

# Feeding comparisons of four batoids (Elasmobranchii) in coastal waters of southern Brazil

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*Food partitioning between species is a common strategy for avoiding resource competition which allows the coexistence of two or more species in the same place. In order to evaluate the feeding of four species of batoids regularly caught by artisanal fisheries in southern Brazil, the present study aimed to analyse and compare the diet of the four batoid species. The Chola guitarfish, *Rhinobatos percellens*, had a specialized diet, consisting predominantly of blue crabs *Callinectes* sp., followed by teleost fish. The Lesser guitarfish *Zapteryx brevirostris* also had a very specialized diet, consuming mainly on *Polychaeta*, followed by *Caridea* shrimp. The Cownose ray, *Rhinoptera bonasus*, fed mainly on *Ophiuroidea*, followed by *Gastropoda* and *Bivalvia*. Finally, the Rio skate *Rioraja agassizi*, fed on teleost fish, *Gammaridae*, *Caridea* shrimp and *Dendrobranchiata* shrimp. An analysis of similarity showed significant differences among species in their diet. The trophic levels of the batoids in this study are <4.0, placing them in intermediate trophic levels. The analysis of the diets indicates that feeding differs substantially among the four species, suggesting a partitioning of food resources available in the environment.*

**Keywords:** Rajiformes, Myliobatiformes, diet, partitioning, skates, guitarfish

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## INTRODUCTION

The degree of overlap in the use of available resources among closely related and sympatric elasmobranch species is variable, and interactions are associated, for example, with spatial fluctuations (e.g. *Navia et al.*, 2007; Barausse *et al.*, 2010; Valls *et al.*, 2011), ontogenetic development (e.g. *Navia et al.*, 2011; Brickle *et al.*, 2003; Barausse *et al.*, 2010; Bornatowski *et al.*, 2012) and competition (e.g. Ellis *et al.*, 1996; *Navia et al.*, 2007; Treloar *et al.*, 2007). Food partitioning between species is a common strategy for avoiding resource competition, which allows the coexistence of two or more sympatric species (Schoener, 1974).

Smaller elasmobranchs (<150 cm total length) are commonly consumed by large sharks and are considered mesopredators (Ferretti *et al.*, 2010). The reduction of top predators can lead to a proliferation of mesopredators, leading to a destabilization of marine communities through trophic cascades (Myers & Worm, 2003; Myers *et al.*, 2007; Ritchie & Johnson, 2009; Heithaus *et al.*, 2010; *Navia et al.*, 2010; Bornatowski *et al.*, 2014). Given the influence of mesopredator

population growth on the marine food chain, understanding diet and competition levels in mesopredator elasmobranchs is fundamentally important. These dietary data facilitate construction of network trophic interaction models, which are essential for predicting the possible effects of species presence or absence in an ecosystem (*Navia et al.*, 2010; Braga *et al.*, 2012; Bornatowski *et al.*, 2014).

Batoid fish regularly occupy intermediate trophic levels (total length <4.0) in their communities (e.g. Muto *et al.*, 2002; Mabragna & Gilberto, 2007; *Navia et al.*, 2007; Vaudo & Heithaus, 2009; Barbini & Lucifora, 2011; Bornatowski *et al.*, 2010; López-García *et al.*, 2012) and they are also present in the diet of large sharks (Vaudo & Heithaus, 2011). Therefore, batoids can be considered mesopredators that provide an important link between top predators and lower trophic levels in the marine ecosystem, and play an important role in marine ecosystem dynamics (Vaudo & Heithaus, 2011).

