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Dietary metabarcoding of keystone sardine species reveals the importance of their ichthyoplankton prey in food webs of the Southern Brazilian Bight fisheries

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Abstract

Clupeiform fishes are ecologically and economically important species contributing to industrial and artisanal fisheries worldwide. They represent key links in food webs, influencing the dynamic between trophic levels. The dietary interactions of these species are poorly studied in many regions, yet essential for fisheries management. To elucidate the role of these species in food webs of the Southern Brazilian Bight pelagic fisheries, we used metabarcoding analysis of fish stomach contents of Clupeiformes and possible predators. Onboard sampling from March to September 2016 allowed for processing of 87 stomach samples representing 31 species (including 12 samples representing three species of Clupeiformes). Links between trophic levels showed the predominance of *Sardinella brasiliensis* and *Engraulis anchoita* as important dietary items of a large range of fishes (28 species belonging to 18 families) and representing the majority of the total prey read abundance assigned to clupeiform fishes (~46% and ~32%, respectively). *Opisthonema oglinum* contributed to the diet of 16 species in 13 families and ~18% of total read abundance of clupeiform fishes as prey. The appearance of multiple clupeiform taxa in the diet of predators that are not commonly associated with pelagic prey indicates that ecosystem-based fisheries management should not be separated between pelagic and demersal fisheries. The diet of Clupeiformes revealed an unexpectedly large diversity of fish species and a low proportion of invertebrates (<5% of clupeiform prey reads). This was likely due to a combination of both a limitation of the metabarcoding method (primer bias and low success of invertebrate taxonomic identification) as well as a contribution of early life stages (ichthyoplankton) to the diet of these fishes. The potential role of clupeiform fish populations as a constraint to the recruitment from the

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ichthyoplanktonic phase of other ecologically or commercially important fishes should be considered as an important direction for future studies.

1 | INTRODUCTION

Clupeiformes are ecologically and economically important fishes, playing a fundamental role in industrial and artisanal fisheries worldwide (Anggoro & Saputra, 2019; Nelson et al., 2016; Souza-Conceição & Schwingel, 2011). Members of this order are mainly pelagic marine species inhabiting coastal areas, though some species live in estuaries and freshwaters (Whitehead, 1985a; Whitehead et al., 1988). Their bodies are laterally flattened or rounded, and they live in large shoals, feeding mainly on plankton filtered from water using their branchial arches (Whitehead, 1985a; Whitehead et al., 1988). In the Southern Brazilian Bight (SBB, ∼22–28°S), ichthyoplankton records indicate that the Brazilian sardine (*Sardinella brasiliensis* [Steindachner, 1879]) and Argentine anchovy (*Engraulis anchoita* [Hubbs and Marini, 1935]) are the dominant pelagic fishes (Katsuragawa et al., 2006). They are known as near-shore, schooling, and filter-feeding fishes (Whitehead, 1985b), and as small pelagic fish at middle trophic levels are believed to exert major control on the dynamics of lower and higher trophic levels through their transfer of nutrients and energy (Castello, 2007; Cury et al., 2000; Frederiksen et al., 2006).

S. brasiliensis is the most important pelagic fishery resource in Brazil in terms of biomass (Valentini & de Cardoso, 1991), with catches totaling 74,100 t in 2011 (MPA, 2013). Its landings are concentrated in the states of Rio de Janeiro, São Paulo, and Santa Catarina (Figueiredo & Menezes, 1978; Paiva, 1997; Schroeder et al., 2022). Periods when the mean landings of the Brazilian sardine declined (Rossi-Wongtschowski et al., 1995) have been attributed to overfishing (Valentini & de Cardoso, 1991), and some stocks are now considered over-exploited (Cergole et al., 2005; Cergole & Dias-Neto, 2011). This species is restricted to the SBB and spawns during late-spring and summer (Matsuura et al., 1992), when the water column in the bight shows a strong vertical stratification (Kurtz & Matsuura, 2001). Most research on pelagic fisheries in this region focus on *S. brasiliensis* (de Moraes et al., 2012; Dias et al., 2014; Gigliotti et al., 2010; Matsuura, 1996, 1998; Schroeder et al., 2022). However, 6 genera and 12 species of anchovies are also found in the SBB. *E. anchoita* is the main economically important species among these and has historically mainly been fished by the Argentine and Uruguayan fleets (FAO, 2014). Despite its abundance, *E. anchoita* has not been subjected to significant commercial exploitation by southern Brazilian fleets (Buratti et al., 2020; Costa et al., 2020). Instead, it is primarily used as bait, and the quantities captured for this purpose are relatively low (Buratti et al., 2020). As a result, most research has been focused on stocks from the Argentine and Uruguayan coasts (Auad & Martos, 2012; de Ciechomski, 1965;

Garciarena & Buratti, 2013; Leonarduzzi et al., 2010, 2013; Madirolas et al., 2013; Marrari et al., 2013; Padovani et al., 2011), with fewer studies involving *E. anchoita* from southern Brazil (Carvalho & Castello, 2013; Cooke & Madureira, 2012; Costa et al., 2016; de Torquato & Muelbert, 2014; Weiss, 1977). These anchovies are broadly distributed, spawn year-round in the SBB with a peak during late-spring and beginning of summer (Matsuura et al., 1992). Their eggs are important components (a major constituent of the ichthyoplankton) of the pelagic ecosystem, because they survive in different oceanographic conditions resulting in a wide distribution (Macedo-Soares et al., 2014). *Opisthonema oglinum* (Lesueur, 1818), commonly referred to as the Atlantic thread herring, is another common clupeiform species in the SBB. The species exhibits a well-defined reproductive season, with distinct periods of gonadal maturation and spawning, and its reproductive cycle overlaps with that of *S. brasiliensis*, indicating potential interspecies interactions and competition for resources during these periods (Petermann & Schwingel, 2016). During the spring–summer period from 1995 to 2010, data from midwater trawls in the SBB showed that *O. oglinum* was one of the most abundant species and strongly associated in the combination of the Coastal Water and areas of mixing between Coastal Water and South Atlantic Central Water, alongside two other clupeiform species, *S. brasiliensis* and *Harengula clupeola* (Cuvier, 1829) Contente & Rossi-Wongtschowski, 2016.

