

Research article

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## Divergent isotopic niches of sister species of the Antarctic amphipod genus *Charcotia*

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**Abstract.** Climate change and resource exploitation in the Southern Ocean are important anthropogenic pressures on Antarctic food webs. Understanding the eco-functional roles of Antarctic communities is essential for ecosystem management and conservation. Amphipods are among the most dominant and ecologically important benthic taxa in the Southern Ocean. The amphipod genus *Charcotia* is part of the scavenger guild playing a dominant role in nutrient recycling. To study the trophic habits of two sister species *C. amundseni* and *C. obesa*, stable isotope ratios of carbon and nitrogen were measured along geographical and bathymetrical gradients. *Charcotia obesa* belongs to the fourth and *C. amundseni* to the fifth trophic level, based on significant differences in  $\delta^{15}\text{N}$  values. Both benthic and pelagic primary producers dominate the diet in both species as derived from their low  $\delta^{13}\text{C}$  values. *Charcotia obesa*, the species with the narrowest depth range of the two studied species, did not show a depth-related pattern in isotopic ratios. An increasing geographic gradient of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values was observed for *C. obesa*, ranging from the northern most tip of the Western Antarctic Peninsula to the southwestern most part in the Bellingshausen Sea. This might be linked to nutrient rich glacial meltwater in the latter part of the Southern Ocean. Nitrogen stable isotope ratios of *C. amundseni* showed a significant difference between Crown Bay and the other locations; this might be explained by the close location of the Filchner Area to nutrient rich upwelling in the Weddell Sea Gyre. Our study provides evidence for niche differentiation between two closely related amphipod species. Incorporation of additional samples from other locations and depth ranges in combination with isotope analysis and DNA-based prey identification might clarify the trophic position of benthic amphipods.

**Keywords.** Stable isotopes, trophic ecology, ecological plasticity, benthic, scavenger, Southern Ocean.

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## Introduction

The Southern Ocean (SO) harbours a huge diversity of pelagic and benthic organisms (David & Griffiths 2010; Saucède 2015). The long geographic history and isolation of the SO has led to *in situ* evolution of its marine fauna, with adaptations to the cold environment and high levels of endemism (Poulin *et al.* 2002; Clarke 2008). The Antarctic marine fauna is experiencing increasing anthropogenic pressure from the exploitation of marine resources and climate change (Harley *et al.* 2006; Hoegh-Guldberg & Bruno 2010; Constable *et al.* 2014). In order to conserve the unique Antarctic biota, it is important to understand how biodiversity affects ecosystem functioning.

One of the most dominant groups within the SO benthic communities are the Amphipoda (Crustacea, Peracarida), which show a broad variation in trophic diversity, habitat, lifestyle and size (De Broyer & Jazdzewski 1993, 1996; Dauby *et al.* 2001; De Broyer & Jazdzewska 2014). The superfamily Lysianassoidea is one of the most abundant amphipod taxa in the SO as part of the Antarctic scavenger guild (De Broyer *et al.* 2004; De Broyer & Jazdzewska 2014). Gammaridean amphipods, because of their abundance, play an important role in the energy fluxes of the Antarctic ecosystem, both as scavengers feeding on organic matter and as prey for numerous other organisms (Olaso *et al.* 2000; Cherel *et al.* 2008; Panasiuk *et al.* 2020). Previous studies found that many species within the Antarctic scavenger guild primarily rely on multiple feeding types ranging from suspension feeding to deposit feeding and revert to scavenging, or as far as true necrophagy, when food supply is low (Dauby *et al.* 2001; De Broyer *et al.* 2004; Smale *et al.* 2007). Many of the amphipod species within the guild have a wide dietary spectrum, thus potentially having high trophic plasticity. However, despite their relevance in the Antarctic marine food web, their eco-functional roles remain poorly understood.

Integrating diversity within trophic levels (horizontal diversity, i.e., taxonomic richness (Ives *et al.* 2005)) and between trophic levels (vertical diversity, i.e., food chain length and omnivory (Borer *et al.* 2005)) is one approach to understand the trophic spectra of an ecosystem (Duffy *et al.* 2007). Above the level of true herbivory (i.e., predators, scavengers), food webs are referred to as tangled with omnivores who tend to feed opportunistically, yet display specificity in their trophic niches (Thompson *et al.* 2007; Rakusa-Suszczewski *et al.* 2010; Chikaraishi *et al.* 2014). Key to understanding the functional diversity and stability of Antarctic food webs, and the role and position of the scavenger guild, is to unravel the various bottom-up supplies in these tangled food webs (Bruno & O'Connor 2005; Chikaraishi *et al.* 2014).

Stable isotope (SI) analysis is frequently used to investigate the long-term feeding ecology of organisms worldwide, including in Antarctic food webs (Wada *et al.* 1987; Nyssen *et al.* 2005; Stowasser *et al.* 2012; Guerreiro *et al.* 2015; Michel *et al.* 2019). There is a close relationship between the stable isotope ratios assimilated in an organism and its diet (DeNiro & Epstein 1978, 1981). Since primary food sources (i.e., phytoplankton, phytobenthos, and sea ice algae) may vary in stable isotope composition (Wing *et al.* 2018; Zenteno *et al.* 2019), stable isotopes of carbon ( $^{13}\text{C}$ : $^{12}\text{C}$ ;  $\delta^{13}\text{C}$ ) are used to determine the source of primary carbon in food webs. Stable isotope ratios of nitrogen ( $^{15}\text{N}$ : $^{14}\text{N}$ ;  $\delta^{15}\text{N}$ ) are generally measured to determine nitrogen sources and to assess the trophic position of organisms within the food web (Post 2002). Due to fractionation of isotopes, consumers are generally enriched in  $^{15}\text{N}$  relative to their diet, resulting in a sharp increase of  $\delta^{15}\text{N}$  values with each trophic level (DeNiro & Epstein 1981; Nienstedt & Poehling 2004). Combining C and N isotope ratios allows to compare the isotopic niche (i.e., a proxy of trophic niche) of different species (Newsome *et al.* 2007; Jackson *et al.* 2011).

Our aim was to elucidate the trophic niche of *Charcotia obesa* Chevreux, 1906 and *C. amundseni* d'Udekem d'Acoz, Schön & Robert, 2018 (Crustacea, Amphipoda, Lysianassoidea), previously known as *Waldeckia obesa* (Chevreux, 1906). *Charcotia amundseni*, one of two sister species, was recently described by d'Udekem d'Acoz *et al.* (2018) based on morphological and molecular data.

*Charcotia obesa* occurs in a depth range from 0–150 m (with decreasing occurrences below 120 m), whereas *C. amundseni* is present from 120 to 1000 m depth, resulting in a narrow overlap in depth distribution. Previous dietary studies on *C. obesa* and *C. amundseni* demonstrated a scavenging lifestyle and resistance to starvation (Chapelle *et al.* 1994; Dauby *et al.* 2001; Janecki & Rakusa-Suszczewski 2005). Lysianassoid species of the SO vary strongly in their feeding ecology, even between closely related species (Havermans *et al.* 2010; Seefeldt *et al.* 2018). The morphological differences found by d’Udekem d’Acoz *et al.* (2018) include some minor variations in the appearance of epistome and upper lip between both species. Nevertheless, the differences are relatively small and, moreover, the morphology of the feeding appendages does not allow to identify the feeding type and trophic niche of these species (Dauby *et al.* 2001; Michel *et al.* 2020). Hence, we hypothesize that there is no difference in isotopic niche between the two species. Additionally, we expect spatial variation within each of the two amphipod species in isotopic ratios among sampling stations.

