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Niche partitioning among demersal marine fishes at the southern tip of South America

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ABSTRACT: Niche differentiation is a means by which species can coexist and avoid competition. In marine food webs, large demersal fish often couple different trophic pathways and can be targets of valuable fisheries. This is the case for long tail hake *Macruronus magellanicus*, Patagonian toothfish *Dissostichus eleginoides*, southern blue whiting *Micromesistius australis*, and southern hake *Merluccius australis*, which coexist in the southernmost region of the southwestern Atlantic Ocean. In this study, C and N stable isotope and stomach content analyses were used to evaluate possible niche partitioning among these 4 species. Long tail hake and southern blue whiting mainly eat crustaceans, with great overlap in their diet spectra, but they differentiate in their spatial distribution. Southern hake and Patagonian toothfish mainly feed on fish, including the other 2 species, and exploit prey from a broad spatial area. These results suggest a spatial compartmentation of the food web at lower trophic levels, with demersal fish at the higher levels linking distant compartments. Therefore, results of this study show similarities and differences among these 4 demersal fish species, in the trophic and spatial dimensions of their niches, suggesting niche differentiation and probably different roles in the food web.

KEY WORDS: Niche partitioning · Demersal fish · $\delta^{13}C$ · $\delta^{15}N$ · Southwestern Atlantic Ocean

1. INTRODUCTION

Niche differentiation is a means by which organisms avoid competition and is therefore a key determinant for the coexistence of apparently similar species (Chase & Leibold 2003). In the trophic dimension, segregation can occur through the differential consumption of prey items (i.e. resource partitioning), the differential use of areas where species feed or hunt (i.e. habitat partitioning), or their differential timing of foraging peaks (daily or seasonally, temporal partitioning; Schoener 1974). This niche differentiation in coexisting species can be the result of variable intrinsic ecological traits, which can reduce competition intensity (Pianka 1974), or differentiation can result from constraints imposed by the presence of competitors (Ross 1986, Gerking 1994). The understanding of niche partitioning or overlap among coexisting similar species can be important to identify potential ecological interactions.

Ecological interactions in the ocean are particularly difficult to determine, and suitable comparisons of diets of coexisting fish species can be a helpful tool to identify possible competition or predator–prey interactions (e.g. Sala & Ballesteros 1997, Barbini & Lucifora 2012). Demersal fishes are intermediate predators and usually exhibit temporal and

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spatial variations in their diet (e.g. McClatchie et al. 1997, Connell et al. 2010, Dunn et al. 2010), changing roles in their communities throughout their ontogeny (e.g. Park et al. 2017, Hayden et al. 2019). Some species change their trophic niche while growing by substantially modifying their diet, while others expand their trophic niche by incorporating new items into their diet (Hammerschlag-Peyer et al. 2011). In boreal and temperate regions, large demersal teleost fishes dominate and are typically slow-growing generalist feeders (van Denderen et al. 2018), which can couple different trophic pathways. Demersal fish species coexist and interact among them, and given that they are usually targeted by productive fisheries, it is essential to understand their role and interactions within the food web to include them in management considerations.

The southern tip of South America is inhabited by several demersal fishes (Cousseau et al. 2020), some of which are targeted by valuable fisheries (e.g. Laptikhovsky & Brickle 2005, Tascheri et al. 2010, Alemany et al. 2014, Giussi et al. 2016a,b). Long tail hake *Macruronus magellanicus*, Patagonian toothfish *Dissostichus eleginoides*, southern blue whiting *Micromesistius australis*, and southern hake *Merluccius australis* stand out in the catch records of fleets operating in the southwestern (SW) Atlantic Ocean between 34 and 58° S (e.g. Wöhler et al. 2004, Collins et al. 2010, Giussi et al. 2016a,b, Gorini & Lukaszewicz 2022). All species extend their distribution from the southeastern (SE) Pacific Ocean to the SW Atlantic Ocean, south of Tierra del Fuego and around the Falkland/Malvinas Islands (Wöhler et al. 2004, Collins et al. 2010, Giussi et al. 2016a,b). In the SW Atlantic Ocean, the distribution of these 4 species is closely linked to the sub-Antarctic waters of the Malvinas Current (Wöhler et al. 2004, Collins et al. 2010, Giussi et al. 2016a,b). South of 47° S, all 4 species are found on the continental slope and shelf. However, there are variations in the latitudinal and depth limits that characterize each species. For instance, long tail hake and southern hake are found at shallower depths (50–800 and 100–400 m, respectively) than the other species, and their southern distribution does not extend beyond 56° S (Giussi et al. 2016a,b). On the other hand, southern blue whiting and Patagonian toothfish reach higher latitudes associated with Antarctic waters and greater depths (100–800 m and 2000 m, respectively; Wöhler et al. 2004, Collins et al. 2010). Therefore, although the extent and form of distribution differ among the 4 species (Fig. 1), they coexist in the SW Atlantic Ocean.

The diets of these 4 demersal fish species in the SW Atlantic Ocean show both differences and similarities. The long tail hake and southern blue whiting mainly feed on the same macro-zooplanktonic species (Wöhler et al. 2004, Brickle et al. 2009, Giussi et al. 2016b). The long tail hake reaches greater size (up to 110 cm total length; Giussi et al. 2016b) than the southern blue whiting (up to 60 cm total length; Cassia 2000), and it incorporates fishes and cephalopods into its diet while growing (Brickle et al. 2009, Giussi et al. 2016b). On the other hand, Patagonian toothfish and southern hake are large species (maximum total length = 200 and 100 cm, respectively), and both are characterized as ichthyophagous (Giussi et al. 2016a, Sallaberry-Pincheira et al. 2018, Troccoli et al. 2020), although Patagonian toothfish also consume cephalopods and macro-crustaceans (Sallaberry-Pincheira et al. 2018, Troccoli et al. 2020). All studies on the diet of these demersal fishes were performed encompassing different areas and periods of time; and although results suggest interspecific diet overlap among them, at least during some periods of their ontogeny, this was not directly evaluated in the SW Atlantic Ocean.

Stable isotope analysis (SIA) of C and N is a complementary tool to evaluate hypotheses on predator feeding behavior (e.g. Peterson & Fry 1987, Post 2002). Values of δ^{15}N are indicators of the trophic position of consumers, while δ^{13}C values are useful in determining the primary source of food webs (Peterson & Fry 1987, Post 2002, O'Reilly et al. 2003). Unlike stomach contents that reflect diet over a short time scale (hours or a few days) for a given location, SIA allows the study of trophic relationships by integrating dietary information over relatively long time periods (i.e. several weeks to months; Thomas & Crowther 2015, Vander Zanden et al. 2015). In this context, the δ^{13}C and δ^{15}N values can be used as the main axes within the ecological niche defined by Hutchinson (1957) in a 2-dimensional space called the 'isotopic niche' (Newsome et al. 2007, Jackson et al. 2011). Isotopic niches are a good tool to compare similar species that coexist but might have trophic or habitat segregations avoiding competition (Newsome et al. 2007). On the other hand, stomach contents provide accurate information on the identity of the prey items consumed to determine the trophic spectra of species (Baker et al. 2014). Therefore, in this study, we comparatively evaluated, with stable isotopes and stomach contents, whether there are differences in trophic niches among 4 species of fish of commercial interest that coexist in the SW Atlantic Ocean, from ~52 to ~56° S, during the warm season.

