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Patterns and partitioning of food resources by elasmobranchs in southern Brazil

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Abstract Our study sought to analyze patterns and overlap in prey items consumed by elasmobranch species in southern Brazil through a complex network analysis. We hypothesized that species with the same habitat use would show greater trophic niche overlap and lower diet specialization than species with different habitat use. We conducted a literature survey of the species recorded in southern Brazil and analyzed publications with quantitative data on the diet of each species. We found records of 103 species in the region, of which 58 had their diets analyzed and had quantitative data to contribute to this analysis. The results suggest nested diet patterns in this community. Nestedness may arise for different reasons, and suggests that species might be balancing their high feeding niche overlap through compensatory mechanisms. There are no prior records of such a pattern in elasmobranch communities, which brings to light important information about their feeding niche. Data on prey consumption and temporal and spatial patterns of elasmobranch feeding may yield further insight into how these species are interacting in the environment and assist the investigation of the processes that shaped the current community's trophic structure.

Keywords Diet · Network analysis · Rays · Sharks · Trophic ecology

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Introduction

One of the dimensions of a species' ecological niche is its foraging niche. The foraging niche can be partitioned into three major components: temporal (e.g., period of activity, migration patterns for feeding), spatial (feeding location) and trophic (prey consumed) (Spitz et al. 2011). The limiting similarity principle proposes the existence of a similarity limit between coexisting competing species (Roughgarden 1976). Consequently, divergence in any of the three components of a foraging niche should reduce competition and thus facilitate species coexistence (Pianka 1974). However, in part due to sampling limitations, estimating niche overlap in three dimensions is an arduous task (Pianka 1974). As a result, foraging niche studies usually focus on trophic niche description and analysis, as observed in studies of different vertebrate taxonomic groups such as amphibians (e.g., Asrafuzzaman et al. 2018), fishes (e.g., Olivar et al. 2018), birds (e.g., Faria et al. 2018) and mammals (e.g., Temu et al. 2018).

The compression hypothesis proposes that species co-occurrence may limit the distribution of a given

species while also increasing or maintaining the prey types it consumes (Macarthur and Pianka 1966; Macarthur and Wilson 1967; Schoener et al. 1979; Perry and Pianka 1997). However, these authors have also pointed out that allopatric species would tend to differentiate not only in habitat use, but also in the prey types consumed, promoting greater species specialization and possibly smaller trophic niche overlap.

All animal diets are influenced by available food resources and foraging strategies (Spitz et al. 2011). The success of a species' foraging strategy, in turn, can be influenced by its physiological, morphological and behavioral limitations (Spitz et al. 2011). Additionally, foraging behavior is influenced by external factors (e.g. resource availability and predation risk), internal factors (e.g., age, sex, satiation level) and phylogenetics (e.g. set of conserved behaviors, morphological characteristics) (Perry and Pianka 1997). Thus, diets are the result of the evolutionary processes that shape an animal's characteristics (Spitz et al. 2011). Because resource partitioning may facilitate sympatric occurrence of species, interspecific competition is probably a major driver in the establishment of different foraging strategies among predators (Roughgarden 1976; Spitz et al. 2011).

Elasmobranchs are highly representative marine predator species. This group consists of 501 shark species (Ebert et al. 2013; Weigmann 2016) and 633 ray species (Last et al. 2016), which exhibit high diversity in foraging behaviors and prey capture mechanisms. These include physical attack, electric shocks, suction, and bites (Moss 1972; Frazzetta 1994; Motta and Wilga 2001; Motta 2004). Because they are all carnivores (with the one exception of the omnivore *Sphyrna tiburo*; Leigh et al. 2018), sharks and rays have limited prey breadth compared to other groups. Teleost fish, for example, include herbivorous and omnivorous species in addition to predators (Wetherbee and Cortés 2004). Still, elasmobranchs consume a great diversity of prey items, from microscopic organisms such as plankton to large marine mammals such as whales and seals (Wetherbee and Cortés 2004).

The South American Atlantic coast contains the highest concentration of threatened elasmobranch species and is a priority area for conservation (Dulvy et al. 2014). However, due to their high biodiversity in Brazil and other factors such as difficulties in data collection, the feeding ecology of many elasmobranch species remains poorly understood (Braga et al. 2012). Analysis of patterns in food resource use by sympatric species is also an aspect in their foraging ecology that remains poorly understood (Wetherbee and Cortés 2004).

Community distribution patterns can be analyzed using metrics of modularity and nestedness (e.g., Lomolino 1996; Ganzhorn 1998; Baselga 2010). More recently, these patterns have been explored using species interactions (e.g. Fortuna et al. 2010; Dalsgaard et al. 2013; Valverde et al. 2020), such as predator-prey (consumer-resource) interactions. In food webs, modularity occurs when different groups of species within a community share a certain prey range within a group, but have limited overlap with the prey consumed by other groups (Araujo et al. 2008). Conversely, nestedness in a food web occurs when the diets of specialist species represent a subset of diets of generalist species (Carvalho-Rocha et al. 2018). Therefore, these metrics help us understand the structure and underlying mechanisms of complex networks of species interactions, which is essential to better understanding how communities and ecosystems will respond to global change (Tylianakis et al. 2008; Fortuna et al. 2010).

