PRIMARY RESEARCH PAPER

Dietary and niche analyses of four sympatric batoid species of the subtropical South Atlantic Ocean

Liliam de Lima Lemos⬤ · Hugo Bornatowski⬤ ·
Renato Hajenius Aché de Freitas⬤

Abstract We aimed to characterize the trophic ecology and test the hypothesis of niche overlap between four sympatric batoid species of the subtropical South Atlantic. Data were collected between 2017 and 2022 from two artisanal fishery communities in southern Brazil. Batoid's stomach contents were identified, separated into categories, and weighed. We calculated the Levins, Pianka's, and Prey-specific index of relative dietary importance (PSIRI) and performed a similarity test using PERMANOVA and the similarity percentage (SIMPER) for niche analysis. We analyzed 229 stomachs of four batoid species, 187 containing foods. All species showed a narrow food niche. The most important diet items for each species were *Leptochaela serratorbita* and Onuphidae for *Dasyatis hypostigma*; Nematoda for *Pseudobatos horkelii*; *L. serratorbita*, *Sicyonia dorsalis* and Portunidae for *Rioraja agassizii* and *Achelous spinicarpus* and fish for *Sympterygia bonapartii*. The analyses showed dissimilarity among the species' diets without significant niche overlap. Our results detected the absence of significant niche overlap among batoid species, suggesting other types of niche partitioning and spatiotemporal habitat variation. This information could be considered for local management plans.

Keywords Elasmobranch · Trophic ecology · Diet · Ray · Partitioning

Introduction

Elasmobranchs show various morphological body types and occupy many distinct marine and freshwater habitats (Wetherbee et al., 2012). Elasmobranch's main diet consists of fish, crustaceans, mollusks, and polychaetes (Wetherbee et al., 2012; Belleggia et al., 2019). Their feeding is highly diverse, ranging from planktonic species to whales (Budker, 1971; Wetherbee et al., 2012). Information on elasmobranch feeding preferences helps us better understand their ecology, community structure, morphological and functional adaptations, ontogeny, and niche partitioning (Aguiar & Valentin, 2010; Bornatowski et al., 2014a; Belleggia et al., 2019; Rupp & Bornatowski, 2021). Brazil has approximately 203 described elasmobranch species, where 104 are batoids (dorsoventrally flattened elasmobranchs) (Rosa & Gadig, 2014; Gadig & Rosa, 2023). Batoids are commonly caught

L. de Lima Lemos (✉) · R. Hajenius Aché de Freitas
Laboratório de Biologia de Teleósteos e Elasmobrânquios (LABITEL), Departamento de Ecologia e Zoologia - ECZ, Centro de Ciências Biológicas - CCB, Universidade Federal de Santa Catarina, Roberto Sampaio Gonzaga, s/n, Trindade, Florianópolis, Santa Catarina, Brazil
e-mail: lilihlemos@yahoo.com.br

H. Bornatowski
Centro de Estudos do Mar, Universidade Federal do Paraná, Avenida Beira Mar S/N, Pontal do Sul, Pontal do Paraná, Paraná, Brazil

by artisanal fisheries, especially neonates and juveniles. However, these data are neglected in Brazil. The Santa Catarina state is the leading provider of elasmobranchs in the country (Paiva, 1997; Bornatowski et al., 2011, 2018a; Gallardo et al., 2021). Brazil's environmental protection agency, Ibama, seized 27.6 tons of shark fins (10,000 specimens estimated) for illegal exportation in Santa Catarina, representing the world's largest-ever recorded seizure of shark fins (Ibama, 2023).

Several factors can influence batoid diet composition and foraging habits, such as season, animal size, and dimensions of unique morphological characters (e.g. cranial structure, nose size and form, mouth muscles) (Aguiar & Valentin, 2010; Rezende et al., 2015; Barbini & Lucifora, 2016; Barbini et al., 2018). Morphological variations in skull and teeth can reflect different prey capture strategies and diet specializations (Aguiar & Valentin, 2010; Rezende et al., 2015). Dietary preference and overlap between species (feeding overlap) are essential elements that influence community structure and individual fundamental niches (Krebs, 1999). Phylogenetically close species tend to overlap resources and become potential competitors (Pianka, 1973; Bethea et al., 2006; Heupel et al., 2007; Heithaus et al., 2013). Measuring how species overlay food resources is relevant to analyzing trophic niche width and overlap. On the other hand, niche overlap does not necessarily mean species competition if available resources are abundant or irrelevant for one species (Colwell & Futuyma, 1971).

Artisanal and commercial fishing compromise the life strategy for many elasmobranch species, driving demographic decline (Stevens et al., 2000). Some batoid species use specific coastal areas as nurseries, and female batoids temporarily migrate to coastal areas during reproductive periods (Martins et al., 2018). Batoid younglings remain in these areas because coastal areas usually offer abundant food resources and security against predators (Yokota & Lessa, 2006; Heithaus, 2007; Araújo et al., 2016). Fishing activities, mostly artisanal fishing, remove young individuals from coastal areas, directly affecting the maintenance and recruitment of the batoid population (Stevens et al., 2000; Costa & Chaves, 2006; Martins et al., 2018). Elasmobranchs bycatch fishery can lead species to extinction and impoverishment of marine ecosystems (Ferretti et al., 2010; Dale

et al., 2011; Croll et al., 2012; Pennino et al., 2013; Bornatowski et al., 2014a; Rupp & Bornatowski, 2021). The lack of information about several batoid species, especially about dietary, adds to threats such as fishing, pollution, and natural habitat destruction and places the majority of elasmobranch species as threatened for extinction (Davidson and Dulvy, 2017; Derrick et al., 2020; MMA, 2022).

The elasmobranch's importance for the structure and balance of aquatic trophic food webs emphasized the urgency to understand their feeding ecology. Diet studies are a relevant basis for constructing ecotrophic models (using the Ecopath software) to formulate hypotheses on fisheries management and make inferences about biomass declines (e.g. Bornatowski et al., 2018b; Rupp & Bornatowski, 2021). Urgency is even more imminent when we consider the lack of data and current threats of extinction. Knowledge of the elasmobranch diet can improve sustainable fishing, including managing and conserving elasmobranch populations. Since batoid species are usually sympatric bottom mesopredators and tend to consume similar resources, the knowledge about sympatric species diets is relevant to understanding trophic niche information and their ecological importance. The diet information can provide new ecological information about sympatric threatened species. This study aimed to characterize the trophic niche and to test the hypothesis of niche overlap among four sympatric batoid species using stomach content analysis in a popular tourist destination in the South of Brazil.

Material and methods

Data collection

Four sympatric batoid species from the subtropical South Atlantic Ocean were collected in two artisanal fisheries communities in coastal Southern Brazil (27° 22' S, 48° 20' W, Fig. 1). The species collected and their IUCN's category of threatened of extinction are *Dasyatis hypostigma* Santos & Carvalho, 2004—EN, *Pseudobatos horkelii* (Müller & Henle, 1841)—CR, *Rioraja agassizii* (Müller & Henle, 1841)—VU and *Sympterygia bonapartii* Müller & Henle, 1841—NT (IUCN, 2020). Samples were collected on 12 samples occasions, in an opportunistic form, through the contact of the fisheries, in the following years: 2017

Fig. 1 Map representing the two sample points in the study area on the south coast of Brazil, from which the four sympatric batoid species (*Dasyatis hypostigma*, *Pseudobatos horkelii*, *Rioraja agassizii*, and *Sympterygia bonapartii*) were collected
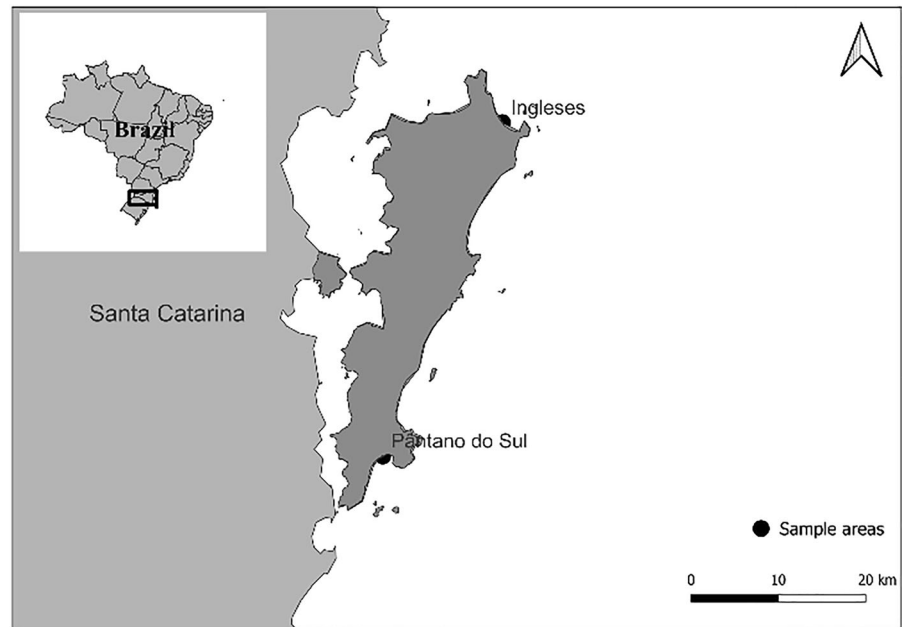
(August, September, and December), 2018 (May), 2019 (March, August and October), 2020 (February and November), 2021 (January), and 2022 (January and February). The samples were grouped into two seasons: warm (October to March) and cold (May to September). The biometric data (total length—TL, disk width—DW, weight, sex, maturation stage) were recorded for all batoid specimens. Stomachs were removed, fixed in 10% formalin, and sorted in the laboratory. The content was identified to the lowest possible taxonomic level, quantified, and weighed for each batoid species. We used family identification as the lowest taxonomic level to compare diet between species (i.e. Portunidae, Varunidae, Onuphidae, Sicyonidae). Seaweed and substrate were considered accidental ingestion and excluded from analysis (Aguiar & Valentin, 2010).

