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On the trophic role of pelagic fishes and fishery landings shifts in the South Brazil Bight

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ABSTRACT

Knowledge of the feeding habits of pelagic fishes off the Brazilian coast is scarce, making the analysis of trophic interactions often inaccurate. Here, we investigated the diet and trophic role of 12 pelagic fish species by revisiting samples obtained by the ECOSAR II Program (FURG/IO/IBAMA) between 23°S and 28°40'S, an area also known as South Brazil Bight. In addition, we analyzed their biomass and fisheries landings in order to examine shifts over time. The content of 432 stomachs was analyzed at the lowest taxonomic level possible. The frequencies of occurrence were used to cluster species, revealing three trophic guilds: "Planktivorous Clupeiformes", "Planktivorous Carangiformes", and "Piscivores". Most Carangidae consumed mainly copepods and other small crustaceans, except *Selene setapinnis* which clustered in the piscivorous guild together with Scombriformes specimens. In terms of biomass, the dominance of *Trachurus lathami*, *Sardinella brasiliensis*, and *Trichiurus lepturus* was evident. The species' trophic levels ranged from 2.98 to 4.5, showing that these fishes occupied intermediate to high trophic position. Comparing fisheries landings in two study periods (1986-2002 and 2003-2019), six species showed a decrease, while three an increase. Correlations between landings of the Brazilian sardine (*Sardinella brasiliensis*) and other pelagic fishes indicate that when the former's decreases, the catch of alternative species, such as *Opisthonema oglinum* and *Chloroscombrus chrysurus*, increases. The intermediate position of small pelagics in the food web may affect the availability of commercial species by controlling the abundance of lower and upper trophic-level organisms. These findings fill essential gaps for ecosystem modeling, suggesting that ecosystem-based fisheries management should address multispecies issues of the pelagic realm rather than only single-species approaches. Combining past survey data with yield trends provides evidence for both natural and human-induced ocean changes.

Descriptors: Pelagic resources, Diet composition, Trophic level, Southwest atlantic, Fishing statistics.

INTRODUCTION

The South Brazil Bight (SBB) comprises a moderate productive region in which a significant portion of the country's fishery yield is concentrated. Key species in marine ecosystems are small pelagic fishes that inhabit transition areas of the continental shelf (Jordán, 2009; Branch et al., 2010). Most of the fish production in the SBB is composed of r-strategists species that are short-lived and endemic to the Argentine Province (Vazzoler et al., 1999), such as anchovy and sardines. The Brazilian sardine (*Sardinella brasiliensis*) is the most abundant and with the most substantial fishery yield in Brazilian waters (Matsuura, 1998; Cergole et al., 2002) and along with it, other pelagic fish are captured by the purse-seining fleet (Gasalla and Rossi-Wongtschowski, 2004).

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However, *S. brasiliensis,* like other small pelagic species, has shown a marked variability in its stock abundance, alternating between periods of high production and a drastic decline in commercial catches (Barange et al., 2009).

Due to the decreasing trend of national sardine yield, going from more than 220,000 tons in 1973 to about 100,000 tons in 1976 (IBAMA, 2000), the federal government of Brazil implemented the ECOSAR Program (abbreviation translated as: "Acoustic exploration and assessment of Brazilian sardinella and Argentine anchovy biomass in the Southeast Region of Brazil"). In ECOSAR I (1988), the biomass of *S. brasiliensis* was estimated as much lower than past values. Owing to a fishery's potential collapse in the region, the government also promoted the following cruises (from 1995 to 2010) to evaluate other pelagic resources of the area that could be alternatives to *S. brasiliensis* stock, especially other sardines such as *Opisthonema oglinum* and *Chloroscombrus chrysurus* (Rossi-Wongtschowski et al., 1996; Jablonski, 2007). Most of the species mentioned above consist of the bulk of fisheries bycatch of the operating fleets in the region; thus, information on their feeding habits and prey selectivity is scarce (Hofling et al., 2000; Corrêa et al., 2005; Martins et al., 2005; Carvalho and Soares, 2006; Muto et al., 2008). However, information on the trophic ecology of small pelagic fish is crucial to understand their role in energy transfer through the food web (Pikitch et al., 2012; Essington et al., 2015). The intermediate trophic position that small pelagic fish hold in the food web of marine ecosystems suggests that they may function as regulators, controlling both the availability of zooplankton and predatory fishes (Rice, 1995; Smith et al., 2011).

Research on fish feeding habits provides information necessary to understand ecological roles concerning environmental fluctuations and food availability (Gasalla and Soares, 2001; Bennemann et al., 2006; Christensen and Walters, 2004; Gasalla et al., 2007; Soares et al., 2018). Moreover, estimating trophic levels (TL) depicts the trophic position of organisms in the food web, considering both the food composition and the TL of each prey consumed (Pauly et al., 2000; Vasconcellos and Gasalla, 2001; Shannon et al., 2014).

The frequency of occurrence of ingested prey items is a proxy that has been widely used to calculate the trophic position of the ichthyofauna, and together with quantitative indices, allow the construction of ecosystem models that help to understand the impact of fishing on the environment (Hahn and Delariva, 2003; Gasalla, 2004; Gasalla and Rossi-Wongtschowki, 2004; Gascuel et al., 2008; Garrido et al., 2015). Similarly, diet information may be used to define trophic guilds, i.e., groups of species that exploit common or similar feeding traits. Associate the concept of trophic guilds with quantitative information on diets seems fundamental for understanding energy distribution and resilience within pelagic communities (Aguiaro and Caramaschi, 1998; Gasalla and Rossi-Wongtschowski, 2004; Specziár and Rezsu, 2009). However, such data are still scarce regarding pelagic fish on the Brazilian coast.

Knowing the trophic role of pelagic fish is essential in ecological studies and modeling, given their effects on the food web, but also for fisheries sustainability. Estimating the species' TL is essential to measure the marine capture fisheries' average TL, so-called the Marine Trophic Index (MTI) (Pauly et al., 1998; Vasconcellos and Gasalla, 2001). The MTI was considered one of the eight indicators of ecosystem health by the Convention on Biological Diversity (CBD) in 2004, and its fluctuations reflect the trophic interactions in an ecosystem (Pauly and Watson, 2005). A decrease in MTI may reflect a shift in fisheries from high TL fishes to small pelagic planktivorous (Pauly et al., 1998). As a result, TL estimates may contribute to assessing fishing impacts on the structure and functioning of ecosystems (Pitcher, 1995; Gasalla, 2004; Gasalla and Rossi-Wongtschoski, 2004; Gasalla et al., 2007; Gascuel et al., 2008).

Given the ecosystem relevance and socioeconomic significance of pelagic fish in Southeastern Brazil, here we investigate their trophic ecology aiming to provide insights to better understanding and managing marine resources. To that end, we revisited survey data collected and archived by the ECOSAR II Project by assessing stomach content analysis and both dietary similarity indexes and species TLs. Outcomes are contextualized to relevant fisheries data (e.g., landings) to explore temporal shifts and MTI estimates. This study also aims to contribute to the field of trophic ecology with new data on diet, trophic relationships, and yields of economically important species.

METHODS

Data collection

The area covered by the ECOSAR Program (Federal University of Rio Grande (FURG)/ Oceanographic Institute of the University of São Paulo (IOUSP)/Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA)) prospecting cruises correspond to the "São Paulo Bight" or South Brazil Bight, with a northern limit at Cabo Frio (23°S) and a southern limit at Santa Marta Grande Cape (28°40'S) up to the 200 m isobath (Figure 1). The oceanographic and ichthyofauna data were obtained in the winter of 1995 during the ECOSAR II cruise onboard the RV "Atlântico Sul" (FURG), which was held from 06/11/1995 to 07/02/1995. In order to collect specimens, 26 hauls were conducted during the survey using a midwater trawl from which 24 caught pelagic fish. The survey was carried out on pre-established stations during the day and night, at a mean speed of 10 knots (Contente and Rossi-Wongtschowski, 2016). Particular details on the grid sampling, methods of acoustic data, and procedures of fishing operations were described in Soares et al. (2005), Madureira and Rossi-Wongtschowski et al. (2005), and Contente and Rossi-Wongtschowski (2016).

The ichthyofauna collected was frozen on board and then processed by the expert teams at the IOUSP under the coordination of Drs. Suzana Anita Saccardo (IBAMA), Carmen L. D. B. Rossi-Wongtschowski (IOUSP) and Lauro Saint-Pastous Madureira (FURG). Stomachs of the most abundant species were extracted and conditioned in storage glasses to be posteriorly analyzed in Santos (Instituto de Pesca). In ECOSAR II, a total of 53 species of pelagic fish were recorded (Madureira and Rossi-Wongtschowski, 2005), while the present study assesses the 12 most abundant of these species covering three orders and six distinct families (Table 1). The species identification guides used are listed in Rossi-Wongtschowski et al. (2014), who grouped species' occurrence in the surveys regarding geographical position and depth. The food items found in the stomach contents were identified

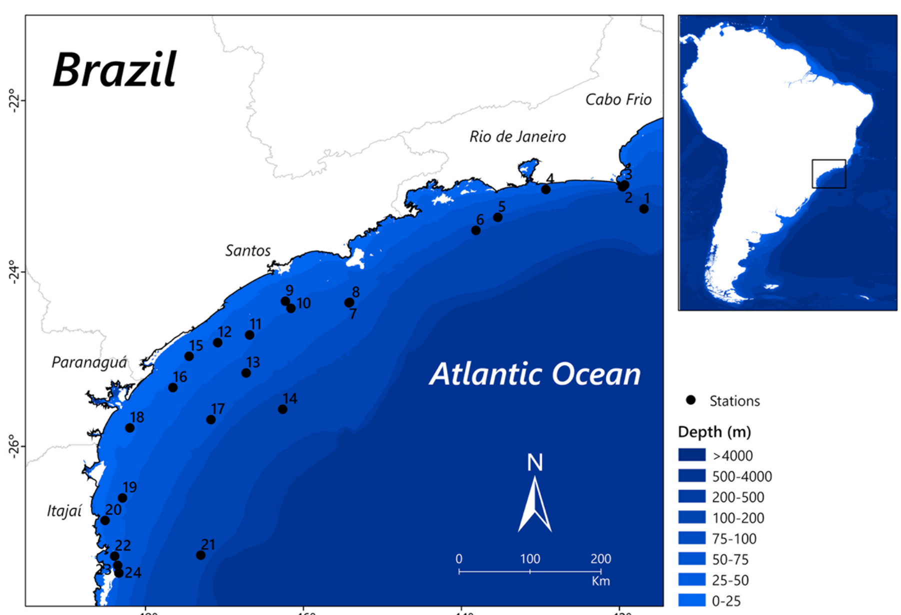

Figure 1. Sample area and collection stations of the ECOSAR II cruise in South Brazil Bight in June and July of 1995.