In this study, we used meta-analysis to investigate both the use of prey items by elasmobranchs in southern Brazil, as well as the trophic niche partitioning and overlap between these species using modularity and nestedness metrics. Based on the compression hypothesis, we expected that species with similar habitat use would show high trophic niche overlap. Additionally, we expected species with different habitat use to have more differentiated diets and consequently low trophic niche overlap.

Material and methods

Study area

Southern Brazil is a region that comprises three states: Parana, Santa Catarina and Rio Grande do Sul, and the South Atlantic Ocean bathes its whole coast. Brazil's southern region is home to a shark and ray community with high richness and endemism (Lucifora et al. 2011; Dulvy et al. 2014), in addition to acting as a nursery area for several species (Mazzoleni 2006; Bornatowski 2008; Kotas et al. 2008; Bornatowski et al. 2011; Kotas et al. 2017).

Data collection

We compiled a list of sharks and rays species with records in southern Brazil through reading of publications with occurrence data and distribution (Gadig 2001; Soto 2001; Gomes et al. 2010; Bornatowski and Abilhoa 2012; Rosa and Gadig 2014). When in doubt, we checked available data on species' distribution at IUCN website (2018) and FishBase (Froese and Pauly 2018). After compilation, we obtained information about species' diet through articles search. Using as keywords each species' name, as well as the words "diet" and "feeding", we searched for publications with data on elasmobranchs' diet composition, obtained through stomach content analysis, in the databases: Scopus, Web of Science and Google Scholar. We selected only articles providing quantitative data (e.g. number, frequency and weight of food resources consumed), and included in the analysis only species that had more than 30 stomachs analyzed. At this stage, we evaluated studies carried out worldwide, not restricting the search spatially. However, in order to minimize the regional influence on species' diet, standardize data with different prey taxa resolution, and assist in the calculation of the standardized diet composition, prey items were grouped into 11 prey categories (adapted from Cortes 1999; Ebert and Bizzarro 2007) (Table 1).

Considering that we found more than one article per species which met the criteria mentioned above, we calculated a standardized diet composition index, proposed by Cortes (1999) and applied by Ebert and Bizzarro (2007). This index is based on relative sample size, determines the proportion of each prey category in the species' diet, and is calculated using the formula:

$$\mathrm{P}jk = \sum_{i=1}^{\mathrm{n}} \frac{Pij*Ni}{\sum_{j=1}^{m} *\sum_{i=1}^{n} (Pij*Ni)}$$

where, Pij is the proportion of prey category j obtained from source i for species k;

Ni is the number of stomach samples from species k containing food that were used to calculate Pij from source i; n is the number of sources; m is the total number of prey categories.

Thus, the sum of Pjk equals 1. According to Ebert and Bizzarro (2007), we used the following hierarchical criteria to obtain each prey category's proportion (Pij) for each k species: when available, the Standardized Index of Relative Importance (IRI%) or the Alimentary Index (IAi%). When these composite indices weren't available, or more than one simple index has been used to describe the diet (e.g., relative biomass (RB%) and relative frequency (RF%)), we calculated a geometric importance index by obtaining the average of these, as suggested by Assis (1996) (e.g., (RF% + RB%) / 2); if only a simple index was available, we used it. When the frequency of occurrence, an index of non-additive proportions, was the only data available, we standardized it in order to equalize each index's contribution to the diet composition. The formula for calculating frequency of occurrence and the formula used to standardize its values were, respectively:

$$FO\% = \left(\frac{n}{N}\right)*100$$

where n = number of stomachs in which the food item occurred; N = total number of analysed stomachs.

$$F\% = ((FOi\%*100)/(FOt\%))$$

Where $FOi\%$ is the food item's occurrence percentage; $FOt\%$ is the sum of all food items' occurrence percentage.

Our analysis did not consider unidentified organic matter and accidentally ingested materials such as sediment, debris and plant matter. Likewise, we did not consider items consumed with low frequency, possibly accidentally. We identified these items as those that had a numerical contribution of less than 0.01%. This value also aimed to avoid the disposal of prey consumed intentionally, even if at low frequency. Finally, species' classification regarding their habitat use was determined according to the classification provided by FishBase (Froese and Pauly 2018).

Table 1 Determined prey categories

FISH	Teleost fishes
CHON	Chondrichthyan fishes (sharks, skates, rays, and chimaerids)
BIR	Seabirds
REP	Marine reptiles (sea turtles)
MAM	Marine mammals (cetaceans, pinnipeds, mustelids)
CEPH	Cephalopods (squids, octopuses)
MOL	Molluscs (excluding cephalopods) and unidentified molluscs
CRU	Decapod crustaceans (shrimps, crabs, prawns, lobsters)
OCRUST	Other non-decapod crustaceans and unidentified crustaceans
POLY	Polychaetes and other marine worms
INV	Other invertebrates

Following this classification, we attributed species to six different environments (demersal, reef associated, pelagic-oceanic, bathypelagic, bathydemersal or benthopelagic). Considering the occurring species in southern Brazil, we categorized them as sympatric when presenting similar habitat use, and those that differed in this aspect as allopatric. Even though we are aware that some species can possibly use more than one habitat, we classified them according to their main one, detailed in FishBase (Froese and Pauly 2018). We emphasize that throughout the text, mentions to habitat use by the analyzed species refer to this classification.

