FEATURE ARTICLE

Trophic structure of southern marine ecosystems: a comparative isotopic analysis from the Beagle Channel to the oceanic Burdwood Bank area under a wasp-waist assumption

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ABSTRACT: Understanding the structure and functioning of marine ecosystems has become a critical issue to assess the potential short- and long-term effects of natural and anthropogenic impacts and to determine the knowledge needed to conduct appropriate conservation actions. This goal can be achieved in part by acquiring more detailed food web information and evaluating the processes that shape food web structure and dynamics. Our main objective was to identify large-scale patterns in the organization of pelagic food webs that can be linked to a wasp-waist (WW) structure, proposed for the southwestern South Atlantic Ocean. We evaluated 3 sub-Antarctic marine areas in a regional context: the Beagle Channel (BC), the Atlantic coast of Tierra del Fuego (CA) and the oceanic Burdwood Bank area (BB). We used carbon and nitrogen isotopic information of all functional trophic groups, ranging from primary producers to top predators, and analyzed them through stable isotope-based Bayesian analyses. We found that BC and BB have a more pronounced WW structure compared to CA. We identified species at mid to low trophic positions that play a key role in the trophodynamics of each marine area (e.g. Fuegian sprat *Sprattus fuegensis*, longtail southern cod *Patagonotothen ramsayi* and squat lobster *Munida gregaria*) and considered them as the most plausible WW species. The identification of the most influential species within food webs has become a crucial task for conservation purposes in local and regional contexts to maintain ecosystem integrity and the supply of ecosystem services for the southwestern South Atlantic Ocean.
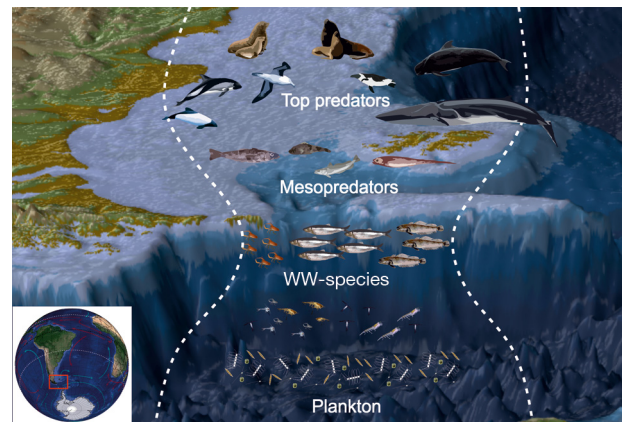
The Southwestern Atlantic Ocean has a large number of species linked by an intermediate trophic level with a few biological components of ecological importance.

Image: Luciana Riccialdelli

1. INTRODUCTION

Marine ecosystems are being profoundly transformed by humans affecting the integrity and stability of subpolar and polar ecosystems with long-lasting consequences (Hoegh-Guldberg & Bruno 2010,

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Widdicombe & Somerfield 2012, Constable et al. 2014). Anthropogenic and climate-induced impacts are known to affect individual species (e.g. by modifying their distributions and abundances), but they can also change the connections that each species has with its prey and predators (e.g. species trophic interactions; Constable et al. 2014, Lynam et al. 2017).

Food-web organization can be described by these trophic interactions and the energy flows between species in a community, and thus is considered an excellent tool to represent ecosystem complexity (Thompson et al. 2012, Young et al. 2015). The propagation of any impact throughout the food web would depend, though only in part, on the type of processes that shape its structure and dynamics (Young et al. 2015), since the dynamic process of trophic interactions, or trophodynamics, is not the only source of ecosystem regulation and structuring (Hunt & McKinnell 2006). Therefore, the propagation of such impacts will show differences if the food web is controlled by predators (i.e. top-down control), by resources (i.e. bottom-up control) or by dominant mid-trophic level species (i.e. wasp-waist control) (Cury et al. 2003, Lynam et al. 2017).

Generally, oceanic food webs are thought to be constrained by resource availability, or bottom-up control, whereby the productivity and abundance of populations at any trophic level positively correlate with and are limited by food supply (e.g. controlled by the productivity and abundance or biomass of populations at lower trophic levels) (Cury et al. 2003, Madigan et al. 2012). However, due to their size, mobility and energetic requirements, top predators, such as marine mammals, also have important effects on the ecosystems where they live and feed, by regulating populations of their prey (e.g. Reisinger et al. 2011). The abundance or biomass of lower trophic levels therefore also depends on effects from consumers above them (top-down control, Cury et al. 2003).

In upwelling regions and many other productive marine areas, so-called 'wasp-waist' (WW) control has been proposed as an alternative model. These systems are regulated primarily by small pelagic forage fish (e.g. sardines) or other low to mid-trophic level pelagic species (e.g. crustaceans) or 'WW species'. A low diversity, but high abundance, of these species could exert top-down control of lower levels (e.g. primary producers) and bottom-up control of meso- and top-predators (e.g. seabirds and marine mammals), thereby regulating the energy transfer between these trophic levels (Cury et al. 2000, Bakun 2006). Food webs with a WW structure are considered to be more vulnerable to collapse, if the abundances of WW species decline for any reason (e.g. climate change, fisheries), because of the critical energetic links they have with the rest of the food web (Cury et al. 2003). Despite the importance of the WW level with respect to energy transfer to the upper trophic levels, recent isotope studies have suggested that WW systems could be more complex than previously assumed, offering predators alternative food supply pathways (e.g. Madigan et al. 2012, Cardona et al. 2015). Undoubtedly, trophic structure and dynamics of food webs are more complex than we thought, and multiple types of control can be operating at different spatial and temporal scales with complex interactions under the effect of different stressors (Hunt & McKinnell 2006, Reisinger et al. 2011, Lynam et al. 2017).

The southwestern South Atlantic Ocean, a marine ecosystem influenced by the Malvinas Current, has been proposed to be under WW control (e.g. Padovani et al. 2012, Arkhipkin & Laptikhovsky 2013, Saporiti et al. 2015). As in other WW systems, this region has a particular community structure, with a diverse pool of species at the lowest and at the highest trophic levels. This large number of species is linked by an intermediate trophic level with only a few biological components of ecological importance, which play a key role in the structure and functioning of this large marine ecosystem. Crustaceans (i.e. the amphipod *Themisto gaudichaudii* and the squat lobster *Munida gregaria*) and fish (i.e. Fuegian sprat *Sprattus fuegensis* and longtail southern cod *Patagonotothen ramsayi*) have been proposed as WW species in previous studies (e.g. Padovani et al. 2012, Arkhipkin & Laptikhovsky 2013, Diez et al. 2018). These species fulfill several criteria to be considered WW species, including: (1) they are species with high regional abundances (Madirolas et al. 2000, Padovani et al. 2012, Arkhipkin & Laptikhovsky 2013), (2) they seem to occupy low to mid-trophic positions (TPs) in food webs (Ciancio et al. 2008, Riccialdelli et al. 2010), (3) many predators feed on them (Raya Rey et al. 2007, Riccialdelli et al. 2010, 2013, Scioscia et al. 2014), and (4) the population dynamics of these species appear to depend on the environment (e.g. climatic variations) (Diez et al. 2016, 2018). There is a need for better identification of WW species as an essential functional trophic group to improve food-web models, but particularly for conservation purposes. In addition, the southern sector of this ecosystem has been subject of the establishment of Argentina's first oceanic marine protected area (MPA), the Namuncurá–Burdwood Bank (MPAN-

BB), created by national law no. 26 875 in 2013, and more recently the Namuncurá–Burdwood Bank II (MPAN-BBII) and Yaganes, created by national law no. 27 490 in 2018. These MPAs have been created because the areas were considered as hotspots[1] (Falabella 2017), based on conservation priorities (e.g. seabed biodiversity) and because they individually or in networks contribute to protect and strengthen the functioning of this southern region to maintain global ocean health. To assess the potential short- and long-term effects of environmental and anthropogenic impacts and conduct appropriate conservation actions in those marine areas, it is critical to understand their structure and functioning.

This goal can be achieved by acquiring more detailed food-web information (Young et al. 2015). Stable isotope analyses (e.g. carbon, $\delta^{13}C$; and nitrogen, $\delta^{15}N$) have the potential to distinguish the origins of organic matter in a community and track them across consumers (Wada et al. 1991). Therefore, by providing information on energy flow and trophic relationships, isotopic studies allow the construction of general food-web models (e.g. Abrantes et al. 2014, Riccialdelli et al. 2017a). Moreover, since baseline $\delta^{13}C$ and $\delta^{15}N$ values (e.g. phytoplankton and zooplankton) can change between and within ocean basins, isotopic differences between consumers have also been linked to foraging habitats in space and time (e.g. Graham et al. 2010). By providing information about different aspects of species' trophic niches, for example through the use of Bayesian mixing models (Parnell et al. 2010, Jackson et al. 2011), it is possible to identify food-web connections and explore the trophic diversity or specialization and possible niche partitioning between species within a community. Moreover, community-wide trophic metrics, as proposed by Layman et al. (2007) and developed under a Bayesian approach by Jackson et al. (2011), help evaluate food-web interactions and provide insight into the vertical and basal trophic structure and the overall trophic diversity of the communities (e.g. Abrantes et al. 2014, Demopoulos et al. 2017). The application of this approach allows com-

parisons across marine areas for overall patterns in food-web structure (Saporiti et al. 2015) and to study the effects of different impacts on such community metrics (e.g. Layman et al. 2007).

Our goal was to compare the main components of the pelagic food web of 3 sub-Antarctic marine areas in the southwestern South Atlantic Ocean: the Beagle Channel (BC), the Atlantic coast of Tierra del Fuego (CA, based on 'Costa Atlántica') and the oceanic Burdwood Bank (BB) area. We focused specifically on the BB, as it is a little-known oceanic area recently declared an MPA (MPAN-BB and MPAN-BBII). Therefore, the study of this area is relevant in the context of its management policies. We hypothesized that the BB has the same trophic structure (WW) proposed for its adjacent marine areas. In this regard, we proposed: (1) to identify differences and similarities between areas and check if there is a pattern that could corroborate our hypothesis of the presence of WW species in a regional context, and (2) to identify these WW species within each marine area.

Based on the hypothesis that a WW structure would dominate regionally, we expected: (1) a short vertical structure. In WW systems, the species that occupy the mid- to low TPs are a major food supply for predators, thus a short food web is expected (Cury et al. 2000); (2) a low trophic diversity and a high trophic redundancy for those marine areas with a more pronounced WW structure. This means a high interspecific overlap in trophic niches, which is an expected outcome in WW systems since a large proportion of species would show similar trophic habits (e.g. feeding on the same prey); (3) the presence of few WW species for each marine area with similar but not identical trophic niches. WW species usually differ in several aspects of their ecological niche (e.g. TP and general habits); thus, their influence on the trophic web is expected to be different (Bakun 2006).

2. MATERIALS AND METHODS

2.1. Study site

The study site covers the sub-Antarctic zone at the southwestern portion of the South Atlantic Ocean, next to the Tierra del Fuego Archipelago, from ~52° to 56° S and from ~57° to 69° W (Fig. 1). We compared 3 different marine areas: (1) the BC, including the marine zone at the southeastern tip of Tierra del Fuego; (2) the CA, including the northern part of Staten Island; and (3) the BB, including the plateau and its adjacent slope break.

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[1]The term 'hotspot' in pelagic marine ecosystems is not restricted only to areas of high biodiversity and endemism; it has also been used for areas of low biodiversity, but with high abundances, or areas of high primary productivity and high energy transfers (Young et al. 2015). Here, we defined a hotspot by a combination of factors including the conservation priorities established by Argentine law, oceanographic features (e.g. seamounts, shelf break), highly dynamic (in space and time) oceanographic conditions and high biodiversity
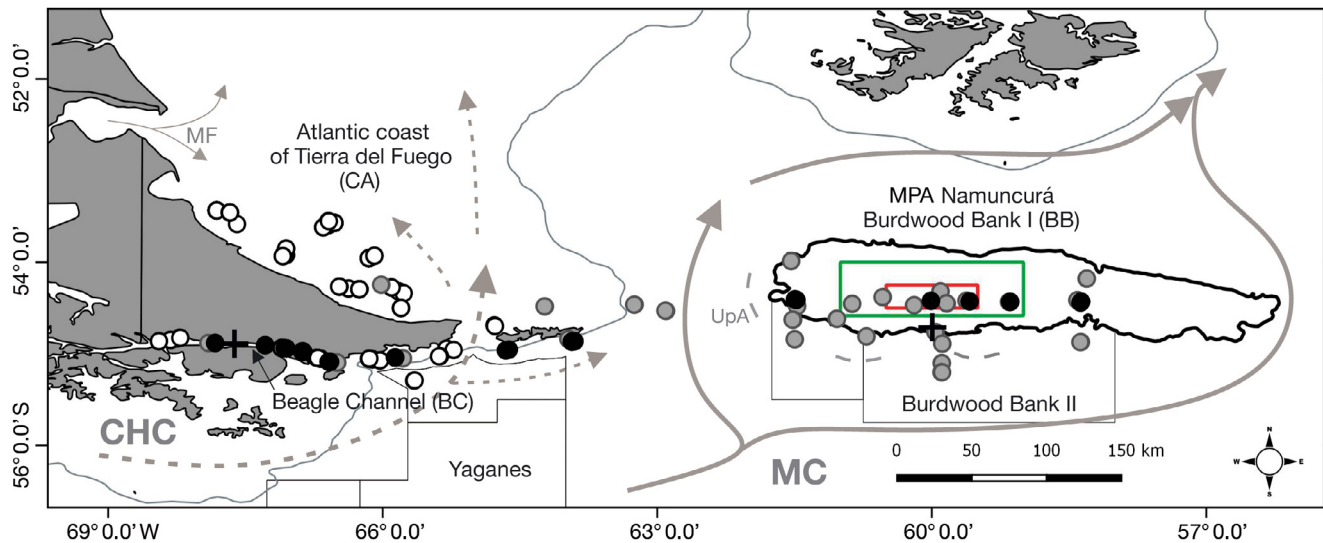
Fig. 1. Marine areas studied: Beagle Channel, Atlantic coast of Tierra del Fuego, and Burdwood Bank, including the Marine Protected Areas of Argentina Namuncurá – Burdwood Bank I (red line: core area, green line: buffer area, black line: transition area), Burdwood Bank II and Yaganes. Solid and dashed lines are used for illustrative purposes to distinguish the currents/fronts. Sampling stations are indicated, where open circles: BODPMar2014 survey, black circles: TANGOFeb2015 survey, gray circles: BOPDApr2016 survey, black cross: VA1418 survey. CHC: Cape Horn Current; MC: Malvinas Current; MF: Magellan Front, UpA: upwelling areas

The region is influenced by the Malvinas Current, which originates from the Antarctic Circumpolar Current, the Cape Horn Current that gets into the area around the southern tip of Tierra del Fuego, freshwater discharges from Tierra del Fuego, and the Strait of Magellan and its strong tidal currents (Piola & Rivas 1997). The CA area is affected by a seasonal but persistent front, the Magellan Front, related to the influx of freshwater (of low salinity <32) from the Pacific to the Atlantic via the Strait of Magellan and from the Cape Horn Current (with slightly saltier waters <33.9) (Acha et al. 2004, Belkin et al. 2009). BB is particularly affected by both branches of the Malvinas Current that flow around the bank, causing more oceanic and polar conditions where surface water temperatures range from ~5°C (autumn) to 6°C (spring), with salinities of ~34 (García Alonso et al. 2018). The BB is an undersea plateau found at 50–200 m depth and surrounded by deep channels (>1000 m depth). It is located about 150 km east of Staten Island and 200 km south of the Falkland/ Malvinas Islands. The BB is also the site where Argentina established the open-sea MPAN-BB (Falabella 2017) and the MPAN-BBII (at the present time, both MPAs are under a unification process).

