Isotope-based inferences of skipjack tuna feeding ecology and movement in the southwestern Atlantic Ocean

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ABSTRACT

Skipjack tuna (*Katsuwonus pelamis*) sustain a large-scale fishery in the southwest Atlantic Ocean (SWA), but information about its foraging ecology in this region is still limited. Here we use carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis of muscle from individuals collected in 2017–2018 (n = 383) to quantify diet composition and characterize movement patterns. We found a relatively small degree of variation in δ^{13}C (range: -18.9 to -16.5‰) in comparison to δ^{15}N values (6.7–14.7‰). At higher latitudes in the southern area (30–34°S), individuals had higher mean (±SD) δ^{15}N values (12.2 ± 1.3‰) in comparison to those collected in the northern area (9.7 ± 1.5‰) between 20–26°S. At the northern area, isotope mixing models with informative priors showed that lanternfish (median: 50%) and krill (31%) were the primary foods. In the southern area, lanternfish (53%), krill (23%) and small pelagic fish (23%) were the primary food sources. Spatial shifts in diet composition were related to warming events that likely resulted in low abundance of sardines in the northern area. The latitudinal pattern in skipjack and krill δ^{15}N values mirrored that of regional zooplankton isoscapes, suggesting residency at the timescale of isotopic turnover for muscle (~2–4 months), and that geographical variation in the baseline isotopic composition can be exploited to characterize seasonal movements of skipjack and other top marine consumers in this region.

1. Introduction

Understanding trophic links and energy flux in exploited ecosystems is a primary component of ecosystem-based fisheries management, whose primary objective is to sustain healthy marine ecosystems and the fisheries they support (Cury et al., 2008; Hilborn et al., 2020). Tunas (family Scombridae) support extensive fisheries worldwide in terms of landings and economic value (Brill and Hobday, 2017; FAO, 2018). Like marine mammals and seabirds, tunas evolved to take advantage of places and times that are best-suited to different phases of their life cycle, often migrating long distances for breeding and feeding (Dufour et al., 2010). Some tuna species reach sexual maturity quickly and have the fastest growth rates among fishes (Murua et al., 2017) as a consequence of their anatomical, biochemical, and physiological adaptations for a high energy expenditure lifestyle that is fueled by generalist foraging strategies (Olson et al., 2016).

Skipjack tuna (*Katsuwonus pelamis*) have a global distribution in tropical and sub-tropical oceans (Wild and Hampton, 1993) and have been consistently placed in the top three marine species that contribute to food security worldwide (FAO, 2018). In the southwestern Atlantic Ocean (SWA), the species has a high social and economic relevance for fishers, producers, and markets that sustain the tuna canning industry in Brazil (Schmidt et al., 2019). Brazilian catches averaged 23,566 t/year from 2000 to 2018, reaching a peak of 32,438 t in 2013 followed by a 56% decrease to 18,133 t two years later (ICCAT, 2019). This decrease in catches was not related to overfishing, but rather to sea surface temperature (SST) anomalies, specifically an extreme heating episode in the SWA (Manta et al., 2018) that also impacted the sardine fishery in Brazil (Schmidt et al., 2019).

The annual lifecycle of skipjack in the SWA involves movements

between spawning and feeding grounds located at tropical and sub-tropical areas, respectively (Matsuura 1986; Castello and Habiaga, 1989; Matsuura and Andrade, 2000). Spawning occurs in waters with SST >24 °C and can occur year-round in the Guiana Current off the northeast coast of Brazil, and seasonally in the Brazil Current (BC) off the southwest coast of Brazil (Matsuura, 1986). Skipjack feeding grounds are located near the Subtropical Convergence (30–36°S) formed by the confluence of the warm and oligotrophic waters carried by the BC and the nutrient-rich and cold subantartic waters of the Malvinas Current (Garcia, 1997). Over the continental shelf, primary production in this region is also boosted by the Rio de la Plata and Patos Lagoon drainages (Möller et al., 2008). Consequently, this region sustains a large biomass of pelagic forage fish like Argentine anchovy (*Engraulis anchoita*) and lanternfish (*Maurolicus stehmanni*) (Matsuura and Andrade, 2000; Madureira et al., 2009), which represent important food resources for numerous top predators such as pelagic and demersal fish, seabirds, and marine mammals (Castello, 1997; Velasco and Castello, 2005; Marques et al., 2018).

The fishing season for skipjack in the SWA starts during the austral spring (October–December) when schools are swimming southwards following the BC. The peak of the fishing season and relative abundance of the species in the region occurs during the summer (January–March) when SST reaches its maximum. During the fall (April–June), the schools move northwards again as the SST decreases with the advance of the Malvinas Current from the south (Andrade and Garcia, 1999; Lima et al., 2000; Coletto et al., 2019).

Several studies based on stomach content analysis (SCA) have shown that skipjack diet is affected by prey distribution, migration, and oceanographic conditions (e.g. Roger, 1994; Potier et al., 2002). Euphausiids (i.e. krill) and small pelagic fish are the primary prey of skipjack in the eastern Pacific Ocean (Alverson, 1963). Krill is the primary prey of skipjack in coastal Baja California, while flying-fishes are important prey in offshore areas (Alatorre-Ramíres et al., 2017). The lightfish (*Vinciguerria nimbari*) can be an important prey item for skipjack in the eastern tropical Atlantic Ocean (Dragovich and Potthoff, 1972). A recent study found that krill (*Meganyctiphanes norvegica*), flying fish (*Exocoetus volitans*), and the anchovy (*Engraulis encrasicolus*) were the primary prey of skipjack in the Balearic Sea, Alboran Sea, and Gulf of Cadiz respectively in the Mediterranean Sea (Varela et al., 2019). In the SWA off Brazil, the primary prey of skipjack in the 1990's were lanternfish (*M. stehmanni*) and krill (*Euphausia similis*), and the importance of the latter prey type decreased with increasing skipjack size (Anken-brandt, 1985). In the southern region of the SWA, the Argentine anchovy (*Engraulis anchoita*) has also been noted as an important source of prey (Vilella, 1990).

Conventional dietary techniques such as SCA, however, can only provide a snapshot of ingested foods and likely underestimate diet items that are quickly assimilated by the consumer (Chipps and Garvey, 2007). Additionally, the high frequency of empty stomachs of species like skipjack, or those filled with bait species, are also limitations of using SCA to study the diet of commercially exploited species like tunas over large spatial and temporal scales (Vooren 1976; Ankenbrandt, 1985; Vilella, 1990; Roger, 1994; Varela et al., 2013). Given these limitations and the overall paucity of information on the diet of skipjack in the SWA, additional proxies are needed to better characterize dietary shifts across a range of latitudes and ontogeny to understand the energy pathways that sustain large-scale fisheries in this region.

Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes are widely used as intrinsic biochemical tracers of animal diet composition and movement (Phillips et al., 2014; Hobson and Wassenaar, 2019). The main premise of stable isotope analysis (SIA) is that the δ^{13}C and δ^{15}N values of consumer tissues mirror those of its food, but are slightly offset due to physiologically-mediated processes associated with assimilation and tissue synthesis, often called trophic discrimination. The systematic enrichment in the heavier isotope with increasing trophic level is greater for δ^{15}N (2–4‰) than for δ^{13}C (0–2‰) (DeNiro and Epstein, 1978, 1981)

and as such nitrogen isotopes are often used to estimate trophic position (Post, 2002), while carbon isotopes are used to assess the relative influence of different primary producers in fueling the food webs utilized by the consumer (Peterson and Fry, 1987). One of the primary advantages of SIA over conventional dietary proxies like SCA is that it can provide a time-integrated measure of dietary inputs depending on the tissue analyzed (Martinez del Rio et al., 2009). Some tissues (e.g. liver) have rapid isotopic incorporation rates that reflect information about the ecology and physiology of organisms from days to weeks, while others like muscle or bone collagen reflect ecological information integrated over month to year timescales (Pinnegar and Polunin, 1999; Martinez del Rio et al., 2009; Martinez del Rio and Carleton, 2012).

Often the most complete dietary information is obtained when SCA and SIA are combined because the advantages of one technique offset the disadvantages of the other (Phillips et al., 2014; Swan et al., 2019). Specifically, SIA integrates information on resource and habitat use over multiple timescales but does not typically provide taxon-specific data on diet composition, which is an advantage of SCA. As such, SCA and SIA can be combined to estimate the contribution of different sources (prey) to a mixture (consumer) via isotopic mixing models (Phillips et al., 2014) that use informative priors based on SCA identification of prey species consumed by the population (Moore and Semmens, 2008; Franco-Trecu et al., 2013; Swan et al., 2019).

Studies focused on niche partitioning and resource use often quantify isotopic niches of individuals and/or populations, which provide a proxy for resource and/or habitat use (Newsome et al., 2007). The most common metric used to estimate isotopic niches is the standard ellipse area calculated by means of frequentist or Bayesian methods (Jackson et al., 2011). However, the elliptical nature of SEAs does not adequately capture the multi-modal structure of some datasets, which can lead to inaccurate estimates of the isotopic niche (Franco-Trecu et al., 2014). More recently, an approach based on kernel densities has been applied to isotopic data as it is less sensitive to extreme (outlier) values and performs well with more structured multi-modal datasets (Eckrich et al., 2019).

In this study, we aimed to quantify skipjack diet composition and characterize movement patterns in the SWA. We combined δ^{13}C and δ^{15}N values of skipjack muscle and their primary prey with data from SCA to generate quantitative estimates of the assimilated diet in the primary feeding grounds of the species in this region. Lastly, we used kernel isotopic niche estimates to explore habitat use and seasonal movement patterns across ontogeny along the range of latitudes (20–34°S).

