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Uncovering the trophic relationship between *Themisto gaudichaudii* and *Salpa thompsoni* in the Antarctic Polar Frontal Zone

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ABSTRACT: Trophic dynamics of 2 abundant macrozooplankton species *Salpa thompsoni* and *Themisto gaudichaudii* were studied during the austral summer at 2 locations near the Antarctic Polar Front with contrasting low and high chlorophyll *a* (chl *a*) concentrations. Compound-specific stable isotope analysis, complemented by gut content and bulk isotope analyses, were used to investigate trophic interactions between species, and to assess their trophic positions in the pelagic food web. The results of the compound-specific stable isotope analysis placed *S. thompsoni* at the second trophic level and approx. 1 trophic level below *T. gaudichaudii*. Two forms of *T. gaudichaudii* appeared to feed at different trophic levels, with *T. gaudichaudii bispinosa* feeding at a higher trophic level (~3.3) than *T. gaudichaudii compressa* (~2.8). Isotope data coupled with gut content analysis indicated a regular consumption of salps in both areas, although a higher contribution of gelatinous prey was encountered in a chl *a* poor area. The food web baseline values (bulk $\delta^{13}C$) varied regionally, highlighting 2 independent food webs albeit with a similar trophic structure. Overall, our findings suggested that in areas where *S. thompsoni* is highly abundant, *T. gaudichaudii* may be a significant predator of this species.

KEY WORDS: Salps · Amphipods · Gut content · Nitrogen isotopic composition · Amino acids · Trophic position

INTRODUCTION

The pelagic tunicate *Salpa thompsoni* and the hyperiid amphipod *Themisto gaudichaudii* are 2 conspicuous and abundant macrozooplankton species in the Southern Ocean, particularly in the sub-Antarctic region and Antarctic Polar Frontal zone (Kane 1966, Pakhomov et al. 2002). Among Southern Ocean metazoans, *S. thompsoni* ranks first in terms of wet mass and third in terms of dry or carbon mass (Voronina 1998). This species has been identified as one of the most important filter-feeders in the Southern Ocean, and may at times consume the entire daily primary production (e.g. Dubischar & Bathmann 1997, Perissinotto & Pakhomov 1998a, Pakhomov et al. 2002). By packaging small particles into large fast sinking fecal pellets, *S. thompsoni* likely also contributes significantly to vertical carbon flux from the surface ocean to the deep interior and seafloor (Le Fèvre et al. 1998, Perissinotto & Pakhomov 1998b, Walsh et al. 2001).

T. gaudichaudii is thought to occur in 2 distinct forms: forma *compressa*, characterized by a subequal length of the fifth (P5) and sixth pereopod (P6); and forma *bispinosa*, where the P5 is approx. twice as long as the P6 (Sheader & Evans 1974). A wide range of intermediate forms has been observed between

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these 2 extremes (Sheader & Evans 1974). Based on gut content analyses, *T. gaudichaudii* has generally been considered to be an opportunistic carnivorous omnivore (Pakhomov & Perissinotto 1996, Froneman et al. 2000, Lange 2005). Near South Georgia, it has been estimated that during summer *T. gaudichaudii* may consume up to 2% of the available mesozooplankton biomass daily, or up to 70% of mesozooplankton daily productivity (Pakhomov & Perissinotto 1996, Watts & Tarling 2012). *T. gaudichaudii* may even control the recruitment of the larval Antarctic krill *Euphausia superba* and Mackerel icefish *Champsocephalus gunnari* (Watts & Tarling 2012). It has been suggested that morphological differences between *compressa* and *bispinosa* forms may result in different prey compositions (Sheader & Evans 1975).

Both *S. thompsoni* and *T. gaudichaudii* seem to play a significant role in the diet of various Antarctic top predators (reviewed by Pakhomov et al. 2002, Shreeve et al. 2009, Waluda et al. 2010) and they are therefore important ecological links between primary producers/consumers and top consumers. However, despite their importance in Southern Ocean food webs, their actual trophic roles, and particularly that of *T. gaudichaudii*, are not clearly understood. *S. thompsoni* is generally considered to represent the first consumer level feeding directly on phytoplankton (Cherel et al. 2008, Richoux & Froneman 2009, Stowasser et al. 2012). Although diatoms are predominant items in the gut contents of *S. thompsoni* (Tanimura et al. 2008, von Harbou et al. 2011), fatty acid trophic biomarkers and molecular analyses of gut contents indicated a substantial year-round contribution of flagellates to their diet (von Harbou et al. 2011, Metfies et al. 2014). Stomach content analysis for *T. gaudichaudii* revealed a predominantly carnivorous diet (Pakhomov & Perissinotto 1996), although there is limited evidence that phytoplankton may also be an important dietary item for this species (Hopkins 1985). Bulk stable isotope analyses have been quite ambiguous for *T. gaudichaudii*, suggesting a variable trophic level (TL) of this species ranging from 2.2 to 2.9 (Cherel et al. 2008, Richoux & Froneman 2009, Stowasser et al. 2012).

During the 2012 austral summer cruise of the RV 'Polarstern' (ANT XXVIII-3), observations of *S. thompsoni* and *T. gaudichaudii* population dynamics near the Polar Front indicated that there may be a direct trophic link between these 2 species. Their co-occurrence yet inverse density distributions suggested that *T. gaudichaudii* predation may have prevented the development of *S. thompsoni* blooms in some instances (Pakhomov & Hunt 2013). This has implications for both trophic transfers and vertical fluxes in the region. Most previous studies on the feeding behavior of these 2 species have used either gut contents or bulk stable isotope analyses. Both methods have their limitations. Gut contents are often difficult to identify due to a high degree of digestion, and this method only gives a snapshot of the diet ingested. Bulk stable isotope values, which have widely been used to investigate food web structures in a number of ecological studies (Fry 2006), integrate diet information over a longer period of time but do not provide species level information of prey consumed. In addition, to estimate organism TL with this method it is necessary to characterize the $\delta^{15}N$ values of the food web baseline. This is often problematic, since there may be several food sources with overlapping isotopic compositions, which sometimes leads to a substantial error in the estimated TL (± 1 unit or more, e.g. Stowasser et al. 2012). The $\delta^{15}N$ values of source materials may also have high spatial and temporal variability (Michener & Schell 1994, Cabana & Rasmussen 1996).

