



Trophic structure of Southern Ocean squid: a cross-basin analysis of stable isotopes in archived beaks from predator stomachs

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ABSTRACT: Cephalopods are an important component of Southern Ocean food webs, but aspects of their trophic ecology remain unresolved. Here, we used archived squid (order Teuthida) beaks, collected from stomach contents of predators at Macquarie and Kerguelen Islands, to investigate the trophic structure within an assemblage of pelagic squids (*Alluroteuthis antarcticus*, *Filippovia knipovitchi*, *Gonatus antarcticus*, *Histioteuthis eltaninae*, *Martialia hyadesi* and *Brachioteuthis linkovskyi*). We combined bulk nitrogen stable isotopes ($\delta^{15}\text{N}_{\text{bulk}}$) with compound-specific isotope analysis of amino acids (CSIA-AA) to estimate the trophic position (TP) of species and to assess isotopic relationships with body size at the species, community, and ocean basin levels. We observed significantly higher mean $\delta^{15}\text{N}_{\text{bulk}}$ values for species at the Kerguelen Islands compared to conspecifics at Macquarie Island. This result was explained by regional variability in $\delta^{15}\text{N}$ values of phenylalanine ($\delta^{15}\text{N}_{\text{Phe}}$), suggesting that predator species were accessing different isotopic baselines at each region. This may highlight the different foraging strategies of both species. The overlap in species TP estimates from CSIA-AA (TP_{CSIA}) between the 2 communities (Macquarie Island TP_{CSIA} min: 2.3, max: 5.3; Kerguelen Islands TP_{CSIA} min: 2.7, max: 5.3) indicated a similar trophic structure at both locations. We note unrealistically low TP_{CSIA} for some species, which we attribute to uncertainty of trophic discrimination factors. TP estimates suggested that squid encompass 3 trophic levels from mid-trophic levels to higher predators. We did not find strong or consistent relationships between TP and body size at either the species- or community-level. One of the largest squid species, *M. hyadesi*, occupied the lowest TP in both communities. These new insights into the trophic structure of the Southern Ocean squid community have important implications for the future representation of pelagic squids in ecosystem models.

KEY WORDS: Allometry · Biochemical tracers · CSIA-AA · Nitrogen · Trophic position · Cephalopods · Antarctic · Mesopelagic

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1. INTRODUCTION

Cephalopods are an important component of Southern Ocean food webs, but substantial knowledge gaps remain regarding their ecology, distribution, and trophic role (Collins & Rodhouse 2006, Xavier

et al. 2018, Cherel 2020). Of the Southern Ocean cephalopods, squids (order Teuthida) are the most dominant group in the pelagic ecosystem (Rodhouse et al. 2014, Cherel 2020) and are a key trophic component for many predators (Cherel 2020) such as toothfish (Cherel et al. 2004, Seco et al. 2016, Queirós

et al. 2021), marine mammals (Field et al. 2007, Harrington et al. 2017, Cherel 2021) and seabirds (Cherel et al. 1996, Xavier et al. 2003, Jimenez et al. 2017). Southern Ocean squids also play an important role as predators, notably of myctophid fishes (Pethybridge et al. 2013), other cephalopods and crustaceans such as amphipods (Phillips et al. 2003, Pethybridge et al. 2013). Thus, they support the flow of energy through alternative non-krill-based trophic pathways from primary producers to higher order predators across various regions and seasons in the Southern Ocean (Rodhouse & White 1995, Murphy et al. 2016, McCormack et al. 2019a). Despite being identified as a key component of the food web, data on squid are limited due to their low catchability with scientific nets and because few surveys dedicated to the study of oceanic cephalopods are being undertaken (Rodhouse et al. 2014). The increasing threats posed by climate change and harvesting have heightened the need for ecosystem models that can provide robust predictions of the ecological implications of environmental change (Murphy et al. 2012, 2016, Constable et al. 2017, Trebilco et al. 2020). Such modelling efforts will ultimately require improved quantification of energy pathways dominated by key groups such as squids to ensure they are accurately represented in such models.

Squids have been found to display a high degree of trophic diversity spanning multiple trophic levels (Navarro et al. 2013). However, their representation in current Southern Ocean ecosystem models is limited to a single functional group (Murphy et al. 2012) or broad trophic groupings (Gurney et al. 2014) based on their taxonomic identity. An alternative to modelling frameworks that aggregate functional groups based on species are size-based food web models. These models represent the flow of biomass and energy through communities from smaller to larger individuals (Blanchard et al. 2017). Grouping by body size is based on the premise that this is a stronger determining factor of feeding interactions than taxonomic identity in marine ecosystems (Andersen et al. 2016, Blanchard et al. 2017). Body size is thought to be an important determinant for the trophic structure of the squid community (Rodhouse & Nigmatullin 1996), and so quantifying relationships between trophic position (TP) and body size will be important to resolving their representation in ecosystem models (Murphy et al. 2012, McCormack et al. 2019a).

Cephalopod predators can be used as biological samplers to overcome some of the limitations of net sampling. Cephalopod beaks, composed of indiges-

tible material, chitin, accumulate in the stomachs of their predators (Cherel & Hobson 2005, Cherel et al. 2009b) and can be identified to species-level based on morphology (Xavier & Cherel 2021). A further advantage is that predators catch larger specimens and a greater diversity of species than nets (Rodhouse & Yeatman 1990, Cherel et al. 2004). Analysing biochemical tracers in beaks can then be used to gain insight into the functional role of cephalopods in food webs (i.e. their trophodynamics; Cherel & Hobson 2005, Hobson & Cherel 2006, Cherel et al. 2009b, 2019, Queirós et al. 2018, 2021). Stable isotopes are the most widely used biochemical tracers in ecology (Peterson & Fry 1987, Bearhop et al. 2004, Layman et al. 2012, Pethybridge et al. 2018b, McCormack et al. 2019b). One of the most used elements is nitrogen, which is measured in consumer proteins and expressed as a ratio of heavy to light isotopes ($^{15}\text{N}:$ ^{14}N , $\delta^{15}\text{N}$ values), relative to international standards of atmospheric nitrogen. Following assimilation, consumer tissues metabolically excrete lighter isotopes (^{14}N) in waste products, resulting in a gradual increase in $\delta^{15}\text{N}$ values per trophic transfer (Pethybridge et al. 2018b). Typically, this increase, known as the trophic enrichment factor, falls within the range of ~ 2.4 – 4.2 ‰, and 3.4 ‰ has been widely used as a default (Minagawa & Wada 1984, Pethybridge et al. 2018b), although the flaws in assuming a single fixed value are recognised (Hussey et al. 2014). Regardless, $\delta^{15}\text{N}$ provides an indicator of consumer TP and nitrogen sources fuelling the food web (Post 2002).

Bulk nitrogen stable isotope analysis (SIA) of squid beaks has been successfully applied to beaks collected from various Southern Ocean predators (Cherel & Hobson 2005, Ruiz-Cooley et al. 2006, Guerreiro et al. 2015, Seco et al. 2016, Queirós et al. 2018) and has revealed new information on the isotopic niches occupied by different squid species (Guerreiro et al. 2015), the trophic structure within different communities and ontogenetic shifts in diet (Cherel et al. 2009b, Queirós et al. 2021). Yet, interpretation of bulk $\delta^{15}\text{N}$ values comes with several caveats. A global review and synthesis of available isotope data from squids has highlighted the influence of local biogeochemistry on consumer $\delta^{15}\text{N}$ values (Navarro et al. 2013). Marine food webs can be fuelled by different nitrogen sources (e.g. upwelled nitrate or atmospheric nitrogen), causing a variation in baseline $\delta^{15}\text{N}$ values which is propagated through the food web influencing consumer $\delta^{15}\text{N}$ values (Hannides et al. 2009).

