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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 ($\delta^{13}C$, $\delta^{15}N$) 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.

KEY WORDS: Benthic community · Ophiuroidea · Trophic ecology · Isotopic niche · Canadian Arctic Ocean

1. INTRODUCTION

Arctic marine offshore ecosystems are mainly sustained by seasonal organic carbon pulses from phytoplankton (i.e. open water algae) and sympagic (i.e. ice-associated algae) communities (Tamelander et al. 2009). When light conditions and inorganic nutrient supplies are favorable during spring, the beginning of a limited period of sea-ice algal production begins, followed by a phytoplankton bloom (Hegseth 1998, Leu et al. 2011, 2015). The duration of phytoplankton and ice algal production is comparable, but in terms

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of biomass, phytoplankton generally exceeds sea-ice algae (Leu et al. 2011). Once the organic matter is produced, the vertical export of particulate organic matter (POM) varies considerably during seasons and among regions according to biological and physical processes (e.g. zooplankton grazing pressure, microbial processes), which ultimately control the final amount and quality of POM that reaches the benthos (Herndl & Reinthaler 2013).

The Arctic is warming faster than any other region on Earth (AMAP 2017). As a result, the Arctic seascape changes abruptly, exhibiting accelerated reductions in the thickness and extent of sea ice, with predictions estimating a seasonally ice-free Arctic Ocean by 2040 (Comiso et al. 2008, Kędra et al. 2015). Sea ice plays a vital role in the Arctic Ocean ecosystem by mediating physical and biological processes such as primary production (Hunt et al. 2002, Gradinger 2009, Ramírez et al. 2017), but also by serving as a habitat for a large number of organisms (e.g. from bacteria to marine mammals) and as a base substrate for ice algae (Garrison 1991, Werner 2005). Consequently, sea ice loss may affect the magnitude of the set of interactions between habitats (i.e. sympagic–pelagic and sympagic–benthic coupling) in which exchanges of energy, mass, or nutrients occur (Wassmann & Reigstad 2011). Benthic fauna depends largely upon the supply of organic carbon from primary producers (pelagic and sympagic); thus, benthic consumers and food web structure are sensitive to changes in the timing, nature, quality, or abundance of nutrients (Kędra et al. 2012). Therefore, the knowledge of the ecological and biological mechanisms that drive trophic ecology and support species co-occurrence is important to predict how environmental changes may affect trophic interactions, species coexistence, and food web dynamics.

In the Arctic Ocean, the benthic community structure varies significantly due to ecological (e.g. species interactions, resource availability, seasonality) and environmental gradients (e.g. temperature, salinity, depth, currents, sediment type, bottom topography) (Kędra et al. 2013, Roy et al. 2014). Ecological drivers that include niche complexity coupled with species interactions shape benthic composition and influence the transfer of energy through trophic levels (Collin et al. 2011, Roy et al. 2014). Stable isotope analysis (SIA; carbon and nitrogen), which provides time- and space-integrated insight on diet and habitat use by consumers, has emerged as a common approach to examine the structure and dynamics of ecological communities and carbon flow in food webs (Post 2002, Layman et al. 2007, Jackson et al. 2011). In turn, the use of the isotopic niche, a low-dimensional specification of the 'Hutchinsonian niche' (Hutchinson 1957), which consists of the area occupied by individuals in the isotopic niche space, has served to analyze patterns of interactions in various ecological resolutions (Shipley & Matich 2020), and to interpret levels of dietary specialization of individuals (Araújo et al. 2007, Karlson et al. 2015). The characteristics of the niche vary according to intrinsic (e.g. intra- and interspecific competition) and extrinsic factors (e.g. sea-ice cover, resource availability, seasonality) that influence the dimensions of the niche (Costa-Pereira et al. 2017, Shipley & Matich 2020). Furthermore, individual levels of dietary specialization within a population may drive the variability of the niches (Araújo et al. 2009, Semmens et al. 2009).

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

Even though we have expanded our knowledge about the diet of brittle stars in the Arctic (e.g. Graeve et al. 1997, Gallagher et al. 1998), there are still many knowledge gaps in the trophic ecology of most ophiuroids and how they coexist using the same resources while avoiding interspecific competition. In the present study, we examined changes in the isotopic niche structure of ophiuroids in response to variation in sea-ice conditions, local productivity, and individual-level differences in feeding behavior. Three species of coexisting ophiuroids were chosen as models to test the following hypotheses: (1) depending on sea-ice concentration (SIC), patterns in species niche structure (i.e. segregation and overlap of niches) will change across regions, where a higher overlap of niches will be linked to regions with more SIC due to brittle stars exploiting more similar food items; (2) changes in the isotopic niche width of ophiuroids will be closely related to sediment $\delta^{13}C$ carbon composition and individual feeding behaviors, in which niche width reduction will be linked to regions with higher abundance of resources where consumers ingest the more abundant sources; and (3) a decrease in niche overlap will be associated with regions with higher heterogeneity of resources in which brittle stars can use a higher spectrum of resources.