To more closely assess the trophic dynamics of *S. thompsoni* and *T. gaudichaudii* from samples collected during ANT XXVIII-3, we have here used a combination of 3 different methods: compound-specific nitrogen isotope analysis of individual amino acids (CSIA-AA), complemented by bulk carbon and nitrogen isotope analysis, and gut content analysis. The first method allows an estimation of the trophic position without knowing the baseline $\delta^{15}N$ values of the primary producer sources (McClelland & Montoya 2002, McCarthy et al. 2007, Popp et al. 2007, Chikaraishi et al. 2009, 2014). A comparison of the $\delta^{15}N$ values for glutamic acid and phenylalanine has been shown to be most useful (Chikaraishi et al. 2009). Glutamic acid enriches (+8.0 ± 1.2‰) with each TL due to reactions (e.g. transamination or deamination) that cleave the carbon–nitrogen bond, whereas phenylalanine shows little change in $\delta^{15}N$ values (+0.4 ± 0.5‰) because its dominant metabolic processes neither form nor cleave bonds related to the nitrogen atom (Chikaraishi et al. 2007, 2009, Ohkouchi et al. 2015). Thus, TLs can be estimated with an analytical error (1σ of accuracy) of 0.12 for aquatic organisms (Chikaraishi et al. 2009). Although the amino acid method is still in the development stage, it has been applied to food web studies spanning primary producers, invertebrates and fish (e.g. Chikaraishi et al. 2007, 2014, Loick et al. 2007, Hannides et al. 2009, Olson et al. 2010).

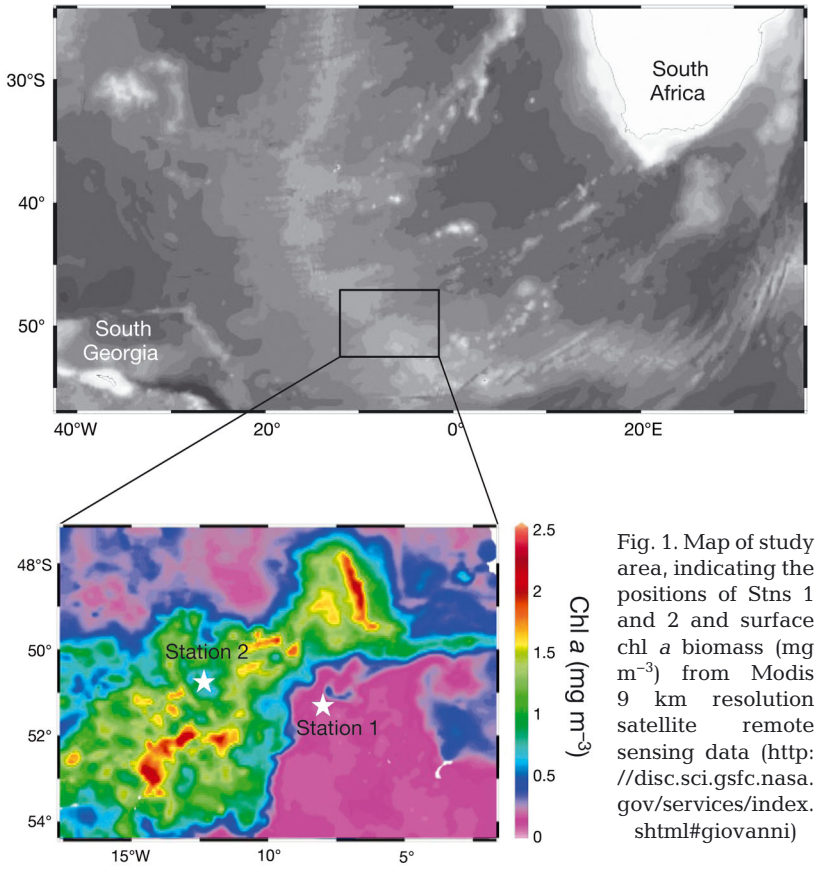

Fig. 1. Map of study area, indicating the positions of Stns 1 and 2 and surface chl *a* biomass (mg m^{-3}) from Modis 9 km resolution satellite remote sensing data (http://disc.sci.gsfc.nasa.gov/services/index.shtml#giovanni)

The goals of this study were (1) to analyze the diet of *T. gaudichaudii* near the Antarctic Polar Front during the austral summer, (2) estimate the trophic position of *S. thompsoni* and *T. gaudichaudii* in pelagic food webs, (3) assess potential trophic interactions between these species, and (4) to examine the trophic niche differences between the 2 forms of *T. gaudichaudii*, namely *bispinosa* and *compressa*.

MATERIAL AND METHODS

Sampling

Sampling was performed at 2 stations in the Atlantic sector of the Southern Ocean during a summer expedition of the RV 'Polarstern' (ANT XXVIII-3; Fig. 1). Stn 1 (2 samples) was located at 52.0°S 8.0°W and was completed on 26 January 2012. Stn 2 was situated at 51.2°S 12.7°W and was sampled between 31 January and 17 February 2012. Stn 2 was sampled 8 times (mostly for *Themisto gaudichaudii* dietary analyses) at regular intervals. While Stn 1 was characterized by low chlorophyll *a* (chl *a*) concentrations (<0.2 mg m^{-3}), high chl *a* concentrations were measured at Stn 2 (>1 mg m^{-3}) (Fig. 1). These patches persisted for several months, both before and after the cruise (unpubl. data). Zooplankton samples were collected from the upper 250 m of the water column with a Rectangular Midwater Trawl (RMT 1+8), equipped with 1 m^2 (0.33 mm mesh size) and 8 m^2 (4.5 mm mesh size) nets. Additional samples were collected using a Bongo net (60 cm mouth diameter, 0.3 mm mesh size) in the top 200 m water layer.

Individuals of *Salpa thompsoni* and *T. gaudichaudii* were taken from zooplankton samples. *S. thompsoni* was measured from the oral to the atrial opening (OAL) and *T. gaudichaudii* from the anterior part of the head to the end of the uropods. The 2 forms of *T. gaudichaudii*, *bispinosa* and *compressa*, were identified according to Vinogradov et al. (1996) and separated. Samples of both species were preserved in a 4% formaldehyde and seawater solution for gut content analysis, and either directly frozen at −20°C or oven-dried at 50°C, weighed, crushed and then stored for later bulk and compound-specific stable isotope analysis (CSIA).

