Ontogenetic changes in stable isotope (δ^{13}C and δ^{15}N) values in squid *Gonatus fabricii* (Cephalopoda) reveal its important ecological role in the Arctic

Alexey V. Golikov[1,*], Filipe R. Ceia[2], Rushan M. Sabirov[1], Zarina I. Zaripova[1], Martin E. Blicher[3], Denis V. Zakharov[4], José C. Xavier[2,5]

[1]**Kazan Federal University, Department of Zoology, 420008 Kazan, Russia**
[2]**Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, 3001-401 Coimbra, Portugal**
[3]**Greenland Institute of Natural Resources, Greenland Climate Research Centre, 3900 Nuuk, Greenland**
[4]**Polar Research Institute of Marine Fisheries and Oceanography, Laboratory of Coastal Research, 183038 Murmansk, Russia**
[5]**British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, CB3 0ET Cambridge, UK**

ABSTRACT: *Gonatus fabricii* is the most abundant cephalopod species in Arctic waters, and the only squid that completes its entire life cycle there. In order to understand its ecological role in the Arctic, we conducted stable isotope analyses of beaks from all ontogenetic groups from west and east Greenland waters and the Barents Sea, complemented with morphological data. The values of both δ^{13}C and δ^{15}N of *G. fabricii* were not related to sex. Values of δ^{13}C showed a small ontogenetic increase, and these values were geographically distinct, with highest levels found in the western part of the study area. Values of δ^{15}N showed a dramatic ontogenetic increase (i.e. 10.0‰ δ^{15}N; 2.6 trophic levels), from epipelagic juvenile forms to large bathypelagic adults, without significant geographical variation. The observed maximum value of δ^{15}N (14.9‰) is the highest ever recorded in cephalopod beaks. The estimated trophic level (up to 5.1) compares only to top vertebrate predators in the Arctic: large piscivorous fishes, seals and toothed whales or large benthic scavenging fishes. Thus, *G. fabricii* is a top invertebrate predator in the Arctic, with the widest isotopic niche observed to date for any species there. Among cephalopods its trophic level is only exceeded by its Antarctic congener, *G. antarcticus*, and by the Antarctic colossal squid *Mesonychoteuthis hamiltoni*. Thus, polar squids occupy higher trophic positions than do squids living in warmer regions. Finally, our study shows that *G. fabricii* descends to bathypelagic layers during ontogenesis, continuously increasing its trophic level by changing prey types and sizes, and avoiding predation pressure.

KEY WORDS: Gonatidae · Oegopsid squid · Arctic marine food webs · Trophic ecology · Feeding · Allometric equations · Beak · Morphology

INTRODUCTION

Cephalopods play an important role in marine ecosystems worldwide (Jereb et al. 2010), reaching annual estimates of global biomass up to 375 million tonnes (Rodhouse & Nigmatullin 1996). Their main predators are fishes, seabirds, pinnipeds and whales (Clarke 1996, Croxall & Prince 1996, Klages 1996, Smale 1996), while their main prey are crustaceans, fishes and other cephalopods (Nixon 1987, Rodhouse & Nigmatullin 1996, Ibanez & Keyl 2010). An ontogenetic shift in cephalopod diet, meaning changing prey types and sizes due to growth, is expected (Rodhouse & Nigmatullin 1996), although evidence is available only for some species (*Todarodes sagittatus*, *Dosidicus gigas*, *Berryteuthis magister*) through stomach content

studies (Breiby & Jobling 1985, Shchetinnikov 1989, Hunsicker et al. 2010). Thus, in general, cephalopods occupy a broad trophic niche in marine ecosystems, which is expected to change throughout their life cycle. This underlines the urgency of studying the diet and trophic niche of squids, to aid our understanding of the global functioning of marine ecosystems, where different species of squids usually occupy high trophic levels with high biomass and abundance (Rodhouse & Nigmatullin 1996, Navarro et al. 2013). It is particularly crucial under a climate change context, as the warming has been shown to cause changes in the geographical distribution of cephalopods (Golikov et al. 2012, 2013, 2014, Xavier et al. 2018). In this context, cephalopod beaks are useful (Clarke 1986, Xavier et al. 2007, 2016b), since equations relating beak rostral length to mantle length (ML) and total mass are used to estimate the sizes of cephalopods eaten by predators (Clarke 1962a,b, 1986) (Table S1 in the Supplement at www.int-res.com/articles/suppl/ m606p065_supp.pdf). In addition, stable isotope analyses of nitrogen (δ^{15}N) and carbon (δ^{13}C) in the beaks allow estimation of the trophic level occupied by the individuals (Cherel & Hobson 2005, Cherel et al. 2008, 2009) and determination of the primary source of productivity in a geographic sense (i.e. the foraging areas within the range) (Cherel & Hobson 2005, Guerreiro et al. 2015), respectively. An ontogenetic shift in the diet of squids has already been demonstrated by stable isotope analyses of their beaks (e.g. *B. magister* in the Pacific, *Architeuthis dux* in the Atlantic and many species of Antarctic squids; Cherel & Hobson 2005, Guerra et al. 2010, Hunsicker et al. 2010, Seco et al. 2016). Thus, it is possible to estimate the ecological role of squids by studying their beaks, combining morphology and stable isotope analysis (Xavier et al. 2007, 2016b).

Polar ecosystems have been recognised as vulnerable due to a wide range of effects caused by environmental change (Meltofte 2013, Constable et al. 2014, Xavier et al. 2016a). Currently, there are 10 cephalopod species that live in the Arctic throughout their complete life cycle, which is much fewer than in other parts of the World Ocean (Golikov et al. 2013, Xavier et al. 2018). The common Arctic squid *Gonatus fabricii* (Lichtenstein, 1818) is the only squid species among Arctic cephalopods and is the most abundant cephalopod species in the Arctic (Nesis 1987, Golikov et al. 2013). *G. fabricii* is known to exhibit a significant descent, from epipelagic to bathypelagic layers, during ontogenesis (referred to as ontogenetic descent in this paper), with females undergoing gelatinous degeneration at a late maturing

stage in bathypelagic layers, during which they stop feeding (Kristensen 1981, 1984, Bjørke & Hansen 1996, Bjørke et al. 1997, Arkhipkin & Bjørke 1999). A list of *G. fabricii*'s known prey and predators (Tables S2 & S3 in the Supplement) also suggests that there are ontogenetic changes in its ecological role. The size and taxonomic composition of their prey ranges from epipelagic copepods to large bathypelagic fishes (Table S2). Seabirds and small/ medium-sized fishes prey on squid of smaller sizes, while large fishes, seals and toothed whales prey on larger squid; *G. fabricii* is known to comprise the majority of the diet of at least 4 species of fishes, 3 seabird species, 1 seal species and 3 species of toothed whales in different areas of the Arctic (Table S3). Therefore, *G. fabricii* is a valuable ecological component of the Arctic, being both an important prey and a predator of high abundance (Kristensen 1984, Bjørke & Gjøsaeter 1998, Bjørke 2001). However, estimation of its biomass from predators has only been based on allometric equations of lower rostral length (LRL) obtained from specimens from Disko Bay and adjacent areas in west Greenland (Zumholz & Frandsen 2006) and from the Norwegian Sea (Wiborg et al. 1982). Other allometric equations of LRL are rare and often do not include enough samples to adequately represent their respective areas, such as the 'North Atlantic' in broad terms (Clarke 1986). Published length–mass relationship equations also have the same issue (Kristensen 1984, Clarke 1986, Arkhipkin & Bjørke 1999, Zumholz & Frandsen 2006). Stable isotope analyses of δ^{15}N have been conducted previously on muscles of *G. fabricii* to estimate the trophic level (TL) occupied by this species (Lawson & Hobson 2000, Hooker et al. 2001, Linnebjerg et al. 2016). However, these studies were limited to small sample sizes of *G. fabricii* and on individuals of small or medium ML (often collected from predators). Moreover, these studies were focused on the Arctic biota as a whole or on a predators' diet, and did not assess the biology, ecology and distribution of *G. fabricii*, including ontogenetic shift in diet or changes in TL.