Data analysis

We examined trophic niche overlap between species through network analysis proposed by Araujo et al. (2008). For this, we built a unipartite network, in which nodes represent species and edges connecting them represent diet overlap. Thus, species that eat items of the same prey category are connected by an edge. The thickness of the edge connecting two species represents the degree of trophic niche overlap, which is calculated using the W*ij* index:

$$\mathrm{W}ij = 1 - 0.5 \sum_{k=1}^{k} |\mathrm{P}ik - \mathrm{P}jk|$$

where P*ik* is the frequency of prey category *k* in individual *i*'s diet; P*jk* is the frequency of prey category *k* in individual *j*'s diet.

This formula was adapted from Schoener (1968) by Araujo et al. (2008). The Wij index ranges from 0 to 1, with 0 indicating no diet overlap and 1 indicating total overlap. Thus, species with a higher degree of trophic niche overlap will be connected by thicker edges than those with low overlap. We performed the calculations of Wij values in DIETA1 program (Araujo et al. 2008).

Using the unipartite network, we tested the degree of elasmobranchs' dietary specialization using the E index (Araujo et al. 2008). This index is based on the average density of connections between species in the network, being calculated through the equation:

$$E = 1 - \overline{O}$$

where $\overline{O}$ is the average network density of connections, calculated through the following formula:

$$O = \left(\sum Wij\right) / (n(n-1)/2)\Big).$$

where $\sum Wij$ is the total sum of pairwise overlap in the individual niche overlap network;

(n(n-1)/2) is the number of edges of a completely connected network with *n* individuals.

The E index ranges from 0 to 1, with 0 representing no variation in diet between species and 1 representing total variation (Araujo et al. 2008). We performed the E-value significance test using a bootstrap resampling procedure, with 10.000 iterations. The null hypothesis of no diet specialization in the community can be rejected when the observed E value (E_{obs}) is greater than 95% of the E values generated by resampling (E_{boot}). The adjusted E index (E_{adj}), which is the E_{boot} values average, is used to balance stochasticity of samples for diet analysis (e.g., Carvalho-Rocha et al. 2018). Thus, we used the E_{adj} value as a metric for diet specialization degree observed in the community. We performed the calculation and significance test of the E index in R program (R Core Team 2017), using RInSp package (Zaccarelli et al. 2013).

To assess the pattern of prey category consumed by elasmobranchs, we created a bipartite consumer-prey network, in which lines of the matrix represent species while columns represent prey categories, featuring two distinct classes of elements that interact exclusively with each other and not between the classes itself. Thus, the edges connecting elements of different classes represent the consumption of a prey category by a determined species.

Aiming to quantify the bipartite network's modularity, we used the Q_B index proposed by Barber (2007), utilizing the simulated annealing algorithm (Guimerà and Amaral 2005), in order to maximize the Q value. The calculation of Q_B is given through the formula:

$$Q_B = \sum_{i=1}^{NM} \left[\frac{Ei}{E} - \left(\frac{KiC * KiR}{E^2} \right) \right]$$

where N_M is the number of modules; *Ei* is the number of edges in module *i*; *E* is the total number of edges in the network; Ki^C is the total number of edges of the species within module *i* that belongs to class C (consumers); Ki^R is the total number of species links within module *i* that belongs to class R (resources).

To quantify nestedness among species' diets, we used the NODF metric, which utilizes only presence-absence data (Almeida-Neto et al. 2008). This index can range from 0 (no nesting) to 100 (fully nested). To test Q and NODF values' significance, we used a null

probabilistic model that exchanges the presence of prey items consumption by elasmobranchs in bipartite networks, using the lines sum (number of food categories consumed by a species) and the columns (number of species that consumed a certain food category) (null model 2; Bascompte et al. 2003). We used 1000 replications for each metric, creating a theoretical distribution of Q and NODF values. Empirical values were considered significant if they fell outside the 95% confidence interval of the theoretical distributions generated by the null model. We performed both calculation and test of Q significance in the MODULAR program (Marquitti et al. 2014), and performed the calculation and NODF's significance test index in the R program (R Core Team 2017), using the vegan (Oksanen et al. 2015) and igraph (Csardi and Nepusz 2006) packages.

Intending to verify if diet composition between species with different habitat use differed, we performed 10 PERMANOVAS, testing all combinations between environments, pair by pair. The bathypelagic environment was excluded of this analysis, since only one species was classified with this habitat use (*Isistius brasiliensis*). We used Bray-Curtis dissimilarity index for the analysis, considering a level of significance of 0.05. We performed PERMANOVAS analyzes in the R program (R Core Team 2017), using the vegan package (Oksanen et al. 2015). We designed the bipartite network of species-prey interaction and the unipartite network of species-species interaction in the PAJEK 28 program (http://vlado.fmf.uni-lj.si/pub/networks/pajek/). The bipartite matrix of species-prey category was built in the R program (R CORE TEAM 2017) using the bipartite package (Dormann et al. 2008).

Results

We found 103 species of elasmobranchs (65 sharks and 38 rays) in southern Brazil (Online Resource 1). However, only 58 species (39 sharks and 19 rays) had sufficient diet composition data to be analyzed according our criteria (Table 2). To calculate the standardized diet composition index for each species, we analyzed a total of 99 scientific papers, 1 thesis and 1 book chapter (Online Resource 1).