Compound-specific stable isotope analysis of amino acids (CSIA-AA) complements traditional 'bulk' stable

isotope data by distinguishing between baseline primary production sources and trophic effects, allowing for more accurate estimates of TP (Pethybridge et al. 2018b). Amino acids such as phenylalanine show no change in $\delta^{15}\text{N}$ values from the base of the food web to the consumer and are often termed 'source' amino acids (McClelland & Montoya 2002). In contrast, amino acids such as glutamic acid show large enrichments in ^{15}N with each trophic transfer and are termed 'trophic' amino acids. Measuring the $\delta^{15}\text{N}$ values of source and trophic amino acids in a consumer eliminates the need to separately measure the isotopic baseline of a food web (Bradley et al. 2015, Pethybridge et al. 2018b). This method was recently validated on squid beaks collected from predator stomachs in the Southern Indian Ocean to produce reliable estimates of food web baseline and associated uncertainty, thus resulting in improved TP estimates (Cherel et al. 2019). Further, this study noted the ability of CSIA-AA to overcome the chitin effect, which is a significant confounding factor to the interpretation of bulk isotope data (Cherel et al. 2019). This study aside, current TP estimates for Southern Ocean pelagic squid species have been calculated for only a few species and using bulk stable isotope data only (Cherel et al. 2008, Navarro et al. 2013).

Here we used an existing prey library of squid beaks collected from 2 major predators to investigate the trophic structure and energy flow within an assemblage of 6 pelagic squid species in the West Pacific and Indian sectors of the Southern Ocean. Squid beaks were sampled from southern elephant seals at Macquarie Island in the West Pacific and wandering albatross at the Kerguelen Islands in the Indian sector. We combined bulk nitrogen SIA with

CSIA-AA to estimate the TP ($\delta^{15}\text{N}_{\text{bulk}}$ and TP_{CSIA} , respectively) of species within each community and to assess relationships with body size at the species-, community-, and ocean basin-level. In the Southern Indian Ocean, previous studies have demonstrated a species-level enrichment in ^{15}N with size (Cherel & Hobson 2005, Cherel et al. 2009a), and evidence suggests that the role of squids in Southern Ocean food webs varies regionally (McCormack et al. 2021). We focused on 2 key questions: (1) Is there variability in trophic roles for individual squid species across the 2 communities; and (2) How strong is size-based trophic structure in the pelagic squid assemblage?

2. MATERIALS AND METHODS

2.1. Sample collection and preparation

Squid beaks were collected from existing prey libraries held in Australia at the Institute for Marine and Antarctic Studies (IMAS) and in France at the Centre d'Etudes Biologiques de Chizé. Beaks were previously sampled from the stomach contents of juvenile and adult southern elephant seals *Mirounga leonina* at Macquarie Island (Fig. 1) during the period of September 1999 to September 2000 (Field et al. 2007). At the Kerguelen Islands (Fig. 1) beaks were collected from regurgitates of wandering albatross chicks *Diomedea exulans* during the breeding season from June to October 1998 (Cherel et al. 2017). Beaks were cleaned at the time of collection and stored in 70 % ethanol until isotopic analysis was conducted. Previous research has demonstrated a

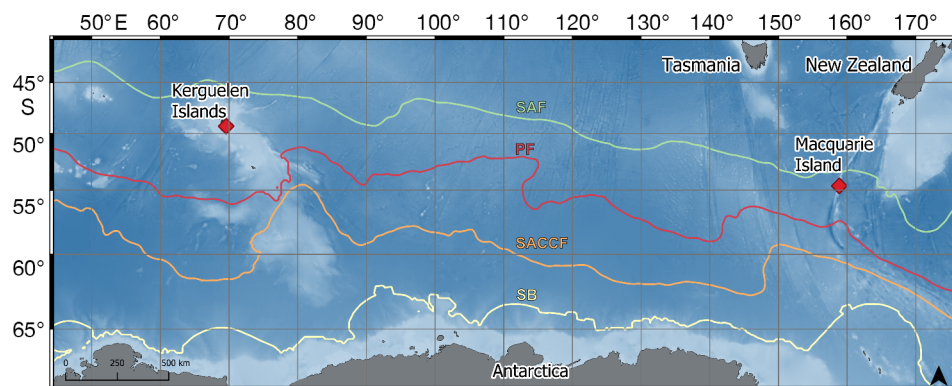


Fig. 1. Sampling locations (red diamonds) of squid beaks from 2 sites in the Indian and Pacific sectors of the Southern Ocean. Squid beaks were collected from wandering albatross *Diomedea exulans* at the Kerguelen Islands during the winter field season of 1998 and from southern elephant seals *Mirounga leonina* at Macquarie Island during the summer and winter field season for 1999. Coloured lines indicate mean frontal positions (Sokolov & Rintoul 2007). SAF: Subantarctic Front; PF: Polar Front; SACCF: Southern Antarctic Circumpolar Current Front; SB: southern boundary of the Antarctic Circumpolar Current

negligible effect of ethanol preservation on the bulk nitrogen isotope values of squid beaks (Ruiz-Cooley et al. 2011).

The lower beaks of 5 species (*Alluroteuthis antarctica*, *Filippovia knipovitchi*, *Gonatus antarcticus*, *Histioteuthis eltaninae* and *Martialia hyadesi*) that were abundant in the stomach contents of both predators at both locations (Field et al. 2007, Cherel et al. 2017), and are thought to be among the most abundant species in the Southern Ocean (Cherel 2020), were selected from archived samples. Beaks from an additional species, *Brachioteuthis linkovskyi*, were also selected from Macquarie Island elephant seals, as this species was among the most abundant in these stomach samples. However, it was absent in albatross samples from Kerguelen Islands precluding comparisons with the same species from Macquarie Island. For each species, up to 15 lower beaks were selected from both locations (where possible), spanning the range of sizes present (Table 1). In the laboratory, lower beaks were cleaned thoroughly with distilled water and identified to species level based on their morphology (Xavier & Cherel 2021). The lower rostral length (LRL), from the rostral tip to the jaw angle, was measured to the nearest 0.01 mm using vernier callipers. We used the LRL to estimate dorsal mantle length (ML; equivalent to body size) from published allometric equations using the R package *solong* (Raymond 2021) from the Southern Ocean Diet and Energetics Database (Scientific Committee on Antarctic Research 2018; Table S1; www.int-res.com/articles/supp/m685p137_supp.pdf). The LRL may be used as proxy for body size among individuals of the same species (Xavier & Cherel 2021). We prepared the whole lower beak for SIA, as this gives an integrated view of diet and foraging location across a consumer's lifetime with bias towards the most recent period of growth (Guerreiro et al. 2015). Further, this allowed us to draw comparisons with previous studies (e.g. Cherel et al. 2008, Guerreiro et al. 2015).

2.2. Bulk stable isotope analysis

In preparation for SIA, beaks were oven-dried at 60°C and ground to a homogeneous powder using a mortar and pestle. We weighed ground squid beak into tin capsules using a microbalance (ranging from 0.4–0.5 mg). Bulk stable isotope compositions were measured using an Isoprime 100 mass spectrometer coupled to an Elementar vario PYRO cube elemental analyser at the Central Science Laboratory, Univer-

Table 1. Attributes of the lower beaks of 6 different squid species collected from predator stomachs at Kerguelen and Macquarie Islands ordered according to lower rostral length (LRL) size (low to high). Values are sample size (n), minimum and maximum values for measured LRL (range) and estimated mantle length (ML) (range), mean bulk $\delta^{15}\text{N}$ values with SD, minimum and maximum bulk $\delta^{15}\text{N}$ values (range). The p-values are reported from Tukey HSD post-hoc test for pairwise comparisons of bulk $\delta^{15}\text{N}$ values for like species across locations. * Statistically significant Tukey comparison ($p < 0.05$)