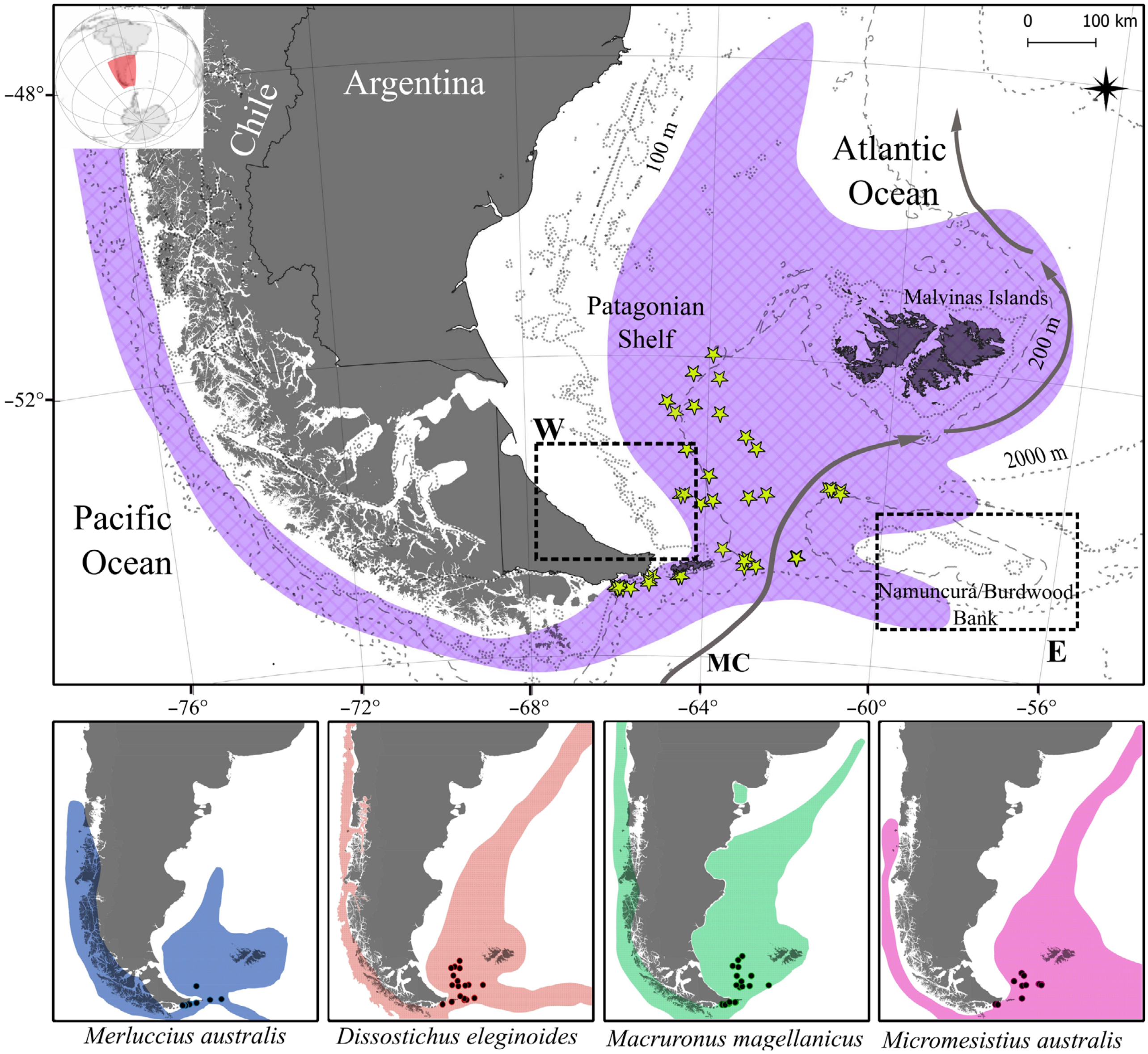

Fig. 1. Study area in the southwestern Atlantic Ocean, geographic references, and circulation patterns. The violet area represents the zone where the 4 study species coexist, and stars are sampling stations. Dashed lines indicate the 100, 200, and 2000 m isobaths, while arrows indicate the Malvinas Current (MC). Dotted rectangles represent the west (W) and east (E) zones. Small maps show the sampling stations and distribution of each species: southern hake *Merluccius australis* (adapted from Giussi et al. 2016a), Patagonian toothfish *Dissostichus eleginoides* (adapted from Collins et al. 2010), long tail hake *Macruronus magellanicus* (adapted from Giussi et al. 2016b), and southern blue whiting *Micromesistius australis* (adapted from Wöhler et al. 2004), provided by the Remote Sensing Program of INIDEP

2. MATERIALS AND METHODS

2.1. Study area

The study was performed in the southern portion of the SW Atlantic Ocean between ~52 and ~56° S, from 130 to 1250 m depth. The area includes part of the Patagonian shelf and shelf break, and an area south of Tierra del Fuego (Fig. 1). Samples of long tail hake, Patagonian toothfish, southern blue whiting, and southern hake were taken on commercial fishing vessels by personnel of the Fisheries Research Assistants Program of the National Institute for Fisheries Research and Development (INIDEP, Argentina). Sampling occurred between October (2016) and April (2017), which is considered the 'warm period' (Rivas

& Pisoni 2010). All vessels used bottom trawls to fish in the area for variable periods of time, throughout the entire 24 h day, until the net was full.

2.2. Sample collection

Individuals of each species were collected (n = 96 long tail hake, 61 Patagonian toothfish, 53 southern blue whiting, and 25 southern hake) and immediately frozen (−20°C) to later perform SIA of C and N and stomach content analysis. Total length (TL) to the lower cm was recorded, and individuals were classified into juveniles or adults according to their length at maturity (TL_{50}; long tail hake = 58 cm, Giussi et al. 2016b; Patagonian toothfish = 82 cm, Prenski & Almeida 2000; southern hake = 59 cm, Giussi et al. 2016a; southern blue whiting = 38 cm, Pájaro & Macchi 2001).

2.3. Sample preparation for SIA

A sample of dorsal muscle tissue was extracted from each individual, dried in an oven (60°C for 72 h), milled, weighed, and packed into tin capsules. Samples were later analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer in the Stable Isotope Facility, University of California, Davis (USA). Stable isotopes were expressed in delta notation as differences (‰) from a standard:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \qquad (1)$$

where R_{sample} refers to the ratio of heavy isotope to light isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$), and $R_{standard}$ is the Vienna Pee Dee Belemnite limestone standard for carbon or the atmospheric N_2 standard for nitrogen (Gonfiantini 1978, Coplen et al. 1992).