Gut content analysis

Gut contents were examined in 6 (2 *compressa*, 4 *bispinosa*) and 87 (18 *compressa*, 69 *bispinosa*) *T. gaudichaudii* individuals in the low and high chl *a* regions, respectively. From individual tows, 6–20 *T. gaudichaudii* (both forms) were examined for stomach contents. After dissecting out the stomach, it was opened under the microscope and its overall fullness (%) was visually determined. In all stomachs, prey items were identified to the lowest possible level, counted and the volumetric contribution of the main prey items/groups to the total food bolus was assessed visually with a precision of ~10% (Burukovsky & Froerman 1974). The results of the stomach content analysis were expressed as frequency of occurrence (%) of main taxonomic groups in stomachs with food. The volumetric contribution was calculated only using stomachs with the overall fullness of ≥50% by summing all percentages of a prey item in stomachs divided by the number of stomachs with food (Burukovsky & Froerman 1974).

Bulk stable isotope analysis

For the analysis of bulk $\delta^{13}C$ and $\delta^{15}N$ values, 6 samples of *S. thompsoni* (3 from each station), and 7 of *T. gaudichaudii* (3 *bispinosa*, 4 *compressa*) were measured (only 1 *bispinosa* from the low chl *a* station). At the high chl *a* station, 2 individuals of *S. thompsoni* were pooled for 2 samples to obtain sufficient biomass for the measurements. Dried samples were weighed on a microbalance (APX-100, Denver Instruments) and then ground into a fine powder with a mortar and pestle. The $\delta^{13}C$ and $\delta^{15}N$ values of untreated subsamples were then measured (n = 1 per sample) using a modified Thermo Finnigan Flash EA (EA1112) coupled to a Thermo Finnigan Delta plus XP IRMS with a ConFlo III interface (Ogawa et al. 2010). The carbon and the nitrogen isotopic compositions are reported in the standard delta (δ) notation relative to the Vienna Peedee Belemnite standard (VPDB) and to atmospheric nitrogen (Air), respectively. The analytical precision, determined by replicate analyses of a standard (tyrosine; Tayasu et al. 2011), was 0.07‰ for $\delta^{13}C$ and 0.25‰ for $\delta^{15}N$. The $\delta^{13}C$ values of both species were lipid corrected ($\delta^{13}C_{cor}$) based on Smyntek et al. (2007), if the atomic C/N ratio (CN) was ≥5:

$$\delta^{13}C_{cor} = \delta^{13}C + 6.3\,[(CN - 4.2)/CN] \quad (1)$$

Therefore the C/N ratios by weight were converted to atomic C/N ratios.

The TL separation (TLS) between *S. thompsoni* and *T. gaudichaudii* was estimated assuming a 3.4‰ (±1.1‰) change in $\delta^{15}N$ per TL (Minagawa & Wada 1984). The propagation of error of TLS was calculated as follows:

$$1\sigma_{TLS} = [(\Delta\delta^{15}N/TDF) \times (1\sigma/\Delta^{15}N)^2 + (1\sigma_{TDF}/TDF)^2\,]^{1/2} \quad (2)$$

where the trophic discrimiation factor (TDF) = 3.4‰ and $1\sigma_{TDF}$ = 1.1‰. $\Delta\delta^{15}N$ describes the average difference between $\delta^{15}N$ of *S. thompsoni* and *T. gaudichaudii.*

Differences in $\delta^{13}C$ and $\delta^{15}N$ between species and regions were statistically analyzed by a Student's *t*-test using R.

Compound-specific stable nitrogen isotope analysis of amino acids

The same individuals that were used for the bulk isotope analyses were also analyzed for the nitrogen isotopic composition of individual amino acids. All subsamples were prepared for CSIA by HCl hydrolysis and *N*-pivaloyl/isopropyl ester (Pv/iPr) derivatization (Chikaraishi et al. 2007). In brief, each sample was hydrolyzed with 12 N HCl at 110°C for 12 to 24 h. The hydrolysate was washed with *n*-hexane/dichloromethane (3/2, v/v) to remove hydrophobic constituents (e.g. lipids). The Pv/iPr derivatives of amino acids were extracted with *n*-hexane/dichloromethane (3/2, v/v), following derivatization with thionyl chloride/2-propanol (1/4, v/v) at 110°C for 2 h and subsequently with pivaloyl chloride/dichloromethane (1/4, v/v) at 110°C for 2 h.

The $\delta^{15}N$ values of the individual amino acids were analyzed by gas chromatography/combustion/isotope ratio mass spectrometry (GC/C/IRMS) using an Agilent 6890N GC coupled to a Thermo Finnigan Delta plus XP IRMS with a GC Combustion Interface III. The amino acid derivatives from samples were injected in triplicate into the GC and separated on an Agilent HP Ultra-2 column (50 m, 0.32 mm i.d., 0.52 µm film thickness). The GC oven temperature was programmed as follows: initial temperature of 40°C for 3 min, ramp up at 15°C min^{-1} to 110°C, ramp up at 3°C min^{-1} to 150°C, ramp up at 6°C min^{-1} to 220°C, and dwell for 13.0 min. The carrier gas (He) flow through the GC column was 1.4 ml min^{-1}. The combustion was then performed at 950°C, the reduction at 550°C. The CO_2 generated in the combustion furnace was eliminated by a liquid nitrogen trap.

The nitrogen isotopic composition is expressed relative to atmospheric N_2 on scales normalized to the $\delta^{15}N$ values of standard amino acids (Chikaraishi et al. 2014). Standard mixtures of 10 amino acids with known $\delta^{15}N$ values were analyzed after every 3 to 5 samples during GC/C/IRMS analytical sessions for normalization purpose, and to confirm the reproducibility of the isotope measurements. Analytical precision of the standards was better than 0.5‰.

TLs were calculated for *S. thompsoni* and *T. gaudichaudii* based on the $\delta^{15}N$ values of glutamic acid ($\delta^{15}N_{Glu}$) and phenylalanine ($\delta^{15}N_{Phe}$). We used the equation for aquatic food webs by Chikaraishi et al. (2009):

$$TL_{Glu/Phe} = (\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4)/7.6 + 1 \quad (3)$$

The potential uncertainty (i.e. propagation of error) in the $TL_{Glu/Phe}$ value, which is calculated by taking into account the propagation of uncertainty on each factor in the following formula, was estimated according to Chikaraishi et al. (2014):

$$1\sigma_{TL} = [(y^2/7.6x) + (1\sigma_{TDF}/TDF)^2]^{1/2}, \quad (4)$$

where $x = \delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4$, $y = [2(1\sigma_m)^2 + (1\sigma_\beta)^2]^{1/2}$, $1\sigma_m$ = 0.5‰, $1\sigma_\beta$ = 0.9‰, and $1\sigma_{TDF}$ = 1.2‰, after Chikaraishi et al. (2009). TL differences between the 2 *Themisto* forms were statistically tested (Student's *t*-test).