In this study, a large and representative sample of beaks throughout the ontogenesis of *G. fabricii*, collected from 3 different parts of the Arctic (i.e. west and east Greenland, and the Barents Sea and adjacent areas), was analysed. We would expect a strong ontogenetic trophic shift in *G. fabricii* based on size increase and ontogenetic descent from small epipelagic forms (about 20 mm ML) to large bathypelagic forms (up to almost 400 mm ML). Bathypelagic males and females have different lifestyles, and thus stable isotope values are expected to reflect

these differences. Finally, geographic (habitat) variation in stable isotope values of *G. fabricii* (especially in $\delta^{13}C$) collected throughout the Arctic is to be expected, because the isotopic signature is affected by the different baseline levels of the respective water masses (Post 2002, Cherel & Hobson 2005, Hansen et al. 2012). Thus, the main goal of this study was to investigate the ecological role of *G. fabricii* in the Arctic, through understanding its habitat and TL (by using stable isotope analysis of beaks) and morphological data on beaks. New equations of the length–mass relationship and rostral length provided herein are crucial to achieving that goal. They will allow the estimation of consumption of the species by the numerous predators in the Arctic. In addition, the list of known prey and predators of *G. fabricii* (with references) provided in this study is of great importance to further our understanding of the ecological role of this species.
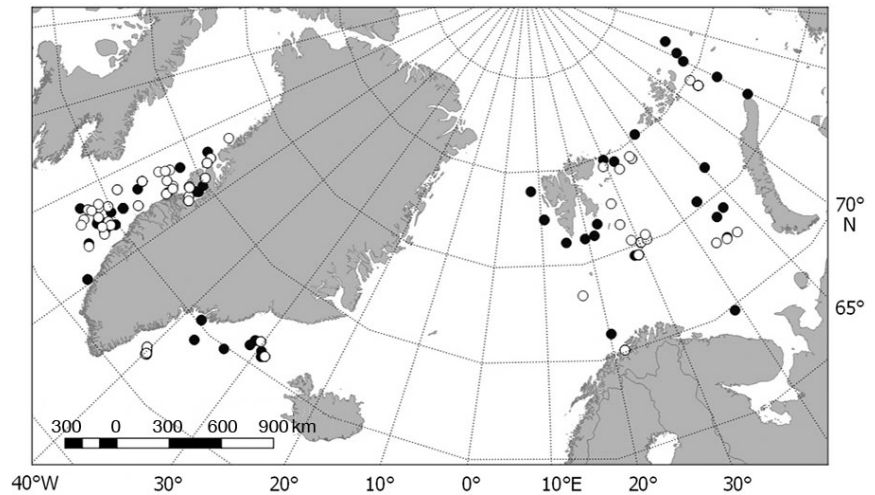

Fig. 1. Sampling locations of *Gonatus fabricii* in west Greenland, east Greenland and the Barents Sea. ●: morphological and stable isotope analysis of beaks; ○: only morphological analysis of beaks

MATERIALS AND METHODS

Study area and samples

Samples of *Gonatus fabricii* were collected in west Greenland waters by the R/V 'Paamiut' (Greenland Institute of Natural Resources) in 2015 and 2016, in east Greenland waters by R/V 'Paamiut' in 2015, and in the Barents Sea and adjacent areas in 2004–2012 and 2016 by the R/Vs 'F. Nansen', 'Smolensk' and 'Vilnius' (Polar Research Institute of Marine Fisheries and Oceanography). Samples were collected in July and August (locations shown in Fig. 1). Overall, 185

upper and lower beaks were collected and measured; stable isotope analyses were performed on 105 lower beaks of those pairs (Table 1; see below). All 185 squid specimens were used for ML to total body mass relationships and allometric relationships between LRL and ML/mass; the same relationships provided for upper rostral length (URL). Maturity stages were assigned on a scale based on Sauer & Lipinski (1990) and Nigmatullin et al. (2003), categorised as 0 to II: immature; III and IV: maturing; V_1: premature; V_2: mature; and V_3: subspent. The approximate sizes of maturity stages in *G. fabricii* are relatively well known (although some gaps do still exist for the later stages because of their rarity in catches) (Golikov et al. 2012), as are the sizes of ecological stages, meaning larvae and epi-, meso- and bathypelagic adult squid (Arkhipkin & Bjørke 1999, Golikov et al. 2012). Accordingly, we determined the following ontogenetic groups of squid:

Table 1. Sample sizes (n) and sampling year of beaks of *Gonatus fabricii* collected during the studied period (2004–2016) for males and females, selected for beak measurements and respective stable isotope analyses in west and east Greenland and the Barents Sea. Range in the mantle length (ML) is also shown

Specimens		Beak measurements			Stable isotope analyses		
		n	Sampling year	ML (mm)	n	Sampling year	ML (mm)
West Greenland	Females	44	2015–2016	15–249	22	2015	15–239
	Males	45	2015–2016	13–273	21	2015	13–257
East Greenland	Females	15	2015	40–178	13	2015	40–178
	Males	14	2015	49–178	12	2015	49–178
The Barents Sea	Females	39	2004–2012, 2016	21–221	21	2004–2012, 2016	29–221
	Males	28	2004–2012, 2016	25–185	16	2004–2012, 2016	26–185

– epipelagic larvae: ML < 15 mm;
– epipelagic immature: ML 15–30 mm, maturity stage 0;
– epipelagic immature: ML 30–60 mm, maturity stage I;
– mesopelagic immature: ML 60–75 mm, maturity stage I.

Afterwards, the groups were categorized differently between sexes; in males:

– mesopelagic immature: ML 75–130 mm, maturity stage II;
– bathypelagic maturing: ML > 130 mm, maturity stage III–IV;
– bathypelagic mature: ML > 160 mm, maurity stage V_2;
– bathypelagic subspent: ML > 160 mm, maturity stage V_3;

and in females:

– mesopelagic immature: ML 75–110 mm, maturity stage II;
– bathypelagic maturing, without gelatinous degeneration: ML > 150 mm, maturity stage III;
– bathypelagic maturing, with gelatinous degeneration: ML > 150 mm, maturity stage IV.

Five specimens were randomly selected (or all, in the case of insufficiency at rare late stages) for each group for length–mass relationship and beak measurements, and 4 specimens (out of the 5) per group were selected for stable isotope analysis. Bathypelagic females after gelatinous degeneration were not included in further statistical analysis, because only 2 individuals were collected, both from the Barents Sea.