The Brazilian fishing industry experienced significant growth in the 1960s, primarily focusing on highly productive pelagic and demersal resources (Paiva, 1997). However, overfishing and the subsequent decline in fish stocks have led to a notable decrease in productivity, resulting in the necessity of implementing conservation policies (Dias-Neto, 2010; Freire et al., 2015). To understand stock dynamics, ecosystem impacts, and human activities, the collection of data during commercial fishing operations is essential (Cunha & Resgalla, 2016; Tamanaha et al., 2016). This would further allow researchers to investigate the effects of changes in fishing fleets' behavior and catch technology, driven by ecological, market-oriented, and legal factors (Arana et al., 2016). Indeed, integrating scientific research and data into fisheries management is crucial to achieve both ecological and economic sustainability. There is a pressing need to update knowledge regarding industrial fisheries in southeastern and southern Brazil while actively identifying innovative solutions for fishing development and management in the region. These efforts are essential for effective conservation practices (Arana et al., 2016). Species captured as bycatch in the Brazilian sardine fishery between 2008 and 2010 indicated better estimates of growth for small pelagic fish (including Clupeiformes) than for larger or more benthic associated fishes, showing the

importance of studies aiming at monitoring populations and treating them accordingly (Vaz-dos-Santos & Rossi-Wongtschowski, 2013).

Traditional dietary studies use visual identification of food items, but this method is dependent on the prey item (whole organism or parts of larval or adult stages) and the level of digestion of the prey as they determine which diagnostic characters are available often limiting species level identification and often require a high level of taxonomic knowledge for reliable characterization across many taxa (Amundsen & Sánchez-Hernández, 2019; Sheppard & Harwood, 2005). Dietary analysis using metabarcoding has been proven to be an effective method for recovering species level interactions in food webs and describing ecological effects associated with habitat use (Hoenig et al., 2021; Leray et al., 2015; Pompanon et al., 2012; Weber et al., 2023), providing a valuable alternative to traditional morphological-based analysis (Alberdi et al., 2019; Cuff et al., 2022). Metabarcoding enables detailed identification helping to better evaluate the variety of dietary items and can provide relative quantification of food items consumed allowing insights into diet choices (Bessey et al., 2019; Casey et al., 2019; Cowart et al., 2015; Dafforn et al., 2014; Elbrecht et al., 2017; Nielsen et al., 2017; Zurdo et al., 2023). The comprehensive access to the wide range of food items with accurate taxonomic identification and relative comparison of abundance offers valuable data for both biodiversity research and management (Ando et al., 2020; Deagle et al., 2019; Ficetola et al., 2018; Kartzinel et al., 2015; Roffler et al., 2021).

Although clupeiform fishes are important in fisheries and aquaculture, in comparison to other commercially important fish, there are often gaps in basic biological information and fishing data at the regional level that can support management decisions (Birge et al., 2021). Because they play a key role in food webs, the knowledge of the dietary interactions of these species is essential for fisheries management (Roslin & Majaneva, 2016). However, obtaining this knowledge can be challenging because (a) taxonomic identification of many clupeiforms can be difficult (Whitehead, 1985a); (b) they eat a diverse array of small organisms, which decreases the accuracy and precision of identifying most of the species in their diets through morphological approaches (Siegenthaler et al., 2019; Takahashi et al., 2020); and (c) the digestive processes further impede the identification of small dietary items and fragments (Ribas et al., 2021). In our study, we used metabarcoding analysis of fish stomach contents to obtain better insights into the role of clupeiform species and their potential predators in the food web of the SBB and help to fill the knowledge gaps currently hampering sustainable fisheries management.

2 | MATERIAL AND METHODS

2.1 | Sampling

Samples were collected from March to September 2016 during on-board fishery monitoring of the pelagic sardine fishery in southeastern Brazil (between Barra Velha, Santa Catarina state, and Rio de Janeiro, Rio de Janeiro state) (Figure 1) as part of a regional ecosystem-based fisheries management project based at the University of São Paulo Oceanographic Institute. Samples covered seven capture events from three fishing embarkations of purse seine fishing vessels (four capture events from one embarkation just west of Ilha Grande, Rio de Janeiro; two capture events from one embarkation just east of Ilha Grande, Rio de Janeiro; and one capture event from an embarkation at Barra Velha, Santa Catarina—see the supporting information). These purse-seine caught samples are ideal for metabarcoding analyses, as they have not consumed bait and have little time to eat co-collected taxa during their capture (Ribas et al., 2021). Nonetheless, records of co-collected taxa were made to control for their possible influence on dietary findings. We collected as many individuals as possible from each species identified in the bycatch (Table 1). A total of 87 samples from 31 species were collected (see Table 1 for further details).

Whole fish were frozen until further processing in the laboratory at the University of São Paulo, USP. Samples and equipment were decontaminated prior fish dissection to remove their stomach contents. Stomach contents were preserved in absolute ethanol in decontaminated storage vessel with external labeling and transferred to the Federal University of Pará, UFPA, for further processing. Samples were collected under SISBIO license number 53022-2 from the "Instituto Chico Mendes de Conservação da Biodiversidade." Work was performed under approval of the UFPA Ethics Committee (CEUA-UFPA—Permit 68/2015).

2.2 | DNA extraction, PCR, and sequencing

All procedures were performed following initial decontamination of all materials and surfaces using bleach and/or UV light exposure. Individual stomach contents were separated from preservative by three cycles of centrifugation, washed with ultrapure, and UV sterilized water. Four 650 μl subsample replicates (a–d) were prepared and stored in separate microcentrifuge tubes (Rosa et al., 2024). DNA from all replicates was extracted using the CTAB/phenol/chloroform protocol (Doyle & Doyle, 1987) in a decontaminated fume hood. Two-hundred sixty-three subsamples representing all 87 samples across 31 species were successfully extracted and sequenced (successful amplification of replicates a–d is indicated in Table S1 as some replicates did not amplify, apparently because of PCR inhibition), as well as multiple negative controls generated at various steps, from sample processing (tubes opened and filled only with ethanol or water during sample preparation—one control between each homogenized sample), to DNA extraction (one negative control in each row of 12 tubes) and amplicon production (a minimum of two spatially separated negative controls on each PCR plate) steps (Rosa et al., 2024).