RESULTS

Gut content

Total lengths of *Themisto gaudichaudii* individuals used for gut content analysis ranged between 18–35 mm and 17.5–25 mm for the *compressa* and *bispinosa* forms, respectively. In the low chl *a* region, 2 individuals had empty guts, 3 contained mostly digested 'jelly-like food' and one had digested chaetognath remains (Fig. 2A). In the high chl *a* region, 6 out of 18 (33%) studied individuals of the *bispinosa* form had empty stomachs, whilst only 11 of 69 (16%) studied specimens of the *compressa* form had empty stomachs. Despite differences in length (*bispinosa* and *compressa* forms were 20.8 ± 2.2 mm and 25.9 ± 4.0 mm long, respectively), diets of both forms were similar (Table 1). The combined diet composition mainly consisted of digested 'jelly-like food' (37.6% by volume) and salps (21.8%) (Fig. 2B). These food items were also the most frequent prey in the stomachs (Table 1). Salps in stomachs were mostly represented by recently released small aggregates. Usually, 3 to 6 salps were found in the single hyperiid

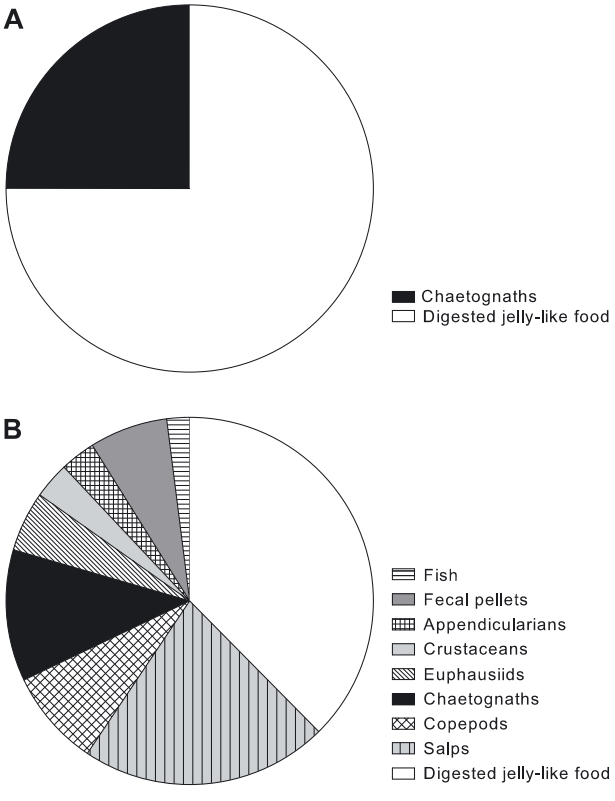

Fig. 2. Stomach content (by volume) of *Themisto gaudichaudii* in regions of (A) low chl *a* and (B) high chl *a* concentrations in the vicinity of the Antarctic Polar Front

Table 1. Diet of *Themisto gaudichaudii* in the region of low and high chl *a* concentrations in the vicinity of the Antarctic Polar Front. Due to the low number of specimens in the low chl *a* region, and only 4 specimens with food in stomachs, data for the 2 forms was combined. In the high chl *a* region *T. gaudichaudii* diets were represented by 12 and 58 stomachs for forma *bispinosa* and *compressa*, respectively. F = frequency of occurrence (% of all stomachs with food), V = mean percentage contribution to stomach volume

Region/form	Copepoda		Euphausiacea		Crustacea		Chaetognatha		Appendicularia		Salpidae		Jelly-like food		Fecal pellets		Fish	
	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)
Low chl *a*	–	–	–	–	–	–	25.0	25.0	–	–	–	–	75.0	75.0	–	–	–	–
High chl *a*																		
Forma *bispinosa*	16.7	5.8	–	–	–	–	25.0	19.2	8.3	4.2	33.3	25.0	41.7	37.5	8.3	8.3	–	–
Forma *compressa*	10.3	9.1	12.1	6.4	6.8	3.8	12.1	10.0	3.4	2.9	29.3	21.2	37.9	37.6	6.9	6.6	3.4	2.4
Both forms	11.4	8.5	10.0	5.3	5.7	3.2	14.3	11.6	4.3	3.1	30.0	21.8	40.4	37.6	7.8	6.9	2.9	2.0

Table 2. Body length (OAL = length from oral to atrial opening), dry weight (DW), atomic C/N ratio, bulk carbon (uncorrected [$\delta^{13}C$] and lipid corrected [$\delta^{13}C_{cor}$]) and nitrogen isotopes ($\delta^{15}N$), as well as nitrogen isotopic composition of amino acids of *Salpa thompsoni* (6 samples) in the low and high chl *a* region (±1σ). TL = trophic level (±1σ, propagation of error); TL and propagation of error were calculated using Eqs. (3) & (4), respectively, in the 'Materials and methods'. Analytical precision of the standards was 0.25‰ and 0.5‰ for bulk and compound-specific analyses of $\delta^{15}N$, respectively