To avoid bias in the interpretation of $\delta^{13}C$ values due to lipid content (Sweeting et al. 2006, Post et al. 2007, Logan & Lutcavage 2008, Matley et al. 2016, Skinner et al. 2016), lipid correction was performed for all species. For long tail hake and Patagonian toothfish, which are species that accumulate high lipid content in their muscle (C:N > 3.5), we used a specific formula for correction. To perform this correction on Patagonian toothfish, a sample of muscle tissue was taken in duplicate from 25 randomly selected specimens to analyze C stable isotopes in subsamples with and without chemically extracted lipids following Elliott et al. (2017). A regression model was adjusted to predict the $\Delta\delta^{13}C$ ($\delta^{13}C$ with − $\delta^{13}C$ without lipid) considering the C:N ratios as the independent variable following Post et al. (2007). The resulting equation is: $\delta^{13}C_{corrected} = \delta^{13}C_{untreated} - 2.52 + 1.01 \times C{:}N$ (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m739p191_supp.pdf). In the case of long tail hake, the same correction was previously performed on a subset of samples from this same data set (Alvarez et al. 2022), resulting in the following equation: $\delta^{13}C_{corrected} = \delta^{13}C_{untreated} - 6.85 + 2.26 \times C{:}N$. In the case of southern blue whiting and southern hake, no specific formula exists and therefore correction was performed following the equation of Post et al. (2007).

2.4. Diet of fish

Stomach contents were extracted and analyzed using the same individuals that were sampled for SIA. Prey items were identified to the lowest possible taxonomic level by using identification keys, illustrative guides, bibliographic background (e.g. Bremec et al. 2003, Roux et al. 2007, Xavier & Cherel 2009), and consultations with specialists. Prey items were counted and weighed to the nearest 0.001 kg. The contribution of each prey to the diet was evaluated by calculating the percentage frequency of occurrence (%F = number of stomachs in which a given prey was found/number of stomachs with food × 100), the numerical percentage (%N = number of a given prey/number of total prey found × 100), and the percentage of weight (%W = weight of a given prey/total weight of prey found × 100). The index of relative importance (IRI) was then calculated as: IRI = %F × (%N + %W) according to Pinkas et al. (1971), expressed as a percentage (%IRI; Cortés 1997).

2.5. Statistical analysis

2.5.1. Size and species effects

In order to evaluate possible differences in $\delta^{13}C$ and $\delta^{15}N$ among species and size, generalized linear models (GLMs) were adjusted, taking $\delta^{13}C$ and $\delta^{15}N$ as response variables and TL and species as continuous and categorical independent variables, respectively. A null model was included in the model selection approach to test the hypothesis that none of the independent selected variables influenced the values of $\delta^{13}C$ and $\delta^{15}N$. All models had a Gaussian error distribution and identity link function (Crawley 2013). Akaike's information criterion (AIC) and Akaike's weight (*w*) were used for model selection (Burnham & Anderson 2002, Burnham et al. 2011). AIC values are presented as AIC differences (ΔAIC). Goodness of fit was assessed by the percentage deviance explained (%DE). Predicted values of $\delta^{13}C$ and $\delta^{15}N$ by the adjusted models for specific values of TL (40, 60, and 80 cm) were calculated and compared among species. For southern blue whiting, 80 cm was not considered, given that this value is out of range of TL values of this species. All model estimations and graphical representations were performed with the packages 'ggeffects' and 'ggplot2' (Lüdecke 2018) in R 4.3.1 (www.R-project.org).

2.5.2. Isotopic niches

Isotopic niches were calculated for each species and life stage. Isotopic niches were estimated for each group as the bivariate ellipses on $\delta^{13}C$ and $\delta^{15}N$ dimensions using Bayesian estimates of standard ellipse area (SEA_B), calculated using the R package 'SIBER' (Jackson et al. 2011). SIBER Markov chain Monte Carlo (MCMC) parameters used were 100 000 iterations, 1000 burn-in, 5% thinning, and 3 independent chains. Coherence among chains was determined for each model parameter using a Gelman-Rubin diagnostic of <1.1. The 95% credible intervals of posterior distributions of SEA_B, as niche width estimates, were calculated for each group, and the groups were considered different when no overlap occurred among them. Percentage overlap of niche space between groups was measured based on SEA_B using the 'bayesianOverlap' function in the R package 'SIBER' (Jackson et al. 2011). The 95% confidence intervals for SEA_B overlap were estimated based on the posterior distributions of the 0.4 and 0.95 fitted ellipses, considered as the core isotopic niche and complete isotopic niche respectively (Buss et al. 2022). The overlap between 2 groups was expressed as the percentage of the area summing both groups, with 100% indicating complete overlap and 0% indicating complete segregation.

2.5.3. Mixing models

The relative contribution of the potential prey items in the diet of juveniles and adults of each species was assessed with a Bayesian stable isotope mixing model using the 'MixSIAR' package in R (Stock et al. 2018). Stable isotope values of the potential prey items were taken from published data by Riccialdelli et al. (2020). Those data come from samples that were taken between 2013 and 2016 in areas near the study site. They found that $\delta^{13}C$ and $\delta^{15}N$ of the potential prey items differed among an area close to Burdwood Bank (east of the study site, hereafter E zone; Fig. 1) and an area close to the shelf and Tierra del Fuego (west of the study site, hereafter W zone; Fig. 1). Given that both zones are potential feeding grounds for the demersal fish species, potential prey from both zones were considered in the mixing model. The purpose of this analysis is to determine the importance in the diet of sources of different spatial origin. Given the similarities in stable isotope values among the different items (Riccialdelli et al. 2020), we were unable to discriminate the particular items, but we could distinguish among 2 large groups: crustaceans and fishes/squids. For crustaceans, mean values of the amphipod *Themisto gaudichaudii*, euphausiids, and the squat lobster *Grimothea* (= *Munida*) *gregaria* were considered. For fishes and squids, mean values of sprats, myctophids, notothenids, and squids (*Illex argentinus* in the W zone and *Dorytheutis gahi* in the E zone; Riccialdelli et al. 2020) were used. Given that long tail hake and southern blue whiting are potential prey items for Patagonian toothfish and southern hake, they were included in the mixing models. MixSIAR models were run for each consumer with maturity stage as a fixed factor (2 levels: juveniles and adults) and uninformative priors. No specific trophic enrichment factors (TEFs) exist for large demersal teleosts; we therefore used classical values (1 and 3.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) but considering higher variability (SD = 1 for both). The TEFs used encompass the different values for teleost marine fishes from recent reviews (from 2.5 to 3.8‰ for $\delta^{15}N$ and between 0.5 and 1.6‰ for $\delta^{13}C$; Canseco et al. 2022, Stephens et al. 2022, 2023). MCMC sampling was conducted using 3 chains, a chain length of 100 000, and a burn-in of 50 000. Convergence was examined with Gelman-Rubin, Heidelberger-Welch, and Geweke diagnostic tests.

3. RESULTS

3.1. Size and species effects on stable isotope values

$\delta^{13}C$ values ranged between −21.7 and −15.8‰. Southern blue whiting had the most depleted ^{13}C values, while long tail hake had the most enriched ones. On the other hand, southern hake showed higher $\delta^{15}N$ values (14.6 ± 1.3‰), while southern blue whiting had the lowest $\delta^{15}N$ values (10.9 ± 0.7‰; Table S1).

$\delta^{13}C$ decreased with TL in Patagonian toothfish, southern blue whiting, and long tail hake, but did not vary with size in southern hake (Table 1, Fig. 2). The rate of decrease was higher for Patagonian toothfish and southern blue whiting compared to long tail hake (Fig. 2). Predicted $\delta^{13}C$ values at all TL levels (40, 60, 80 cm) were higher in long tail hake than in the other species (Table 2). Southern blue whiting showed lower values than the other species, while no differences were found between Patagonian toothfish and southern hake (Fig. 2, Table 2).