PCR amplifications of all subsamples and negative controls targeting the Cytochrome C oxidase subunit I marker (130 bp) were performed using the primers Minibar-Mod-F and Minibar-Mod-R (Berry et al., 2015), following index combinations as described in Fadrosh et al. (2014). PCRs were carried out in 25 μl final volumes with final
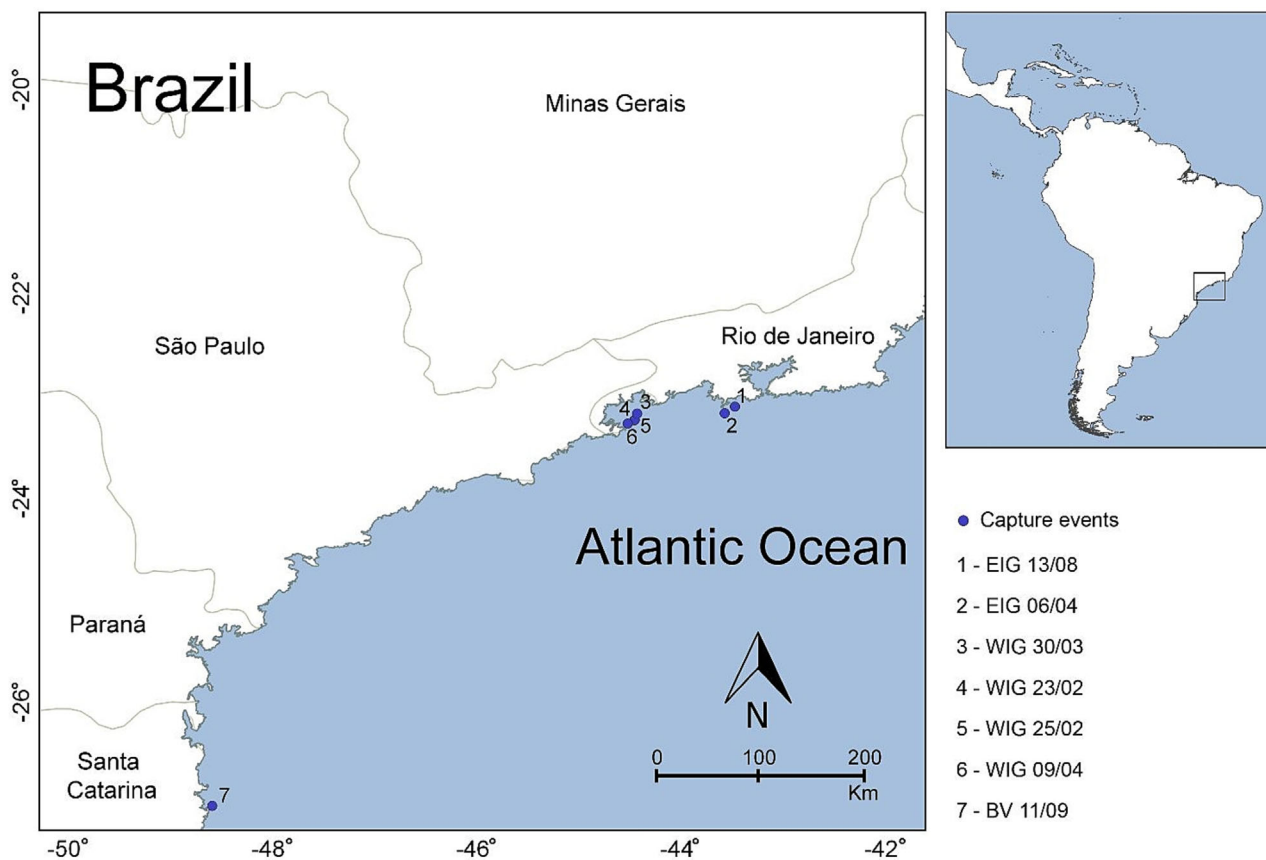
FIGURE 1 Sampling area covering seven capture events during on-board fishery monitoring of the pelagic sardine fishery in southeastern Brazil, from March to September 2016. EIG, East of Ilha Grande, Rio de Janeiro; WIG, West of Ilha Grande, Rio de Janeiro; BV, Barra Velha, Santa Catarina

TABLE 1 Fish taxa collected in the Southern Brazilian Bight sardine fishery for which diet was characterized with DNA metabarcoding

Order	Family	Species	Sample size
Acanthuriformes	Ephippidae	*Chaetodipterus faber* (Broussonet, 1782)	1
Acanthuriformes	Sciaenidae	*Cynoscion guatucupa* (Cuvier, 1830)	2
Acanthuriformes	Sciaenidae	*Cynoscion jamaicensis* (Vaillant and Bocourt, 1883)	1
Acanthuriformes	Sciaenidae	*Menticirrhus americanus* (Linnaeus, 1758)	2
Acanthuriformes	Sciaenidae	*Micropogonias furnieri* (Desmarest, 1823)	4
Acanthuriformes	Sciaenidae	*Paralonchurus brasiliensis* (Steindachner, 1875)	3
Batrachoidiformes	Batrachoididae	*Porichthys porosissimus* (Cuvier, 1829)	5
Beloniformes	Hemiramphidae	*Hemiramphus balao* (Lesueur, 1821)	3
Carangiformes	Carangidae	*Caranx crysos* (Mitchill, 1815)	2
Carangiformes	Carangidae	*Caranx latus* (Agassiz, 1831)	3
Carangiformes	Carangidae	*Chloroscombrus chrysurus* (Linnaeus, 1766)	2
Carangiformes	Carangidae	*Hemicaranx amblyrhynchus* (Cuvier, 1833)	2
Carangiformes	Carangidae	*Oligoplites saliens* (Bloch, 1793)	5
Carangiformes	Carangidae	*Selene setapinnis* (Mitchill, 1815)	3
Carangiformes	Carangidae	*Trachinotus carolinus* (Linnaeus, 1766)	1
Carcharhiniformes	Carcharhinidae	*Rhizoprionodon lalandii* (Valenciennes, 1839)	1
Clupeiformes	**Clupeidae**	***Brevoortia pectinata*** **(Jenyns, 1842)**	**1**
Clupeiformes	**Clupeidae**	***Opisthonema oglinum*** **(Lesueur, 1818)**	**6**

TABLE 1 (Continued)