Statistical analyses

A cumulative prey curve was constructed using the Shannon–Wiener method to assess whether the number of sampled stomachs was enough to describe the diversity of four batoid species. The EstimateS 9 software was used to obtain the Shannon–Wiener index. Sample sufficiency was estimated visually when the graphic reached an asymptote and decreased variance (Magurran, 2004).

For dietary analysis, the following indexes were calculated: Numeric (%N), Gravimetric (%W), Frequency of Occurrence (%FO), Prey-specific abundance (%PN), and Prey-specific weight (%PW) (Cortés, 1997; Brown et al., 2012). Prey-specific Index of Relative Importance (%PSIRI) was calculated to determine the importance of each prey item in the species' diet

$$\%PSIRI = \frac{\%FO * (\%PN + \%PW)}{2}$$

%PN is the specific abundance for prey number, and %PW is the specific abundance for prey weight (Brown et al., 2012).

The width of the trophic niche was determined using Levins'

$$(Bi) : Bi = 1 / \sum P_j^2$$

Pj represents the prey item weight fraction of each feeding category j ($\Sigma Pj = 1$) (Krebs, 1999). Values were standardized (B_A) using the equation:

$$BA = (Bi - 1)/(N - 1)$$

where N is the class number (Krebs, 1999), B_A standardized values varied between 0 and 1. Low B_A values indicate a very specialized diet and high B_A values indicate a generalized diet (Hurlbert, 1978).

The trophic level (TL) was calculated using the equation from Christensen & Pauly (1992):

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

where DC_{ij} is referred to as the diet composition, in the proportion of prey (j), in the species diet (i), and TL_j is the trophic level of prey (j). Preys' Trophic position (TL_j) was based on Ebert and Bizzarro (2007).

Niche overlap was calculated using the Pianka index (1973), using the "niche_null_model" function, "Pianka'' metric, and 1000 replications from the "EcosimR '' package. The values ranged between 0 and 1, and overlap was considered biologically significant when values were above 0.60 (Zaret & Rand, 1971). The biomass data diets of the four batoid species were transformed using the Hellinger method and compared using percentage SIMPER analyses and PERMANOVA similarity (Clarke et al., 2014). Dissimilarity was calculated using the "vegdist" function, "bray" method, "adonis," and "simper" functions, with 1000 replications from the "vegan" package and "parwaise.adonis" from the "pairwiseAdonis" package. We used the "betadisper" and "permutest" functions, with 999 replications, of the "vegan" package to test the overdispersion of the data. Graphic analyses were obtained using non-metric multidimensional scaling (nMDS) using the "metaMDS" function and "bray" method from the "vegan" package. Unidentified digested material was excluded from the analyses. Samples with a feeding category of low occurrence (two or fewer specimens) were identified as outliers and removed from analyses. All analyses were performed using R Language for Statistical Computing (R Core Team, 2022).

Results

A total of 229 individual stomachs belonging to four sympatric batoid species from the Southwestern Atlantic Ocean were analyzed. Food was found in 187 stomachs, of which 87.17% were sampled in the warm season, 8.56% in the cold season, and 4.28% of samples had no season register. *Dasyatis hypostigma* had 60 stomachs analyzed (40 with content and 20 empty stomachs). Of the stomachs with content, ten were of females and 30 of males, with sizes ranging from 45 to 85 cm total length for TL ($\mu = 65.53 \pm 9.63$sd, Fig. 2) and 28 to 48 cm for DW ($\mu = 35.54 \pm 3.34$sd, Fig. 2). All the stomachs were collected in the warm seasons. *Pseudobatos horkelii* had 70 stomachs analyzed (58 with contents and 12 empty). The specimens with stomach content represent 19 females and 40 males. The specimen sizes range from 35 to 125 cm for TL ($\mu = 92.85 \pm 13.35$sd) and 12 to 45 cm for DW ($\mu = 30.33 \pm 5.60$sd). In the cold season, only one specimen was collected (Aug/2019). All the other specimens were sampled in the warm season. *Rioraja agassizii* had 66 stomachs analyzed (60 with content and six empty). Of the stomachs with content, 46 were of females and 14 of males, and the specimens' sizes ranged from 39 to 61 cm for TL ($\mu = 51.18 \pm 5.73$sd) and 21 to 40 cm for DW ($\mu = 33.16 \pm 4.10$sd). Most samples (61.67%) were collected in the warm season, 25.00% in the cold season, and 13.33% had no register for the season. *Sympterygia bonapartii* had 33 stomachs

Fig. 2 Body size variation of batoids species *Dasyatis hypostigma* (dh), *Pseudobatos horkelii* (ph), *Rioraja agassizii* (ra), and *Sympterygia bonapartii* (sb) in the Subtropical South Atlantic. **a** Disk width size, **b** Total length size
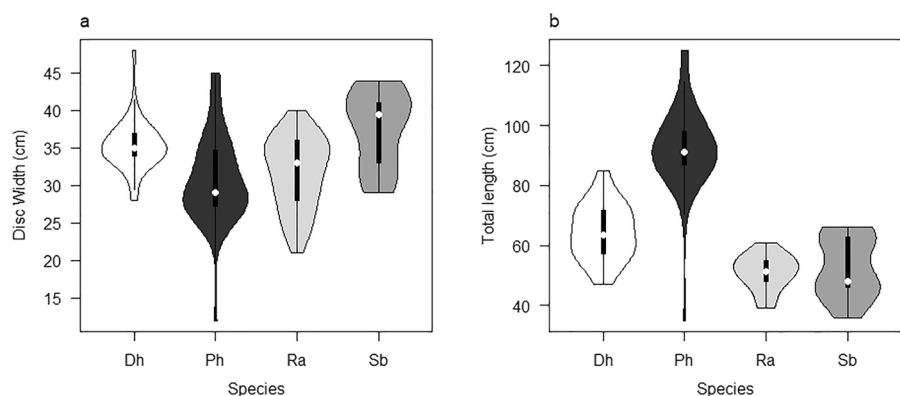
analyzed (29 with content and four empty), with 14 females and 15 males having food in their stomachs. All the samples were collected in the warm season. The specimen sizes ranged from 36 to 68.5 cm for TL ($\mu = 53.72 \pm 10.29$sd) and 29 to 44 cm for DW ($\mu = 37.75 \pm 5.28$sd). The cumulative average prey species graphic indicated that samples reached sufficiency to represent four batoid species diets (Fig. 3). Sample numbers collected in this study were considered insufficient for diet variation analyses (sex, ontogenetic, and temporal variations).

Diet, niche breadth, and trophic position

Stomach content analysis of four batoid species resulted in 55 feeding items identified (Table 1). *Dasyatis hypostigma* has 26 feeding items and shows feeding specialization with narrow niche breadth ($B_A = 0.30$). The trophic position was $T_1 = 3.56$. Polychaeta (47.97% PSIRI) and Crustacea (46.79% PSIRI) were the most important taxon. The main prey items were *Leptochela serratorbita* Spence Bate, 1888 shrimp from the Pasiphaeidae family (22.86%PSIRI) and Polychaetes from the Onuphidae family (18.80%PSIRI). *Pseudobatos horkelii* had 31 feeding items, where unidentified Nematoda (36.84% PSIRI) was the principal feeding item, followed by unidentified Teleostei (13.96% PSIRI) and unidentified crustaceans (12.42% PSIRI). PSIRI analyses showed Crustacea (44.52% PSIRI), Nematoda (36.84% PSIRI), and Teleostei (13.96% PSIRI) as the leading groups of the diet. *Pseudobatos horkelii* presented a narrow niche breadth ($B_A = 0.15$), and the trophic position was $T_1 = 3.60$. The *Rioraja agassizii* diet had 32 feeding items, mainly composed of Crustacea (94.71% PSIRI). The prevalent species were the Caridean shrimp *L. serratorbita* (30.95% PSIRI), the Dendrobranchiata shrimp from the Sicyonidae family, *Sicyonia dorsalis* Kingsley, 1878 (12.64% PSIRI), and Portunidae crabs' family (12.22% PSIRI). *R. agassizii* presented low niche breadth ($B_A = 0.19$), and the trophic position was $T_1 = 3.54$. *Sympterygia bonapartii* had 29 feeding items and a narrow niche breadth ($B_A = 0.16$), indicating high diet specialization. The
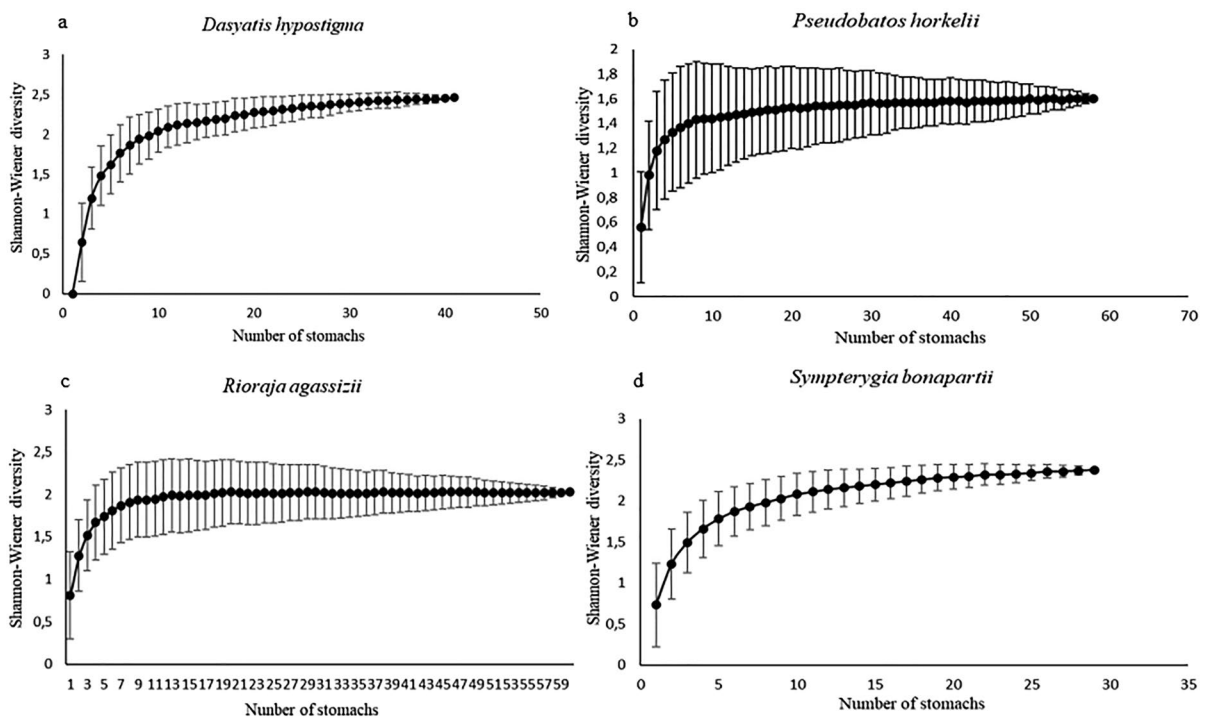