2. Material and methods

2.1. Sample collection

Muscle tissue samples were obtained from skipjack collected during catch landings at Niterói (Rio de Janeiro –RJ) and Rio Grande (Rio Grande do Sul–RS), Brazil between January 2017 and December 2018 as part of the Bonito Project. Fishing positions were plotted using QGIS software (Version 3.4.9). Catches occurred between 20 and 34°S, and skipjack and prey samples were divided into two groups hereafter referred to as northern (20–28°S) and southern (28–34°S) areas (Fig. 1). We chose these areas because they are characterized by distinct oceanographic conditions. The southern area is heavily influenced by the cold waters of Malvinas Current, especially during fall and winter (Garcia, 1997; Lopes et al., 2006) and continental water runoff from Rio de la Plata and Patos Lagoon (Möller et al., 2008). The northern area is dominated by tropical water and coastal and shelf-break upwellings of South Atlantic Central Water driven by the Brazil Current (Campos et al., 1995, 2000; Acha et al., 2004; Lorenzetti et al., 2009). The northern and the southern areas are 1,000–1,200 km distant from each other. The oceanographic processes driving nutrient availability and distribution were found to be responsible for the latitudinal patterns in zooplankton
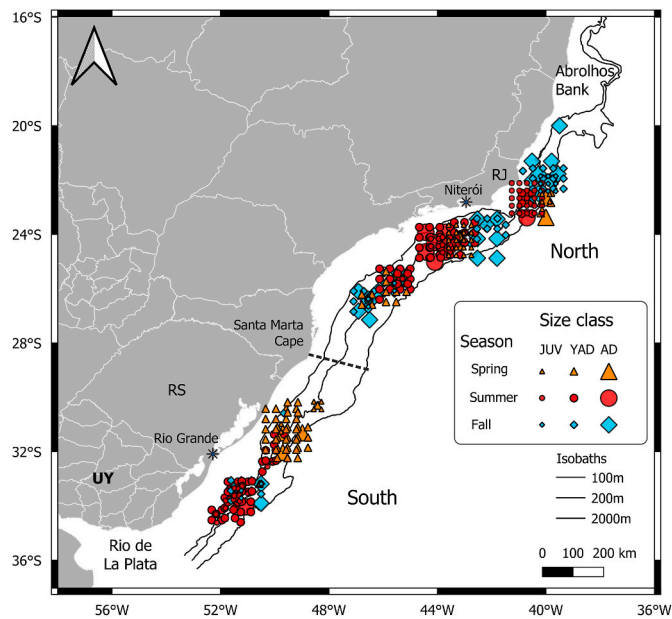
Fig. 1. Seasonal distribution for skipjack tuna in the Southwest Atlantic Ocean. Size classes are denoted by symbol size: juvenile (JUV), young adult (YAD), and adult (AD). Seasons are indicated by symbol shapes and colors: summer (red, Jan–Mar); fall (blue, Apr–Jun); spring (orange, Oct–Dec). No fishing activities occur during the winter (Jul–Sep). The limit (dashed line) between northern and southern areas was defined in Santa Marta Cape (~28°S). Points from the same sampling event are shown as a square grid around the central catch position. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

δ^{13}C and δ^{15}N isoscapes (Troina et al., 2020).

All individuals (n = 383) were measured for straight fork length (SFL), weighed to the nearest gram, and sexed by macroscopic identification of ovaries and testes. Individuals were categorized into size groups according to the SFL that 50% (L_{50} = 46 cm) and 100% (L_{100} = 63 cm) of the specimens are likely to have reached sexual maturity in the SWA (Soares et al., 2019). Size groups were defined as juveniles (SFL < 47 cm), young adults (SFL 47–63 cm), and adults (SFL > 64 cm).

2.2. Stable isotope analysis

We used a scalpel to remove ~5 g of white muscle from the region adjacent to the second dorsal fin of each individual, which was kept frozen (−20 °C) until processing in the laboratory. For isotope analysis, samples were rinsed with distilled water, lyophilized or oven-dried at 60 °C for 48 h, and homogenized with a mortar and pestle (Sulzman, 2007). Aliquots of ~0.5 mg of the resulting powder were weighed into tin capsules and δ^{13}C and δ^{15}N values were measured at the University of New Mexico (UNM) Center for Stable Isotopes (CSI) in Albuquerque, NM or the University of California Davis (UCD) Stable Isotope Facility (SIF) in Davis, CA. Analyses at UNM-CSI were performed with a Costech ECS-4010 elemental analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Bremen, Germany), while analyses at UCD-SIF were performed with a Europa Hydra 20-20 mass spectrometer. Isotope values are reported in δ notation using the equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C and ^{15}N and R is the ratio ^{13}C/^{12}C or ^{15}N/^{14}N (Peterson and Fry, 1987). Internationally accepted standards for δ^{13}C and δ^{15}N are Vienna Pee Dee Belemnite (V-PDB) and atmospheric N$_2$, respectively. Within-run analytical precision (±SD) was estimated via analysis of proteinaceous internal reference materials and estimated to be ±0.1‰ for both δ^{13}C and δ^{15}N. We compared inter-laboratory measurements by analyzing replicates of skipjack muscle (n = 3) measured in both isotope

laboratories. The mean difference for δ^{13}C (0.2‰, paired *t*-test, $t_2 = -8.41$, p = 0.01) and for δ^{15}N (0.1‰, paired *t*-test, $t_2 = 1.37$, p = 0.15) was small and the slope for the linear regression among replicates did not differ from zero for δ^{13}C ($r^2 = 0.98$, $F_{1,1} = 56.86$, p = 0.08). Owing to low mean (±SD) weight percent [C]:[N] ratios of skipjack white muscle (3.2 ± 0.1) that is indicative of pure protein, we did not lipid-extract samples prior to isotope analysis (Post et al., 2007).

2.3. Skipjack potential prey

Ankenbrandt (1985) analyzed skipjack stomachs collected from the commercial pole and line fishery in Brazil between 1981 and 82 and reported krill (*Euphausia similis*) and lanternfish as the primary prey between 22 and 28°S. Vilella (1990) analyzed samples from the commercial pole and line fleet between 1986 and 89, as well as samples from exploratory purse-seine fishing (1983–86). Sardines were the primary prey found in stomachs collected from the commercial pole and line fleet samples, while lanternfish, krill and anchovy were the primary prey of tuna caught in the exploratory purse-seine fishery (Vilella, 1990). Based on this previous work, we selected potential prey items consumed by skipjack in the study area. Isotopic data for these prey species were obtained from published studies conducted in the same area (Troina, 2019; Troina et al., 2020) as well as from samples we collected throughout the study (n = 19) and one sardine purse-seine landing at Rio Grande in May 2019 (n = 12). Prey samples were processed and analyzed following the same protocol we used for skipjack muscle.

2.4. Data analysis

Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in isotope values among skipjack collected in the two areas (northern and southern) and between sex. Permanova was based on Euclidian distance matrix of δ^{13}C and δ^{15}N values. The homogeneity of multivariate dispersion was tested with 'betadisper' function from 'vegan' package (Oksanen et al., 2020). Linear regression analyses were applied to test the relationship between skipjack δ^{13}C values and SFL, and between δ^{15}N values of skipjack and euphausiids latitude of collection. Mann-Whitney rank sum tests were used to verify the differences in skipjack muscle δ^{13}C and δ^{15}N values for the monthly comparisons between areas during the 2017 and 2018 fishing seasons and for comparisons among size classes from each area. Statistical analyses and graphical outputs were performed in R 3.6.0 (R Core Team, 2019).

Because lipids are depleted in ^{13}C, we used tissue- and taxa-specific equations to normalize δ^{13}C values of prey samples that had C:N > 3.5. We used Eqn. 1 and Eqn.2 from Logan et al. (2008) for fish samples (except lanternfish) and for Euphausiids, respectively. Lanternfish δ^{13}C values were normalized following Hoffman and Sutton (2010). Lipid normalization for carbon isotope values of cephalopod muscle was performed following Logan and Lutcavage (2013), that applied a general equation for fish muscle reported in Logan et al. (2008). Food web studies often use hydrochloric acid (HCl) to remove the inorganic C, as calcareous structures may bias δ^{13}C values (Carabel et al., 2006). We choose not to treat prey samples with HCl because studies show that this pretreatment can influence δ^{15}N values (Bunn et al., 1995; Carabel et al., 2006).

To reduce the number of sources for ensuring discriminatory power in our mixing models (Phillips et al., 2014), we grouped sources *a priori* by family and region (northern and southern) and compared their mean δ^{13}C and δ^{15}N values (Mann-Whitney rank sum test). We then grouped families based on their statistical similarity (p > 0.05 for δ^{13}C and δ^{15}N) and considering their ecological function within each region (Phillips et al., 2005). Using mean isotope values for prey groups sources, we simulated mixing polygons through a Bayesian statistical framework with the *sp* and *splancs* packages in R (Bivand et al., 2013; Rowlinson and Diggle, 2017). This is a quantitative method based on a

point-in-polygon premise for assessing whether a proposed mixing model is likely to explain the isotope values of consumers and the accuracy of trophic discrimination factors (TDF; Smith et al., 2013). Mixing polygons were run with 1500 iterations.