On the whole-community level, the most consumed prey category was teleost fishes (48.51%). This was followed to smaller degrees by decapod crustaceans (19.54%), cephalopod molluscs (11.88%), other crustaceans (5.29%), polychaetes and other marine worms (5.20%), other molluscs (3.13%), condrichthyes (3.11%), marine mammals (1.87%), other invertebrates (0.94%), marine reptiles (0.31%) and seabirds (0.22%). For sharks only, the most consumed prey category was also teleost fishes (61.44%), followed by cephalopod molluscs (16.81%), decapod crustaceans (10.46%), condrichthyes (4.60%), marine mammals (2.52%), other crustaceans (1.54%), other invertebrates (0.97%), polychaetes and other marine worms (0.63%), marine reptiles (0.40%), other molluscs (0.35%) and seabirds (0.29%). For rays only, teleost fishes (41%) were still the most consumed prey category, followed by decapod crustaceans (37.10%), polychaetes and other marine worms (13.02%), other crustaceans (11.82%), other molluscs (7.89%), cephalopod molluscs (3.63%), other invertebrates (0.82%) and condrichthyes (0,32%). No records were found of ray predation on marine mammals, marine reptiles, or seabirds. The proportion of each category in the analyzed species diets are shown in Fig. 1, and detailed in Online Resource 1.

Collectively, the 58 analyzed species had a middling level of average trophic niche overlap, considering the index extremes ($(W\overline{ij}) = 0.40 \pm 0.29$) (Fig. 2). The average edge density of the unipartite network of niche overlap between species was smaller than expected by random chance ($E = 0.67$; $E_{boot} = 0.28$; $p < 0.001$), suggesting diet specialization. However, this specialization appears moderate when considering the adjusted index value derived from bootstrap resampling ($E_{adj} = 0.54$; i.e., species share 46% of their diets).

The modularity of the elasmobranch species bipartite network was low and marginally significant ($Q\overline{B} = 0.204$; $CI_{null} = 0.163–0.201$). Conversely, nestedness was higher than expected by random chance within the food category presence-absence bipartite network (NODF = 70,14; $CI_{null} = 51,11–59,86$; Fig. 3).

PERMANOVA analysis indicated a significant difference in demersal species diets when compared to those of reef-associated, pelagic-oceanic and benthopelagic species (Table 3). Comparisons between elasmobranchs diets across all other habitats were not significantly different (Table 3). Species habitat classification according to FishBase (Froese and Pauly 2018) is found in Supplementary Material A1.

Table 2 Alphabetized list of species with diet data for analysis. N = number of articles examined and Ns = total number of stomachs with prey items observed across the articles. Available data on prey items in the diets included relative abundance, frequency, and weight (N%, F%, and W%, respectively), a Standardized Index of Relative Importance (IRI%), and the alimentary index (IAi%). Superscripts represent the articles referenced (Appendix 2)

Species	N	Ns	Data
Alopias superciliosus	2	151	IRI%[50,51]
Alopias vulpinus	1	107	N%[52], W%[52]
Atlantoraja castelnaui	1	255	IRI%[12]
Atlantoraja cyclophora	2	392	IRI%[13], IAi%[14]
Atlantoraja platana	2	834	N%[15], W%[15], IRI%[16]
Bathyraja brachyurops	2	463	IRI%[17], N%[18]
Carcharhinus brachyurus	2	296	N%[69,70], W%[69,70]
Carcharhinus brevipinna	2	87	F%[68], IRI%[72]
Carcharhinus falciformes	1	443	N%[71], W%[71]
Carcharhinus isodon	2	75	IRI%[72], F%[73]
Carcharhinus leucas	2	92	F%[74,75]
Carcharhinus limbatus	3	374	IRI%[72,76], F%[77]
Carcharhinus obscurus	3	1455	IRI%[48], N%[69], W%[69], F%[78]
Carcharhinus plumbeus	3	627	IRI%[79,80], F%[81]
Carcharhinus porosus	1	171	F%[82]
Carcharhinus signatus	1	215	N%[83], W%[83]
Carcharias taurus	2	142	IRI%[48], N%[49]
Carcharodon carcharias	1	225	IRI%[53]
Deania profundorum	1	43	N%[34], W%[34], F%[34]
Discopyge tschudii	2	266	IRI%[8,9]
Echinorhinus brucus	1	113	IRI%[33]
Etmopterus granulosus	1	53	N%[34], W%[34], F%[34]
Etmopterus lucifer	1	67	F%[44]
Galeocerdo cuvier	3	312	F%[84,86], IRI%[85]
Galeorhinus galeus	2	352	IRI%[63,64]
Ginglymostoma cirratum	1	41	N%[47]
Heptranchias perlo	1	88	IRI%[58]
Hexanchus griseus	1	96	N%[59], W%[59], F%[59]
Isistius brasiliensis	1	42	F%[45]
Isurus oxyrinchus	3	705	IRI%[54,56], N%[55]
Lamna nasus	1	501	W%[57]
Mustelus canis	2	475	IRI%[48,65]
Mustelus schmitti	2	924	IRI%[66], N%[67], W%[67]
Myliobatis goodei	2	151	IRI%[29,30]
Myliobatis ridens	1	48	IRI%[29]
Narcine brasiliensis	2	155	IAi%[10], IRI%[11]
Notorynchus cepedianus	2	248	IRI%[60,61]
Prionace glauca	4	1409	IRI%[90], N%[88,89], W%[89], F%[87]
Psammobatis bergi	1	130	IRI%[19]
Psammobatis extenta	2	693	IRI%[20, 21]
Pseudobatos horkelii	1	30	N%[1]
Pseudobatos percellens	4	343	N%[2], W%[2], IRI%[3,4], IAi%[5]