$\delta^{15}N$ decreased with size in Patagonian toothfish and long tail hake, but did not vary with size in southern blue whiting and southern hake (Table 1, Fig. 2). At low values of TL, predicted $\delta^{15}N$ showed similar values for southern hake, Patagonian toothfish, and long tail hake, and lower values for southern blue whiting (Table 2). On the other hand, at 60 and 80 cm TL, all species showed different values (Table 2). Southern hake had the highest values, followed by long tail hake, Patagonian toothfish, and southern blue whiting (Table 2, Fig. 2).

3.2. Comparison of isotopic niches

Differences in isotopic niche areas were found between long tail hake juveniles and adults. The niche area was wider in juveniles than in adults, and both groups showed 44% overlap (SD = 8%). On the other hand, southern blue whiting showed wider niche isotopic area in adults than juveniles, with an overlap of 30% (SD = 8%). Patagonian toothfish did not show a difference in the area but exhibited a 39% overlap (SD = 7%) between juveniles and adults (Fig. 3; Table S2).

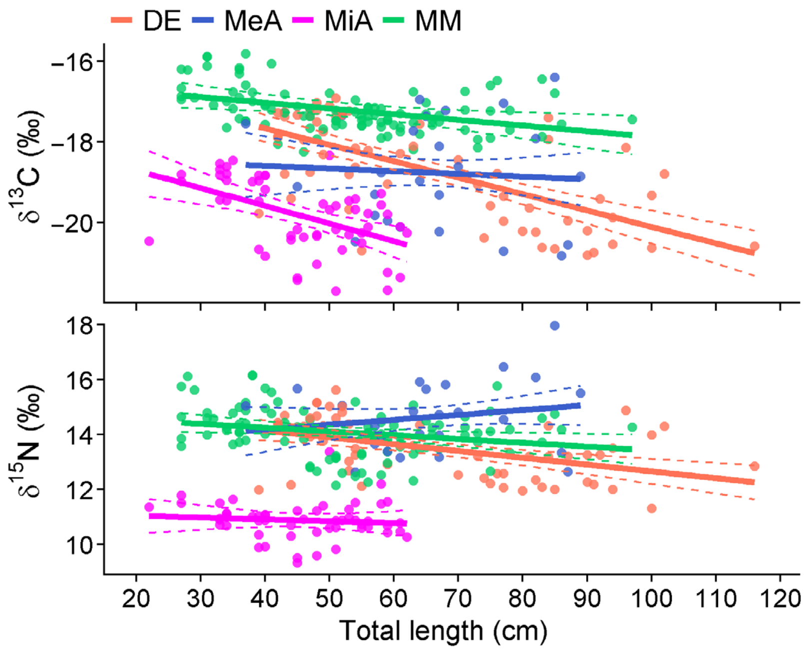

Fig. 2. Generalized linear models (GLMs) with an identity link function and a Gaussian error distribution, that explain $\delta^{13}C$ and $\delta^{15}N$ values as a function of total length for 4 studied demersal fish species in the southwestern Atlantic Ocean. The solid line is the function estimated by the GLM, the dashed lines represent 95% confidence intervals, and the circles represent point values. DE: Patagonian toothfish *Dissostichus eleginoides*; MeA: southern hake *Merluccius australis*; MiA: southern blue whiting *Micromesistius australis*; MM: long tail hake *Macruronus magellanicus*

Table 1. Ranked generalized linear models for $\delta^{13}C$ and $\delta^{15}N$ values of long tail hake *Macruronus magellanicus*, Patagonian toothfish *Dissostichus eleginoides*, southern blue whiting *Micromesistius australis*, and southern hake *Merluccius australis* dorsal muscle. Models in **bold** indicate the top ranked model according to differences in Akaike's information criterion (ΔAIC), AIC weights (*w*), and percentage of deviance explained (%DE)

Response	Model	df	ΔAIC	*w*	%DE
$\delta^{13}C$	**Total length + species + total length × species**	**9**	**0.0**	**0.997**	**67.1**
	Total length + species	6	11.8	0.003	64.5
	Species	5	65.8	<0.001	55.0
	Total length	3	234.3	<0.001	6.3
	Null	2	247.5	<0.001	0
$\delta^{15}N$	**Total length + species + total length × species**	**9**	**0.0**	**0.82**	**70.3**
	Total length + species	6	3.0	0.18	69.2
	Species	5	17.6	<0.001	66.9
	Total length	3	271.4	<0.001	1.0
	Null	2	271.7	<0.001	0

Table 2. Predicted generalized linear model values (95% CI) for the slope of the relationship between isotopic values and total length (TL) for each species and for $\delta^{13}C$ and $\delta^{15}N$ at different levels of TL (40, 60, 80 cm). * indicates significant relationship (beta ≠ 0); different superscript letters indicate significant differences among species (all $p < 0.05$)

Estimates	*Merluccius australis*	*Macruronus magellanicus*	*Dissostichus eleginoides*	*Micromesistius australis*
Beta	−0.03, 0.02	−0.02, 0*	−0.05, −0.03*	−0.07, −0.02*
$\delta^{13}C$				
40 cm	−19.32, −17.86^{a}	−17.24, −16.82^{b}	−18.0, −17.33^{c}	−19.84, −19.34^{d}
60 cm	−19.09, −18.37^{a}	−17.49, −17.13^{b}	−18.69, −18.27^{b}	−20.86, −20.08^{c}
80 cm	−19.33, −18.39^{a}	−17.92, −17.27^{b}	−19.55, −19.04^{b}	–
Beta	−0.01, 0.05	−0.03, 0*	−0.04, −0.01*	−0.03, 0.02
$\delta^{15}N$				
40 cm	13.37, 14.98^{a}	14.02, 14.48^{a}	13.78, 14.51^{a}	10.63, 11.19^{b}
60 cm	14.14, 14.93^{a}	13.77, 14.17^{b}	13.41, 13.88^{c}	10.35, 11.21^{d}
80 cm	14.37, 15.41^{a}	13.34, 14.06^{b}	12.87, 13.43^{c}	–

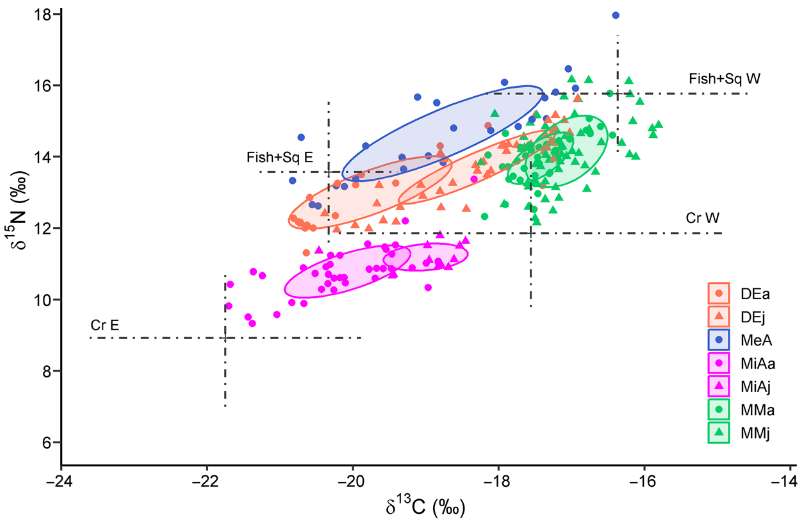

Fig. 3. Individual stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and isotopic niches of juveniles (triangles) and adults (circles) of 4 demersal fish species in the southwestern Atlantic Ocean. Solid lines enclose the standard ellipse (SEA, fits 40% of the data) for each group estimated by SIBER analysis. Species abbreviations as in Fig. 2 (suffixes — a: adults; j: juveniles). Dotted lines correspond to mean (intersection) $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of the most likely food sources, corrected by trophic discrimination factors ($\Delta^{15}N = 3.4 \pm 1$ and $\Delta^{13}C = 1 \pm 1$). Fish+Sq W (Fish+Sq E): fishes and squid from thewest (east) zone; Cr W (Cr E): crustaceans from west (east) zone