Table 1. Brazilian and English popular names, species list, and taxonomic position of the pelagic fishes' species chosen for this study.

Brazilian popular name	English popular name	Species	Order	Family
Xixarro	Rough scad	*Trachurus lathami Nichols*, 1920	Carangiformes	Carangidae
Xixarro-pintado	Round scad	*Decapterus punctatus* (Cuvier, 1829)	Carangiformes	Carangidae
Galo	Atlantic moonfish	*Selene setapinnis* (Mitchill, 1815)	Carangiformes	Carangidae
Palombeta	Atlantic bumper	*Chloroscombrus chrysurus* (Linnaeus, 1766)	Carangiformes	Carangidae
Sardinha-verdadeira	Brazilian sardinella	*Sardinella brasiliensis* (Steindachner, 1879)	Clupeiformes	Clupeidae
Sardinha-cascuda	False herring	*Harengula clupeola* (Cuvier, 1829)	Clupeiformes	Clupeidae
Sardinha-laje	Atlantic thread herring	*Opisthonema oglinum* (Lesueur, 1818)	Clupeiformes	Clupeidae
Manjuba	Shortfinger anchovy	*Anchoa lyolepis* (Evermann and Marsh, 1900)	Clupeiformes	Engraulidae
Manjuba	Piquitinga anchovy	*Anchoa tricolor* (Spix and Agassiz, 1829)	Clupeiformes	Engraulidae
Sardinha-dentuça	Dogtooth herring	*Chirocentrodon bleekerianus* (Poey, 1867)	Clupeiformes	Pristigasteridae
Bicuda/Serrinha	White snake mackerel	*Thyrsitops lepidopoides* (Cuvier, 1832)	Scombriformes	Gempylidae
Peixe-espada	Largehead hairtail	*Trichiurus lepturus Linnaeus*, 1758	Scombriformes	Trichiuridae

and counted under a stereomicroscope at the Fisheries Institute (Instituto de Pesca) in Santos (São Paulo State). A total of 432 stomachs were analyzed. Each sample was observed under an optical microscope to verify the occurrence of phytoplankton. Food items larger than the average size of the organisms found were measured with the aid of a micrometer eyepiece. The expert team identified the items to the lowest taxonomic level possible (Gasalla, 1995). For this study, we retrieved information on species identification and the number of individuals from samples stored at the Fisheries Ecosystems Laboratory (LabPesq) in the IOUSP.

Diet composition

Diet data for all fish were expressed as the frequency of occurrence (FO) (Hynes, 1950; Hyslop, 1980), defined as the number of stomachs in which a prey occurs by the total number of non-empty stomachs. FO is one of the most commonly used diet proxies which can provide information regarding food preference and selectivity, in addition to the extent of trophic niche, although partially (Bowen, 1996; Hahn and Delariva, 2003). Whenever possible, the ECOSAR II teams also recorded the numerical frequencies (%N), where the number of prey individuals is divided by the total number of prey consumed and the visual volumetric frequency (%V) defined as the visible size of the prey by the total sample occupied in the Petri dish. The %N allows establishing information on species selectivity and prey availability in the environment, while %V minimizes the overestimation of items with high abundance but low biomass. For species that consumed macroscopic items, the gravimetric frequency (%M) was estimated by obtaining the wet weight ratio of each prey and dividing it by the total weight of items measured on a precision balance (Hynes, 1950; Hyslop, 1980). This last method allows for analysis with a smaller margin of error, but it is not feasible for extremely small or very digested items.

Based on the %FO of each species, the similarity between the diets was estimated using the Minitab® Statistical 19, considering correlation coefficient distance with the complete linkage method (also called the "furthest neighbor method"). In this method, the similarity between the groups is given by the individuals that least resemble, and in the agglomerative hierarchical clustering, the most similar individuals are established at each stage (Ladds et al., 2018). For this analysis, the food items were divided into "Phytoplankton", "Ichthyoplankton", "Fish", "Polychaeta", "Zooplankton", and "Others" so that there was no repetition of the data included in the following groups. The trophic guilds were based on the formed groups according to Elliott et al. (2007).

Trophic levels

Trophic levels and their standard errors (SE) were estimated at the species level using the TrophLab program (Pauly et al., 2000; version June 2000), which uses the formula proposed by Cortés (1999):

$$TL = 1 + \sum_{j=1}^{G} DC_{ij} \times TL_j$$

where DC_{ij} is the fraction of prey (j) in the diet of i, TL_j is the trophic level of j, and G is the total number of prey categories. The mean values for each category were used in a higher degree of identification to determine the respective trophic positions of the prey, available on TrophLab (Pauly et al., 2000). Quantitative diet composition data (visual volumetric frequency or by weight) as qualitative data (list of items in the diet) can be used (Pauly et al., 2000). To maximize the reliability of the results, we gave priority to the use of %M or %V indexes. These indexes are highly suitable for analyzing the relative importance of the items consumed, as they consider the prey's contribution in terms of weight or volume (Liao et al., 2001). However, as these values were not obtained for all species, %N or %FO was also used when necessary. We compared our TL estimations with data available at Fishbase (Froese and Pauly, 2014),

Biomass

To describe and investigate the abundance of fish aggregations in this study at SBB, data on total biomass, the total frequency of abundance, and the total frequency of occurrence presented by Contente and Rossi-Wongtschowski (2016) on biomass related to ECOSAR III (1995) to VII (2010) were compiled. Such data were adapted for the ECOSAR II species, except for *D. punctatus* and *A. lyolepis*, whose data were not measured. However, the percentage values were calculated concerning the total of the 43 species of pelagic fish sampled. The authors point out that in the ECOSAR IV to VII cruises, the sampling area was different from the ECOSAR IIII cruise, so estimations were treated with caution. Despite this, given the ECOSAR cruises' performance intervals, these data can support understanding the abundance and biomass magnitude of these species in the study area and allow temporal comparisons.

Fisheries production

To investigate the current situation of fish stocks and their fluctuations, fishing statistics were evaluated from the oldest recorded online (1986) until 2019. Data of landings encompassing the states of São Paulo, Rio de Janeiro, Paraná, Santa Catarina, and Rio Grande do Sul were gathered. Statistical bulletins on fisheries production were consulted from the IBAMA, the Program for the Assessment of the Sustainable Potential of Living Resources in the Exclusive Economic Zone (REVIZEE) (Valentini and Pezzutto, 2006), Instituto de Pesca de São Paulo (IP/APTA/SAA/SP, 2021), and other fishing entities in the region such as PMAP/RJ (2021), PMAP/PR (2021), UNIVALI/EMCT/LEMA (2020) and FURG/MPA (2018).

Marine Trophic Index

To investigate whether there is a temporal variation in the average TL of fishing, the MTI was used, a multispecific indicator (Pauly et al., 1998). The MTI measures the change in the average TL of fishing catches by region, i.e., ideally, it should cover all animals killed by fishing (landings and discards). However, only landing data are commonly used due to the lack of discards data availability (Pauly and Watson, 2005). Thus, the calculation was performed as follows:

$$MTI = \frac{\Sigma TL_i \times Y_{ij}}{\Sigma Y_{ij}}$$

where Y_{ij} refers to the landings of species *i* in year *j* and TL_i to the trophic level of each species *i*. For this analysis, we considered the species relevant for fishing among the 12 species from 1986 to 2019.

Other statistical analysis

The fish length and weight data obtained in ECOSAR II were associated with the estimated TLs for each species to verify if there is a significant linear correlation. Using Minitab® Statistical 19 software, analyses were performed using Pearson's correlation coefficient (also known as Pearson's r) and a scatter plot with a fitted regression line. Pearson's ranges from -1 to 1 and analyzes the linear relationship between two continuous variables: the greater the absolute value of the coefficient, the stronger the relationship between the variables (Minitab, 2021). Fish landing data were also correlated using Minitab and Spearman's correlation. Spearman's correlation analyzes the monotonic relationship between two continuous variables, which do not necessarily vary linearly. The significance level for both Pearson's and Spearman's correlations was set to 0.05.

RESULTS

Fish diet

The identified food items were grouped into six different phyla or five groups of organisms such as "Phytoplankton", "Zooplankton" or "Ichthyoplankton". The analyses regarding the %FO and other indexes at the lowest possible taxonomic level are present in Supplementary tables S1 and S2.