Table 2 (continued)

Species	N	Ns	Data
Pteroplatytrygon violacea	2	186	IRI%[27], N%[28], W%[28]
Rhinoptera bonasus	2	105	IRI%[31], N%[32], W%[32]
Rhizoprionodon lalandii	3	218	IRI%[91,92], N%[93]
Rhizoprionodon porosus	1	187	IRI%[94]
Rioraja agassizii	3	1223	IRI%[20,22,23]
Schroederichthys bivius	2	1226	N%[36], W%[62]
Sphyrna lewini	5	1268	IRI%[95,96,97,98,99]
Sphyrna zygaena	3	191	IRI%[101],IAi%[100],N%[69], W%[69]
Squalus acanthias	3	9707	F%[35], N%[36], IRI%[37]
Squalus blainville	3	653	N%[41,43], W%[41,42]
Squalus megalops	4	701	IRI%[38,40],N%[34,39],W%[34], F%[34]
Squatina guggenheim	1	556	N%[46], F%[46]
Sympterygia acuta	1	301	IRI%[25]
Sympterygia bonapartii	1	1024	IRI%[24]
Zapteryx brevirostris	3	399	IRI%[4,6], IAi%[7]
Zearaja chilensis	1	671	IRI%[26]

Discussion

Our study suggests high trophic niche overlap among elasmobranch species in southern Brazil. This pattern was evident regardless of habitat use, refuting our hypotheses. Similarly high levels of trophic niche overlap were found in a study of five shark and ray species within the same habitat on the south coast of Rio de Janeiro, Brazil (Viana et al. 2017). However, another study found low diet overlap among sympatric shark species, while species with different distributions showed high overlap (Papastamatiou et al. 2006). The broad lack of research on higher diversities of shark and ray species taken together greatly diminishes the comparison of such results, as analyses based on only a few species cannot reflect the full complexity of trophic relationships within an elasmobranch community.

Additionally, elasmobranch species in southern Brazil had low diet modularity, suggesting there are no groupings whereby some collection of species preferentially consumes items from the same prey category, and shows little overlap with other groups (Araujo et al. 2008). However, we observed a highly nested diet pattern in the community, in which the prey categories consumed by species that are more specialized represented a subset of the prey consumed by more generalist species. Such patterns of nestedness have also been observed in intrapopulation diet studies of sharks (e.g., Abrantes and Barnett 2011; Matich et al. 2011) and other vertebrates groups (e.g., Araújo et al. 2010; Cantor et al. 2013; Carvalho-Rocha et al. 2018), and in marine, terrestrial, and lake communities (Kondoh et al. 2010).

The compression hypothesis suggests that sympatric predators tend to have high trophic niche overlap, since a high diversity of predator species tends to maintain or increase the diversity of items consumed as prey (Macarthur and Pianka 1966; Macarthur and Wilson 1967; Schoener et al. 1979; Perry and Pianka 1997). On the other hand, for allopatric predators, the hypothesis indicates that there should be less diet overlap, as these animals tend to specialize in different prey types (Macarthur and Pianka 1966; Macarthur and Wilson 1967; Schoener et al. 1979; Perry and Pianka 1997). Our results indicate that some species groups with different habitat use did differ in terms of diet composition. However, diet variation explained only 9 to 13% of this variation. In fact, when we analyzed the elasmobranch trophic overlap network, we found that there was no formation of species groups that had high diet overlap among themselves and low overlap with others, regardless of habitat use classification. There are many possible reasons for this result. First, there are four dimensions for food resource partitioning among predators: microhabitat (e.g., depth and substrate occurrence),