2. MATERIALS AND METHODS

2.1. Study area

Baffin Bay (BB; Fig. 1) is a semi-enclosed ocean basin located between Baffin Island and western Greenland that connects the Arctic Ocean and the northwest Atlantic Ocean (Dunlap & Tang 2006, Hamilton & Wu 2013). Annual sea-ice development in BB begins in late autumn and reaches its maximum extent around March (Stern & Heide-Jørgensen 2003). Excluding the ice-free months between August and September, BB is partially covered by sea ice (Tang et al. 2004).

The Canadian Arctic Archipelago (CAA) to the north-west of BB extends over an area of 3.3×10^6 km^2, and comprises a large number of islands and channels between Banks Island in the west and Baffin and Ellesmere Islands in the east (Melling 2002). In this region, the sea-ice component is a mixture of both first-year and multi-year ice (Kwok 2006). The perennial multi-year ice, located almost entirely on Queen Elizabeth Islands, Western Parry Channel, and M'Clintock Channel, can represent more than 50% of the total area covered by ice before the melt season (Howell et al. 2013).

The North Water Polynya (NOW) is located between Greenland and Canada on the northern end of BB. This region is characterized by low SIC and exhibits one of the highest levels of primary productivity recorded for the Arctic Ocean (Barber et al. 2001). Polynyas are areas of open water or with minimal sea-ice coverage surrounded by a contiguous ice pack (Barber & Massom 2007).

2.2. Sample collection

The Canadian research icebreaker CCGS 'Amundsen' visited 15 stations from 19 August to 1 September 2018 and from 20 July to 23 August 2019 to collect sediment and brittle stars (i.e. *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis*) in 3 different Canadian Arctic regions (Fig. 1). Brittle stars were found and collected at 9 of the 15 stations (Table S1 in the Supplement at www.int-res.com/articles/suppl/m683p081_supp.pdf) for subsequent SIA using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm. In addition, surface sediment samples were collected from 13 stations (Table 1), from the upper 1 cm of a box core (0.125 m^2). Sediment samples were not collected at Stns E1 and 177 in BB. From each box core, sediments were collected for SIA (1 sample per station) using 60 ml truncated syringes and for pigment content analysis (3 samples per station) using 10 ml truncated syringes. Since carbon isotope ratios ($\delta^{13}C$) vary substantially among primary producers, but change little between each trophic level (0–1‰; Peterson & Fry 1987, Post 2002, Layman et al. 2007), the carbon isotopic composition of surface sediment was used in the present study as a proxy to determine the relative contribution of primary carbon food sources in the diet of ophiuroids. In addition, sediment surface chlorophyll *a* (chl *a*) concentration, a short-term proxy of productivity, was carried out at Laval University, Quebec, Canada, following the modified protocols of Riaux-Gobin & Klein (1993) and Link et al. (2011). After collection, all samples were frozen for subsequent SIA and pigment analysis.

2.3. Stable isotope analyses

Sediment and brittle star samples were freeze-dried at −50°C and ground to a fine powder with a mortar and pestle. For sediments, carbonates were removed using 1 N HCl until bubbling ceased. For brittle stars, a total of 92 individuals were used for SIA (Table S1). Lipid extraction was carried out in brittle stars using a solution of dichloromethane:methanol (2:1). Brittle star samples were then decarbonated by exposing them to HCl vapors for 48 h in an airtight container. After acidification, to verify the total removal of car-