The most common prey items in the gut contents of Clupeiformes were zooplankton and phytoplankton (Figure 2). It is worth mentioning that the 'Fish' category was relevant for *O. oglinum* due to the fish scales found in the guts content (Figure 3). Specifically, there is a high %FO of Calanoid, Poecilostomatoid, and Harpacticoid copepods, and marine shrimp Penaeidae and Caridea (Table S1). For fish of the Engraulidae family (*A. tricolor* and *A. lyolepis*), Calanoid and Poecilostomatoid copepods were the most frequent prey in the stomach contents of both species, with almost 100% of FO. Bivalve mollusks and gastropods were also part of the food composition of *A. lyolepis*, while polychaetes occurred in the stomachs of *A. tricolor*.

On the other hand, *S. brasiliensis* sardine was the species among the Clupeiformes with the highest %FO of ichthyoplankton, although zooplankton, phytoplankton, and fish were present. Also, *S. brasiliensis* had the greatest diversity of zooplankton prey. For *O. oglinum*, a significant part of the FO was represented by zooplankton that was already digested, therefore not being classified at

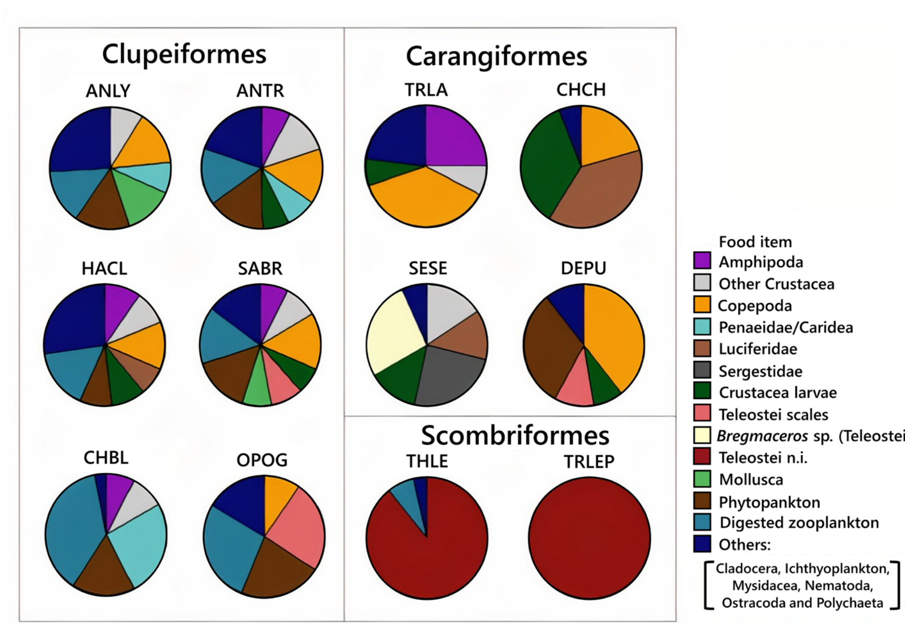

Figure 2. Percentage of the frequency of occurrence (%FO) of the main food items of the species: *Trachurus lathami* (TRLA), *Thyrsitops lepidopoides* (THLE), *Sardinella brasiliensis* (SABR), *Selene setapinnis* (SESE), *Trichiurus lepturus* (TRLEP), *Harengula clupeola* (HACL), *Decapterus punctatus* (DEPU), *Opisthonema oglinum* (OPOG), *Chloroscombrus chrysurus* (CHCH), *Chirocentrodon bleekerianus* (CHBL), *Anchoa lyolepis* (ANLY), and *Anchoa tricolor* (ANTR).

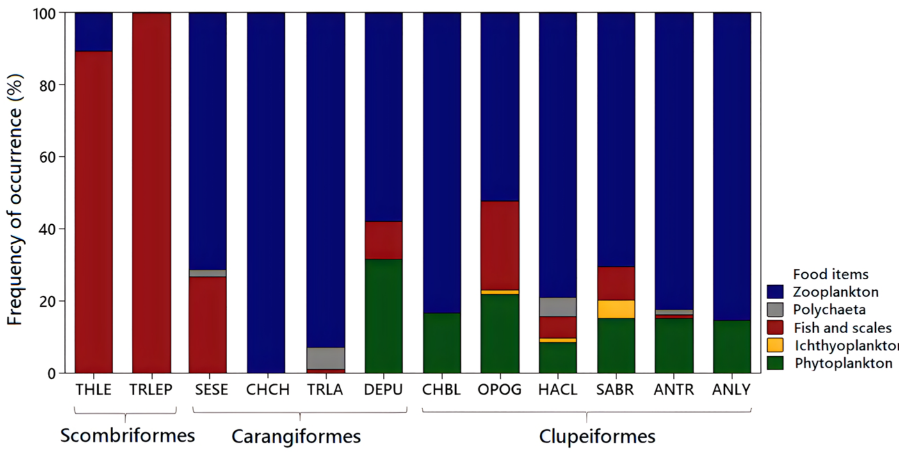

Figure 3. Frequency of occurrence (FO) of the main food items divided into large taxonomic categories of the species of the Order Scombriformes (*Thyrsitops lepidopoides* (THLE) and *Trichiurus lepturus* (TRLEP)), Carangiformes (*Trachurus lathami* (TRLA), *Chloroscombrus chrysurus* (CHCH), *Selene setapinnis* (SESE) and *Decapterus punctatus* (DEPU)) and Clupeiformes (*Anchoa lyolepis* (ANLY), *Anchoa tricolor* (ANTR), *Harengula clupeola* (HACL), *Sardinella brasiliensis* (SABR), *Chirocentrodon bleekerianus* (CHBL) and *Opisthonema oglinum* (OPOG)).

a more specific taxonomic level. However, there is a high %FO of teleost fish scales and phytoplankton, resulting in *O. oglinum* obtaining the highest percentage in the "Fish" grouping compared to the other Clupeiformes (Figure 3). When analyzing only the %FO of *H. clupeola*, there is diversification of food items; however, there is a predominance of zooplankton through copepods and amphipods. On the other hand, *C. bleekerianus* had a food preference for Penaeidae and Caridea shrimp, in addition to unidentified digested zooplankton.

As for Carangiformes, the high %FO of zooplanktonic organisms is also remarkable. Among these, copepods were highly frequent in stomachs, with 68.54% of FO for *T. lathami* and 100% for *D. punctatus* (Copepoda: Calanoida) (Table. S1). Decapod crustaceans of the Luciferidae family were present in most of the stomach contents of *C. chrysurus*, in addition to Crustacea larvae in the Zoea stage. The Atlantic moonfish *S. setapinnis* primarily ingested zooplankton while it frequently preyed on *Bregmaceros* sp., a teleost fish, unlike the rest of the studied Carangiformes. The other fishes, of the order Scombriformes (*T. lepturus* and *T. lepidopoides*), ingested practically only Teleostei that were not identified. Overall, when analyzing the %FO for all these pelagic fishes, it is possible to notice a general food preference for zooplanktonic organisms - however, some species consumed mainly teleost fish.

Similarity

The similarity between species was estimated by cluster analysis and based on the %FO (Figure 4). It was feasible to use a final partition of three clusters, with a similarity of approximately 58%. The first grouping (far left) comprises *T. lathami*, *D. punctatus,* and *C. chrysurus*, all of the Carangidae family, thus naming them "Planktivorous Carangiformes". The second group comprises three species, *T. lepidopoides*, *S. setapinnis,* and *T. lepturus*, which primarily preyed on fish. The third group comprises all the fishes of the order Clupeiformes in the study (*S. brasiliensis*, *H. clupeola*, *O. oglinum*, *C. bleekerianus*, *A. lyolepis,* and *A. tricolor*), which were identified as "Planktivorous Clupeiformes". Thus, it is observed that although the trophic guilds were not built based on the species phylogeny, there was a high similarity between the groupings and the taxonomy. It is also verified that the highest similarity indices are given between *T. lepturus* and *T. lepidopoides*, with 99.80, followed by *A. lyolepis* and *A. tricolor* with 95.52.

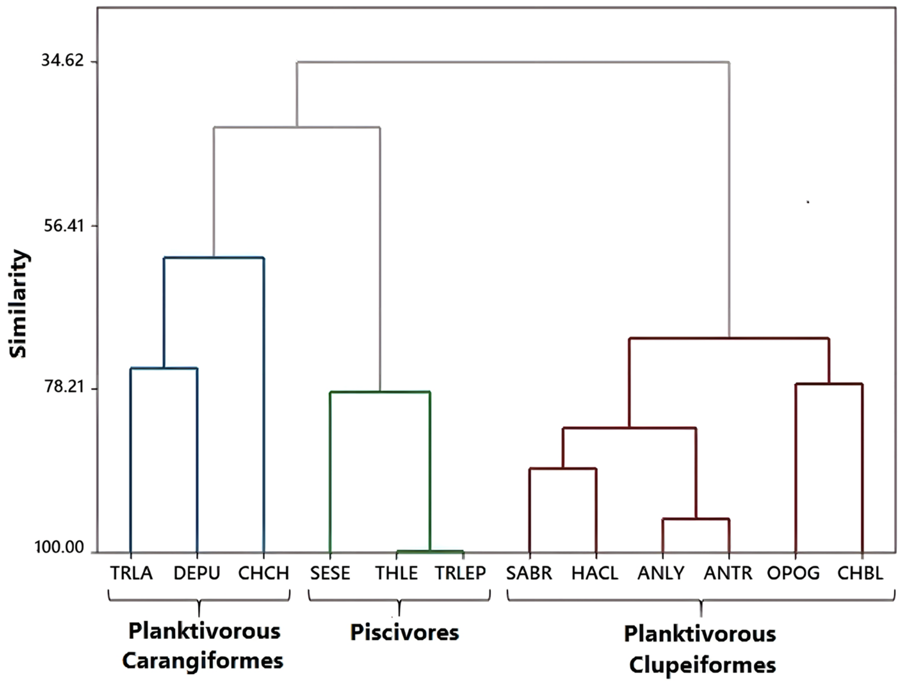

Figure 4. Cluster of similarity between the species *Trachurus lathami* (TRLA), *Decapterus punctatus* (DEPU), *Chloroscombrus chrysurus* (CHCH), *Selene setapinnis* (SESE), *Trichiurus lepturus* (TRLEP), *Thyrsitops lepidopoides* (THLE), *Sardinella brasiliensis* (SABR), *Harengula clupeola* (HACL), *Anchoa lyolepis* (ANLY), *Anchoa tricolor* (ANTR), *Opisthonema oglinum* (OPOG), and *Chirocentrodon bleekerianus* (CHBL).