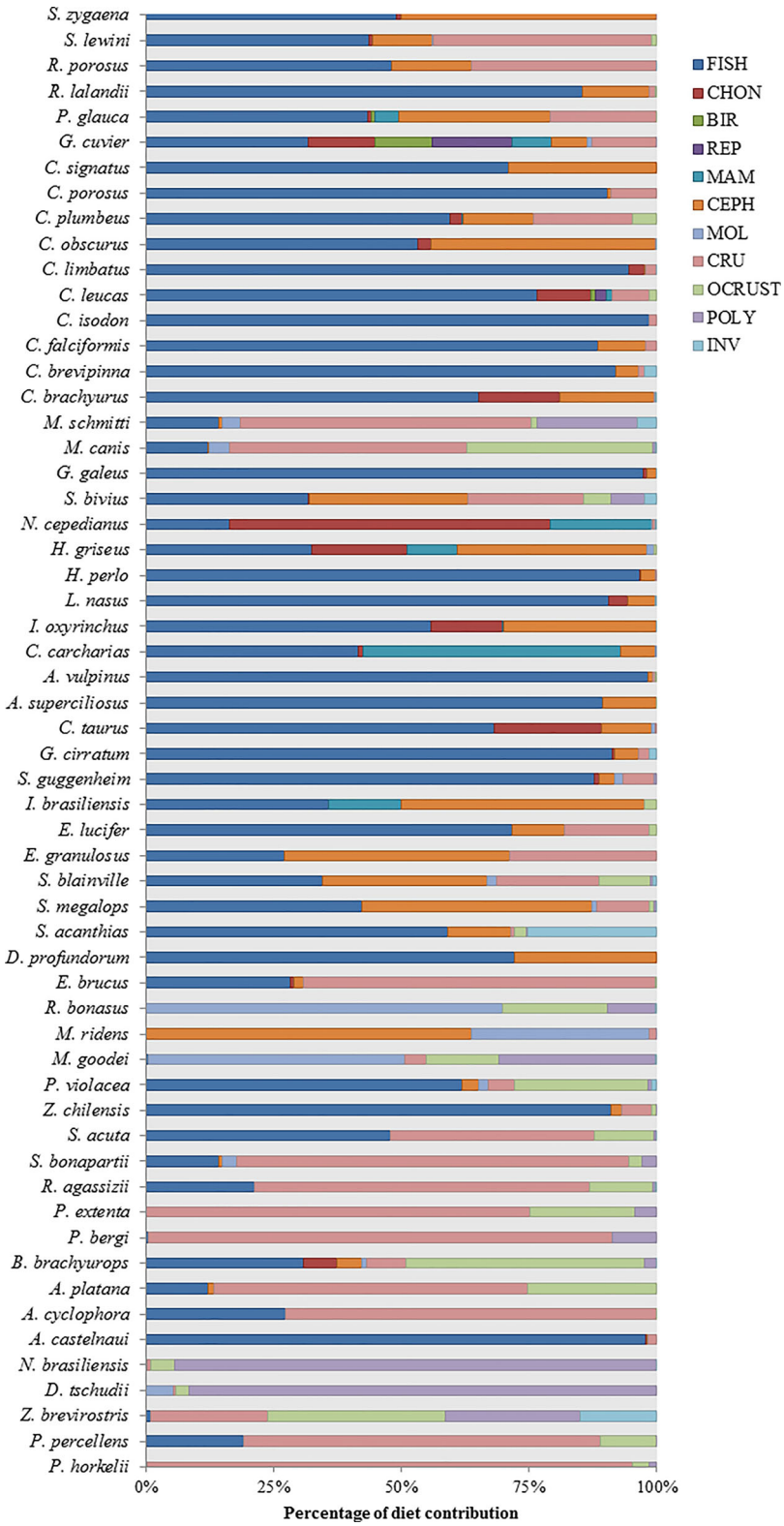

Fig. 1 Prey category's proportion in the diet of the elasmobranch species analyzed. FISH: teleost fishes; CHON: chondrichthyan fishes (sharks, skates, rays, and chimaerids); BIR: seabirds; REP: marine reptiles; MAM: marine mammals; CEPH: cephalopods; MOL: molluscs (excluding cephalopods) and unidentified molluscs; CRU: decapod crustaceans; OCRUST: other non-decapod crustaceans and unidentified crustaceans; POLY: polychaetes and other marine worms; INV: other invertebrates

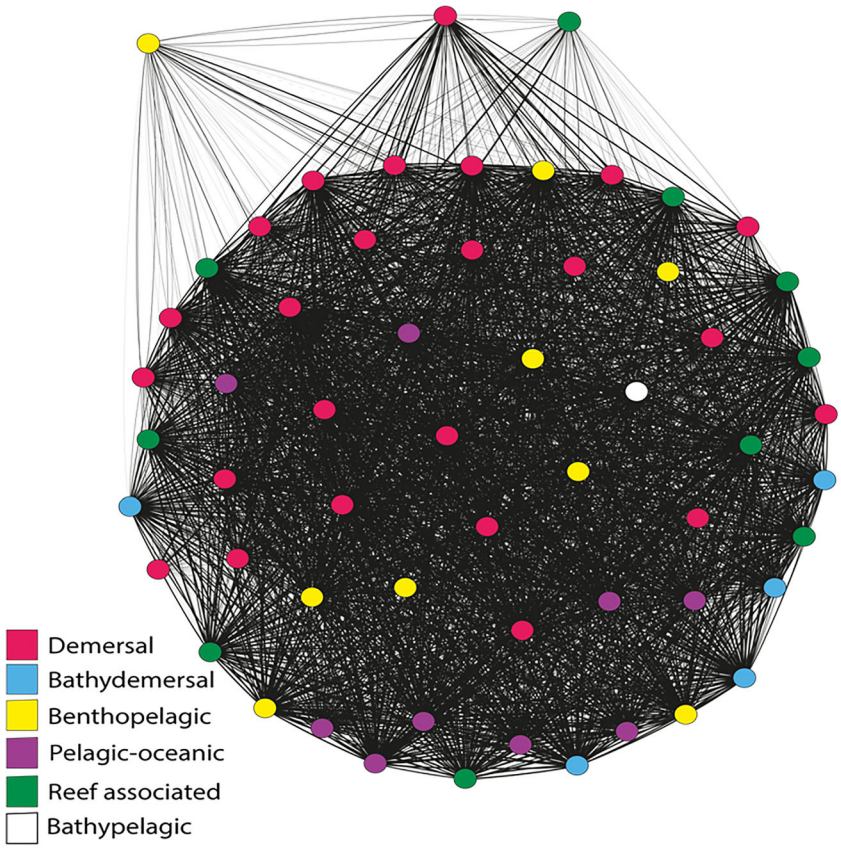

Fig. 2 Network representation of quantitative interaction between shark and rays species. Nodes represent each of the 58 species and the thickness of the edges represents. The degree of trophic niche overlap between species. Colors represent species' habitat use according to FishBase classification (Froese and Pauly 2018).

structural habitat (environment type; e.g., reef), prey taxa, and prey size (Schoener et al. 1979). We analyzed niche partitioning and overlap with respect to only two of these dimensions (structural habitat and prey taxa), and it is possible that sharks and rays are differentiating in the other microhabitat and prey size dimensions. Future studies may yield further insight into this possibility. Finally, it is important to note that our study, by virtue of using meta-analysis, was forced to group prey taxa into broader categories. Diet differentiation nuances within a given category may thus have been obscured.