Order	Family	Species	Sample size
Clupeiformes	**Clupeidae**	***Sardinella brasiliensis* (Steindachner, 1879)**	**5**
Gerreiformes	Gerreidae	*Eucinostomus gula* (Quoy and Gaimard, 1824)	5
Istiophoriformes	Sphyraenidae	*Sphyraena tome* (Fowler, 1903)	3
Lutjaniformes	Haemulidae	*Orthopristis ruber* (Cuvier, 1830)	3
Perciformes	Priacanthidae	*Priacanthus arenatus* (Cuvier, 1829)	2
Perciformes	Sparidae	*Pagrus pagrus* (Linnaeus, 1758)	1
Perciformes	Triglidae	*Prionotus punctatus* (Bloch, 1793)	1
Scombriformes	Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)	4
Scombriformes	Scombridae	*Euthynnus alletteratus* (Rafinesque, 1810)	2
Scombriformes	Scombridae	*Scomber colias* (Gmelin, 1789)	8
Scombriformes	Trichiuridae	*Trichiurus lepturus* (Linnaeus, 1758)	2
Syngnathiformes	Dactylopteridae	*Dactylopterus volitans* (Linnaeus, 1758)	3
Tetraodontiformes	Monacanthidae	*Aluterus monoceros* (Linnaeus, 1758)	1

Note: Clupeiform samples are in bold text.

concentration of 1X Q5 High-Fidelity master mix (New England Biolabs), 2X Q5 enhancer (New England Biolabs), 100 nM of each primer, and 2–3 ng of template DNA (including unique combinations of dual-indexing barcodes) (Ribas et al., 2021; Rosa et al., 2024). The PCR amplification protocol was as follows: initial denaturation at 98°C for 30 s; followed by 30 cycles of denaturation at 98°C for 10 s, annealing at 45°C for 15 s, and extension at 72°C for 15 s; and final extension of 2 min at 72°C.

Amplicons were visualized on agarose gels and quantified using ImageLab Software v6.0. (Bio-Rad Laboratory). Amplicons were then normalized using a Biomek 4000 liquid handling robot (Beckman Coulter). The DNA libraries were cleaned using 1.0X AMpure beads (Beckman Coulter), and sequence adapters ligated to the dual-indexed amplicons using the NEBNext Fast DNA Library Prep Set for Ion Torrent (New England Biolabs). The amplified libraries were size selected using BluePippin (Sage Science). The final libraries were quantified on a Fragment Analyzer (Agilent) instrument using the High Sensitivity Genomic DNA Kit (Agilent) and sequenced on two 530 chips on an Ion GeneStudio S5 system (Thermo Fisher).

2.3 | Bioinformatics: Sequence data processing

We used the pipeline PIMBA (Oliveira et al., 2021) to process the sequencing data. The raw sequencing data were first demultiplexed using the dual-index barcodes. The demultiplexed FASTQ files were then cleaned to remove low-quality bases (PHRED < 20) using PRINSEQ (Schmieder & Edwards, 2011), with the *pimba_prepare* module. Then, we used QIIME (Caporaso et al., 2010) and VSEARCH (Rognes et al., 2016) pipelines in the *pimba_run* module to perform dereplication, discard singletons, trim sequences to 130 bases, remove chimeric sequences, and cluster molecular operational taxonomic units (MOTUs) using similarity thresholds of 97% and 99%. Using

pimba_run, MOTUs were aligned with the *nt* reference database from NCBI using BLAST to perform taxonomic assignment, including the use of LULU (Frøslev et al., 2017) to remove erroneous MOTUs and PIMBA script to check for and exclude MOTUs representing nuclear mitochondrial pseudogenes (NUMTs) based on descriptors considering the 10 most similar sequences identified by BLAST. Assignment was performed using minimum thresholds of 90% similarity, and similarity to the most similar taxon was recorded. This step was included since extensive reference databases for much of the fauna in the sampled geographic region are not available, and we aimed at identifying as many taxa as possible in the diet during post-processing (see below). The outputs from the different clustering levels were evaluated to determine their effectiveness at recovering taxa without producing multiple MOTUs with the same taxonomic assignment.

Rarefaction curves for each replicate were performed to assess whether adequate sequencing depth had been achieved, using random sampling of 999 sequences without replacement in the "rarecurve" function from *vegan* (Oksanen et al., 2020) in R 4.1.0 (R Core Team, 2021).

2.4 | Bioinformatics: Taxonomic assignment and statistics

To remove false positives and possible contaminants or sequencing errors, we applied the following rules: (i) the maximum number of reads detected in the controls was removed for each MOTU from all samples; (ii) MOTUs containing fewer than 10 reads were discarded; and (iii) obvious non-target species or MOTUs likely originating from carry-over contaminations were removed from the dataset (Ushio et al., 2018; Ribas et al., 2021; Rosa et al., 2024). The final assignments of dietary items were inferred based on similarity values and knowledge on geographic distributions in the literature accessed

through FishBase (Froese & Pauly, 2022) and SeaLifeBase (Palomares & Pauly, 2022) to confirm the taxonomic identification. Species identity was considered confirmed for similarities above 97%, and the most probable geographically local representatives of the same genus or family identified when similarities were between 90% and 97% (Rosa et al., 2024). For example, a sample assigned with a similarity of 90–97% could be subsequently assigned at family level, genus level, or even a specific species in the genus known from the region if only one species is known for the region. A minimum of 90% similarity was used, as reassignment based on lower similarities than this becomes unlikely. As no blocking primers were used in this study, the predator's DNA was co-amplified alongside dietary items. These data were used to confirm predator identification but removed for subsequent dietary analyses.

Detection of prey taxa was normalized, and secondary consumption of items was evaluated according to Rosa et al. (2024), by using both thresholds of relative read abundance (RRA) within samples (<1% for exclusion and 1–5% as a flag to assess secondary consumption) and comparative data from the literature and from within the global metabarcoding dataset produced in this study. The number of reads was then averaged across subsamples (to avoid inflation of read abundance in samples with more subsamples, e.g., 4 vs. 3 vs. 2 subsamples) (Rosa et al., 2024). The dietary links of clupeiform fishes were visualized using Sankey diagrams. Figures were produced using the *ggplot2* package (Wickham, 2016) under R 4.1.2 (R Core Team, 2021). R scripts are available as a file in the supporting information.