The presence of batoid fish is common in fisheries along the southern Brazilian coast (Vooren & Klippel, 2005; Costa & Chaves, 2006) which target commercially important species such as *Paralichthys* spp., *Micropogonias furnieri*, *Genidens barbatus* and *Cynoscion* spp. In order to evaluate the competition between species of batoids regularly caught by artisanal fisheries in southern Brazil (Costa & Chaves, 2006; Bornatowski *et al.*, 2009), the present study aimed to analyse and compare the diet of the four batoid species, *Rhinobatos percellens*, *Zapteryx*

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*brevirostris*, *Rioraja agassizi* and *Rhinoptera bonasus*. The results will provide useful information on the trophic ecology of captured species along the southern Brazilian coast, thus helping us to explain the coexistence and the role played by these mesopredator batoids on the marine food webs in this area.

## MATERIALS AND METHODS

Observations of fish landings were conducted at the artisanal fishing communities of the central coast of the State of Paraná, southern Brazil (from 25°49'S 48°31'W to 25°36'S 48°20'W) (Figure 1) from April 2010 to March 2012. Mesh sizes used by the gillnet fishery include 7, 9, 11, 16 and 18 cm stretch mesh. Gillnets (no pre-established sizes) were set a maximum of 20 km from the coast in water depths up to 20 m.

For *R. percellens* and *Z. brevirostris* the total length (TL, cm) was recorded, while for *R. agassizi* and *R. bonasus* total disc width (DW, cm) was recorded for each individual. Stomachs were removed, fixed in 10% formalin and subsequently analysed in the laboratory. The food items were separated, identified to the lowest possible taxonomic level, counted, and weighed. We used the main prey to compare diet between species (i.e. fish, Dendrobranchiata, Caridea, Gammaridae, Brachyura, Cephalochordata, Ophiuroidea, Gastropoda and Bivalvia).

In order to investigate the effect of sample size in estimating the batoids' diets (Ferry & Cailliet, 1996; Cortés, 1997), cumulative prey curves were created. A cumulative prey curve was constructed using the Shannon–Wiener method to evaluate whether the number of sampled stomachs was sufficient to describe the diversity of diet of four batoid species, and the samples were randomized 50 times with the routine 'sample-based rarefaction' using the EstimateS 7.5 software (Colwell, 2005). Sample size was considered sufficient if the curves visually reached an asymptote (Magurran, 2004).

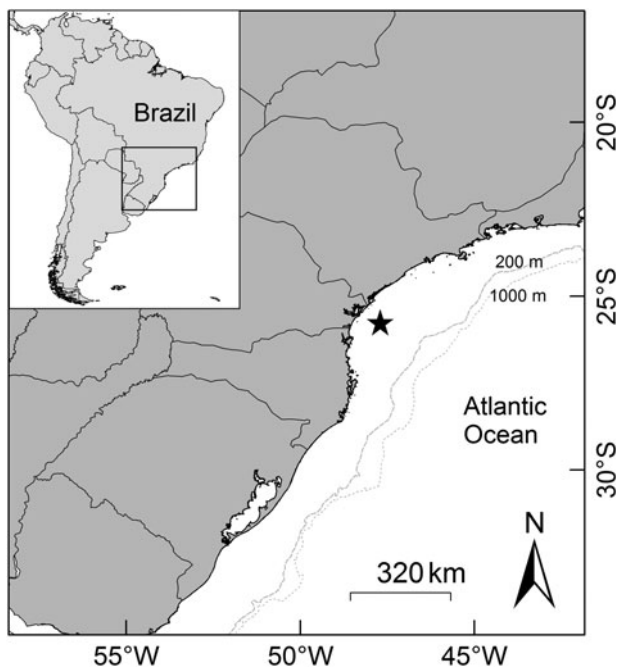


Fig. 1. Central coast of the State of Paraná, southern Brazil. Black star represents where the sampling was conducted.