Biometric data

Biometric data of weight and total body length (BL) corresponding to 1764 individuals of the twelve species studied were retrieved (Table 2). The number of individuals per species used for the calculations ranged from 30 to 374. The average BL ranged from 72 to 384 mm, while the average weight for each species reached from 2 to 88 g, species with different weight and length standards. The BL shows that the species with the largest specimens in ECOSAR II were *T. lepturus* and *T. lepidopoides*, which can be considered medium-sized, and all other species are small pelagic.

Trophic level and correlation with biometric data

The TLs of the fishes studied varied from 2.98 to 4.5, with an average of 3.49 and a SE of 0.45 (Table 3). In general, trophic levels are defined such that organisms with a value between 1 and 2 are primary producers, 2 and 3 are herbivores, 3 and 4 omnivores, and 4 to 5 are carnivores/piscivores (Pauly and Christensen, 2000). Thus, *T. lathami*, *S. brasiliensis*, *H. clupeola*, *D. puntactus*, *O. oglinum*, *C. bleekerianus*, *C. chirocentrodon*, *A. lyolepis*, and *A. tricolor* can be considered omnivores, that is, feeding on more than one trophic level, while *T. lepturus*, *T. lepidopoides,* and *S. setapinnis* were identified as piscivores. To assist in the comprehension of the trophic positions and illustrate the studied species, an illustrative diagram of the analyzed fish with their respective TLs was constructed (Figure 5), as well as a conceptual diagram representing the trophic relationships observed in this study based on dietary trophic and trophic levels calculation (Figure 6).

Comparing with the TL of each species available in the Fishbase database, also calculated based on stomach composition, it can be noticed that *S. setapinnis* and *T. lepturus* have lower TLs values than those found in the study. However, the associated SE allows classifying such species as piscivorous. Even though there are differences due to the different study sites, the type of collection, the classification of fisheries, and the size of individuals, among other factors, the results generally follow the Fishbase literature.

Table 2. Mean, minimum, and maximum body weight and length of fish collected in the ECOSAR II Program; where 'n' is the number of individuals sampled.

Species	n	Average length (mm) [min-max]	Average weight (g) [min-max]
Anchoa lyolepis	30	72 [66-93]	2 [1.6-5.6]
Chirocentrodon bleekerianus	62	88 [74-107]	3.9 [1.9-7.1]
Anchoa tricolor	68	110 [77-129]	9.2 [2,8-16.3]
Trachurus lathami	323	116 [85-173]	14.2 [4.7-46.1]
Haregula clupeola	82	155 [106-188]	43.1 [11.1-68.1]
Sardinella brasiliensis	374	158,7 [90-247]	33.9 [2.9-115.2]
Decapterus punctatus	30	168 [158-179]	41.3 [34.7-53.3]
Selene setapinnis	113	171 [102-285]	53.2 [12.1-261.7]
Chloroscombrus chrysurus	142	176 [104-275]	56.1 [10.1-169.3]
Opisthonema oglinum	80	198 [114-272]	72.3 [11.2-196,4]
Thyrsitops lepidopoides	105	246 [157-347]	88 [5.8-290,9]
Trichiurus lepturus	355	384 [63-1380]	23.6 [0.1-1947]

Table 3. Trophic level (TL) and standard error (SE) associated with the species: *Trachurus lathami* (TRLA), *Decapterus punctatus* (DEPU), *Chloroscombrus chrysurus* (CHCH), *Selene setapinnis* (SESE), *Trichiurus lepturus* (TRLEP), *Thyrsitops lepidopoides* (THLE), *Sardinella brasiliensis* (SABR), *Harengula clupeola* (HACL), *Anchoa lyolepis* (ANLY), *Anchoa tricolor* (ANTR), *Opisthonema oglinum* (OPOG) and *Chirocentrodon bleekerianus* (CHBL), based on percentage indices of frequency of occurrence (FO), numerical (N), visual volumetric (V), or gravimetric frequency (M); Right side: TL and se of each species available in Fish Base (Froese and Pauly, 2000).

Present study				Fishbase	
Species	Indexes (%)	TL	SE	TL	SE
TRLEP	N	4.5	0.8	4.20	0.75
THLE	M	4.5	0.8	3.86	0.63
SESE	M	4.16	0.71	3.72	0.52
OPOG	V	3.5	0.5	3.60	0.50
HACL	V	3.3	0.41	3.53	0.51
ANLY	M	3.26	0.4	3.40	0.45
SABR	V	3.17	0.44	3.10	0.30
TRLA	FO	3.16	0.35	3.27	0.34
ANTR	V	3.14	0.32	3.40	0.40
CHBL	V	3.12	0.33	3.27	0.43
CHCH	M	3.1	0.3	3.53	0.44
DEPU	N	2.98	0.05	3.26	0.43
Mean		3.49	0.45	3.51	0.48

A scatter plot between the estimated TLs and the maximum BL of each species (Figure 7) shows a positive relationship between the two variables, with R^2 of 0.56 and Pearson's correlation coefficient (r) of 0.68. Thus, such a moderate linear relationship may mean that the TLs of pelagic fish tend to increase with fish size. The mean BL also had a significantly strong linear and positive relationship with the TL, with R^2 of 0.89 and Pearson's correlation coefficient of 0.76. The correlation between the average weight and TL had a R^2 of 0.71 and r of 0.45 (Figure 7). Thus, the positive relationship between the three biometric variables and TLs indicates that species with greater lengths and weights tend to hold a higher trophic position in the food web than those with smaller sizes. The

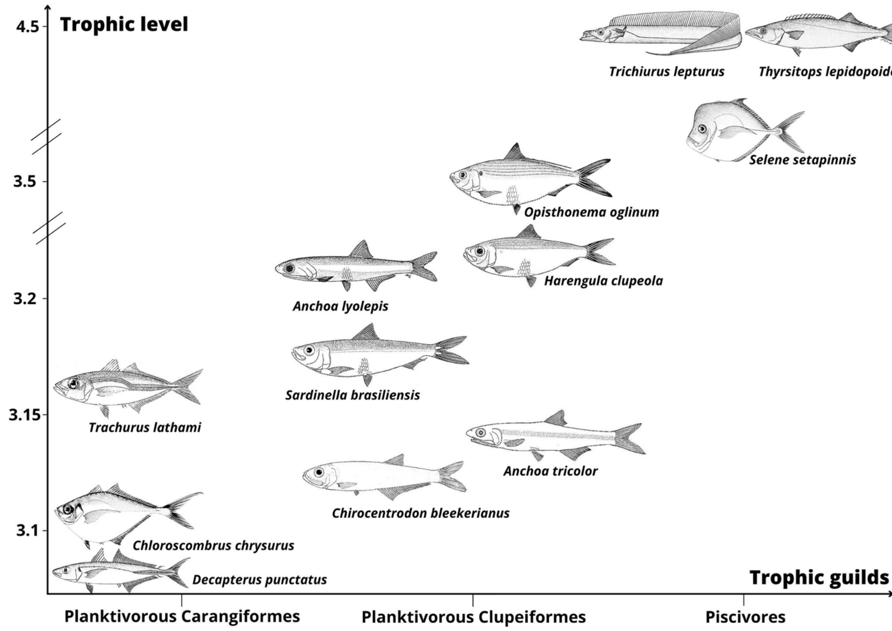

Figure 5. Illustrative diagram of trophic guilds (x axis) and estimated trophic levels (y axis) using diet composition data from TrophLab software (Pauly et al., 2000). Source of fishes images: Figueiredo and Menezes, 1978; Whitehead, 1988.