## Material and methods

### Sample collection

Specimens from the genus *Charcotia* were obtained from collections curated at various scientific institutes (viz. the University of Lodz, Poland; Alfred Wegener Institute, Bremerhaven, Germany; Université Libre de Bruxelles, Brussels, Belgium; Muséum national d’Histoire naturelle, Paris, France and the Royal Belgian Institute of Natural Sciences, Brussels, Belgium). Specimens were collected from various locations and depths in the SO during several scientific expeditions (Table 1). Amphipods were caught using epibenthic sledge or baited traps, sorted, identified and preserved in pre-cooled molecular grade ethanol (96–99%) at -20°C. Samples originated from four geographic areas (Fig. 1): the Weddell Sea near the Filchner Area, the West Antarctic Peninsula (WAP), Queen Maud Land and the Adélie Coast. *Charcotia obesa*, was sampled in nine locations, five off the north-west shelf of the Antarctic

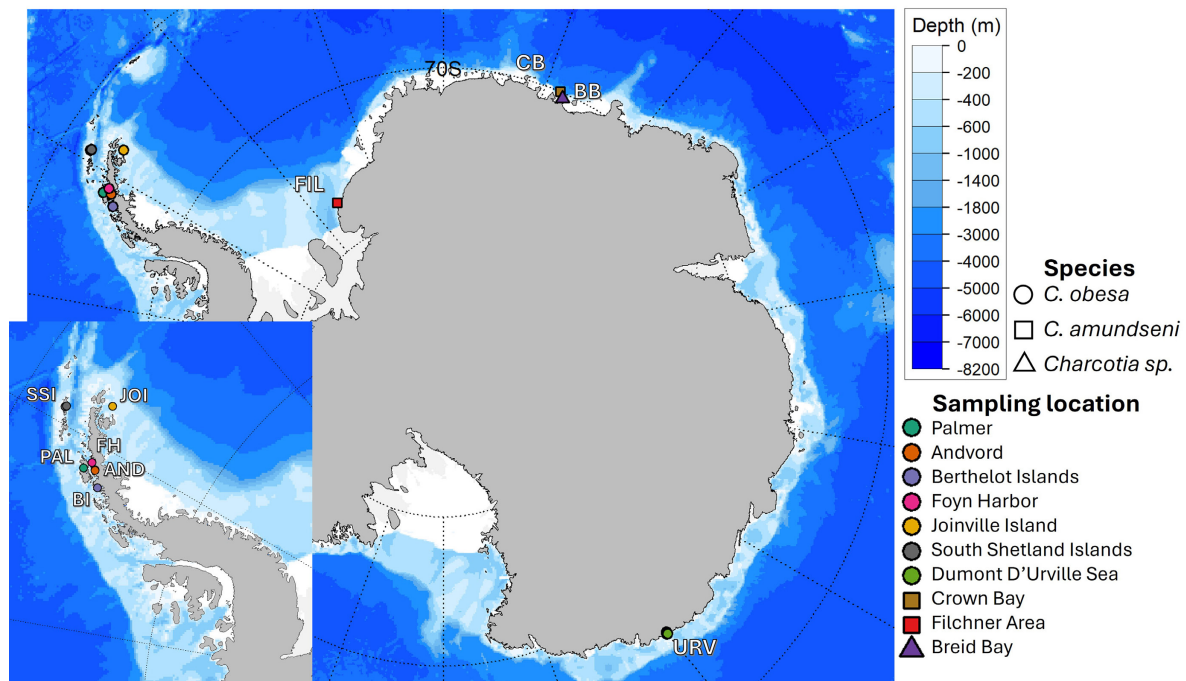


Fig. 1 – Sampling locations of *Charcotia obesa* (circles) and *C. amundseni* (squares) as well as one sampling location where both species were sampled (triangle). The map was made in R using the CCAMLRGIS package (ver. 4.2.1).

TABLE 1 (continued on next page)

Sampling stations of *Charcotia amundseni* and *C. obesa* chronologically ordered and greyscale highlighted per expedition. Including the number of individuals sampled at each location, expedition, sampling event date, coordinates (decimal\_Latitude, decimal\_Longitude), the depth and from which collection the samples originated. For the exact geographic locations around the Antarctic continent, please refer to Figure 1.

Location	Species	n	EXPEDITION	Sampling_Date (dd/mm/yyyy)	dec_Lat	dec_Long	Depth (m)	Collection*
Crown Bay	<i>C. amundseni</i>	17	Belare 08-09	23/12/2008	-70.000	23.000	230	AWI
Filchner Area	<i>C. amundseni</i>	19	PS 82 ANT XXIX/9	18/01/2014	-76.970	-32.940	260–274	AWI
Breid Bay	<i>C. amundseni</i>	5	Belare 22-12	24/01/2022	-70.350	23.945	260	ULB
South Shetland Islands; Admiralty Bay	<i>C. obesa</i>	26	Polish Antarctic IPY Expedition	01/04/2007	-62.158	-58.445	205–210	U Lodz EBS2/07
	<i>C. obesa</i>	1	REVOLTA I	13/01/2010	-66.663	139.990	30	MNHN6616
	<i>C. obesa</i>	3		16/01/2010	-66.761	139.867	102–106	MNHN6597
	<i>C. obesa</i>	21	REVOLTA I -	21/05/2010	-66.667	139.992	36	MNHN6203
	<i>C. obesa</i>	7	hivernage	01/06/2010	-66.667	139.992	36	MNHN6223
	<i>C. obesa</i>	2		10/01/2011	-66.645	139.949	91–93	MNHN6209
	<i>C. obesa</i>	18		11/01/2011	-66.618	140.004	103–107	MNHN6435
	<i>C. obesa</i>	6	REVOLTA II	18/01/2011	-66.602	140.030	130–131	MNHN6244
	<i>C. obesa</i>	3		24/01/2011	-66.680	139.971	32–37	MNHN6213
	<i>C. obesa</i>	5		04/02/2011	-66.633	140.023	88–90	MNHN14208
Dumont D'Urville Sea	<i>C. obesa</i>	2	REVOLTA III -	01/05/2012	-66.665	139.992	30	MNHN14204
	<i>C. obesa</i>	26	hivernage	13/05/2012	-66.665	139.992	30	MNHN6469
	<i>C. obesa</i>	1		11/01/2013	-66.658	139.905	60	MNHN5118
	<i>C. obesa</i>	11	REVOLTA IV	12/01/2013	-66.685	139.940	100	MNHN5132
	<i>C. obesa</i>	1		19/01/2013	-66.725	139.946	133	MNHN5116
	<i>C. obesa</i>	1		24/01/2013	-66.633	139.920	125–129	MNHN5120

TABLE 1 (continued)

Palmer	<i>C. obesa</i>	10	03/02/2019	-64.321	-32.923	22	RBINS
Andvord	<i>C. obesa</i>	17	05/03/2019	-64.843	-62.534	10	RBINS
Berthelot Islands	<i>C. obesa</i>	3	Belgica121	-64.854	-62.602	0-44	RBINS
Foyn Harbor	<i>C. obesa</i>	21	14/03/2019	-65.328	-64.137	18	RBINS
south of Joinville Island	<i>C. obesa</i>	4	18/03/2019	-64.548	-61.995	20	RBINS
South Shetland Islands; Admiralty Bay	<i>C. obesa</i>	1	PolarStern118	-64.021	-55.909	403-405	RBINS
	<i>C. obesa</i>	4	30/12/2019	-62.117	-58.475	120	RBINS
	<i>C. obesa</i>	2	ANTARXXVII	-62.121	-58.478	120	RBINS
Breid Bay	<i>C. obesa</i>	10	03/01/2020	-62.162	-58.360	57	RBINS
	<i>C. obesa</i>	2	BELARE 22-12	-70.350	23.945	260	ULB

\*AWI = Alfred Wegener Institute; ULB = Université Libre de Bruxelles; U Lodz = University of Lodz; MNHN = Muséum national d'Histoire naturelle; RBINS = Royal Belgian Institute of Natural Sciences



Peninsula (AP) (South Shetland Island (SSI); Foyn Harbor (FH); Palmer Island (PAL); Andvord (AND); Berthelot Islands (BI)), one on the north-east shelf of the AP (south of Joinville Island (JOI); later excluded as outlier, see below), one on the south-east coast (Dumont d'Urville Sea (URV)) and one near Queen Maud Land in the north-east (Bleid Bay (BB)). Samples in the north-west are subcategorized as one location in the north (SSI), three central (FH, PAL, AND) and one in the south (BI), respectively. *Charcotia amundseni* was collected at two geographical locations, one in the Weddell Sea (Filchner Area (FIL)) and two off the coast of Queen Maud Land (Bleid Bay (BB); Crown Bay (CB)). The final dataset contained 205 *C. obesa* individuals and 41 *C. amundseni* individuals, based on morphological identification and confirmation with mitochondrial DNA COI sequences.

### Stable isotope analysis

Two to four pleopods (depending on size) including muscles were dissected from each *Charcotia* specimen and air-dried for at least 72 h. By using the same tissue (i.e., mostly soft tissue muscles) for all samples, we exclude potential bias and underestimations due to the analysis of different tissue (Søreide & Nygård 2012). The protocol allows to conserve collection specimens for taxonomic purpose and future studies. Pleopods were weighted in tin cups; dry mass ranged from 0.1 to 0.4 mg. Samples were analysed at the University of Liège, using an Isotope Ratio Mass Spectrometer (IRMS) (precisION, Elementar) coupled to an elemental analyser (vario MICRO, Elementar). Delta ( $\delta$ ) notations of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) were used to express isotope ratios, which are calculated here as parts per thousand (‰) (Coplen 2011). We used blank tin cups, secondary analytical material (glycine and European sea bass *Dicentrarchus labrax* reference material) and certified material from the International Atomic Energy Agency (IAEA, Vienna, Austria), IAEA C-6 (sucrose;  $\delta^{13}\text{C} = -10.8 \pm 0.5$  ‰) and IAEA-N1 (ammonium sulphate;  $\delta^{15}\text{N} = 0.4 \pm 0.2$  ‰). The isotope ratios are expressed as mean values  $\pm$  SD for each species and calculated according to sampling station and depth.