Species	Kerguelen Islands			Macquarie Island			ANOVA			
	n	LRL range (mm)	$\delta^{15}\text{N}$ (‰) Mean (SD)	n	LRL range (mm)	$\delta^{15}\text{N}$ (‰) Mean (SD)	Tukey tests $\delta^{15}\text{N}$ (‰) p	ANOVA Tukey tests $\delta^{15}\text{N}$ (‰) p		
<i>Histioteuthis eltaninae</i>	15	2.7–3.8	6.9 (0.5)	6.1–7.9	10	2.7–3.9	62–91	5.4 (1.1)	3.3–7.6	<0.05*
<i>Brachioteuthis linkovskyi</i>	0				10	3.6–4.2	88–100	4.8 (1.3)	3.3–6.8	
<i>Alluroteuthis antarcticus</i>	10	4.9–6.2	6.7 (0.3)	6.4–7.3	12	3.8–5.6	129–193	4.9 (1.1)	2.8–7.1	<0.05*
<i>Gonatus antarcticus</i>	10	5.4–8.1	8.8 (0.5)	8.0–9.8	7	3.1–5.8	89–204	5.6 (0.8)	4.6–6.9	<0.05*
<i>Martialia hyadesi</i>	10	4.9–7.4	3.1 (0.8)	2.4–5.2	14	4.1–8.2	223–344	1.8 (1.8)	0.1–4.8	<0.05*
<i>Filippovia knipovitchi</i>	10	6.8–9.2	7.2 (0.6)	6.7–8.6	14	3.7–6.4	125–291	5.0 (0.8)	3.3–6.4	<0.05*

sity of Tasmania, Hobart, Australia. Stable isotope ratios are presented in delta (δ) notation as parts per thousand (‰) and calculated according to the following formula:

$$\delta X(\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \right] \quad (1)$$

where X is ^{15}N and R is the corresponding ratio of heavy to light isotopes, $^{15}\text{N}/^{14}\text{N}$, relative to international standards of atmospheric N_2 . International reference standards with known isotopic composition (glutamic acid: USGS 40, USGS 41; ammonium sulphate: USGS 25, IAEA-N1, IAEA-N2) were used to correct for instrumental drift and quality assurance purposes. Instrumental precision was 0.1‰, and a minimum of 1 international reference standard was run for every 6 samples.

2.3. Compound-specific isotope analysis of amino acids

Samples were prepared for CSIA-AA following the methods outlined in Dale et al. (2011) and Hofmann et al. (2003). The $\delta^{15}\text{N}$ isotope composition of the amino acids (AA) was measured with a Trace GC gas chromatograph coupled to a Delta V Plus isotope ratio mass spectrometer (IRMS), through a GC-C combustion furnace (980°C), reduction furnace (650°C), and liquid N_2 cold trap.

All samples were analysed in triplicate, with each set bracketed by a standard suite of AAs with known $\delta^{15}\text{N}$ values. Measured $\delta^{15}\text{N}$ values of sample AAs were then normalised using the average of the standard runs immediately before and after the sample repeats. Within sample reproducibility associated with the analysis of both Glx (glutamate and glutamine) and phenylalanine averaged 0.44‰ (1SD) and ranged from 0.06 to 0.85‰.

TP was calculated using the difference between the trophic AA Glx (the method used here combines glutamate and glutamine, termed Glx; Fuller & Petzke 2017) and phenylalanine, a source AA, according to Cherel et al. (2019):

$$\text{TP}_{\text{CSIA}} = \frac{\delta^{15}\text{N}_{\text{Glx}} - \delta^{15}\text{N}_{\text{Phe}} - \text{TDF}_1 - \beta}{\text{TDF}_2} + 2 \quad (2)$$

where $\delta^{15}\text{N}_{\text{Glx}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ represent the nitrogen isotopic values of glutamic acid/glutamine and phenylalanine in the consumer, respectively; β is the isotopic difference in $\delta^{15}\text{N}$ between glutamic acid and phenylalanine in primary producers (2.9‰; Nielsen et al. 2015); TDF_1 is the trophic discrimination factor

which represents the change in ^{15}N enrichment of glutamic acid relative to phenylalanine with each trophic transfer (7.6‰; Chikaraishi et al. 2009); and TDF_2 is the trophic discrimination factor specifically for cephalopods (5.0‰; McMahon & McCarthy 2016).

Additionally, we used relative trophic position (RTP) as a proxy for TP to assess community and basin level body size relationships. This was calculated using the following equation:

$$\text{RTP}(\text{‰}) = \delta^{15}\text{N}_{\text{Glx}} - \delta^{15}\text{N}_{\text{Phe}} \quad (3)$$

The advantage of RTP is that it requires no prior assumptions of β and TDF values, which is a major limitation of CSIA-AA (Chikaraishi et al. 2009, McMahon & McCarthy 2016). Instead, it utilises the relative differences in food web position (Choy et al. 2015).

2.4. Statistical analysis

All statistical analyses were performed using R, version 4.0.4 (R Core Team 2021) and a significance level of $\alpha = 0.05$. Currently, there is no standard method for integrating data from bulk nitrogen SIA and CSIA-AA, and so we followed previous examples in the literature to help guide our analysis (Choy et al. 2012, Cherel et al. 2019).

2.4.1. Comparison of isotopic values and trophic positions

We compared the isotopic values and TP of species to determine whether their trophic roles varied across the 2 communities. We performed a 2-way ANOVA with a Tukey HSD post-hoc test for pairwise comparisons to test for significant differences in bulk $\delta^{15}\text{N}$ values (proxy for TP) between species across and within both locations. Due to the unbalanced sampling design (different sample sizes for each species) and a significant interaction effect between location and species, we repeated the ANOVA based on type III sum of squares. Next, to determine whether bulk $\delta^{15}\text{N}$ values could be used as a proxy for TP, we modelled the relationship between TP_{CSIA} and bulk $\delta^{15}\text{N}$ values using linear regression models.

We investigated the influence of regional variability in primary production sources on bulk $\delta^{15}\text{N}$ values at the 2 sampling locations using the R package lme4 (Bates et al. 2015) to fit a linear mixed-effects (LME)

model. We used the $\delta^{15}\text{N}$ values of phenylalanine (a source amino acid; $\delta^{15}\text{N}_{\text{Phe}}$), location (Kerguelen Islands and Macquarie Island) and an interaction term between $\delta^{15}\text{N}_{\text{Phe}}$ and location to predict bulk $\delta^{15}\text{N}$ values. Sampling was undertaken during summer 1999, winter 1998 and winter 1999. To determine whether we needed to include field season as a random effect within the model, we performed a likelihood ratio test to compare the full model (with the random effect, field season) to a reduced version of the model (without the random effect, field season). Likelihood ratio tests supported the inclusion of the random effect term of field season (change in Akaike's information criterion, ΔAIC , of 6). Next, we assessed the performance of the full model against corresponding reduced models with AIC (Akaike 1974, Burnham & Anderson 2004). The best fit models were those with ΔAIC values ≤ 2 (where $\Delta\text{AIC}_i = \text{AIC}_i - \text{AIC}_{\text{min}}$; Burnham & Anderson 2004). We assessed the fit of the final model using the marginal and conditional r^2 (Nakagawa & Schielzeth 2013). The full model and corresponding reduced model formulations can be viewed in Table S2a.

2.4.2. Relationships between body size and trophic position

To determine the strength of size-based trophic structure within the pelagic squid assemblage, we assessed the relationships between body size and TP at the species, community, and ocean basin levels. At the species level, we fit species-specific linear regression models at both locations to investigate species-level ontogenetic shifts in bulk $\delta^{15}\text{N}$ (a proxy for TP) using LRL as the predictor variable. We used bulk $\delta^{15}\text{N}$ as a proxy for TP as we did not have a large enough sample size from CSIA-AA for each species to assess species-specific relationships. We used measured LRL as a proxy for body size to assess species-level relationships rather than ML estimated from allometric equations. This eliminates some of the variability associated with the use of estimates. Next, we fit LME models to investigate community and basin level relationships between body size and bulk $\delta^{15}\text{N}$ and RTP. We modelled community and basin level relationships using estimated ML, loca-

tion, and an interaction term to predict $\delta^{15}\text{N}$ values and RTP. We used ML for community level investigations, as 2 different species may have the same beak size (LRL) but different body sizes (ML). Thus, ML is estimated from species-specific allometric equations which accounts for this variability. Consequently, ML was a better metric for body size than LRL for this analysis. Species and field season were included in both models as random effects. We assessed the performance of the full models against corresponding reduced models following the same procedure as outlined above. The full model and corresponding reduced model formulations can be viewed in Table S2b,c.