The mixing polygon for skipjack collected in the northern area was simulated with the following prey groups: (1) krill (Euphausiidae); (2) cephalopods and fish (Carangidae, Ommastrephidae); (3) lanternfish (*Maurolicus stehmanni*); and; (4) small pelagic fish (Clupeidae). The mixing polygon for skipjack collected in the southern area was simulated with the following prey groups: (1) krill (Euphausiidae); (2) cephalopods (Ommastrephidae); (3) lanternfish (*Maurolicus stehmanni*) and; (4) small pelagic fish (Clupeidae, Engraulidae). For each polygon simulation, we used three sets of trophic discrimination factors (TDF) to correct for isotopic offset between skipjack and prey sources: (1) *Thunnus orientalis* reported in Madigan et al. (2012) ($\Delta^{13}C$ 1.8 ± 0.4‰, $\Delta^{15}N$ = 1.9 ± 0.4‰); (2) adult *Thunnus thynnus* ($\Delta^{13}C$ −0.2 ± 0.6‰; $\Delta^{15}N$ = 1.6 ± 0.2‰ reported in Varela et al., 2011) and; (3) juvenile *Thunnus thynnus* ($\Delta^{13}C$ 0.3 ± 0.1‰; $\Delta^{15}N$ = 1.5 ± 0.1‰ reported in Varela et al., 2012) (Appendix 1, Fig. A1). We chose to use the TDF estimates reported in Madigan et al. (2012) for reasons discussed below.

The relative contribution of prey groups to skipjack diet was estimated with Stable Isotope Mixing Models in R (SIMMR; Parnell, 2019). SIMMR were run with uninformative priors (SIMM-UP) and with informative priors (SIMM-IP) for each site and size class. We used the previously mentioned Bonito Project SCA dataset to construct informative priors for the SIMM-IP. We specified priors means and standard deviations and generated prior distributions through "*simmr_elicit*" function in the SIMMR package. We used prey mass as priors because it is considered the best measure of relative importance of prey in animal diet (Swan et al., 2019). When estimating total biomass for small pelagic fish, we removed anchovies and sardines that had a low degree of digestion and assumed they were ingested as bait. Mean (±SD) isotope values for prey groups and informative priors used in mixing models are shown in Table 1. Models were fitted using 10,000 iterations, 1000 burn-in, with a thinning interval of 10 and four Markov Chain Monte Carlo (MCMC) chains. Convergence was first checked before further consideration. Results are reported as the median and (2.5–97.5%) credible interval for the contribution of each prey group to skipjack diet. Differences in prey contribution between size groups were compared through "*compare_groups*" function in SIMMR and reported with probabilities.

Finally, we used the rKIN package (Eckrich et al., 2019) to estimate a Kernel Utilization Density (KUD) isotopic niche for skipjack from each area (northern and southern) or ontogenetic group (juvenile, young adults, adults). Similar to standard ellipse analysis, we assumed that the overlap of KUD provides an estimate for isotopic niche overlap between area and ontogenetic groups. Niche size and overlap are reported for 50%, and 75% KUD contours.

3. Results

3.1. Skipjack $\delta^{13}C$ and $\delta^{15}N$ values

Mean $\delta^{13}C$ and $\delta^{15}N$ (±SD) values and sample sizes for each area and ontogenetic group are reported in Table 2. Straight fork length (SFL) for all individuals ranged from 37 to 80 cm (mean ± SD: 51.6 ± 8.4 cm) and total body mass ranged from 0.9 to 12.0 kg (mean ± SD: 3.3 ± 2.0 kg). No differences were detected between sexes with PERMANOVA (p = 0.61). Isotopic values differed between areas (p < 0.001), and multivariate dispersion did not differ between areas (p > 0.05), suggesting that differences were not due to multivariate dispersion. $\delta^{13}C$ values increase with skipjack SFL ($F_{1,381}$ = 57.54, p < 0.001; supplementary Figure A1a). $\delta^{15}N$ values increased towards higher latitudes in both skipjack muscle ($F_{1,381}$ = 308.4, p < 0.001) and euphausiids ($F_{1,41}$ = 43.3, p < 0.001; supplementary Figure A1b). $\delta^{15}N$ values differed among size groups within each area, with higher values observed in young adults. Adults from the southern area, however, did not differ from any other size group in either areas for both $\delta^{13}C$ and $\delta^{15}N$ isotopes (Table 2, Appendix 1; Table A2).

No differences in $\delta^{13}C$ values were observed between areas in the monthly comparison (except on March 2017), although a slight increase occurred over time in both fishing seasons (Fig. 2). $\delta^{15}N$ values differed consistently across areas, but became similar after March–April (Fig. 2, Appendix 1; Table A3).

Table 2
Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) for areas (northern and southern) and size classes of skipjack collected in the Southwest Atlantic Ocean (n = 383). Size groups not connected by the same superscript letter are significantly different (p < 0.05).

		n	$\delta^{13}C$ mean ± SD	$\delta^{13}C$ Range	$\delta^{15}N$ mean ± SD	$\delta^{15}N$ Range
Northern		242	−17.6 ± 0.4	−18.9 to −16.5	9.7 ± 1.5	6.7 to 13.9
	Juveniles	78	−17.9 ± 0.2[a]	−18.5 to −17.3	9.0 ± 1.2[a]	6.7 to 13.3
	Young Adults	130	−17.5 ± 0.5[b]	−18.9 to −16.5	10.2 ± 1.6[b]	7.1 to 13.9
	Adults	34	−17.4 ± 0.4[bc]	−18.2 to −16.7	9.5 ± 1.0[c]	8.0 to 13.1
Southern		141	−17.7 ± 0.5	−18.6 to −16.6	12.2 ± 1.3	9.0 to 14.7
	Juveniles	26	−17.9 ± 0.6[ad]	−18.6 to −16.6	11.2 ± 1.2[d]	9.5 to 13.5
	Young Adults	108	−17.6 ± 0.4[e]	−18.9 to −16.7	12.5 ± 1.1[e]	10.1 to 14.7
	Adults	7	−17.7 ± 0.3[abcde]	−18.1 to −17.1	10.9 ± 2.2[bcde]	9.0 to 13.9

Table 1
Mean measured $\delta^{13}C$, $\delta^{13}C$ normalized for lipid contents ($\delta^{13}C_{norm}$), $\delta^{15}N$ values (‰), weight percent carbon-to-nitrogen (C:N) ratios, and informative priors of four prey categories used in mixing models for skipjack tuna collected in the northern and southern areas of Southwest Atlantic Ocean.

Area	Prey Group	Stable Isotope Values					Informative Prior
		n	$\delta^{13}C$ ± SD	$\delta^{13}C_{norm}$ ± SD	$\delta^{15}N$ ± SD	C:N ± SD	Biomass proportion ±SD
North	krill	20	−21.0 ± 1.2	−19.1 ± 0.5	3.7 ± 1.1	4.9 ± 1.4	0.065 ± 0.052
	cephalopods and fish	15	−18.6 ± 0.4	−18.0 ± 0.5	6.7 ± 1.4	3.4 ± 0.2	0.148 ± 0.073
	lanternfish	27	−20.3 ± 0.4	−20.3 ± 0.4	10.0 ± 1.0	3.8 ± 0.2	0.057 ± 0.054
	small pelagic fish	6	−17.0 ± 1.3	−17.0 ± 1.3	11.7 ± 0.8	3.3 ± 0.1	0.729 ± 0.132
South	krill	23	−21.8 ± 0.7	−19.8 ± 0.5	5.6 ± 1.2	4.8 ± 0.7	0.855 ± 0.060
	cephalopods	23	−19.6 ± 0.6	−18.1 ± 0.5	8.5 ± 1.7	3.6 ± 0.2	0.046 ± 0.039
	lanternfish	41	−20.5 ± 0.9	−20.1 ± 0.4	10.6 ± 1.4	4.2 ± 0.9	0.047 ± 0.039
	small pelagic fish	15	−18.2 ± 0.5	−17.8 ± 0.5	13.6 ± 0.6	3.4 ± 0.2	0.053 ± 0.037

Fig. 2. Monthly variation in mean δ¹³C and δ¹⁵N values of skipjack in the northern and southern areas of the Southwest Atlantic Ocean during 2017 and 2018 fishing seasons. Error bars represent SD. Asterisks denote statistical significance of monthly comparison on isotope values between areas. ***p < 0.001, **p < 0.05 (see Table A3 for more details).

3.2. Isotope mixing models

The highest proportion of individuals inside the 95% probability contours in both the northern and southern mixing polygons were obtained with TDF values reported by Madigan et al. (2012) (supplementary Figure A2). Median estimates and credible intervals from mixing models with uninformative (SIMM-UP) and informative (SIMM-IP) priors for both areas and all size classes are reported in Table 3. In the northern area, SIMM-UP indicated that diet was composed of lanternfish (median: 50%) and krill (31%), followed by cephalopods and fish (12%), and lastly small pelagic fish (7%). SIMM-IP estimates were

very similar for this area, indicating that diet was composed of lanternfish (50%) and krill (29%), cephalopods and fish (14%) and small pelagic fish (7%) (Fig. 3). In the southern area, SIMM-UP indicated lanternfish as the main prey (64%), followed by similar proportions of small pelagic fish (14%), cephalopods (13%) and krill (9%). SIMM-IP estimates slightly differed for this area and indicated lanternfish as the main prey (53%), followed by krill (23%), small pelagic fish (23%) and cephalopods (1%) (Fig. 3).