Morphological data

Beaks were dissected from the buccal masses after freezing and thawing them several times. The measurements were taken following Clarke (1962a, 1986) and Wolff (1982); 6 measurements were performed from each upper beak (n = 185 beaks) and 4 from each lower beak (n = 185) (see detailed measurements in Fig. 2). Dispersion analysis was used to assess differences in mean values (i.e. ecological groups, geographical areas and sexes); groups were compared using the non-parametric Kruskal-Wallis *H* and Mann-Whitney *U*-tests (Zar 2010). Regression analysis was used to find the equations fitting our data. All tests were performed using a significance value of α = 0.05. Statistical analysis, calculations and
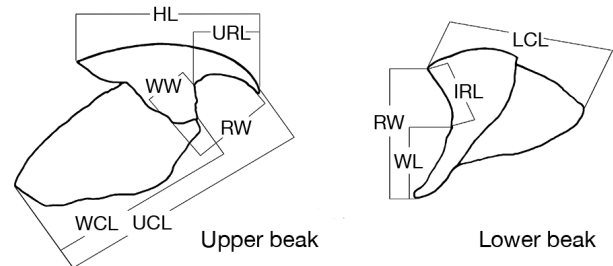

Fig. 2. Beak measurements obtained in *Gonatus fabricii*, following Clarke (1962a, 1986) with modifications of Wolff (1982). HL: hood length; LCL: lower crest length; LRL: lower rostral length; RW rostral tip to inner margin of wing; UCL: upper crest length; URL: upper rostral length; WCL: wing to crest length; WL: wing length; WW: width of the wing

plots were performed with Statistica 10 (Statsoft), PAST 3.15 (Hammer et al. 2001) and MS Excel 2010. Beaks were photographed with different optical stereomicroscopes and a digital videomicroscope (Hirox KH-7700).

Stable isotope analysis

All the beaks from west and east Greenland used for stable isotope analyses were collected in 2015. The beaks from the Barents Sea were collected over different years (2004–2012, 2016) (Table 1). Lower beaks selected for the analysis were dried at 60°C and ground into a fine powder. Powder sub-samples were weighed (~0.3 mg) with a microbalance scale and sterile-packed in tin containers. Stable isotope values were determined by a Flash EA 1112 series elemental analyser coupled online via a Finnigan ConFlo II interface to a Delta VS mass spectrometer (Thermo Scientific). The carbon and nitrogen isotope ratios were expressed in delta (δ) notation relative to Vienna-PDB limestone (V-PDB) for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. Replicate measurements of internal laboratory standards (acetanilide STD: Thermo Scientific PN 338 36700) in every batch (n = 14) indicated precision <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Similar statistical analyses were used for stable isotope and beak measurements. Stable isotopic niche widths were estimated and plotted with standard ellipse area corrected for small sample sizes (SEAc; an ellipse that contains 40% of the data regardless of sample size) and the Layman metric of convex hull area (TA); their areas and overlaps were estimated using R 2.15.2 (R Development Core Team, 2011) (Layman et al. 2007, Jackson et al. 2011, Ceia et al. 2014) and AreaS 2.1 (A. N. Permyakov; www.ssaa.ru).

Values of $\delta^{15}N$ in cephalopod beaks, in contrast to $\delta^{13}C$ values, are typically from 3.1 to 6.1‰ (mean 4.8‰) lower than values from muscle tissue (Cherel & Hobson 2005, Hobson & Cherel 2006, Cherel et al. 2008, Ruiz-Cooley et al. 2011). Therefore, we corrected the 'muscle' values of $\delta^{15}N$ obtained from the literature for comparison with our data by subtracting 4.8‰. However, when estimating TL, this value was added to our 'beak' values of $\delta^{15}N$, as proposed by Cherel et al. (2008). It was important to find the appropriate equations based on $\delta^{15}N$ and baseline values of $\delta^{15}N$ to estimate TL, because it is used as a tool to avoid biases when comparing specimens from different areas (Cherel et al. 2008, Linnebjerg et al. 2016). TL equations were chosen from among the following, applicable for the Arctic: (1) general classical equation for the World Ocean, trophic enrichment factor (TEF) of $\delta^{15}N$ is 3.4 (Post 2002); (2) equation for the Arctic with TEF 3.8 for all taxa except birds (Hobson & Welch 1992, Hobson et al. 2002); and (3) new equation for the World Ocean with scaled TEF (Hussey et al. 2014a,b), adapted for the Arctic (Linnebjerg et al. 2016). The last model was chosen, as it was the most recent and is supposed to show more significant results at higher TLs due to the scaled approach to TEF. Reference values of TL 2.0, required for the equation, were $\delta^{15}N$ 7.92‰ in Greenland waters (i.e. mean value of *Calanus finmarchicus*; Linnebjerg et al. 2016), and $\delta^{15}N$ 7.20‰ in the Barents Sea (i.e. mean value of *C. glacialis*; Søreide et al. 2013). The TLs obtained were then compared between groups (i.e. ecological groups, geographical areas and sexes). TLs of other cephalopods (data from the literature) were compared with our results estimated using the equation for Antarctic waters with TEF 3.2, the only one specifically used for cephalopods prior to our research (referred to as the 'Antarctic model') (Cherel et al. 2008).

Compilation of prey and predator lists (Tables S2 & S3) of *G. fabricii* were carried out to evidence and strengthen our conclusions and theories based on stable isotope analysis. Overlap in prey of epi-, meso- and bathypelagic stages of *G. fabricii*'s life cycle were estimated using the prey list in Table S2 and standard procedures for calculation.

RESULTS

Beak morphology and allometric equations

Beaks of the epipelagic *Gonatus fabricii* (maturity stages 0–I; n = 93) had URL values from 0.4 to 2.4 mm (mean ± SE: 1.4 ± 0.08 mm) and LRL values from 0.4 to 2.5 mm (1.5 ± 0.08 mm). No significant differences between sexes (U = 1017.5, p = 0.77) or regions ($H_{2,93}$ = 2.73, p = 0.09) were found. Beaks of meso-pelagic *G. fabricii* (maturity stages I–II; n = 63) were larger: URL from 1.1 to 4.0 mm (2.7 ± 0.13 mm), LRL from 1.3 to 4.0 mm (2.7 ± 0.12 mm). No significant differences between sexes (U = 418.5, p = 0.48) or regions ($H_{2,63}$ = 3.46, p = 0.11) were found. Beaks of bathypelagic *G. fabricii* (maturity stages after late II; n = 29) were the largest: URL from 3.0 to 6.5 mm (5.4 ± 0.25 mm), LRL from 3.3 to 6.5 mm (5.1 ± 0.14 mm). Again, no significant differences between sexes (U = 55, p = 0.10) or regions ($H_{2,29}$ = 2.09, p = 0.07) were found. Among all the measurements, the most useful were URL, hood length (HL) of the upper beak and LRL, as these parts most often remained intact when collected. In contrast, the crests and wings of the beaks are fragile and were often broken in our samples; thus these measurements were less useful. The shape and proportions of beaks did not change significantly during ontogeny (Fig. 3, Table 2).

Growth of both URL and LRL had significant positive correlations to ML: URL = $0.0543ML^{0.8725}$ (n = 183, R^2 = 0.95, p = 0.010) and LRL = $0.0592ML^{0.8528}$ (n = 183, R^2 = 0.98, p = 0.009) (Fig. 4). These showed slightly negative allometric growth in the upper and lower rostrums, meaning beaks grew more slowly, proportionally, than ML. The rostral growth was continuous, with no sharp increases, and tended to slow down in late ontogenesis. Both URL (U = 298, p = 0.032) and LRL (U = 296, p = 0.031) grew slightly faster in females; their allometric coefficients were higher (Fig. 4, Table S1). Similar results were found in all the studied regions (Table S1).