	Low chl *a*			High chl *a*		
OAL (mm)	33	30	33	20, 20	24, 17	36
DW (mg)	64.0	49.3	76.5	35.3	27.7	48.2
C/N	5.4	5.6	5.4	4.8	4.8	4.6
Bulk $\delta^{13}C$ (‰)	−26.3	−27.9	−26.4	−22.4	−22.3	−22.5
Bulk $\delta^{13}C_{cor}$ (‰)	−24.9	−26.3	−24.9	−22.4	−22.3	−22.5
$\delta^{15}N$ (‰, relative to Air)						
Bulk	0.6	0.1	0.6	1.4	1.8	3.3
Alanine	10.0 ± 0.7	10.4 ± 0.2	14.0 ±0.1	11.4 ± 0.1	8.5 ± 0.2	9.4 ± 0.4
Glycine	−1.6 ± 0.2	1.3 ± 0.4	−0.7 ± 0.3	1.7 ± 0.8	−4.0 ± 0.2	1.3 ± 0.3
Valine	8.8 ± 0.4	11.0 ± 0.2	9.6 ±0.1	8.1 ± 0.4	5.1 ± 0.3	11.6 ± 0.4
Leucine	0.9 ± 0.3	4.5 ± 0.2	3.1 ± 0.3	2.2 ± 0.4	−0.7	3.7 ± 0.4
Isoleucine	3.5 ± 0.4	8.2 ± 0.3	4.0 ± 0.1	3.7 ± 0.1	1.0	6.2 ± 0.1
Glutamic acid	12.0 ± 0.1	11.1 ± 0.4	11.3 ± 0.2	11.1 ± 0.4	10.2 ± 0.4	9.8 ± 0.4
Phenylalanine	0.9 ± 0.3	0.3 ± 0.2	0.6 ± 0.1	0.7 ± 0.8	−0.6 ± 0.2	−1.0 ± 0.4
$TL_{Glu/Phe}$	2.0 ± 0.21	2.0 ± 0.22	2.0 ± 0.22	1.9 ± 0.22	2.0 ± 0.22	2.0 ± 0.22

stomach. However, in one instance a large *compressa* form (33 mm) was recorded with up to 20 small aggregates. It was not possible to identify the digested 'jelly-like food' but under careful scrutiny it did not contain any hard remains, e.g. hooks of chaetognaths, pieces of pteropod shells, setae or chitin pieces of crustaceans. Salps were followed by chaetognaths that accounted on average for ~12% of the stomach volume (Fig. 2B) and were usually represented by a single specimen. Crustaceans overall contributed ~17% of the mean stomach volume (Table 1). Of these, copepods, identified as *Metridia gerlachei* and *Rhincalanus gigas* copepodites (up to 3 copepods per stomach) constituted 8.5%, followed by 5.3% euphausiid remains (mostly the eyes and legs of *Thysanoessa* spp.) (Fig. 2B). Appendicularians and fish larvae were only occasionally found in stomachs and contributed 3.1 and 2.0% to stomach volume, respectively (Fig. 2B). It is noteworthy that several stomachs were filled with an amorphic mass usually of brownish or greenish coloration resembling large fecal pellets, possibly of *Salpa thompsoni* adults. Classified as fecal pellets, they accounted on average for 6.9% of the stomach volume (Fig. 2B).

$\delta^{13}C$ and $\delta^{15}N$ values of bulk tissues

Individuals of *S. thompsoni* used for stable isotope analyses measured between 17 and 36 mm in OAL (Table 2), while *T. gaudichaudii* total length ranged between 18 and 26 mm (Table 3).

The average lipid corrected $\delta^{13}C$ values of *S. thompsoni* were −25.4 ± 0.8‰ in the low chl *a* area and −22.4 ± 0.1‰ in the high chl *a* area (*t*-test; $p < 0.01$) (Table 2, Fig. 3). The bulk $\delta^{15}N$ values were also significantly lower at the low chl *a* (0.4 ± 0.3‰) compared to the high chl *a* area (2.2 ± 1.0‰) ($p < 0.05$).

The bulk stable isotope values of *T. gaudichaudii* were more enriched than those of *S. thompsoni* (Table 3, Fig. 3). The $\delta^{13}C$ values for *T. gaudichaudii* were −23.8 ± 0.9‰, and −21.5 ± 0.5‰ in the low and high chl *a* regions, and differed significantly between these regions ($p < 0.01$) (Table 3). Similarly, bulk $\delta^{15}N$ values of 5.4 ± 1.4‰ and 4.4 ± 0.7‰ were measured in the low and high chl *a* areas, respectively ($p > 0.05$). The average difference in $\delta^{15}N$ between *S. thompsoni* and *T. gaudichaudii* was 4.93 ± 1.45‰ ($p < 0.01$) in the low and 2.24 ± 1.21‰ ($p < 0.05$) in the high chl *a* areas (Fig. 3). Assuming a 3.4 ‰ change between TLs we can calculate a 1.45 ± 0.48 TLS between *S. thompsoni* and *T. gaudichaudii* in the low chl *a* area and a 0.66 ± 0.55 TLS in the high chl *a* area. Interestingly, *T. gaudichaudii* forma *bispinosa* had a more enriched average nitrogen signature than forma *compressa* in both the high and low chl *a* areas (Table 3, Fig. 3).

$\delta^{15}N$ values of individual amino acids

The $\delta^{15}N$ values of the amino acids ranged from −4.0 to 14.0‰ for *S. thompsoni* (Table 2), and from −6.5 to 23.6‰ for *T. gaudichaudii* (Table 3). An ob-

Table 3. Body length (L), dry weight (DW), atomic C/N ratio, bulk carbon (uncorrected [$\delta^{13}C$] and lipid corrected [$\delta^{13}C_{cor}$]) and nitrogen isotopes ($\delta^{15}N$), as well as nitrogen isotopic composition of amino acids of both forms of the amphipod species *Themisto gaudichaudii* (7 samples) in the low and high chl *a* region (±1σ). TL = Trophic level (±1σ, propagation of error); TL and propagation of error were calculated using Eqs. (3) & (4), respectively, in the 'Materials and methods'. Analytical precision of the standards was 0.25‰ and 0.5‰ for bulk and compound-specific analyses of $\delta^{15}N$, respectively