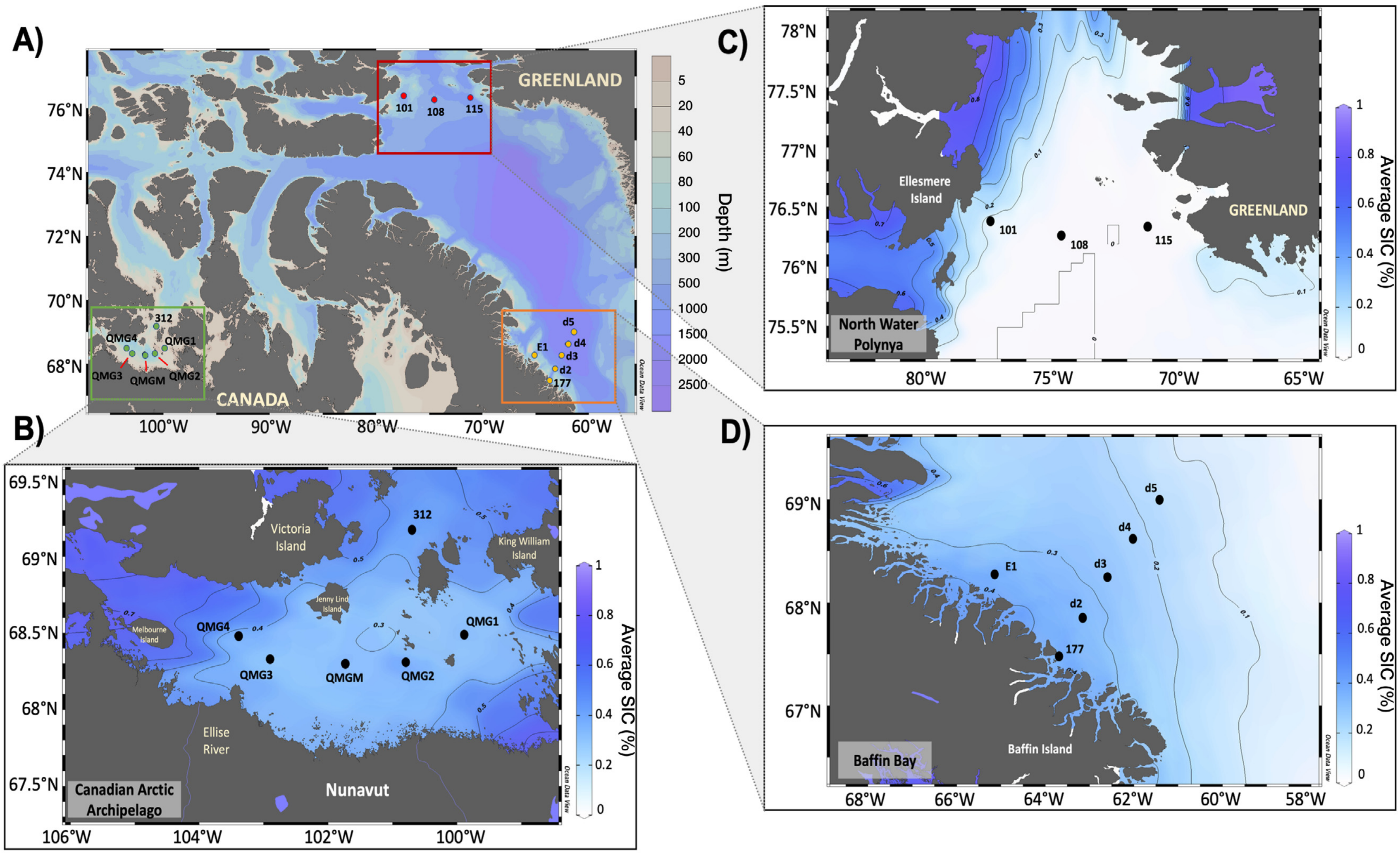

Fig. 1. Location of sampling stations with bathymetric gradients. (A) Red dots represent the stations in the North Water Polynya, green dots in the Canadian Arctic Archipelago, and orange dots in Baffin Bay. (B–D) Average sea-ice concentrations (SIC) for the regions studied, ranging from 0 to 100 % (expressed here between 0 and 1; gray lines), in the summer (June to August, between 2018 and 2019) were derived from the National Snow and Ice Data Center (https://nsidc.org/data/nsidc-0051)

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

Stn	Depth (m)	Date (yyyy-mm-dd)	Latitude (°N)	Longitude (°W)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SIC (‰)	nChl	Chl *a* (±SD) ($\mu g\ g^{-1}$)
CAA									
312	67	2018-08-19	69.17	100.70	−16.5	7.3	45	3	0.07 ± 0.0
QMG1	39	2018-08-21	68.49	99.89	−22.9	6.7	34	3	0.64 ± 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 ± 0.1
QMG4	70	2018-08-22	68.48	103.43	−23.0	7.9	36	2	0.02 ± 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 ± 0.1
108	447	2019-07-22	76.26	74.60	−22.3	5.9	1	10	0.48 ± 0.3
115	663	2019-07-20	76.31	71.24	−22.3	5.5	0	3	0.19 ± 0.1
BB									
d5	1838	2019-08-26	69.00	61.41	−21.0	8.6	0	3	0.01 ± 0.0
d4	1809	2019-08-25	68.62	62.01	−21.0	7.8	1	4	0.02 ± 0.0
d3	1570	2019-08-25	68.24	62.59	−21.5	7.9	1	3	0.02 ± 0.0
d2	266	2019-08-25	67.86	63.15	−22.8	6.0	3	3	0.06 ± 0.0

bonate in the samples, drops of acid were applied to dried material (champagne test) to check that no more bubbles (i.e. CO_2 that would be produced by the chemical dissociation of the carbonates) formed.

Stable nitrogen and carbon isotope ratios were measured using a continuous-flow isotope ratio mass spectrometer (Thermo Electron Delta Advantage) in the continuous-flow mode (Thermo Electron ConFlo III) with an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies) in the oceanography laboratory at Laval University. Replicate measurements of international standards (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) established measurement errors of ≤0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios were expressed in delta (δ) units ($\delta^{13}C$, $\delta^{15}N$) as the per mil (‰) difference with respect to standards: δX (‰) = $[(R_{Sample} - R_{Standard})/R_{Standard}] \times 10^3$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards were calibrated against the international references Vienna PeeDee Belemnite for carbon and atmospheric air for nitrogen.

2.4. Trophic positions

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

$$\delta^{15}N_c = \delta^{15}N_b + \Delta N(TP - \lambda) \qquad (1)$$

where $\delta^{15}N_c$ corresponds to the nitrogen stable isotope value of the consumer for which the TP is estimated, $\delta^{15}N_b$ represents the nitrogen isotope ratio of surface sediment bulk organic matter for each region studied; ΔN corresponds to the trophic discrimination factor (TDF) for nitrogen, and λ is the TP of baseline sources. TP of basal primary producers was set to 1.0, meaning that TP ≤2 (low trophic level) represents primary consumers, >2 TP <3 (intermediate trophic level) represents secondary consumers (e.g. omnivores), and TP ≥3 (high trophic level) represents top consumers and scavengers.