The stable shape and proportions, together with continuous growth of rostral length, made the beaks ideal tools to estimate the ML of *G. fabricii* consumed by predators. Significant length–mass relationship equations to estimate the mass of *G. fabricii* consumed by predators are provided in Table S1. The general relationship (for both sexes combined) is mass = $0.0003ML^{2.4777}$ (n = 183, R^2 = 0.97, p = 0.009), based on 185 specimens from 3 major parts of the *G. fabricii* range in the Arctic.

Stable isotope analysis

Values of $\delta^{13}C$ in the lower beaks of *G. fabricii* ranged from −23.0 to −18.4‰ (−20.8 ± 0.10‰). Overall, no significant differences were found between sexes (U = 1137, p = 0.18) nor within any of the stud-
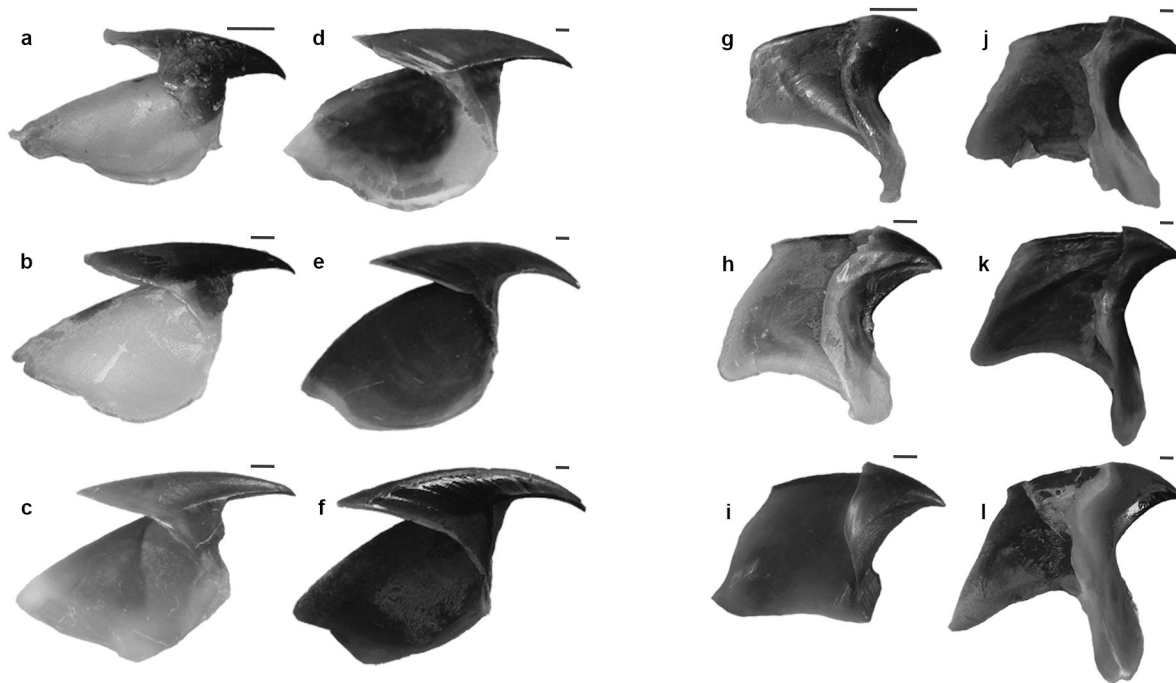
Fig. 3. Morphology of the beak in *Gonatus fabricii*: (a,g) upper and lower beak of epipelagic squid, maturity stage 0; (b,h) upper and lower beak of epipelagic squid, maturity stage I; (c,i) upper and lower beak of mesopelagic squid, maturity stage II; (d,j) upper and lower beak of mesopelagic squid, maturity stage III; (e,k) upper and lower beak of bathypelagic squid, maturity stage IV; (f,l) upper and lower beak of bathypelagic squid, maturity stage V_3. Scale bars: 0.5 mm (a,b,g,h), 1 mm (c–f, i–l)

Table 2. Changes in relative proportions of *Gonatus fabricii* beaks: upper rostral length (URL) relationship to hood length (HL) and to upper crest length (UCL), lower rostral length (LRL) relationship to lower crest length (LCL) during *Gonatus fabricii* ontogenesis. Values are mean ± SE

	URL/HL (%)	URL/UCL (%)	LRL/LCL (%)
Kruskal-Wallis *H*-test	$H_{3,185}$ = 3.908, p = 0.06	$H_{3,185}$ = 1.513, p = 0.22	$H_{3,185}$ = 1.023, p = 0.80
Epipelagic	32.89 ± 0.73	23.49 ± 1.10	39.87 ± 0.90
Mesopelagic	36.00 ± 0.86	26.53 ± 0.82	39.91 ± 1.46
Bathypelagic	40.04 ± 1.47	28.79 ± 1.28	37.16 ± 2.31
Bathypelagic after gelatinous degeneration (females only)	37.63 ± 0.41	27.62 ± 1.19	41.37 ± 5.36

$0.0074\,ML - 21.391$ (n = 103, R^2 = 0.16, p = 0.23), or LRL: $\delta^{13}C = 0.3272\,LRL - 21.59$ (n = 103, R^2 = 0.18, p = 0.21).

On the other hand, $\delta^{13}C$ values in the lower beaks of *G. fabricii* showed highly significant geographic differences ($H_{2,105}$ = 37.68, p < 0.001), being highest in west Greenland (from −22.0 to −19.0‰, mean −20.2 ± 0.10‰), followed by east Greenland (from −22.2 to −18.4‰, mean −20.8 ± 0.19‰) and the Barents Sea (from −23.0 to −19.6‰, mean −21.5 ± 0.15‰) (Table 4). Bathypelagic females from the Barents Sea after gelatinous degeneration (values

ied regions: west Greenland (*U* = 191, p = 0.33), east Greenland (*U* = 1197, p = 0.11) or the Barents Sea (*U* = 162, p = 0.86). The ontogenetic increase of $\delta^{13}C$ values was small, with bathypelagic stages only having significantly higher values (−20.0 ± 0.21‰), than mesopelagic (−20.8 ± 0.13‰) and epipelagic (−21.1 ± 0.17‰) squid (Table 3). The values of $\delta^{13}C$ were −19.6 and −20.5‰ in the 2 bathypelagic females after gelatinous degeneration. No significant correlations were found between $\delta^{13}C$ values and ML: $\delta^{13}C$ =

Table 3. Ontogenetic comparison of $\delta^{13}C$ values in the lower beaks of *Gonatus fabricii*. Kruskal-Wallis *H*-test and Mann-Whitney *U*-test for between-groups comparisons are provided in the table. Significant p-values are in **bold**