Ontogenetic diet shifts were consistent between SIMM-UP and SIMM-IP model types in both areas (Table 3; Fig. 4). In both areas, the contribution of krill decreased from juveniles to young adults (Probability > 0.98). In the northern area, the proportion of cephalopods and fish and small pelagic fish increased in young adults and adults, in
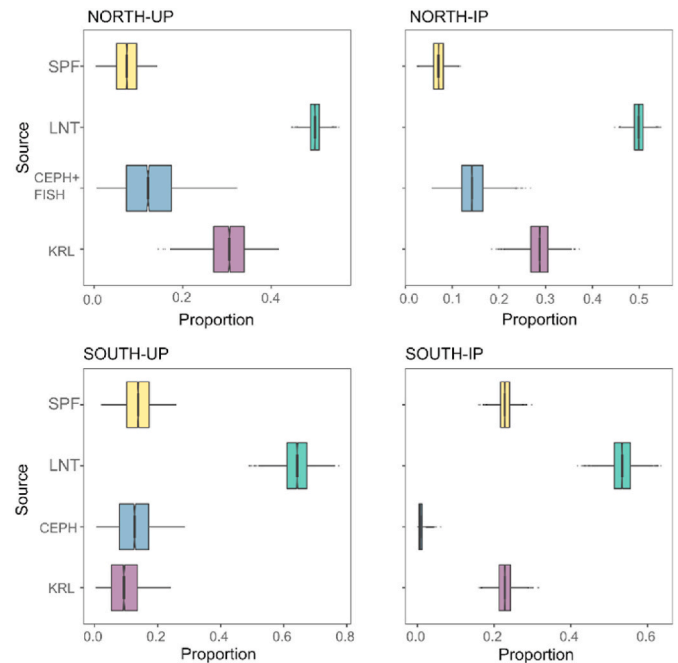

Fig. 3. Posterior mixing models estimates for skipjack diet composition. Contribution of prey sources to skipjack diet in the northern (top plots) and southern (bottom plots) areas of Southwest Atlantic Ocean estimated with mixing models using uninformative (SIMM-UP) and informative (SIMM-IP) priors. Table 3 reports medians and 95% credible intervals for each prey type: krill (KRL), cephalopods and fish (CEPH + FISH), lanternfish (LNT), and small pelagic fish (SPF).

Table 3
Estimates of diet proportions (medias and 95% credible intervals in parentheses) based on stable isotope mixing models with uninformative (SIMM-UP) and informative (SIMM-IP) priors for skipjack captured in the northern and southern areas of the Southwest Atlantic Ocean and of various sizes. Juveniles (JUV), young adults (YAD), adults (AD).

|		SIMM-UP	SIMM-IP	JUV-UP	JUV-IP	YAD-UP	YAD-IP	AD-UP	AD-IP
Northern	krill	0.31 (0.21–0.38)	0.29 (0.23–0.33)	0.42 (0.37–0.46)	0.38 (0.33–0.43)	0.21 (0.07–0.32)	0.20 (0.13–0.27)	0.31 (0.15–0.43)	0.30 (0.20–0.38)
	cephalopods/fish	0.12 (0.02–0.26)	0.14 (0.09–0.21)	0.04 (0.01–0.08)	0.07 (0.04–0.10)	0.18 (0.03–0.38)	0.19 (0.11–0.28)	0.18 (0.03–0.41)	0.19 (0.11–0.31)
	lanternfish	0.50 (0.47–0.53)	0.50 (0.47–0.53)	0.53 (0.49–0.56)	0.52 (0.49–0.56)	0.51 (0.46–0.55)	0.50 (0.47–0.55)	0.40 (0.34–0.46)	0.39 (0.33–0.45)
	small pelagic fish	0.07 (0.02–0.12)	0.07 (0.04–0.10)	0.02 (0.00–0.04)	0.02 (0.01–0.04)	0.10 (0.02–0.18)	0.11 (0.07–0.15)	0.10 (0.02–0.18)	0.12 (0.07–0.17)
Southern	krill	0.09 (0.01–0.19)	0.23 (0.19–0.27)	0.24 (0.12–0.36)	0.35 (0.26–0.49)	0.08 (0.02–0.17)	0.21 (0.17–0.26)		
	cephalopods	0.13 (0.02–0.23)	0.01 (0.00–0.03)	0.08 (0.02–0.22)	0.01 (0.00–0.07)	0.11 (0.02–0.20)	0.01 (0.00–0.03)		
	lanternfish	0.64 (0.55–0.72)	0.53 (0.47–0.59)	0.60 (0.44–0.73)	0.57 (0.35–0.71)	0.63 (0.55–0.70)	0.52 (0.46–0.59)		
	small pelagic fish	0.14 (0.05–0.22)	0.23 (0.20–0.26)	0.06 (0.01–0.16)	0.05 (0.01–0.18)	0.18 (0.10–0.25)	0.26 (0.22–0.29)		
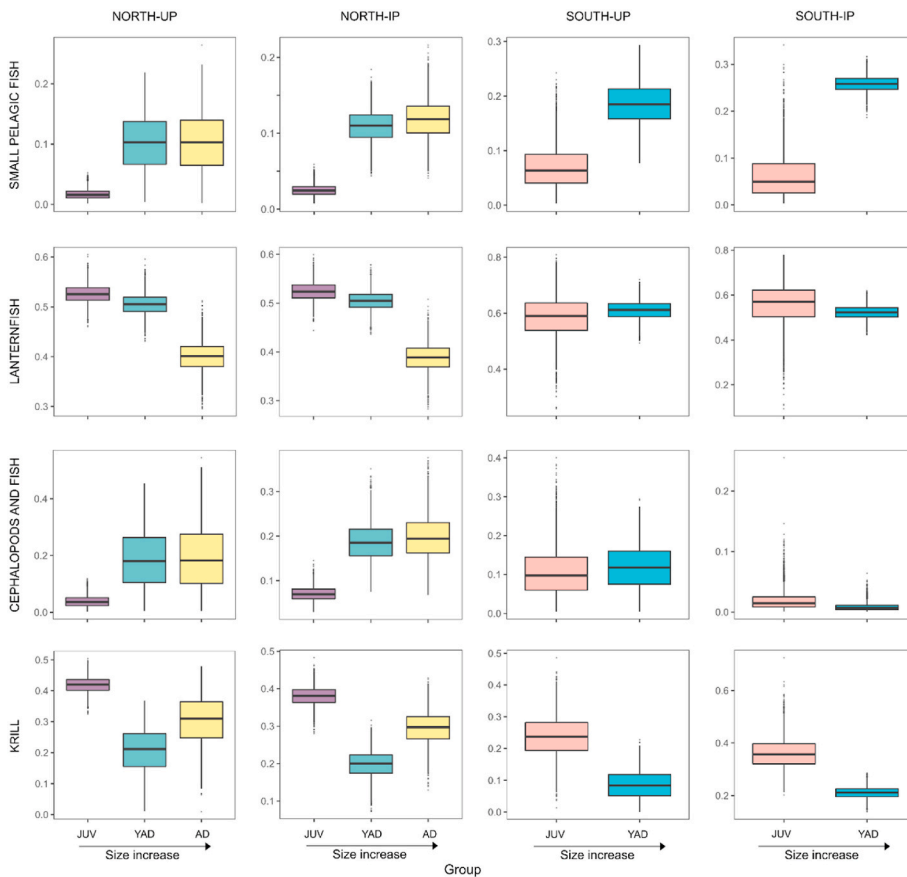
Fig. 4. Ontogenetic shifts in prey proportion on skipjack diet estimated by mixing models with uninformative (UP) and informative (IP) priors. The proportion of krill and lanternfish decreased, while the contribution from cephalopods and fish and small pelagic fish increased with skipjack size, respectively. Colors denotes size groups: JUV (juvenile); YAD (young adult); AD (adult). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

comparison to juveniles (P > 0.94). In the southern area, the importance of small pelagic fish increased with skipjack size (P > 0.97). Lanternfish importance decreased with skipjack size in the northern area (P > 0.75), while no ontogenetic shifts in lanternfish consumption were evident in the south. No shift in the proportion of cephalopods occurred among size classes in the southern area. Due to small sample size (n = 7), we were not able to estimate diet composition of adult skipjack captured in the southern area.

3.3. Isotopic niche width

Isotopic niche estimates were larger for skipjack collected in the northern area, in comparison to the south (Fig. 5a), and individuals (n = 26) collected in the northern area were observed inside the KUD contours defined by skipjack captured in the southern area and vice-versa (n = 12). Isotopic niche overlaps between areas varied from 0% to 64.7% depending on the KUD of inference (Table 4).

KUD estimates for ontogenetic groups showed that young adults have larger isotopic niches in comparison to juveniles and adults (Fig. 5b). Contours for KUD showed differences in the isotopic niche among skipjack size classes. The core area for juveniles, denoted by 50% contour, had the lowest $\delta^{13}C$ and $\delta^{15}N$ values, whereas young adults were distributed across the entire isotopic space and appeared to have two core areas: a larger one defined by relatively high $\delta^{15}N$ values and a smaller one with intermediate to low $\delta^{15}N$ values (Fig. 5b). Finally, the core area of adults had similar (low) $\delta^{15}N$ values to juveniles, while adult $\delta^{13}C$ values were higher than other size classes. Overlap estimates for 50% contours were greatest among adults and young adults (36.3%), adults and juveniles (35.7%) and juveniles and adults (33.4%) (Table 4).

4. Discussion

We applied complementary approaches to study skipjack tuna foraging ecology and movement in the Southwest Atlantic Ocean. Mixing models showed that the primary prey for skipjack is lanternfish in both the northern and southern feeding grounds. Krill was also important prey in both areas, while cephalopods and fish and small pelagic fish (e.g. anchovy and sardine) were the secondary prey in the northern and southern areas, respectively. In regards to ontogenetic dietary patterns, the importance of krill and lanternfish decreased, while the contributions from cephalopods and fish, and small pelagic fish increased with increasing skipjack size. Latitudinal trends in skipjack muscle tissue were consistent with those of regional isoscapes of zooplankton (Troina et al., 2020), suggesting a degree of residency similar in timescale to the isotopic incorporation of tuna muscle (2–4 months) (Graham, 2007), and that baseline $\delta^{15}N$ gradients may be useful for tracking movement of skipjack and other top marine consumers in this region. Lastly, the isotope-based ontogenetic patterns in skipjack seasonal movements agree with data on size structure dynamics gleaned from fishery landings.