2.5. Sea-ice concentration data

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

2.6. Statistical analyses

All statistical analyses were performed using R Studio version 1.4.1106 (R Core Team 2019) and graphical procedures with Ocean Data View version 5.1.7 (https://odv.awi.de). Homogeneity of variance and normality of residuals were verified using the Shapiro-Wilk test on residuals. Linear models were employed to simultaneously evaluate the effect of environmental variables (i.e. depth and SIC) and their interactions on $\delta^{13}C$ and $\delta^{15}N$ values found in sediment and the ophiuroid samples. A Kruskal-Wallis test was conducted to examine the differences in stable isotope ratios of carbon and nitrogen in brittle stars among species, stations, and regions. Significant effects implicating categorical factors (SIC, depth, regions, and species) were further analyzed with Tukey post hoc tests using the 'emmeans' package (v2.27-61) (Lenth & Lenth 2018). The core isotopic niche space occupied by brittle stars was calculated using the standard ellipse area in the 'SIBER' package in R (Jackson et al. 2011). Furthermore, the probabilistic method of Jackson et al. (2011) was used to estimate the mode and the credible interval of the Bayesian-simulated standard ellipse areas. Specifically, we used the sample size-corrected standard ellipse area (SEAc), which is a more robust approach that encompasses the core (around 40%) of the isotopic observations within each species group and is therefore less sensitive to sample size and isotopic outliers (Jackson et al. 2011). SEAc credibility intervals were based on 1 000 000 iterations and a burn-in of 100 000.

3. RESULTS

3.1. Isotopic composition of sediments

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

3.2. Trophic position and isotopic composition of brittle stars

TPs of brittle stars ranged between the second and the fifth trophic level. *Ophiacantha bidentata* had the highest modal TP (mean = 4.33), while *Ophiocten sericeum* showed the lowest modal TP (mean = 2.63) in the CAA region (Fig. 2). The greatest modal TP of *O. sericeum* (mean = 3.99) was evidenced mainly in the NOW, where all brittle stars predominantly occupied high TPs compared to BB. The greatest modal TP of *Ophiopleura borealis* (mean = 4.05) was found in the CAA region. The greatest ranges of TPs were observed for all 3 species of brittle stars in BB (Fig. 2).

Brittle stars displayed a wide range of isotopic compositions among stations and regions (Table 2, Fig. 3). Linear models revealed a significant effect of SIC and depth on $\delta^{13}C$ values of brittle star species among regions ($p < 0.001$; Table S2) and also an interactive effect of SIC and depth on $\delta^{13}C$ values of ophiuroids (p = 0.03; Table S2). In addition, linear models showed an interactive effect of SIC and chl *a* concentration on $\delta^{13}C$ values of ophiuroids ($p < 0.001$). However, chl *a* content alone was not an environmental variable that significantly affected the $\delta^{13}C$ values of ophiuroids (p = 0.33). Significant differences in $\delta^{13}C$ values across species (Kruskal-Wallis, chi-squared = 41.94, df = 2, $p < 0.001$) and

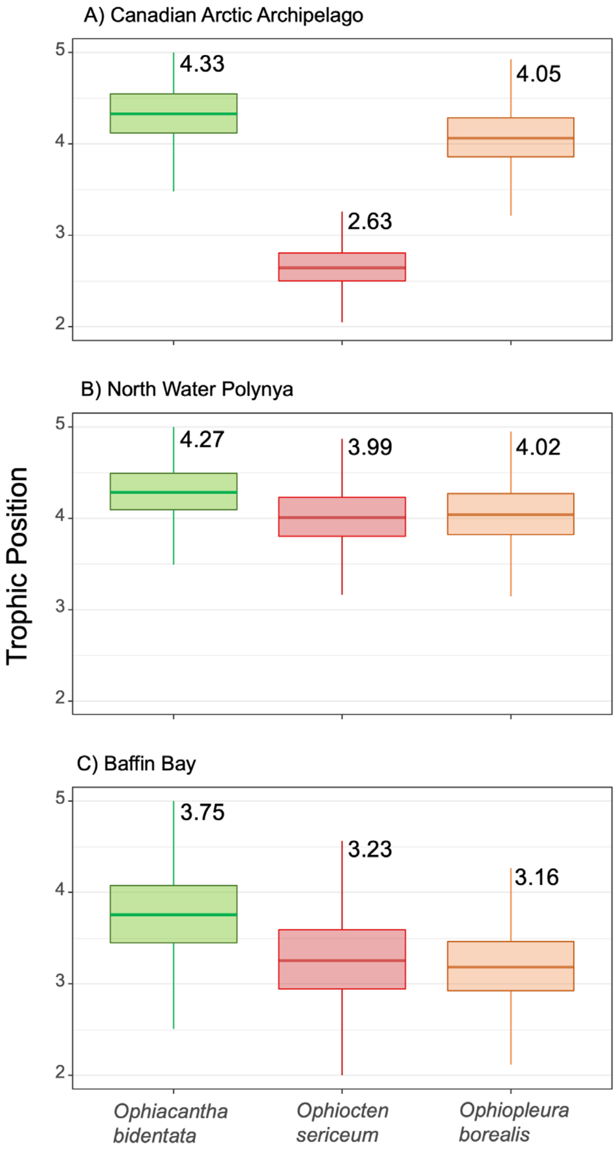

Fig. 2. Estimated trophic position (TP) of brittle stars. Horizontal lines represent the modal TP occupied by different brittle star species (mean TP values given above the boxes; black numbers). The middle part of the boxes represents the interquartile range, i.e. the middle quartiles (or the 75th minus the 25th percentile). The whiskers represent the variability outside the 75th and 25th percentile. Estimates were made using the 'tRophicPosition' model across the Arctic regions: (A) the Canadian Arctic Archipelago, (B) the North Water Polynya, and (C) Baffin Bay