Lastly, within this region, the BC is a particular marine environment that can be as much as 30 km wide at its eastern mouth and extends nearly 200 km to the west, connecting the Pacific and the Atlantic Oceans (Isla et al. 1999). Pushed by the preponderance of west and southwesterly winds, the diluted waters of the BC, originating from high precipitation and glacial melting, flow towards the Atlantic (Balestrini et al. 1998). Surface water temperatures range from ~4°C in winter to ~9°C in summer, and salinity ranges from 27 to 31 from the inner part of the BC to the eastern mouth (Balestrini et al. 1998). The third MPA, Yaganes, is located at the southeast section of the BC and south of Staten Island from the 500 m isobaths towards the polar front.

2.2. Sample collection and processing

We conducted most of the biological sampling (organic matter in sediments, primary producers and consumers) during 3 research cruises at the end of the austral summer and autumn (February–April) in 2014, 2015 and 2016, onboard the RV 'Puerto Deseado' (cruises BOPDMar2014 and BOPDApr2016), a vessel belonging to the Argentine National Scientific and Technical Research Council (CONICET); the 'SB-15 Tango' (TANGOFeb2015), a vessel belonging to the Argentine Coastguard (Prefectura Naval); and onboard small vessels (i.e. zodiacs) belonging to the Austral Center for Scientific Research (CADIC-CONICET). We increased samples for specific and important species (e.g. *Sprattus fuegensis*) that could be collected onboard the RV 'Victor Angelescu', a vessel belonging to the Argentine National Institute for

Fisheries Research (INIDEP), during an oceanographic research cruise in November 2018 (VA1418).

We sampled marine mammals through stranded animals found on beach surveys along the northeastern and southern coast of Tierra del Fuego (L. Riccialdelli on-going long-term studies under the Investigaciones en Mamíferos Marinos Australes [IMMA] Project), and seabirds were sampled in their breeding colonies from the BC (Martillo and Bridges Islands) and Staten Island (A. Raya Rey on-going long-term studies). To complement our fieldwork, we also used isotopic data of specific species and also from basal sources (e.g. sediment particulate organic matter [SPOM], benthic baselines) that were previously published (e.g. Saporiti et al. 2014, Riccialdelli et al. 2017a, Bas et al. 2019, 2020) or unpublished data available for the region.

2.2.1. Primary producers

We collected phytoplankton samples at 37 sampling stations distributed in the 3 marine areas with a 25 μm net during vertical trawling from 20 m depth. We pre-filtered each sample onboard with a 115 μm mesh (to remove organisms >115 μm) and then filtered samples onto pre-combusted (450°C for 4 h) GF/F type fiber filters of 0.7 μm nominal pore size. Filters with phytoplankton were kept frozen (−20°C) until drying at 60°C for 48 h. We collected macroalgae at 25 sampling stations in BC and 7 in CA by hand during coastal surveys and onboard small boats (zodiacs) from CADIC-CONICET. We cleaned the fronds of macroalgae by rinsing them with distilled (DI) water and cleaned them of epibionts and debris.

2.2.2. Consumers

We collected zooplankton at 40 sampling stations with a 200 μm net during 5 min of oblique trawling from 100 m depth to the surface water, and kept frozen (−20°C) onboard until processing. In the laboratory, we separated zooplankton samples into taxonomical groups (e.g. euphausiids, copepods, amphipods), using a Leica stereoscope. We collected invertebrates (e.g. crustaceans, mollusks) and fish species at 19 sampling stations (BC = 5, CA = 6 and BB = 8) during 10 min of bottom trawling. We only sampled muscle from these organisms, but when the individual was too small, we pooled the entire organism (e.g. zooplankton groups, small crustaceans).

2.2.3. Predators

Among the pool of samples that we had available for top predators, and based on previous knowledge from the literature and our personal observations, we chose only a few species that we considered representative of each marine area. We collected skin and muscle samples from only fresh and recently stranded (<24 h) marine mammals, since decomposition is not a significant source of isotope variation within that time (Payo-Payo et al. 2013). Samples were frozen (−20°C) until processing. To avoid the effects on $\delta^{13}C$ values associated with the presence of lipids, we performed a lipid extraction with a 2:1 chloroform:methanol solution. While this extraction does not significantly alter skin $\delta^{15}N$ values (Newsome et al. 2018), we also analyzed the same samples without treatment to assure unbiased $\delta^{15}N$ values. We collected and cleaned feathers and blood samples from seabirds following Raya Rey et al. (2012). All samples (macroalgae to top consumers) were lyophilized (48 h), ground and mixed (homogenized).

2.2.4. SPOM

We collected samples from surface sediments with dredges at 18 sampling stations during the BOP-DApr2016 survey cruise and kept them frozen (−20°C) onboard in plastic bags. The sediment contains organic and inorganic C in the form of carbonates. Since carbonates may be enriched in ^{13}C compared to organic C, it is necessary to remove the carbonates from the sediment to avoid their influence. Thus, we divided each sample in 2 and removed most of the carbonates in the first HCl fumigation, following Harris et al. (2001). During this treatment, we placed ~40 mg of dried sediment (previously oven-dried at 60°C for 48 h) in Eppendorf tubes and added DI water (~75 μl) to moisten the sediment. Later, we exposed these samples to HCl (12N) vapor for 12 h in a closed glass desiccator cabinet. After acid fumigation, we again dried each sample at 60°C for 4 h. We used the second half of the sample (untreated) to obtain an estimation of $\delta^{15}N$.

2.3. Stable isotope analysis

We weighed an aliquot (0.6 to 3.0 mg, depending on the sample type) of dried sample into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. We analyzed samples

from BOPDMar2014 and TANGOFeb2015 oceanographic surveys and samples of top predators with a Thermo DELTA V Advantage isotope-ratio mass spectrometer at the Institute of Geochronology and Isotopic Geology (Instituto de Geocronología y Geología Isotópica, INGEIS, UBA-CONICET). We analyzed samples from BOPDApr2016 and VA1418 oceanographic surveys with a Thermo Scientific DELTA V Advantage isotope-ratio mass spectrometer at the Environmental Sciences Stable Isotope Laboratory (Laboratorio de Isótopos Estables en Ciencias Ambientales, LIECA, IANIGLA-CONICET). In general, we analyzed 1 sample per collected individual (or pooled individuals), but to have a better characterization of the basal resources (phytoplankton), we carried out double analyses in samples with sufficient material. We expressed isotope results in delta (δ) notation; units are expressed as ‰, using the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards were Vienna Pee Dee Belemnite limestone for carbon and air (atmospheric N_2) for nitrogen (Gonfiantini 1978, Coplen et al. 1992). All isotope measures are reported as mean ± SD. We were able to quantify the analytical precision via repeated analysis of internal reference standards. Based on 3 internal standards (caffeine, sugar and collagen TRACE), the within-run standard deviation (SD) was 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ for samples analyzed at INGEIS. Based on 3 internal standards (caffeine IECA 17, collagen IECA17 and USGS41a) the within-run SD was 0.06‰ for $\delta^{13}C$ and $\delta^{15}N$ for samples analyzed at LIECA. We also measured the weight percent carbon and nitrogen concentration of each sample, which is reported as a [C]/[N] ratio. Since we did not conduct lipid-extraction of our samples (except top predators) prior to isotopic analysis, we normalized $\delta^{13}C$ values, following Post et al. (2007), and we applied a correction factor of -0.022 yr^{-1} to all sample carbon isotope values to the most present sample (2018 yr) to account for the Suess effect, or the anthropogenic decrease in the $\delta^{13}C$ of atmospheric CO_2 due to the burning of fossil fuels (Francey et al. 1999).

We sampled skin and muscle of a calf (i.e. lactating) Burmeister's porpoise *Phocoena spinipinnis* and minke whale (*Balaenoptera* sp.) and used a general trophic correction to approximate values of an adult of each species (see Section 2.4.2). We corrected bone collagen data with a general tissue fractiona-

tion factor of ~4‰ for $\delta^{13}C$ to approximate muscle (Hedges et al. 2005). We divided pinniped data (Drago et al. 2009) into CA and BC individuals according to the location of death, based on source data provided by the RNP Goodall Foundation.

2.4. Data treatment

To perform stable isotope analysis and to identify patterns in food web structure, we selected a pool of species that were the most abundant in the oceanographic surveys and/or have been identified as important species for the structure and dynamics of each marine area (for details, see Table 1). We grouped these organisms into 6 functional trophic groups, considering a combination of ecological and taxonomic characteristics: (1) inputs (primary producers and SPOM), (2) zooplankton (copepods, euphausiids and amphipods), (3) pelagic fish and crustaceans, (4) benthopelagic species (crustaceans, fish and squids), (5) demersal species (fish) and (6) top predators (seabirds and marine mammals).

2.4.1. Trophic structure: community-wide metrics and isotopic niche estimation

We described the trophic structure of each community through the Bayesian approach of Layman metrics (Layman et al. 2007, Jackson et al. 2011), using the Stable Isotope Bayesian Ellipses in R (SIBER) package of SIAR in R (Parnell et al. 2010, Jackson et al. 2011, R Development Core Team 2019) based on the $\delta^{13}C$ and $\delta^{15}N$ values of 612 biological components for the entire region. Specifically, for each area, we analyzed 19 species/groups (n = 234) from the BC; 22 (n = 204) from CA and 21 (n = 174) from the BB area. We calculated the Bayesian estimate of the community metrics originally proposed by Layman et al. (2007) and comparatively analyzed them among the 3 marine areas under study (Jackson et al. 2011). The nitrogen range (NR) describes the vertical structure (trophic length) of each community (e.g. larger range suggests more trophic levels). Nitrogen isotope ratios ($^{15}N:^{14}N$, $\delta^{15}N$) generally show higher increases of ~2–5‰ between consumers and their food and thus, in addition to reflecting food sources, are often used as an indicator of TP and food chain length (Post 2002). The carbon range (CR) represents the basal structure of each community and can give an estimate of the trophic diversity at the base of each community with varying $\delta^{13}C$ values. The natu-

Table 1. Biological components analyzed from the Beagle Channel, the Atlantic coast of Tierra del Fuego and Burdwood Bank marine areas. The trophic groups reported are those used to estimate the standard ellipse areas and Layman metrics in SIBER. $\delta^{13}C$ values are reported as: (1) raw values with no corrections ($\delta^{13}C_{raw}$), (2) raw values corrected by lipid normalization ($\delta^{13}C_{norm}$) (Post et al. 2007) and (3) raw values corrected by lipid normalization and Suess effect ($\delta^{13}C_{suess}$). All top predator samples were lipid extracted. C:N values of sediment particulate organic matter (SPOM) correspond to acidified samples. Abb: species/group abbreviations. Empty cells: no data