	Low chl *a*			High chl *a*			
Species form	*bispinosa*	*compressa*	*compressa*	*bispinosa*	*bispinosa*	*compressa*	*compressa*
L (mm)	25	26	25	25	18	22	18
DW (mg)	38.7	25.0	29.3	17.5	14.5	12.1	16.8
C/N	5.3	4.5	5.3	5.2	6.5	4.9	5.3
Bulk $\delta^{13}C$ (‰)	−24.9	−22.9	−26.1	−22.2	−23.6	−22.3	−22.8
Bulk $\delta^{13}C_{cor}$ (‰)	−23.6	−22.9	−24.7	−21.0	−21.4	−22.3	−21.5
$\delta^{15}N$ (‰, relative to Air)							
Bulk	6.5	5.9	3.8	5.1	4.3	3.5	4.7
Alanine	22.3 ± 0.5	23.6 ± 0.6	20.0 ± 0.5	19.1 ± 0.5	20.2 ± 0.1	20.7 ± 0.1	22.0 ± 0.2
Glycine	−0.7 ± 0.9	−0.1 ± 0.0	2.3 ± 0.4	1.0 ± 0.4	2.0 ± 0.6	−6.5 ± 0.5	2.0 ± 0.4
Valine	17.4 ± 0.1	19.8 ± 0.1	13.1 ± 0.2	18.4 ± 0.3	14.8 ± 0.3	17.9 ± 0.2	17.1 ± 0.3
Leucine	10.6 ± 0.5	12.8 ± 0.6	12.1 ± 0.5	14.3 ± 0.2	8.4 ± 0.5	12.3 ± 0.2	13.1 ± 0.2
Isoleucine	13.4 ± 0.4	14.7 ± 0.2	10.2 ± 0.4	15.7 ± 0.2	10.6 ± 0.3	13.1 ± 0.1	11.4 ± 0.1
Glutamic acid	21.8 ± 0.2	18.4 ± 0.4	19.4 ± 0.2	22.3 ± 0.5	21.9 ± 0.3	19.9 ± 0.3	18.7 ± 0.1
Phenylalanine	1.4 ± 0.4	1.0 ± 0.3	2.0 ± 0.4	0.6 ± 0.4	0.6 ± 0.1	2.3 ± 0.3	1.3 ± 0.2
$TL_{Glu/Phe}$	3.2 ± 0.18	2.8 ± 0.19	2.8 ± 0.19	3.4 ± 0.18	3.3 ± 0.18	2.9 ± 0.19	2.8 ± 0.19

vious difference in the values between the areas of different chl *a* concentrations could not be observed within the 2 species. Generally, alanine, valine, leucine, isoleucine and glutamic acid were enriched in $\delta^{15}N$ relative to the bulk material, whereas glycine and phenylalanine tended to be depleted (Tables 2 & 3). Compared to *S. thompsoni*, *T. gaudichaudii* was generally enriched in alanine (10.5 and 10.8‰ in low and high chl *a* area, respectively),

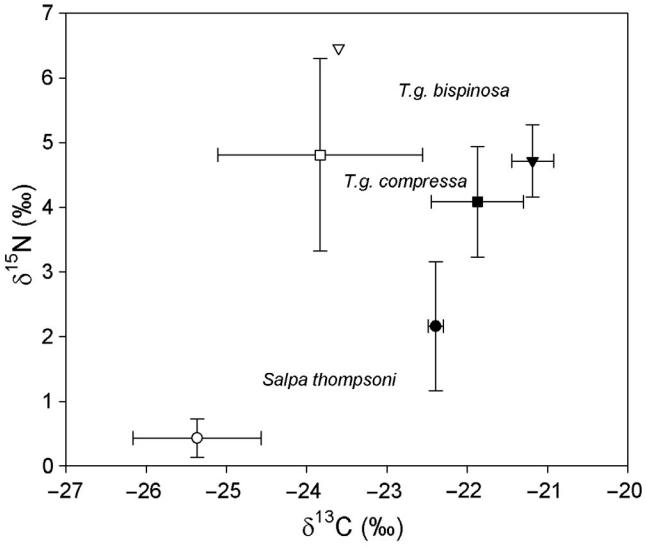

Fig. 3. Bulk carbon (lipid corrected) and nitrogen isotopes (‰, ±1σ) of *Salpa thompsoni* (●,○), *Themisto gaudichaudii* (*bispinosa*: ▼,▽; *compressa*: ■,□) in the high (filled symbols) and low (open symbols) chl *a* regions

valine (7.0 and 8.8‰), leucine (8.9 and 9.6‰), isoleucine (7.3 and 8.3‰) and glutamic acid (8.4 and 10.3‰, Fig. 4). The values of glycine and phenylalanine were only slightly higher in *T. gaudichaudii* than in S. thompsoni (low chl a: 0.9‰ both amino acids; high chl a: 0.0 and 1.5‰, respectively). The $\delta^{15}N$ of phenylalanine showed some variation, but overlapped between the high and the low chl *a* region (Fig. 5). TL estimation based on the $\delta^{15}N$ values for glutamic acid and phenylalanine positioned *T. gaudichaudii* at TL 3 and *S. thompsoni* at TL 2 (Tables 2 & 3; Fig. 6). As in the bulk isotope analysis, *T. gaudichaudii bispinosa* had a slightly higher TL (~3.3) than *T. gaudichaudii compressa* (~2.8) (*t*-test; $p < 0.001$), as shown by higher $\delta^{15}N$ values in glutamic acid (Table 3, Figs. 5 & 6).

DISCUSSION

Source at the base of the food web

The $\delta^{15}N$ values of the amino acid phenylalanine, a measure of the food web baseline, for the combined samples of *Salpa thompsoni* and *Themisto gaudichaudii* ranged from 0.3 to 2.0‰ and −1.0 to 2.3‰ in the low and high chl *a* regions, respectively. This indicated that the nitrogen source at the base of the food web was similar for both species, and between regions. The nitrogen isotopic composition of phenylalanine has been shown to vary substantially be-

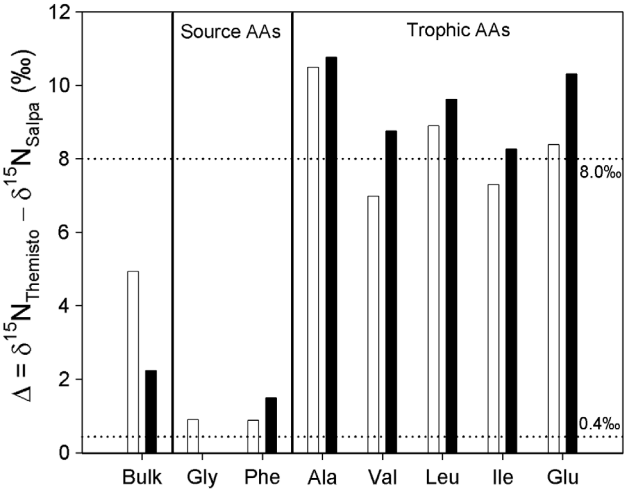

Fig. 4. Average ^{15}N-enrichment factors (Δ) between *Themisto gaudichaudii* (consumer) and *Salpa thompsoni* (food source) in regions of low (□) and high (■) chl *a* concentrations. Source AAs = amino acids shown not to change between trophic levels, trophic AAs = amino acids shown to change between trophic levels. Lines demarcating 8‰ and 0.4‰ indicate the enrichment factors per trophic level for glutamic acid and phenylalanine, respectively, in an aquatic food web, according to Chikaraishi et al. (2009)