The importance of various prey taxa to the batoids' diets, was assessed by calculating the index of relative importance (IRI; Pinkas *et al.*, 1971):

$$\text{IRI} = (\%N + \%W) * \%FO,$$

where %N is the number of a given prey type as a percentage of the total number of prey; %W is the weight of a given prey type as a percentage of the total weight of prey; and %FO is the percentage of frequency of occurrence of each prey type (Hyslop, 1980). The IRI values were standardized in percentage values according to Cortés (1997):

$$\% \text{IRI} = (\text{IRI} / \sum \text{IRI}) * 100$$

Diet niche breadth was estimated using Levin's ( $B_i$ ):  $B_i = 1 / \sum P_j^2$ , where  $P_j$  is the fraction by IRI of each food in the diet ( $\sum P_j = 1$ ) (Krebs, 1999). The values were standardized ( $B_A$ ) so that it ranges from 0 to 1 by using the equation  $B_A = (B_i - 1) / (N - 1)$ , where N is the number of classes (Krebs, 1999). Low values indicate diets dominated by few prey items (specialist predators) while higher values indicate generalist diets.

Niche overlap was calculated with the IRI of each prey using the Pianka index with EcoSim 7.72 software (Gotelli & Entsminger, 2005). Overlap was considered biologically significant when values exceed 0.60 (Zares & Rand, 1971). The overlaps found were compared with a distribution of expected values based on simulations (1000 repetitions) of a null model to evaluate the statistical significance of estimated overlaps. Observed values were considered statistically different from the null distribution values if they were higher or lower than 95% of the simulated indices (Gotelli & Graves, 1996). Lower values suggest differences in diets or resource partitioning, while higher values suggest similar diets or strong resource competition.

The standardized trophic levels of batoids were calculated using the trophic index (TR), proposed by Cortés (1999):

$$\text{TR} = 1 + \left( \sum_{j=1}^n P_j * \text{TR}_j \right),$$

where  $\text{TR}_j$  is the trophic level of each prey taxon  $j$  (see Cortés, 1999) and  $P_j$  is the proportion of each prey taxa in the diet based on %IRI values.

To test for variation between the diets of batoid species, a similarity matrix with the transformed estimated contribution values of food items, based on weight of preys, was then generated using the Bray–Curtis similarity coefficient. Diet similarity was analysed with non-metric multidimensional scaling analysis (nMDS). Data were then investigated using one-way analysis of similarity (ANOSIM), with individuals as samples and species as factor. This test was used to verify similarities (distance) within defined groups (factors = species) against similarities between groups and also calculates the statistic  $\rho = R$ , which varies between  $-1$  and  $+1$  (Clarke & Gorley, 2006). The significance ( $P$  values) was assessed using a random permutation test 999 times and  $R$  was calculated for each total permutation. In the context of this study, the  $R$  value of zero represents the null hypothesis (there are no differences between our factor groups or subset samples—stomach),

**Table 1.** Diet composition of four batoid species caught along the Paraná coast, southern Brazil expressed in percentage by number (%N), weight (%W), frequency of occurrence (%FO), and percentage of the index of relative importance of food (% IRI).