Functional trophic group/SIBER	Species	Abb	N	$\delta^{13}C_{raw}$ Mean	SD	$\delta^{13}C_{norm}$ Mean	SD	$\delta^{13}C_{suess}$ Mean	SD	$\delta^{15}N$ Mean	SD	C:N	Sampling year	Reference
Beagle channel (BC)														
Group 1: inputs	Phytoplankton[a]	Phyto	22	−20.2	2.6			−20.3	2.6	10.6	2.8	6.9	2014/2015	This study
	Macroalgae (Macrocystis pyrifera)	Macro	25	−15.1	1.5			−15.2	1.5	8.4	0.9	15.2	2014	This study
	SPOM	SPOM	3	−18.9	1.5	−18.9	1.5	−19.0	1.4	9.4	1.3	10.1	2010/2016	Riccialdelli et al. (2017a), this study
Group 2: zooplankton	Copepods[a]	Cope	19	−21.9	2.6	−18.9	2.3	−19.0	2.3	9.8	2.0	6.4	2014/2015/2016	This study
	Euphausiids[a]	Eupha	4	−21.8	1.5	−20.3	1.4	−20.4	1.4	10.8	1.1	4.8	2016	This study
	Munida gregaria – pelagic[a]	MGP	11	−19.7	2.5	−18.0	2.6	−18.0	2.6	9.9	0.9	5.1	2014/2015/2016	This study
	Themisto gaudichaudii[a]	TG	4	−22.0	1.7	−20.2	1.6	−20.2	1.6	9.2	3.7	5.1	2014/2015/2016	This study
Group 3: pelagic fish and crustaceans	Munida gregaria – benthic	MGB	19	−16.7	0.5	−16.3	0.4	−16.5	0.5	14.0	0.8	3.7	2009/2014	Riccialdelli et al. (2017a), this study
	Odontesthes smitti	Osmitt	6	−13.9	1.0	–		−14.2	1.0	15.7	1.6	3.2	2008	L. Riccialdelli (unpubl. data)
	Sprattus fuegensis	Sfueg	20	−17.6	0.6	−16.5	1.0	−16.6	1.0	13.3	0.7	4.5	2013/2018	L. Riccialdelli (unpubl. data), this study
Group 4: benthopelagic species	Patagonotothen cornucola	Pcorn	3	−15.2	0.6	−14.6	0.5	−14.7	0.5	15.9	0.7	3.9	2014	This study
	Patagonotothen tessellata	Ptesse	15	−16.9	1.1	−16.4	1.0	−16.5	1.0	13.7	2.0	3.9	2009/2014	Riccialdelli et al. (2017a), this study
	Patagonotothen ramsayi	Pram	4	−16.9	0.4	−16.5	0.2	−16.6	0.2	12.4	0.9	3.7	2014/2016	This study
	Eleginops maclovinus	Emaclo	20	−15.5	0.9	−15.5	0.7	−15.7	0.7	16.4	0.4	3.4	2010/2014	Riccialdelli et al. (2017a), this study
Group 5: demersal species	Cottoperca trigloides	Ctrigl	6	−16.2	0.4	−15.9	0.5	−16.0	0.4	14.3	0.3	3.6	2014/2016	This study
Group 6: top predators	Arctocephalus australis[b]	Aaust	8	−16.9	1.2			−14.6		20.6			2009	Saporiti et al. (2015), Bas et al. (2019)
	Otaria flavescens[b]	Oflav	5	−13.4	0.9			−13.8	1.0	20.7	1.4		1981 to 2007	Drago et al. (2009), Bas et al. (2019)
	Phocoena spinipinnis[c]	Pspin	1(2)	−14.5	0.1			−14.5	0.1	16.6	0.2	3.2	2016	This study
	Seabirds (Spheniscus magellanicus, Phalacrocorax atriceps, Leucophaeus scoresbii)	SeaB	38	−16.7	0.6	−16.6	0.5	−16.6	0.5	16.2	0.5	3.5	2014	A. Raya Rey (unpubl. data)
Atlantic coast of Tierra del Fuego (CA)														
Group 1: inputs	Phytoplankton[a]	Phyto	18	−16.2	2.6			−16.2	2.6	8.3	2.0	6.5	2014/2015	This study
	Macroalgae (Macrocystis pyrifera)	Macro	7	−11.2	2.8			−11.3	2.8	12.5	1.0	8.8	2013	L. Riccialdelli (unpubl. data)
	SPOM	SPOM	1	−20.6				−20.7		6.6		5.4	2016	This study
Group 2: zooplankton	Copepods[a]	Cope	14	−20.7	1.9	−17.1	1.5	−17.2	1.5	7.4	1.1	7.0	2014/2015/2016	This study
	Euphausiids[a]	Eupha	4	−21.4	1.1	−20.1	1.0	−20.1	1.0	7.7	1.1	4.6	2014/2016	This study
	Munida gregaria – pelagic[a]	MGP	7	−20.9	1.0	−19.1	1.2	−19.2	1.2	8.6	0.9	5.1	2014/2016	This study
	Themisto gaudichaudii	TG	7	−20.9	1.9	−18.3	1.5	−18.3	1.5	8.1	1.1	6.0	2014/2015/2016	This study
Group 3: pelagic fish and crustaceans	Munida gregaria – benthic[a]	MGB	2	−18.7	0.0	−18.1	0.0	−18.2	0.0	11.0	0.0	3.9	2014	This study
	Odontesthes smitti	Osmitt	5	−15.3	0.5			−15.5	0.5	17.3	0.1	3.2	2007	Riccialdelli et al. (2010, 2013)
	Sprattus fuegensis	Sfueg	11	−21.8	2.0	−18.1	1.4	−18.2	1.4	12.1	0.7	7.0	2014	This study
Group 4: benthopelagic species	Macruronus magellanicus	Mmage	5	−16.1	0.4			−16.4	0.4	15.1	0.3	3.1	2007	Riccialdelli et al. (2010, 2013)
	Patagonotothen ramsayi	Pram	19	−17.2	0.5	−17.0	0.7	−17.1	0.7	12.5	0.7	3.5	2014/2016	This study
	Eleginops maclovinus	Emaclo	9	−13.9	2.2			−14.1	2.2	17.3	1.3	3.1	2007	Riccialdelli et al. (2010, 2013)
	Salilota australis	Saust	13	−16.3	1.0			−16.5	1.0	14.9	1.4	3.4	2007/2008/2014	Riccialdelli et al. (2010, 2013), this study
	Squids (Illex argentinus, Doryteuthis gahi)	Squid	11	−17.5	1.0	−16.9	0.9	−17.0	0.9	12.5	1.3	4.0	2014	This study
Group 5: demersal species	Cottoperca trigloides	Ctrigl	6	−17.4	2.8	−17.1	2.9	−17.2	2.9	13.3	1.4	3.6	2014/2016	This study
	Merluccius australis	Maust	14	−15.9	0.5			−16.2	0.5	17.7	0.7	3.1	2007/2008	Riccialdelli et al. (2010, 2013)
	Merluccius hubbsi	Mhubb	3	−16.6	0.2			−16.9	0.2	17.7	0.3	3.2	2008	Riccialdelli et al. (2010, 2013)
	Dissostichus eleginoides	Deleg	1	−16.5				−16.8		16.3		3.1	2007	L. Riccialdelli (unpubl. data)

Table 1 (continued)

Functional trophic group/SIBER	Species	Abb	N	δ13C_raw Mean	SD	δ13C_norm Mean	SD	δ13C_suess Mean	SD	δ15N Mean	SD	C:N	Sampling year	Reference
Group 6: top predators	Cephalorhynchus commersonii	Ccomm	17	−15.1	0.5			−15.2	0.5	16.5	0.7	3.4	2009 to 2013	This study
	Otaria flavescens[b]	Oflav	16	−13.0	0.6			−13.3	0.5	20.7	0.9		1981 to 2007	Drago et al. (2009)
	Seabirds (Spheniscus magellanicus)	SeaB	14	−18.1	0.2	−17.7	0.2	−17.8	0.2	15.5	0.3	3.8	2014	A. Raya Rey (unpubl. data)
Burdwood Bank (BB)														
Group 1: inputs	Phytoplankton[a]	Phyto	10	−26.0	4.3			−26.1	4.3	3.8	0.4	7.7	2015	This study
	SPOM	SPOM	16	−24.9	0.9	−24.9	0.9	−24.9	0.9	5.2	1.1	6.4	2016	This study
Group 2: zooplankton	Copepods[a]	Cope	20	−26.6	1.7	−22.2	2.1	−22.4	2.2	3.6	0.9	7.8	2015/2016	This study
	Euphausiids[a]	Eupha	22	−24.9	1.3	−23.5	1.5	−23.6	1.5	5.6	1.3	4.8	2015/2016	This study
	Munida gregaria – pelagic[a]	MGP	1	−25.0				−22.2		7.4		6.2	2016	This study
	Themisto gaudichaudii[a]	TG	21	−25.4	1.2	−23.1	1.7	−23.1	1.7	5.5	1.1	5.7	2015/2016	This study
Group 3: pelagic fish and crustaceans	Munida spinosa	Mspin	7	−20.6	0.5	−19.7	0.4	−19.8	0.4	8.6	0.3	4.2	2016	This study
	Sprattus fuegensis	Sfueg	5	−20.8	0.1	−20.7	0.2	−20.7	0.2	9.1	0.1	3.4	2018	This study
Group 4: benthopelagic species	Macruronus magellanicus	Mmage	2	−18.0	1.5			−18.1	1.5	13.8	0.1		2009/2010	Quillfeldt et al. (2015)
	Patagonotothen elegans	Pele	3	−21.1	2.9	−21.2	2.8	−21.3	2.8	11.9	1.5	3.3	2016	This study
	Patagonotothen ramsayi	Pram	12	−21.3	1.2	−21.3	1.2	−21.3	1.2	9.5	1.4	3.3	2016	This study
	Salilota australis	Saust	1	−19.9				−20.4		10.3		2.8	2016	This study
	Semirossia tenera	Sten	1	−21.7				−21.5		11.3		3.6	2016	This study
	Squid–oceanic (Gonatus antarcticus, Kondakovia longimana)	Squid	4	−22.0	0.6			−22.0	0.6	9.5	2.2	3.2	2016	Alvito et al. (2015)
Group 5: demersal species	Cottoperca trigloides	Ctrigl	10	−21.8	2.6	−21.9	2.5	−22.0	2.5	12.1	1.2	3.2	2016	This study
	Dissostichus eleginoides	Deleg	4	−22.3	1.8	−21.9	0.4	−21.5	0.9	11.8	1.3	4.2	2016	This study
Group 6: top predators	Globicephala melas edwardii	Gmelas	6	−16.6	0.6			−16.7	0.6	15.9	1.5	3.6	2015	This study
	Lagenorhynchus cruciger[b]	Lcruc	7	−21.3	0.9			−21.8	1.1	10.2	0.6	3.0	1977 to 2011	Riccialdelli et al. (2010, unpubl. data)
	Balaenoptera sp.[c]	Minke	3	−24.7	1.0			−24.7	1.0	5.3	0.2	3.2	2016	This study
	Seabirds (Eudyptes chrysocome)	SeaB	18	−22.6	0.7	−22.2	0.7	−22.3	0.7	10.6	0.5	3.8	2014	A. Raya Rey (unpubl. data)
	Ziphius cavirostris	Zcavi	1	−17.4				−17.4		13.8		3.2	2014	This study

[a]Pooled individuals in each sample; [b]Samples based on bone collagen; [c]Calf

ral occurrence of ^{13}C to [12]C (expressed in δ notation as $\delta^{13}C$) can vary substantially between primary producers with different photosynthetic pathways (e.g. C3 plants vs. C4 plants or phytoplankton vs. macroalgae; France 1995, Peterson 1999), and exhibit a small increase (~0–2‰) between consumers and their food (Rau et al. 1983). Therefore, $\delta^{13}C$ is commonly used as a source indicator in food-web studies. The mean distance to the centroid (CD) gives a measure of the average degree of trophic diversity within a community. The mean nearest-neighbor distance (MNND) assesses the overall similarity of trophic niches among species within a community, and the SD of MNND provides a measure of the evenness of the distribution of the trophic niches in bi-blot space (e.g. $\delta^{13}C$ and $\delta^{15}N$). The convex hull area (TA) was estimated; however, it is known that it may have large biases due to sample size (Jackson et al. 2011). In order to overcome the limitation of TA, we also calculated the standard ellipse area corrected for small sample size (SEA_C, expressed in ‰^{2}). SEA_C was fitted to 40% of the data to represent isotopic niche width for each trophic group in a given community (Jackson et al. 2011). For statistical comparisons of the isotopic niche area between trophic groups, we calculated the Bayesian estimate of the standard ellipse area (SEA_B) using SIBER (Jackson et al. 2011). The SEA_B provides a description of the isotopic niche of a population or community, and it is not affected by bias associated with sample size or number of groups (Jackson et al. 2011), allowing us to compare the 3 marine areas with a different number of biological components.

In addition, to evaluate a potential bias introduced by differences in the ranges of $\delta^{13}C$ and $\delta^{15}N$ values, we also computed the community metrics (diversity metrics) in a standardized multidimensional space, following Cucherousset & Villéger (2015) and using the equation:

$$\delta k_{st} = (\delta k - \min(\delta k)) \ / \ (\max(\delta k) - \min(\delta k)) \quad (2)$$

where δk_{st} is the standardized value of each stable isotope (δk) that is scaled to have the same range (0–1). With respect to basal and vertical structure, we saw no need to standardize these values, since the comparison between these measures between communities is independent of each other, and in fact, these differences are accounted for when calculating and comparing these metrics between communities (Cucherousset & Villéger 2015).

2.4.2. WW species

To identify possible groups of WW species for each marine area and analyze their importance in the trophic dynamics of each community, we:

(1) performed a cluster analysis for each community based on $\delta^{13}C$ and $\delta^{15}N$ values of each species. To create each cluster, we used the complete linkage method and Euclidean distances;

(2) estimated the relative TP of each species/group within each functional trophic group, respectively, using 2 different models:

Model 1: TP was estimated using the equation proposed by Post (2002):

$$TP_i = [(\delta^{15}N_i - (\alpha \times \delta^{15}N_{b1} + (1 - \alpha) \times \delta^{15}N_{b2}))/TDF] + TP_b \quad (3)$$

where TP_i is the TP of each consumer i (individual/species/group) considered, and $\delta^{15}N_i$ is the nitrogen isotope composition of each consumer i. This model considered 2 baselines, thus $\delta^{15}N_{b1}$ and $\delta^{15}N_{b2}$ are the mean nitrogen isotope composition of baseline 1 (pelagic) and 2 (benthic), and TP_b represents the TP of both baselines in each marine area. TDF is the trophic discrimination factor for nitrogen values (TDF = $\Delta^{15}N$). To solve this equation, α is calculated as the contribution of baseline 1 to the diet of the consumer with a mixing model based on carbon and considering the isotopic fractionation of carbon ($\Delta^{13}C$):

$$\alpha = (\delta^{13}C_i - \delta^{13}C_{b2} + \Delta^{13}C \ / \ (\delta^{13}C_{b1} - \delta^{13}C_{b2}) \quad (4)$$

where $\delta^{13}C_i$, $\delta^{13}C_{b1}$ and $\delta^{13}C_{b2}$ are the mean nitrogen carbon isotope composition of each consumer, baseline 1 (pelagic) and baseline 2 (benthic), respectively.