The abundance of food resources in the environment is another factor that directly influences competition between species as well as diet composition (Heithaus 2004; Martinho et al. 2012; Bornatowski et al. 2014a, b). The compression hypothesis is based on the premise that all environments occupied by sympatric species have the same limiting resources (Schoener et al. 1979; Perry and Pianka 1997). However, when prey is abundant, competition ceases to occur (Bornatowski et al. 2014a, b), and species can meet their energy requirements without being subject to spatial or trophic limitations. In our study, we saw that the most consumed prey category was teleost fishes (49.97%). This was the category in which the highest number of species was grouped, but this result nonetheless suggests that this grouping could be the overall most abundant resource in the area. Additionally, elasmobranchs are highly mobile fish (Simpfendorfer and Heupel 2004) and are active predators. Due to their motility, they may have small areas of spatial overlap even between species with the same habitat use. This explanation has been used previously for other vertebrates; for example, Dickman (1986) invoked species mobility as one of the reasons why he couldn't find the expected food resource use pattern in his study of marsupials from Australia.

The modularity in shark and rays species diets was low and marginally significant. This suggests the absence of species groups that share similar prey within a group but not across groups and points to the presence of opportunistic species in the community (Araujo et al. 2008). In fact, when observing the unipartite network of species trophic niche overlap and the bipartite network

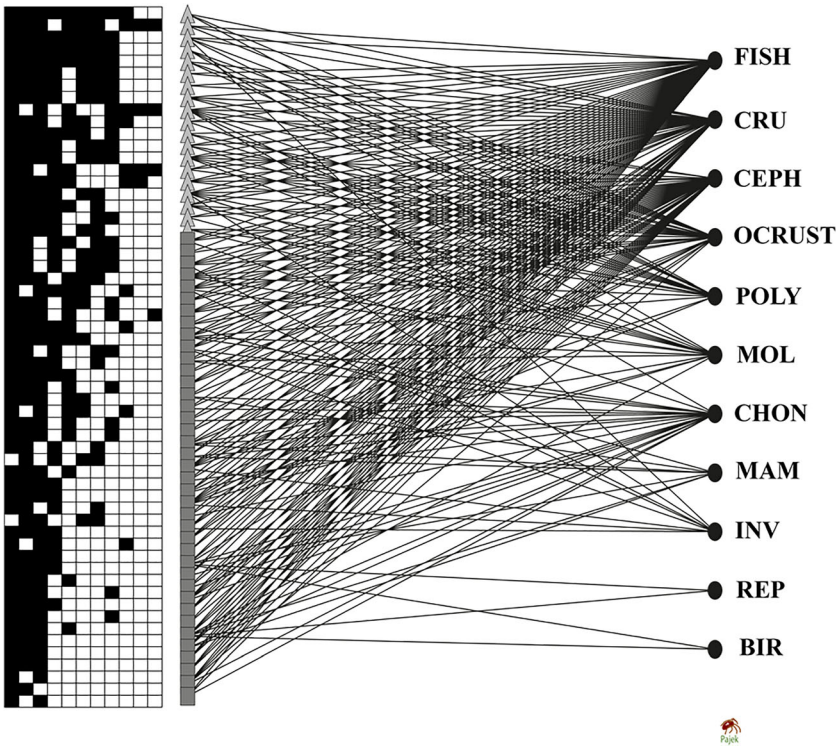

Fig. 3 Matrix and network of qualitative interaction between species and prey categories in graphic representation. In the matrix, lines represent species, while columns represent prey categories and black cells indicate the consumption of a given category by a given species. In the network, dark triangles represent shark species, light squares represent rays species, the black circles represent the prey categories and connecting lines represent the consumption of a category by a species. The order of the prey categories in the matrix is the same represented in the interaction network. FISH: teleost fishes; CHON: chondrichthyan fishes (sharks, skates, rays, and chimaerids); BIR: seabirds; REP: marine reptiles; MAM: marine mammals; CEPH: cephalopods; MOL: molluscs (excluding cephalopods) and unidentified molluscs; CRU: decapod crustaceans; OCRUST: other non-decapod crustaceans and unidentified crustaceans; POLY: polychaetes and other marine worms; INV: other invertebrates

of the consumption of prey categories by species, both point to a non-modular pattern. On the other hand, the bipartite matrix of species prey consumption showed a nested pattern. This indicates that sharks and rays with more specialized diets consumed a subset of the food resources used by more generalist ones. Nested patterns have already been observed in several food chains across a great range of habitats, suggesting their presence in groups with antagonistic interactions (e.g. predator-prey) is more common than previously theorized (Kondoh et al. 2010).