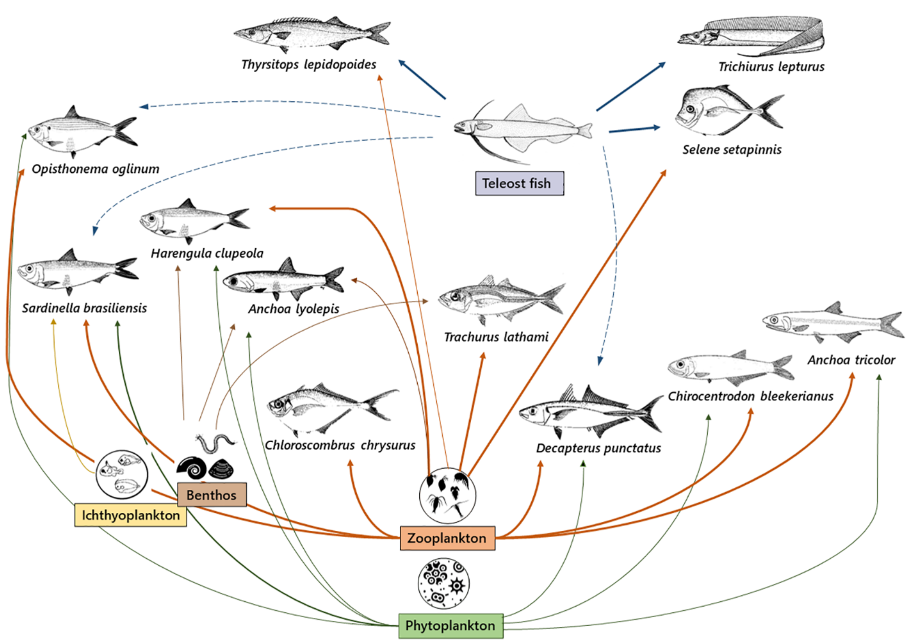

Figure 6. Diagram of the trophic relationships of the pelagic fish in the study, in which the preys are grouped into large categories and there are two levels of arrows: thin lines represent weak feeding relationships while thicker ones indicate moderate to strong importance. The dotted arrow represents indirect consumption of the item in the form of teleost scales. Figures are not to scale. Source of illustrations: Figueiredo and Menezes, 1978; Whitehead et al., 1988.

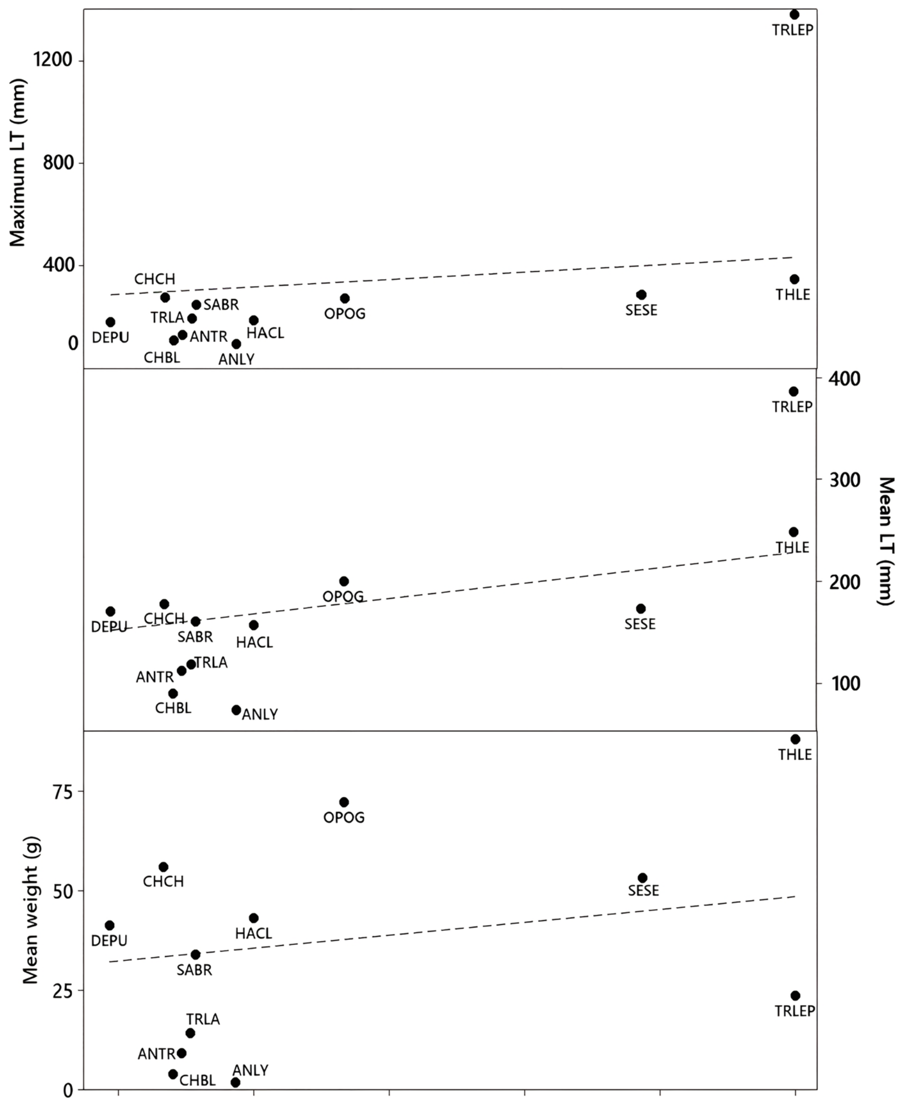

Figure 7. Correlation between the trophic level with the mean weight, maximum and mean body length (BL) of the species collected in ECOSAR II Program: *Trachurus lathami* (TRLA), *Decapterus punctatus* (DEPU), *Chloroscombrus chrysurus* (CHCH), *Selene setapinnis* (SESE), *Trichiurus lepturus* (TRLEP), *Thyrsitops lepidopoides* (THLE), *Sardinella brasiliensis* (SABR), *Harengula clupeola* (HACL), *Anchoa lyolepis* (ANLY), *Anchoa tricolor* (ANTR), *Opisthonema oglinum* (OPOG) and *Chirocentrodon bleekerianus* (CHBL).

species *O. oglinum*, in particular, had the highest TL among the Clupeiformes and was also the species in that order with the highest weight and BL of ECOSAR II. Also noteworthy is the inversion between *T. lepidopoides* and *T. lepturus* in the weight and length graphic, indicating that *T. lepturus* tends to grow more in length than in weight.

Biomass

It was found that *T. lathami*, *T. lepturus,* and *S. brasiliensis* were three of the five dominant species on ECOSAR cruises, making up 34.2% of the total biomass (Table 4). The most common species in the aggregations sampled was *T. lepturus*, with a total frequency of occurrence of

Table 4. Frequency of abundance for each ECOSAR cruise from 1995 to 2010 (biomass; %B), total frequency of abundance (% FBt) and total frequency of occurrence (FOt) of the species sampled in the ECOSAR cruises from 1995 (III) to 2010 (VII) covering the study. The symbol (-) indicates %B<0.1%. Source: Contente and Rossi-Wongtschowski (2016).

Species	Cruzeiro (%B)						
	III	IV	V	VI	VII	%FBt	FOt
Trachurus lathami	9.1	7.3	24.3	6.8	27.8	15.6	26.1
Trichiurus lepturus	5.0	7.5	5.7	8.1	15.2	9.3	58.7
Sardinella brasiliensis	2.4	2.2	6.1	20.0	11.8	9.3	40.2
Anchoa tricolor	1.7	–	0.5		10.1	3.3	8.7
Harengula clupeola	2.7	1.0	0.5	3.8		1.5	22.8
Opisthonema oglinum	0.3	1.8		3.0		1.1	13.0
Selene setapinnis	0.4	2.5		0.1	0.8	0.9	13.0
Thyrsitops lepidopoides	0.1	0.7	0.8	1.5	0.2	0.7	23.9
Chloroscombrus chrysurus	0.1	1.2	0.8	0.5	0.4	0.6	20.7
Chirocentrodon bleekerianus	0.3	–		0.7		0.2	10.9

58.7%, followed by S. *brasiliensis* and *T. lathami*, which demonstrates a continuity of the abundance of the stocks in the study area over the years. As seen on REVIZEE cruises, *T. lepturus* was found in more than 50% of catches on ECOSAR cruises (Soares et al., 2005). Other species, such as *A. tricolor* and *C. bleekerianus,* showed low abundance and frequency, which may represent a connection with dominant species or dispersed clusters of low biomasses.

Fishing landing

For some of the species, data from the Fisheries Statistics Area of Score-Sul/REVIZEE from 1986 to 2004 were utilized (Valentini and Pezzutto, 2006). For the remaining years and species without REVIZEE data available, state fisheries databases were examined to obtain information on total marine landings (both industrial and artisanal) by species and year. States such as Paraná and Rio de Janeiro only collected fishing data in specific years, and some states also lacked data on artisanal fisheries. No occurrence was found in the databases for two species in the study (*C. bleekerianus* and *D. punctatus*). The species *A. lyolepis* and *A. tricolor* were grouped in the landings because there was no differentiation between the two species in the records.

The fishing landing values from 1986 to 2019 in the SBB ranged from 182.3 tons (*T. lepidopoides*) to 1854732.1 tons (*S. brasiliensis*) (Table 5). The sardine *S. brasiliensis* showed the highest levels of landings, with an order of magnitude higher on average than all other species studied. Comparing the annual averages of landings in two study periods, 1986-2002 and 2003-2019, it is observed that six of the nine species analyzed suffered a decrease in the second period (*S. setapinnis, T. lepturus, T. lathami, S. brasiliensis, H. clupeola, A. tricolor, and A. lyolepis*) (Table 5). The three remaining species that showed an increase were *O. oglinum*, *C. chrysurus*, and *T. lepidopoides*. It is worth noting that *T. lathami* had the steepest drop in landings, with a reduction of more than 80% from 2003, and was more intensively landed until 1994. It is also notable that *S. brasiliensis* is responsible for most of the fishing landings in the region compared to other small pelagic, with 81.2% of the total percentage in that period. When considering the total landings of the here-called "Piscivores" and "Planktivorous Carangiformes" together, the "Planktivorous Clupeiformes" are almost ten times more important for fisheries in the region. "Planktivorous Clupeiformes" represent approximately 91% of the total landing in this period evaluated, while the "Planktivorous Carangiformes" and "Piscivores" account for 5.38% and 4% of the total landings, respectively (Table 5).