regions (Kruskal-Wallis, chi-squared = 21.36, df = 2, $p < 0.001$) were found in this study. Among species, the most ^{13}C-enriched value (δ^{13}C = −18.2‰) was found in *O. bidentata* in the NOW region, while the most ^{13}C-depleted value (δ^{13}C = −24.9‰) corresponded to *O. sericeum* in the CAA region (Table S1). Average δ^{13}C values ranged from −24.5 ± 0.2‰ (*O. sericeum*) to −19.0 ± 0.4‰ (*O. bidentata*) in the CAA region; from −20.2 ± 0.4‰ (*O. sericeum*) to −19.1 ± 1.5‰ (*O. bidentata*) in the NOW; and from −20.5 ± 0.5‰ (*O. sericeum*) to −19.3 ± 0.4‰ (*O. bidentata*) in BB (Table 2).

Linear models revealed an effect of depth on δ^{15}N values of brittle star species among regions ($p < 0.01$) and an interaction effect of SIC and depth on δ^{15}N values of ophiuroids ($p < 0.001$; Table S3). Likewise, significant differences in δ^{15}N values among stations were found (chi-squared = 24.15, df = 8, p = 0.002). However, δ^{15}N values showed no significant differences across regions (chi-squared = 0.32, df = 2, p = 0.85). δ^{15}N varied across species (chi-squared = 26.41, df = 2, $p < 0.001$). The most ^{15}N-depleted values were found in *O. sericeum* (10.1‰) in the CAA, and the most ^{15}N-enriched value in *O. bidentata* (15.2‰) in the BB region (Table S1). Average δ^{15}N values ranged from 10.2 ± 0.1‰ (*O. sericeum*) to 14.5 ± 0.4‰ (*O. bidentata*) in the CAA; from 11.6 ± 0.8 to 13.8 ± 1.3‰ (*O. sericeum*) in the NOW; and from 12.6 ± 0.4‰ (*O. borealis*) to 13.9 ± 0.84‰ (*O. bidentata*) in BB (Table 2).

3.3. Isotopic niche widths and niche overlap of brittle stars

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

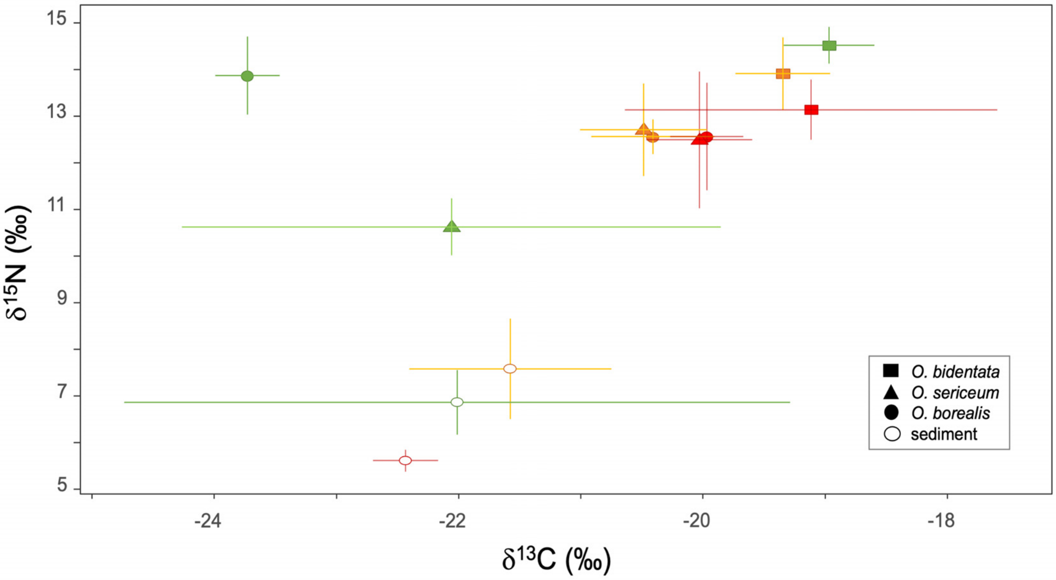

Fig. 3. Carbon and nitrogen isotopic composition of sediment and ophiuroids. Stable isotope bi-plots illustrating the isotopic composition of the brittle star species *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis* across the Arctic Ocean regions: the Canadian Arctic Archipelago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