Table 3 PERMANOVA results on differences in diet composition between elasmobranch species with different habitat use according to FishBase (Froese and Pauly 2018)

Habitat	F	R^2	*P*
Demersal vs Reef associated	5.62	0.15	**< 0.01**
Demersal vs Bathydemersal	2.00	0.69	0.13
Demersal vs Pelagic-oceanic	5.44	0.15	**< 0.01**
Demersal vs Benthopelagic	3.03	0.09	**0.03**
Reef associated vs Bathydemersal	1.47	0.10	0.18
Reef associated vs Pelagic-oceanic	0.78	0.04	0.65
Reef associated vs Benthopelagic	1.71	0.09	0.14
Bathydemersal vs Pelagic-oceanic	1.02	0.08	0.36
Bathydemersal vs Benthopelagic	1.13	0.09	0.38
Pelagic-oceanic vs Benthopelagic	1.85	0.10	0.18

Interactions between species with different body sizes have already been identified as a factor that influences the nestedness of diet patterns in trophic webs (Woodward et al. 2005; Nordstrom et al. 2015). In fact, Nordstrom et al. (2015) observed that as the predator body size was positively correlated with more generalist consumption of a wider range of prey items. This phenomenon has been observed not only in marine environments but also in terrestrial and lake ecosystems (Digel et al. 2011). Meanwhile, smaller predators had

more specialized diets (Nordstrom et al. 2015), which agrees with Yvon-Durocher et al. (2008) who note that smaller species tend to have a less diverse diet and hunt prey of smaller size and weight. We found only partial support for these hypotheses in our study. We observed that some large species did consume a greater variety of prey categories (e.g., *Galeocerdo cuvier*, *Isurus oxyrinchus*, *Carcharodon carcharias*), but smaller species also consumed a high diversity of food resources (e.g., Squalus sp. from the megalops group, *Rioraja agassizii*, *Psammobatis bergi*). Our results may be biased, however, as a result of the meta-analysis approach that necessarily grouped all prey into broader categories and only took into account the presence or absence of prey categories. In fact, body size has already been identified as a factor influencing the diet structure of elasmobranchs, and ontogenetic changes in diet have been observed for several sharks (e.g., Preti et al. 2012; Bornatowski et al. 2014a) and rays (e.g., Brickle et al. 2003; Barbini and Lucifora 2011; Spath et al. 2013). This variation may be related to changes in energy demand, greater experience in prey capture, and an increase in jaw size as an animal grows, as well as habitat use change and decreased vulnerability to predators (Wetherbee and Cortés 2004; Lucifora et al. 2009; Bornatowski et al. 2014a, b). In short, the interaction between species with different body sizes may be the driving factor underlying the nested pattern of food resources use.

Nested patterns in trophic network consumer-resource interactions increase diet overlap among consumers (Kondoh et al. 2010). The principle of limiting similarity suggests that high niche overlap between species decreases their chances for coexistence (Macarthur and Levins 1967; Roughgarden 1976). Nestedness is therefore expected to negatively influence the stability of antagonistic trophic interaction systems (Kondoh et al. 2010; Thébault and Fontaine 2010) and to interfere with community function (e.g., by reducing secondary production within an ecosystem; Poisot et al. 2013). However, the presence of nested structures in several biological communities suggests that different compensatory mechanisms may exist to limit possible negative effects on species coexistence and allow community persistence (Kondoh et al. 2010). For example, the temporal partitioning of resources shared by consumers can increase energy transfer in the community (Nordstrom et al. 2010), and other partitioning may arise from interactions and species not explicitly described in the bipartite consumer-resource trophic network (Kondoh et al. 2010). For example density controls on populations of competing elasmobranch species by a given predator could reduce the negative effects of species coexistence.

Spatiotemporal differentiation in elasmobranch alimentary niches has already been observed in different studies (e.g. Papastamatiou et al. 2006; Kubodera et al. 2007; Martinho et al. 2012). Nonetheless, the patterns underlying nestedness and compensatory mechanisms for trophic web stability may vary depending on the distribution of prey (Kondoh et al. 2010). Thus, we must research not only diet, but also the temporal and spatial patterns of prey abundance and food consumption to fully elucidate the pattern-forming processes of foraging niches within a community.

Conclusions

Our study revealed both a large trophic niche overlap between co-occurring shark and ray species in southern Brazil as well as a nested diet pattern. This suggests that more specialized species consumed a subset of prey consumed by more generalist species. However, this work has limitations due to prey items generalization in broader categories, and the data reduction process required for meta-analysis. Documentation of such food resource use patterns for a community composed exclusively of elasmobranchs, brings new and important information about the feeding habitats of these animals. Despite the high extinction pressure on many elasmobranch species, there is still a great knowledge gap about basic aspects of their diet. Therefore, we highlight the need to carry out more detailed studies concerning the feeding ecology of sharks and rays, especially at a local level.

Information on the spatiotemporal patterns of food resource use can also help our general understanding of how these species interact in the environment, and allow investigation of processes that may have shaped the current structure of resource use. Increased levels of taxonomic and biometric detail on the prey items analyzed in diet studies will also enable more nuanced analysis of trophic niche partitioning in the dimensions of prey taxonomy and size. In addition, research covering a greater number of species may yield better comprehension of the patterns of food resource use by elasmobranch communities. Provision of such

information concerning resource partitioning, habitat use, prey selection, risk effects, competition, and energy transfer can then assist in management measures and decision making for species conservation.

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Declarations

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