4.1. Skipjack diet composition

Our results show that three primary prey types sustain the skipjack population in SWA feeding grounds: lanternfish, and krill in the northern area, and lanternfish, krill and small pelagic fish in the southern area. Skipjack forages mostly on fish and crustacean prey in the Atlantic Ocean (Olson et al., 2016). The lightfish (*Vinciguerria nimbari*) have been identified as an abundant food source in eastern tropical Atlantic (Dragovich and Potthoff, 1972). In the area between 22 and 28°S corresponding to the northern area in our study, Ankenbrandt (1985) found that the main prey consumed in the 1981–82 fishing season were
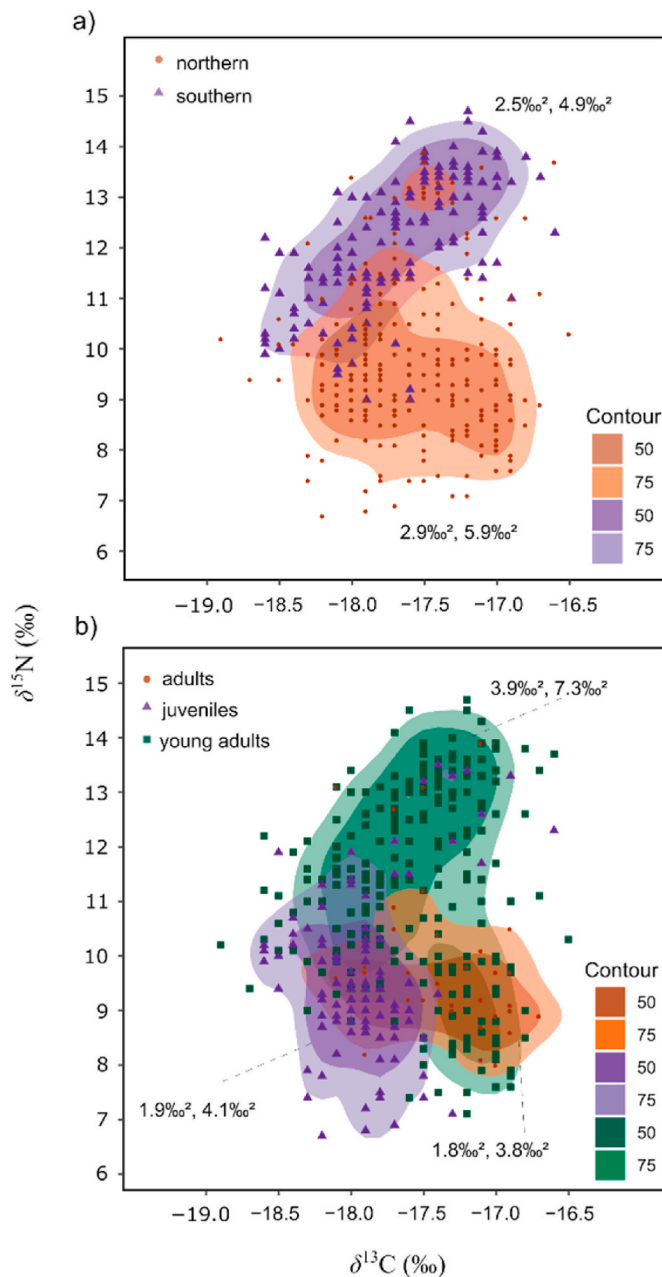
Fig. 5. δ^{13}C and δ^{15}N isotopic niche widths for skipjack tuna (*Katsuwonus pelamis*) in the Southwest Atlantic Ocean. Bi-plots for the (a) northern and southern areas, and (b) ontogenetic groups are shown. Kernel utilization density and niche width (insets) were generated for 50% (darker colors), and 75% (lighter colors) contour levels. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Estimates of isotopic niche overlap for skipjack by area and ontogenetic group according to kernel utilization densities at 50% and 75% contours. Overlaps are percentage of the first group area over the second.

	Groups	50%	75%
Site	North x South	0	22.7
	South x North	0.1	27.6
Size Groups	Juveniles x Young Adults	15.7	42.8
	Juveniles x Adults	33.4	36.9
	Young Adults x Juveniles	7.5	24.2
	Young Adults x Adults	16.2	37.2
	Adults x Juveniles	35.7	40.6
	Adults x Young Adults	36.3	72.2

occurred in the southern area (Madureira et al., 2005). Overall, these patterns suggest that there is a strong trophic link between skipjack and lanternfish in the SWA.

Skipjack was also reported to consume krill in the Pacific and Indian Oceans (Olson et al., 2016; Vooren, 1976), while north Atlantic krill (*Meganyctiphanes norvegica)* was the primary food source in the Balearic Sea (Varela et al., 2019). Dense patches of euphausiids are common in oceanographic fronts between oligotrophic and cold nutrient-rich waters in the Southern California Bight (Fiedler and Bernard, 1987). These conditions are similar to those associated with skipjack foraging behavior and fishing activity in the SWA (Andrade, 2003; Coletto et al., 2019) where *Euphausia similis* occurs in the convergence of subtropical and subantartic waters masses that generate favorable conditions for krill growth, providing large nutrient-rich patches of forage for pelagic top consumers (Antezana and Brinton, 1981; Lopes et al., 2006).

Mixing models show higher proportion of small pelagic fish in skipjack diet in the southern area in comparison to the northern area. Also, the ontogenetic shift in the importance of small pelagic fish with increasing size was more pronounced in the southern area, suggesting a greater availability of this prey at higher latitudes. The reduced contribution of small pelagic fish in the northern area may be related to the low abundance of the Brazilian sardine (*Sardinella brasiliensis*), as indicated by the lowest ever catch recorded by the Brazilian industry in 2017 (Schmidt et al., 2019). Several impacts of climate change have been documented on marine fisheries in the SWA, with evidences that sardine is moving to the south of its traditional range (23–29°S) (Franco et al., 2020), which appear to be related to positive SST anomalies and the southward influence of the Brazil Current (Gianelli et al., 2019; Schmidt et al., 2019; Franco et al., 2020). It is likely that the spatial and ontogenetic variation on skipjack diet observed here are further elucidating effects of the extreme warming events recorded during recent years in the SWA (Manta et al., 2018).

Our mixing models indicate ontogenetic shifts in skipjack diet. Lanternfish and krill importance decreased with skipjack size, while the proportion of cephalopods and fish and small pelagic fish increased. Ankenbrandt (1985) found that smaller skipjack relied more on krill, while the importance of lanternfish and fish in general increased with skipjack size. Vilella (1990), however, found no shifts in diet with respect to skipjack size. Graham et al. (2007) found that a critical size threshold of ~45 cm for yellowfin tuna (*Thunnus albacares*) was likely associated with an endothermic capability to access larger prey in deeper, colder waters. Likewise, the average size of prey increased with the size of bigeye tuna (*Thunnus obesus*) and yellowfin tuna from the Indian Ocean (Ménard et al., 2006) and the eastern Pacific off Ecuador (Varela et al., 2017). The asymmetric shape of prey size distribution, however, suggests that tunas may continue to feed on small prey when they reach larger body sizes (Young et al., 2010), which is consistent with the more even proportions of prey groups in adult skipjack diet observed in the northern area of the SWA (Table 3 and Fig. 4).

The relatively small but notable occurrence of skipjack with outlying δ^{15}N values at both areas indicates that a few individuals were not in equilibrium with the isotopic composition of local prey. The inclusion of

lanternfish (*Maurolicus stehmanni*) and krill (*Euphausia similis*) that represented 26.7% and 22.2% of stomach content by volume (V), respectively. Vilella (1990) also found that lanternfish was the primary prey for skipjack (45% V) between 30 and 34°S from 1983 to 86, followed by krill (12% V), and anchovy (*Engraulis anchoita;* 8% V). Hydroacoustic cruises conducted between 1995 and 1997 indicated that lanternfish occurs between 22 and 34°S in the SWA, and the highest abundances for the species were found near the shelf break and slope areas, where the South Atlantic Central Water meets the Tropical Water from Brazil Current (Madureira et al., 2005). During winter, the greatest lanternfish abundance was found in the northern area off Rio de Janeiro, while during the fall and spring-summer surveys, the highest abundance

these individuals in our mixing models may bias the estimates of dietary composition to some degree, however, these outliers represent a low proportion (~11%) of the individuals we sampled. Future isotope-based studies could address this potential uncertainty by focusing on tissues (e. g. liver or blood plasma) with faster isotopic incorporation rates.

The posteriors for cephalopods contribution in our SIMM-IP in the southern area mirrored the informative priors. Since only hard parts such as beaks accumulate in predator stomachs with minimal digestion (Clarke, 1986), biomass estimates may underestimate cephalopod contribution to skipjack diet. The importance of cephalopods is minimal regardless of the index we used as priors in mixing models; i.e. biomass <2%; frequency of occurrence, FO 2–3% (Supplementary Table A1). Ankenbrandt (1985) reports Ommastrephidae as the most frequent cephalopod family in skipjack stomach contents (1.7% FO), followed by Argonautidae (1% FO). Data from Vilella (1990) shows that Teutoidea contributed only 1.3% of stomach content volume and had 6% FO in experimental purse seining, while only representing of 0.13% volume and 0.75% FO in commercial fishing. Santos and Haimovici (2002) reviewed the role of cephalopods in SWA food webs, and classified skipjack as an occasional predator (i.e. < 10% FO) for Ommastrephidae and Argonautidae. Overall, these patterns generally agree with our mixing model results, however, it is worth noting that dietary data based on SCA may be biased because some Ommastrephidae are diel migrants and pole and line fishing depends on visual sighting of tuna at the surface during the day (Lima et al., 2000).