Fig. 3 Cumulative average (solid line) and standard deviation (vertical lines) of Shannon–Wiener diversity index for samples of the studied batoid species in Subtropical South Atlantic **a** *Dasyatis hypostigma*; **b** *Pseudobatos horkelii*; **c** *Rioraja agassizii*; **d** *Sympterygia bonapartii*

Table 1 Feeding item list for four batoid species expressed in percentage

Feeding items	Dasyatis hypostigma				Pseudobatos horkelii				Rioraja agassizii				Sympterygia bonapartii			
	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%
TELEOSTEI				**1.78**				**13.96**				**2.97**				**27.56**
Telostei un	17.62	53.46	5.00	1.78	12.21	190.16	13.79	13.96*	11.52	24.51	15.00	2.70	17.25	45.58	37.93	11.92*
Urophycis brasiliensis (Kaup, 1858)									11.52	21.19	1.67	0.27				
Sardinella brasiliensis (Steindachner, 1879)													13.55	440.09	6.90	15.64*
CRUSTACEA				**46.79**				**44.52**				**94.71**				**58.33**
Crustacea un	19.22	15.80	27.50	4.82	14.83	88.10	24.14	12.42*	11.52	17.93	3.33	0.49	13.55	1.10	10.34	0.76
Decapoda un	17.62	15.43	12.50	2.07	13.43	51.17	17.24	5.57	17.91	24.48	15.00	3.18	27.10	0.71	3.45	0.48
Brachyura un	17.62	59.96	2.50	0.97	12.21	41.19	12.07	3.22	15.36	30.95	10.00	2.32	27.10	7.68	6.90	1.20
Portunidae	17.62	7.59	2.50	0.32	24.42	22.03	8.62	2.00	27.97	76.79	23.33	12.22*	20.33	19.16	13.79	2.72
Achelous sp									23.03	2.22	1.67	0.21				
Achelous spinicarpus Stimpson, 1871									23.03	45.79	3.33	1.15	102.25	91.20	37.93	36.69*
Callinectes sp					12.21	17.34	3.45	0.51	14.40	6.43	6.67	0.69	27.10	16.41	10.34	2.25
Grapsoidea									11.52	5.98	3.33	0.29	13.55	4.69	3.45	0.31
Varunidae													13.55	8.05	13.79	1.49
Parthenopidae					12.21	2.61	1.72	0.13								
Calappidae									11.52	32.06	3.33	0.73				
Leucosiidae									11.52	8.20	5.00	0.49				
Shrimp un	17.62	70.92	10.00	4.43	12.21	12.21	6.90	0.84	19.58	15.33	33.33	5.82	21.68	7.09	17.24	2.48
Dendrobranchiata un	35.24	5.86	2.50	0.51	16.28	51.72	20.69	7.03	20.15	24.52	13.33	2.98	13.55	16.15	10.34	1.54
Pleoticus muelleri (Spence Bate, 1888)	17.62	71.85	2.50	1.12					20.73	108.89	8.33	5.40				
Artemesia longinaris Spence Bate 1888									23.03	15.92	1.67	0.32	40.65	64.84	6.90	3.64
Sicyonia dorsalis Kingsley, 1878					52.91	92.07	5.17	3.75	34.55	31.39	38.33	12.64*	27.10	9.53	6.90	1.26
Sicyonia typica (Boeck 1864)									23.03	16.38	3.33	0.66				
Rimapenaeus constrictus (Stimpson, 1871)					12.21	108.43	3.45	2.08	14.40	22.87	6.67	1.24	13.55	19.83	3.45	0.58
Caridea un					18.32	1.65	6.90	0.69	19.19	2.03	5.00	0.53				
Alpheus heterochaelis Say, 1818									23.03	18.85	1.67	0.35				
Alpheus sp													13.55	2.55	3.45	0.28
Ogyrides alphaerostris (Kingsley, 1880)	17.62	22.57	7.50	1.51	12.21	0.00	1.72	0.11	15.36	7.04	10.00	1.12	13.55	0.08	3.45	0.23

Table 1 (continued)

	Dasyatis hypostigma				Pseudobatos horkelii				Rioraja agassizii				Sympterygia bonapartii			
	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%
Leptochela serratorbita Spence Bate 1888	81.06	40.85	37.50	22.86*	53.73	15.05	8.62	2.96	116.05	26.81	43.33	30.95*	13.55	2.20	3.45	0.27
Periclemenes sp	17.62	0.66	2.50	0.23	12.21	1.91	1.72	0.12					108.41	2.30	3.45	1.91
Amphipoda																
Gammaridae									11.52	0.39	3.33	0.20	13.55	0.57	3.45	0.24
Cumacea									11.52	1.26	1.67	0.11				
Isopoda	35.24	6.60	5.00	1.05	36.63	17.71	1.72	0.47	11.52	0.02	1.67	0.10				
Stomatopoda	70.48	38.81	7.50	4.10	12.21	24.02	1.72	0.31								
Gibbesia neglecta (Gibbes, 1850)									11.52	580.99	3.33	9.88				
Hippoidea	23.49	51.10	7.50	2.80	15.26	51.85	6.90	2.31	11.52	27.00	3.33	0.64				
CNIDARIA				**1.01**												
Scyphozoa	17.62	63.10	2.50	1.01												
SIPUNCULA				**1.36**				**0.42**								**1.05**
Sipuncula un	52.86	55.96	2.50	1.36	24.42	24.59	1.72	0.42					18.07	2.18	10.34	1.05
MARINE WORMS				**0.26**				**0.20**				**0.43**				
Marine worms un	17.62	3.55	2.50	0.26	12.21	11.01	1.72	0.20	34.55	17.35	1.67	0.43				
POLYCHAETA				**47.97**				**3.23**				**1.59**				**4.01**
Polychaeta un	20.56	39.43	15.00	4.50	17.44	8.74	12.07	1.58	17.27	12.80	3.33	0.50	81.31	21.81	3.45	1.78
Onuphidae	46.57	60.83	35.00	18.80*	24.42	4.92	1.72	0.25	15.36	28.18	5.00	1.09	54.21	3.22	6.90	1.98
Glyceridae	35.24	35.99	2.50	0.89												
Goniadidae	70.48	5.36	2.50	0.95												
Lumbrineridae	45.81	34.37	12.50	5.01	12.21	50.09	1.72	0.54								
Lumbricalus sp	40.28	62.74	17.50	9.01	12.21	3.13	1.72	0.34								
Captilidae	58.74	54.89	15.00	8.52	36.63	6.75	1.72	0.16								
Arenicolidae					12.21	0.74	3.45	0.22								
Pilargidae	17.62	5.61	2.50	0.29												
Opheliidae													13.55	0.86	3.45	0.25
Terebilidae					12.21	4.57	1.72	0.14								
CHORDATA								**0.23**								**0.26**
Ascidecea					24.42	2.00	1.72	0.23					13.55	1.52	3.45	0.26
NEMATODA								**36.84**				**0.31**				**7.76**

Table 1 (continued)

	Dasyatis hypostigma				Pseudobatos horkelii				Rioraja agassizii				Symptergia bonapartii			
	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%	PN%	PW%	FO%	PSIRI%
Nematoda un					107.86	10.86	62.07	36.84*	11.52	0.70	5.00	0.31	36.14	1.38	41.38	7.76
MOLLUSCA								**0.21**								**1.04**
Cephalopoda					12.21	12.62	1.72	0.21					13.55	8.21	3.45	0.38
Bivalvia													13.55	3.06	3.45	0.29
Aplysiidae													13.55	7.98	3.45	0.37
BRYOZOA			**0.86**					**0.36**								
Bryozoa un	17.62	50.97	2.50	0.86	12.21	29.16	1.72	0.36								