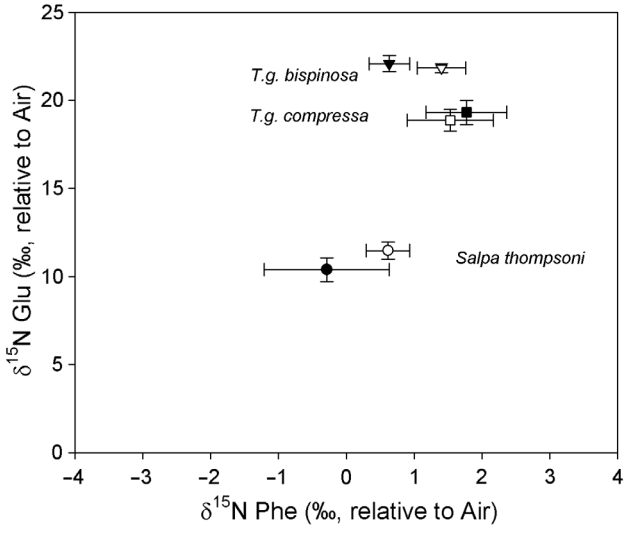

Fig. 5. Nitrogen isotopic composition (‰ ± 1σ) of phenylalanine (Phe) and glutamic acid (Glu) in *Salpa thompsoni* (●, ○) and *Themisto gaudichaudii* (*bispinosa*: ▼, ▽; *compressa*: ■, □) in the high (filled symbols) and low chl *a* regions (open symbols)

tween regions (Choy et al. 2012), between primary producers (Chikaraishi et al. 2009), and between seasons (Hannides et al. 2009). The relatively small difference in the δ^{15}N of phenylalanine in this study indicated that the 2 zooplankton species considered relied on a similar nitrogen source in both regions, and that this had been consistent for at least several weeks. Bulk carbon isotopes have also been used as indicators of carbon sources used in a food web. Unlike nitrogen isotopes, bulk δ^{13}C values differed between high and low chl *a* regions for both species and were generally enriched by ~2.7‰ in high chl *a* regions (Figs. 3 and 6). Bulk δ^{13}C values in any specific area may be strongly influenced by phytoplankton growth rates and the availability of aqueous CO_2, which in turn is largely determined by seawater temperature (Francois et al. 1993, Trueman & Moore 2007). Both of these factors may have come into play in determining zooplankton δ^{13}C in this study. Higher phytoplankton growth rates and surface

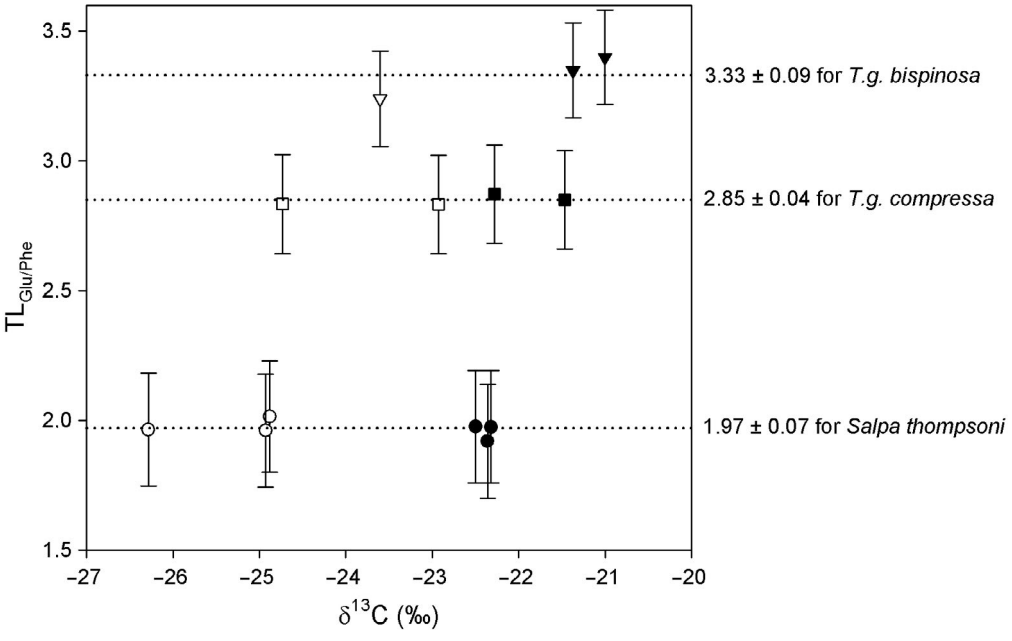

Fig. 6. Lipid corrected bulk carbon (‰) and average trophic levels ($TL_{Glu/Phe}$, ±1σ, propagation of error) of *Salpa thompsoni* (●, ○) and *Themisto gaudichaudii* forms: *bispinosa* (▼, ▽), and *compressa* (■, □) in the high (filled symbols) and low chl *a* regions (open symbols). Dotted lines indicate the average trophic level for each species (±1σ)

water temperatures elevated by ~2°C in the high compared to low chl *a* area most likely led to the enrichment of phytoplankton $\delta^{13}C$ values in the high chl *a* area. The difference in $\delta^{13}C$ values between areas was consistent in both species, demonstrating that regional biochemical differences were propagated through the food web.

Trophic interactions and the role of the 2 *Themisto* forms

The diets of the *T. gaudichaudii* differed substantially between the 2 sites, being completely dominated by chaetognaths and 'digested jelly-like food' in the low chl *a* area and being far more varied, including ~17% crustacean prey by volume, in the high chl *a* area. However, the high chl *a* area was also characterized by a large contribution of gelatinous prey, including 'digested jelly-like food'. Almost complete dominance of the zooplankton community by salps in the low chl *a* area suggested that in all likelihood digested jelly-like food at this station comprised salps (Pakhomov & Hunt 2013). In the case of the high chl *a* area, salps were clearly identified as contributing ~22% to gut content volume, with an additional 37.6% from 'digested jelly-like food'. It is likely that at least a portion of the latter category comprised salps, though other gelatinous groups cannot be excluded based on the gut content analysis alone. Hopkins (1985) has already documented that *T. gaudichaudii* may consume salps. However, other mesozooplankton prey, including copepods, euphausiids, pteropods and chaetognaths, have typically been found to dominate in *T. gaudichaudii* diets (Hopkins 1985, Pakhomov & Perissinotto 1996). Our study found that *Themisto* was targeting small aggregates recently released by solitary forms of *Salpa thompsoni*. In addition, larger (> 25 mm long) specimens of *Themisto* likely were able to consume larger 'jelly-like' organisms (including salps) by biting pieces of them.