Model 2: we performed a Bayesian estimation of TP, using the full model of 'tRophic Position' in R (Quezada-Romegialli et al. 2018) that accounts for the same data as Model 1, but calculates TPs in a Bayesian framework.

We used as baselines the isotope composition of primary consumers since it integrates seasonal and spatial variation in the stable isotope composition of producers (Cabana & Rasmussen 1996). Pelagic primary consumers were considered as baseline 1 (b1), and we used the $\delta^{15}N$ and $\delta^{13}C$ values of mixed zooplankton (copepods+euphausiids) of each marine area to incorporate the entire isotopic variability at the base (mean values in Table 1). Benthic primary consumers were considered as baseline 2 (b2). We used the $\delta^{15}N$ and previously published $\delta^{13}C$ values (mean ± SD) of *Nacella magellanica* for CA ($\delta^{15}N$ = 11.9 ± 0.3‰ and $\delta^{13}C$ = −8.5 ± 2.0‰, Bas et al. 2020); *N. deaurata* for BC ($\delta^{15}N$ = 12.1 ± 0.6‰ and $\delta^{13}C$ = −15.1 ± 1.4‰, Riccialdelli et al. 2017a) and ascidians for BB ($\delta^{15}N$ = 4.2 ± 0.8‰ and $\delta^{13}C$ = −21.7 ± 1.1‰, L. Riccialdelli unpubl. data). Both pelagic and benthic baselines were assumed to be herbivorous and to occupy a TP of 2. We used a general TDF of 3.4 ± 0.98‰ for ΔN and 0.39 ± 1.3‰ for ΔC, estimated as the difference in $\delta^{15}N$ or $\delta^{13}C$ values between consumers and their prey for a wide variety of animal taxa when experimental TDFs are unavailable, as in our case (Post 2002).

We expected that the WW group identified by these analyses may result in a different arrangement of species than those in the SIBER analysis (see Section 2.4.1), such as a combination of small pelagic and benthopelagic species, since these should ultimately respond to a combination of their feeding habits and TPs occupied in the trophic web. After identifying a middle-level group for each marine area, we selected the most probable WW species, based on previous knowledge about their abundances and trophic interactions within each marine area, since not all species within this middle group can be considered as WW. In addition, we have taken into account a small number of additional possible species considered as WW by previous studies (e.g. low trophic level species, such as pelagic crustaceans, the pelagic form of *Munida gregaria* and *Themisto gaudichaudii*). We compared these species through the Bayesian approach described in Section 2.4.1 to find some differences in their isotopic niches e.g. differences in the width of their isotopic niche area (SEA, expressed as ‰^{2}) and/or in the extent of overlap in their SEAs as a reflection of different trophic habits.

2.4.3. Statistical analysis

We tested for significant differences in isotope values between groups and estimates of TPs (Model 1)

between species/groups of different communities. When data met parametric requirements, as assessed by a Kolmogorov-Smirnov test and *F*-test, we used a 1-way ANOVA with a Tukey post hoc test and a Student's *t*-test for pairwise comparisons. Otherwise, we used a nonparametric Kruskal-Wallis *H*-test and Mann-Whitney *U*-test. We used a Bayesian procedure to evaluate the probability that the Bayesian Layman metrics and the isotopic niche widths of each group differed between and within each marine area using SIBER (Jackson et al. 2011). In addition, we also used a Bayesian approach to compare the posterior sample of TP (Model 2) between groups/species with the function 'pairwiseComparisons()' in 'tRophicPosition' (Quezada-Romegialli et al. 2018). We used R software v3.5.3 (R Development Core Team 2019) for data analysis. For all calculations, we tested significance at $\alpha = 0.05$.

3. RESULTS

3.1. Baseline isotope variation among communities

We found a large degree of variation and significant differences in $\delta^{13}C$ and $\delta^{15}N$ values among all of the components analyzed at the base of the food web of the 3 marine areas (Fig. 2, Table 1; see also Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m655p001_supp.pdf). We registered the lowest values in both $\delta^{13}C$ and $\delta^{15}N$ in BB, compared to the other areas in terms of phytoplankton, SPOM, mixed zooplankton (used as the baseline), copepods and euphausiids (for statistical comparisons see Table S1). For $\delta^{15}N$, we found the highest values in BC in all components, and the highest values for $\delta^{13}C$ in CA were found in phytoplankton, mixed zooplankton and copepods.

For macroalgae, we found significantly higher $\delta^{13}C$ and $\delta^{15}N$ values in CA than in BC (Table S1, Fig. S2). We did not find macroalgae during any oceanographic surveys in the BB area. In addition, we did not statistically compare SPOM values from CA due to small sample size (n = 1).

3.2. Trophic structure: community-wide metrics and isotopic niche estimation

We found differences between communities through the Bayesian estimates of SEAs and Layman metrics (Fig. 3, Table 2). Based on the scaled isotope values, we found a similar trend for all community metrics as well as those calculated with unscaled values. Specifically, we found similar isotopic niche areas (SEA$_B$) occupied by the whole community of BB and BC, but both of them had smaller SEA$_B$ compared to CA. We found differences in the food-web length (NR) between communities, with the longest food chain (higher NR values) in CA and similar lengths in BB and BC (Figs. 2 & 3). The basal structure (CR) also differed between areas; BB had the widest basal structure, and BC and CA were similar. We also detected slight differences in trophic diversity (CD), with decreasing values from CA > BB > BC, indicating higher trophic overlap in BC. We also found higher trophic redundancy (low values of MNND and SD of MNND) in BB and BC compared to CA.

Regarding the niche widths within groups among communities, the predicted SEA$_B$ showed significant differences (for data and pairwise comparisons see Tables S2 & S3 and Fig. 4). Specifically, with respect to inputs (Group 1), we registered a smaller isotopic niche (low SEA$_B$) in BB, while it was larger (high SEA$_B$) and similar in BC and CA. The zooplankton group (Group 2) had the smallest isotopic niche in BC and the largest niche in CA. The group formed by small pelagic species and crustaceans (Group 3) had the smallest niche in BB and the largest in CA. Both benthopelagic (Group 4) and demersal species (Group 5) had the lowest SEA$_B$ in BC; while G4 had similar SEA$_B$ between CA and BB, and G5 had the largest SEA$_B$ in CA. Top predators (Group 6) showed the largest SEA$_B$ in BB and the smallest in BC.

3.3. WW species

3.3.1. Cluster analysis

The cluster analysis was useful to detect different trophic groups based on $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 5). From the base to the top of each food web, the species were grouped according to their main trophic habits and their estimated TPs. As expected, these new groups showed a different arrangement of species than the SIBER groups (see Section 2.4); therefore, we identified them with a prime (') superscript (i.e. Group 1', Group 2', etc.). For example, the top predator group (Group 6 used in SIBER) showed discrete groups of consumers with different TPs, such as low trophic level-foragers (e.g. whales), crustacean- and fish-eating taxa (e.g. seabirds and small dolphins) and benthopelagic predators (e.g. ziphiids, pinnipeds). We detected a large overlap between the basal groups (Groups 1' and 2') of pelagic (e.g.
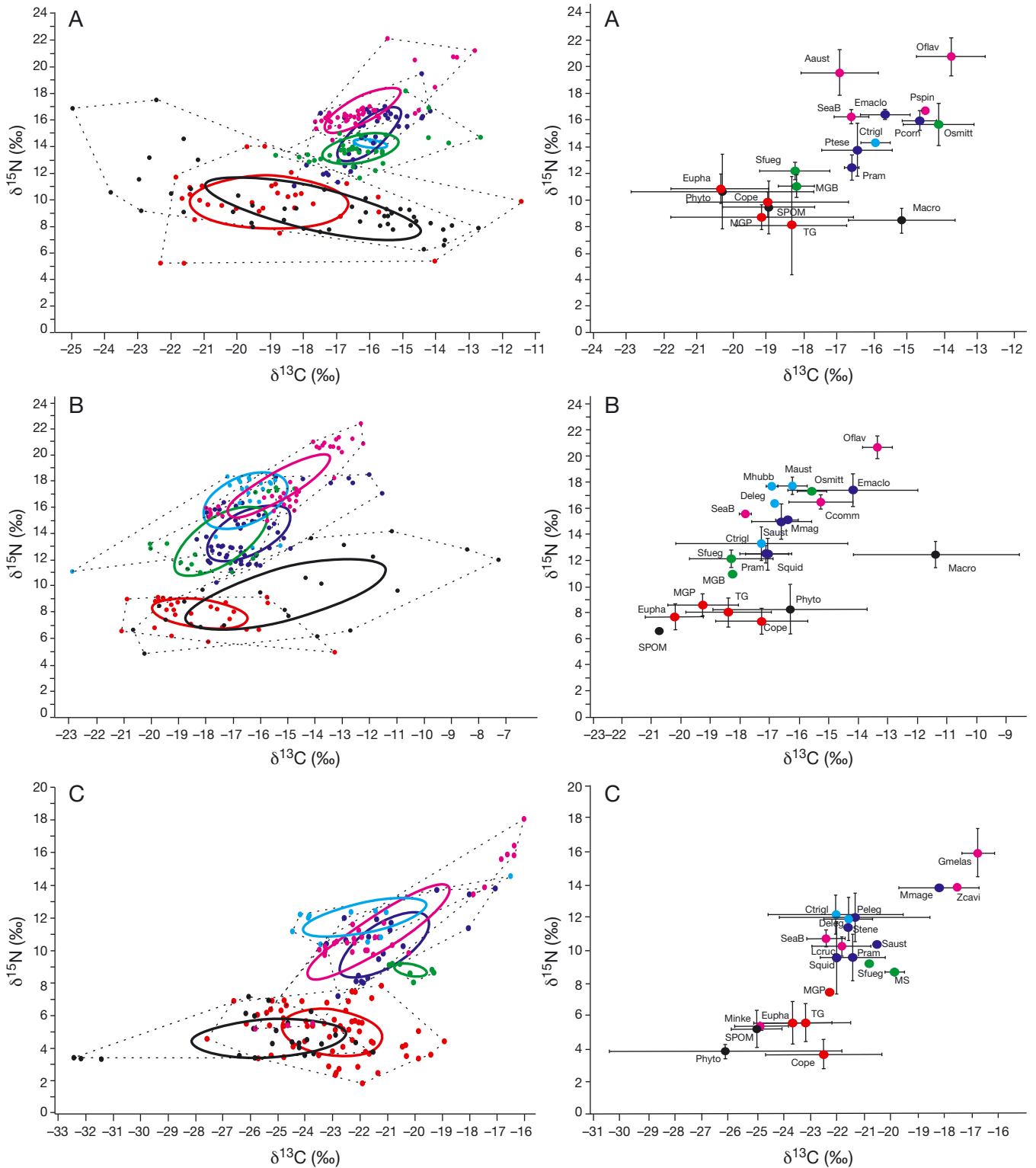
Fig. 2. Trophic structure (left panels) and mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of each species/group (right panels) of (A) Beagle Channel, (B) Atlantic coast of Tierra del Fuego and (C) Burdwood Bank marine areas. Solid lines represent standard ellipse areas corrected for small sample size (SEA$_C$, fits 40% of the data). Dashed lines represent convex hull area. Black: Group 1 (inputs: primary producers and sediment particulate organic matter), red: Group 2 (zooplankton); green: Group 3 (small pelagic fish and crustaceans); blue: Group 4 (benthopelagic species); cyan; Group 5 (mesopelagic species); magenta: Group 6 (top predators). For species/group abbreviations, see Table 1
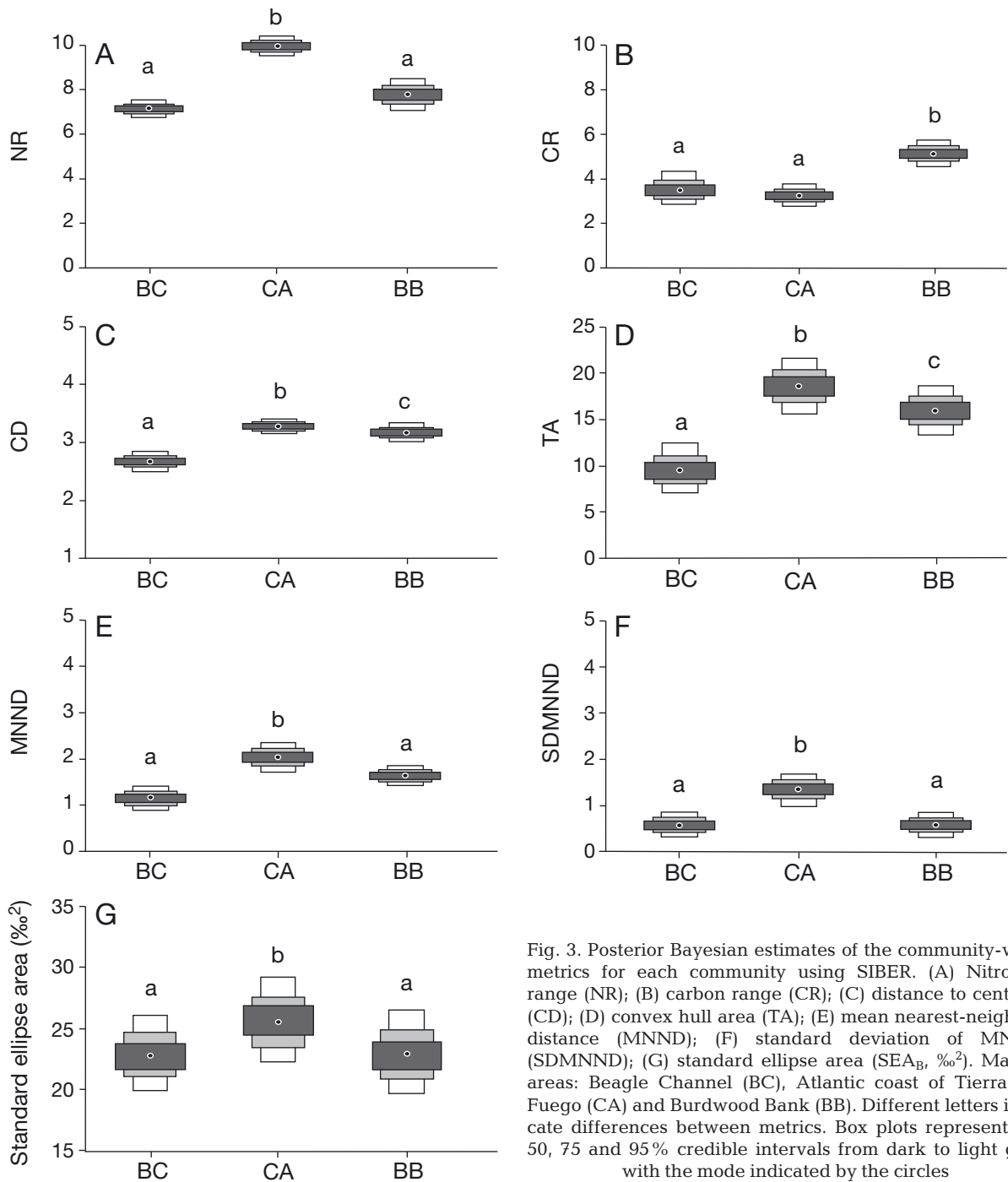
Fig. 3. Posterior Bayesian estimates of the community-wide metrics for each community using SIBER. (A) Nitrogen range (NR); (B) carbon range (CR); (C) distance to centroid (CD); (D) convex hull area (TA); (E) mean nearest-neighbor distance (MNND); (F) standard deviation of MNND (SDMNND); (G) standard ellipse area (SEA$_B$, ‰^{2}). Marine areas: Beagle Channel (BC), Atlantic coast of Tierra del Fuego (CA) and Burdwood Bank (BB). Different letters indicate differences between metrics. Box plots represent the 50, 75 and 95% credible intervals from dark to light gray with the mode indicated by the circles