### Data analysis

A correction was applied to account for differences in SI values of primary producers (i.e., isotopic baseline) at different geographical locations, when comparing SI data between the two species. This correction was taken from (Le Bourg *et al.* 2021) and applied to remove the impact of isotopic baseline variability among localities (Equation 1):  $corX_{ij} = X_{ij} - (\bar{X}_j - \bar{X})$ , where  $X$  is the variable (i.e.,  $\delta^{13}\text{C}$ ),  $i$  denotes the individual and  $j$  the sampling station.  $X_{ij}$  describes a value belonging to individual  $i$  at station  $j$ ,  $\bar{X}$  is the overall mean of all values and  $\bar{X}_j$  is the mean value at station  $j$ . Accordingly, transformed data are displayed as  $\delta^{13}\text{C}_{corr}$  and  $\delta^{15}\text{N}_{corr}$ . The same formula was used when comparing values from different depth ranges to correct again for possible isotopic baseline shift effects. When comparing localities within each species, this correction was not needed, since the analysis was done for each species separately.

Isotopic niches and overlaps were determined by calculating Standard Ellipse Areas (SEA) in bivariate  $\delta^{13}\text{C}$  vs  $\delta^{15}\text{N}$  isotopic spaces, using the SIBER package (ver. 2.1.9; Jackson *et al.* 2011) in Rstudio (ver. 4.1.2, R Core Team 2021) for first comparisons between the two species and between location within each species. To quantify and compare isotopic niches, the Total Area (TA) was calculated, encompassing the whole isotopic niche. The SEA corrected for small sample size ( $SEA_c$ ) was also calculated to measure the core isotopic niche area ( $\pm 40\%$  of the data), thus providing an estimate of the central tendency, and the Bayesian Standard Ellipse Area ( $SEA_B$ ; based on  $2 \cdot 10^6$  iterations, 2 chains,  $10^4$  initial discards and a thinning interval of 10) was also calculated. The  $SEA_B$  accounts for uncertainty in the data (i.e., small and uneven data) using a Bayesian framework and generates posterior distributions of the ellipse areas, which enables the estimation of the mode with 95% credible intervals (CI). Plots were made using the R package ggplot2 (ver. 3.5.1; Wickham 2016). When assessing differences in SI ratios at various depths, recorded sample depths were clustered in increments of 50 m, creating four groupings of *C. obesa* samples at depths of  $< 50$  m ( $n = 115$ ), 50 to 100 m ( $n = 29$ ), 100 to 150 m ( $n = 34$ )

and > 150 m (n=25) (Appendix Table 1S). *Charcotia amundseni* samples were not considered for such analysis as all samples were within 50 m from each other, at a depth range from 230 to 274 m.

To estimate the trophic position (TP) of both species, the tRophic position package (ver. 0.8.0; Quezada-Romegialli *et al.* 2018) was used. To establish a baseline, we used collated data on Particulate Organic Matter (POM) from an earlier study (St John Glew *et al.* 2021) and compared the uncorrected data to this Antarctic pelagic baseline. TP is noted as the statistical mode with a 95 % Credibility Interval (CI<sub>95</sub>) of posterior estimations.

For statistical analysis, data outliers for both  $^{13}\text{C}_{\text{corr}}$  and  $^{15}\text{N}_{\text{corr}}$  were detected and removed per species using the Rosner test; this resulted in the removal of three samples from *C. obesa*, one outlier of  $^{13}\text{C}_{\text{corr}}$  came from the single sample of JOI and two outliers from URV; one of the latter outlier included both, values for  $^{13}\text{C}_{\text{corr}}$  and  $^{15}\text{N}_{\text{corr}}$ , while the other was an outlier of  $^{15}\text{N}_{\text{corr}}$ . Normality was tested with the Shapiro-Wilkes' test and homoscedasticity with the Levene's test. Since parametric assumptions were not met, Mann Whitney U tests, Kruskal-Wallis tests and Chi-squared tests were used. *Post hoc* testing was performed with Dunn tests (Bonferroni corrected). A significance level of p-value < 0.05 was used in all tests.

## Results

### Comparing SI ratios between two *Charcotia* species

Uncorrected  $\delta^{13}\text{C}$  ranged from -20.3 ‰ to -25.6 ‰ and  $\delta^{15}\text{N}$  varied from 8.2 ‰ to 13.6 ‰ among the 205 samples of *C. obesa*. The total dataset of 41 *C. amundseni* samples resulted in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranging from -20.8 ‰ to -24.3 ‰ and from 11.1 ‰ to 15.0 ‰, respectively (Appendix Fig. 1S). Having corrected for variation of SI ratios between locations for interspecific comparisons *C. amundseni* displayed a significantly higher mean  $\delta^{15}\text{N}_{\text{corr}}$  of  $12.9 \pm 0.7$  ‰ (min. 10.9–max. 14.4 ‰) compared to the  $\delta^{15}\text{N}_{\text{corr}}$  of *C. obesa* of  $10.7 \pm 0.6$  ‰ (min. 9.1–max. 12.1 ‰) (Fig. 2; Table 2; (W = 8276, p-value < 0.001)). In contrast,  $\delta^{13}\text{C}_{\text{corr}}$  values for both species were rather similar and not significant (W = 4542, p-value = 0.4143) (Fig. 2; Tables 2–3). Ellipse-based metrics showed no measurable overlap (< 0.01%) between both *Charcotia* species (Fig. 2; Table 2), with *C. amundseni* having the largest SEA<sub>B</sub> (1.0 ‰<sup>2</sup>; CI 0.7–0.9 ‰<sup>2</sup>) of the two species (Table 6). Finally, using the uncorrected  $\delta^{15}\text{N}$  values from both species, we calculated a trophic position of 4.19 (CI<sub>95</sub>: 3.66–4.97) for *C. obesa*, and 5.14 (CI<sub>95</sub>: 4.46–6.17) for *C. amundseni* (Fig. 3). Our trophic position model suggested that this difference was significant, with the probability of *C. amundseni* occupying a higher trophic position being 96.1%.

### Comparing SI ratios between geographic locations

This study showed that there were significant differences in SI ratios of carbon and nitrogen at the intraspecific level for *Charcotia obesa* ( $\delta^{13}\text{C}$ ;  $\chi^2 = 154.72$ , p-value = < 0.0001 and  $\delta^{15}\text{N}$ ;  $\chi^2 = 132.48$ , p-value = < 0.0001) between the sampled regions of the Antarctic continental shelf (Table 3). When checking for a possible geographic grouping of locations within *C. obesa*, individuals belonging to the northern group (SSI) had significantly lower  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (p-value < 0.001) compared to individuals found in the central (PAL, FH & AND) and the southern group (BI) (p-value < 0.001; Table 5a). Within-group pairwise comparisons of locations around the WAP of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , indicated that adjacent stations are non-significant, with the exception of  $\delta^{15}\text{N}$  in the central group, (Table 5b–c) and an increasing gradient from north to south of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Table 4). The only sampling station (Dumont d'Urville Sea, URV) in the south-east differed significantly from all other stations in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  except for Foyen Harbor (FH). Berthelot Islands (BI) had the largest SEA<sub>B</sub> (1.1 ‰<sup>2</sup>; CI 0.8–1.8 ‰<sup>2</sup>) followed by AND (0.9 ‰<sup>2</sup>; CI 0.6–1.4 ‰<sup>2</sup>) and SSI (0.8 ‰<sup>2</sup>; CI 0.6–1.2 ‰<sup>2</sup>) (Table 6). Standard ellipse overlap was minimal between all locations (< 1 %), except for AND and BI with an SEA<sub>B</sub> overlap of 30.95 % (Figs 4a, 5a; Table 5d).

TABLE 2

Mean  $\pm$  SD  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values calculated for *Charcotia obesa* and *C. amundseni*. Corrected values (corr) are location adjusted values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for their respective locations. Overlap of isotopic niches between the two species, displayed in percentages.