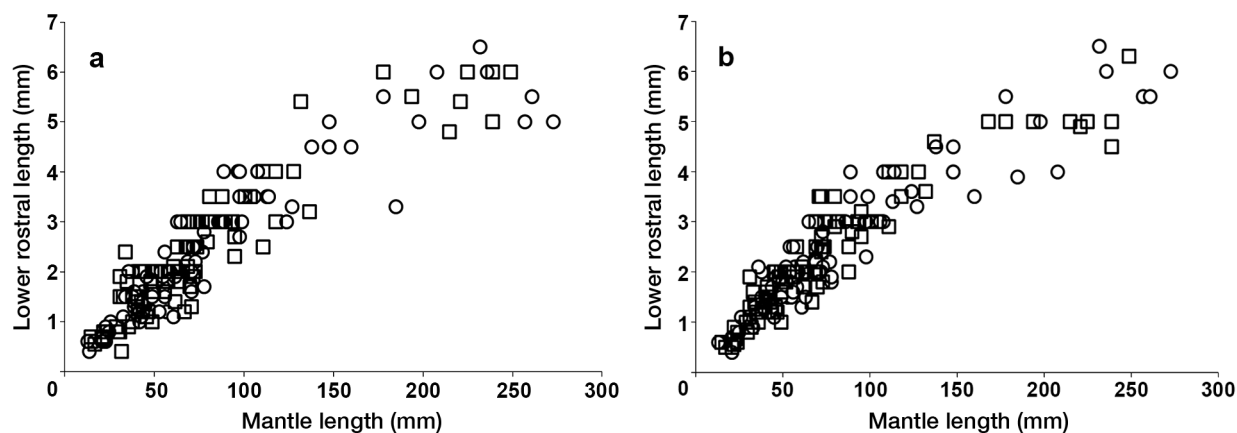|	
All specimens	$H_{2,105}$ = 12.98, df = 2, **p = 0.002**
Epipelagic vs. Mesopelagic	*U* = 771, p = 0.10
Epipelagic vs. Bathypelagic	*U* = 112, **p = 0.002**
Mesopelagic vs. Bathypelagic	*U* = 135.5, **p = 0.003**

Fig. 4. Growth of beak rostral length in *Gonatus fabricii*: (a) upper rostral length (URL); (b) lower rostral length (LRL). ML: mantle length; circles: males; squares: females. (a) Females: URL = $0.0532\,ML^{0.8778}$ (n = 99, R^2 = 0.92, p = 0.010), Males: URL = $0.0551\,ML^{0.8681}$ (n = 84, R^2 = 0.97, p = 0.009); (b) Females: LRL = $0.057\,ML^{0.8642}$ (n = 99, R^2 = 0.98, p = 0.009), Males: LRL = $0.0607\,ML^{0.8439}$ (n = 84, R^2 = 0.98, p = 0.008)

Table 4. Geographic comparison of $\delta^{13}C$ values in the lower beaks of *Gonatus fabricii*. Kruskal-Wallis *H*-test and Mann-Whitney *U*-test for between-groups comparisons are provided in the table. Significant p-values are in **bold**. BS: Barents Sea; EG: east Greenland; WG: west Greenland

All specimens	$H_{2,105}$ = 37.68, **p < 0.001**	Epipelagic	$H_{2,43}$ = 21.06, **p < 0.001**
BS vs. EG	*U* = 257, **p = 0.006**	BS vs. EG	*U* = 16, **p = 0.011**
BS vs. WG	*U* = 189, **p < 0.001**	BS vs. WG	*U* = 18, **p < 0.001**
EG vs. WG	*U* = 265, p = 0.001	EG vs. WG	*U* = 19, **p < 0.001**
Mesopelagic	$H_{2,43}$ = 19.10, **p < 0.001**	Bathypelagic	$H_{2,17}$ = 16.073, **p = 0.038**
BS vs. EG	*U* = 29, **p < 0.001**	BS vs. EG	*U* = 3, **p = 0.035**
BS vs. WG	*U* = 27, **p < 0.001**	BS vs. WG	*U* = 5, **p = 0.034**
EG vs. WG	*U* = 20, **p < 0.001**	EG vs. WG	*U* = 8, **p = 0.041**

given above) fit well into the general picture of a west-ward-directed increase in $\delta^{13}C$ values in *G. fabricii*.

Values of $\delta^{15}N$ in the lower beaks of *G. fabricii* ranged from 4.9 to 14.9‰ (8.7 ± 0.18‰). There were no significant overall differences in $\delta^{15}N$ values between the sexes (*U* = 1262, p = 0.60) or between sexes during the ontogenesis, i.e. among epipelagic (*U* = 211, p = 0.86), mesopelagic (*U* = 254.5, p = 0. 97) and bathypelagic males and females (*U* = 15, p = 0.53). Similar results were obtained when we added the 2 females after gelatinous degeneration to the rest of the bathypelagic females (*U* = 15, p = 0.12). Moreover, no significant differences were found in $\delta^{15}N$ values between regions ($H_{2,105}$ = 2.54, p = 0.08).

Highly significant differences were found between the ontogenetic stages of *G. fabricii*: $\delta^{15}N$ values ranged from 4.9 to 10.2‰ (7.7 ± 0.22‰) in epipelagic; from 5.5 to 11.2‰ (8.7 ± 0.19‰) in mesopelagic; and

from 8.6 to 14.9‰ (11.1 ± 0.46‰) in bathypelagic squid ($H_{2,105}$ = 31.98, p < 0.001) (Fig. 5a). The 2 bathypelagic females after gelatinous degeneration had similar $\delta^{15}N$ values, i.e. 13.5 and 13.2‰. Epipelagic larvae (4 specimens from west Greenland) did not show significant differences from the rest of the epipelagic squid (*U* = 17, p = 0.18), despite lower mean $\delta^{15}N$ values: 6.4 ± 0.59‰. These patterns of ontogenetic differences were similar in all the 3 studied regions (Table 5). Thus, $\delta^{15}N$ values in the lower beaks significantly increased during ontogenesis in all regions, with the growth of ML and LRL.

Isotopic niche and trophic level

Overall, the isotopic niche of *G. fabricii* was wide, from −23.0 to −18.4‰ in $\delta^{13}C$ and from 4.9 to 14.9‰ in $\delta^{15}N$ (Fig. 5b). The niche width was similar in all studied regions and differed between ontogenetic stages. The niche of the epipelagic squid had the largest area in all the studied regions (both SEAc and TA). The known prey of *G. fabricii* (Table S2) also supports these results: 25 taxa of crustaceans, 3 of molluscs, 5 of chaetognaths and 9 of fish larvae from all 49 known prey taxa of *G. fabricii* were known to be consumed by epipelagic squid. The niche of
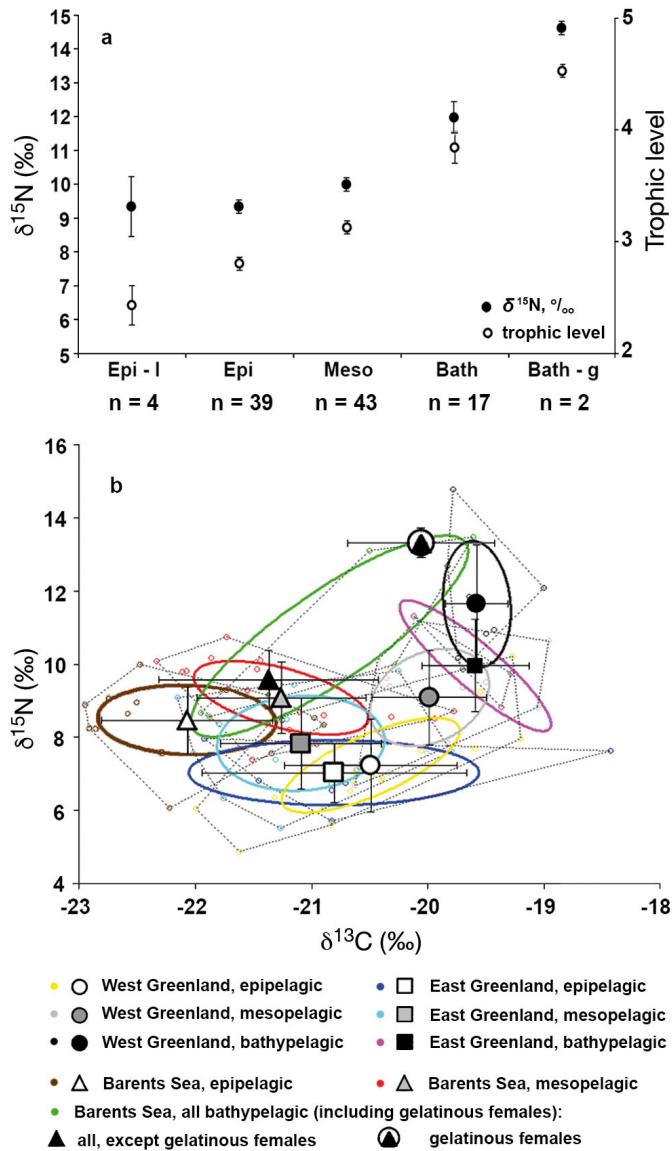
Fig. 5. Stable isotope values and trophic level changes in *Gonatus fabricii*. (a) Increase of δ¹⁵N values and trophic levels during ontogenesis. Values are mean ± SE. Epi – l: epipelagic larvae (mantle length [ML] 14.3 ± 0.5 mm); Epi: epipelagic squid (ML 39.0 ± 1.3 mm); Meso: mesopelagic squid (ML 85.2 ± 1.9 mm); Bath: bathypelagic squid (ML 173.4 ± 9.8 mm); Bath – g: bathypelagic females after gelatinous degeneration (ML 220.3 ± 2.9 mm). (b) Isotopic niches: standard ellipse area corrected for small sample sizes (coloured ellipses) and layman metric of convex hull area (dotted lines). Large symbols: mean ± SD