3. RESULTS

3.1. Comparison of isotopic values and trophic positions

Isotopic values of squid beaks varied by location and species. The $\delta^{15}\text{N}_{\text{bulk}}$ values for squid beaks collected from Kerguelen Islands ranged from 2.4‰ (*Martialia hyadesi*) to 9.8‰ (*Gonatus antarcticus*), while those from Macquarie Island ranged from 0.1‰ (*M. hyadesi*) to 7.6‰ (*Histioteuthis eltaninae*; Table 1, Fig. 2). A broader range of $\delta^{15}\text{N}_{\text{bulk}}$ values were seen within all species groups at Macquarie Island compared to those at Kerguelen Islands (Table 1, Fig. 2). We detected a statistically

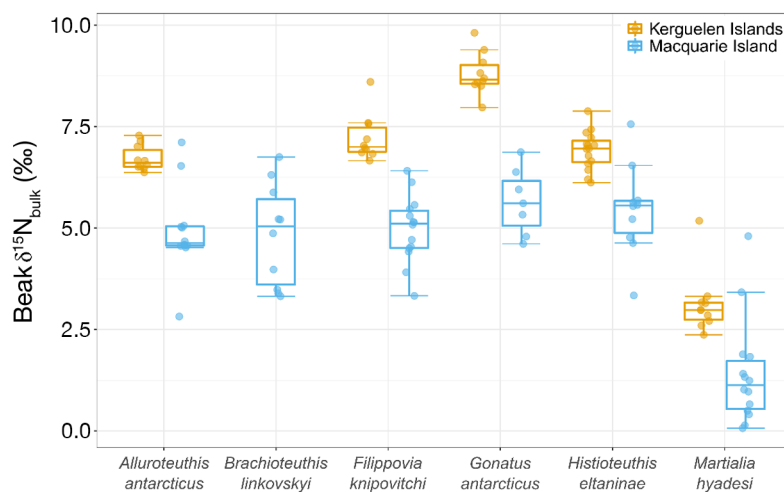


Fig. 2. Bulk $\delta^{15}\text{N}$ values of squid lower beaks (beak $\delta^{15}\text{N}_{\text{bulk}}$) collected from predator stomachs at Kerguelen (yellow) and Macquarie Islands (blue). Points show individual data points. Boxplot ends are the lower and upper quartiles; horizontal line within each plot shows the median value; whiskers are defined as quartile 1 – $1.5 \times$ interquartile range (IQR) and quartile 3 + $1.5 \times$ IQR. Points outside of the whiskers are outliers

significant interaction between location and species on mean $\delta^{15}\text{N}_{\text{bulk}}$ values (ANOVA; $F_{4,111} = 2.59$, $p < 0.05$). The Tukey HSD post hoc test showed significantly higher mean values for species at the Kerguelen Islands compared to conspecifics at Macquarie Island ($p < 0.05$ for all comparisons; Table 1, Fig. 2). Within location comparisons at Kerguelen Islands showed a significantly higher mean $\delta^{15}\text{N}_{\text{bulk}}$ value for *G. antarcticus* ($8.8 \pm 0.5\text{‰}$) and a significantly lower mean $\delta^{15}\text{N}_{\text{bulk}}$ value for *M. hyadesi* ($3.1 \pm 0.8\text{‰}$) compared to all other species within the community ($p < 0.05$ for all comparisons). At Macquarie Island, *M. hyadesi* ($1.8 \pm 1.8\text{‰}$) had a significantly lower mean $\delta^{15}\text{N}_{\text{bulk}}$ value compared to all other species present within the community ($p < 0.05$ for all comparisons).

We found a statistically significant positive relationship between $\delta^{15}\text{N}_{\text{bulk}}$ values and TP_{CSIA} at both locations (Fig. 3), indicating a consistent trophic effect on $\delta^{15}\text{N}_{\text{bulk}}$ values. Species occupied the same relative position within each community for $\delta^{15}\text{N}_{\text{bulk}}$ values and TP_{CSIA} , with 2 exceptions. At the Kerguelen Islands, TP_{CSIA} estimates for *G. antarcticus* (TP_{CSIA} range: 4.7–5.0; Table S3) were in line with those of *Alluroteuthis antarcticus* (TP_{CSIA} range: 4.6–5.3), both occupying a higher relative TP_{CSIA} compared to other species in the community. Conversely, at Macquarie Island, TP_{CSIA} estimates placed *G. antarcticus* above all other species (TP_{CSIA} range:

5.3–5.3). Bulk $\delta^{15}\text{N}$ values grouped the different squid species into approximately 3 isotopically distinct groups at Kerguelen Islands and 2 at Macquarie Island (see Fig. 3 density plot). *M. hyadesi* occupied the lowest isotopic position in both communities and *G. antarcticus* occupied the highest isotopic position at the Kerguelen Islands (Figs. 2 & 3). Conversely, TP_{CSIA} estimates segregated species by 2.6 TP_{CSIA} at Kerguelen Islands and 3.0 TP_{CSIA} at Macquarie Island (a difference of 0.4 TP_{CSIA} ; Fig. 3). *M. hyadesi* spanned a total of 1.0 and 1.3 TP_{CSIA} at Kerguelen Islands and Macquarie Island, respectively, showing overlap in TP_{CSIA} between the 2 communities (Kerguelen Islands TP_{CSIA} range: 2.7–3.7; Macquarie Island TP_{CSIA} range: 2.3–3.6). Remaining species encompassed a range of 1.4 TP_{CSIA} at Macquarie Island and 1.2 TP_{CSIA} at Kerguelen Islands (Macquarie Island TP_{CSIA} range: 3.9–5.3; Kerguelen Islands TP_{CSIA} range: 4.1–5.3; Table S3).

We found evidence of varying primary production sources at the 2 locations. Model comparisons for the relationship between $\delta^{15}\text{N}_{\text{bulk}}$ values and $\delta^{15}\text{N}_{\text{Phe}}$ (and regional variation in the relationship) showed the full model to be best supported (with the lowest AIC), and all reduced versions of the full model showed ΔAIC values of >2 (Table S2a). We found a significant interaction effect (Figs. 4 & S1), indicating a difference in trends between the 2 locations. At the Kerguelen Islands there was a positive association