3 | RESULTS

Raw sequencing data can be found in GenBank databases under the Project accession ID PRJNA642914. The overall dataset shows saturation in the number of MOTUs recovered per sample with increasing sequencing coverage and recovery of all the same prey taxa using clustering at the lower level of 97%. Our decontamination procedures were successful, and we obtained fewer than 10 reads of human DNA or other contaminants (i.e., other species being worked on elsewhere by the researchers) in any given sample. Following contaminants and sequencing errors removal as in Ribas et al. (2021), we confirmed the taxonomic identification of the specimens from which the stomach contents were analyzed using their most abundant MOTU. After the rule-based automated data cleaning and manual curation, a few remaining MOTUs were considered to represent likely secondary consumption within each species and removed from further analysis.

Only a few identified dietary items were also caught in the same net as the fish whose stomach contents were analyzed. These were only maintained as probable dietary items when the RRA of the item was greater than that of other items, which were not caught in the same net as the same sample. Almost all these items were also identified in the diet of individual samples that were not collected from the same net. A final table of accepted predators of Clupeiformes was produced that included taxa belonging to 13 orders, 18 families,

29 genera, and 31 species (Table S2; Figure 2), and the accepted prey items of Clupeiformes included taxa belonging to three phyla, 12 orders, 13 families, 22 genera, and 24 species (Table S3, Figure 3).

3.1 | Clupeiformes as dietary items

S. brasiliensis and *E. anchoita* were the principal prey items (dominant read count and most frequently encountered across all samples of potential clupeiform predators) and are found as either a probable dietary item or as a major component of the diet of fishes from 11 and 10 orders (14 and 13 families and 22 and 23 species each), respectively, and represent the majority of the total RRA assigned to clupeiform fishes (~46% and ~32% each). *S. brasiliensis* was not found as a prey item of the sampled fishes from the orders Carcharhiniformes (family Carcharhinidae) and Istiophoriformes (family Sphyraenidae), while *E. anchoita* was not found to be consumed in samples of fishes from the orders Beloniformes (family Hemiramphidae), Perciformes (families Priacanthidae, Sparidae, and Triglidae), and Syngnathiformes (family Dactylopteridae). *O. oglinum* was found in the diet of fishes from 12 orders, 13 families, and 16 species, contributing with a lower percentage of the RRA (~18%); *Harengula jaguana* (Poey, 1865) was consumed by fishes from two species (*O. oglinum* and *Paralonchurus brasiliensis* [Steindachner, 1875]); and *Anchoa* sp. was found as a dietary item from only one fish species (*Sphyraena tome* Fowler, 1903—Istiophoriformes: Sphyraenidae) (Figure 2).

3.2 | Clupeiformes diet

Many species identified in the diet of the clupeiform fishes (Figure 3) likely represent the consumption of early life stages as they include many fish taxa (including various members of the families Carangidae, Sciaenidae, and Scombridae as well as the bluefish, *Pomatomus saltatrix* [Linnaeus, 1766]; the largehead hairtail, *Trichiurus lepturus* [Linnaeus, 1758]; the flying gurnard, *Dactylopterus volitans* [Linnaeus, 1758]; and the unicorn leatherjacket, *Aluterus monoceros* [Linnaeus, 1758]) that when adults are much larger than the clupeiform fishes whose stomachs were analyzed. Although invertebrate zooplankton (a pteropod mollusk—*Creseis virgula* [Rang, 1828] and a branchiopod crustacean—*Penilia avirostris* [Dana, 1849]) were identified in the diet of *O. oglinum*, they were found at very low RRA, and only fish were identified in the diet of *B. pectinata* and *S. brasiliensis*. The most diverse diet among the Clupeiformes was identified in *O. oglinum* that included 12 orders, 15 families, and 20 species, compared to 8 orders, 10 families, and 14 species in *S. brasiliensis* and only three orders, three families, and three species in *B. pectinata*. *O. oglinum* was found to consume three other Clupeiformes (*E. anchoita*, *H. jaguana*, and *S. brasiliensis*), while *S. brasiliensis* consumed *E. anchoita* and *O. oglinum*, and *O. oglinum* was also found in the diet of *B. pectinata*. This reciprocal consumption between species (Clupeiformes found to be predators and prey of each other) was common. This further highlights the role of early life stages
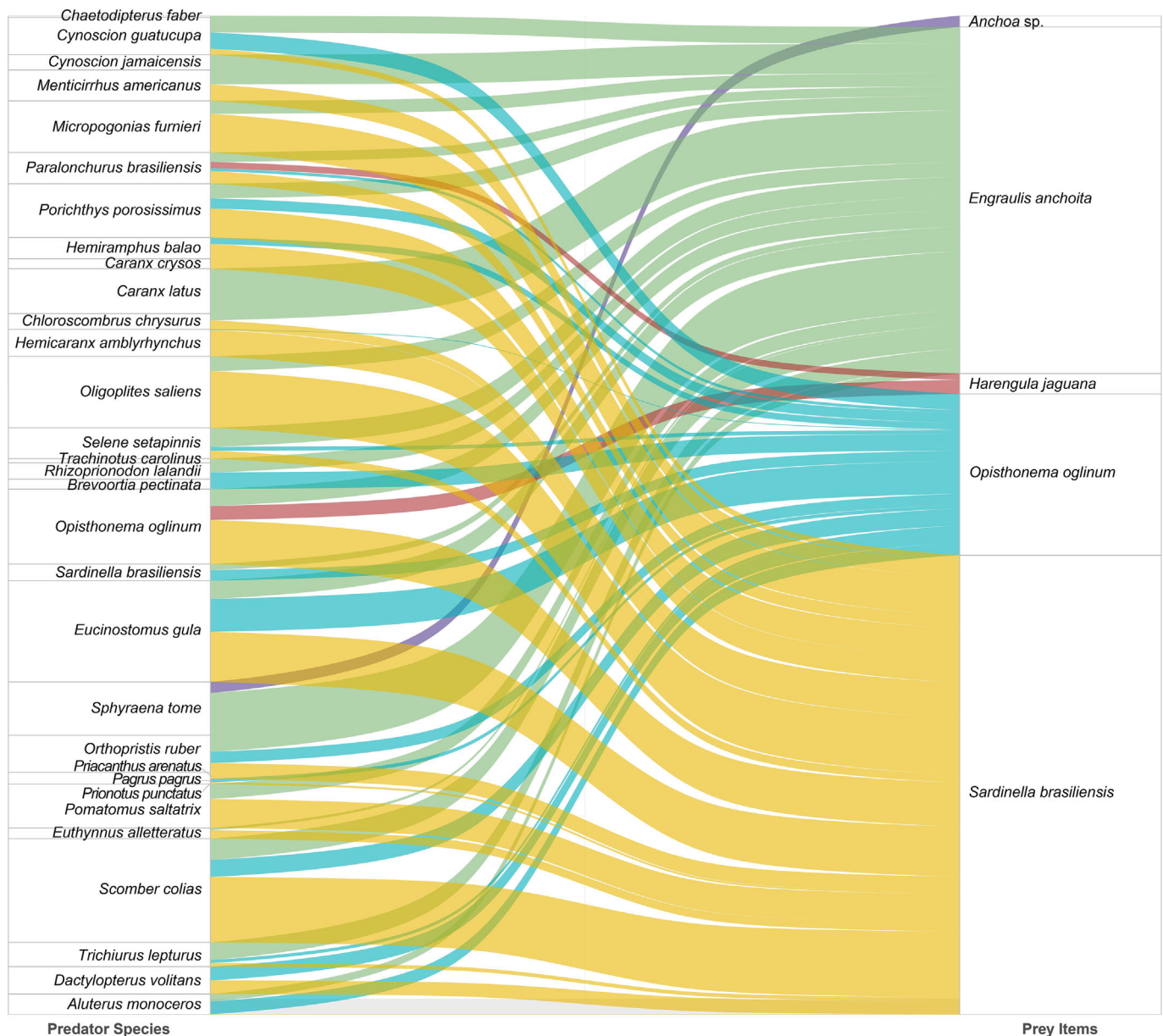
FIGURE 2 Clupeiform fishes identified as prey (right) of fishes caught as bycatch in the southern Brazilian sardine purse seine fishery (left) based on COI minibar metabarcoding of stomach contents. Width of lines are related to read counts.