Species	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}_{\text{corr}}$ (‰)	$\delta^{15}\text{N}_{\text{corr}}$ (‰)	Overlap
<i>Charcotia obesa</i>	205	$-23.7 \pm 1.0$	$10.7 \pm 1.2$	$-23.7 \pm 0.4$	$10.7 \pm 0.6$	<0.01 %
<i>Charcotia amundseni</i>	41	$-23.6 \pm 0.6$	$12.9 \pm 0.9$	$-23.7 \pm 0.5$	$12.9 \pm 0.7$	

TABLE 3

Results of Mann Whitney U tests, Kruskal-Wallis and Chi<sup>2</sup> tests assessing the influence of species, locations and depths on stable isotope values of carbon and nitrogen. Significant p-values (<0.05) are indicated in bold.

$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)		
Mann Whitney U test		W	p-value		W	p-value
Species		4542	0.4143		8276	<b>&lt;0.001</b>
Kruskal-Wallis test	df	$\chi^2$	p-value	df	$\chi^2$	p-value
Locations <i>C. obesa</i>	5	154.72	<b>&lt;0.001</b>	5	132.48	<b>&lt;0.001</b>
Locations <i>C. amundseni</i>	2	20.303	<b>&lt;0.001</b>	2	17.058	<b>&lt;0.001</b>
Chi <sup>2</sup> test	df	$\chi^2$	p-value	df	$\chi^2$	p-value
Depths <i>C. obesa</i>	3	15.007	<b>0.002</b>	3	15.552	<b>0.001</b>

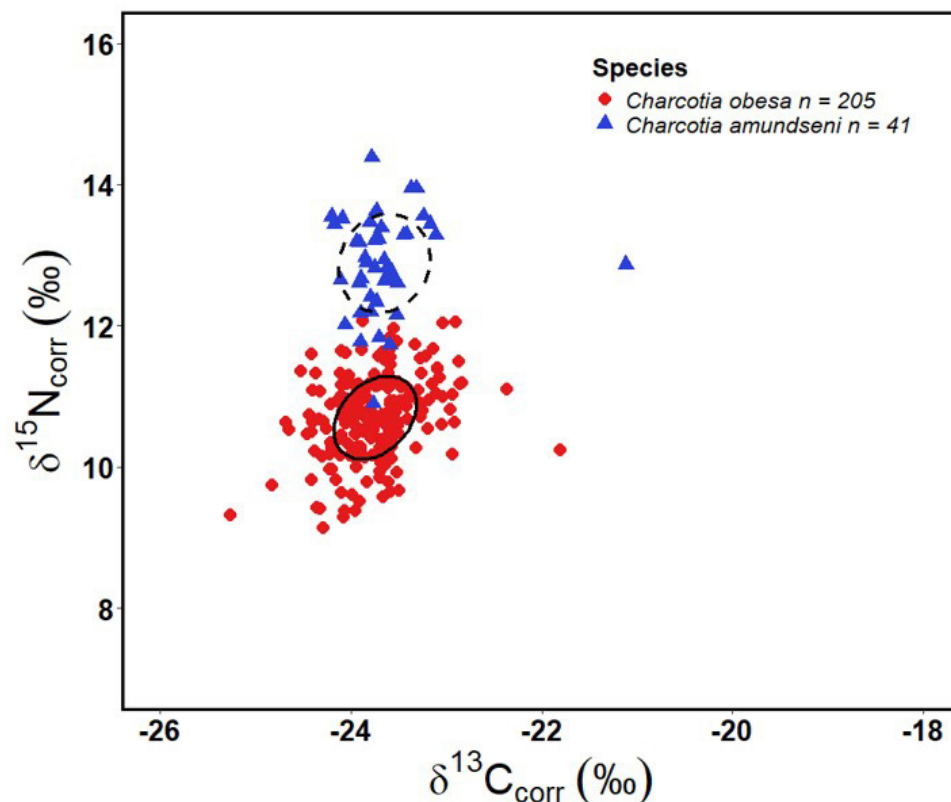


Fig. 2 – Standard Ellipse Areas of individual stable isotope values of  $\delta^{13}\text{C}_{\text{corr}}$  and  $\delta^{15}\text{N}_{\text{corr}}$  and its isotopic niche, of *Charcotia obesa* (red circles, black ellipse) and *C. amundseni* (blue triangles, dashed ellipse).



TABLE 4

Sample size (n) and mean  $\pm$  SD  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values calculated for *Charcotia obesa* and *C. amundseni*; values are grouped per sampling location.

Species	Locations	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Charcotia obesa</i>	South Shetland Islands	40	$-24.8 \pm 0.4$	$9.5 \pm 0.7$
	Palmer Station	10	$-24.9 \pm 0.3$	$11.6 \pm 0.3$
	Foyn Harbor	4	$-23.3 \pm 0.1$	$12.1 \pm 0.6$
	Andvord	20	$-22.0 \pm 0.6$	$12.2 \pm 0.5$
	Berthelot Islands	21	$-22.2 \pm 0.7$	$12.6 \pm 0.6$
	Dumont D'Urville Sea	108	$-23.9 \pm 0.4$	$10.3 \pm 0.6$
<i>Charcotia amundseni</i>	Breid Bay	5	$-24.1 \pm 0.2$	$11.8 \pm 0.7$
	Crown Bay	17	$-23.9 \pm 0.2$	$12.6 \pm 0.5$
	Filchner Area	19	$-23.4 \pm 0.7$	$13.5 \pm 0.9$

Three locations were sampled for *C. amundseni* (Fig. 4b). An increasing trend in both isotope ratios was found from the Filchner Area (FIL) to the two locations in Queen Maud Land (Table 4).  $\delta^{13}\text{C}$  differed significantly between specimens from the FIL compared to Crown Bay (CB) (p-value=0.001) and Breid Bay (BB) compared to CB (p-value=0.001). The same patterns are shown for  $\delta^{15}\text{N}$  with significant differences between BB and the FIL (p-value <0.001) and between the FIL and CB (p-value=0.006). Overall, the location within the Weddell Sea (FIL) and two locations of Queen Maud Land (CB and BB) showed significant differences in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}$ ;  $\chi^2=20.30$ , p-value=<0.0001 and  $\delta^{15}\text{N}$ ;  $\chi^2=17.06$ , p-value=<0.0001) (Table 3), whereas the variation between the two adjacent sites is much

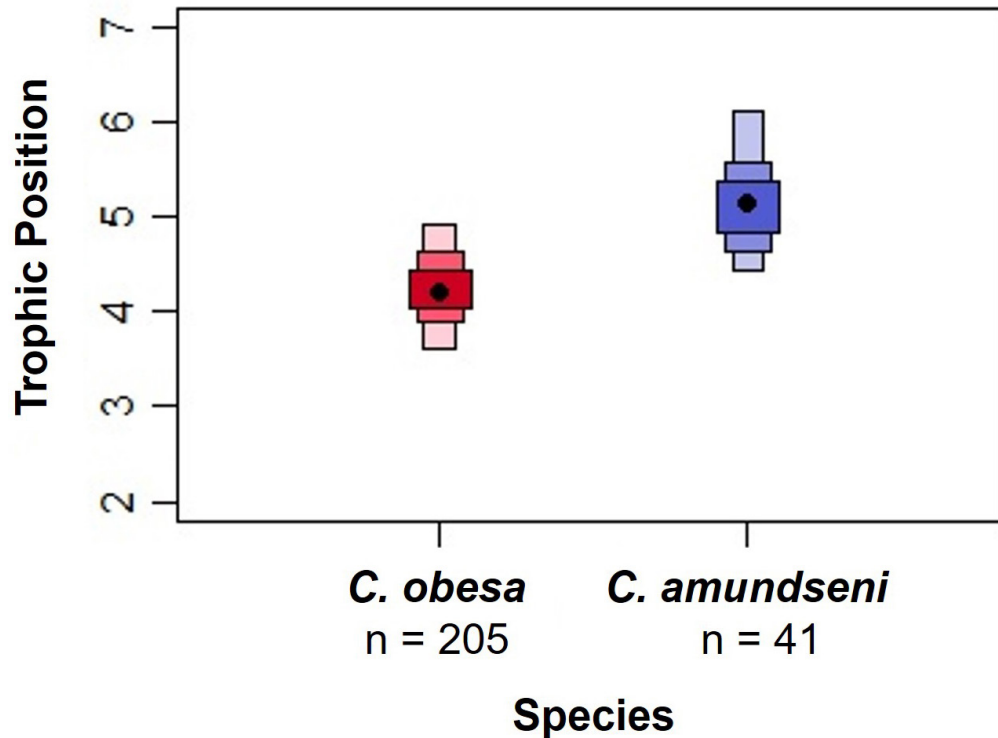


Fig. 3 – Trophic positions calculated for *Charcotia obesa* (red) and *Charcotia amundseni* (blue). Boxplots show credibility intervals of 50, 75 and 95 %. Black dot denotes the mode of each species' trophic position.