phytoplankton, zooplankton) and benthic (e.g. SPOM) components. Macroalgae were identified as a very different basal resource compared to phytoplankton and SPOM. In addition, we identified a middle trophic group in each food web, Group 3′, which was considered a WW level group represented by few species. Among these, *Sprattus fuegensis*, *Patagonotothen ramsayi* and *Munida* spp. (benthic form) were present within all 3 food webs. In Group

2′, we classified the pelagic form of *M. gregaria* and the amphipod *Themisto gaudichaudii*, also considered a key species in the literature.

3.3.2. TP estimations

We estimated the TP occupied by each consumer analyzed in our study based on 2 different models

Table 2. Isotopic niche width and Layman metrics of each community (BC: Beagle Channel; CA: Atlantic coast of Tierra del Fuego; BB: Burdwood Bank). SEA: standard ellipse area; SEA_C: SEA corrected for small sample sizes; SEA_B: Bayesian estimate of SEA. SEAs fit 40% of the data. NR: range in $\delta^{15}N$, CR: range in $\delta^{13}C$, TA: convex hull area, CD: mean distance to centroid, MNND: mean nearest-neighbor distance, SDMNND: standard deviation of MNND. All metrics were calculated with unscaled and scaled values

Metric	Unscaled values			Scaled values		
	BC	CA	BB	BC	CA	BB
SEA	23.62	25.59	22.85	0.03	0.04	0.03
SEA_C	23.72	25.72	22.98	0.03	0.04	0.03
SEA_B	23.50	25.50	22.90	0.03	0.04	0.04
NR	7.69	9.78	7.39	0.37	0.47	0.36
CR	3.04	3.17	5.16	0.09	0.10	0.16
TA	8.83	19.11	15.71	0.01	0.03	0.02
CD	2.67	3.27	3.13	0.12	0.15	0.14
MNND	1.10	2.12	1.52	0.05	0.08	0.06
SDMNND	0.65	1.09	0.72	0.03	0.04	0.02

(Table 3, Fig. 5), but we did not find a large difference between them. In general, lower TP estimations were made in BC and higher estimations in CA and BB ($H = 61.84$, df = 2, p < 0.001 and p < 0.005 for all pairwise comparisons between the same group/species). Based on our data set, and considering both models, 2 pinniped species, namely South American fur seal *Arctocephalus australis* and South American sea lion *Otaria flavescens*, were the top predators in BC and *O. flavescens* in CA, while the long-finned pilot whale *Globicephala melas* occupied the highest positions estimated in the oceanic BB area.
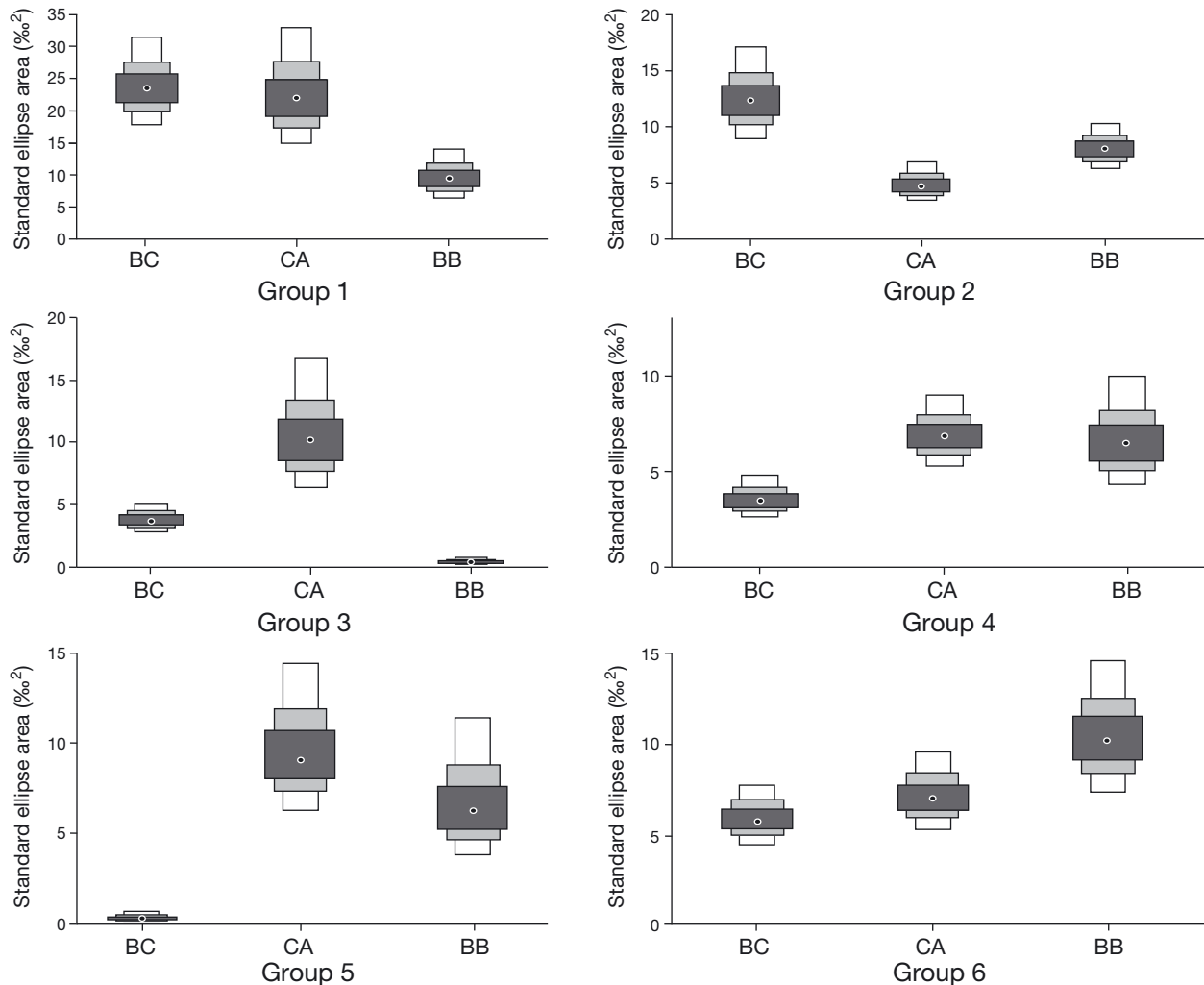

Fig. 4. Posterior Bayesian estimates of the standard ellipse areas (SEA_B, ‰²) for each functional group through SIBER. Group 1: inputs (primary producers and sediment particulate organic matter); Group 2: zooplankton; Group 3: pelagic fish and crustaceans; Group 4: benthopelagic species; Group 5: demersal species; Group 6: top predators. Beagle Channel (BC), Atlantic coast of Tierra del Fuego (CA) and Burdwood Bank (BB). Box plots represent the 50, 75 and 95% credible intervals from dark to light gray. Circles correspond to the mode of SEA_B for each group
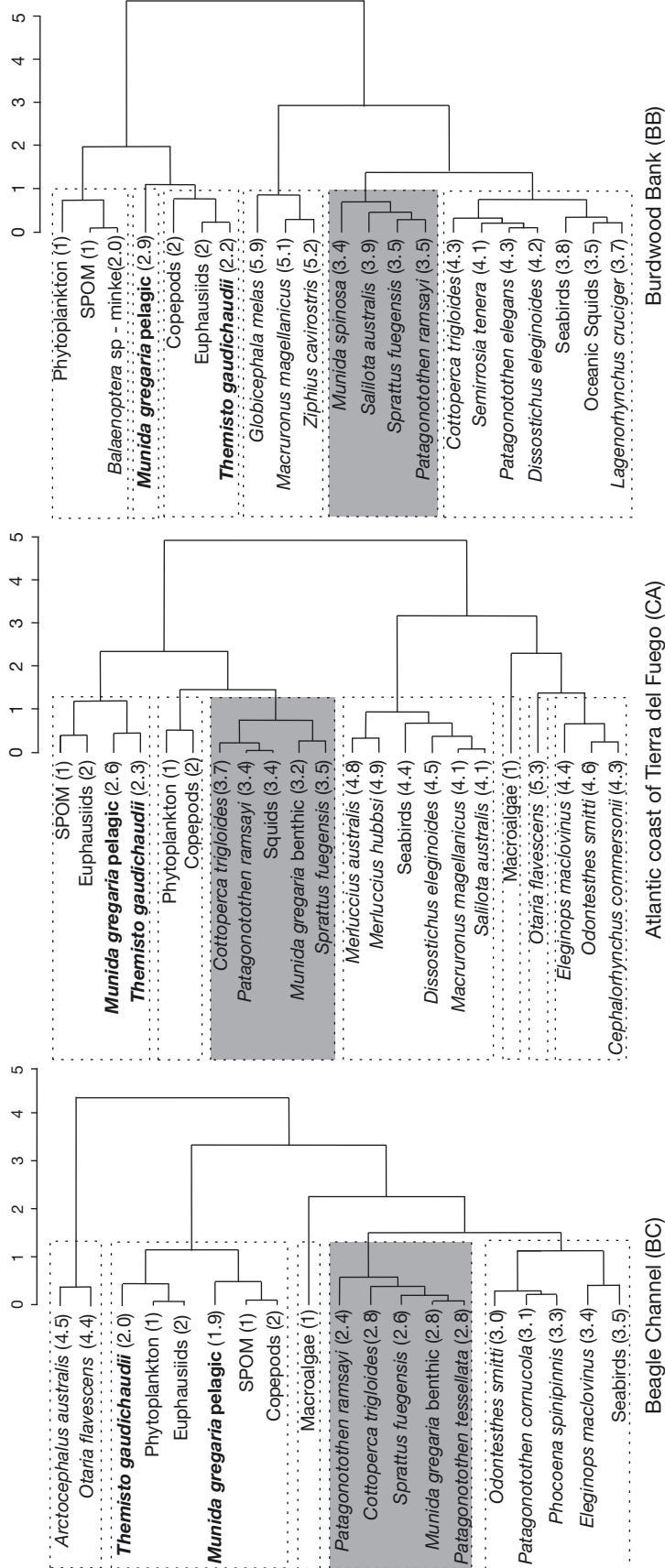
Fig. 5. Cluster analysis (complete linkage method and Euclidean distance) for 612 biological components of the 3 marine areas under study based on δ^{13}C and δ^{15}N values. The *x*-axis represents the distance metric (Euclidean). Numbers in parentheses are the estimated trophic position (TP) (Model 1). The major organic primary producers and organic sources (sediment particulate organic matter, SPOM) are assumed to represent the first trophic level. The area in gray indicates the group with possible wasp-waist (WW) species of mid-level TPs for each marine area. Dashed boxes represent different trophic groups. Species in **bold** have been considered in the literature as WW species occupying low TPs

The species considered in the literature and in this study as possible WW species had estimated TPs between 2.0 and 3.5. Overall, species in BC had lower estimated TPs compared to those in CA and BB (F = 15.79, df = 2, p < 0.001, for Model 1), except for *T. gaudichaudii*, which showed no differences between marine areas (for all pairwise comparisons, see Table S4). The pelagic form of *M. gregaria* had a lower TP (ranging from 2.0 to 2.2), compared to its benthic counterpart (ranging from 2.8 to 3.1). In BB, we only sampled 1 individual of the pelagic form, and therefore it was not included in comparisons. However, its isotopic values resembled those of a pelagic organism in CA, which would explain a high estimated TP (2.9, Model 1).

Within each marine area, the WW species had some differences between their TPs in both models. In BB, *T. gaudichaudii* had lower TPs compared to benthic *Munida spinosa*, *P. ramsayi* and *S. fuegensis*, with the last 3 species having similar TPs. In CA, the pelagic form of *M. gregaria* and *T. gaudichaudii* had similar TPs, but lower with respect to *S. fuegensis* and *P. ramsayi*. In BC, the pelagic form of *M. gregaria* had the lowest estimated TP and the benthic form the highest. In addition, *P. ramsayi* and *S. fuegensis* had similar TPs.