Given the dominance of *S. brasiliensis* in the total landings of commercial fisheries in the area, we assessed their relationship to the landings of

Table 5. Trophic guilds, total and average landings in tons, percentage in relation to all species in the study and percentage of variation in fishing landings in two periods (1986-2002 and 2003-2019) considering the South Brazil Shelf Large Marine Ecosystem.

Trophic guilds	Species	Landing (t)	Percentage (%)	Total (t)	Landing averages (t)			Variation (%)
					1986-2019	1986-2002	2003-2019	
	Selene setapinnis	44980.4	1.97		1320.2	1519.8	1063.5	-30
Piscivores	*Trichiurus lepturus*	41007.3	1.80	86170	1200.8	1292.7	1057.3	-18.2
	Thyrsitops lepidopoides	182.3	0.01		5.4	1.2	9	653
Planktivorous Carangiformes	*Chloroscombrus chrysurus*	82827.5	3.63	122688.7	2434.1	1730.6	2967	71.4
	Trachurus lathami	39861.2	1.75		1172.3	1991.1	334	-83.2
	Sardinella brasiliensis	1854732.1	81.20		54459	65860.2	40839.4	-38
Planktivorous Clupeiformes	*Opisthonema oglinum*	215622.1	9.44	2075300	6337.2	5079.9	7181.3	41
	Harengula clupeola	2827.3	0.12		83.2	120.3	43.4	-63.9
	Anchoa sp.	2118.6	0.09		61.9	94.4	28.5	-69.8

Table 6. Spearman's correlations of fishing landings between *Sardinella brasiliensis* and *Trachurus lathami*, *Opisthonema oglinum*, *Selene setapinnis*, *Chloroscombrus chrysurus*, and *Trichiurus lepturus* from 1986 to 2019 in the South Brazil Shelf Large Marine Ecosystem; p-value with "*" indicates non-statistically significant correlation (p>0,05).

Species		Spearman's Correlation	*p*-value
	Trachurus lathami	0.49	0.003
	Opisthonema oglinum	-0.485	0.004
Sardinella brasiliensis	*Selene setapinnis*	0.431	0.011
	Chloroscombrus chrysurus	-0.398	0.02
	Trichiurus lepturus	-0.028	0.875*

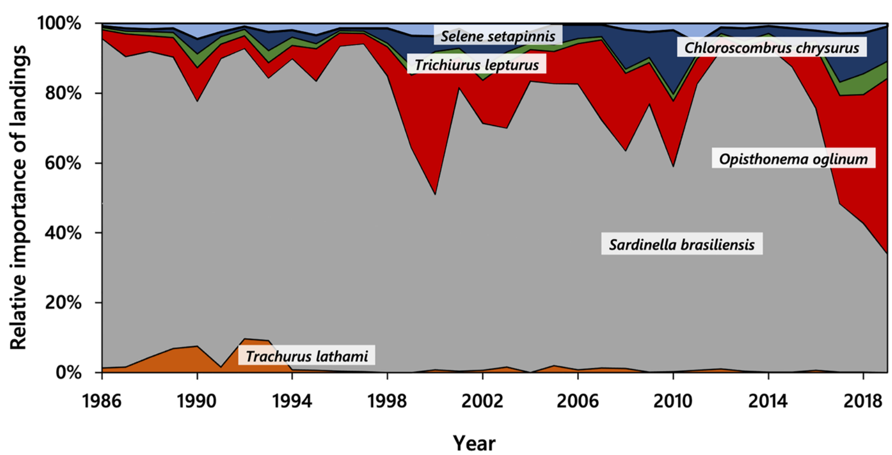

Figure 8. Relative importance of fishing landings of the main pelagic species studied in the South Brazil Shelf Large Marine Ecosystem.

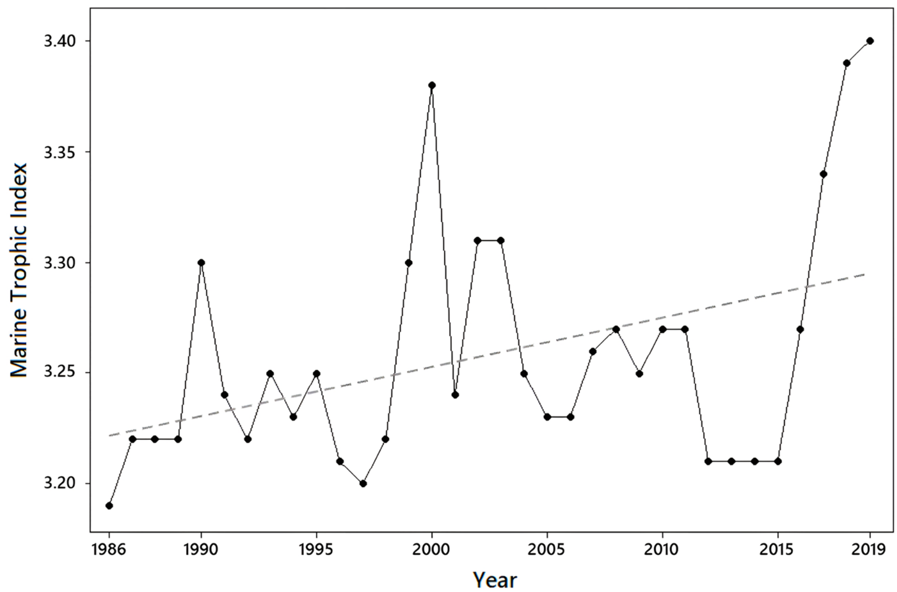

Figure 9. Marine Trophic Index in the South Brazil Shelf Large Marine Ecosystem considering the landing data of nine species of the pelagic fish studied, from 1986 to 2019.

the other significant commercial species (Table 6). A moderate and positive Pearson correlation of 0.49 and 0.43 was found between fishing for *S. brasiliensis* and *T. lathami* and *S. brasiliensis* with *S. setapinnis*, respectively. The *O. oglinum* and *S. brasiliensis* were negatively correlated, as well as *S. brasiliensis* and *C. chrysurus*. As obtained in the correlation values (Table 6) and the relative importance of the main species in annual landings (Figure 8), an increased tendency in the landings of *O. oglinum* and *C. chrysurus* is observed as the landings of *S. brasiliensis* decrease.

Marine Trophic Index

MTI was highly variable from 1986 to 2019, exhibiting an increasing trend over the years (r^2=0.16). However, it was observed that the MTI occupied a relatively small range, with a minimum of 3.19 (1986) and a maximum of 3.4 (2019) (Figure 9). The MTI average considering all the years of the study was 3.26.

DISCUSSION

The TLs calculated here show that the fishes studied occupied an intermediate level in the trophic structure of the region. Garcia and Giarrizzo (2014), when estimating the TL of marine pelagic fishes from the Brazilian coast, found values ranging from 2 to 4.8. In the study by Gasalla et al. (2007), small pelagic fish were classified as “forage fish” representing trophic level 3.0 and the highest biomass for the ecotrophic model. Thus, pelagic fish are both crucial predators and prey in this ecological system. The planktivorous species consumed a wide range of food items, with high diversification of zooplankton items. As Lowe-McConnel (1987) points out, it is typical of tropical regions that many species show plasticity in their diet, although they may specialize in one food item category. The broad feeding spectrum of these fishes reflects not only the wide availability of food resources but the diverse feeding habits of the different ontogenetic stages of pelagic fishes. According to the similarity cluster and trophic levels, the species were grouped in the trophic guilds "Planktivorous Clupeiformes", "Planktivorous Carangiformes", and "Piscivores".

Diet of pelagic fishes

Among the Clupeiformes, the most abundant food items in the stomach contents of *S. brasiliensis* were zooplankton and phytoplankton. The authors Hofling et al. (2000) reported that pre-adult and adult specimens of *S. brasiliensis* have seasonal and geographic variations in their diet, and it is generally considered omnivorous. Such food plasticity is also described by Schneider and Schwingel (1999), where, during winter, phytoplankton constitutes the primary food item, while in autumn and spring, zooplankton is its dominant prey. In the present study, calanoid, cyclopoid, and harpacticoid copepods were present in all stomachs, as documented in the region by Schneider and Schwingel (1999). Even with the preference for zooplankton, the results corroborate the generalist habits of the species, as several sardines can change their feeding strategy according to oceanographic fluctuations and food availability (Matsuura, 1977).

Although piscivory is rarely mentioned in literature for *S. brasiliensis*, in our study we recorded fish of the genus *Bregmaceros* (order Gadiformes) in its gut contents. However, the presence of *Bregmaceros* sp. in the ECOSAR II teams' sampling networks suggests that the consumption of teleost fish by *S. brasiliensis* occurred after capture and not in their natural habitat. This justification can also be associated with the data found by Contente and Rossi-Wongtschowski (2016) that show the presence of *Bregmaceros atlanticus* in ECOSAR cruises with a total frequency of occurrence of 2.2. Thus, it may have been captured simultaneously with *S. brasiliensis*.