*Important feeding items; *un* Unidentified

Prey-specific number (%PN), Prey-specific weight (%PW), Frequency of Occurrence (%FO), and Prey-specific Index of Relative Importance (%PSIRI) from diet batoids species, *Dasyatis hypostigma, Pseudobatos horkelii, Rioraja agassizii*, and *Symptergia bonapartii*

Table 2 Pianka's overlap index between *Dasyatis hypostigma* (Dh), *Pseudobatos horkelii* (Ph), *Rioraja agassizii* (Ra), and *Symptergia bonapartii* (Sb), four sympatric batoids of the subtropical South Atlantic Ocean

Species	Predicted overlap	Observed overlap	P
Dh x Ph	0.15	0.20	0.24
Dh x Ra	0.18	0.25	0.20
Dh x Sb	0.12	0.04	0.67
Ph x Ra	0.15	0.24	0.17
Ra x Sb	0.10	0.47	0.02*
Ph x Sb	0.10	0.29	0.09

*Significant value

*Values with higher overlap than expected and differing from predicted by chance ($P < 0.05$)

trophic position was $T_1 = 3.70$. The diet was represented by Crustacea (58.33% PSIRI) and Teleostei (27.56% PSIRI) taxon and was composed of the crab *Achelous spinicarpus* Stimpson, 1871, from the Portunidae family (36.69% PSIRI). The second important prey item was *Sardinella brasiliensis* (Steindachner, 1879) fish (15.64% PSIRI), followed by Teleostei unidentified fish (11.92% PSIRI).

Feeding similarities and overlap trophic niche

For this analysis, one specimen was removed from *Dasyatis hypostigma*, one from *Pseudobatos horkelii,* and one from *Rioraja agassizii*, identified as outliers. Pianka's overlap index indicated no niche overlap between the four species ($O_{kj} = 0.25$, $P = 0.02$). Pairwise comparison for each species showed no overlap, but, except for *R. agassizii* and *Symptergia bonapartii* pairwise comparison ($O_{kj} = 0.47$, $P = 0.02$, Table 2), the null model results were not significant, which means that it could occur by chance. Nonmetric multidimensional scaling (nMDS) indicated overlap, mostly between *R. agassizii, D. hypostigma,* and *P. horkelii* (Fig. 4). Overlap diet was not confirmed by PERMANOVA and SIMPER analyses. PERMANOVA (Table 3) indicated a significant difference in the diet composition of four batoid species ($R_2 = 0.114$, $P = 0.001$). Pairwise species analysis also showed a significant difference between batoid diets (species x species, $P = 0.006$). SIMPER analyses indicated diet dissimilarity between four batoid species (> 70%). The feed items most important for

Fig. 4 Non-metric multidimensional scaling of the diet overlap of four batoids species *Dasyatis hypostigma* (dh), *Pseudobatos horkelii* (ph), *Rioraja agassizii* (ra), and *Sympterygia bonapartii* (sb) in the Subtropical South Atlantic
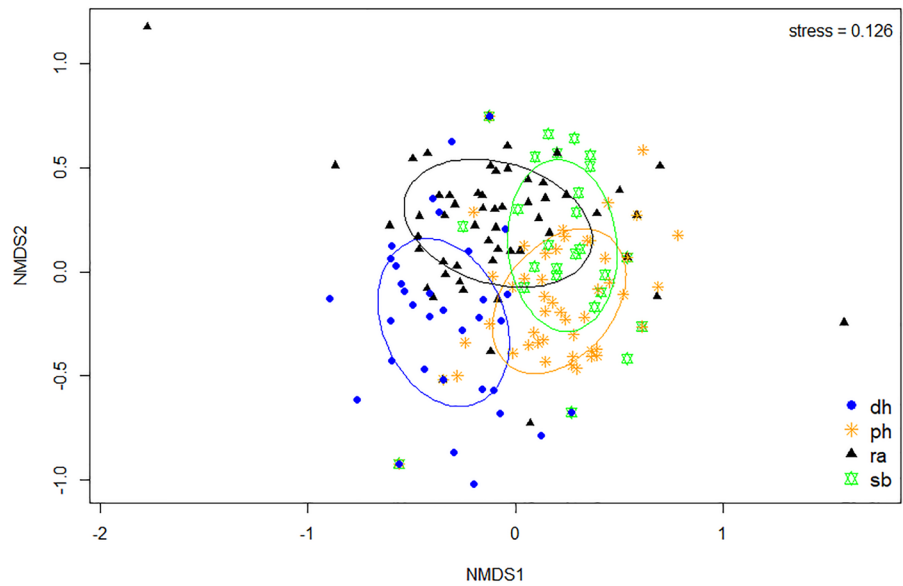

Table 3 PERMANOVA pairwise dissimilarity analyses from the diet of four batoid species sympatric in the subtropical South Atlantic: *Dasyatis hypostigma, Pseudobatos horkelii, Rioraja agassizii,* and *Sympterygia bonapartii*

Species x Species	R^2	P-value
D. hypostigma x *P. horkelii*	0.08	0.006*
D. hypostigma x *R. agassizii*	0.06	0.006*
D. hypostigma x *S. bonapartii*	0.11	0.006*
P. horkelii x *R. agassizii*	0.08	0.006*
P. horkelii x *S. bonapartii*	0.05	0.006*
R. agassizii x *S. bonapartii*	0.05	0.006*

*Significant value

the dissimilarity between *D. hypostigma* and *P. horkelii* are Nematoda (20.1%, $P < 0.01$), Crustacea (11%, $P < 0.01$), Lumbrineridae (36.7%, $P < 0.01$), Onuphidae (44.6%, $P < 0.01$), and Polychaeta (58.2%, $P < 0.01$). The feed items for *D. hypostigma* and *R. agassizii,* Sicyoniidae (21.8%, $P < 0.01$), Pasiphaeidae (12.2%, $P < 0.01$), Onuphidae (45.8%, $P < 0.01$), and Lumbrineridae (52.1%, $P < 0.01$) are the main items that contribute for diet dissimilarity. Portunidae (20.7%, $P < 0.01$), Clupeidae (69.9, $P < 0.01$), Teleostei (32.5%, $P = 0.02$), and Lumbrineridae (55.8, $P = 0.01$) are the feeding items that most contribute for diet dissimilarity for *D. hypostigma* and *S. bonapartii*. Sicyoniidae (10.8%, $P < 0.001$), Pasiphaeidae (31.4%, $P < 0.01$), Nematoda (46.7%, $P < 0.01$), Dendrobranchiata (73.4%, $P = 0.03$), and Decapoda

(53.8%, $P = 0.04$) are the most contributing items for *P. horkelii* and *R. agassizii* diet dissimilarity. The feed items Portunidae (23.5%, $P < 0.01$), Teleostei (38.54, $P < 0.01$), Clupeidae (68.8%, $P < 0.01$), and Nematoda (46.2%, $P = 0.02$) are the most influential feeding items to the diet dissimilarity of *P. horkelii* and *S. bonapartii*. For *R. agassizii* and *S. bonapartii,* the items Portunidae (22.7, $P < 0.01$), Teleostei (34.5%, $P = 0.03$), and Clupeidae (62.7%, $P = 0.02$) are the main items to dissimilarity contributions. We did not confirm trophic niche overlap among the four batoid species.

Discussion

The diet of four batoid species was composed mainly of benthic prey and taxon commonly found as part of the studied species diet (crustaceans, polychaetes, fish), except Nematoda for *Pseudobatos horkelii* (Ruocco & Lucifora, 2016; Belleggia et al., 2019; Chelotti & Gadig, 2023). *Dasyatis hypostigma, Pseudobatos horkelii, Rioraja agassizii,* and *Sympterygia bonapartii* showed a narrow niche breadth, indicating diet specialization in a few prey items (Hurlbert, 1978). The importance of each item has shown differences when compared to the diet of the same species in other locations (e.g. Argentina, São Paulo) (Paesch, 2000; Barbini, 2010; Barbini & Lucifora, 2011; Bornatowski et al., 2014b). Elasmobranchs'

diet specialization can create a complex trophic ecology structure and reinforce their substantial ecological role in marine ecosystems (Wetherbee et al., 2012). Besides, small sharks and batoids can live in complex habitats with environmental variations (e.g. salinity, temperature), and due to their varied habitat occupancy and feeding plasticity, they can show specialized diet (Tricas, 1985; Grubbs, 2010; Motta & Huber, 2012; Freitas et al., 2019; Hayata et al., 2021; Rupp & Bornatowski, 2021). The diet specialization in a few prey species (e.g. bivalves, infauna) also is a mechanism to avoid competition with other large and higher trophic levels elasmobranchs (Vaudo & Heithaus, 2011; Bornatowski et al., 2014c; Hayata et al., 2021). Regarding the trophic level result, all four species studied fit on the third level of the food chain (mesopredator, $T_1 < 4$). The mean trophic level is one of the indicators of ecosystem health used by the Convention on Biological Diversity (Pauly & Watson, 2005). Research with mesopredators (e.g. rays) is essential once significant top predators (e.g. sharks) reduction can change the structure of the food chain and lead to a mesopredator release and a cascading trophic effect in the ecosystem (Bornatowski et al., 2014a; 2014b; 2018b). In the study area, inshore fishing and anthropogenic impacts have occurred since the end of the nineteenth century, with declining catches (Gallardo et al., 2021). Due to the increased fishing efforts in recent decades, Gallardo et al. (2021) suspect a fishing down in the marine food web along the Santa Catarina coast, with biodiversity loss, including high trophic level species.