mesopelagic squid was the second highest in this study (both SEAc and TA). Nineteen taxa of crustaceans, 4 of molluscs, 5 of chaetognaths and 9 of fish were the known prey of mesopelagic squid (Table S2). The isotopic niche overlap between epipelagic and mesopelagic stages was 62.2% (Fig. 5b), with 31 common prey taxa, i.e. 73.8% overlap (Table S2).

The smallest isotopic niche was found in bathypelagic squid (both SEAc and TA). They showed the most notable differences from the niches of mesopelagic squid (i.e. 36.7% overlap in isotopic niches; all the 16 prey taxa were common, meaning 100% overlap in prey) and especially of epipelagic squid (6.9% overlap in isotopic niches with 56.3% overlap in prey, while common prey taxa were the fish only, whose larval and juvenile stages were eaten by small epipelagic *G. fabricii* and adult stages were eaten by large bathypelagic *G. fabricii*).

TL estimates of *G. fabricii* ranged from 2.5 to 5.1 (3.5 ± 0.05). TL did not differ statistically between sexes (U = 1267.5, p = 0.62) or regions, the only exception being east Greenland (Table 6), due to smaller sizes (ML) of the squid sampled in that area. As expected, there were significant differences in TL between the ontogenetic stages: the TL of epipelagic squid was from 2.5 to 4.0 (mean 3.3 ± 0.06), TL in mesopelagic squid was from 2.6 to 4.2 (3.6 ± 0.06) and TL in bathypelagic was from 3.3 to 5.1 (4.1 ± 0.14) (Table 6). Bathypelagic squid showed higher differences from the other groups (Fig. 5c). Mean TL of epipelagic larvae was 3.3 ± 0.27, the same as the means of the other epipelagic *G. fabricii* but with larger standard error values (Fig. 5c). The 2 bathypelagic females after gelatinous degeneration had TLs within the values of the rest of bathypelagic specimens (4.8 and 4.9). Overall, the ontogenetic shift in TL was 2.6. The increase during the epipelagic stage was 1.5 TLs, 1.6 TLs during the mesopelagic stage and 1.8 TLs during the bathypelagic stage.

DISCUSSION

Beak morphology and equations

The lack of significant changes in the shape and proportions of the beaks, as well as their continuous growth, make them useful for estimating the length and mass of *Gonatus fabricii* in the diet of predators. Overall, the equations obtained in this study (Table S1) for 3 major areas of the Arctic (west and east Greenland and the Barents Sea and adjacent waters) are useful throughout the whole range of *G. fabricii* in the Arctic. Previously published allometric equations for estimation of *G. fabricii* sizes using rostral length (Wiborg et al. 1982, Clarke 1986, Zumholz & Frandsen 2006), and equations of length–mass relationships (Kristensen 1984, Clarke 1986, Arkhipkin & Bjørke 1999, Zumholz & Frandsen 2006) were based on limited data and sampling area; here, we provide new equations (Table S1)

Table 5. Ontogenetic comparison of $\delta^{15}N$ values in the lower beaks of *Gonatus fabricii*. Kruskal-Wallis *H*-test and Mann-Whitney *U*-test for between-groups comparisons are provided in the table. Significant p-values are in **bold**

All specimens	$H_{2,105} = 31.98$, **p < 0.001**	The Barents Sea	$H_{2,37} = 6.281$, **p = 0.040**
Epipelagic vs. Mesopelagic	$U = 531.5$, **p < 0.001**	Epipelagic vs. Mesopelagic	$U = 21$, **p = 0.046**
Epipelagic vs. Bathypelagic	$U = 30$, **p < 0.001**	Epipelagic vs. Bathypelagic	$U = 14$, **p = 0.045**
Mesopelagic vs. Bathypelagic	$U = 95$, **p < 0.001**	Mesopelagic vs. Bathypelagic	$U = 24$, **p = 0.047**
East Greenland	$H_{2,25} = 6.688$, **p = 0.035**	West Greenland	$H_{2,43} = 24.89$, **p < 0.001**
Epipelagic vs. Mesopelagic	$U = 9$, **p = 0.042**	Epipelagic vs. Mesopelagic	$U = 47$, **p = 0.002**
Epipelagic vs. Bathypelagic	$U = 3$, **p = 0.023**	Epipelagic vs. Bathypelagic	$U = 3$, **p < 0.001**
Mesopelagic vs. Bathypelagic	$U = 5$, **p = 0.041**	Mesopelagic vs. Bathypelagic	$U = 8$, **p = 0.003**

Table 6. Geographic and ontogenetic comparison of trophic levels of *Gonatus fabricii*. Kruskal-Wallis *H*-test and Mann-Whitney *U*-test for between-groups comparisons are provided in the table. Significant p-values are in **bold**. BS: Barents Sea; EG: east Greenland; WG: west Greenland

All specimens	$H_{2,105} = 12.01$, **p < 0.001**	All specimens	$H_{2,105} = 33.04$, **p < 0.001**
BS vs. EG	$U = 188$, **p < 0.001**	Epipelagic vs. Mesopelagic	$U = 551.5$, **p < 0.001**
BS vs. WG	$U = 626$, p = 0.10	Epipelagic vs. Bathypelagic	$U = 34$, **p < 0.001**
EG vs. WG	$U = 393$, p = 0.11	Mesopelagic vs. Bathypelagic	$U = 116$, **p < 0.001**

with higher coefficients of determination and levels of significance. Also, some of the previously published equations are either linear models or were log-transformed (Wiborg et al. 1982, Kristensen 1984, Clarke 1986), which can cause additional biases comparing to standard power function (Hayes et al. 1995), as this function is the one most commonly used. Described tendencies of overall squid growth and LRL growth for west Greenland resembled those previously published for the region (Zumholz & Frandsen 2006), and the overall pattern of squid growth resembled the one by Arkhipkin & Bjørke (1999) published for the Norwegian Sea (having the most representative size sample prior to our study). Thus, our equations can be used for all studies across the Arctic region, as the samples are representative, both in terms of species ontogeny and sizes, and of geography.