TABLE 5

Results of pair-wise Dunn tests with Bonferroni corrections assessing the influence of location on stable isotope values. (a) pair-wise tests between the North, Central and South clusters of locations. (b) pair-wise tests between locations for  $\delta^{13}\text{C}$  for both *Charcotia* species. (c) pair-wise tests between locations for  $\delta^{15}\text{N}$  for both *Charcotia* species. Significant p-values ( $<0.05$ ) are indicated in bold. (d) overlap of isotopic niches between geographical locations, displayed in percentages.

<i>C. obesa</i>							<i>C. amundseni</i>			
<b>a</b>	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$						
	North	Central	South	North	Central	South				
North	–									
Central	<b>&lt;0.001</b>	–								
South	<b>&lt;0.001</b>	0.347	–							
North				–						
Central				<b>&lt;0.001</b>	–					
South				<b>&lt;0.001</b>	0.243	–				

<b>b</b>	$\delta^{13}\text{C}$						$\delta^{13}\text{C}$		
	SSI	PAL	FH	AND	BI	URV	BB	CB	FIL
SSI	–						BB	–	
PAL	1	–					CB	0.538	–
FH	<b>&lt;0.001</b>	<b>0.003</b>	–				FIL	<b>0.001</b>	<b>0.001</b>
AND	<b>&lt;0.001</b>	<b>&lt;0.001</b>	1	–					–
BI	<b>&lt;0.001</b>	<b>&lt;0.001</b>	1	1	–				
URV	<b>&lt;0.001</b>	<b>0.001</b>	1	<b>&lt;0.001</b>	<b>&lt;0.001</b>	–			

<b>c</b>	$\delta^{15}\text{N}$						$\delta^{15}\text{N}$		
	SSI	PAL	FH	AND	BI	URV	BB	CB	FIL
SSI	–						BB	–	
PAL	<b>&lt;0.001</b>	–					CB	0.392	–
FH	<b>&lt;0.001</b>	1	–				FIL	<b>0.001</b>	<b>0.006</b>
AND	<b>&lt;0.001</b>	1	1	–					–
BI	<b>&lt;0.001</b>	1	1	1	–				
URV	0.002	<b>0.005</b>	0.058	<b>&lt;0.001</b>	<b>&lt;0.001</b>	–			

<b>d</b>	Overlap (%)						Overlap (%)		
	SSI	PAL	FH	AND	BI	URV	BB	CB	FIL
SSI	–						BB	–	
PAL	<b>&lt;0.001</b>	–					CB	13.05	–
FH	0.000	0.000	–				FIL	<b>&lt;0.001</b>	3.52
AND	0.000	0.000	0.000	–					–
BI	0.000	0.000	0.000	30.95	–				
URV	0.000	0.000	0.000	0.000	0.000	–			

TABLE 6

Isotopic niches areas for each species, as well as for each sampling location of each species. Including Total Area (TA), Standard Ellipse Area adjusted for small sample size ( $SEA_C$ ), and Bayesian Standard Ellipse Area ( $SEA_B$ ) mode and 95% credible intervals.

	n	TA	$SEA_C$	$SEA_B$	$SEA_B$ 95% CI
<i>Charcotia obesa</i>	205	6.2	0.8	0.8	0.7–0.9
South Shetland Islands	40	3.0	0.9	0.8	0.6–1.2
Palmer Station	10	0.7	0.4	0.3	0.2–0.6
Foyn Harbor	4	0.2	0.4	0.2	0.1–0.7
Andvord	20	2.8	1.0	0.9	0.6–1.4
Berthelot Islands	21	3.7	1.3	1.1	0.8–1.8
Dumont D'Urville Sea	108	4.1	0.6	0.6	0.5–0.8
<i>Charcotia amundseni</i>	41	5.5	1.1	1.0	0.8–1.4
Breid Bay	5	0.3	0.4	0.3	0.1–1.0
Crown Bay	17	0.9	0.7	0.3	0.2–0.6
Filchner Area	19	5.5	1.9	1.7	1.1–2.9

lower (Table 5b–c). CB had a niche overlap with BB of 13.05 % and a minor overlap with the FIL (3.52 %), whereas BB and FIL had no overlap (Fig. 5b; Table 5d). *Charcotia amundseni* individuals from the FIL had the largest  $SEA_B$  (1.7‰<sup>2</sup>; CI 1.1–2.9‰<sup>2</sup>), while the  $SEA_B$  values of the other two locations were much smaller and very similar (BB: 0.3‰<sup>2</sup>; CI 0.1–1.0‰<sup>2</sup> & CB: 0.3‰<sup>2</sup>; CI 0.2–0.6‰<sup>2</sup>) (Table 6).

### Depth-dependent SI ratios

*Charcotia obesa* displayed a large overlap in isotopic niche between depths (Fig. 2S; Table 1S). Moreover, values for both  $\delta^{13}C_{corr}$  and  $\delta^{15}N_{corr}$  differed only a few decimal points (Table 2S).

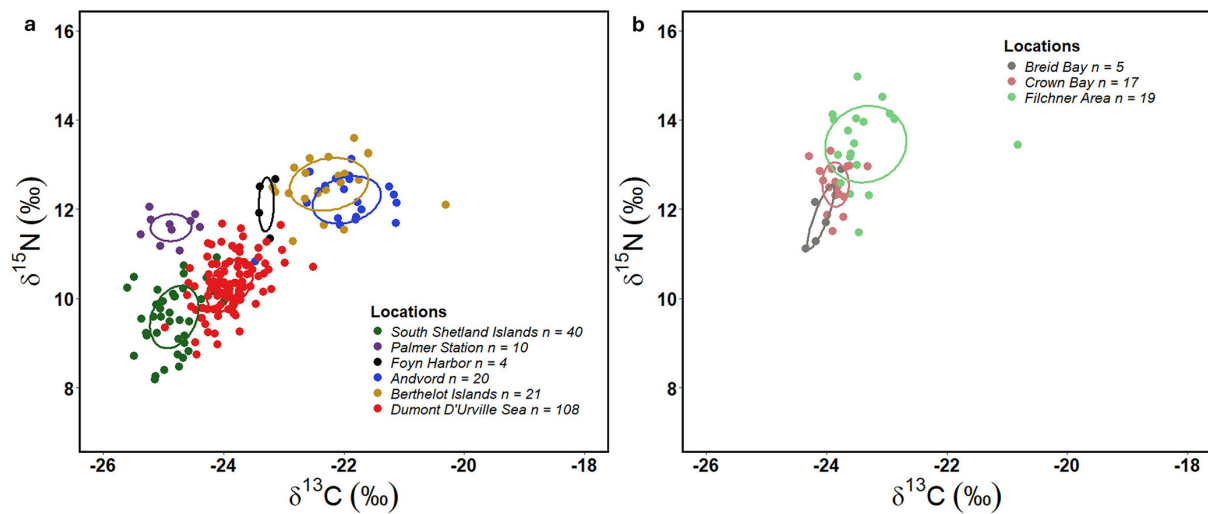


Fig. 4 – Standard Ellipse Areas of individual stable isotope values of  $\delta^{13}C$  and  $\delta^{15}N$  for *Charcotia obesa* (a), *C. amundseni* (b) and their isotopic niches, grouped per location. Locations are indicated by different colours; the sample number per location is provided in the legend.