Regarding diet composition, *Dasyatis hypostigma* had mostly crustaceans and polychaetas as prey items and showed specialized feeding in *Leptochela serratorbita* shrimp and worms of the Onuphidae family. There are few studies about *D. hypostigma* diets that have found Polychaeta as the main item for southwestern Brazilian species, followed by the Penaidae family and Amphipoda for specimens from Argentina (Ruocco & Lucifora, 2016; Domingos et al., 2021). Ontogenetic effects were reported in a study in Argentina, where the small specimens fed mostly Amphipoda, and the large specimens had Polychaeta as the main item in their diet (Ruocco & Lucifora, 2016). Considering that females of *D. hypostigma* are mature with 49.5 cm disk width and males with 30 cm (Last et al., 2016; Gomes et al., 2019), it was assumed that all the specimens captured in our study were small and juvenile. Once that disk widths from females ranged from 35 to 48 cm (only 2 of $10 > 40$ cm), and for males, besides disk width ranging from 28 to 38 cm, the maturity was determined during the collection by clasper rigidity. In this way, ontogenetic prey variation does not influence the results presented, representing juvenile specimens' diet. Our study showed that small specimens had polychaetes as the leading item of their diet, contrasting the findings of Ruocco & Lucifora (2016). Diet's seasonal effects were found in Argentina, where crustaceans were more important in winter, whereas in spring, other taxons were prevalent (e.g. bivalves, fish, gastropoda) (Ruocco & Lucifora, 2016). Otherwise, our results showed Crustaceans and Polychaetas as important prey in warm seasons. Sex is another variable that can influence the diet of elasmobranchs (Wetherbee et al., 2012), and we sampled specimens for both sexes, with males as the majority (Female = 15%, Male = 75%). Although diet differences between sexes for *D. hypostigma* were not tested here, these differences were not evidenced in other research for this species (Ruocco & Lucifora, 2016).

In the diet of *Pseudobatos horkelii,* Nematoda was the most important prey item, followed by crustaceans, showing a specialized diet of benthic prey. The groups commonly found as relevant prey items (Polychaeta and Teleostei) for *P. horkelii* and other species from the *Pseudobatos* genus were not evidenced in the present research as representative prey in the diet of *P. horkelii* (e.g. Amaral & Migotto, 1980; Bornatowski et al., 2010, 2014b; Belleggia et al., 2019; Chelotti & Gadig, 2023). Crustaceans are also less important in the diet of *P. horkelii* in the present study, unlike specimens from other locations in Brazil (e.g. Paraná, São Paulo) and Argentina (e.g. Amaral & Migotto, 1980; Soares et al., 1992; Casselberry & Carlson, 2015; Martins et al., 2017; Chelotti & Gadig, 2023). Some studies considered Nematoda an accidental ingestion (Chelotti & Gadig, 2023), which was not evidenced in other studies (Amaral & Migotto, 1980; Soares et al., 1992; Belleggia et al., 2019). Furthermore, we found Nematoda as a significantly important prey (36.84% PSIRI), which could be the reflex of local feeding variety, according to geographical differences, prey availability, and abundance (Last et al., 2016; Motta et al., 2016; Reys-Ramírez et al., 2022). Seasonal, ontogenetic, and sex effects on diet

were not considered in our analysis because, except for one, all the specimens were sampled in warm seasons. Also, the majority (94.83%) of specimens were assumed to be adults, according to size mature reference (> 750 mm TL) (Vooren et al., 2005), and for sex comparison, the samples were insufficient. Thus, this study represents the diet of adults in the warm season for *P. horkelii.* It is noteworthy that sex and maturity stage did not influence the diet of *P. horkelii* in other researchers, and there is no information about the diet seasonality (Belleggia et al., 2019; Chelotti & Gadig, 2023).

Rioraja agassizii, as expected, showed a carcinophagus benthic diet, in which Crustacea were the most relevant category prey (Soares et al., 1992; Muto et al., 2001; Barbini & Lucifora, 2011; Bornatowski et al., 2014b; Motta et al., 2016; Viana et al., 2017; Belleggia et al., 2019). In contrast, other taxa, such as Teleostei and Polychaeta, were unusual prey, presenting low importance in the diet. These findings partially contrast with the *R. agassizii* diet from specimens in São Paulo, which find Caridean and fishes as predominant prey (Muto et al., 2001). Body size, sex, and season variation were evidenced for the *R. agassizii* diet (Muto et al., 2001), where the consumption of small crustaceans, such as Amphipoda, was related to smaller specimens (< 180 mm) and to the spring season, and fish consumption was linked to adult females on winter (480 mm). Still, Caridea was a predominant prey for all body sizes (Muto et al., 2001). Here, adult females were the majority of our sample (53.33%), but fish and polychaetes were less representative, contrasting findings in other locations (Soares et al., 1992; Muto et al., 2001; Barbini & Lucifora, 2011; Bornatowski et al., 2014b; Motta et al., 2016; Belleggia et al., 2019). In contrast, another study found fish as important prey in winter, with no distinction between sexes, and the increasing importance of Crustaceans (e.g. crabs and shrimps), according to increase in the body size, which goes with the results shown in the present study (Barbini & Lucifora, 2011). Despite *R. agassizii* having shown ontogenetic, seasonal, and annual variances, caridean shrimps, including *Leptochela serratorbita,* seem prevalent (Muto et al., 2001). This prey was important in winter, autumn, and spring, such in adults as juveniles (Muto et al., 2001). Accordingly, we evidenced this prey as crucial as well, but the majority (61.67%) of specimens were collected in the warm

season (mainly summer). *Sicyonia dorsalis* and Portunidae crabs have also been found as prevailing prey, corroborating our results (Soares et al., 1992; Muto et al., 2001; Bornatowski et al., 2014b). Some studies have shown some distinctions in the diet of *R. agassizii* over different years, but the diet was composed of the same prey groups, with changes in the order of importance of shrimps, brachyurans, and fish (Muto et al., 2001; Motta et al., 2016).

The feeding habit of *Sympterygia bonapartii* showed a high specialization diet in a few benthopelagic preys. Similar patterns of feeding items, consisting of crabs and fish, were found in other locations, such as Argentina and Uruguay (Paesch, 2000; Barbini, 2010; Estalles et al., 2016; Belleggia et al., 2019). The *S. bonapartii* diet can show differences attributed to variations in sex, ontogenetic, and seasonality due to changes in mouth morphology, ability improvement, and swimming speed. These variations allow adults to consume larger prey, like fish (Estalles et al., 2016). In the present study, seasonal effects were not analyzed, but these results showed the *S. bonapartii* diet in warm seasons since all the stomachs were collected in warm months. However, the *S. bonapartii* diet's results deserve caution since the samples represented specimens for both sexes similarly and ranged in body size (Fig. 2). Most specimens sampled (72%) had a total length between 51 and 75 cm and could be considered adults, once male adult sizes are between 61 and 74 cm and females between 50 and 69 cm (Basallo & Oddone, 2014; Gomes et al., 2019). According to Estalles et al. (2016), the larger the body size of skates, the smaller the contribution of crustaceans to the diet, and large-body females increased the importance of fish. Although most specimens were adults, our results showed Crustaceans as the most important prey. The importance observed in *Sardinella brasiliensis* as prey is due to the high weight found in a few samples (2 out of 29), which increased the prey-specific weight percentage. Besides, specimens considered juveniles also had fish in the stomach content, and both females and males consumed Teleostei. So, this difference between the sizes and sex may not be apparent, considering our sample design.

Dasyatis hypostigma, Pseudobatos horkelii, and *Rioraja agassizii* showed spatial diet variation compared to other studies with the same species in distinct geographical locations (e.g. Argentina, Paraná, São

Paulo) (Amaral & Migotto, 1980; Barbini & Lucifora, 2011; Bornatowski et al., 2014b; Belleggia et al., 2019; Domingos et al., 2021; Hayata et al., 2021; Chelotti & Gadig, 2023). These preys' variations could be related to abiotic variables (e.g. sea temperature, salinity) and oceanography (e.g. depth, sea currents) differences that influence local biodiversity and prey availability (Barbini & Lucifora, 2011; Motta et al., 2016). The island of Santa Catarina is surrounded by 32 other coastal islands, forming an archipelago with a diversity of coastal ecosystems, highlighting 117 sandy beaches and nine pebble beaches (Horn Filho et al., 1999), dunes, lagoons, as well as mangroves and salt marshes (Horn Filho, 2004). The ecosystems are continually modeled due to the joint action of factors such as wind, currents, and waves. They are related to sea variation and climate change, where the winds from the south and north quadrants are the main physical agents of Santa Catarina Island hydrodynamics (Cruz, 1998). Furthermore, the dynamics of sea currents in southern Brazil (ACAS, Santa Marta resurgence, Brazil-Malvinas Confluence (BMC)), together with continental shelf width, geomorphological and submarine characteristics of this region, exert influence in local primary productive and biodiversity (Pereira et al., 2009). The southern region of Brazil has a large biomass of demersal and pelagic fish and, consequently, the largest fishing fleet in the country due to these characteristics (Matsuura, 1987). In this way, the diet of the four batoid species presented here can be influenced by local prey diversity and resource availability, which is a consequence of the local ecosystem dynamics due to the oceanographic and geomorphological differences of Santa Catarina Island, which goes by the theory of the organism's consumption of available resources in the environment (Barbini & Lucifora, 2011; Reys-Ramírez et al., 2022).