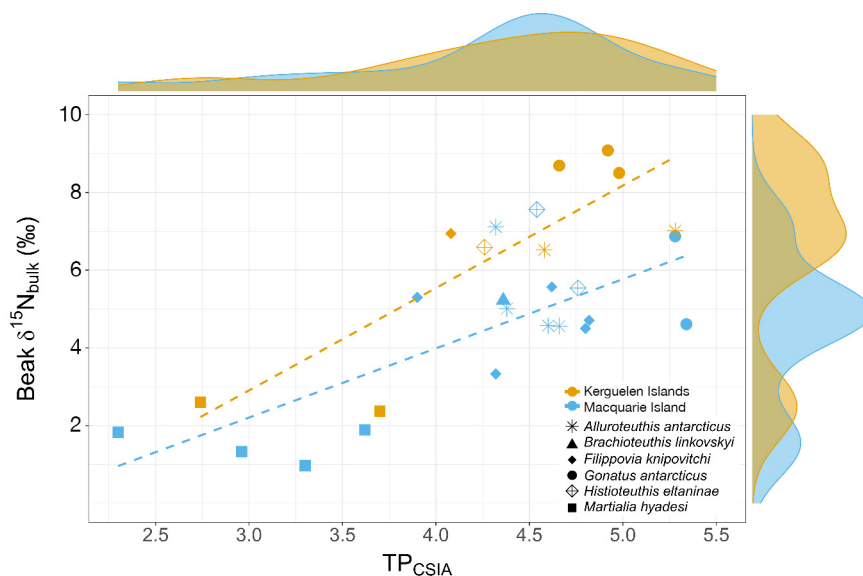


Fig. 3. Community-level linear regression models demonstrating the relationship between bulk $\delta^{15}\text{N}$ values of lower squid beaks (beak $\delta^{15}\text{N}_{\text{bulk}}$) and corresponding estimated trophic positions from compound specific isotopic analysis of individual amino acids (TP_{CSIA}). Point shapes represent different squid species. Dashed yellow line and surrounding points represent the linear regression for the community at the Kerguelen Islands ($y = -4.99x + 2.63$, $F_{1,7} = 16.01$, $r^2 = 0.65$, $p = 0.005$); blue dashed line and points indicate the relationship at Macquarie Island ($y = -3.13x + 1.78$, $F_{1,16} = 17.98$, $r^2 = 0.50$, $p = 0.0006$). Density plots (outer axis) coloured by location illustrate the spread of the data and isotopic or trophic distinctness between groups

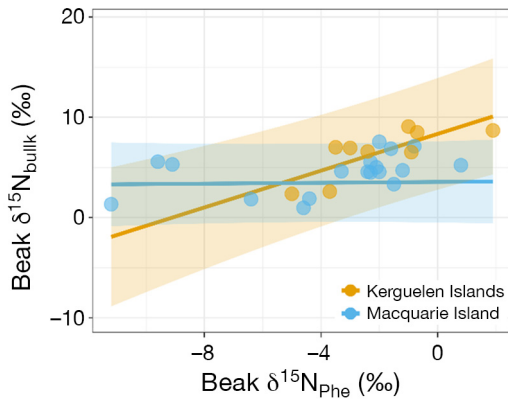


Fig. 4. Relationship between bulk $\delta^{15}\text{N}$ values of squid beaks (beak $\delta^{15}\text{N}_{\text{bulit}}$) and the $\delta^{15}\text{N}$ values of phenylalanine (a source amino acid; beak $\delta^{15}\text{N}_{\text{Phe}}$) for the Southern Ocean squid assemblage. Regression lines and shaded areas (yellow: Kerguelen Islands; blue: Macquarie Island) represent the prediction and SE from the best fit model which was the full model (marginal $r^2 = 0.47$; conditional $r^2 = 0.76$; Table S2a). The figure depicts a significant interaction effect between beak $\delta^{15}\text{N}_{\text{Phe}}$ and location (Table S2a, Fig. S1)

between of $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{bulit}}$ values (Figs. 4 & S1). In contrast, the slope did not differ significantly from zero at Macquarie Island. Overall, the model showed that the relationship between $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{bulit}}$ values varied depending on the location (marginal $r^2 = 0.47$; Figs. 4 & S1).

3.2. Relationships between body size and trophic position

H. eltaninae was the smallest species at both locations, with the lowest LRL and estimated ML (Table 1). Conversely, *Filippovia knipovitchi* at the Kerguelen Islands was the largest species, with the highest LRL and estimated ML (Table 1). Species-specific linear regression models showed a significant increase in $\delta^{15}\text{N}_{\text{bulit}}$ values with increasing LRL for *H. eltaninae* at the Kerguelen Islands ($F_{1,13} = 5.93$, $r^2 = 0.31$, $p < 0.05$; Fig. 5, Table S4). This relationship was not consistent across both locations with the absence of a significant relationship at Macquarie Island, despite a similar range in LRL of 2.7–3.9 mm. At Macquarie Island, *A. antarcticus* was the only species to show a significant positive relationship ($F_{1,10} = 6.22$, $r^2 = 0.32$, $p < 0.05$, respectively). Remaining species groups showed no significant positive or negative relationships between $\delta^{15}\text{N}_{\text{bulit}}$ and LRL at the size ranges we sampled.

Further, we modelled the relationship between $\delta^{15}\text{N}_{\text{bulit}}$ values and estimated ML at Kerguelen and Macquarie Islands to investigate community-level relationships between body size and TP (Fig. 6). The full model, which included both predictors, mantle length and location, as well as their interaction, was not the best fit model but a reduced version with ML

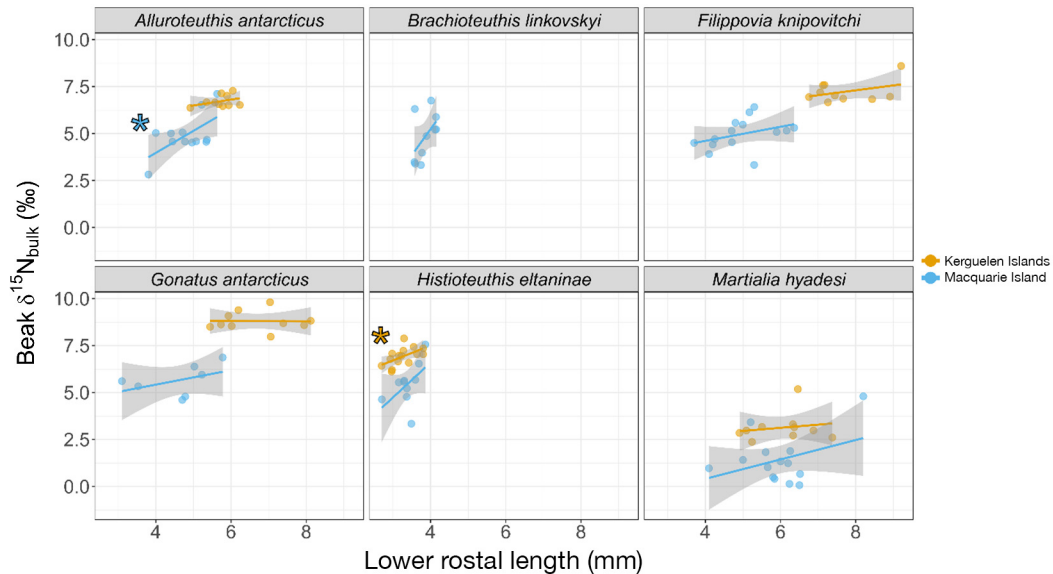


Fig. 5. Species-specific linear regression models demonstrating the relationship between bulk $\delta^{15}\text{N}$ values of lower squid beaks (beak $\delta^{15}\text{N}_{\text{bulit}}$) and the lower rostral length (mm) by species at the Kerguelen Islands (yellow) and Macquarie Island (blue). Statistically significant linear relationships ($p < 0.05$) are indicated by the asterisks positioned next to associated regression models. Asterisks are colour-matched by location. Regression equations for significant linear relationships are as follows, blue asterisks: $y = -0.71x + 1.17$, $F_{1,10} = 6.22$, $r^2 = 0.38$, $p < 0.05$; yellow asterisks: $y = 4.32x + 0.796$, $F_{1,3} = 5.93$, $r^2 = 0.31$, $p < 0.05$. See Table S3 for all other regression equations and statistics

as the only predictor (Table S2b, Fig. 6). However, a ΔAIC of <2 still provided substantial support for the full model (Table S2b). Closer inspection of estimates and confidence intervals from the full model showed them to overlap with zero (Fig. S2), indicating no significant difference in trends between the 2 communities and slopes that do not differ significantly from zero. Overall, the models showed that ML was a poor predictor of community-level patterns in $\delta^{15}\text{N}_{\text{bulk}}$ values at both locations (marginal $r^2 = 0.28$ for the full model; Fig. 6).