(particularly eggs and larvae) as components of the diet of clupeiform fishes in the SBB.

4 | DISCUSSION

The results of the present study confirm that clupeids are consumed by many species. Such findings have been previously observed in other taxon-specific dietary studies conducted in various habitats (Arantes, 2014; Bornatowski et al., 2012, 2014; Braga et al., 2018; Haluch et al., 2009; Lima et al., 2000; Lucena et al., 2000; Martins & Haimovici, 2020; Paiva & Motta, 1999). We found exceptions (newly identified predators) such as *Chaetodipterus faber* (Broussonet, 1782)

(Acanthuriformes: Ephippidae), previously only known to feed on a variety of prey, but mainly on hydroids, anthozoans, and polychaetes, but also showing herbivorous habits (Barros et al., 2013; Bittencourt, 1990; Couto & de Vasconcelos, 1980; Hayse, 1990; Reid et al., 1956). *Eucinostomus gula* (Quoy & Gaimard, 1824) (Gerreiformes: Gerreidae), was previously only known to consume polychaetes, copepods, amphipods, isopods, bivalves, ostracods, cnidarians, hydrozoans, nematodes, and algae as prey items, but with teleost fish parts (unidentifiable) also found in analyses (Bouchereau & Chantrel, 2009; Brook, 1977; Cruz et al., 2018; Kerschner et al., 1985; Marancik & Hare, 2007; Odum & Heald, 1972; Springer & Woodburn, 1960). Other predator species investigated in our study, but previously not known to feed on Clupeiformes included:
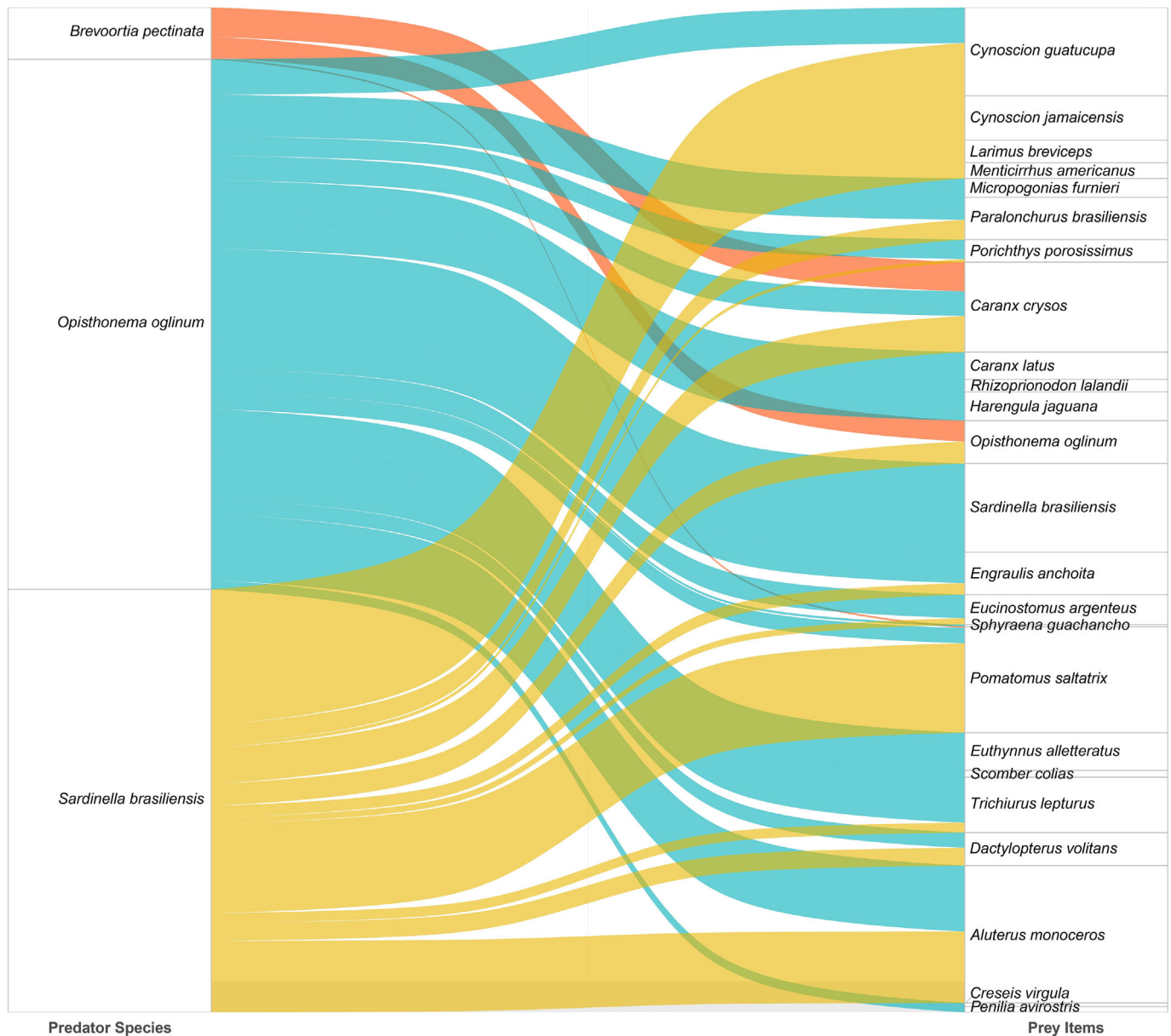
FIGURE 3 Dietary items identified (right) for the Clupeiform species (left) caught as target or as bycatch of the southern Brazilian sardine purse seine fishery using COI minibar metabarcoding of from stomach contents. Width of lines are related to read counts.