The results of the CSIA agreed well with previous studies that have shown *S. thompsoni* to be a primary consumer which feeds directly on diatoms and flagellates (e.g. von Harbou et al. 2011). The estimated trophic positions based on the $\delta^{15}N$ values of glutamic acid and phenylalanine placed *S. thompsoni* at TL 2 (1.97 ± 0.07). *T. gaudichaudi* was approx. 1 TL higher than *S. thompsoni* in both regions, indicating that this species preys primarily on primary consumers. These data therefore support the results of the gut content analysis, which showed salp predation by *T. gaudichaudii* and the contention that the 'digested jelly-like food' was mostly comprised of salps. If there was a high incidence of other gelatinous groups such as carnivorous medusa and siphonophores, a higher TL would be expected. The $\delta^{15}N$ values of amino acids therefore identified a similar trophic structure between the 2 areas sampled (Fig. 6) despite the regional difference in temperature and phytoplankton productivity.

The bulk isotope data TL estimates differed somewhat from the compound-specific estimates. The TL of ~3.4 (TLS of 1.45 ± 0.48) estimated for the low chl *a* area (assuming *S. thompsoni* to be at TL 2) indicated a higher contribution of secondary consumers to the *T. gaudichaudii* diet. Indeed, there was evidence of this in the presence of chaetognaths in their guts. In the high chl *a* region, a TL of ~2.7 (TLS of 0.66 ± 0.55) indicated a higher contribution of primary producers to the *T. gaudichaudii* diet. This may have come through direct grazing or alternatively through consumption of *S. thompsoni* food bolus (and/or fecal pellets) which can have high phytoplankton content. Although the propagation of error for the TLS is relatively high, the slightly different results between the bulk and compound-specific analyses are noteworthy. They highlight the need for closer scrutiny of the latter technique in particular, focusing on changes in amino acid $\delta^{15}N$ between TLs (Steffan et al. 2013, Bradley et al. 2014). Nonetheless, as they stand, both isotope methods lend support to the gut content analysis and significant predation by *T. gaudichaudii* on *S. thompsoni*. The regional differences in bulk isotope values and corresponding estimated TLs point to regional differences in food web structure as the primary cause of differences in TL reported in the literature for this species (Cherel et al. 2008, Richoux & Froneman 2009, Stowasser et al. 2012).

The stable isotope results in this study indicate a difference between the 2 *Themisto* forms, with *T. gaudichaudii bispinosa* appearing to feed at a slightly higher TL than *T. gaudichaudii compressa* (TL = 3.33 ± 0.09 vs. TL = 2.85 ± 0.04 according to CSIA) of a similar size. Given the small sample size this is not conclusive and indeed the stomach content data show a high degree of similarity in diet between the 2 forms. However, the morphological differences between them indicate this is something that should be investigated further in the future. In forma *bispinosa*, the fifth pereopod (P5) is twice as long as the sixth pereopod (P6), and in forma c*ompressa* both P5 and P6 are almost equal in length and substantially shorter than P5 in forma *bispinosa*. The main function of these pereopods (especially P3-P7) is to

capture and restrain the prey (Kane 1963, Nemoto & Yoo 1970). Hence, it is possible that forma *compressa* may consume smaller and possibly lower trophic position prey than forma *bispinosa* of comparable size (Sheader & Evans 1975).

Generally, both forms of *T. gaudichaudii* can be found over a wide geographic range in the Southern Ocean. However, Kane (1966) reported low percentages of *bispinosa* at low latitudes (9% at 33–37°S), but increasing numbers moving southwards, with a contribution of 75% to the *T. gaudichaudii* population at higher latitudes (68–72°S). This distribution pattern, combined with the findings in this study of forma *bispinosa* having a higher TL than forma *compressa*, may explain the change in TL with latitude previously observed for this species across the Sub-Tropical Front (STF, Richoux & Froneman 2009). Richoux & Froneman (2009) estimated the TL of *T. gaudichaudii* at 2.2 ± 0.1 to the north of the STF and 2.9 ± 0.1 to the south. Experiments have shown that development into either *bispinosa* or *compressa* is dependent on the length of the intermoult period, which in turn is probably mostly influenced by temperature, but also by sex, and nutrition level (Sheader 1975). *T. gaudichaudii* moults into a *compressa* form when temperatures are high (>7°C) and/or food conditions are good, and into a *bispinosa* form if temperatures (<6°C) or food concentrations are low (Sheader 1975). Because zooplankton tends to be larger in colder waters, the temperature-related changes in feeding appendage morphology may be an adaptation to larger prey species (Sheader 1975). The wide array of diets previously noted for *T. gaudichaudii* may in part be related to the differences in feeding morphology outlined above, but the overriding factor is most likely an opportunistic and highly flexible feeding behavior. As a consequence it is not surprising that a broad range of TLs is covered by this amphipod.

In view of the overlapping centers of distributions of *S. thompsoni* and *T. gaudichaudii*, it is possible that trophic interactions between these 2 species may reflect an evolutionary prey–predator relationship, with *T. gaudichaudii* feeding morphology being an adaptation to preying on *S. thompsoni*. Such a contention however requires detailed analysis of *T. gaudichaudii* population dynamics and/or genetics. Whatever the case, it is apparent from this study that when *S. thompsoni* is highly abundant, *T. gaudichaudii* may be a significant predator of this species. Previous studies have suggested that the southward shift of *S. thompsoni* during the last half century (Pakhomov et al. 2002, Atkinson et al. 2004) has been due to a reduction of the stock and the productivity of Antarctic krill (Pakhomov et al. 2002, Atkinson et al. 2008) or a decrease in ice cover and overall water warming (Atkinson et al. 2004). The findings of this study suggest that a southward extension in the distribution of *S. thompsoni* may in fact be augmented by release from predation by *T. gaudichaudii*, which remains primarily distributed at the Polar Front (Kane 1966).

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