When comparing species, southern hake exhibited the largest isotopic niche area, which was around 30% larger than those of the other 3 species (Fig. 3; Table S3). The isotopic niche area of juvenile Patagonian toothfish was similar to that of juvenile long tail hake and adult southern blue whiting (Fig. 3; Table S3). The narrowest areas were observed in long tail hake adults and southern blue whiting juveniles (Fig. 3; Table S3). Considering the complete niche, southern blue whiting juveniles showed a low overlap (<5%, SD = 6%) with the other groups (for all pairwise comparisons, see Tables S2 & S4). The greatest mean overlaps found were between juvenile Patagonian toothfish and adults (32%, SD = 6%) and juveniles (32%, SD = 4%) of long tail hake (Table S2). There were also overlaps between southern hake and both adults (41% SD = 7%) and juveniles (28% SD = 5%) of Patagonian toothfish (Table S2).

3.3. Contribution of sources according to mixing models

The posterior distributions of the mixing models showed different contributions of sources for the different demersal fish species. Fishes and squid, and crustaceans from the W zone were the main components in the diet of long tail hake, with no differences between juveniles and adults (Fig. 4). High correlations (−0.78) between fishes/squid and crustaceans from the W zone were found, adding uncertainty in differentiating the contributions of these 2 sources, but both contributed more than 85% to their diet. On the other hand, for adult southern blue whiting, the contribution of crustaceans was higher from the E zone (57.2 ± 8.7%) than from the W zone (18.1 ± 10.2%). However, for juveniles, the contribution of crustaceans of the E zone (39.6 ± 9.6%) was similar to that of the W zone (35.4 ± 14.1%). For Patagonian toothfish, similar contrib-

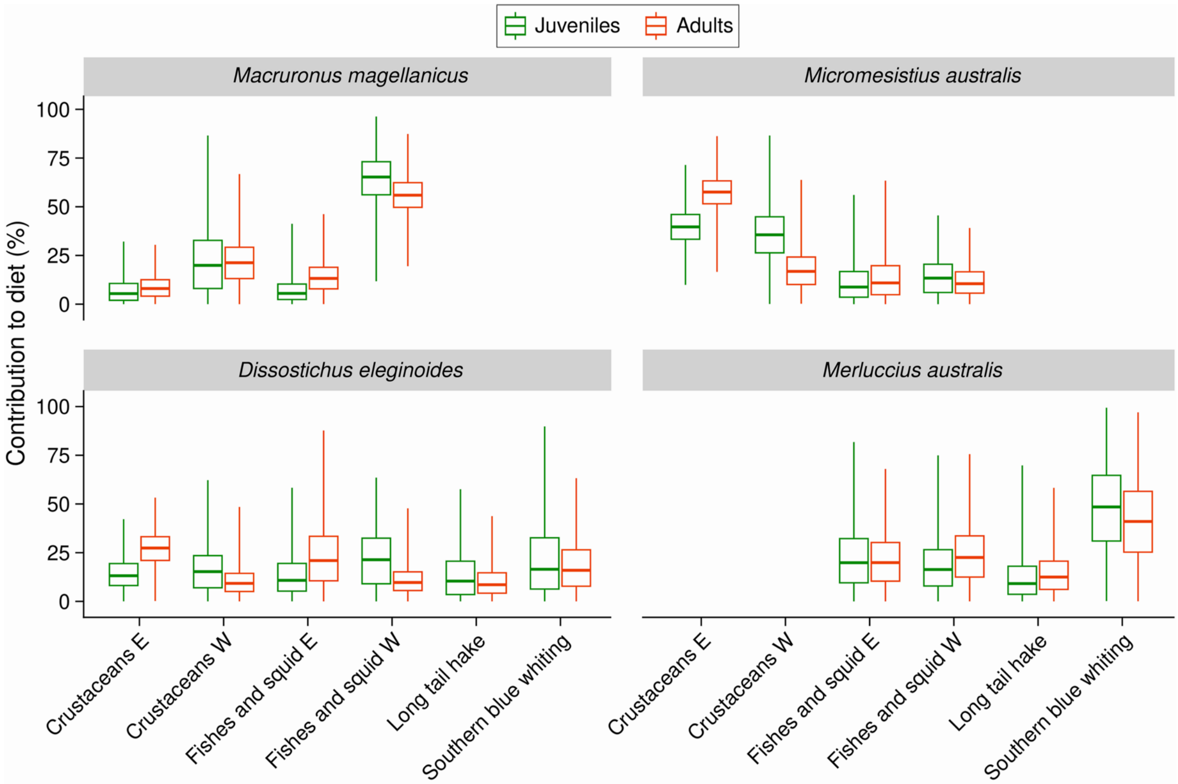

Fig. 4. Percentage of the contribution of the different prey items in the diet of 4 demersal fish species in the southwestern Atlantic Ocean, estimated by the posterior distribution of stable isotope Bayesian mixing models, considering juveniles and adults. Bar: median; box: interquartile range; whiskers: min.—max. E: east zone; W: west zone (see Fig. 1)

utions of all sources were found, with no differences between juveniles and adults except for a higher contribution of crustaceans in the E zone in adults (27.0 ± 9.3%; Fig. 4). For southern hake, the model showed a high proportion of southern blue whiting contribution in their diet, with no difference between adults and juveniles and a similar contribution of long tail hake and fishes/squid from both zones (Fig. 4).

3.4. Diet of fish

Stomachs of long tail hake juveniles almost exclusively contained zooplanktonic crustaceans. Euphausiids were the main prey item, followed by the amphipod hyperiid *Themisto gaudichaudii* and the squat lobster *Grimothea gregaria* (Table 3). The stomach contents of long tail hake adults were also mainly composed of crustaceans, particularly *G. gregaria* (Table 3). The second most important prey items were fishes, which were found highly digested, with myctophids the only group that could be identified (Table 3). Stomachs of juvenile Patagonian toothfish primarily contained fish species such as the morid cod *Notophycis marginata* and southern blue whiting (Table 3). Crustaceans and cephalopods were found in low quantities. Adults, on the other hand, consumed both fish and crustaceans in similar proportions. Among the fish groups, myctophids were the only identifiable taxon due to the degree of digestion of stomach contents. The most consumed crustacean was the shrimp *Acanthephyra pelagica*, and cephalopods were poorly represented (Table 3). Stomachs of southern blue whiting showed that they mainly fed on zooplanktonic crustaceans, particularly euphausiids (Table 3). Stomachs of southern hake revealed that they mostly consumed fish; in particular, Fuegian sprat *Sprattus fuegensis* and southern blue whiting could be identified (Table 3). Crustaceans, mainly euphausiids and *G. gregaria*, were scarce in the diet (Table 3).