In the southern area, estimates of diet composition based on SIMM-IP were considered more realistic in comparison to SIMM-UP. The effect of priors on mixing model posteriors is greater when the isotopic variation among sources is limited (Franco-Trecu et al., 2013; Swan et al., 2019), and the discriminatory power of mixing models is directly related to the degree of isotopic differences among sources of prey that defines the geometry of the mixing space (Phillips et al., 2014). The incorporation of priors into mixing models has the advantage of setting the range of feasible solutions for each source in a given model (Moore and Semmens, 2008), but caution should be taken with this approach as the priors can transfer biases from other methods (e.g. SCA) into dietary estimates derived from mixing models (Franco-Trecu et al., 2013; Swan et al., 2019).

4.2. Skipjack habitat use

Skipjack caught in the southern area had higher mean $\delta^{15}N$ values than fish captured in the northern area. This pattern could be related to diet (i.e. trophic level) as krill had a greater importance for skipjack in the northern area in comparison to the southern area. More importantly, the trend of increasing $\delta^{15}N$ values with latitude was clear in $\delta^{15}N$ values of prey collected from the two regions: e.g. krill $\delta^{15}N$ values on average were ~1.9‰ higher in the south in comparison to the north. Also, $\delta^{15}N$ values for both skipjack and krill increased with latitude, suggesting that baseline patterns were likely the cause of differences on both prey and skipjack $\delta^{15}N$ values between areas. Published basin-scale isoscapes show that zooplankton $\delta^{15}N$ values are ~4‰ near the upper margin of the northern area at Abrolhos Bank (Fig. 1), and increase to ~6‰ near the southern area of our study (McMahon et al., 2013), which is likely driven by the greater influence of N_2 fixation by phytoplankton in the oligotrophic waters of the northern area versus higher nutrient availability and primary production in the southern area (Troina et al., 2020). The latitudinal trend in skipjack and krill $\delta^{15}N$ composition is consistent with previous work with pelagic predators from other ocean basins. Yellowfin tuna and mesozooplankton $\delta^{15}N$ values varied consistently with latitude in the Eastern Tropical Pacific (Popp et al., 2007). Swordfish (*Xiphias gladius*) and yellowfin tuna also reflected spatial variation in baseline $\delta^{15}N$ values in the Indian Ocean (Ménard et al., 2007), while the $\delta^{15}N$ values varied with sampling location for dolphinfish (*Coryphaena hippurus*) and yellowfin tuna in the North Atlantic Ocean (Logan and Lutcavage, 2013). $\delta^{13}C$ can also vary with latitude of

sampling locations as shown for bigeye (*Thunnus obesus*), albacore (*Thunnus alalunga*) and yellowfin tunas (Logan et al., 2020). These patterns suggest that the baseline variation in $\delta^{15}N$ is likely the primary driver of the latitudinal trend in skipjack muscle $\delta^{15}N$ values in the SWA.

To reflect gradients in baseline isotope composition, mobile predators should have a degree of residency that is similar to or greater than the isotopic incorporation rates of their tissues (Graham et al., 2010). Fisheries data show that skipjack occurs in the southern foraging grounds of the SWA from October–September until May–June of the following year (Coletto et al., 2019). It is important to note that our opportunistic sampling effort occurred for a period of 6–7 months during two years (2017 and 2018) in both the northern and southern areas. Isotopic incorporation is directly related to growth rates (Martinez del Rio et al., 2009), and since skipjack have the fastest growth rates among tunas (Murua et al., 2017), incorporation rates should be higher than those estimated for Pacific bluefin tuna (~5.5 months; Madigan et al., 2012), but are likely more similar to those estimated for juvenile yellowfin tuna (~2–4 months; Graham, 2007). Therefore, the increase in skipjack muscle $\delta^{15}N$ values observed at higher latitudes suggests a degree of residency on the timescale of a few months in the productive southern foraging grounds.

In addition to nitrogen isotope difference between the northern and southern areas, we observed temporal patterns in skipjack $\delta^{15}N$ that are likely the product of seasonal latitudinal movements. Some skipjacks captured in the northern area had higher $\delta^{15}N$ values (>12.5‰) than expected based on the 50% KUD niche estimates that were more similar to mean $\delta^{15}N$ values of skipjack captured in the southern area. Most of these outlier individuals (n = 16 or 76%) were caught during April and May. When comparing skipjack isotope composition between areas over time, we found that $\delta^{15}N$ values were different during summer months (January–March), but during April–May $\delta^{15}N$ values for individuals captured in the northern area increase and become similar to those for individuals captured in the southern area, which can be explained by the seasonal movement of skipjack from south to north in the fall. Skipjack latitudinal movements in the SWA are driven by seasonal displacements of the Subtropical Convergence Area and the warm waters of the BC that determine the seasonal distribution of SST across this region (Castello and Habiaga, 1989; Vilella and Castello, 1993; Andrade, 2003; Coletto et al., 2019). Skipjack seasonal migration following the displacements of BC in the area were observed through fishing effort and catch dynamics (Andrade 2003; Coletto et al., 2019), and also by tag and recovery experiments, as individuals released in the southern area were subsequently recaptured in the northern area (Luckhurst, 2014; Fonteneau, 2015; ICCAT, 2016).

We also observed a smaller number of individuals (n = 3) captured in the southern area that had surprisingly low $\delta^{15}N$ values (<9.2‰) similar to those of skipjack captured in the northern area. All three individuals were adults, significantly larger (SFL = 67–73) than most fish caught in the southern area. This pattern suggests that adult skipjack primarily forage at lower latitudes, but move towards the productive foraging areas at higher latitudes during the fall. Length frequency analysis shows a seasonal modal progression, with smaller sized individuals occurring during spring and larger individuals in the fall (Ankenbrandt, 1985; Andrade and Kinas, 2004; Soares et al., 2019). Larvae/egg distribution and size at sexual maturity suggest that spawning rarely takes place in the southern area, but instead during the summer months near Abrolhos Bank (~18°S) near the northern margin of the northern area (Matsuura, 1986; Vilella and Castello, 1993; Matsuura and Andrade, 2000; Soares et al., 2019). The higher occurrence of larger individuals during the fall could explain the increase in $\delta^{13}C$ values observed at both sites towards the end of the fishing seasons, as $\delta^{13}C$ increase with skipjack size. Patterns in the isotopic niche of different size groups thus appear to be linked to skipjack lifecycle. Specifically, there was a large overlap in the 50% KUD contours between juveniles and adults, whose $\delta^{15}N$ values are lower in comparison to young adults. In contrast, young adults have higher $\delta^{15}N$ values because they primarily forage in the most productive

southern foraging grounds at higher latitudes near the subtropical convergence, where baselines have higher δ^{15}N values, and they also consume higher trophic level prey (e.g. cephalopods and fish, and small pelagic fish), while juveniles primarily consume lanternfish and krill.

5. Conclusion

Understanding trophic links and energy flux in exploited ecosystems is imperative for fisheries management. As opportunistic predators, tuna foraging strategies evolved to satisfy their high energetic demands by maximizing intake of energy-rich foods (Olson et al., 2016). The opportunistic strategy for skipjack includes the consumption of energy-rich and abundant prey such as lanternfish and krill, which form strong trophic links in the pelagic food webs of the SWA. Lanternfish and krill were the main prey regardless of skipjack size, and young adults and adults also consume cephalopods and fish (i.e. Omastrephidae, Carangidae) in the northern area, and small pelagic fish (i.e. Clupeidae and Engraulidae) in the southern area. We also show that the observed differences in skipjack δ^{15}N values between the northern and southern areas reflect baseline trends in the nitrogen isotopic composition of zooplankton near the base of the pelagic food webs. Since this pattern was conserved from primary consumers to a higher trophic level pelagic predator, skipjack may have a degree of residency in the order of ~2–4 months in the northern or southern SWA foraging grounds based on isotopic incorporation rates for similar sized yellowfin tuna. Finally, we recommend that the foraging patterns of the SWA skipjack population be continuously monitored to better understand how oceanographic conditions influence skipjack distribution patterns in this highly dynamic pelagic environment.

Ethics approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors. All authors have approved the manuscript submission to *Marine Environmental Research*.

Sample credit author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.105246.

References

Acha, E.M., et al., 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. J. Mar. Syst. 44, 83–105. https://doi.org/10.1016/j.jmarsys.2003.09.005.

Alatorre-Ramíres, V.G., et al., 2017. Trophic segregation of mixed schools of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) caught in the eastern tropical Pacific Ocean. Fish. Bull. 115, 252–268. https://doi.org/10.7755/FB.115.2.11.

Alverson, F.G., 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean: Inter-Am Trop. Tuna Comm. Bull. 7, 293–396.

Andrade, H.A., Garcia, C.A.E., 1999. Skipjack tuna fishery in relation to sea surface temperature in the southern Brazilian coast. Fish. Oceanogr. 8, 245–254. https://doi.org/10.1046/j.1365-2419.1999.00107.x.

Andrade, H.A., 2003. The relationship between the skipjack tuna (*Katsuwonus pelamis*) fishery and seasonal temperature variability in the south-western Atlantic. Fish. Oceanogr. 12, 10–18. https://doi.org/10.1046/j.1365-2419.2003.00220.x.