Ecology feeding analyses indicated no trophic niche overlap between the four sympatric Southwestern Atlantic batoid species. These findings show niche partitioning between *Dasyatis hypostigma, Pseudobatos horkelii, Rioraja agassizii*, and *Sympterygia bonapartii*, which is a strategy that sympatric and ecologically close species can adopt to avoid competition and has already been described for other sympatric batoid species (Platell et al., 1998; Platell & Potter, 2001; Marshall et al., 2008; Siepielski & Mcpeek, 2010; Kinney et al.,

2011; Bornatowski et al., 2014b; Hayata et al., 2021). The niche partitioning strategy allows the coexistence of sympatric species through partial or complete trophic niche overlap, thus limiting direct competition for resources (Belleggia et al., 2019). The difference found in resource uses between *R. agassizii*, *P. horkelii*, and *D. hypostigma* diets could be related, firstly, to a temporal difference between the samples but also to the distinct characteristics in specific foraging areas (e.g. biodiversity, resource viability), morphologies (e.g. body sizes, teeth), and ecologies between the species (e.g. foraging time, time spent in prey capture, feeding plasticity) (Wetherbee et al., 2012; Belleggia et al., 2019). The batoid species in the present study had morphological differences (e.g. disk width, total length, dental plates, snout size), which could influence their diet dissimilarity. Morphology and feeding behavior are the first influences in batoids diets, followed by the composition and abundance of available prey (Pillay, 1952). The diet of sharks (e.g. Squaliformes) and batoids of different orders and families (e.g. Dasyatidae, Rajidae, Rhinobatidae) has already been associated with morphological variations (Dean et al., 2007; Wilga et al., 2007; Pasquino, 2010; Motta & Huber, 2012). Batoids had a flat body and ventral mouth that suggest a benthic feeding habitat, as shown by our findings. Other batoid characteristics such as mouth width and small teeth are connected to prey size, captured by suction, and selection of edible from inedible food (e.g. separate sediment from the food) (Motta & Huber, 2012; Rezende et al., 2015). The suction mechanisms of Rajidae enable it to ingest benthic invertebrates, like the crabs consumed by *R. agassizii* and *S. bonapartii* (e.g. *Achelous spinicarpus*) (Moyle & Cech-Jr., 1988). Besides, snout and fin size, as the *P. horkelii*, could help in the capture and manipulation of buried prey (Lucifora et al., 2000; Grubbs, 2010; Pasquino, 2010; Sommerville et al., 2011; Motta & Huber, 2012; Rezende et al., 2015). Once different prey capture strategies allow populations to coexist (Macarthur, 1958; Belleggia et al., 2019), all the differences in morphology, life stage, sex, and feeding strategies combined could explain the dissimilarity found, allowing and contributing to the coexistence of sympatric batoids in the study area.

Conclusion

This study provides feeding ecology information for four endangered sympatric batoid species (*Dasyatis hypostigma*, *Pseudobatos horkelii*, *Rioraja agassizii*, and *Sympterygia bonapartii*) that showed specialized diet and fed mostly on benthic preys, indicating feeding activity in the same habitat type. Significant trophic niche overlap was not detected, suggesting any direct resource competition between them. While the ecological importance of these results, it is important to reinforce that trophic niche occupation can vary according to species sex, life stage (ontogenetic), and feeding-specific periods (e.g. day/ night period) and can show variances through the seasons and years. These variables could influence our results once they were not tested separately, especially for the temporal difference between the samples, considering that prey species can show fluctuations in abundance through the seasons and years, which could change the diet composition (Macarthur, 1958; Hurlbert, 1978; Slobodchikoff & Schulz, 1980; Cardillo & Warren, 2016). Multiple ecological factors, such as other niche dimensions (e.g. temperature, depth, photoperiod, sex, season, ontogenetic), must be analyzed to fully understand the species diets and niche trophic overlaps (Macarthur, 1958; Hurlbert, 1978). Artisanal fishing (benthic prey-specific) is the major benthic batoids threatened once these batoids show a specialized diet in shrimps and crabs and tend to be more impacted by the reduction of resource availability. Besides limitations in diet and trophic niche analyses, we provide basic ecological information about threatened sympatric batoid species' diet and trophic niche, including the endemic species of Southern Atlantic Ocean *Dasyatis hypostigma* and *Pseudobatos horkelii*. These results could be used to model biomass loss and fishing impacts on elasmobranch populations.

Declarations

References:

Aguiar, A. A. & J. L. Valentin, 2010. Biologia e ecologia alimentar de elasmobrânquios (Chondrichthyes: Elasmobranchii): uma revisão dos métodos e do estado da arte no Brasil. Oecologia Australis 14: 464–489. https://doi.org/10.4257/oeco.2010.1402.09.

Amaral, A. C. Z. & A. E. Migotto, 1980. Importância dos anelídeos poliquetas na alimentação da macrofauna demersal e bentônica da região de Ubatuba. Boletim Do Instituto Oceanográfico 29: 31–35. https://doi.org/10.1590/S0373-55241980000200006.

Araújo, P. R. V., M. C. Oddone & G. Velasco, 2016. Reproductive biology of the stingrays, *Myliobatis goodei* and *Myliobatis ridens* (Chondrichthyes: Myliobatidae), in Southern Brazil. Journal of Fish Biology 89: 1043–1067. https://doi.org/10.1111/jfb.13015.

Barbini, S. A. & L. O. Lucifora, 2011. Feeding habits of the Rio skate, *Rioraja agassizii* (Chondrichthyes: Rajidae), from off Uruguay and north Argentina. Journal of the Marine Biological Association of the United Kingdom 91: 1175–1184. https://doi.org/10.1017/S0025315410001529.

Barbini, S. A. & L. O. Lucifora, 2016. Big fish (and a smallish skate) eat small fish: diet variation and trophic level of *Sympterygia acuta*, a medium-sized skate high in the food web. Marine Ecology 37: 283–293. https://doi.org/10.1111/maec.12273.

Barbini, S. A., D. E. Sabadin & L. O. Lucifora, 2018. Comparative analysis of feeding habits and dietary niche breadth in skates: the importance of body size, snout length, and

depth. Reviews in Fish Biology Fisheries 28: 625–636. https://doi.org/10.1007/s11160-018-9522-5.

Barbini, A. S. Ecología trófica de las rayas (Chondrichthyes, Rajidae) en el ecosistema costero bonaerense y Uruguayo, 2010. PhD Thesis. Universidad Nacional de Mar del Plata.

Basallo, A. & M. C. Oddone, 2014. Reproductive biology of the skates *Sympterygia acuta* Garman, and *S. bonapartii* Müller & Henle, (Chondrichthyes: Rajoidei) in south Brazil. Neotropical Ichthyology 12: 4. https://doi.org/10.1590/1982-0224-20130097.

Belleggia, M., C. Battagliotti, F. Cortés & J. H. Colonello, 2019. Feeding together: a global diet analysis of twenty-three species of Chondrichthyes on a feeding ground area. Hydrobiologia 842: 77–99. https://doi.org/10.1007/s10750-019-04027-w.

Bethea, D. M., J. K. Carlson, J. A. Buckel & M. Satterwhite, 2006. Ontogenetic and site related trends in the diet of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from the northeast Gulf of Mexico. Bulletin of Marine Science 78: 287–307.

Bornatowski, H., M. C. Robert & L. Costa, 2010. Feeding of guitarfish *Rhinobatos percellens* (Walbaum, 1972) (Elasmobranchii, Rhinobatidae), the target of artisanal fishery in southern Brazil. Brazilian Journal of Oceanography 58: 45–52. https://doi.org/10.1590/S1679-87592010000100005.

Bornatowski, H., J. R. S. Vitule, V. Abilhoa & M. F. M. Corrêa, 2011. Unconventional fishing for large sharks in the State of Paraná, southern Brazil: a note of concern. Journal of Applied Ichthyology 27: 1108–1111. https://doi.org/10.1111/j.1439-0426.2010.01600.x.

Bornatowski, H., A. F. Navia, R. R. Braga, V. Abilhoa & M. F. M. Correa, 2014a. Ecological importance of sharks and rays in a structural food web analysis in southern Brazil. ICES Journal of Marine Science 71: 1586–1592. https://doi.org/10.1093/icesjms/fsu025.

Bornatowski, H., N. Wosnick, W. P. D. Carmo, M. F. Corrêa & V. Abilho, 2014b. Feeding comparisons of four batoids (Elasmobranchii) in coastal waters of southern Brazil. Journal of the Marine Biological Association of the United Kingdom 94: 1491–1499. https://doi.org/10.1017/S0025315414000472.

Bornatowski, H., R. R. Braga, V. Abilhoa & M. F. M. Corrêa, 2014c. Feeding ecology and trophic comparisons of six shark species in a coastal ecosystem off southern Brazil. Journal of Fish Biology 85: 246–263. https://doi.org/10.1111/jfb.12417.

Bornatowski, H., R. R. Braga & R. P. Barreto, 2018a. Elasmobranchs Consumption in Brazil: Impacts and Consequences. In Rossi-Santos, M. R., C. W. Finkl (eds), Advances in Marine Vertebrate Research in Latin America Springer, Cham: 251–262. https://doi.org/10.1007/978-3-319-56985-7_10.