3.3.3. Isotopic niche widths within WW species groups

Within each marine area, we found differences in the isotopic niche (SEA$_B$) occupied by the WW species considered (for data and pairwise comparisons, see Tables S5 & S6

Table 3. Trophic position (TP) estimations. Model 1: two baselines with the trophic discrimination factor (TDF) for N and C (Post 2002), Model 2: Bayesian full model with 2 baselines and TDF for N and C (Quezada-Romegialli et al. 2018). Functional trophic groups reported are the ones used with SIBER. Phytoplankton, macroalgae and sediment particulate organic matter (SPOM) were assigned as TP 1, and copepods and euphausiids as TP 2 in all models; '*': not estimated due to low sample size (n ≤ 2). Results are shown as means ± SD for Model 1. Bayesian posterior estimates for Model 2 are shown as mode and 95% credibility interval lower and upper limits

Functional trophic group/SIBER	Species	N	TP Model 1 Mean	SD	TP model 2 Mode	95%CI Lower	Upper
Beagle channel (BC)							
Group 1: inputs	Phytoplankton[a]	22	1.0		1.0		
	Macroalgae (*Macrocystis pyrifera*)	25	1.0		1.0		
	SPOM	3	1.0		1.0		
Group 2: zooplankton	Copepods[a]	19	2.0		2.0		
	Euphausiids[a]	4	2.0		2.0		
	Munida gregaria – pelagic[a]	11	1.9	0.4	2	2.0	2.1
	Themisto gaudichaudii[a]	4	2.0	1.0	2.2	1.5	3.0
Group 3: pelagic fish and crustaceans	*Munida gregaria* – benthic	19	2.8	0.2	2.7	2.6	3.1
	Odontesthes smitti	6	3.0	0.5	2.9	2.5	3.9
	Sprattus fuegensis	20	2.6	0.2	2.6	2.4	2.9
Group 4: benthopelagic species	*Patagonotothen cornucola*	3	3.1	0.1	2.9	2.1	3.9
	Patagonotothen tessellata	15	2.8	0.5	2.6	2.3	3.2
	Patagonotothen ramsayi	4	2.4	0.2	2.3	1.9	2.6
	Eleginops maclovinus	20	3.4	0.2	3.4	3.2	3.7
Group 5: demersal species	*Cottoperca trigloides*	6	2.8	0.1	2.8	2.6	3.1
Group 6: top predators	*Arctocephalus australis*[b]	8	4.5	0.5	4.5	4.0	5.2
	Otaria flavescens[b]	5	4.4	0.5	4.4	4.0	5.5
	Phocoena spinipinnis[c]	1(2)	3.3	0.0	*	*	*
	Seabirds (*Spheniscus magellanicus, Phala crocorax atriceps, Leucophaeus scoresbii*)	38	3.5	0.1	3.4	3.3	3.8
Atlantic coast of Tierra del Fuego (CA)							
Group 1: inputs	Phytoplankton[a]	18	1.0		1.0		
	Macroalgae (*Macrocystis pyrifera*)	7	1.0		1.0		
	SPOM	1	1.0		1.0		
Group 2: zooplankton	Copepods[a]	14	2.0		2.0		
	Euphausiids[a]	4	2.0		2.0		
	Munida gregaria – pelagic[a]	7	2.6	0.4	2.2	2.0	2.6
	Themisto gaudichaudii	7	2.3	0.3	2.1	1.9	2.3
Group 3: pelagic fish and crustaceans	*Munida gregaria* – benthic[a]	2	3.2	0.0	*	*	*
	Odontesthes smitti	5	4.6	0.1	4.7	4.2	4.9
	Sprattus fuegensis	11	3.5	0.4	3.4	3.0	3.6
Group 4: bentho pelagic species	*Macruronus magellanicus*	5	4.1	0.1	4.1	3.7	4.4
	Patagonotothen ramsayi	19	3.4	0.2	3.4	3.1	3.6
	Eleginops maclovinus	9	4.4	0.3	4.5	3.8	4.9
	Salilota australis	13	4.1	0.5	4.1	3.6	4.4
	Squids (*Illex argentinus, Doryteuthis gahi*)	11	3.4	0.4	3.5	3.0	3.7
Group 5: demersal species	*Cottoperca trigloides*	6	3.7	0.3	3.8	2.8	4.2
	Merluccius australis	14	4.8	0.2	4.7	4.5	5.1
	Merluccius hubbsi	3	4.9	0.1	4.7	4.0	5.7
	Dissostichus eleginoides	1	4.5		*	*	*
Group 6: top predators	*Cephalorhynchus commersonii*	17	4.3	0.2	4.3	4.0	4.6
	Otaria flavescens[b]	16	5.3	0.2	5.3	4.8	5.7
	Seabirds (*Spheniscus magellanicus*)	14	4.4	0.1	4.3	4.0	4.6
Burdwood Bank (BB)							
Group 1: inputs	Phytoplankton[a]	10	1.0		1.0		
	SPOM	16	1.0		1.0		
Group 2: zooplankton	Copepods[a]	20	2.0		2.0		
	Euphausiids[a]	22	2.0		2.0		
	Munida gregaria – pelagic[a]	1	2.9		*	*	*
	Themisto gaudichaudii[a]	21	2.2	0.3	2.2	2.0	2.9

Table 3 (continued)

Functional trophic group/SIBER	Species	N	TP Model 1 Mean	TP Model 1 SD	TP model 2 Mode	TP model 2 95%CI Lower	TP model 2 95%CI Upper
Group 3: pelagic fish and crustaceans	*Munida spinosa*	7	3.4	0.1	3.1	2.5	3.7
	Sprattus fuegensis	5	3.5	0.0	3.3	2.2	4.3
Group 4: bentho pelagic species	*Macruronus magellanicus*	2	5.1	0.2	3.9	2.0	6.1
	Patagonotothen elegans	3	4.3	0.7	3.6	2.3	5.3
	Patagonotothen ramsayi	12	3.5	0.5	3.3	3.0	4.1
	Salilota australis	1	3.9		*	*	*
	Semirrosia tenera	1	4.1		*	*	*
	Squid – oceanic (*Gonatus antarcticus, Kondakovia longimana*)	4	3.5	0.7	3	2.2	4.8
Group 5: demersal species	*Cottoperca trigloides*	10	4.3	0.5	4.1	3.8	4.7
	Dissostichus eleginoides	4	4.2	0.4	4	3.2	5.1
Group 6: top predators	*Globicephala melas edwardii*	6	5.9	0.5	5.2	4.6	6.4
	Lagenorhynchus cruciger[b]	7	3.7	0.2	3.6	3.3	4.1
	Balaenoptera sp.[c]	1(3)	2.0	0.1	2.2	2.0	2.4
	Seabirds (*Eudyptes chrysocome*)	18	3.8	0.2	3.7	3.5	4.1
	Ziphius cavirostris	1	5.2		*	*	*

[a]Pooled individuals in each sample; [b]Samples based on bone collagen; [c]Calf

and Fig. 6). We did not compare the pelagic form of *M. gregaria* in BB or the benthic form of the same species in CA due to small sample sizes. *T. gaudichaudii* had the most extensive isotopic niche area (SEA$_B$) in the 3 food webs. Also, this species overlapped its isotopic niche only with the pelagic form of *M. gregaria*, corresponding to 13 and 40% of their respective SEA$_C$ in BC and to 8 and 43% of their SEA$_C$ in CA.

The isotopic niches of *S. fuegensis* and *P. ramsayi* overlapped in the 3 food webs. The overlaps corresponded to 98% and almost 2% of their respective isotopic niche area (SEA$_C$) in BB; 13 and 25% of their respective SEA$_C$ in CA; and 14 and 39% of their respective SEA$_C$ in BC (Fig. 6). In addition, we estimated a wider isotopic niche area (SEA$_B$) for *P. ramsayi* than for *S. fuegensis* only in BB, while the opposite occurred in BC and CA (Tables S5 & S6).

In BC, the benthic form of *M. gregaria* had a high isotopic niche overlap with *S. fuegensis*, corresponding to 49 and 28% of their SEA$_C$, and also overlapped with *P. ramsayi*, but to a lesser extent, corresponding to 5 and 8% of their SEA$_C$, respectively (Fig. 6).

4. DISCUSSION

The southwestern South Atlantic Ocean is a marine region influenced by different complex oceanographic processes and interactions (e.g. upwelling and mixing processes) with significant impacts on the biogeochemistry of the local ecosystems under study (Matano et al. 2019). By taking advantage of the isotopic differences at a regional scale, we were able to differentiate the 3 marine areas under study (BC, CA and BB). We utilized an appropriate isotopic baseline determined from a large data set of isotopic information of the biological components at the base of the food webs (e.g. sediments, primary producers) that covered the full range of the isotopic variability recorded in previous studies. In terms of their isotopic values, the BB was the most different area, characterized by oceanic and polar conditions. We also included isotopic information of all functional trophic groups, from the main inputs (primary producers and SPOM) to top predators (marine mammals and seabirds). We found similar trophic metrics (e.g. topology) between the 3 food webs; however, BC and BB showed the most pronounced WW structure (e.g. short food webs). In addition, we identified both locally and regionally probable WW species. The Fuegian sprat *Sprattus fuegensis* was present in all 3 areas, occupying the WW level along with the longtail southern cod *Patagonotothen ramsayi* in BB and CA and with the squat lobster *Munida gregaria* in BC.

4.1. Baseline isotopic variation

We detected important spatial variation in carbon (δ^{13}C) and nitrogen (δ^{15}N) composition at the base of
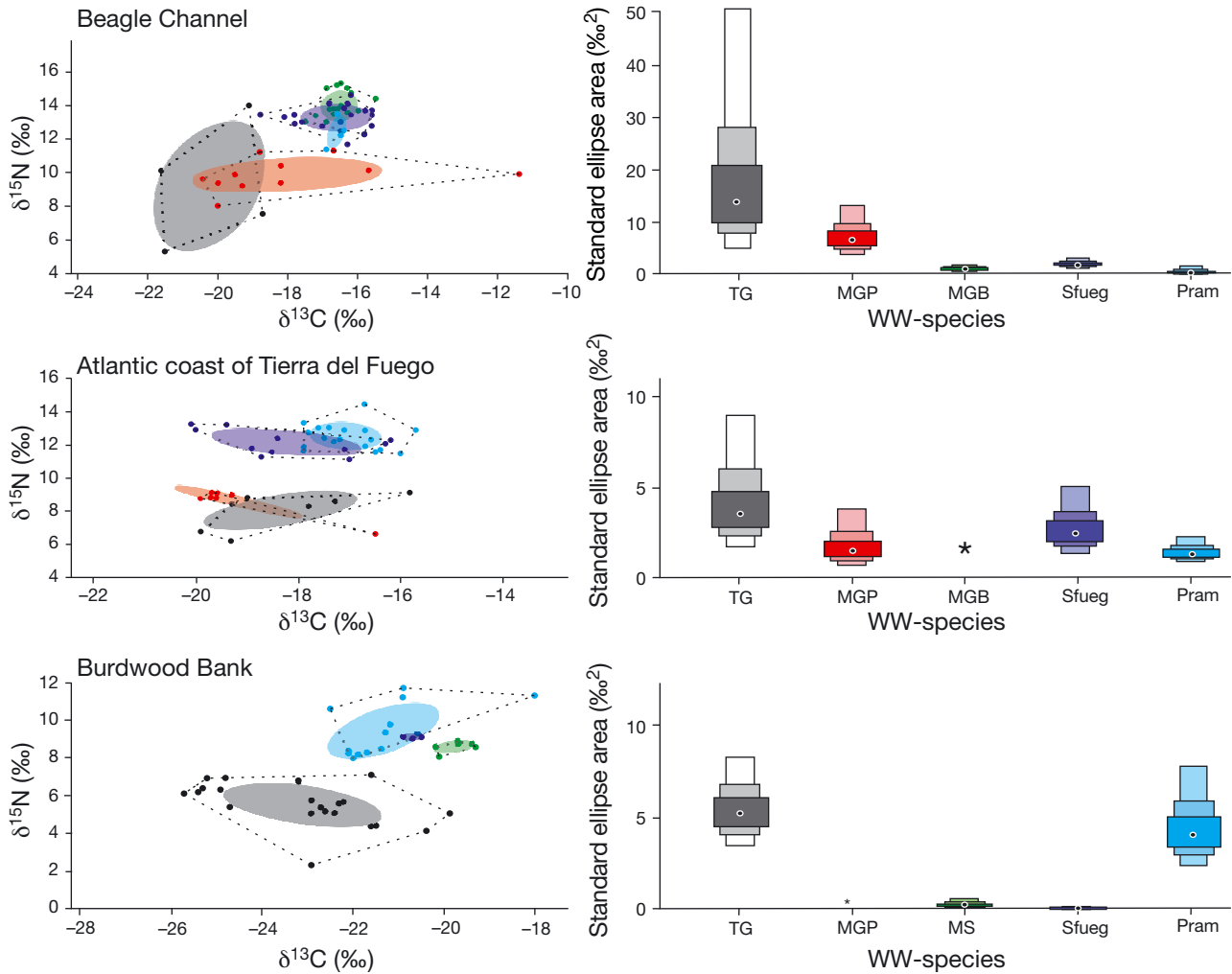
Fig. 6. Isotopic niche of wasp-waist (WW) species for each marine area. Standard ellipse areas corrected for small sample-size (SEA$_C$, fits 40% of the data, colored lines) and convex hull (TA, dashed lines) and posterior Bayesian estimates of the standard ellipse areas (SEA$_B$, ‰^{2}) for each WW species per community. Box plots represent the 50, 75 and 95% credible intervals from dark to light colors. Circles correspond to the mode of SEA$_B$ for each WW species. TG: *Themisto gaudichaudii* (black); MGP: *Munida gregaria* – pelagic (red); MGB: *Munida gregaria* – benthic (green); MS: *Munida spinosa* (green); Sfueg: *Sprattus fuegensis* (purple); Pram: *Patagonotothen ramsayi* (cyan). '*': not estimated due to small sample size

the food web among the 3 marine areas under study. Chemical, physical and biological factors are known to influence the isotopic composition of phytoplankton communities, which is transferred to upper trophic levels (Graham et al. 2010). Water temperature is one of the main driving forces of variability in $\delta^{13}C$ values (Goericke & Fry 1994). In Patagonian waters, Lara et al. (2010) found a highly significant positive correlation between temperature and $\delta^{13}C$ values in POM towards polar waters. Since the concentration of dissolved CO_2 varies with temperature, a significant effect on isotopic fractionation by marine phytoplankton is expected (Rau et al.1982, Goericke & Fry 1994). As with the case of carbon, the abundance and various forms of the inorganic nitro-

gen pool affect nitrogen composition, which is ruled mostly by a complex combination of different processes that occur in marine waters (e.g. the recycling of nitrogen in the euphotic zone, N_2 fixation, the influx of nitrate-rich upwelling, nitrogen from runoff and melting glaciers) (Montoya 2007). The types of primary producers also introduce isotopic variation (Peterson 1999). Phytoplankton is the only primary producer in oceanic waters, such as the BB area. Nevertheless, high spatial and seasonal variability in the plankton community (e.g. in terms of biomass and composition) was observed in previous studies from coastal to offshore regions. Moreover, in coastal areas of BC and CA, macroalgae, which are typically more enriched in ^{13}C than phytoplankton (France