Among regions, the isotopic niches ($\delta^{13}C$ vs. $\delta^{15}N$ biplots) revealed differences in overlap of consumers (Fig. 5). Niche analysis showed that the NOW was the only region where the 3 brittle stars shared isotopic niche space. However, in other regions, our results showed marked differences in isotopic composition, and brittle stars either did not share niche space (i.e. CAA), or niche overlap only occurred between 2 species (i.e. BB; Fig. 5). The area of overlap comprised between 13 and 54 % of the total isotopic niche area among all regions. The greatest niche overlaps occurred between *O. sericeum* and

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

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

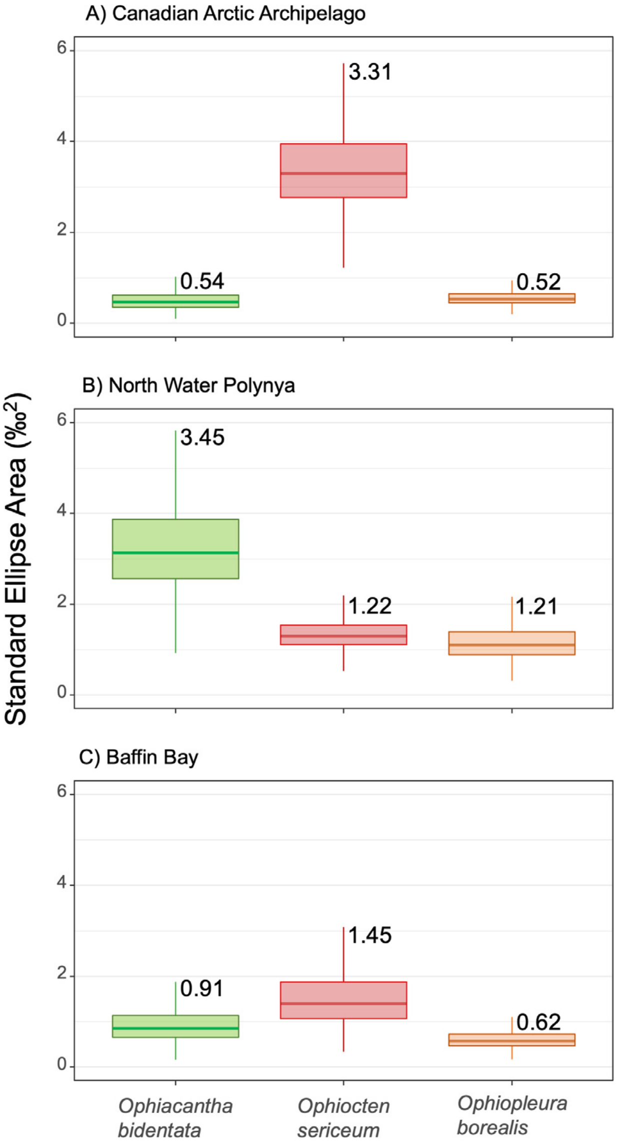

Fig. 4. Variation in standard ellipse areas for each brittle star species using SIBER. The sample size-corrected standard ellipse area (SEAc; numerical value given above the boxes) of the 3 brittle stars: *Ophiacantha bidentata*, *Ophiocten sericeum*, and *Ophiopleura borealis* for 3 Canadian Arctic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

O. borealis, which shared at least 54 and 29% of the isotopic niche area in the NOW and BB regions, respectively (Fig. 5B,C). Moreover, biplots showed differences in resource use among species on a local and regional scale, revealing greater variability in resource use by ophiuroids in the CAA than in the other 2 regions. Finally, isotopic niche and TP models indicated that *O. sericeum* encompassed a greater degree of isotopic variability in its prey, feeding at lower trophic levels than the other ophiuroids, whereas individuals of the species *O. bidentata* fed high in the food chain.

4. DISCUSSION

4.1. Isotopic composition and carbon use by consumers

Previous studies denoted a pattern in the δ^{13}C and δ^{15}N values of benthic fauna in both the Arctic and Antarctic Oceans with respect to fluctuations in local oceanographic conditions such as SIC (e.g. Norkko et al. 2007, Michel et al. 2019, Yunda-Guarin et al. 2020) and depth (Stasko et al. 2018b). Together, these studies highlighted the key indirect control of environmental conditions (e.g. SIC and depth) in the isotopic composition and availability of food resources, which ultimately induced benthic food web structure shifts. For instance, seasonal changes in oceanographic conditions (e.g. depth, SIC, water temperature) and variability in the composition of food items proved to be 2 important factors altering the isotopic composition of Arctic amphipods by inducing changes in nitrogen and carbon turnover rates (Kaufman et al. 2008). Isotopic values may also reflect a range of varying proportions of food items assimilated by individuals over time (Bearhop et al. 2004) or similar food items with different δ^{13}C isotopic compositions. In our study, SIA did not provide high resolution of dietary information of brittle stars according to oceanographic conditions or food availability. However, δ^{13}C values of surface sediment organic matter in this study were a useful indicator of the relative contribution of primary organic carbon sources to ophiuroids. Considering that δ^{13}C values in surface sediments in the Arctic Ocean typically range between −22 and −30‰ (average −26.8‰) for terrestrial sources and between −17 and −22‰ for marine sources (average −20.6‰) (Koziorowska et al. 2016, Kumar et al. 2016, Włodarska-Kowalczuk et al. 2019), δ^{13}C values found in surface sediments in this study suggested a mix of carbon sources available for benthic consumption (Table 1). In addition, the δ^{13}C values of primary sources calculated in previous studies ranged from −13.4 to −20.7‰ in BB, from −7.1 to −25.3‰ in the CAA, and from −8.9 to −14.1‰ in the NOW for sympagic algae, and from −20.1 to −26.3‰ in BB, from −23.2 to −27.4‰ in the CAA, and from −22.1 to −27.6‰ in the NOW for suspended POM (SPOM) (Roy 2014, Friscourt 2016, Yunda-Guarin et al. 2020, M. Gosselin unpubl. data). Hence, δ^{13}C values of surface sediments found in this