Stable isotope values and ecological role of *G. fabricii* in the Arctic

Values of $\delta^{13}C$ in the lower beaks of *G. fabricii* showed only a slight ontogenetic increase, demonstrated in all studied regions. The explanation is that bathypelagic stages of *G. fabricii* live in different water masses from where epi- and mesopelagic stages live: cold Arctic waters below 800 m depth (Coachman & Barnes 1963), which obviously have a different isotopic signature from the mixed Arctic and Atlantic waters above 800 m (Coachman & Barnes 1963). Squid species that stay in one water mass throughout their entire life span show no ontogenetic increase in $\delta^{13}C$ values (Cherel & Hobson 2005). Values of $\delta^{13}C$ of *G. fabricii* were significantly different geographically, increasing gradually westward from the Barents Sea to east Greenland, and onwards to west Greenland. All groups (i.e. epi-, meso- and bathypelagic squid), showed this tendency (see 'Results'). Published $\delta^{13}C$ values of *G. fabricii* are similar to our study: from the Norwegian Sea (Hooker et al. 2001; from −19.6 to −19.2‰, higher than our maximum values in the Barents Sea), from west Greenland (Linnebjerg et al. 2016; −18.8 ± 0.5‰) and from Newfoundland (Lawson & Hobson 2000; −18.5 ± 0.4‰), with these 2 latter regions exhibiting higher values than our maximum values in west Greenland.

Typically, there is a latitudinally decreasing global pattern of $\delta^{13}C$ values in phytoplankton and in the associated trophic chain (Sackett et al. 1965, Rau et al. 1982, Goericke & Fry 1994), including squid (Takai et al. 2000). In this study, a longitudinal westward increase of $\delta^{13}C$ values in the northernmost Atlantic and the Arctic was found in *G. fabricii*. Despite not being previously reported in Arctic biota, this can also be noticed in planktonic and benthic invertebrates, fishes, seabirds and marine mammals

(data for comparison were taken from Hobson & Welch 1992, Hooker et al. 2001, Hobson et al. 2002, Søreide et al. 2006, 2013, Tamelander et al. 2006, Hansen et al. 2012, Linnebjerg et al. 2016, Dixon et al. 2017). Values of $\delta^{13}C$ within species are lower in the Barents Sea and surrounding waters than in west Greenland and the North Water polynya. Occasionally, there are differences even within the same region. This is a natural consequence of regional differences in $\delta^{13}C$ values at the base of the food web (i.e. phytoplankton), as shown in a recent study (Magozzi et al. 2017). Interestingly, in the Antarctic, $\delta^{13}C$ values in beaks of 9 squid species, including *Gonatus antarcticus*, showed a longitudinal eastward increase from South Georgia (South Atlantic Ocean) through Crozet to Kerguelen (South Indian Ocean) (Guerreiro et al. 2015), contrasting with *G. fabricii* in the Arctic Ocean. This could be explained by annual $\delta^{13}C$ values of phytoplankton distribution (Magozzi et al. 2017) and the clockwise direction of the Antarctic Circumpolar Current.

Values of $\delta^{13}C$ in cephalopod beaks are assumed to be directly comparable to those obtained from cephalopod muscles (Cherel & Hobson 2005, Hobson & Cherel 2006, Ruiz-Cooley et al. 2011). Some of the published studies were performed on muscle (e.g. Hobson & Welch 1992, Lawson & Hobson 2000, Takai et al. 2000, Das et al. 2003, Ruiz-Cooley et al. 2006, Hunsicker et al. 2010, Braid & Bolstad 2014, Linnebjerg et al. 2016); others were performed on beaks (e.g. Cherel & Hobson 2005, Hobson & Cherel 2006, Ruiz-Cooley et al. 2006, Cherel et al. 2008, 2009, Guerra et al. 2010, Guerreiro et al. 2015, Fang et al. 2016, Seco et al. 2016). However, no global pattern or relationships can be derived at this point due to limited data. In the Pacific, Atlantic and Antarctic there are cephalopods having both lower and higher $\delta^{13}C$ values than that of *G. fabricii* from the Arctic. Still, *G. fabricii* demonstrated the second highest range of $\delta^{13}C$ values (i.e. 4.6‰) with *G. antarcticus* showing the highest range (i.e. 7.3‰). Also from the Antarctic, *Alluroteuthis antarcticus* showed a range close to that of *G. fabricii* (i.e. 4.5‰; Guerreiro et al. 2015). These results suggest that polar squid may have more variation in habitat use than do more warm-water squid species.

G. fabricii demonstrated a significant ontogenetic increase in $\delta^{15}N$ values in their lower beaks, as expected. All stages (epi-, meso- and bathypelagic) were significantly different among all regions. Such a high magnitude of $\delta^{15}N$ increase (i.e. 10.0‰) corresponds to an ontogenetic shift of 3.0 TLs, assuming the most commonly applied enrichment factor of 3.4 (Post 2002). Specifically, with our model, using a scaled enrichment factor (Linnebjerg et al. 2016), the increase was 2.6 TL. The most dramatic increase of 1.8 TL was observed during the bathypelagic life stage, where the squid attained their largest sizes. No significant differences in TL or $\delta^{15}N$ values were found between sexes, despite the gelatinous degeneration in large bathypelagic females; their values were within the range of other bathypelagic squid. The highest estimated TL of *G. fabricii* was 5.1. The largest *G. fabricii* in this study had an ML of 257 mm, and the largest ever recorded *G. fabricii* had an ML of 389 mm (Sennikov et al. 1989). Thus, the TL of *G. fabricii* could potentially increase further.

Values of $\delta^{15}N$ in beaks reported from this study exceeded the range of previously published $\delta^{15}N$ values in muscles of *G. fabricii* from the Norwegian Sea (Hooker et al. 2001; from 13.4 to 14.6‰), in west Greenland (Linnebjerg et al. 2016; 13.1 ± 1.7‰) and in Newfoundland (Lawson & Hobson 2000; 12.3 ± 0.7‰). Overall, with $\delta^{15}N$ values reaching 14.9‰, our study showed that *G. fabricii* has one of the highest values among the Arctic invertebrates. There are only a few exceptions, all of which are scavenging benthic animals: some species of gastropods (*Buccinum* spp.), amphipods (*Anonyx* spp. and *Stegocephalus* spp.) and asteroids (*Crossaster papposus* and *Poraniomorpha tumida*) had values of $\delta^{15}N$ ranging from 11.9 to 17.4‰ (Table S4 in the Supplement) (Dunton et al. 1989, Hobson & Welch 1992, Tamelander et al. 2006). Values of $\delta^{15}N$ in *G. fabricii* also exceeded those of most Arctic fishes, except for large specimens of 15 species of teleost fish, large specimens of thorny skate *Ambliraja radiata* and all specimens of Greenland shark *Somniosus microcephalus* (Table S4); all these species are large piscivorous forms or benthic scavengers, eating scavenging invertebrates (Hobson & Welch 1992, Hobson et al. 2002, Tamelander et al. 2006, Hansen et al. 2012, Linnebjerg et al. 2016). All the Arctic seabirds show lower values of $\delta^{15}N$ than does *G. fabricii*, with the exception of the glaucous gull *Larus hyperboreus* (Table S4 in the Supplement) (Hobson & Welch 1992, Hobson et al. 2002, Linnebjerg et al. 2016). However, in the Canadian high Arctic, seabirds have significantly higher values of $\delta^{15}N$ than in other parts of the Arctic (Hobson & Welch 1992), and higher values of $\delta^{15}N$ than *G. fabricii* during this study, probably due to birds' dietary specifics there. Values of $\delta^{15}N$ in *G. fabricii* also surpassed many of the Arctic marine mammals (Hobson & Welch 1992, Abend & Smith 1995, Walker & Macko 1999, Lawson & Hobson 2000, Hooker et al. 2001, Hobson et al. 2002, Fontaine et al.