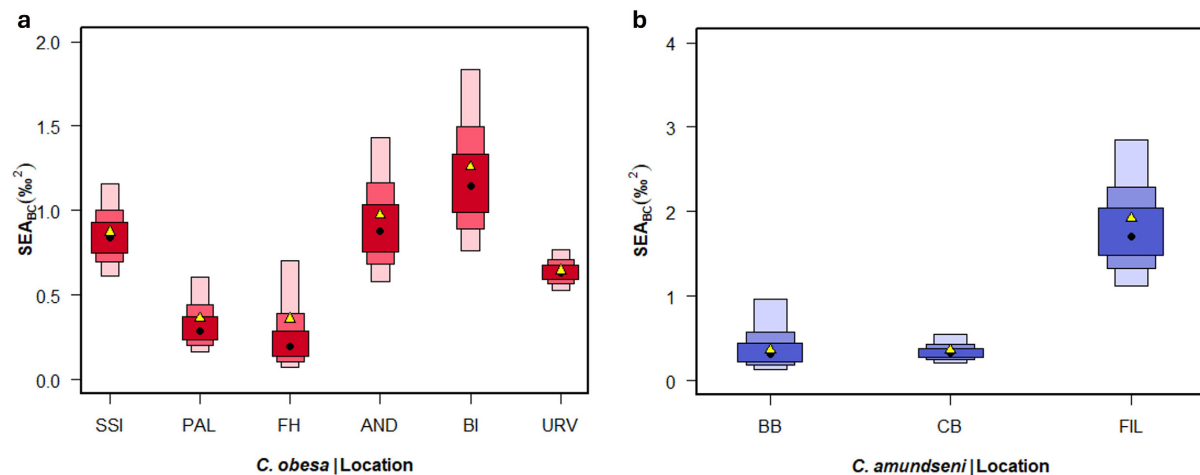


Fig. 5 – Standard Ellipse Areas of stable isotope values of geographical locations for both *Charcotia obesa* (a, red) and *Charcotia amundseni* (b, blue). Black dots denote the Bayesian estimate of  $SEA_B$  while yellow triangles indicate the computed  $SEA_C$ .

## Discussion

The isotopic composition of carbon ( $\delta^{13}C$ ) and nitrogen ( $\delta^{15}N$ ) of two *Charcotia* sister species (*C. obesa* Chevreux, 1906 and *C. amundseni* d’Udekem d’Acoz, Schön & Robert, 2018) were analysed to compare their trophic position in the Antarctic food web. Significant differences in nitrogen isotope ratios were found between the two sister species. Based on the high nitrogen values, high trophic levels were estimated for both species. Significant differences in both stable isotopes between regions were found within each species. An increasing trend in both stable isotopes in *C. obesa* was found from the north to south off the WAP. Significant differences were also observed in *C. amundseni* from sampling locations in the Weddell Sea and Queen Maud Land.

### Nitrogen SI ratios and trophic positions

$\delta^{15}N$  values for both species were high, corroborating a high position in the trophic web and, probably, a necrophagous scavenging behaviour (Dauby *et al.* 2001; Nygård *et al.* 2012). *Charcotia* individuals, in past studies showed  $\delta^{15}N$  values of  $11.6 \pm 0.3\text{‰}$  in the eastern Weddell Sea (Nyssen *et al.* 2002) and lower values along the Antarctic Peninsula ( $7.3 \pm 0.7\text{‰}$ ) (Nyssen *et al.* 2005). Michel *et al.* (2019) have reported  $\delta^{15}N$  values of  $9.1 \pm 1.6\text{‰}$  of *C. obesa* individuals in East Antarctica (Adélie Land), which differs slightly with the isotopic ratio of *C. obesa* in our study ( $10.3 \pm 0.6\text{‰}$ ).  $\delta^{15}N$  values in the previous studies match the range found in our study (min. 7.3–max. 12.2‰). Other scavenging amphipods investigated by Zenteno *et al.* (2019) had  $\delta^{15}N$  values ranging from  $4.4 \pm 0.6\text{‰}$  to  $5.9 \pm 0.3\text{‰}$ , with the highest  $\delta^{15}N$  value ( $6.6 \pm 0.4\text{‰}$ ) for a carnivore predatory amphipod. One species included in the latter study was *Cheirimedon femoratus* Pfeffer, 1888 (Crustacea, Amphipoda, Lysianassoidea), which is considered an omnivorous scavenger from the same scavenging guild as *Charcotia* (De Broyer *et al.* 2004; Seefeldt *et al.* 2017, 2018). *Cheirimedon femoratus* occupies a broad trophic range within the guild, with a  $\delta^{15}N$  value of  $4.4 \pm 0.6\text{‰}$  (Seefeldt *et al.* 2017; Zenteno *et al.* 2019). This species is notably smaller than *Charcotia* and has a different mandible morphology, feeding on carcasses (when available) and algae during austral summer (Núñez-Pons *et al.* 2012; Seefeldt *et al.* 2017). *Charcotia* feeds on carcasses from outside to inside, while smaller species obtain access either through orifices in the body or from openings created by larger scavengers, such as *Charcotia* (Seefeldt *et al.* 2017). *Charcotia amundseni* and *C. obesa* displayed different  $\delta^{15}N_{corr}$  values, suggesting a different trophic position (TP; Post 2002). *Charcotia amundseni* (TP of 5.14) presumably belonged to the fifth trophic level and *C. obesa*, with

an estimated TP of 4.19, to the fourth trophic level. A first explanation could be that, although the two species are opportunistic scavengers *C. amundseni* which is found deeper feeds on carcasses occupying a higher trophic position than *C. obesa*. *Charcotia* are feeding episodically and are often found on large dead animals at depth (Jażdżewska 2009; Bolstad *et al.* 2023). We hypothesize that in shallow areas, the diversity of dead prey is larger and belongs to more diverse trophic positions than in deeper areas. Deep-sea carcasses are typically dominated by larger organic falls of organisms from higher trophic levels (Bolstad *et al.* 2023), which, consequently, could explain the lower trophic position of *C. obesa* compared to *C. amundseni*. The lack of any overlap in the trophic niche based in the SEA (Fig. 2; Table 2) further supports the different trophic position of both species. Anyway, our modelled results show that the two species occupy very high trophic positions, much higher than observed by Michel *et al.* (2019) (*C. obesa*, TP: 2.4) for example. This difference is huge in terms of energy flow and could indicate that *C. obesa* has higher feeding plasticity than initially thought. In East Antarctic *C. obesa* was caught at shallow depths (20 m), preying likely on dead invertebrates occupying a lower trophic position. Our *Charcotia* species are at a higher trophic position than smaller scavenging amphipods investigated by Zenteno *et al.* (2019), showing that the scavengers guild does not necessarily depend on the same prey and comprises organisms occupying different trophic positions in the Antarctic food web (Smale *et al.* 2007). Niche partitioning might allow scavenging amphipods to co-exist in the same habitat.

Differences in trophic position and thus in realized ecological niche support the coexistence of morphologically similar species and contribute to the diversification of sister species (Klarner *et al.* 2013; Bessa *et al.* 2014). Nevertheless, a second hypothesis could be that both species display eco-physiological differences. Isotopic fractionation is associated with starvation, leading generally to an increase of  $\delta^{15}\text{N}$  values (Doi *et al.* 2017). Impacts of diet quality and starvation on nitrogen isotopic fractionation have been reported in other arthropods (Haubert *et al.* 2005) and crustaceans (Fantle *et al.* 1999; Trochine *et al.* 2019). Starvation has been reported for *Charcotia* (Chapelle *et al.* 1994), as an opportunistic omnivorous scavenger feeding episodically. The higher  $\delta^{15}\text{N}$  values observed in *C. amundseni* as opposed to *C. obesa*, might indicate that *C. amundseni*, living in deeper water, cope with starvation more frequently and for more elongated periods of time than the shallow water *C. obesa* individuals (Scheer *et al.* 2022). Additionally, recent research found that differences in gut microbiome composition and specific symbiotic relationships aid deep sea invertebrates to cope with surviving in these unusual environments. Microbiome diversity leads to variable host physiology, behaviour and ecology (Osman & Weinnig 2021) and provides an alternative explanation for the trophic differences found in this study.

### Carbon SI ratios and food sources

No significant difference was found between the mean  $\delta^{13}\text{C}_{\text{corr}}$  values of both species (Table 3).  $\delta^{13}\text{C}$  values are generally indicative of the primary food source of an organism (France 1995; Michener & Kaufman 2007) with more negative  $\delta^{13}\text{C}$  values ( $\pm -25\text{‰}$  to  $\pm -30\text{‰}$ ) being characteristic of pelagic primary producers (Espinasse *et al.* 2019; Michel *et al.* 2019), intermediate  $\delta^{13}\text{C}$  values ( $\pm -25\text{‰}$  to  $\pm -10\text{‰}$ ) of mainly benthic primary producers and less negative  $\delta^{13}\text{C}$  values ( $\pm -20\text{‰}$  to  $\pm -8\text{‰}$ ) being characteristic of sea ice microbial communities (Gillies *et al.* 2012a, 2013; Michel *et al.* 2019). *Charcotia obesa* had the largest range in  $\delta^{13}\text{C}$ , which might be attributed to the larger sample size, but could also reflect a wide diversity of primary food sources (both pelagic and benthic) and larger diversity in dead organic matter in the shallower depth range in which they occur. The range of  $\delta^{13}\text{C}$  values of *C. amundseni* falls within the predetermined range of both pelagic and benthic primary producers as primary food source, which is in agreement with organisms feeding on carcasses of pelagic animals (Gillies *et al.* 2012b; Michel *et al.* 2019). A range of  $3.5\text{‰}$  in  $\delta^{13}\text{C}$  values supports their scavenging foraging feeding behaviour (Amsler *et al.* 2014; Aumack *et al.* 2017). The study by Zenteno *et al.* (2019) found  $\delta^{13}\text{C}$  values for scavenging amphipods ranging from  $-14.7 \pm 0.6\text{‰}$  to  $-21.5 \pm 0.6\text{‰}$ , aligning with our results. The availability of



multiple primary food sources is one of the key features that enables the stability of Antarctic food webs (Zenteno *et al.* 2019).