Similarly, ML explained little of the variability in RTP within the squid community (marginal $r^2 = 0.24$; Fig. 7). Model comparisons did not provide support for the full model ($\Delta\text{AIC} > 2$; Table S2c). The best fit model was a reduced version with ML as the only fixed effect (Table S2c), demonstrating a non-significant location effect. Model trends indicated a negative relationship between RTP and ML. *M. hyadesi*,

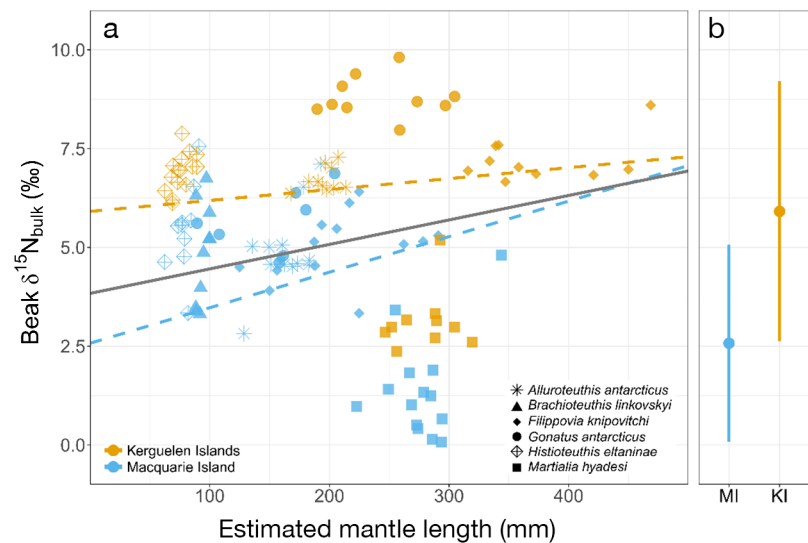


Fig. 6. Relationship between bulk $\delta^{15}\text{N}$ values of squid beaks (beak $\delta^{15}\text{N}_{\text{bulk}}$) and squid mantle length (mm; estimated from beak size based on allometric equations in Table S1) for 2 communities of Southern Ocean squids: (a) regression lines from the full model (marginal $r^2 = 0.24$; conditional $r^2 = 0.91$) for the community at the Kerguelen Islands (yellow dashed line and points) and Macquarie Island (blue dashed line and points) and the best fit model (grey solid line; marginal $r^2 = 0.06$; conditional $r^2 = 0.89$); (b) intercept and the 95% confidence intervals from the full model for both locations (KI: Kerguelen Islands; MI: Macquarie Island) for ease of visualisation of confidence intervals

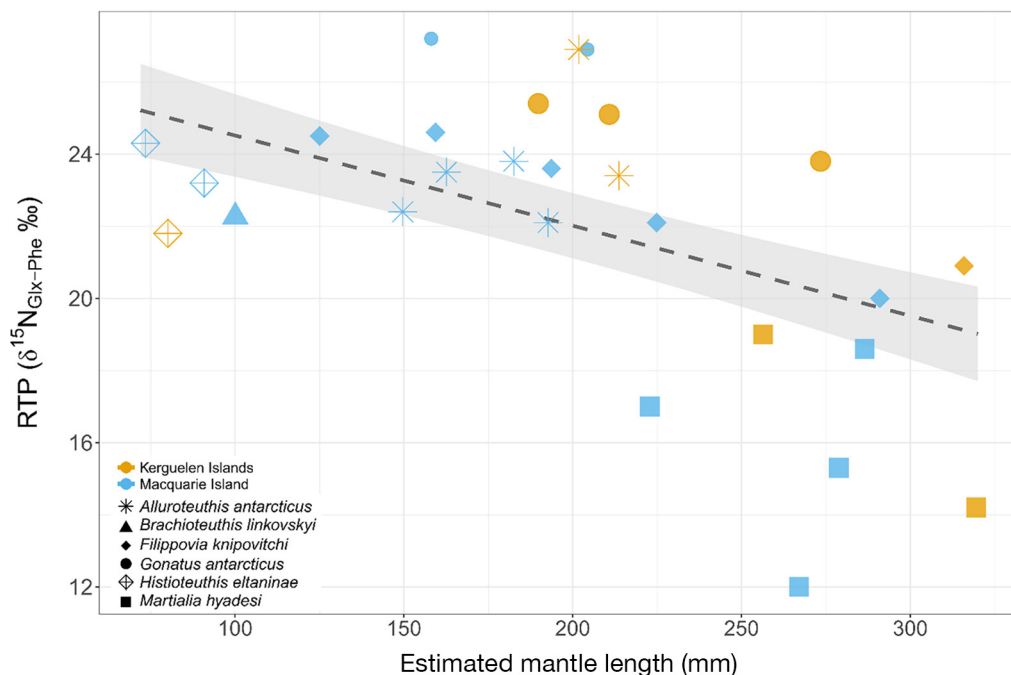


Fig. 7. Relationship between estimated relative trophic position (RTP) and squid mantle length (mm; estimated from beak size based on allometric equations in Table S1) for the Southern Ocean squid assemblage. Dashed grey line and shaded area: prediction and SE from the best fit model (marginal $r^2 = 0.24$; conditional $r^2 = 0.81$). Point shapes: the different squid species; colours: squid from either the Kerguelen Islands (yellow) or Macquarie Island (blue)

one of the largest squid species in the study occupied the lowest RTP (RTP range: 12–19‰; Table S3). Conversely, *H. eltaninae*, the smallest species in the study, occupied a RTP of 22–24‰. Overall, the full model estimates, and confidence intervals overlapped with zero demonstrating a weak relationship between RTP and ML, suggesting that other factors are influencing TP within the squid community (Fig. S2).

4. DISCUSSION

This study combines bulk and compound-specific stable isotope analyses to provide new insights into the trophodynamics of pelagic squids across 2 major oceanic sectors in the Southern Ocean, with the first TP estimates from CSIA data of the assemblage in the West Pacific sector and novel comparisons with the relatively well-studied squid community of the Indian sector (Cherel et al. 2004, Cherel & Hobson 2005, Guerreiro et al. 2015). Further, we present the first TP estimates from CSIA data for *Alluroteuthis antarcticus* and the poorly studied species *Brachioteuthis linkovsky* (Jereb & Roper 2010). The application of CSIA-AA allowed us to overcome the chitin effect (Cherel & Hobson 2005, Cherel et al. 2009a, Cherel 2019) and disentangle the effects of regional biogeochemistry from trophic structure leading to increased certainty in TP estimates (Pethybridge et al. 2018b).

The positive relationship between $\delta^{15}\text{N}_{\text{bulk}}$ values and TP_{CSIA} at both locations is consistent with a trophic effect on bulk $\delta^{15}\text{N}$ values. However, we found significantly higher $\delta^{15}\text{N}_{\text{bulk}}$ values at the Kerguelen Islands. Despite the regional variability in $\delta^{15}\text{N}_{\text{bulk}}$ values, species broadly occupied the same relative isotopic positions within their communities. Bulk $\delta^{15}\text{N}$ values showed that species occupied 3 distinct isotopic positions at Kerguelen Islands, with *Martialia hyadesi* and *Gonatus antarcticus* occupying separate positions below and above the other species (*A. antarcticus*, *Filippovia knipovitchi* and *Histioteuthis eltaninae*) in the food web, respectively. At Macquarie Island, species occupied 2 distinct isotopic positions, again with *M. hyadesi* occupying a distinct position below all other species (*A. antarcticus*, *F. knipovitchi*, *G. antarcticus*, *H. eltaninae* and *B. linkovsky*). Our findings align with those from communities at Crozet Islands and South Georgia, where although $\delta^{15}\text{N}_{\text{bulk}}$ values were consistently higher for squid species at South Georgia, the relative positioning of species within their community was the same (Guerreiro et al. 2015). There are 2

possible explanations for this: either conspecifics have different feeding preferences between communities, or there are regional differences in primary production sources.