4. DISCUSSION

Our results show the trophic relationships of 4 demersal fish species in the SW Atlantic Ocean, suggesting intra- and interspecific trophic and spatial

Table 3. Diet composition of 4 demersal fish species in the southwestern Atlantic Ocean, expressed by the percentage frequency of occurrence (%F), the numerical percentage, (%N), the percentage of weight (%W), and the index of relative importance (%IRI), for juveniles and adults. Empty stomachs were not taken into account

Prey items	*Macruronus magellanicus* Juveniles (N = 37) %F	%N	%W	%IRI	*Macruronus magellanicus* Adults (N = 17) %F	%N	%W	%IRI	*Dissostichus eleginoides* Juveniles (N = 26) %F	%N	%P	%IRI	*Dissostichus eleginoides* Adults (N = 12) %F	%N	%W	%IRI	*Micromesistius australis* Adults (N = 20) %F	%N	%W	%IRI	*Merluccius australis* Adults (N = 10) %F	%N	%W	%IRI
Crustaceans	**97.3**	**99.6**	**97.4**	**99.9**	**76.5**	**90.8**	**14.5**	**64.9**	**15.4**	**13.3**	**1.9**	**1.6**	**75.0**	**32.4**	**31.7**	**43.1**	**90.0**	**90.5**	**57.6**	**93.3**	**40.0**	**26.7**	**0.1**	**7.7**
Euphausiids	40.5	73.2	19.6	60.4	17.6	12.5	0.3	3.8	–	–	–	–	–	–	–	–	60.0	60.3	23.5	74.5	20.0	15.4	0.2	9.7
Themisto gaudichaudii	37.8	20.7	14.2	21.2	5.9	0.8	–	0.1	–	–	–	–	–	–	–	–	30.0	9.5	11.9	9.5	–	–	–	–
Grimothea gregaria	18.9	2.7	46.8	15.0	52.9	77.5	14.2	82.1	–	–	–	–	–	–	–	–	–	–	–	–	10.0	7.7	–	2.4
Gammaridae	10.8	1.9	2.2	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthephyra pelágica	–	–	–	–	–	–	–	–	7.7	8.3	2.4	3.4	33.3	13.5	19.6	16.5	–	–	–	–	–	–	–	–
Pasiphaea acutifrons	–	–	–	–	–	–	–	–	–	–	–	–	16.7	10.8	8.9	4.9	–	–	–	–	–	–	–	–
Mysidae	2.7	0.1	9.7	0.4	–	–	–	–	–	–	–	–	–	–	–	–	10.0	11.1	6.0	2.5	–	–	–	–
Unidentified decapod	2.7	0.1	0.5	–	–	–	–	–	3.9	4.2	–	0.7	–	–	–	–	15.0	4.8	8.7	3.0	–	–	–	–
Unidentified crustaceans	21.6	0.9	4.4	1.7	–	–	–	–	3.9	4.2	0.3	0.7	25.0	8.1	3.3	4.3	15.0	4.8	7.6	2.7	7.7	0.2	2.5	–
Fish	**8.1**	**0.4**	**2.6**	**0.1**	**47.1**	**6.7**	**85.3**	**34.9**	**80.8**	**76.7**	**97.4**	**97.9**	**50.0**	**54.1**	**62.0**	**52.0**	**20.0**	**6.4**	**37.5**	**6.1**	**80.0**	**60.0**	**99.9**	**91.4**
Notophycis marginata	–	–	–	–	–	–	–	–	15.4	20.8	5.0	16.5	–	–	–	–	–	–	–	–	–	–	–	–
Sprattus fuegensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10.0	15.4	45.2	19.0
Micromesistius australis	–	–	–	–	–	–	–	–	3.9	4.2	83.0	13.9	–	–	–	–	–	–	–	–	10.0	7.7	50.6	18.3
Myctophidae	–	–	–	–	5.9	0.8	83.8	8.4	7.7	8.3	0.4	2.8	8.3	21.6	11.6	4.1	10.0	3.2	26.3	4.4	–	–	–	–
Unidentified fish	8.1	0.4	2.6	0.4	41.2	5.8	1.5	5.1	30.8	37.5	8.1	58.4	50.0	32.4	50.5	61.9	10.0	3.2	11.2	2.1	40.0	30.8	3.8	43.3
Unidentified cephalopods	–	–	–	–	–	–	–	–	**7.7**	**6.7**	**0.6**	**0.4**	**33.3**	**10.8**	**4.8**	**4.7**	–	–	–	–	–	–	–	–

segregation among them. According to stomach contents, southern blue whiting and long tail hake are intermediate predators with similar diets, but their isotopic niches show complete segregation. In contrast, southern hake and Patagonian toothfish are mainly fish feeders and show broad isotopic niches with some overlap between them and long tail hake. We distinguished 2 trophic pathways in the 2 species at lower trophic levels (i.e. southern blue whiting and long tail hake), with the other 2 predator species (i.e. southern hake and Patagonian toothfish) linking them (Fig. 5).

Southern blue whiting and long tail hake consume similar resources and are potential competitors. Both species feed mainly on crustaceans (Wöhler et al. 2004, Brickle et al. 2009, Giussi et al. 2016b, Alvarez et al. 2022, this study), but their isotopic niches showed complete segregation. The difference between them is that there is a higher proportion of fish in the stomachs of long tail hake than in those of southern blue whiting. In addition, the squat lobster *Grimothea gregaria* is an important crustacean food item of long tail hake (Alvarez et al. 2022, this study) and was not found in southern blue whiting. On the other hand, myctophids were found more frequently in the stomachs of southern blue whiting than in those of long tail hake. However, these differences in diet are not sufficient to explain their completely different isotopic niches, given that the different prey items have similar isotopic values (Ricciardelli et al. 2020). The differences in isotopic niches do not always reflect different proportions of prey consumed (Cummings et al. 2012), but they can be the result of foragers exploiting the same prey in different locations with variable