Andrade, H.A., Kinas, P.G., 2004. Estimation of birthdates and catch-at-age using length frequency analysis (LFA), with application for skipjack tuna (*Katsuwonus pelamis*) caught in the Southwest Atlantic. ICES J. Mar. Sci. 61, 798–811. https://doi.org/10.1016/j.icesjms.2004.03.002.

Ankenbrandt, L., 1985. Food habits of bait-caught skipjack tuna, *Katsuwonus pelamis*, from the southwestern Atlantic Ocean. Fish. Bull. 83, 379–393.

Antezana, T., Brinton, E., 1981. Euphausiacea. In: Boltovskoy, D. (Ed.), Atlas del zooplancton del Atlantico sudoccidental y métodos de trabajo con zooplancton marino. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, pp. 681–698.

Bivand, R.S., Pebesma, E., Gomez-Rubio, V., 2013. Applied Spatial Data Analysis with R, second ed. Springer, NY.

Brill, R.W., Hobday, A.J., 2017. Tunas and their fisheries: safeguarding sustainability in the twenty-first century. Rev. Fish Biol. Fish. 27, 691–695. https://doi.org/10.1007/s11160-017-9500-3.

Bunn, S.E., et al., 1995. Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications studies using multiple stable isotopes. Limnol. Oceanogr. 40, 622–625. https://doi:10.4319/lo.1995.40.3.0622.

Campos, E.J.D., Gonçalves, J.E., Ikeda, Y., 1995. Water mass characteristics and geostrophic circulation in the South Brazil Bight: summer of 1991. J. Geophys. Res. 100, 18537–18550. https://doi.org/10.1029/95JC01724.

Campos, E.J.D., Velhote, D., Silveira, I.C.A., 2000. Shelf break upwelling driven by Brazil Current cyclonic meanders. Geophys. Res. Lett. 27, 751–754. https://doi.org/10.1029/1999GL010502.

Carabel, S., et al., 2006. An assessment of sample processing methods for stable isotope analyses of marine food webs. J. Exp. Mar. Biol. Ecol. 336, 254–261. https://doi.org/10.1016/j.jembe.2006.06.001.

Castello, J.P., Habiaga, R.P., 1989. The skipjack tuna fishery in southern Brazil. ICCAT Col. Vol. Sci. Pap. 30, 6–19.

Castello, J.P., 1997. A anchoita (*Engraulis anchoita*, Engraulididae, Pisces) no sul do Brasil. In: Dissertation, Universidade Federal do Rio Grande.

Chipps, S.R., Garvey, J.E., 2007. Assessment of Food Habits and Feeding Patterns. In: Guy, C., Brown, M. (Eds.), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, MD, USA, pp. 473–514.

Clarke, M.R., 1986. A Handbook for the Identification of Cephalopod Beaks. Claredon Press, Oxford.

Coletto, J.L., Pinho, M.P., Madureira, L.S.P., 2019. Operational oceanography applied to skipjack tuna (*Katsuwonus pelamis*) habitat monitoring and fishing in south-western Atlantic. Fish Ocenogr. 28, 82–93. https://doi.org/10.1111/fog.12388.

Cury, P.M., et al., 2008. Ecosystem oceanography for global change in fisheries. Trends Ecol. Evol. 23, 338–346. https://doi.org/10.1016/j.tree.2008.02.005.

DeNiro, M.J., Epstein, J., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochem. Cosmochim. Acta 42, 495–506.

DeNiro, M.J., Epstein, J., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochem. Cosmochim. Acta 45, 341–351.

Dragovich, A., Potthoff, T., 1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. Fish. Bull. 70, 1087–1110.

Dufour, F., Arrizabalaga, H., Irigoien, X., Santiago, J., 2010. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. Prog. Oceanogr. 86, 283–290. https://doi.org/10.1016/j.pocean.2010.04.007.

Eckrich, C.A., et al., 2019. rKIN: kernel-based method for estimating isotopic niche and overlap. J. Anim. Ecol. 89, 757–771. https://doi.org/10.1111/1365-2656.13159.

FAO, 2018. The state of world fisheries and agriculture. In: Meeting the Sustainable Development Goals Rome, 211pp. http://www.fao.org/3/I9540EN/i9540en.pdf. (Accessed 10 August 2020).

Fiedler, P.C., Bernard, H.J., 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. Continent. Shelf Res. 7, 871–881. https://doi.org/10.1016/0278-4343(87)90003-3.

Fonteneau, A., 2015. On the movement patterns and stock structure of skipjack (*Katsuwonus pelamis*) in the Atlantic: how many skipjack stocks in the Atlantic Ocean? ICCAT Col. Vol. Sci. Pap. 71, 205–220.

Franco, B.C., et al., 2020. Climate change impacts on the atmospheric circulation, ocean, and fisheries in the southwest South Atlantic Ocean: a review. Climatic Change. https://doi.org/10.1007/s10584-020-02783-6.

Franco-Trecu, et al., 2013. Bias in diet determination: incorporating traditional methods in bayesian mixing models. PloS One 8, e80019. https://doi.org/10.1371/journal.pone.0080019.

Franco-Trecu, V., Aurioles-Gamboa, D., Inchausti, P., 2014. Individual trophic specialization and niche segregation explain the contrasting population trends of two sympatric otariids. Mar. Biol. 161, 609–618. https://doi.org/10.1007/s00227-013-2363-9.

Garcia, C.A.E., 1997. Physical oceanography. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments: the Coastal and Sea in the Southwestern Atlantic. Springer, Berlin, pp. 94–96.

Gianelli, I., Ortega, L., Marín, Y., Piola, A.R., Defeo, O., 2019. Evidence of ocean warming in Uruguay's fisheries landings: the mean temperature of the catch approach. Mar. Ecol. Prog. Ser. 625, 115–125. https://doi.org/10.3354/meps13035.

Graham, B.S., 2007. Trophic Dynamics and Movements of Tuna in the Tropical Pacific Ocean Inferred from Stable Isotope Analyses. Dissertation. University of Hawaii at Manoa.

Graham, B.S., Grubbs, D., Holland, K., Popp, B.N., 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. Mar. Biol. 150, 647–658. https://doi.org/10.1007/s00227-006-0360-y.

Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., et al. (Eds.), Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping, pp. 299–318. https://doi.org/10.1007/978-90-481-3354-3_14.

Hilborn, R., Amoroso, R.O., et al., 2020. Effective fisheries management instrumental in improving fish stock status. Proc. Natl. Acad. Sci. Unit. States Am. 117, 2218–2224. https://doi.org/10.1073/pnas.1909726116.

Hobson, K.A., Wassenaar, L.I., 2019. Tracking Animal Migration with Stable Isotopes. Academic Press, London.

Hoffman, J.C., Sutton, T.T., 2010. Lipid correction for carbon stable isotope analysis of deep-sea fishes. Deep Sea Reas. Deep-Sea Res. Part I 57, 956–964. https://doi.org/10.1016/j.dsr.2010.05.003.

ICCAT, 2016. ICCAT manual. International commission for the conservation of Atlantic tuna. In: ICCAT Publications [on-Line]. Updated 2016. ISBN (Electronic Edition): 978-92-990055-0-7 Chap. 2.1.3 Skipjack Tuna.

ICCAT, 2019. International commission for the conservation of Atlantic tunas. Stat. Bull. 45. https://www.iccat.int/sbull/SB45-2019/index.html#. (Accessed 10 June 2020).

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Lima, J.H.M., Lin, C.F., Menezes, A.A.S., 2000. A description of the baitboat fishery off the South and southeast Brazil. ICCAT Col. Vol. Sci. Pap. 51, 416–462.

Logan, J.M., et al., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical and modelling methods. J. Anim. Ecol. 77, 838–846. https://doi.org/10.1111/j.1365-2656.2008.01394.x.

Logan, J.M., Lutcavage, M.E., 2013. Assessment of trophic dynamics of cephalopods and large pelagic fishes in the central North Atlantic Ocean using stable isotope analysis. Deep-Sea Res. Part II 95, 63–73. https://doi.org/10.1016/j.dsr2.2012.07.013.

Logan, J.M., et al., 2020. Global patterns and inferences of tuna movements and trophodynamics from stable isotope analysis. Deep-Sea Res. Part II. 175, 104775. https://doi.org/10.1016/j.dsr2.2020.104775.

Lopes, R.M., et al., 2006. O zooplâncton marinho na região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Rossi-Wongtschowski, C.L.D.B., Madureira, L.S.P. (Eds.), O Ambiente oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. Editora da USP, São Paulo, pp. 219–264.

Lorenzetti, J.A., Stech, J.L., Mello-Filho, W.L., Assireu, A.T., 2009. Satellite observation of Brazil Current inshore thermal front in the SW South Atlantic: space/time variability and sea surface temperatures. Continent. Shelf Res. 29, 2061–2068. https://doi.org/10.1016/j.csr.2009.07.011.

Luckhurst, B.E., 2014. Elements of the ecology and movement patterns of highly migratory fish species of interest to ICCAR in the Sargasso Sea. ICCAT Col. Vol. Sci. Pap. 70, 2183–2206.

Madigan, D.J., et al., 2012. Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, pacific bluefin tuna (*Thunnus orientalis*). PloS One 7, e49220. https://doi.org/10.1371/journal.pone.0049220.