### Effect of location

The primary food sources in Antarctic food webs (phytoplankton, macroalgae, and detrital matter) are highly dependent on sea-ice coverage, and therefore also shaped by location and seasonality (Norkko *et al.* 2007). While we could not study seasonality as we used an opportunistic approach to analyse existing samples, our results confirm spatial variation, as there is limited overlap between sites on the  $\delta^{13}\text{C}$  -axis for each of the two species (Fig. 4a–b). When investigating the trophic ecology within each species, carbon isotope ratios of *C. obesa* individuals showed significant geographical differences between localities off the Antarctic continent (Tables 3, 5b–c). Lowest mean  $\delta^{13}\text{C}$  values ( $-24.8\text{‰}$ ) were estimated around the SSI while the highest mean  $\delta^{13}\text{C}$  value ( $-22.0\text{‰}$ ) was measured in Andvord (AND) (Table 4). Interestingly, Dumont d’Urville Sea (the only south-east sampling location) differed significantly in the mean  $\delta^{13}\text{C}$  value from all other locations except Foyn Harbor (with the lowest sample size per location), and showed no overlap in isotopic niche (Figs 4a, 5a; Table 5d). The only locations with an overlap of 30.95% were the Andvord and Berthelot Islands, which are located relatively close in the WAP. The biogeochemistry of the Southern Ocean differs regionally, which affects primary production (Henley *et al.* 2020; Fraser *et al.* 2023) and is reflected in our isotope data. For *C. amundseni*, samples from three locations were included in the current study and we found a significant difference between the Weddell Sea location (Filcher Area (FIL) and both locations in Queen Maud Land (Breid Bay (BB); Crown Bay (CB) (Table 5b). The carbon stable isotope ratio is highly influenced by sea surface temperature and  $\text{CO}_2$  availability for photosynthesis (Lara *et al.* 2010; Espinasse *et al.* 2019). Additionally, primary production is negatively correlated with sea ice coverage, leading to an increase of detritus consumption by benthic consumers, which is reflected in higher  $\delta^{13}\text{C}$  values (Norkko *et al.* 2007).  $\delta^{15}\text{N}$  values, on the other hand, are strongly influenced by sea ice dynamics and upwelling, since the availability of nitrogen (in the form of nitrate) is the limiting factor and will cause an increase in stable isotope values (Difiore *et al.* 2010; Zenteno *et al.* 2019). The lowest mean value of  $\delta^{15}\text{N}$  ( $9.5\text{‰}$ ) in *C. obesa* was estimated in the South Shetland Islands (SSI), while the highest mean value ( $12.6\text{‰}$ ) was found in Berthelot Islands (BI), showing an increasing gradient of  $3\text{‰}$  from the northernmost sampling location around the WAP to the most southwest sampling location close to the Bellingshausen Sea. A similar pattern was found by Brault *et al.* (2018) in zooplankton species from the WAP to the Ross Sea. The authors attributed this pattern to the abundant polynyas and higher productivity due to glacial inputs of iron in the Amundsen and Ross Sea, leading to higher  $\delta^{15}\text{N}$  values phytoplankton (Brault *et al.* 2018). Similar meltwater input has been reported in the Bellingshausen Sea, which could explain the observed pattern of increasing  $\delta^{15}\text{N}$  in our study (Holland *et al.* 2010; Sheehan *et al.* 2023). Significant differences in nitrogen stable isotopes of *C. amundseni* were found between FIL and both other locations (CB and BB), and confirmed by the lack of or minimal overlap in the SEA. The Filchner Area is located at the east side of the Weddell Sea, adjacent to the Weddell Gyre which contributes to upwelling of nutrient rich deep-sea water. The latter might be linked to the higher  $\delta^{15}\text{N}$  values (Gordon *et al.* 2001; Nicholls *et al.* 2009; Vernet *et al.* 2019).

### Depth effect

*Charcotia obesa* samples originated from four depth ranges along the shelf of the Antarctic continent (see Appendix Fig. 2S, Tables 1S and 2S). Distance to the continent and consequently also depth may strongly influence both isotopic ratios. Usually, coastal environments show higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, which decrease with distance to the shore (Lara *et al.* 2010; Zhang *et al.* 2014). The decrease in the carbon isotope ratio is generally steeper than for the nitrogen isotope (El-Sabaawi *et al.* 2012; St John Glew *et al.* 2021). However, in our data, this decrease is not very pronounced and the four depth ranges show complete overlap in the SEA analysis (Appendix Fig. 2S).

### Suggestions for future studies

Our study illustrates that a limited number of geographical stations can produce valuable novel insights. Increasing the sampling size to at least five individuals equally distributed per location and a more structured distribution of locations and depths around the Antarctic continent makes the statistical analyses across variables more robust. Isotopic measurements of POM during sampling would also be advisable to provide baseline values for the species of interest (Michel *et al.* 2016). Sampling outside of the Austral summer is recommended, although challenging if not next to impossible. Increasing the temporal resolution and year-round sampling could further improve the accuracy of observed patterns and also unravel seasonal patterns (Kolts *et al.* 2013; de Lima *et al.* 2022).

Stable isotopes are a powerful tool to estimate trophic niches of organisms but may lack resolution especially when spatiotemporal variation in the ecosystem is high. Including dietary studies by sampling the stomach content might provide a more detailed, albeit snapshot, insight in the diet and starvation periods. Metabarcoding of the stomach content has proven to be a useful tool at a higher resolution than visual dietary assessments (Maes *et al.* 2022). Therefore, a combination of trophic markers, molecular and morphological methods will result in information at the highest resolution and predict a species' trophic niche most accurately (Gerringer *et al.* 2017).

### Conclusion

Based on the data presented here, we observe that even closely related sister species, which occupy similar habitats and have similar feeding strategies differentiate their isotopic niche. The plasticity in feeding habits of scavenging amphipods might have important implications in the face of climate change. Polar regions are one of the fastest warming regions in the world, more specifically the Antarctic Peninsula is affected to a great extent (Wallis *et al.* 2023; Engel *et al.* 2024). Decreasing sea ice cover might alter the effective niche of certain species and reduce suitable habitat (Parkinson & Cavalieri 2012). Trophic plasticity of Antarctic benthic organisms could be a strategy to ensure survival, however potentially leading to different responses of each group (Michel *et al.* 2016). Therefore, future focus on trophodynamics is essential in terms of insights in ecosystem functioning and conservation of the pristine Antarctic environment.

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## Appendix

Supplementary Tables and Figures.

TABLE 1S

Sample size (n) and mean  $\pm$  SD  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values calculated for *Charcotia obesa*. Corrected values (corr) are adjusted for locations. Values are grouped according to sampling depth.

Species	Depth	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}_{\text{corr}}$ (‰)	$\delta^{15}\text{N}_{\text{corr}}$ (‰)
<i>C. obesa</i>	<50 m	115	-23.2 $\pm$ 1.0	11.2 $\pm$ 1.1	-23.7 $\pm$ 0.5	10.7 $\pm$ 0.6
	50–100 m	29	-24.4 $\pm$ 0.5	9.7 $\pm$ 0.9	-24.0 $\pm$ 0.3	10.3 $\pm$ 0.6
	100–150 m	34	-24.1 $\pm$ 0.2	10.3 $\pm$ 0.6	-23.8 $\pm$ 0.3	10.8 $\pm$ 0.6
	>150 m	25	-24.9 $\pm$ 0.3	9.8 $\pm$ 0.5	-23.8 $\pm$ 0.3	10.9 $\pm$ 0.5

TABLE 2S

Results of pair-wise Dunn tests with Bonferroni corrections assessing the influence of depths on corrected stable isotope values of carbon and nitrogen for *Charcotia obesa*. Significant p values (<0.05) are indicated in bold.