As for *H. clupeola*, this species had a diversified diet where zooplankton predominated in the stomach contents, e.g., Amphipoda, Copepoda, Zoea larvae, and other small crustaceans. This habit of eating zooplankton resembles that found by Hofling et al. (2000) and Stefanoni (2008). The authors Ortaz et al. (1996) report a predominance of copepods and crustacean larvae secondarily, having also found fish in the food composition of *H. clupeola* in Venezuela. In Chaves and Vendel (2008) study, the diet found is predominantly planktivorous with diatoms and copepods. Still, it is emphasized that there may be changes in trophic habits depending on local availability.

We observed that the diet of the Atlantic thread herring (*O. oglinum*) was dominated predominantly by zooplankton and, at a lower level, phytoplankton and fish scales. The predominance of zooplankton or phytoplankton in the diet of *O. oglinum* is reported in the literature (Hofling et al. (2000), Paiva and Pereira (2003), Vasconcelos-Filho (1979)). Benthic crustaceans and fish were classified as seasonally crucial for this species by Veja-Cendejas et al. (1997), while Vasconcelos Filho et al. (2010) reported a predominance of microcrustaceans and diatoms in the species' feeding habits. According to Bomfim et al. (2020), the main food category of *O. oglinum* was crustaceans, followed by sediments as the accessory category. It is a species that can be categorized as opportunistic, according to Veja-Cendejas et al. (1997), as it adapts to the most available and adequate food supply throughout its life cycle.

The dogtooth herring (*C. bleekerianus*) of the family Pristigasteridae ingested mostly decapod crustaceans Penaeidae or Caridea and other items of zooplankton. In the literature, *C. bleekerianus* is described as the only species of small size among Clupeiformes predators that consume fish and exploit relatively large prey, as they have well-developed teeth (Whitehead et al., 1988; Sazima et al., 2004; Nelson et al., 2016). However, this study's analyses did not document fish or other large prey in the stomach of this sardine. Corrêa et al. (2005), when studying the food composition of the species off the coast of Paraná, found planktonic organisms with a predominance of copepods and diatoms. In the present study, shrimp was an essential item for the diet, following what was found by Muto et al. (2008), who reported mainly planktonic crustaceans given by copepods and sergestid shrimp. Food preference for larger organisms or small crustaceans may be associated with food availability and individual size (Zavala-Camin, 1996).

The feeding habits of the anchovies (*Anchoa* sp.) are generally inferred through the pattern of the Engraulidae family as being based on small zooplanktonic organisms (DeLancey, 1989). The species *A. tricolor* fed mainly on items of zooplankton, being relevant to the copepods Calanoida and Cyclopoida, in addition to the decapods Penaeidae and Caridea. Medeiros (2017), when investigating the diet of this species, classified it as zooplanktivorous, being Brachyura an important food item. The species *A. lyolepis*, on the other hand, fed mainly on unidentified zooplankton and other crustaceans and little on phytoplankton. For this species, Chaves and Vendel (2008) recorded a high consumption of copepods, diatoms, gastropods, and bivalves in the estuary. According to Mazzetti (1984), the diet of *A. lyolepis* is similar to that of *E. anchoita*, which is composed of crustaceans, mollusks, and phytoplankton. Although a greater diversity of food items of *A. tricolor* can be pointed out in relation to *A. lyolepis*, both species feed mainly on plankton and may have very similar habits depending on the fish's development stage (Mazzetti, 1984; Whitehead et al., 1988). A high similarity between the diets of anchovies was found by analyzing the proximity in the food similarity grouping made with the FOs, also reaching similar TL values. Mazzetti (1984) also observed greater prey diversification in *A. tricolor* compared to *A. lyolepis* and points out that it may be due to this first species reaching larger sizes and discusses the possibility that the larger the fish, the more diversified its food.

The main components of the Clupeiformes diet in this study were zooplanktonic organisms, especially crustaceans such as copepods and decapods. This can be related to morphological characteristics, such as the environmental variables of the ecosystem. Silva et al. (2009) described the morphophysiological patterns of the digestive tract with eating habits, in which, for the sardine, the large and sinuous intestine allows greater absorption and storage of food for periods of limited availability. Besides, fish's digestive system morphology is related to food composition, so evolutionary adaptations occur according to dietary needs (Seixas Filho et al., 2001; Rotta, 2003).

Among the Carangiformes, *C. chrysurus* had a feeding preference for the Luciferidae family's decapod crustaceans. According to the study by Carvalho and Soares (1997), they usually feed on planktonic crustaceans and mollusks. Vasconcelos Filho et al. (2010) report a predominant habit by Crustacea (44% of the items found), mangrove plants/remnants (15%), and Teleostei (4%), while Cunha et al. (2000) reported that the most important food items for *C. chrysurus* were, in order of frequency: crustaceans, mollusk larvae, fish and algae. The rough scad (*T. lathami*) was the fish with the greatest number of stomachs studied, which contained, above all, Copepoda, Gammaridae (Amphipoda), and other crustaceans. In the study by Carvalho and Soares (2006), *T. lathami* mainly ingested calanoid copepods and other crustaceans, mollusks, chaetognaths, and teleost fish. In general, zooplankton constitutes its passive food, while benthic organisms are part of the species' active food (Saccardo and Katsuragawa, 1995). As for the round scad (*D. punctatus*), the most significant contributions to the diet were made by Copepoda of the order Calanoida and diatoms. Furthermore, there was a frequent consumption of phytoplankton, which was not identified at the taxonomic level. Copepods and mollusks were identified as important prey for this species by Hales and Stanton (1987), although their diet varies seasonally.

The significance of copepods in the diets of Clupeiformes and Carangiformes could be attributed to their abundance and diversity in coastal ecosystems. Lopes et al. (2006), when investigating the distribution of zooplankton in SBB, reported high diversity values of planktonic species towards the outer shelf and high abundance values in upwelling sites. In fact, Muxagata (1999), studying the contribution of zooplanktonic biomass in the ECOSAR II region, recorded that copepods and other small crustaceans are associated with upwelling events on the Brazilian coast with high abundance values being recorded from Cabo Frio to the off the Cape of Santa Marta Grande. Other authors (Bakun, 2006; Garrido et al., 2015) have related the herbivorous habits of small pelagics with their abundance in upwelling areas, possibly due to the ability of these species to use primary producers efficiently.

Larger pelagic fishes are also extremely important for maintaining the food web in the region. Piscivorous species are often economically significant and have a high trophic level, playing a crucial role in marine ecosystems as the top of the food web (Van Denderen et al., 2017). As fish size increases, it is expected that they will consume larger prey, thus increasing their mean TL. A positive correlation between the mean TL and fish size was observed in this study and the ones performed by Romanuk et al. (2011) and Garcia and Giarrizzo (2014). According to Karpouzi and Stergiou (2003), this is associated with the feeding strategy, especially of piscivorous fish, where the

TL was expressed as an asymptotic function of the mouth area. Cohen et al. (1993) investigated that prey and predator sizes are always positively correlated, while Jennings et al. (2002) pointed out that body size is a predictor of TL within the community, providing an empirical basis for integrating trophic analyses.

The largehead hairtail (*T. lepturus*) is a benthopelagic shoal-forming fish, mainly preying on pelagic fish and squid and is considered opportunistic in terms of food (Martins and Haimovici, 2000; Bittar et al., 2008). Fishes corresponded to all their stomach contents, which corroborates with the predominantly piscivorous eating habit, particularly on Clupeiformes, recorded by other authors (Martins and Haimovici, 2000; Magro, 2006; Bittar et al., 2008; Soares et al., 2008). In the study by Muto et al. (2005), teleost fishes predominated in their diet, and the importance of the Engraulids in the winter of the platform region of Rio de Janeiro and São Paulo was highlighted. In addition, consumption of *T. lathami* by the largehead hairtail was recorded on the continental shelf of Santa Catarina and Paraná, although another unidentified Teleostei represents the most significant importance of the food index of the prey consumed. On the South coast of Brazil, *T. lepturus* was investigated by Martins et al. (2005), who showed that juveniles eat almost exclusively calanoid copepods, while adults consume fish such as anchovy besides cephalopods, Euphausiacea, and coastal shrimps.

The white snake mackerel (*T. lepidopoides*) also showed a high intake of Teleostei, such as *Trachurus* sp. and others not identified. This result agrees with Nakamura and Parin (1993), who documented a carnivorous food preference for small fish for this species. Although it is a Carangid, the Atlantic moonfish (*S. setapinnis*) fed mainly on Teleostei *Bregmaceros* sp. and decapod crustaceans, thus being grouped according to their eating habits and not by phylogeny. Small planktonic fish and crustaceans were incorporated as the main elements of their diet in Carvalho and Soares (1997), while Hofling et al. (2000) recorded a diet based on decapods, fishes, and organic matter. However, the high consumption of teleost fish may be restricted to adults, as juveniles feed primarily on zooplankton crustaceans and, secondarily, on fish and cephalopods in the study by Gorni and Loibel (2014). Oliveira-Silva and Lopes (2007) point out with *Selene vomer*'s research that the eating habits of this fish correspond to the morphology of the digestive tract, being piscivorous. Bastos et al. (2005) also classified this species' diet as predominantly piscivorous, where the importance of Teleostei in the diet increased with the size of the fish.

Fishing landings and biomass

The highest abundances of pelagic fish aggregations in the SBB were given by medium to high trophic level species, especially by *T. lepturus*, *T. lathami,* and *S. brasiliensis*. This was also observed by Soares et al. (2005) when studying SBB in the REEVIZE program. The dominance and high biomass of these species in this region indicate that they play a crucial role in the pelagic ecosystem at depths of 100 m.