Bornatowski, H., R. Angelini, M. Coll, R. R. P. Barreto & A. F. Amorim, 2018b. Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. Reviews in Fish Biology and Fisheries 28: 241–259. https://doi.org/10.1007/s11160-017-9492-z.

Brown, S. C., J. J. Bizarro, G. M. Cailliet & D. A. Ebert, 2012. Breaking with tradition: redefining measures

for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). Environmental Biology of Fishes 95: 3–20. https://doi.org/10.1007/s10641-011-9959-z.

Budker, P., 1971. The life of sharks, Columbia University Press, New York. 222.

Cardillo, M. & D. L. Warren, 2016. Analyzing patterns of spatial and niche overlap among species at multiple resolutions: Spatial and niche overlap. Global Ecology and Biogeography 25: 951–963. https://doi.org/10.1111/geb.12455.

Casselberry, G. A. & J. K. Carlson. 2015. Endangered Species Act Status Review of the Brazilian guitarfish (*Rhinobatos horkelii*). Report to the National Marine Fisheries Service, Office of Protected Resources. SFD Contribution PCB-15-08. Retrieved from https://repository.library.noaa.gov/view/noaa/17717.

Chelotti, L. D. & O. B. F. Gadig, 2023. Comparative trophic ecology of two sympatric guitarfishes *Pseudobatos* (Chondrichthyes, Rhinobatidae) from Southeast Brazil, southwestern Atlantic. Journal of Fish Biology 102: 248–257. https://doi.org/10.1111/jfb.15257.

Christensen, V. & D. Pauly, 1992. ECOPATH II. A software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61: 169–185. https://doi.org/10.1016/0304-3800(92)90016-8.

Clarke, K. R., R. N. Gorley, P. J. Somerfield & R. M. Warwick, 2014. Change in marine communities: an approach to statistical analysis and interpretation Primer-E Ltda, Plymouth: 144.

Colwell, R. K. & D. J. Futuyma, 1971. On the Measurement of Niche Breadth and Overlap. Ecological Society of America 52: 567–576. https://doi.org/10.2307/1934144.

Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54: 726–738. https://doi.org/10.1139/cjfas-54-3-726.

Costa, L. & P. T. C. Chaves, 2006. Elasmobrânquios capturados pela pesca artesanal na costa sul do Paraná e norte de Santa Catarina, Brasil. Biota Neotropica 6: 3. https://doi.org/10.1590/S1676-06032006000300007.

Croll, D. A., K. M. Newton, K. Weng, F. Galván-Magaña, J. O'sullivan & H. Dewar, 2012. Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean. Marine Ecology Progress Series 465: 193–200. https://doi.org/10.3354/meps09900.

Cruz, O. 1998. A Ilha de Santa Catarina e o continente próximo; um estudo de geomorfologia costeira Editora da UFSC, Florianópolis: 280.

Dale, J. J., N. J. Wallsgrove, B. N. Pop & K. N. Holland, 2011. Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. Marine Ecology Progress Series 433: 221–236. https://doi.org/10.3354/meps09171.

Davidson, L. N. K. & N. K. Dulvy, 2017. Global marine protected areas to prevent extinctions. Nature Ecology & Evolution 1: 40. https://doi.org/10.1038/s41559-016-0040.

Dean, M. N., J. J. Bizzaro & A. P. Summers, 2007. The evolution of cranial design, diet and feeding mechanisms in

batoid fishes. Integrative and Comparative Biology 47: 70–81. https://doi.org/10.1093/icb/icm034.

Derrick, D. H., J. Cheok & N. K. Dulvy, 2020. Spatially congruent sites of importance for global shark and ray biodiversity. PLoS ONE 15: e0235559. https://doi.org/10.1371/journal.pone.0235559.

Domingos, J. F. S., B. Paiva, C. E. M. Bruno & A. F. Amorim, 2021. Diet of elasmobranchs captured in the fishing of pink shrimp off southern Brazil. Brazilian Journal of Animal and Environmental Research 4: 637–658.

Ebert, D. A. & J. J. Bizzarro, 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). Environment Biology of Fishes 80: 221–237. https://doi.org/10.1007/s10641-007-9227-4.

Estalles, M. L., M. R. Perier & E. E. Giacomo, 2016. Trophic ecology of the smallnose fanskate *Sympterygia bonapartii* in the San Matías Gulf, northern Patagonia, Argentina. Ichthyology Research 63: 207–217. https://doi.org/10.1007/s10228-015-0489-0.

Ferretti, F., B. Worm, G. L. Britten, M. R. Heithaus & K. L. Heike, 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecology Letters 13: 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x.

Freitas, R. H. A., A. A. Aguiar, A. K. C. H. A. Freitas, S. M. Q. Lima & J. L. Valentin, 2019. Unravelling the foraging behavior of the southern stingray, *Hypanus americanus* (Myliobatiformes: Dasyatidae) in a Southwestern Atlantic MPA. Neotropical Ichthyology 17: e180131. https://doi.org/10.1590/1982-0224-20180131.

Gadig, O. B. F., R. S. Rosa, 2023. Diversidade de peixes cartilaginosos do Brasil. In Kotas, J. E., E. P. Vizuete, R. A. Santos, M. R. Baggio, P. G. Salge, R. Barreto (eds), PAN Tubarões: Primeiro Ciclo do Plano de Ação Nacional para a Conservação dos Tubarões e Raias Marinhos Ameaçados de Extinção ICMBio/CEPSUL, Brasília: 45 -85.

Gallardo, S. S., D. F. Herbest, A. Begossi, L. G. Silva & A. C. Colonese, 2021. 150 years of anthropogenic impact on coastal and ocean ecosystems in Brazil revealed by historical newspapers. Ocean & Coastal Management 209: 105662. https://doi.org/10.1016/j.ocecoaman.2021.105662.

Gomes, U. L., C. N. Signori, O. B. F. Gadig, H. R. S. Santos, M. M. Vicente, 2019. Guia para identificação dos tubarões, raias e quimeras do estado Rio de janeiro (Chondrichthyes: Elasmobrachii e Holocephali). Revista Nordestina de Biologia 27: 1. https://doi.org/10.22478/ufpb.2236-1480.2019v27n1.47122.

Grubbs, R. D., 2010. Ontogenetic shifts in movements and habitat use. In Carrier, J. C., J. A. Musick & M. R. Heithaus (eds), Sharks and their relatives II: biodiversity, adaptive physiology, and conservation Taylor & Francis Group, New York: 319–350.

Hayata, M. A., H. Bornatowski & R. H. A. Freitas, 2021. Patterns and partitioning of food resources by elasmobranchs in southern Brazil. Environmental Biology of Fishes 104: 437–450. https://doi.org/10.1007/s10641-021-01082-y.

Heithaus, M. R., J. J. Vaudo, S. Kreicker, C. A. Layman, M. Krützen, D. A. Burkholder, K. Gastrich, C. Bessey, R. Sarabia, K. Cameron, A. Wirsing, J. A. Thomson & M. M. Dunphydaly, 2013. Apparent resource partitioning and trophic structure of large bodied marine predators in

a relatively pristine seagrass ecosystem. Marine Ecology Progress Series 481: 225–237. https://doi.org/10.3354/meps10235.

Heithaus, M. R., 2007. Nursery areas as essential shark habitats: a theoretical perspective. In McCandless, C. T., N. E. Kohler & H. L. Pratt Jr (eds), Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States, American Fisheries Society, US: 3–13.

Heupel, M. R., J. K. Carlson & C. A. Simpfendorfer, 2007. Shark nursery areas: Concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337: 287–297. https://doi.org/10.3354/meps337287.

Horn Filho, N. O., 2004. Estudo Morfossedimentares nas praias da Ilha de Santa Catarina, SC, Brasil: Uma síntese. Gravel 2: 5257.

Horn Filho, N. O., L. F. Diehl, P. C. Leal, 1999. Mapping the Santa Catarina Island's coast, Santa Catarina, southeastern, Brazil, Coastal Zone 99, San Diego: 401-403.

Hurlbert, S. H., 1978. The measurement of niche overlap and some relatives. Ecology 59: 67–77. https://doi.org/10.2307/1936632.

Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (Ibama)., (2023). Retrieved from https://www.gov.br/ibama/pt-br/assuntos/noticias/2023/operacao-do-ibama-apreende-28-7-toneladas-de-barbatanas-de-tubarao-com-origem-irregular.

Kinney, M. J., N. E. Hussey, A. T. Fisk, A. J. Tobin & C. A. Simpfendorfer, 2011. Communal or competitive? Stable Isotope analysis provides evidence of resource partitioning within a communal shark nursery. Marine Ecology Progress Series 439: 263–276. https://doi.org/10.3354/meps09327.

Krebs, C. J.,1999. Ecological Methodology, Benjamin Cummings, Menlo Park: 620.

Last, P., W. White, M. De Carvalho, B. Séret, M. Stehmann & G. Naylor, 2016. Rays of the world, CSIRO Publishing, Clayton: 832. https://doi.org/10.1071/9780643109148.

Lucifora, L. O., J. L. Valero, C. S. Bremec & M. L. Lasta, 2000. Feeding habitats and prey selection by the skate *Dipturus chilensis* (Elasmibranchii: Rajidae) from the southwestern Atlantic. Journal of the Marine Biological Association of the United Kingdom 80: 953–954. https://doi.org/10.1017/S002531540000299X.

Macarthur, R. H., 1958. Population Ecology of Some Warblers of Northeastern Coniferous Forests. Ecology 39: 599–619. https://doi.org/10.2307/1931600.

