophiopleura</i>								
<i>borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-23.54	14.42
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-23.61	14.97
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-23.64	14.27
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-24.13	13.06
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-23.94	14.59
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-23.85	13.94
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-24.01	12.51
<i>O. borealis</i>	QMGM	CAA	112	22/08/2018	68.30	-101.74	-24.03	12.31
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.88	13.46
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.32	14.33
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.38	14.95
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.70	14.01
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.35	14.17
<i>O. borealis</i>	QMG4	CAA	70	22/08/2018	68.48	-103.43	-23.81	13.25
<i>O. borealis</i>	108	NOW	447	22/07/2019	76.26	-74.60	-19.87	13.74
<i>O. borealis</i>	108	NOW	447	22/07/2019	76.26	-74.60	-20.39	12.85
<i>O. borealis</i>	108	NOW	447	22/07/2019	76.26	-74.60	-19.76	13.77
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.61	14.08
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.77	11.34
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-20.22	12.17
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-20.20	12.74
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-20.26	11.18
<i>O. borealis</i>	115	NOW	662	29/08/2018	76.33	-71.18	-19.64	11.21
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.44	12.17
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-19.66	12.59
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.81	11.95
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.39	12.60
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.77	13.20
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.42	12.59
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-19.87	12.39
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-19.93	12.44
<i>O. borealis</i>	E1	BB	447	23/08/2019	68.28	-65.14	-20.45	12.63

1
2

1 **Table S2.** Summary of main effects and significant two-way interaction effects on $\delta^{13}\text{C}$ values of ophiuroids.

Main effects and significant interaction effects	Model				Post-hoc		
	Degrees of freedom	F-value	p-value	Effect size (slope)	Significant effect	p-value	Effect size
Depth	1	36.04	<0.0001	8.113e-04			
SIC	1	89.27	<0.0001	2.944e-01			
Region	2	70.61	<0.0001		NOW > CAA BB > CAA	<0.0001 <0.0001	11.580 11.222
Species	2	8.19	0.0006		<i>O. bidentata</i> > <i>O. borealis</i> <i>O. bidentata</i> > <i>O. sericeum</i>	0.0024 0.0005	1.105 1.108
Depth x SIC*	1	4.56	0.0356		($\delta^{13}\text{C}$ ~ Depth) SIC 0-3 > SIC 32-45		

2 *Sea-ice concentration (SIC)

3
4 **Table S3.** Summary of main effects and significant two-way interaction effects on $\delta^{15}\text{N}$ values of ophiuroids.

Main effects and significant interaction effects	Model				Post-hoc		
	Degrees of freedom	F-value	p-value	Effect size (slope)	Significant effect	p-value	Effect size
Depth	1	7.94	0.0060	0.0023			
Species	2	38.23	<0.0001		<i>O. bidentata</i> > <i>O. borealis</i> <i>O. bidentata</i> > <i>O. sericeum</i> <i>O. borealis</i> > <i>O. sericeum</i>	0.0006 <0.0001 <0.0001	0.960 1.970 1.010
Depth x SIC*	1	12.81	0.0006		($\delta^{15}\text{N}$ ~ Depth) SIC 0-3 > SIC 32-45		
Depth x Species	2	40.57	<0.0001		($\delta^{15}\text{N}$ ~ Depth) <i>O. sericeum</i> > <i>O. bidentata</i> ($\delta^{15}\text{N}$ ~ Depth) <i>O. sericeum</i> > <i>O. borealis</i>	<0.0001 <0.0001	0.006 0.007

5 *Sea-ice concentration (SIC)

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