Consumer $\delta^{15}\text{N}_{\text{bulk}}$ values are influenced by regional biogeochemical processes at the base of the food web (Choy et al. 2012). The unique isotopic signatures generated by these processes are transferred through the food web from primary producers to consumers (Post 2002). Thus, estimating the TP of a consumer is dependent upon an accurate assessment of the isotopic baseline (Jennings & van der Molen 2015, Pethybridge et al. 2018a). In this study, we found the relationship between $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ values varied depending on the location. Upon further analysis we found an overlap in TP_{CSIA} estimates between the 2 locations, suggesting that differences in $\delta^{15}\text{N}_{\text{bulk}}$ values were explained by regional variability in baseline $\delta^{15}\text{N}$ values rather than TP. The wandering albatross population at Kerguelen Islands have been shown to forage mainly in the eastern vicinity of the islands (Cherel et al. 2017). This area is recognised for a high level of productivity generated by the vertical mixing from the interaction of the Antarctic Circumpolar Current (ACC) with surrounding topographic features (Park & Vivier 2009). The increased availability of iron promotes phytoplankton growth and bloom development increasing nitrate utilization (Trull et al. 2008, Dragon et al. 2009). During assimilation, phytoplankton preferentially retain ^{14}N -nitrate which progressively enriches the nitrate pool in ^{15}N . This results in a concurrent ^{15}N enrichment of phytoplankton with bloom progression (Trull et al. 2008). Thus, high nitrate utilization in this area will lead to an increase in baseline $\delta^{15}\text{N}$ which is propagated through the food web to consumers. This may explain the relatively higher $\delta^{15}\text{N}_{\text{bulk}}$ values for beaks from the Kerguelen Islands compared to those from Macquarie Island. In contrast, the southern elephant seal population at Macquarie Island forage mainly in offshore environments (Field et al. 2007). Here, the high-nutrient low-chlorophyll waters of the inter-frontal zones are relatively iron-replete and nitrate utilization is low (Sedwick et al. 1997, Moore & Abbott 2002, Somes et al. 2010), so the baseline for $\delta^{15}\text{N}$ may be expected to be lower or less variable. This highlights the very different oceanographic regimes in which our predator species foraged. In addition to the differences in foraging locations (Kerguelen Islands vs. Macquarie Island), foraging strategies between predator species were unique. For example, elephant seals can forage at great depths and are wide-ranging species (Field

et al. 2001). Conversely, albatross forage in both slope and oceanic waters (Cherel et al. 2017). This is likely to be a further contributing factor to the variability in $\delta^{15}\text{N}$ values of squid beaks at our study locations.

The variable chitin content of squid beaks may also play a role in observed differences in $\delta^{15}\text{N}_{\text{bulk}}$ values between locations. The ratio of chitin to protein is variable within and between squid beaks; for example, small undarkened beaks have a higher chitin content compared to larger darkened beaks (Rubin et al. 2010). Given that chitin is depleted in ^{15}N , higher chitin content will lead to erroneously low $\delta^{15}\text{N}_{\text{bulk}}$ values. Thus, the relatively high $\delta^{15}\text{N}_{\text{bulk}}$ values at Kerguelen Islands may be the result of a larger proportion of squid beaks with low chitin content.

The uniformity in TP_{CSIA} estimates across ocean basins suggests that the trophic structuring of the squid community is similar at both locations. The observed broad range in TP_{CSIA} from 2.3 to 5.3 agrees with previous estimates obtained from $\delta^{15}\text{N}_{\text{bulk}}$ values of squid beaks in the Indian sector (Table S3; Cherel & Hobson 2005, Cherel et al. 2008) and highlights that Southern Ocean squids occupy multiple trophic roles within the ecosystem, from mid-trophic levels to higher predators. The trophic diversity found here is not constrained to the Southern Ocean. The ability of squids to occupy a broad range of trophic levels has been documented globally across different oceans and ecosystem types (Coll et al. 2013, Navarro et al. 2013, Choy et al. 2017), reflecting their versatile role in marine food webs.

TP_{CSIA} estimates broadly clustered species into 2 groups at both locations. *M. hyadesi* spanned a total of 1.6 TP at the lowest TP in the community, indicating a diverse range of resources and a generalist feeding strategy. Studies from the Atlantic sector of the Southern Ocean have shown that *M. hyadesi* predominantly feed on amphipods, euphausiids, other squids and a large proportion myctophid fish (Collins & Rodhouse 2006 and references therein). However, TP_{CSIA} estimates from our study were lower or at a similar level to that of myctophids (Cherel et al. 2010), suggesting a diet dominated by zooplankton. Surprisingly, we recorded a TP as low as 2.3 for this species. Previous studies have suggested that this reflects some feeding on suspended particles (Stowasser et al. 2012, Gloeckler et al. 2018). However, we suggest that this reflects the uncertainty surrounding appropriate values for TDF. One of the main assumptions of CSIA-AA is that TDF values are constant across a range of environments, taxa, and tissue types (McClelland & Montoya 2002, Chika-

raishi et al. 2009, McMahon & McCarthy 2016). It is now recognised that this assumption frequently leads to underestimates of TP_{CSIA} (Lorrain et al. 2009, Dale et al. 2011, Choy et al. 2012, Bradley et al. 2014). In the context of this study, the surprisingly low TP_{CSIA} estimates for *M. hyadesi* are most likely a consequence of inappropriately large TDF values. This highlights the need for further research, such as controlled feeding experiments, on a range of organisms from low to high trophic levels across different environments (Bradley et al. 2014) and investigation into the mechanisms controlling amino acid metabolism (Miura & Goto 2012). Until such time absolute TP values will be surrounded by uncertainty. Subsequently, we used RTP as a proxy for TP to assess sized-based community-level relationships later in the study.

Remaining species in our study showed a broad and overlapping range in TP_{CSIA} values (TP_{CSIA} 3.9–5.3). TP estimates were more in line with those of predator species such as king penguins (TP 4.5; Lorrain et al. 2009, Cherel et al. 2010); southern elephant seals (TP 4.6; Cherel et al. 2008) and Procelariiformes (TP 3.7–5.2; Stowasser et al. 2012). *In situ* observations of gonatid species have shown high levels of cannibalism and predation on myctophids, demonstrating the role of cephalopods as predators in the oceanic ecosystem (Hoving & Robison 2016, Choy et al. 2017). In our study, *G. antarcticus* and *A. antarcticus* had the highest recorded TP (TP_{CSIA} max 5.3), which aligns with their previously documented diet of fish and other squids (Collins & Rodhouse 2006 and references therein).

Body size is recognised as a major determinant of energy flow and trophic structure in aquatic food webs (Jennings et al. 2001, Blanchard et al. 2017). In the Southern Ocean, previous studies have demonstrated a species-level enrichment in ^{15}N with size, consistent with ontogenetic shifts in diet for cephalopods (Cherel & Hobson 2005, Cherel et al. 2009a). For example, *Todarodes filippovae* of the Ommastrephid family, was shown to increase almost 2 trophic levels from juvenile to adult life stages corresponding to a dietary shift from lower to higher trophic levels with squid growth. This relationship holds true for cephalopods of other marine ecosystems across the globe (Cherel et al. 2009b, Staudinger et al. 2019, Murphy et al. 2020), including for the Arctic species *Gonatus fabricii*, a congener of *G. antarcticus* (Golikov et al. 2018). Here, we found little evidence of this, with only 2 species displaying higher $\delta^{15}\text{N}_{\text{bulk}}$ values at larger sizes compared to their smaller counterparts. Similarly, mixed results were observed for oceanic cephalopods in the west-

ern Tasman Sea (Murphy et al. 2020). One possible explanation for this variable result is the ability of juvenile squids to feed closer to their adult life stages (Rodhouse & Nigmatullin 1996). The rapid growth and maturation of prehensile arms and tentacles during juvenile life stages enables the capture of large prey (Vidal 1994, Rodhouse & Nigmatullin 1996). The use of arms and tentacles allow squid to grasp on to their prey during consumption, and so they are less limited by gape size than fish (Rodhouse & Nigmatullin 1996, Hoving & Robison 2016). However, the lack of statistically significant trends at the species-level may also be due to the limited size range of individuals available for inclusion in our analysis (Galvan et al. 2010). We were constrained by the size range of beaks available in predator stomach contents, which is largely determined by the size range targeted by the predators (Field et al. 2007). A further factor which may have limited our analysis is sample size. The statistical power of a linear regression is not only dependent on the strength of the correlation but also the sample size (Galvan et al. 2010). Thus, our sample size of 7–15 observations per species may have been insufficient.