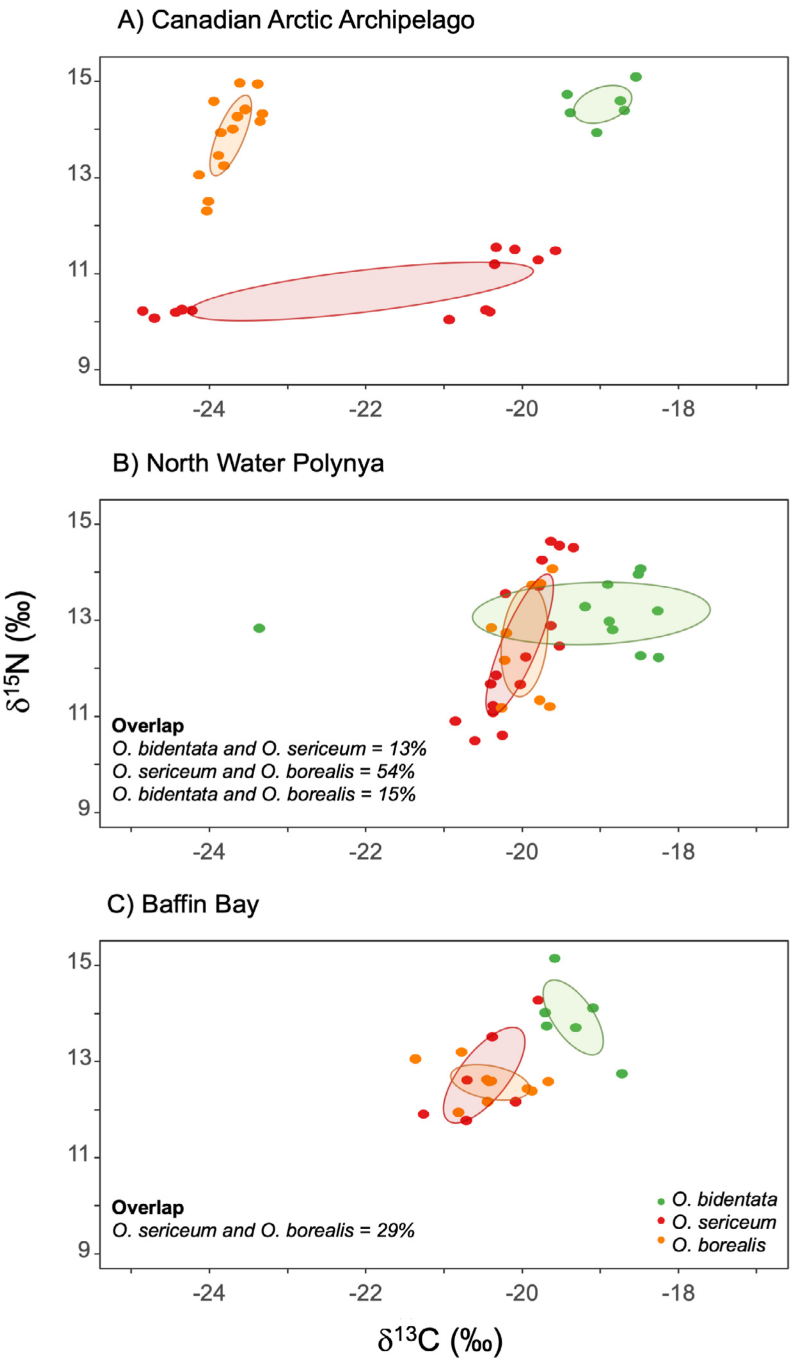

Fig. 5. Stable isotope bi-plots for each region, illustrating the isotopic niche and overlap of the 3 Ophiuroidea species. Standard ellipses (solid lines) enclose the core isotopic niches of the brittle stars: *Ophiacantha bidentata* (green), *Ophiocten sericeum* (red), and *Ophiopleura borealis* (yellow)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

study implied that ophiuroid diet was influenced by carbon items from different origins. On the one hand, depleted δ^{13}C values in ophiuroids (<–23‰) suggested that brittle stars could use a mix of mostly marine-derived carbon sources of benthic or pelagic origin such as SPOM. On the other hand, in the NOW, BB, and the east part of the CAA, δ^{13}C values suggested that brittle stars could rely on at least 2 food sources: marine-derived carbon and detritus enriched by microbial activity.