1995, Peterson 1999), constitute an important food source for several benthic organisms and contribute to the pelagic realm through different pathways (e.g. grazing and suspension-feeding) (Riccialdelli et al. 2017a). It is important to note that the isotope values registered in the basal component of the food webs (e.g. SPOM, phytoplankton, zooplankton) can be subject to spatial and temporal variation in association with oceanographic parameters, such as sea surface temperatures. Although small marine organisms tend to show greater temporal variability due to faster turnover rates compared to larger organisms (Cabana & Rasmussen 1996), the isotopic variation at the base may propagate through the entire food web.

Along the continental shelf areas of Tierra del Fuego, from ~46° to ~54° S, $\delta^{13}C_{POM}$ values ranges from −18.35 to −23.07‰ (Lara et al. 2010), which agrees with the $\delta^{13}C$ value of phytoplankton measured in CA. We also measured $\delta^{13}C$ values of zooplankton similar to values mentioned in previous studies (e.g. −19.8‰, Ciancio et al. 2008). $\delta^{15}N_{POM}$ values range from ~5.7 to ~2.5‰, decreasing towards southern latitudes and reflecting biological fractionation and/or isotopic differences in the nitrogen pool (Lara et al. 2010, Barrera et al. 2017). In fact, the Cape Horn Current that influences the southwestern South Atlantic Ocean transports waters from the South Pacific with ¹⁵N-depleted ammonium that is available to phytoplankton (Lara et al. 2010). The $\delta^{15}N$ values that we measured in phytoplankton and zooplankton groups are in agreement with values previously reported for the area (7.3‰ for $\delta^{15}N$, Ciancio et al. 2008, Lara et al. 2010).

In the BC, water temperature is the main factor that explains most of the variation in $\delta^{13}C_{POM}$ values, which are within a range of −24.5 to −20.9‰ and with a mean value of −23.0 ± 0.9‰ (Barrera et al. 2017). $\delta^{13}C$ values measured in phytoplankton in our study in BC are in agreement with the ranges reported by Barrera et al. (2017) and with a previous food-web study that reported $\delta^{13}C_{POM}$ values of −23.9 ± 0.7‰ and $\delta^{13}C_{phytoplankton}$ values of −21.0 ± 0.5‰ (Riccialdelli et al. 2017a). In addition, the availability of ammonium in the system (Cardona Garzón et al. 2016, Barrera et al. 2017) may influence $\delta^{13}C_{phytoplankton}$ values due to its effect on the β-carboxylation pathway for C fixation (Dehairs et al. 1997). Also, the availability of ¹⁵N-enriched ammonium, derived from runoff in the inner BC, could explain high $\delta^{15}N_{POM}$ (6.9‰), $\delta^{15}N_{phytoplankton}$ (8.9 ± 0.6‰) and $\delta^{15}N_{macroalgae}$ (10.3 ± 0.6‰) values reported previously (Barrera et al. 2017, Riccialdelli et al. 2017a) and in our study. During the austral summer, phytoplanktonic cells

like diatoms, such as *Chaetoceros* sp. and *Thalassiosira* sp., can represent between 20 and 45% of total phytoplankton in coastal areas of Tierra del Fuego (e.g. Almandóz et al. 2011, Barrera et al. 2017). This group is the main feeding input to the zooplankton, such as copepods (e.g. *Calanus australis, Oithona similis, Drepanopus forcipatus*) and amphipods (e.g. *Themisto gaudichaudii*) (Sabatini & Álvarez Colombo 2001, Sabatini et al. 2004, Aguirre et al. 2012). Towards the open ocean, diatoms decrease in abundance (~7%) and dinoflagellates (~93%) dominate (Barrera et al. 2017). The same pattern occurs during austral autumn in BC (Almandóz et al. 2011).

In the oceanic BB area, complex oceanographic conditions generate an internal spatial heterogeneity, mainly along its longitudinal axis, and consequently plankton communities respond with different spatial distributions (Bertola et al. 2018a, García Alonso et al. 2018). The plankton community changes to different pools of oceanic species of primary producers (e.g. the diatom *Rhizosolenia* sp., Olguín Salinas et al. 2015, Bertola et al. 2018a,b) and zooplankton like euphausiids (e.g. *Euphausia lucens, E. valentini*), copepods (e.g. *Neocalanus tonsus*) and chaetognaths (e.g. *Sagitta* spp.) (Sabatini & Álvarez Colombo 2001, Sabatini et al. 2004, Aguirre et al. 2012). Interestingly, satellite color imagery showed generally lower chlorophyll blooms over BB with respect to coastal areas like CA and BC (Matano et al. 2019). However, in BB, phytoplankton blooms can develop in deeper layers and not on the surface (Bertola et al. 2018a). Our isotopic data in that area are similar to published information for zooplankton of the Antarctic Circumpolar Current (e.g. euphausiids range from −26.0 to −22.0‰ and from 3.5 to 5.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively; Schmidt et al. 2003, Stowasser et al. 2012). Between the shelf and oceanic sub-Antarctic waters, from ~55° to ~58° S, mean $\delta^{13}C_{POM}$ values were −26.93 ± 0.61‰ (Lara et al. 2010), near what we measured for marine phytoplankton in BB (−26.1 ± 4.3‰). $\delta^{15}N_{POM}$ values also decrease within a range of 1 to 4‰ and drop to −1.6 to 1‰ at the Drake Passage (Lara et al. 2010). These are waters of low temperatures (~5.1°C) and salinities (~34), where the Malvinas Current, the main current that influences the BB marine area, originates (Matano et al. 2019). In agreement with previous studies in oceanic and southern waters (e.g. Schmidt et al. 2003, Lara et al. 2010, Stowasser et al. 2012), we also measured low $\delta^{15}N_{phytoplankton}$ values (3.8 ± 0.04‰) in BB. The main reason for the low $\delta^{15}N$ value in these waters seems to be the phytoplankton

uptake of isotopically light ammonium that comes from oceanic zooplankton excretions and the intense mineralization of the organic matter in surface waters (Lara et al. 2010). Thus, the BB area is influenced by typical oceanic and polar water masses, characterized by very low $\delta^{13}C$ and $\delta^{15}N$ values that create a unique marine area compared to the other investigated areas.

4.2. Trophic structure

Based on the scaling procedure, the unbiased stable isotope space showed reduced differences between communities (Cucherousset & Villéger 2015), but did not blur the quantification of the estimated trophic community metrics and allowed us to identify large-scale patterns in food-web organization across the 3 marine areas. Interestingly, the topologies of the food webs and the associated isotopic community metrics showed similar results with and without scaling the data. This was due to the fact that the full range in $\delta^{13}C$ (min−max = 25‰) and $\delta^{15}N$ (min−max = 21‰) values among the 3 marine areas was similar, with a difference between both axis of only 4‰.

The food webs were quite similar among the 3 marine areas studied in terms of structure, species composition and clustering, although we found some differences. Across a latitudinal gradient, the topology of Patagonian food webs exhibits a reduction in vertical structure and trophic diversity towards the south (Saporiti et al. 2015), meaning that food webs tend to be shorter and more redundant towards subpolar and polar waters as an outcome of a more pronounced WW structure (Ducklow et al. 2007, Saporiti et al. 2014). We evaluated the topology of food webs mainly in a longitudinal axis, from inshore (BC, CA) to offshore waters (BB). However, among the 3 food webs studied, CA is closer to central and northern Patagonia and was the area that showed metrics similar to the southern area studied by Saporiti et al. (2015). From CA towards BB and BC, a more pronounced WW structure was evident in the isotopic metrics. Marine areas can differ in species composition and functional groups, and therefore spatial segregation of taxa can influence food-web topology (Montoya et al. 2015). Overall, we found shorter food-chain lengths at BB and BC, compared to CA. Few pelagic/benthopelagic species, such as *S. fuegensis*, *M. gregaria*, *P. ramsayi* and *T. gaudichaudii*, are known to dominate the mid to low TPs in this southern region (Padovani et al. 2012, Arkhipkin &

Laptikhovsky 2013, Diez et al. 2016, 2018). The high abundance of few prey species at this level of the food web (e.g. Saporiti et al. 2015) imposes a certain feeding dependence on southern predators, shortens food-web length and increases the trophic overlap and redundancy of the overall food web (Cury et al. 2000). Several mesopredators in the CA area (e.g. hakes *Merluccius hubbsi* and *M. australis*, among others) represent important links of mobile and large-bodied species with different trophic habits increasing the food-chain length, reducing interspecific niche overlap and trophic redundancy in this marine area. Therefore, higher consumers can diversify their diet, thereby increasing omnivory and generalism (e.g. Nye et al. 2020).

In addition, higher habitat heterogeneity, as well as warmer and more productive marine areas, can sustain a higher number of species with different feeding strategies that require high resource availability (Kortsch et al. 2019). Such environmental conditions have been positively associated with food-web complexity metrics (Saporiti et al. 2015, Kortsch et al. 2019). We found low trophic diversity with lower CD values compared to those reported by Saporiti et al. (2015), considering that we have taken into account top predator data (i.e. marine mammals and seabirds), which may increase Layman metrics. Among the 3 marine areas studied, BC and BB had the most restricted trophic diversity and a high trophic redundancy and evenness, as would be expected towards Antarctic waters. These results are in agreement with the smaller isotopic niche area occupied by these communities. Limited primary productivity and lower temperatures, such as those occurring in polar waters, reduce food-web complexity, which is sustained by smaller-sized fish and crustaceans acting as important links between lower and higher trophic levels (Kortsch et al. 2019). This scenario is in agreement with environmental conditions in BC and BB (Lara et al. 2010, Almandóz et al. 2011, Barrera et al. 2017, Matano et al. 2019). In combination, all of these metrics and SEA analyses imply a slightly more structurally complex food web in CA, compared to the BB and BC marine areas.

Food-web structure, as well as the type of control that can be operating in a given marine area, is a dynamic process linked to the presence and distribution of species in a community (Young et al. 2015). Our findings may also contribute to the understanding of the structure of ancient food webs at coastal areas. A number of retrospective studies have examined food web changes over time based on the iso-

topic analysis of skeletal remains of marine fauna from shell middens in the southwestern Atlantic Ocean (e.g. Saporiti et al. 2014, Zangrando et al. 2016, Vales et al. 2017, Bas et al. 2019, 2020, Nye et al. 2020). Specifically, a reduction in the basal structure characterizes modern and coastal food webs, when compared to ancient ones (e.g. Saporiti et al. 2014, Bas et al. 2019). Higher temperatures in the past could have caused more freshwater run-off and a major supply of C3 plant debris being input into coastal marine waters (Bas et al. 2019). Since C3 plant debris is ^{13}C-depleted compared to marine phytoplankton and macroalgae (Riccialdelli et al. 2017a), its greater contribution may have increased the range of δ^{13}C baseline values measured in the past.

Furthermore, in our study, BB showed significantly lower δ^{13}C values and a broader basal structure compared to coastal areas. In BB, multiple primary resource types do not cause the isotopic variation measured at the base of its food web, since phytoplankton seems to be the only primary producer. Instead, other main driving forces have been identified, including water temperature (see Section 4.1). Consequently, a greater influence of oceanic waters in coastal areas could also have helped to spread the range in basal structure of ancient food webs.