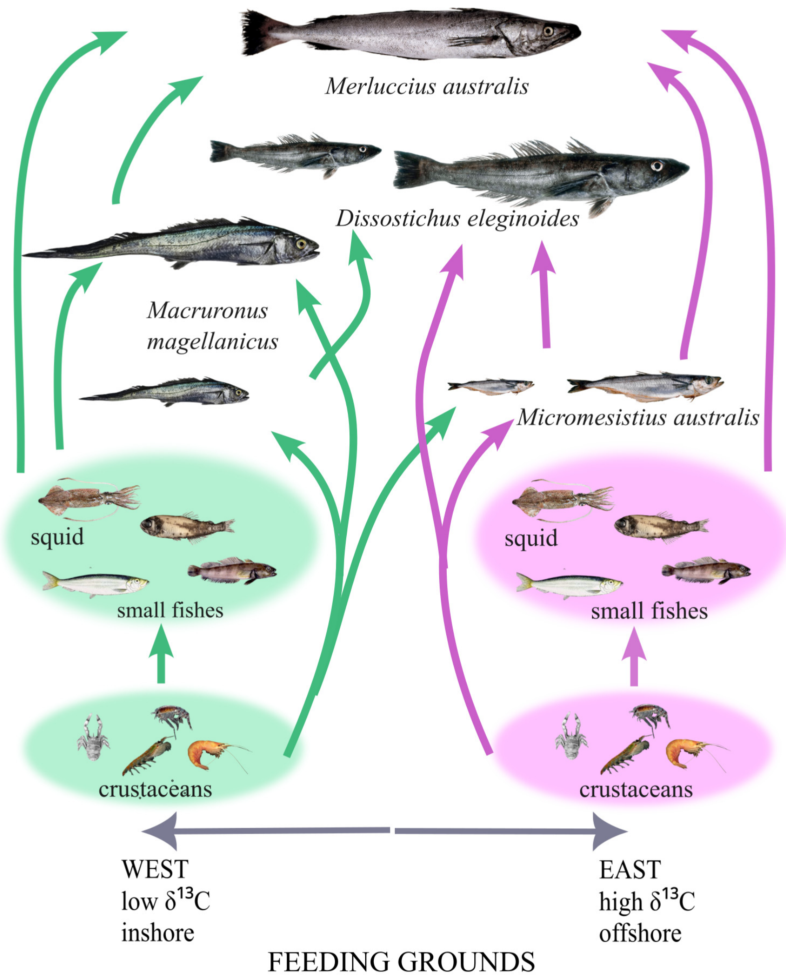

Fig. 5. Trophic interactions among 4 demersal fish species in the southwestern Atlantic Ocean and their potential prey from the west (W) and east (E) zones. The green and pink arrows indicate trophic pathways from the different zones. Species drawings were provided by the INIDEP Photographic Office; they are illustrative and are not to scale

isotopic composition (Bearhop et al. 2004, Jackson et al. 2011, Cummings et al. 2012). Our results suggest that the latter occurs between southern blue whiting and long tail hake in the area of study.

The spatial segregation suggested by the different isotopic niches is supported by isotopic mixing models given that southern blue whiting mostly consume crustaceans from the E zone, whereas long tail hake consume sources from the W zone. This result is consistent with the spatial distribution and movements of these 2 species. Southern blue whiting are associated with sub-Antarctic waters occurring off Chile, New Zealand, and the SW Atlantic Ocean (Ryan et al. 2002, Wöhler et al. 2004, Niklitschek et al. 2010). This species concentrates in a spawning area southwest of the Malvinas Islands, mainly from August to October (Pájaro & Macchi 2001, Agnew 2002), with high site fidelity (Arkhipkin et al. 2009). After spawning, adults disperse (Agnew et al. 2003) and then migrate to the southern tip of South America and Antarctic waters (Agnew et al. 2003, Wöhler et al. 2004). In this study, sampling was performed after the spawning period, and most of the organisms obtained were adults. Our sampling site, including the Burdwood Bank, is one of the main summer feeding grounds of this species, which explains the offshore origin of their sources (Agnew et al. 2003). On the other hand, long tail hake, the most abundant species in the studied area (Giussi et al. 2016b), were usually associated with the Patagonian shelf (Giussi et al. 2016b, Alemany et al. 2018). However, their largest concentrations in recent years were found in feeding grounds located in an area between 53 and 56° S and following the 200 m isobaths (Alvarez et al. 2022). Some of the main prey items of long tail hake, found in this and previous studies, are squat lobster and Fuegian sprat (Giussi et al. 2016b, Alemany et al. 2018, Alvarez et al. 2022), both associated with shelf waters (Diez et al. 2018), which can explain the shelf origin of the trophic pathway for this species (Fig. 5). In conclusion, our results show that southern blue whiting and long tail hake incorporate sources from different areas, and given that they are prey of other demersal fishes (i.e. southern hake and Patagonian toothfish), they both act as intermediate predators linking zooplankton from different spatial origins with higher trophic levels in the food web.

The ichthyophagous species, i.e. southern hake and Patagonian toothfish, have $\delta^{15}N$ values that indicate a high trophic level. The main components in the stomachs of southern hake were fishes, including Fuegian sprat and southern blue whiting, which is consistent with previous results (e.g. Arkhipkin et al. 2015). In addition, a high proportion of unidentified, highly digested fishes was present, with potential prey items being macrourids and merluccid fishes (Dunn et al. 2010). As in southern hake, fishes were the main components in the stomachs of Patagonian toothfish (García de la Rosa et al. 1997, Marí & Sánchez 2002, Arkhipkin et al. 2003, Sallaberry-Pincheira et al. 2018, Troccoli et al. 2020, this study), but crustaceans were also important, coincident with their opportunistic behavior (García de la Rosa et al. 1997). The $\delta^{15}N$ values indicated a higher trophic level in southern hake than in Patagonian toothfish, which may be explained by the above differences in diet between them. However, both species are fish predators that show opportunistic behavior, and similar to other large demersal fishes, they can probably link different trophic pathways in the food webs (van Denderen et al. 2018).

The linkage between trophic pathways is due to predator–prey interactions among the studied demersal fishes. Both Patagonian toothfish and southern hake feed on southern blue whiting, among other prey items. Southern hake have also been reported as predators of long tail hake (Sanchez 1999, Giussi et al. 2016a), reaching up to 90% of their diet by mass in the Pacific Ocean (Lillo et al. 2008, 2011). Nevertheless, although our results did not find identifiable traces of long tail hake in the stomachs, the stable isotope values of southern hake suggest that both long tail hake and southern blue whiting could be part of their diet, with the latter being an important component. Mixing models should be used with caution because there are potential sources for these species that were not considered (e.g. *Moroteuthopsis* [= *Onykia*] *ingens*; Giussi et al. 2016a), and no specific discrimination factors were used, which may bias the model results (Auerswald et al. 2010). However, contrasting what was found for long tail hake and southern blue whiting, mixing models did not show different contributions of E or W sources in these species. Moreover, the wide isotopic niche of both southern hake and Patagonian toothfish, particularly in the $\delta^{13}C$ dimension, could be the result of diverse prey items and the incorporation of sources from different areas. Hence, given that they are slow-growing (Collins et al. 2010) and long-lived (Yates et al. 2018), these demersal top predators are capable of incorporating energy from distant areas, acting as important links in the food web, particularly in the spatial dimension.