4.2. Niche structure under local oceanographic conditions and food supply

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

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

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

4.3. Species-specific dietary selectivity and niche dynamics

In general, brittle stars are considered generalist species and employ a large variety of foraging behaviors to access a wide diversity of resources (Pearson & Gage 1984). These feeding attributes have led different ophiuroid species to be recognized as ecologically equivalent species that share habitat and food sources (Pearson & Gage 1984). Nevertheless, foraging behaviors in consumers are dynamic and tend to vary over time as a response to multiple variables including prey availability, seasonality, competition, and even the physiological state of the consumer (Yeakel et al. 2016). Since tendencies in generalist species towards a particular diet only exist on a short time scale, it is difficult to establish with precision the fluctuations in the isotopic composition of these individuals, especially when their isotopic composition probably reflects an average of different food items ingested over time (Bearhop et al. 2004). As expected, our results showed high variability in resource-use patterns (i.e. changes in the dietary niche width) among brittle star species and differences in species-specific feeding selectivity, which ultimately led to significant changes in niche width of these ophiuroids. Based on the isotopic composition of brittle stars, changes in the relative contribution of primary sources seem to have affected the interspecific characteristics of the feeding mode of ophiuroids. Interestingly and contrary to what is specified in most of the literature (see Section 1), brittle stars displayed high inter-individual variability in feeding behavior across stations in which each individual showed its own pattern of feeding. Accordingly, the species niche width varied significantly due to intraspecific variability in foraging behaviors and individual species trends in dietary selectivity linked to ecological processes such as productivity (Semmens et al. 2009, Araújo et al. 2011). For instance, consumers exhibited greater differences in resource use in the less productive regions of the CAA and BB, increasing the segregation of the niches (Robinson & Strauss 2020). Notably, in the CAA region, a broad isotopic niche (SEAc) occurred in *O. sericeum*, which suggested variation in its feeding selectivity at the individual level across stations, leading to an expansion of its trophic diversity. In contrast, in the same region, a reduction of the isotopic niche width (i.e. low trophic diversity) in *O. bidentata* and *O. borealis* suggested high feeding selectivity or low dietary evenness over time (Bearhop et al. 2004). This is also supported by the field experiment conducted by Mäkelä et al. (2017a) with benthic macrofauna, showing that differences in food utilization by polychaetes, bivalves, and crustaceans were site-specific, with no taxa exclusively exhibiting higher rates of ice algal uptake, suggesting high feeding plasticity.

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

TP estimates showed that brittle stars fed at various trophic levels. In most regions, ophiuroids occupied intermediate to high trophic levels, suggesting that ophiuroids were predominantly mobile deposit feeders and omnivores (including carnivores/scavengers). However, brittle stars did not always show a similar range of TPs within the same region. For example, in the CAA region, *O. sericeum* had the most ^{15}N-depleted values of the 3 study species, which suggested that individuals predominantly fed on lower trophic levels than the other species. In contrast, in other regions, such as the NOW, ophiuroids shared higher mean trophic levels, implying that consumers relied primarily on heterotrophic prey or reworked organic matter typically ^{15}N-enriched by microbial activity (Mäkelä et al. 2017b). Finally, brittle stars in the BB region showed the broadest range in TPs, indicating that individuals adopted predominantly omnivorous behavior to exploit a broad spectrum of trophic resources (i.e. trophic generalists or intermediate feeding specialists). Based on our results, it seems likely that individuals within each species do not always share similar diets and have varied preferences towards different food items. The inter-individual dietary flexibility observed in brittle stars would suggest that ophiuroids play an important role in benthic food webs from the point of view of increasing the number of trophic links and energy flow pathways from one trophic level to the next. Considering the high densities that ophiuroids represent in benthic ecosystems of the Arctic, for example >400 ind. m^{-2} in Young Sound, Greenland, and the Barents Sea (Piepenburg & Schmid 1996, Blicher & Sejr 2011), brittle stars could be critical ecological species driving dynamics, functioning, and stability of benthic food webs.

4.4. Niche overlap and brittle star co-occurrence

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

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

4.5. Concluding remarks

Climate change is expected to lead to shifts in the availability and abundance of food sources for benthic consumption in the future Arctic Ocean that are not yet identified and may affect the dynamics and stability of food webs (Kędra et al. 2015). Despite the ecological importance of ophiuroids as key species in benthic assemblages and trophic cascades in the Arctic Ocean (Pearson & Gage 1984), only a few studies have been carried out to date to better understand the mechanisms that drive feeding ecology and trophic niches of Arctic brittle star species. Here, ecological niche analyses of 3 syntopic brittle star species using the isotopic niche approach provided insight into the mechanisms driving niche dynamics, feeding behavior, and co-occurrence of ophiuroids. We found some evidence that SIC is an important driver of niche structure in ophiuroids. Greater interspecific niche segregation was indeed associated with regions with greater SIC. Additionally, changes in organic carbon composition highlighted a strong influence of species-specific degrees of dietary selectivity shaping niche structure and overlap. Since the Arctic Ocean ecosystem is experiencing strong changes in abiotic conditions due to climate change that could affect ecosystem functioning, more studies of this type are needed to better understand the role of individual species in the functioning and stability of benthic food webs. Finally, our results revealed the great ability of some individuals to adjust their dietary behaviors according to fluctuations in resource composition, highlighting the difficulty of generalizing feeding modes of benthic consumers and the lack of information about trophic interactions, diets, and habitat use by benthic species.

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

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