Species	Depths	p-value $\delta^{13}\text{C}_{\text{corr}}$ (‰)	p-value $\delta^{15}\text{N}_{\text{corr}}$ (‰)
<i>C. obesa</i>	<50 m – 50 to 100 m	<b>0.006</b>	<b>0.011</b>
	<50 m – 100 to 150 m	0.092	1
	<50 m – >150 m	0.339	0.729
	50 to 100 m – 100 to 150 m	1	<b>0.010</b>
	50 to 100 m – >150 m	1	<b>0.002</b>
	100 to 150 m – >150 m	1	1



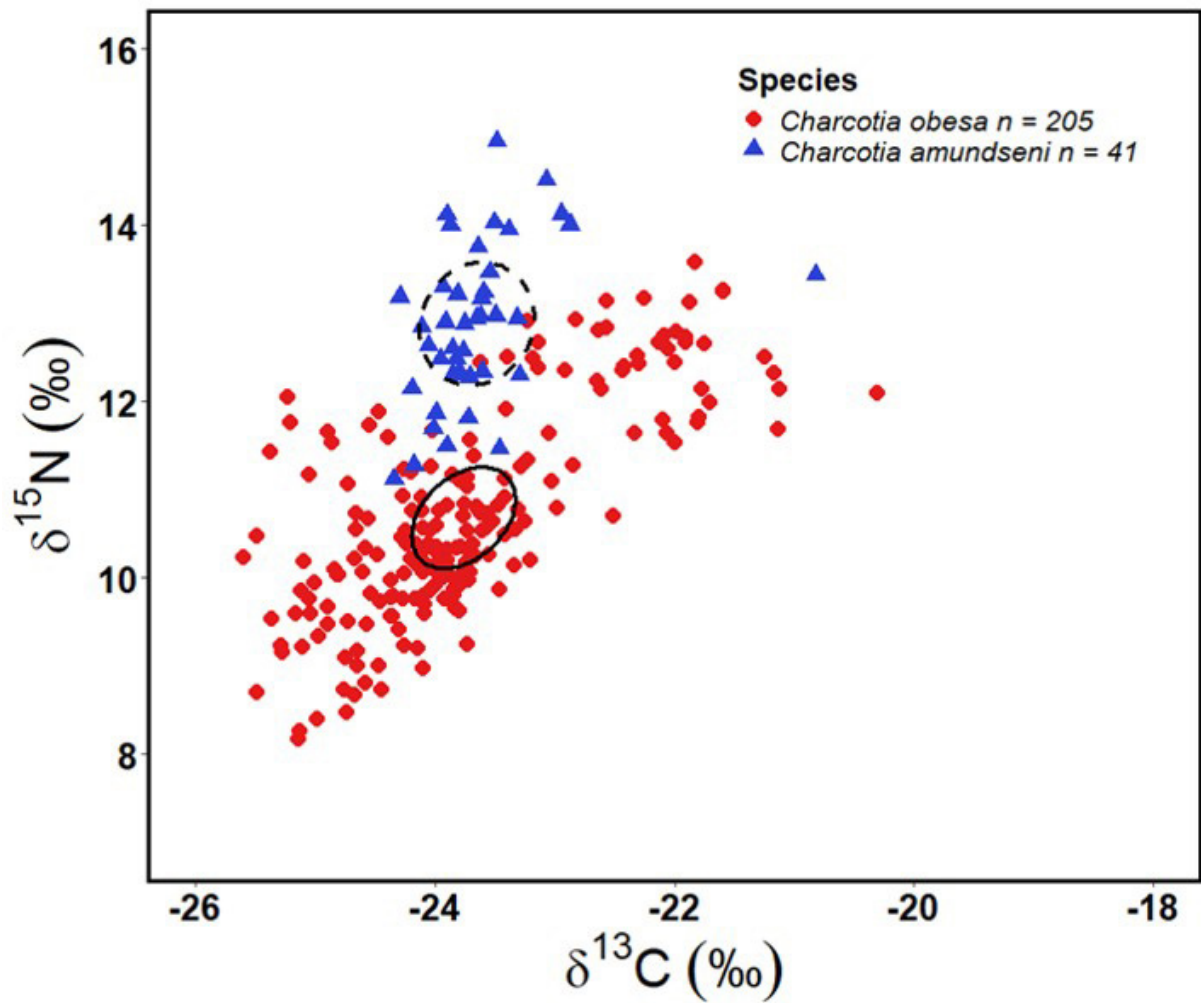


Fig. 1S – Standard Ellipse Areas of individual uncorrected stable isotope values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and its isotopic niche of *Charcotia obesa* (red circles) and *C. amundseni* (blue triangles).

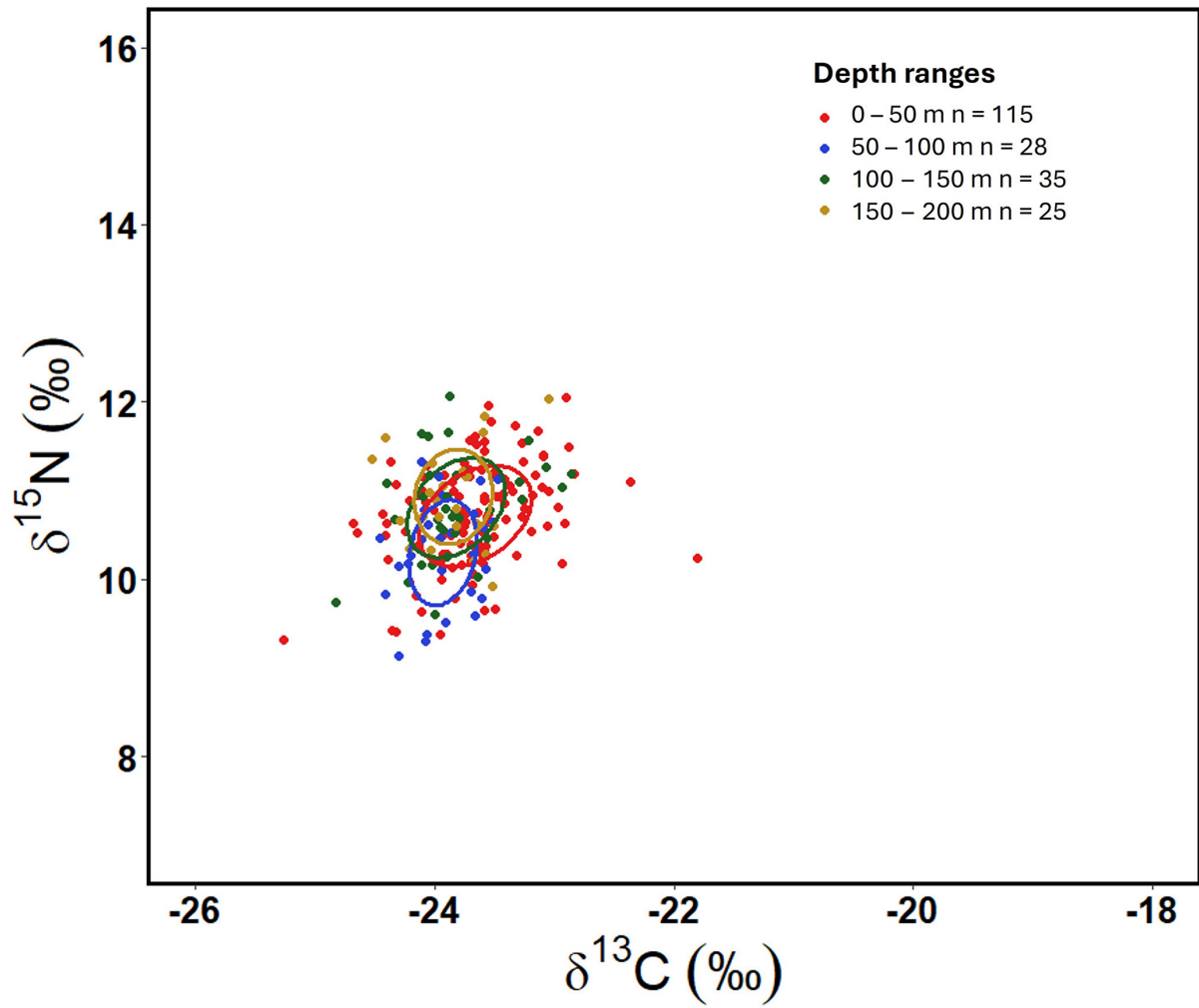


Fig. 2S – Standard Ellipse Areas of individual stable isotope values of  $\delta^{13}\text{C}_{\text{corr}}$  and  $\delta^{15}\text{N}_{\text{corr}}$  for *Charcotia obesa* and its isotopic niche, grouped per depth. Different depths are indicated by different colours; the sample number per species is also provided.