Micropogonias furnieri (Desmarest, 1823) (Carozza et al., 2004; Figueiredo & Vieira, 2005; Morasche et al., 2010), *Pagrus pagrus* (Linnaeus, 1758) (Capitoli & Haimovici, 1993; Goldman et al., 2016), and *P. brasiliensis* (Steindachner, 1875) (Branco et al., 2005; de Robert et al., 2007).

Since the previously unidentified predators of clupeiform fishes identified above are all generally fishes that exhibit a benthic feeding behavior or primarily feed near the bottom of the water column, this indicates that the role of pelagic fish in the diet of fishes from lower strata in the water column is probably overlooked and molecular-based studies using metabarcoding identification of stomach contents can provide additional and more accurate information of predator diets that could be missed through traditional diet analysis

(Amundsen & Sánchez-Hernández, 2019). This is especially the case when small or degraded food items present in the stomach cannot be identified at the species level, such as the presence of larval stages or eggs of clupeiforms with a rapid rate of digestion, so few identifiable hard structures are left for carrying out a proper and effective identification based on traditional methods (Amundsen & Sánchez-Hernández, 2019).

In the present study, most of the items identified in the diet of clupeiforms were other fishes, which initially appears to contradict this existing knowledge. Clupeiforms are considered to be generalized planktonic feeders, with many studies indicating that crustaceans, such as adult copepods, are important food items for their growth and successful recruitment (Chícharo et al., 2012; Quah et al., 2022).

However, diet is recorded as varying considerably with food availability, the size of the individuals sampled and the taxonomic groups to which they belong. Larvae of the dorosomatid sardines *S. brasiliensis* (Kurtz & Matsuura, 2001) and *Sardina pilchardus* (Yebra et al., 2019) often consume the most abundant copepods in their environment. A prevalence of copepods was also identified in the diet of adult *S. brasiliensis* (Schneider & Schwingel, 1999), but in a recent study, this species also showed the highest occurrence of ichthyoplankton, along with zooplankton, phytoplankton, and fish in its gut contents, indicating a diverse diet (Olher & Gasalla, 2023).

In our study, fish were identified as the dominant source of prey for *S. brasiliensis*, but the pteropod mollusk *C. virgula* was also found. The dorosomatid *O. oglinum* has also been described as having a feeding preference for crustaceans (Bomfim et al., 2020; Couto & de Vasconcelos Filho, 1986; de Chaves & Vendel, 2008; Olher & Gasalla, 2023; Vega-Cendejas et al., 1997), but some of the cited studies found food items that were only classified as "unidentified fish" (Couto & de Vasconcelos Filho, 1986; Vega-Cendejas et al., 1997), or Teleostei remains (scales and bones), otoliths, juveniles, or animal matter (Bomfim et al., 2020; Olher & Gasalla, 2023). In our study, fish were identified as the dominant source of prey for *O. oglinum*, though some invertebrates (*P. avirostris* and *C. virgula*) were also detected in its diet. A predominance of copepods is recorded for the diet of engraulid anchovy species including *E. anchoita* (Schwingel, 1998), but *Anchoa tricolor* and *Anchoa lyolepis* were recorded to have also consumed bivalve mollusks, gastropods, and polychaetes (Olher & Gasalla, 2023). The discrepancies between known diets and the finding in this study indicate that the contribution of fish and their larval forms might be significantly underestimated and that they could potentially constitute a large part or even the majority of dietary items because they are soft, more quickly digested and grouped into "unidentified fish remains" as they are difficult to identify because of the digestive processes.

The inconsistency of results here in comparison to expectations from the literature may indicate that fish are preferentially targeted as prey items. An alternative, though not mutually exclusive, explanation for the mismatch between our results and previous morphological analyses may be bias in our assays towards amplifying fish DNA. There are limitations inherent in the metabarcoding technique (i.e., primer bias, poor reference database for the region's fauna, and low efficiency of taxonomic identification for invertebrates) (Carugati et al., 2015; Elbrecht & Leese, 2015). Amplification bias exists within taxonomic groups (Elbrecht et al., 2017), but stronger effects are known between major taxonomic groups (Berry et al., 2015) so greater amplification of vertebrate DNA compared to invertebrate DNA may be related to primer matching, especially considering that crustacean DNA is known to be difficult to amplify using some primers for the COI fragment (Zhan et al., 2014). Reference databases are generally more incomplete for invertebrate taxa than for vertebrates (Keck et al., 2023), and there is also variation in terms of which species are present in reference datasets for the different molecular markers (Marques et al., 2021), with lower coverages in general for species that are not commercially important and for geographic

regions where funding is traditionally limited (Ficetola et al., 2021; Keck et al., 2023; Marques et al., 2021). The combination of amplification bias and poor reference databases are factors that could explain the contrast between our results and previous morphological analyses. An important area for further investigation is the use of multiple markers in metabarcoding studies to improve loss of false negative taxa (Burian et al., 2023), and this should also help to improve the accuracy of information on food webs. This does not detract from the fact that many of the prey identified here using metabarcoding would be difficult to identify using traditional morphological methods due to the rapid digestion of food items.