In addition, a higher vertical structure was estimated for modern food webs compared to ancient ones (Saporiti et al. 2014, Bas et al. 2019). This difference is related to a change in the foraging strategy of pinnipeds between pre- and post-hunting settings. Reductions in their populations produced a release of inter- and intraspecific competition that may have led to the consumption of more benthic and higher trophic level prey with respect to the ones consumed in the past in the same habitat (Vales et al. 2017, Bas et al. 2019). An increase in trophic diversity and a decrease in trophic redundancy was reported between ancient and modern food webs in coastal areas and was explained by a trophic segregation between species of marine mammals and seabirds towards modern times (Saporiti et al. 2014, Bas et al. 2019). Warmer (e.g. Argentine hake *M. hubbsi*, Bas et al. 2020) and oceanic shoaling pelagic species (e.g. snoek *Thyrsites atun*, Zangrando et al. 2016) may have played an important role as WW species in the past. If this group of species was a common prey for top predators, this would explain the overlap in their isotopic niches found in the past (e.g. Bas et al. 2019). However, at present, these species are not common in shallow waters and could have been replaced by other WW species, such as *S. fuegensis*. Further-

more, ancient food webs were reconstructed with a skewed vision of the isotopic baselines of the open waters adjacent to Tierra del Fuego. In light of our data set, oceanic fish had lower δ^{15}N values compared to coastal ones. Thus, if oceanic species had been common prey also inhabiting coastal areas in the past (e.g. *T. atun*), a higher consumption of these ^{15}N-depleted prey, but at high TPs (Zangrando et al. 2016), would offer another possible explanation for the change registered in nitrogen stable isotope values in top predators from ancient to modern food webs. Climatic variation may affect the distribution of these oceanic prey through time (Bas et al. 2019), thereby altering trophic interactions along coastal areas of Tierra del Fuego. This scenario is in synergy with modern human impacts that may have pushed top predators to forage in greater areas, increasing the range of dietary sources and niche size over time (Nye et al. 2020). Future studies should further explore these hypotheses. The present research provides crucial background information regarding modern isotopic niche space and topologies of food webs to understand the effects of different natural and/or anthropogenic impacts, during past and future settings.

4.3. WW species

TP estimates represent a powerful metric to compare the position of each species/group and the whole food-chain length among regions and time periods (Young et al. 2015). The estimation of TP is particularly important in WW ecosystems, since the availability of a few species has profound consequences on the entire food web. The TDFs used in this study are an important aspect in the estimation of TP and food change length. TDFs range widely among animals, in relation to the tissue analyzed, the species, the nutritional condition of the animal, the quality of diet and body size, among many other factors (Post 2002). We acknowledge that the use of fixed values of TDF oversimplified trophic structure (e.g. food-web length) and species interactions (Hussey et al. 2014). However, we analyzed many species that have a poorly characterized diet and therefore we had the same bias in the 3 food webs analyzed. Furthermore, we estimated TPs with 2 different models with no substantial differences between them.

Within the 3 marine areas under study, a mid-trophic level group (WW level) formed by small pelagic and benthopelagic species that feed on the

planktivorous fraction and constitute a link to upper consumers, was identified through the cluster analysis. In addition to this middle group, 2 lower trophic level species, the hyperiid amphipod *Themisto gaudichaudii* and the pelagic form of *Munida gregaria*, have been suggested by previous studies to also be important links to upper consumers (e.g. Padovani et al. 2012, Diez et al. 2016, 2018). As has been observed across the major WW ecosystems of the world, the WW level can be dominated by the coexistence of 2 or more (but still relatively few) WW species that alternate, due to fluctuations in their abundances (Bakun & Broad 2003). The fluctuation of these populations has been visible on multi-annual time scales mainly attributed to a set of factors, including climate variability, density-dependent processes and fishing pressure (Bakun 2006). Thus, when the dominant species declines, the subordinate opportunistically replaces the first. The species we considered to be WW in the studied areas exhibited differences in their isotopic niche, such as niche width and TP estimated. Thus, the availability of these WW species may have important implications in the structure of the overall trophic webs, by affecting their putative predators and their own prey, as has been detected between ancient and modern food webs in the region.

In our study case, the Fuegian sprat constitutes the only pelagic species with abundances high enough to be considered the most important species in the trophodynamics of CA and BC (Sánchez et al. 1995, Madirolas et al. 2000, Sabatini et al. 2004, Diez et al. 2018). In addition, it is an important prey item for many top marine predators in the region (e.g. Raya Rey et al. 2007, Riccialdelli et al. 2013, Scioscia et al. 2014, Haro et al. 2016, Harris et al. 2016). The MPAN-BB has also been identified as a major spawning and nursery ground for *S. fuegensis* (García Alonso et al. 2018).

We analyzed adult individuals collected in BB (during cruise VA1418 in November), and a school of *S. fuegensis* was sighted during winter in the area (L. Riccialdelli pers. obs., BOPDAGO-2018). The low $\delta^{13}C$ and $\delta^{15}N$ values of muscle from these individuals indicate a feeding period in the oceanic food web of BB, but not in any other area near it (e.g. CA or BC), or even in the nearest marine environment of the Falkland/Malvinas Islands (see Quillfeldt et al. 2015). The importance of *S. fuegensis* in each marine area seems to be a clear consequence of its special position in the food webs as has been seen for other pelagic organisms in other marine regions (e.g. krill in Antarctic waters, Ducklow et al. 2007, Jordán

2009). Furthermore, based on our estimations, *S. fuegensis* exhibited different estimated TPs (with the lowest in BC), but occupied mid to low TPs in all 3 study areas, meaning that it has a similar trophic role in a regional context. Myctophids are known to be a dominant mesopelagic group at a tertiary level in oceanic waters that play a key role in pelagic food webs (Saunders et al. 2014). In the BB area, larval stages of myctophids have been collected onboard the same research vessels used in the present work (D. Bruno unpubl data), but neither juvenile nor adult stages were collected with the used fishing gear. Thus, for now, *S. fuegensis* constitutes the only pelagic planktivorous species in the BB area, and based on the isotope values, this population could represent a different stock from the coastal sprat, at least from an ecological point of view. However, further studies should be conducted to investigate this possibility.

The longtail southern cod is one of the most abundant benthopelagic nototheniids in southern Patagonia, including BB, and also constitutes an important prey for meso and top consumers (Arkhipkin & Laptikhovsky 2013). This species can feed over a wide range of planktonic (e.g. copepods, *T. gaudichaudii*, euphausiids, jellyfish and salps) and benthic organisms (e.g. *Munida* spp., isopods, amphipods) and can easily switch diet from plankton to benthos (Laptikhovsky & Arkhipkin 2003, Arkhipkin & Laptikhovsky 2013). This plasticity in the diet explains the broader isotopic niche area that characterized our isotopic data set in relation to this species. In the BB and CA areas, *P. ramsayi* was the most abundant fish collected during the research cruises. Its isotopic niche also does not overlap entirely with that of *S. fuegensis* in any of these marine areas, and thus this species and sprat are the 2 most important WW species in both areas.

Several species of *Patagonotothen* are also present in BC; however, they are mostly benthic and coastal species (Ceballos et al. 2019). In addition, during the research cruises, we collected only a few individuals of *P. ramsayi* with the bottom trawling operations in this area. The squat lobster *M. gregaria* is one of the most abundant crustaceans and is prey for many species in BC and southern Patagonia (e.g. Scioscia et al. 2014, Diez et al. 2016). This species also links the benthic and the pelagic realm, contributing to the vertical carbon flow. In particular, *M. gregaria* has 2 morphotypes, '*subrugosa*' with full benthic habits as adults and '*gregaria*' that has both pelagic and benthic forms during the adult stage (Lovrich & Thiel

2011). The pelagic form of *M. gregaria* occurs at high densities in BC (Diez et al. 2016, 2018) in an analogous manner to Antarctic krill *Euphausia superba* in Antarctic waters (Ducklow et al. 2007).

Polar water zooplankton, like copepods and krill, tend to accumulate lipids for overwintering and reproduction (Hagen & Auel 2001). *M. gregaria* stores lipids mainly in the hepatopancreas and uses this energy supply for reproduction and molting (Romero et al. 2006). Burkholder et al. (1967) found that *M. gregaria* from Tierra del Fuego had a higher fat content and caloric value than Antarctic krill. *M. gregaria* and *S. fuegensis* had similar energy density (7.15 vs. 7.5 kJ g^{-1}, respectively; Romero et al. 2006, Ciancio et al. 2007, Scioscia et al. 2014), much higher than all the fishes reported to date in BC (4.21– 6.26 kJ g^{-1}, Fernández et al. 2009). These estimations were made on benthic *Munida*. Until now, there has been no proximal analysis or energy density estimation made on the pelagic form. However, to remain in the water column, the pelagic form reduces its density by increasing its water content and reducing ash and calcium content (Lovrich & Thiel 2011). Also, it optimizes its energetic budget with a higher capacity for aerobic metabolism than the benthic form (C. Avalos & G. Lovrich unpubl. data, cited by Lovrich & Thiel 2011), which may directly influence its fat storage. In addition, in Baja California, Smith et al. (1975) found no differences in chemical composition between the pelagic and benthic form of *Pleuroncodes planipes*, a key species in that system.

Furthermore, the availability of pelagic swarms of *M. gregaria* has increased in terms of occurrence and abundance over the last 10 yr in BC and southern Patagonia (Diez et al. 2016, 2018). Hydroacoustic surveys revealed that pelagic aggregations of *M. gregaria* and *S. fuegensis* occur in BC throughout the year. However, a negative and more intense interaction between them seems to occur during summer, when they showed greater spatial overlap (Diez et al. 2018). In this sense, the pelagic form of *M. gregaria* constitutes an easy and highly valuable energy source, and thus may constitute an important prey item in the diet of upper consumers, which require high prey concentrations to gain energy.

In BC, previous studies have found no isotopic differences between the benthic forms of both morphotypes ('*subrugosa*' and '*gregaria*'), having similar TP estimations (Pérez Barros et al. 2010, Riccialdelli et al. 2017a) to each other and to those from northern Patagonian waters (e.g. San Jorge Gulf, Funes et al. 2018). We estimated lower TPs for the pelagic stage of '*gregaria*' than for the benthic form. The same pattern was reported by Funes et al. (2018) in the San Jorge Gulf, which could be the result of the different contribution of the pelagic and benthic energy pathways in the food webs. The TP occupied by both forms/stages (pelagic and benthic) gives them an important role in potentially shortening the food-web length.

In this way, *M. gregaria* and *S. fuegensis* can be considered WW species in light of their mid to low TPs and because of the key role they play in terms of energy transfer in the trophodynamics of the BC area. In the BB area, we analyzed only 1 sample of pelagic *M. gregaria*, which is not common in the area. In contrast, the species commonly found in BB are fully benthic forms, *M. spinosa* and *M. gregaria* '*subrugosa*' (not analyzed), which probably play the same trophic role as their benthic counterparts in CA and BC.

The functional group of mesopredators, such as the Patagonian grenadier *Macruronus magellanicus*, Argentine and southern hakes, Patagonian toothfish *Dissostichus eleginoides*, southern blue whiting *Micromesistius australis* and thornfish *Cottoperca trigloides*, are also important for the food-web structure (being both predators and prey). As juveniles, these species can at least temporally dominate the WW level, but as adults, they became semi-demersal or demersal predators (Bakun 2006). These mesopredators may constitute an important alternate food supply available to top predators in CA (Bas et al. 2020, Nye et al. 2020), where we found a more complex system than in the BC and BB areas (e.g. higher values of community-wide metrics).

4.4. Top predators

Generally, seabirds and marine mammals are considered top predators. However, based on our estimations, they occupied from the third to the fifth TPs. The highest positions in the oceanic BB were occupied by offshore cetaceans, such as long-finned pilot whales. Offshore predators are known to have wide foraging grounds, and thus high estimated SEA$_B$, preferring the Patagonian slope break around islands and upwelling areas, such as the ones we found around the BB area (Riccialdelli et al. 2010, 2017b). Meanwhile in coastal ecosystems, South American sea lions and South American fur seals were the most important and highest predators of the analyzed food webs, as also reported in previous studies (Drago et al. 2009, Vales et al. 2017). An important point to consider is the fact that both spe-

cies are known to forage on a wide range of habitats from inshore to offshore areas, thereby increasing their isotopic niche (Nye et al. 2020).

Meanwhile, coastal dolphins (e.g. Commerson's dolphin *Cephalorhynchus commersonii*) and porpoises (e.g. Burmeister's porpoise), seabirds (e.g. cormorants, penguins) and oceanic whales (e.g. *Balaenoptera* sp.) mainly feed on mid to low trophic level species (Riccialdelli et al. 2010, 2013, Raya Rey et al. 2012, Scioscia et al. 2014, Haro et al. 2016, Harris et al. 2016). Thus they exhibit lower TPs, as we found in this study and in accordance with previous information. Minke whale samples were considered as a proxy for oceanic whales that are known to forage on small pelagic crustaceans (euphausiids) in sub-Antarctic and Antarctic waters (Van Waerebeek et al. 2010), and consequently occupy low TPs. However, other species of whales like fin whales *Balaenoptera physalus* that have been seen in the BB area (N. Dellabianca unpubl. data), or humpback whales *Megaptera novaeangliae*, a common cetacean for the Fuegian archipelago, are known to forage on pelagic crustaceans (euphausiids and pelagic *M. gregaria*) and small pelagic fish (*S. fuegensis*) (Haro et al. 2016). Thus, as we expected, these species occupy mid-level TPs as a reflection of their known diet.

Since many top predators can be considered generalists, their ability to exert top-down control may depend on the variety of alternate prey species available to them (Madigan et al. 2012), but also would depend on the distances they move and how much time they spend foraging in each marine area in terms of inshore versus offshore waters. Nonetheless, the WW species considered for each area may constitute an important part of predator diets; they also depend on a wide variety of prey species, such as benthic organisms that were not considered in their full context in this study, but that contribute to a high level of omnivory.

4.5. Concluding remarks

In light of our results, the BC and BB areas seem to have a more pronounced WW structure than CA. Identifying the most influential species in these food webs is particularly important to maintain ecosystem integrity and the supply of ecosystem services (Jordán 2009). WW species can be considered as major interactors, having many links to other members of the food web. A long-term plan for managing biodiversity loss should focus on the protection of

these species, but also on key areas for them. The fact that BB has been identified as a spawning and nursery ground for *S. fuegensis* and *P. ramsayi*, considered as 2 WW species in a regional context, gives this oceanic sector additional relevance for conservation. It is necessary to continue to use different approaches to identify unusually important or influential species and specific areas of importance for them (e.g. spawning areas). In addition, continuing with the examination of regional variation and long-term changes (e.g. responses to top-down and bottom-up forces) is crucial to systematically compile information on the integrity, structure and functioning of these subpolar ecosystems in a way that would help to assess the potential short- and long-term consequences of natural and anthropogenic impacts.

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