2007, Mendes et al. 2007, Linnebjerg et al. 2016): walruses *Odobenus rosmarus*, subadult harp seals *Phoca groenlandica*, long-finned pilot whales *Globi-cephala melas*, harbour porpoises *Phocoena pho-coena*, sperm whales *Physeter macrocephalus* and northern bottlenose whales *Hyperoodon ampullatus* (Table S4). Interestingly, the last 2 species are known to be the most important predators of *G. fabricii* (Table S3). This suggests that only the large adult specimens of whales and seals in the Arctic prey upon large bathypelagic specimens of *G. fabricii*.

The estimated TL of *G. fabricii* was higher than all the Arctic invertebrates (again, some benthic scav-engers probably have a higher TL, if treated with the more suitable model). And with ontogenetic increase of 10.0‰ in δ^{15}N, meaning 2.6 TL, *G. fabricii* has the widest isotopic niche and the highest ontogenetic shift in TL among the Arctic invertebrates. Also, its TL was higher than most of the fish, seabirds, walrus, subadult seals and toothed whales in the Arctic (Table S4). It was well within the upper values in the range of TL of large piscivorous fishes, seals and toothed whales or of large benthic scavenging fishes (Hobson & Welch 1992, Abend & Smith 1995, Walker & Macko 1999, Lawson & Hobson 2000, Hooker et al. 2001, Hobson et al. 2002, Tamelander et al. 2006, Fontaine et al. 2007, Mendes et al. 2007, Hansen et al. 2012, Linnebjerg et al. 2016) (Table S4). This sug-gests that most of the 47 known taxa of predators of *G. fabricii* (Table S3), except one taxon of elasmo-branches, 7 taxa of teleost fish and 7 taxa of toothed whales, do not usually eat large bathypelagic squid or do so only occasionally, while mesopelagic *G. fabricii* of smaller sizes are known to be their im-portant prey (Table S3). Small epipelagic squid, on the contrary, are important prey for many species of predators from different taxonomic groups (Table S3). Thus, during ontogenetic descent down-wards to bathypelagic layers, coupled with continu-ous growth, *G. fabricii* increases its TL, changing its prey from small epipelagic plankton to larger crus-taceans, molluscs and fishes, and then increasing the ratio and sizes of fishes in its diet, while avoiding predation pressure itself.

To our knowledge, *G. fabricii* has the highest δ^{15}N values (i.e. 14.9‰) of any other studied cephalopod species; none of the studied cephalopods showed δ^{15}N values in beaks higher than 14.25‰ (the value was up to 18.5‰ in muscle, but 'muscle' values for comparison were corrected by subtracting 4.8‰, as explained above). Thus, even the largest and/or most active hunting squids, such as *Mesonychoteuthis hamiltoni* (Cherel & Hobson 2005, Cherel et al. 2008,

2009), *Architeuthis dux* (Cherel & Hobson 2005, Cherel et al. 2008, 2009, Guerra et al. 2010), *Idio-teuthis cordiformis* (Braid & Bolstad 2014), *Taningia danae* (Cherel & Hobson 2005, Cherel et al. 2008, 2009, Guerreiro et al. 2015), *Dosidicus gigas* (Ruiz-Cooley et al. 2006), *Ommastrephes bartramii* (Takai et al. 2000, Fang et al. 2016) and *Sthenoteuthis oualaniensis* (Takai et al. 2000) showed lower δ^{15}N values than did the *G. fabricii* in our study. Among the species whose TL was estimated in the literature (always by the 'Antarctic model'), the following showed the highest TL: *M. hamiltoni* (TL 6.1), *G. antarcticus* (TL 5.2), *Mastigoteuthis psychrophila* (TL 5.0), *Chiroteuthis veranyi* (TL 5.0) from the Antarctic, *D. gigas* (TL 6.5) from the Gulf of Califor-nia and *I. cordiformis* (TL 6.1) from New Zealand waters (Cherel et al. 2008, Braid & Bolstad 2014). The latter species from the Pacific were excluded from further comparison because there is no correct model to estimate their TL (the 'Antarctic model' is not suit-able, as it uses the Antarctic pelagic tunicate's value of δ^{15}N as a reference for TL 2.0). Among the Antarc-tic squids, 2 species exceeding the TL of *G. fabricii* in the Arctic are the active large- (or even giant-) sized hunters *M. hamiltoni* and *G. antarcticus*. Surpris-ingly, *M. psychrophila* and *C. veranyi*, small, fragile, supposedly plankton-eating species (Cherel & Hob-son 2005), show TL values almost reaching those of *G. fabricii*.

Conclusions and future directions

The habitat (δ^{13}C values) and TL (δ^{15}N values) of *G. fabricii* were not related to sex, despite ontogenetic sexual differences in its life cycle. Values of δ^{13}C showed low ontogenetic increases, while being significantly different geographically: a westward increase was found, from the Barents Sea to east Greenland and further to west Greenland. This habi-tat pattern in δ^{13}C values, despite not being reported previously in any groups of Arctic biota, was identi-fied in many taxa, from phytoplankton to marine mammals elsewhere, showing regional differences in δ^{13}C values in the Arctic. In terms of the TLs (and δ^{15}N values) of *G. fabricii*, the results showed no geo-graphical variation in the Arctic. However, a highly significant ontogenetic increase (10.0‰ δ^{15}N; 2.6 TL) from epipelagic larval and juvenile forms to large bathypelagic adult stages was found. While juveniles showed a TL of 2.5–4.0, close to those of large pelagic crustaceans and small or medium-sized fishes, adults reached high values (3.3–5.1), similar to large pisciv-

orous fishes, seals and toothed whales or large benthic scavenging fishes. Thus, *G. fabricii* is a top invertebrate predator in the Arctic, with the widest isotopic niche observed to date for any species there: during ontogenetic descent to bathypelagic layers, coupled with its continuous growth, it changes prey types and avoids predator pressure.

This study highlights the ecological role of *G. fabricii* in the Artic as the most important cephalopod species, clearly playing a relevant role in the marine food web of the region. To our knowledge, *G. fabricii* has the highest values of $\delta^{15}N$ ever recorded in cephalopod beaks, i.e. 14.9‰. Therefore, comparing its TL with those published for other cephalopods, *G. fabricii* is exceeded only by its congener species from the Antarctic Ocean, *G. antarcticus*, and by the Antarctic colossal squid *M. hamiltoni* (Antarctic data from Cherel et al. 2008). This strongly suggests that in polar ecosystems, squid occupy higher trophic positions than in the rest of the World Ocean.

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