We must also consider that if these results do represent true variation in diet, that this may be a result of the life stages of the sampled specimens and/or the food available in the local environment at the place and time of sampling, reflecting natural variability that is always associated with the number of samples available, and considering that our sampling is limited both spatially and temporally as well as by the overall number of samples per species. Indeed, prey selection is a complex behavioral response that depends on sensory bias (i.e., search image), relative prey availability and many factors relating to the state of the predator (gape size, feeding mechanism, current satiation, and physiological demands for specific nutrients) (Croy & Hughes, 1991; Einfalt & Wahl, 1997; Gill, 2003; Gill & Hart, 1994; Strubbe & van Dijk, 2002). For example, the clupeid *Clupea harengus* (Linnaeus, 1758) has been speculated to target fish eggs when otherwise predominant crustacean prey were less abundant (Segers et al., 2007).

Another issue is raised by the appearance of the shark *Rhizoprionodon lalandii* in the diet of *O. oglinum*. The size difference between the two at any life stage indicates that the consumption of a whole shark by the sardine is impossible, as *Rhizoprionodon* are viviparous (Motta et al., 2007). This raises the importance of consumption of fragments of larger organisms as contributors to the diet of filter feeders, either from natural causes or as a result of fisheries activities. The role of fisheries discards has previously been shown to considerably alter the diet of seabirds that consumed shark (especially shark livers) from long-line fishery discards (Bugoni et al., 2010). Therefore, independently from prey selection, it is also important to consider the minimum filtration ability of the predator's gill rakers, as it directly impacts the capacity to retain prey. Using plastic particles, different minimum filtration sizes were previously estimated and measured based on gill raker morphology for adults of three different Clupeiformes (Collard et al., 2017). *S. pilchardus* and *Engraulis encrasicolus* were estimated to filter smaller particles (214 or 216 μm, respectively) than *C. harengus* (323 μm), but the smallest particles retained by *E. encrasicolus* (~220 μm) were also generally smaller than those retained by *S. pilchardus* by around 30 μm (Collard et al., 2017). These minimum sizes are consistent with mesoplankton consumption, including adult copepods, other crustaceans and fish eggs and larvae.

Reciprocal consumption follows findings in Carangidae (Rosa et al., 2024) but is probably found much more frequently in Clupeiformes than in other taxa due to their role as zooplankton filter feeders. Previous research on Atlantic herring (*C. harengus*) has

revealed cannibalistic interactions, particularly during certain life stages, such as the larval and juvenile phases (Corten, 2013; Hourston et al., 1981), and another study have reported cannibalism in spring-spawning Norwegian herring, where juvenile and adult individuals have been observed consuming early larvae, as evidenced by the presence of larval remains in their stomach contents (Holst, 1992). Our findings support the ecological importance of zooplanktivory of early life stages of fishes, most likely eggs, larvae in ichthyoplankton or small juveniles, and raise its implications for recruitment and fisheries dynamics, according to food availability in the environment. However, we recognize that the generalization of these findings requires further effort considering the limitations of sampling (sample size and spatio-temporal variation in collections) and the possible variations in results because of marker amplification bias and available reference sequences.

5 | CONCLUSION

Our study conducting metabarcoding analysis on the stomach contents of fishes found in the southwest Atlantic region revealed a mix of known and previously unrecorded predators of Clupeiformes, such as *C. faber* and *E. gula*. This showcases the potential of molecular-based techniques for dietary assessment including a large number of taxa identified to species level in the diet, in order to provide additional information on fish diets, particularly when traditional methods fail to identify small or degraded prey items. The inclusion of various clupeiform taxa in the diet of predators not typically associated with pelagic prey highlights the need for integrated ecosystem-based fisheries management that considers both pelagic and demersal fisheries as interconnected components of the ecosystem. Early life stages of other fishes (ichthyoplankton) are also important food sources highlighting an important role in clupeiform growth and recruitment. Future studies should place importance on exploring the potential impact of clupeiform fish on the recruitment of ecologically or commercially significant fishes from the ichthyoplanktonic phase. The identified challenges related to vertebrate DNA amplification bias and the limited taxonomic identification of invertebrates in metabarcoding studies may contribute to the discrepancy with previous literature. Furthermore, we associate filtration capability based on gill raker morphology to the consumption and quick digestion of early life stages of fishes as a mechanism to explain why consumption of fish as prey may have been previously underestimated. The presence of reciprocal consumption and previous known cannibalistic interactions further elucidates the complex feeding dynamics, particularly during specific life stages. Overall, our study demonstrates the value of molecular approaches in unraveling dietary patterns and advancing our understanding of fish feeding ecology, providing insights into the role of clupeiforms in the food web of the southwest Atlantic.

CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHOR CONTRIBUTIONS

Anna Karolina Oliveira de Queiroz: Methodology; investigation; data curation; writing—original draft; writing—review & editing. **Maria A. Gasalla**: Conceptualization; resources; writing—review & editing; supervision; project administration; funding acquisition. **Marcele Laux**: Software; formal analysis; resources; data curation; writing—review & editing. **Renato Renison Moreira Oliveira**: Software; formal analysis; resources; data curation; writing—review & editing. **Fabricio dos Anjos Santa Rosa**: Methodology; formal analysis; investigation; writing—original draft; writing—review & editing. **Audun Schrøder-Nielsen:** Investigation; data curation; writing—review & editing. **Felippe A. Postuma**: Investigation; resources; data curation; writing—review & editing. **João Bráullio de Luna Sales**: Methodology; data curation; resources; writing—original draft; writing—review & editing. **Hugo de Boer**: Resources; supervision; writing—review & editing; funding acquisition. **Quentin Mauvisseau**: Methodology; data curation; resources; writing—original draft; writing—review & editing. **Jonathan Stuart Ready**: Conceptualization; methodology; data curation; resources; writing—original draft; writing—review & editing; supervision; project administration; funding acquisition. All authors revised the manuscript before submission.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.