Madureira, L.S.P., et al., 2005. Distribuição, abundância e interações ambientais de espécies pelágicas na região sudeste-sul do Brasil, entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Madureira, L.S.P., Rossi-Wongtschowski, C.L.D.B. (Eds.), Prospecção de recursos pesqueiros pelágicos na Zona Econômica Exclusiva da Região Sudeste-Sul do Brasil: hidroacústica e biomassas. Série Documentos REVIZEE – Score Sul. Instituto Oceanográfico – USP, São Paulo, pp. 63–126.

Madureira, L.S.P., et al., 2009. Current and potential alternative food uses of the Argentine anchoita (*Engraulis anchoita*) in Argentina, Uruguay and Brazil. In: Hasan, M.R., Halwart, M. (Eds.), Fish as Feed Inputs for Aquaculture: Practices, Sustainability and Implications. FAO Fisheries and Aquaculture Technical Paper. No. 518. Rome, FAO, pp. 269–287.

Manta, G., et al., 2018. The 2017 record marine heatwave in the Southwestern Atlantic shelf. Geophys. Res. Lett. 28, 12449–12456. https://doi.org/10.1029/2018GL081070.

Marques, F.P., et al., 2018. Trophic ecology of Magellanic penguins (*Spheniscus magellanicus*) during the non-breeding period. Estuar. Coast Shelf Sci. 210, 109–122. https://doi.org/10.1016/j.ecss.2018.06.001.

Martinez del Rio, C., et al., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. 84, 91–111. https://doi.org/10.1111/j.1469-185X.2008.00064.x.

Martinez del Rio, C., Carleton, S., 2012. How fast and how faithful: the dynamics of isotopic incorporation into animal tissues. J. Mammal. 93, 353–359. https://doi.org/10.1644/11-MAMM-S-165.1.

Matsuura, Y., 1986. Distribution and abundance of skipjack larvae off the coasts of Brazil. Proc. ICCAT Intl. Skipjack Year Prog 1, 285–289.

Matsuura, Y., Andrade, H.A., 2000. Synopsis on biology of skipjack tuna population and related environmental conditions in Brazilian waters. ICCAT Col. Vol. Sci. Pap. 51, 395–400.

McMahon, K.W., Hamady, L.L., Thorrold, S.R., 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol. Oceanogr 58, 697–714. https://doi.org/10.4319/lo.2013.58.2.0697.

Ménard, F., et al., 2006. Opportunistic predation on tuna: a size-based approach. Mar. Ecol. Prog. Ser. 323, 223–231. https://doi.org/10.3354/meps323223.

Ménard, F., et al., 2007. Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. Mar. Biol. 153, 141–152. https://doi.org/10.1007/s00227-007-0789-7.

Möller, O.O., et al., 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. Cont. Shelf. Res. 28, 1607–1624. https://doi.org/10.1016/j.csr.2008.03.012.

Moore, J.W., Semmens, B.X., 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecol. Lett. 11, 470–480. https://doi.org/10.1111/j.1461-0248.2008.01163.x.

Murua, H., et al., 2017. Fast versus slow growing tuna species: age, growth, and implication for population dynamics and fisheries management. Rev. Fish Biol. Fish. 27, 733–773. https://doi.org/10.1007/s11160-017-9474-1.

Newsome, S.D., et al., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436. https://www.jstor.org/stable/20440730.

Oksanen, J., et al., 2020. vegan: community Ecology Package. R package version 2.5.7. https://CRAN.R-project.org/package=vegan.

Olson, R.J., et al., 2016. Bioenergetics, trophic ecology, and niche separation of tunas. In: Curry, B.E. (Ed.), Advances in Marine Biology, vol. 74. Academic Press, , Oxford, pp. 199–344.

Parnell, A., 2019. Simmr: a stable isotope mixing model. R package version 0.4.1. https://CRAN.R-project.org/package=simmr.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Off. Syst. 18, 293–320.

Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527. https://doi.org/10.1007/s00442-004-1816-8.

Phillips, D.L., et al., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92, 823–835. https://doi.org/10.1139/cjz-2014-0127.

Pinnegar, J.K., Polunin, N.V.C., 1999. Differential fractionation of δ^{13}C and δ^{15}N among fish tissues: implications for the study of trophic interactions. Funct. Ecol. 13, 225–231. https://doi.org/10.1046/j.1365-2435.1999.00301.x.

Popp, B.N., et al., 2007. Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson, T.D., Siegwolf, T.R.W. (Eds.), Stable Isotopes as Indicators of Ecological Change, Amsterdam. Elsevier/Academic Press, pp. 173–190. https://doi.org/10.1016/S1936-7961(07)01012–01013.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITEP]2.0.CO;2.

Post, D.M., et al., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189. https://doi.org/10.1007/s00442-006-0630-x.

Potier, M., et al., 2002. On-going research activities on trophic ecology of tuna in equatorial ecosystems of the Indian Ocean. IOTC Proc. 5, 368–374.

R Core Team, 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL. https://www.R-project.org/.

Roger, C., 1994. Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. Fish. Oceanogr. 3, 133–141. https://doi.org/10.1111/j.1365-2419.1994.tb00055.x.

Rowlingson, B., Diggle, P., 2017. Splancs: Spatial and Space-Time Point Pattern Analysis. R Package Version 2.01-40.

Santos, R.A., Haimovici, M., 2002. Cephalopods in the trophic relations off Southern Brazil. Bull. Mar. Sci. 71, 753–770.

Schmidt, J.O., et al., 2019. Future ocean observations to connect climate, fisheries and marine ecosystems. Front. Mar. Sci. https://doi.org/10.3389/fmars.2019.00550.

Smith, J.A., et al., 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. Methods Ecol. Evol. 4, 612–618. https://doi.org/10.1111/2041-210X.12048.

Soares, J.B., et al., 2019. Size structure, reproduction, and growth of skipjack tuna (*Katsuwonus pelamis*) caught by the pole-and-line fleet in the southwest Atlantic. Fish. Res. 212, 136–145. https://doi.org/10.1016/j.fishres.2018.12.011.

Sulzman, E.W., 2007. Stable isotope chemistry and measurement: a primer. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell, Oxford, pp. 1–18.

Swan, G.J.F., et al., 2019. Evaluating Bayesian stable isotope mixing models of wild animal diet and the effects of trophic discrimination factors and informative priors. Methods Ecol. Evol. 11, 139–149. https://doi.org/10.1111/2041-210X.13311.

Troina, G.C., 2019. Ecologia e interações tróficas de cetáceos no Atlântico sul ocidental. In: Dissertation, Universidade Federal do Rio Grande.

Troina, G.C., et al., 2020. Zooplankton-based δ13C and δ^{15}N isoscapes from the outer continental shelf and slope in the subtropical western South Atlantic. Deep-Sea Res. Part I 159, 103235. https://doi.org/10.1016/j.dsr.2020.103235.

Varela, J.L., Cañavate, J.P, Medina, A., Mourente, G., 2019. Inter-regional variation in feeding patterns of skipjack tuna (*Katsuwonus pelamis*) inferred from stomach content, stable isotope and fatty acid analyses. Mar. Environ. Res. 152, 104821. https://doi.org/10.1016/j.marenvres.2019.104821.

Varela, J.L., de la Gándara, F., Ortega, A., Medina, A., 2012. [13]C and ^{15}N analysis in muscle and liver of wild and reared young-of-the-year (YOY) Atlantic bluefin tuna. Aquaculture 354-355, 17–21. https://doi.org/10.1016/j.aquaculture.2012.04.040.

Varela, J.L., Intriago, K.M., Flores, J.C., Lucas-Pilozo, C.R., 2017. Feeding habits of juvenile yellowfin tuna (*Thunnus albacares*) in Ecuadorian waters assessed from stomach content and stable isotope analysis. Fish. Res. 194, 89–98.

Varela, J.L., Larrañaga, A., Medina, A., 2011. Prey-muscle carbon and nitrogen stable-isotope discrimination factors in Atlantic bluefin tuna (*Thunnus thynnus*). J. Exp. Mar. Biol. Ecol. 406, 21–28. https://doi.org/10.1016/j.jembe.2011.06.010.

Varela, J.L., Rodríguez-Marín, E., Medina, A., 2013. Estimating diets of pre-spawning Atlantic bluefin tuna from stomach content and stable isotope analyses. J. Sea Res. 76, 187–192. https://doi.org/10.1016/j.seares.2012.09.002.

Velasco, G., Castello, J.P., 2005. An ecotrophic model of southern Brazil continental shelf and fisheries scenarios for *Engraulis anchoita* (Pisces, Engraulididae). Atlantica 27, 59–68. https://doi.org/10.5088/atlântica.v27i1.2210.

Vilella, M.J.A., 1990. Idade, crescimento, alimentação e avaliação do estoque de bonito listado, *Katsuwonus pelamis* (SCOMBRIDAE: THUNNINI), explorado na região sudeste – sul do Brasil. In: Dissertation, Universidade Federal do Rio Grande.

Vilella, M.J.A., Castello, J.P., 1993. Dinamica poblacional del barrilete (*Katsuwonus pelamis*) explotado en la region sudeste – sur del Brasil em el período 1980-1986. Frente Maritimo 14, 111–124.

Vooren, C.M., 1976. Biological data on skipjack in New Zeland waters, 1973-76. In: Proceeding of the Skipjack Tuna Conference, July 1976. Fisheries Research Division, Occasional Publication No. 11.

Wild, A., Hampton, J., 1993. A review of biology and fisheries for skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean FAO Fisheries Tech. In: Paper 336 Rome, pp. 1–51.

Young, W.Y., et al., 2010. Feeding ecology and niche segregation in oceanic top predator off eastern Australia. Mar. Biol. 157, 2347–2368. https://doi.org/10.1007/s00227-010-1500-y.