Considering that SBB fish species account for about half of the country's yearly catch, it is crucial to comprehend the current scenario and the temporal changes in these fisheries resources (Valentini and Pezzuto, 2006). When analyzing the biomass data from the ECOSAR cruises, it is clear that *T. lepturus*, *T. lathami*, and *S. brasiliensis* had the highest dominance among all studied species. However, even though *T. lepturus* and *T. lathami* had larger biomasses than *S. brasiliensis* (apart from ECOSAR VI/2009), this species had higher fishing landings during the entire period. Indeed, *S. brasiliensis* was the studied species with the highest amount of landings in the last 33 years at SBB, and according to Neto and Dias (2015), it represents the most important fish for the Brazilian consumer's food security.

With oscillations, the decline of *S. brasiliensis* began in the 1980s, followed by large landed amounts from 1994 to 1998, culminating in a decrease in the following years. In addition to the high consumption of this species by the Brazilian population, *S. brasiliensis* is still used as live bait in the capture of the *Katsuwonus pelamis* (Linnaeus, 1758), which contributes to the decrease in its biomass, and, consequently, in fishing (Neto and

Dias, 2015). Such a reduction may still be associated with the characteristics of its life cycle, but it is possible that failures in managing the sustainable use of the resource were the main reason for the decline in its stock (Cergole and Dias-Neto, 2011). As for *T. lathami,* there have been sudden reductions in landings since 1994, even though it had a high biomass detected on ECOSAR cruises. This species was fished in association with *S. brasiliensis*, being one of the main resources in periods of little sardine production (Saccardo et al., 2005). As shown in the study, the moderate positive correlation between the landings of these species may indicate the role of *T. lathami* as a bycatch of *S. brasiliensis*. From 1994 onwards, the decline in landings of *T. lathami* may be related to the lack of accessibility of the fish by the fishing fleet, given that the species was widespread on the ECOSAR and REVIZEE cruises (Saccardo et al., 2005).

On the other hand, *S. setapinnis*, usually recorded together with *Selene vomer*, could be considered an alternative to *S. brasiliensis* (Valentini and Pezzuto, 2006), although a significant negative variation of this species was observed in the analyzed time intervals. Bastos et al. (2005) point out that it is necessary to protect stocks by assessing data on length and maturation since most of these species' fisheries are concentrated on juveniles. Another commonly exploited species is *T. lepturus*, with a high representation in terms of biomass for the Southeast-South region of Brazil (Haimovici et al., 2007). In the past, *T. lepturus* was not a target of fisheries and was usually discarded on boats, which may have led to overfishing (Magro, 2006). As it is representative of fisheries off the Brazilian coast, studies should be carried out to improve the use and protect the species' stock.

Some species whose fishing activities are not as relevant to the study area were also investigated: *T. lepidopoides, Anchoa* sp., and *H. clupeola.* Although not prominent in industrial fisheries, *Anchoa* sp. is captured as a bycatch in large-scale and artisanal fisheries (Figueiredo and Menezes, 1978; Sergipense et al., 1999). Such small pelagic species do not have the potential to sustain the fisheries in the Southeast-South region of Brazil. Still, changes in their spatial-temporal distributions are reflected in the abundance of their predators, usually fish of great commercial importance (Bernardes and Rossi-Wongtschowski, 2007).

It is important to note the species that increased in annual landings between 1986-2019: *O. oglinum* and *C. chrysurus*. The increase in landings may represent a greater number of fish available, improvement of fishing gear used, or more availability of information since, in the past, there were fewer means of collection, communication, and distribution of artisanal fishing data. The negative correlations calculated in this study suggest that the fisheries for *O. oglinum* and *C. chrysurus* are more intense in periods of decline for *S. brasiliensis*. Haimovici et al. (2007) point out that the fisheries of all small pelagic fish are related to the availability of *S. brasiliensis*, so when its abundance decreases, the fleet targets the rest of the small pelagic (Haimovici et al., 2007). Nevertheless, although the landing of some small pelagic has increased significantly over the period studied, they do not replace *S. brasiliensis* due to the high importance of this species for SBB fisheries. For Neto and Dias (2011), *O. oglinum* can be a fundamental species for maintaining sardines in the fishing sector since its nutritional characteristics and flavor are very similar to that of *S. brasiliensis*. Valentini and Pezzuto (2006) pointed out that even with the decline of *S. brasiliensis*, an intense fleet operation continued, indicating that the biomass of alternative stocks is not so considerable in the region.

Trophic role and fisheries of pelagic fishes

Like landing studies, information on pelagic fishes feeding helps assess the potential for exploitation of fishery resources through trophic aspects (Gasalla and Soares, 2001; Gasalla et al., 2007). The TL's knowledge of fisheries-relevant species is crucial for estimating and monitoring the MTI to maintain sustainable fisheries. Since 1990 the MTI of landed fish has been decreasing globally at a rate of 0.1 per decade; that is, worldwide, catches have shifted from piscivorous top predators to small pelagic planktivorous (Pauly et al., 1998; Pauly et al., 2000). One of the main reasons for such a reduction may be due to species with high TL being preferred for fishing activities, giving rise to the expression "fishing down food webs". Authors such as Essington et al. (2006) and Pauly et al. (1998) state that the sequential addition of low TL species (an effect known in the literature as "fishing through food webs") also has a significant effect on the decrease of the world MTI.

In this way, both the excessive removal of top-of-chain fishes and the exacerbated increase of species with lower TL can, over time, induce a reduction in the MTI. Due to the close relationship between TL and fish size, MTI can reflect changes in size composition and position in the food web and, therefore, trophic roles. In the present study, a slight increase in the MTI was observed from 1986 to 2019, going against the forecast expected by the CBD. Pincinato and Gasalla (2010) and Damasio (2020), when studying the Southeast-South region of Brazil, also estimated an increase in the MTI over the decades. Freire and Pauly (2010) point out that the collapse of *S. brasiliensis*, a low trophic level species, might be one of the leading causes of the upward trend of the MTI observed in Brazilian marine waters from 1978 to 2000.

Bornatowski et al. (2017) point out that in SBB, pelagic predators are key species, and decreases in their biomass impact the pelagic ecosystem as a whole, reducing the MTI. Thus, the decrease in landings of *T. lepturus*, a piscivorous species with an estimated TL of 4.5, could be a reason for the decline in the MTI. However, as observed in this study, *S. brasiliensis* and other Clupeiformes occupy a much more significant position for landings in the region. Thus, the decline in sardine categories with low to medium TL may reflect much more firmly on the rise in MTI at SBB. Vasconcelos and Gasalla (2001) highlight the consequences of the "fishing down food webs" effect in Brazil, as fisheries targeting small pelagic planktivorous have the potential to reduce productivity by interrupting the main energy routes for exploited high TL species. Essington et al. (2006) add that the effects of declines in average TL on catches can be complex and challenging, as the increase in fish with low to medium TL can also occur for environmental reasons. Pauly and Watson (2005) point out that small pelagic can significantly influence the MTI value, but often due to their natural fluctuations in the ecosystem and not necessarily due to increased fishing effort.

The SBB's average MTI calculated here may be underestimated since not all species significant for regional fisheries were included. Studies that cover the impacts of top predators such as sharks and tuna on the whole ecosystem are needed. Analysis of fishing efforts coupled with ecological studies are also critical, given that it may provide information about fishing capacity and changes in the structure of the food web. Lastly, it is crucial to monitor changes in species TLs constantly, as these may vary over time and space (Pauly et al., 1998).

CONCLUSION

The data presented provide a compilation of feeding data for species captured during the ECOSAR II Program surveys. The trophic role of 12 pelagic fish species in SBB was investigated, and, according to the estimated trophic levels, nine can be considered zooplanktivorous and three piscivorous. The three trophic guilds obtained (Planktivorous Clupeiformes, Planktivorous Carangiformes, and Piscivores) show these species' different roles in the trophic web of SBB. Zooplanktonic organisms constituted the primary food resource used by fish of the Clupeiformes and Carangiformes orders, emphasizing copepod and decapod crustaceans' items. Most species obtained a broad food spectrum, despite their consumption preferences being consistent with the existing bibliography. The Atlantic moonfish *S. setapinnis* was the exception among the predominantly planktivorous habit of Carangiformes, being classified as piscivore in the food guild due to the high consumption of teleost fish together with the Scombriformes *T. lepturus* and *T. lepidopoides*. Nevertheless, most fish studied here have great commercial or potential importance in the region. The fish landing data showed the variations between them, emphasizing the decline in the volumes of *S. brasiliensis*, *T. lathami*, *T. lepturus*, *S. setapinnis*, and *H. clupeola*. Also noteworthy is the positive correlation between the fishing of *S. brasiliensis* with *T. lathami* and

S. setapinnis, and a negative correlation with *O. oglinum* and *C. chysurus*. The calculated MTI time series shows a slight increase over these years. Even so, the decrease in species relevant to Brazilian fishing activity leads to the need to assess stocks effectively and implement management measures to avoid overfishing processes. The results regarding feeding habits, trophic position, and its relationship with fishing can support further trophic studies regarding these species, their prey, competitors, and predators to provide relevant information for quantitative modeling and management actions in the SBB. Thus, more studies covering spatial and temporal variations in this area are encouraged, given their importance for management actions on the SBB and the scarcity of information on the food ecology of most species studied.

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AUTHOR CONTRIBUTIONS

J.P.O.: Conceptualization; Methodology; Software and data analysis; Writing- original draft; Writing- review & editing.

M.A.G.: Conceptualization; Methodology; Stomach content analysis; Data storage; Supervision; Writing - review & editing.

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