Magurran, A. E., 2004. Measuring biological diversity, Blackwell Publishing, Oxford: 272.

Marshall, A. D., P. M. Kyne & M. B. Bennett, 2008. Comparing the diet of two sympatric urolophid elasmobranchs (*Trygonoptera testacea* Müller & Henle and *Urolophus kapalensis* Yearsley & Last): evidence of ontogenetic shifts and possible resource partitioning. Journal of Fish Biology 72: 883–898. https://doi.org/10.1111/j.1095-8649.2007.01762.x.

Martins, A. P. B., M. R. Heupel, A. Chin & C. A. Simpfendorfer, 2018. Batoids nurseries: definition, use and importance. Marine Ecology Progress Series 595: 253–267. https://doi.org/10.3354/meps12545.

Martins, A. S., P. A. S. Costa, M. Haimovici, A. C. Braga & M. M. Mincarone, 2017. Ecologia trófica do nécton demersal

da plataforma e talude continental da Bacia de Campos. In Curbelo-Fernandez, M. P., A. C. Braga (eds), Comunidades Demersais e Bioconstrutores: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste Elsevier Habitats, Rio de Janeiro: 167–185. https://doi.org/10.1016/B978-85-352-7295-6.50007-5.

Matsuura, Y., 1987. Recursos pesqueiros: Avaliação dos recursos pesqueiros no Brasil. In Ogawa, M. & J. Koike (eds), Manual de Pesca Associação dos Engenheiros de Pesca do Estado do Ceará: 61–91.

Motta, P. J. & D. R. Huber, 2012. Prey Capture Behavior and Feeding Mechanics of Elasmobranchs. In Carrier, J. C., J. A. Musick & M. R. Heithaus (eds), Biology of Sharks and Their Relatives CRC Press: 153–210.

Motta, N. S., N. Della-Fina, C. C. A. Souza, E. S. Rodrigues & A. F. Amorim, 2016. Analysis of food habits of skate *Rioraja agassizii* (Elasmobranchii, Rajidae) from southern Brazil. Brazilian Journal of Biology 76: 469–475. https://doi.org/10.1590/1519-6984.21414.

Muto, E. Y., L. S. H. Soares & R. Goitein, 2001. Food resource utilization of the skates *Rioraja agassizii* (Müller and Henle, 1841) and *Psammobatis extenta* (Garman, 1913) on the continental shelf off Ubatuba, South-Eastern Brazil. Revista Brasileira De Biologia 61: 217–278. https://doi.org/10.1590/S0034-71082001000200005.

Paesch, L., 2000. Hábitos alimentarios de algunas especies de elasmobranquios en el frente oceânico del Río de La Plata. Frente Marítimo 18: 71–90.

Paiva, M. P., 1997. Recursos pesqueiros estuarinos e marinhos do Brasil, EUFC, Fortaleza: 278.

Pasquino, A. F., 2010. Ecomorfologia alimentar comparada de duas espécies de raias simpátricas, *Zapteryx brevirostris* e *Rioraja agassizi* (Chondrichthyes, Elasmobranchii) da costa de São Paulo. MSc Thesis, Universidade Estadual Paulista.

Pauly, D. & R. Watson, 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. Royal Society 360: 415–423. https://doi.org/10.1098/rstb.2004.1597.

Pennino, M. G., F. Muñoz, D. Conesa, A. López-Quílez & J. M. Bellido, 2013. Modeling sensitive elasmobranch habitats. Journal of Sea Research 83: 209–218. https://doi.org/10.1016/j.seares.2013.03.005.

Pereira, M. D., C. A. F. Schettini & C. Y. Omachi, 2009. Caracterização de feições oceanográficas na Plataforma de Santa Catarina através de imagens orbitais. Revista Brasileira De Geofísica 27: 81–93.

Pianka, E. R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53–74. https://doi.org/10.1146/annurev.es.04.110173.000413.

Pillay, T. V. R., 1952. A Critique of the Methods of Study of Food of Fishes. Journal of the Zoological Society of India 4: 185–200.

Platell, M. E. & I. C. Potter, 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. Journal of Experimental Marine Biology and Ecology 261: 31–54. https://doi.org/10.1016/s0022-0981(01)00257-x.

Platell, M. E., I. C. Potter & K. R. Clarke, 1998. Resource partitioning by four species of elasmobranchs (Batoidea:

Urolophidae) in coastal waters of temperate Australia. Marine Biology 131: 719–734. https://doi.org/10.1007/s002270050363.

Portaria MMA Nº 148, (MMA)., (2022). Lista Nacional de Espécies Ameaçadas de Extinção, Diário Oficial da União, Brasília. Retrieved from https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2020/P_mma_148_2022_altera_anexos_P_mma_443_444_445_2014_atualiza_especies_ameacadas_extincao.pdf.

R Core Team, 2022. A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna. Retrieved from http://www.r-project.org/index.html.

Reys-Ramírez, H., A. Tripp-Valdez, F. R. Elorriaga-Verplancken, A. Piñón-Gimate, M. I. Z. Rejón & F. Galván-Magaña, 2022. Feeding guilds among batoids in the northwest coast of the Baja California Sur. Mexico. Marine Ecology 43: e12728. https://doi.org/10.1111/maec.12728.

Rezende, G. A., R. R. Capitoli & C. M. Vooren, 2015. Dieta e morfologia da cabeça, boca e dentição de duas raias simpátricas, *Myliobatis goodei* e *M. ridens* (Batoidea: Myliobatiformes). Boletim Do Museu De Biologia Mello Leitão 37: 255–270.

Rosa, R. S. & O. B. F. Gadig, 2014. Conhecimento da diversidade dos Chondrichthyes marinhos no Brasil: a contribuição de José Lima de Figueiredo. Arquivos De Zoologia 45: 89–104. https://doi.org/10.11606/issn.2176-7793.v45iespp89-104.

Ruocco, N. L. & O. L. Lucifora, 2016. Ecological singularity of temperate mesopredatory myliobatoidei rays (Chondrichthyes: Myliobatiformes). Marine and Freshwater Research 68: 1098–1111. https://doi.org/10.1071/MF15469.

Rupp, A. & H. Bornatowski, 2021. Food web model to assess the fishing impacts and ecological role of elasmobranchs in a coastal ecosystem of Southern Brazil. Environmental Biology of Fishes 104: 905–921. https://doi.org/10.1007/s10641-021-01120-9.

Siepielski, A. M. & M. A. Mcpeek, 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology 91: 3153–3164. https://doi.org/10.1890/10-0154.1.

Slobodchikoff, C. N. & W. C. Schulz, 1980. Measures of Niche Overlap. Ecology 61: 1051–1055. https://doi.org/10.2307/1936823.

Soares, L., C. L. Rossi-Wongtschowski, L. A. C. Alvares, E. Y. Muto & M. L. A. Gasalla, 1992. Grupos tróficos de peixes demersais da plataforma continental interna de Ubatuba, Brasil. I. Chondrichthyes. Boletim Do Instituto Oceanográfico 40: 79–85. https://doi.org/10.1590/S1679-87591992000100006.

Sommerville, E., M. Platell, W. T. White, A. A. Jones & I. Potter, 2011. C. Partitioning of food resources by four abundant, co-occurring elasmobranch species: relationships between diet and both body size and season. Marine and Freshwater Research 62: 54–65. https://doi.org/10.1071/MF10164.

Stevens, J. D., R. Bonfil, N. K. Dulvy & P. A. Walker, 2000. The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems.

ICES Journal of Marine Science 57: 476–494. https://doi.org/10.1006/jmsc.2000.0724.

The IUCN Red List of Threatened Species (IUCN)., (2020). Version 2020, Retrieved from https://www.iucnredlist.org.

Tricas, T. C., 1985. Feeding ethology of the White Shark, *Carcharodon carcharias*. Memoirs 9: 81–91.

Vaudo, J. J. & M. R. Heithaus, 2011. Dietary niche overlap in a nearshore elasmobranch mesopredator Community. Marine Ecology Progress Series 425: 247–260. https://doi.org/10.3354/meps08988.

Viana, A. F., J. L. Valentin & M. Vianna, 2017. The Feeding ecology of elasmobranch species in southeastern Brazil. Neotropical Ichthyology 15: e160176. https://doi.org/10.1590/1982-0224-20160176.

Vooren, C. M., R. P. Lessa, S. Klippel, 2005. Biologia e status de conservação da viola *Rhinobatos horkelii.* In Vooren, C. M., S. Klippel (eds), Ações para a conservação de tubarões e raias no sul do Brasil, Igaré, Porto Alegre: 33–56.

Wetherbee, B. M., E. Cortés, J. J. Bizarro, 2012. Food consumption and feeding habits. In Carrier, J. C., J. A. Musick & M. R. Heithaus (eds), Biology of Sharks and their Relatives second ed, RC Press, USA: 239–264. https://doi.org/10.1201/b11867-11.

Wilga, C. D., P. J. Motta & C. P. Sanfordz, 2007. Evolution and ecology of feeding in elasmobranch. Integrative and Comparative Biology 47: 55–69. https://doi.org/10.1093/icb/icm029.

Yokota, L. & R. P. Lessa, 2006. A nursery area for sharks and rays in Northeastern Brazil. Environmental Biology of Fishes 75: 349–360. https://doi.org/10.1007/s10641-006-0038-9.

Zaret, M. & S. Rand, 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336–342. https://doi.org/10.2307/1934593.