Spatial variability in diet may also be associated with the movements of species among feeding grounds as they grow, thus adding temporal variability in their roles in the food web. Ontogenetic variation in diet was found for all species except southern hake. This may be because the individuals of southern hake evaluated were larger than 38 cm TL, and in previous results in the SE Pacific Ocean, differences were found between small juveniles (9 to 25 cm TL) feeding mainly on crustaceans and larger individuals feeding almost exclusively on fishes (Toledo et al. 2020). In the case of long tail hake, an ontogenetic shift in the diet was revealed by stable isotope values, which decreased with size, and by stomach contents, which showed a higher proportion of fish in adults than in juveniles, as previously reported (e.g. Giussi et al. 2016b, Alvarez et al. 2022). However, differences between juveniles and adults were not reflected in mixing models or in the isotopic niches, which showed a high overlap. This is probably because the major differences in the isotopic values are due to spatial variability, and given that this species exclusively feeds in the W zone, the mixing model was not able to differentiate between the importance of the different prey items in this species. In contrast, Patagonian toothfish and southern blue whiting showed ontogenetic and spatial dietary shifts reflected by stomach contents and isotopic niches. The variation in the diet of Patagonian toothfish reflected by the mixing model is coincident with what was found here and previously in stomach contents (i.e. Troccoli et al. 2020). While juveniles feed mainly on demersal fish close to the shelf area (W zone), adults feed more on cephalopods, pelagic fishes, and crustaceans offshore (E zone). Therefore, there is a diversification of prey while growing, including scavenging. In the case of southern blue whiting, a low number of juveniles were available for stomach content evaluation, but differences in isotopic niches and mixing models also suggest spatial segregation between adults and juveniles coincident with their main habitat, given that juveniles are usually associated with shallower areas (Ehrlich et al. 1999) and can incorporate isotopic values from sources of both the W and E zones. The large isotopic niche in these species and differences in niche space between juveniles and adults may be the result of changes in habitat use associated with changes in prey availability (Sánchez-Hernández et al. 2022).

Trophic studies often encompass sampling over broad depth ranges or across habitats, and therefore fishes overlapping in trophic habits may have different spatial distributions (e.g. Macpherson 1981). Our results show how diet inferred only from stomach contents can suggest niche overlap given that it reflects a snapshot of the diet in the place where the fish were captured, but SIA is a better determinant of differences in a longer temporal framework. In our system, with the combination of both techniques, the results show some intra- and interspecific segregation among the 4 demersal fishes in their ecological niches according to their prey items and the spatial origin of the food resources they consume (Fig. 6). Southern hake and Patagonian toothfish exploit prey from a

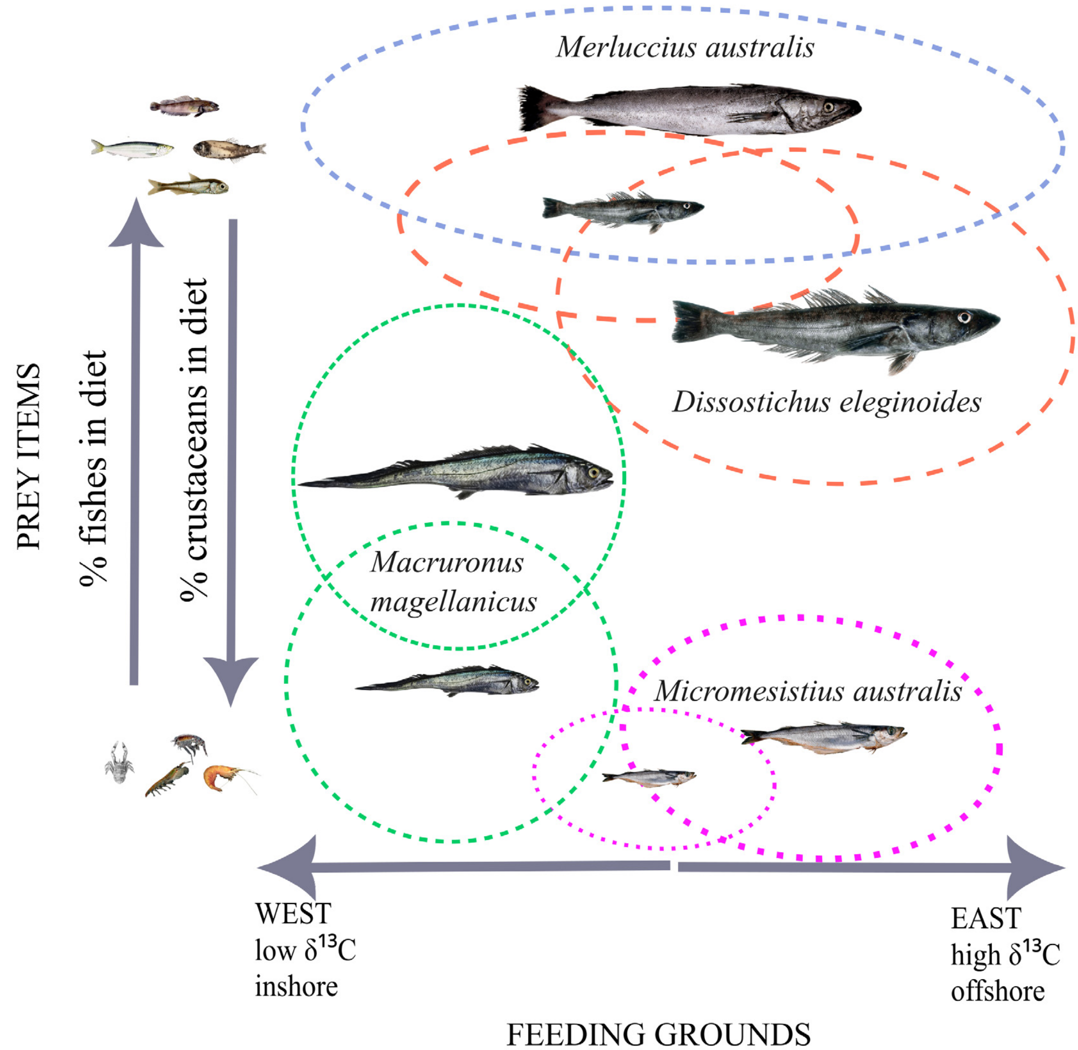

Fig. 6. Schematic representation of the feeding and spatial niche dimensions (ellipses) of 4 demersal fish species in the southwestern Atlantic Ocean. The proportions of crustaceans and fishes and squid as prey items were considered as the feeding dimension, while the proportional use of west (W) and east (E) feeding grounds was considered as the spatial dimension (see Fig. 1). Species drawings were provided by the INIDEP Photographic Office; they are illustrative and are not to scale

broad spatial area and prey on the other 2 species. Although there is a great overlap in diet spectra between long tail hake and southern blue whiting, they differ in the spatial dimension (Fig. 6). Our findings suggest that 4 significant species, which are the targets of fisheries in the SW Atlantic, could interact, but further research is necessary. Understanding these interactions is a crucial factor in moving from single-species to multi-species fishery management.

Niche differentiation at lower trophic levels can reflect a compartmentation of the food web. Compartmentation implies the presence of subsystems (i.e. compartments) in which the interactions among organisms inside those subsystems are more frequent than with organisms from other compartments (Pimm 1979). Although compartmentation is generally associated with robustness and stabilization of communities (Stouffer & Bascompte 2011), models predict that large marine food webs are more stable when subsystems are linked by species that can migrate and interact among compartments (Mougi 2018). Higher-order, mobile, generalist consumers stabilize large food webs by coupling low-level webs in space (McCann et al. 2005, Rooney et al. 2008). In particular, large, demersal, slow-growing fishes are characteristic of temperate and cold environments and usually link trophic pathways (van Denderen et al. 2018). Our results show evidence that southern hake and Patagonian toothfish can have an important role linking distant food web modules. Summing up, the 4 coexisting demersal fish species show similarities and differences in trophic and spatial dimensions, resulting in niche differentiation and probably different roles in the food web in the SW Atlantic Ocean.

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