Further, observed variability may be due to intraspecific differences in the isotopic baseline. In the oceanic environment primary production sources change with depth as well as regionally. Microbial degradation of sinking particulate organic matter leads to an enrichment in ^{15}N with increasing depth (Mintenbeck et al. 2007, Laakmann & Auel 2010). Our study species are predominantly distributed at mesopelagic (200–1000 m) to bathypelagic (>1000 m) depths (Rodhouse et al. 2014) with evidence of daily vertical migration as well as ontogenetic descent in some (Rodhouse & Nigmatullin 1996, Jereb & Roper 2010). A broad range of $\delta^{13}\text{C}$ values have been observed for some squid species, indicative of changes in foraging habitat and multiple isotopic baselines (Staudinger et al. 2019, Murphy et al. 2020). Opportunistic feeding by individuals throughout their habitat range may mask ontogenetic shifts in diet, as individual $\delta^{15}\text{N}$ values will be influenced by multiple isotopic baselines across a range of depths confounding species-level comparisons.

In this study, the absence of community-level relationships between body size and TP also suggested that cephalopods at our study sites do not adhere to a size-based trophic structure typical of fish communities (Jennings et al. 2002, Layman et al. 2005, Cherel et al. 2010, Trebilco et al. 2016). Our findings are congruent with a recent study in the Pacific sector of the Southern Ocean, which failed to find a relationship

between ML and $\delta^{15}\text{N}_{\text{bulk}}$ values of different sections of squid beaks (Queirós et al. 2021). In our study, larger squid species occupied lower TP. *M. hyadesi*, one of the largest species in this study, occupied the lowest TP in both communities. Conversely, RTP estimates positioned *H. eltaninae* up to 2 TP above *M. hyadesi* despite being less than half the size. A recent study found evidence of size-based trophic structure once species were grouped by activity level, which was determined based on different morphological traits (fin to mantle length ratio, fin, and mantle musculature; Murphy et al. 2020). Strong size-based trophic structuring was found for the high activity level group where larger species occupied higher trophic levels compared to smaller species, while those in the low and medium activity level groups occupied a consistent TP across their body size range (Murphy et al. 2020). Our study species predominantly fall into the medium activity level group (Jereb & Roper 2010, Murphy et al. 2020), but we observe a decline in TP with size.

We put forward 2 possible hypotheses for the variation seen here in our TP estimates. First, both southern elephant seals and wandering albatross are known to forage across frontal zones and water masses (Field et al. 2001, Cherel et al. 2017). It is generally recognised that organisms attain larger body sizes in colder, higher latitude regions compared to the warmer waters of the subantarctic or sub-tropical regions (Meiri 2011, Saunders & Tarling 2018). Furthermore, food chain length also varies across the Southern Ocean with short, efficient food chains at high latitudes and progressively longer food chains with more trophic linkages in the north beyond the Southern Antarctic Circumpolar Current Front (Stowasser et al. 2012, McCormack et al. 2021). The short food chains characteristic of Antarctic waters in combination with larger-sized individuals leads to large species occupying low trophic levels. It is possible that the large species in this study were sampled by predators from high latitudes, where they were part of this characteristic short food chain.

For our second hypothesis we suggest that the variation seen here in our TP estimates may in part be explained by prey availability. A recent study demonstrated an increase in trophic niche size of fish species with decreasing levels of productivity (Lesser et al. 2020). They found that species with generalist feeding strategies were able to adjust the size of their niche in response to changes in food availability. High levels of productivity allowed species to narrow their diet to the most energetically favourable resources, while at low levels of productivity species

expanded their niche width to include less favourable resources to meet metabolic demands (Lesser et al. 2020). Other studies have shown an increase in predator–prey mass ratios with size, which indicated larger consumers were feeding on proportionally smaller prey (Barnes et al. 2010, Costa-Pereira et al. 2018). Further, in ecosystems with a high number of closely related species and low prey availability, large consumers showed more variability in their foraging choices (both small and large prey) compared to small consumers (Costa-Pereira et al. 2018). This is particularly relevant to our study system; the pelagic ecosystem is reliant on seasonally pulsed production from the surface waters and the active and passive transport of this carbon to deeper layers of the water column (Smith et al. 2009). An adaptive and generalist feeding strategy would ensure an individual is able to meet their energetic demands in a variable productivity regime. In our study, this may suggest that *M. hyadesi* is adaptively foraging on a range of proportionally smaller prey to meet energetic demands in an environment where preferred prey sources may be rare due to competition with other squid species and low productivity. This would explain the broad range in TP_{CSIA} and unexpectedly low TP for this large species.

5. CONCLUSIONS

We demonstrate the power of combining bulk stable isotopes with CSIA-AA, using archived squid beaks, to provide insights into the trophic structure of 2 squid communities in the Southern Ocean. Compound specific isotope analysis enabled us to disentangle the effects of regional biogeochemistry from trophic structure, facilitating comparisons across ocean basins. We show cross-basin differences in isotopic baselines which might be linked to differences in foraging location between elephant seals and wandering albatross. For example, the higher nitrate utilization at the Kerguelen Islands stimulated by increased availability of iron would lead to an enriched isotopic baseline compared to the iron-replete inter-frontal zones offshore from Macquarie Island. Uniformity in TP_{CSIA} estimates show the trophic structuring of the pelagic squid community to be similar at both locations. We found surprisingly low TP_{CSIA} estimates for *Martialia hyadesi*, which we attribute to the uncertainty of appropriate TDF values when calculating TP_{CSIA} . This highlights the need for species-specific TDF values which necessitates future research that investigates turnover rates of

amino acids. The assemblage of pelagic squid occupies a diverse range of trophic roles, from mid-trophic level consumers (e.g. *M. hyadesi*) to higher predators (e.g. *Gonatus antarcticus*) encompassing 3 trophic levels. The lack of evidence of strong or consistent trophic size-structuring may suggest that feeding mode and/or prey availability play a stronger role than body size in determining TP for these species. Our results suggest that it may not be appropriate to characterise squids as a single functional group within ecosystem models which is consistent with findings in Murphy et al. (2020). This has important implications for the accurate representation of squids in Southern Ocean ecosystem models.

Acknowledgements. The data from Macquarie Island were collected with permits from the Tasmanian Parks and Wildlife Service and ethics approval from the Australian Antarctic Animal Ethics Committee. We thank M. Biuw, J. Harrington, C. McKinley, N. Milius, R. Munro, M. Pauza, K. Wheatley and members of the 51st–53rd ANARE to Macquarie Island for their work in the field. We thank Christian Dietz and Christine Cook at the Central Science Laboratory at the University of Tasmania for their analytical work. Thanks to Kieran Murphy for his guidance and advice on the interpretation of stable isotope data. This project was supported by a Research Enhancement Grant Scheme (REGS) award to R.T. from the University of Tasmania. The data from Kerguelen Islands were collected with ethics approval from the Ethics Committee of the Institut Polaire Français Paul Emile Victor (IPEV). The authors thank S. Caille and D. Secondi, who helped during the field work. The Kerguelen study was supported financially and logistically by the IPEV Programme N°109 (C. Barbraud) and the Terres Australes et Antarctiques Françaises.

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