| Food items                     | <i>Rioraja agassizi</i> |              |              |              | <i>Zapteryx brevirostris</i> |              |              |              | <i>Rhinobatos percellens</i> |              |              |              | <i>Rhinoptera bonasus</i> |              |              |              |
|--------------------------------|-------------------------|--------------|--------------|--------------|------------------------------|--------------|--------------|--------------|------------------------------|--------------|--------------|--------------|---------------------------|--------------|--------------|--------------|
|                                | %N                      | %W           | %FO          | %IRI         | %N                           | %W           | %FO          | %IRI         | %N                           | %W           | %FO          | %IRI         | %N                        | %W           | %FO          | %IRI         |
| <b>TELEOSTEI</b>               | <b>17.82</b>            | <b>60.18</b> | <b>58.82</b> | <b>36.57</b> | <b>6.07</b>                  | <b>17.88</b> | <b>13.13</b> | <b>3.17</b>  | <b>22.98</b>                 | <b>63.98</b> | <b>50.51</b> | <b>33.50</b> | <b>3.54</b>               | <b>23.19</b> | <b>16.67</b> | <b>6.24</b>  |
| Teleostei unidentified         | 12.40                   | 0.15         | 47.06        | 23.92        | 5.14                         | 16.66        | 11.11        | 4.67         |                              |              |              |              | 3.54                      | 23.19        | 16.67        | 7.31         |
| <i>Symphurus tessellatus</i>   | 1.55                    | 0.08         | 5.88         | 0.39         |                              |              |              |              | 6.93                         | 25.40        | 14.81        | 12.24        |                           |              |              |              |
| <i>Etopus crossotus</i>        | 0.78                    | 0.09         | 2.94         | 0.10         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| <i>Diplectrum radiale</i>      | 0.78                    | 0.04         | 2.94         | 0.10         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| Family Congridae               | 2.33                    | 0.33         | 8.82         | 0.95         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| Family Paralichthyidae         |                         |              |              |              |                              |              |              |              | 4.33                         | 7.99         | 9.26         | 2.92         |                           |              |              |              |
| <i>Anchoa</i> sp.              |                         |              |              |              | 0.93                         | 1.09         | 2.02         | 0.08         | 0.87                         | 0.31         | 1.85         | 0.06         |                           |              |              |              |
| <i>Urophycis brasiliensis</i>  |                         |              |              |              |                              |              |              |              | 0.87                         | 5.10         | 1.85         | 0.28         |                           |              |              |              |
| <i>Larimus</i> sp.             |                         |              |              |              |                              |              |              |              | 0.87                         | 3.19         | 1.85         | 0.19         |                           |              |              |              |
| Atherinomorpha                 |                         |              |              |              |                              |              |              |              | 0.87                         | 2.13         | 1.85         | 0.14         |                           |              |              |              |
| <i>Pomadasy corvinaeformis</i> |                         |              |              |              |                              |              |              |              | 1.73                         | 4.92         | 3.70         | 0.63         |                           |              |              |              |
| <b>CRUSTACEA</b>               | <b>77.51</b>            | <b>39.20</b> | <b>67.64</b> | <b>62.93</b> | <b>44.85</b>                 | <b>40.40</b> | <b>68.68</b> | <b>59.00</b> | <b>75.32</b>                 | <b>35.26</b> | <b>78.79</b> | <b>66.46</b> | <b>3.54</b>               | <b>1.24</b>  | <b>12.50</b> | <b>0.83</b>  |
| Brachyura                      | 7.75                    | 0.13         | 23.53        | 7.52         | 1.40                         | 2.44         | 3.03         | 0.22         | 0.87                         | 0.09         | 1.85         | 0.05         |                           |              |              |              |
| Unidentified Crustacea         | 4.65                    | 0.04         | 17.65        | 3.35         | 1.40                         | 1.53         | 2.02         | 0.11         | 4.33                         | 0.55         | 9.26         | 1.15         |                           |              |              |              |
| Shrimp remains                 |                         |              |              |              |                              |              |              |              | 2.60                         | 0.82         | 4.63         | 0.40         |                           |              |              |              |
| <i>Leptochela serratorbita</i> | 14.73                   | 0.02         | 14.71        | 8.79         | 11.21                        | 4.91         | 17.17        | 5.34         | 8.66                         | 1.07         | 7.41         | 1.84         |                           |              |              |              |
| Gammaridae                     | 21.71                   | 0.02         | 26.47        | 23.29        | 1.40                         | 0.06         | 2.02         | 0.06         | 4.33                         | 0.34         | 5.56         | 0.66         |                           |              |              |              |
| Unidentified Caridea           | 16.28                   | 0.05         | 32.35        | 21.40        | 15.42                        | 14.91        | 28.28        | 16.53        | 5.63                         | 0.49         | 4.63         | 0.72         | 3.54                      | 1.24         | 12.50        | 0.98         |
| <i>Alpheus heterochaelis</i>   | 2.33                    | 0.01         | 8.82         | 0.83         | 2.34                         | 1.90         | 5.05         | 0.41         | 2.16                         | 0.27         | 2.78         | 0.17         |                           |              |              |              |
| <i>Ogyrides alphaerostris</i>  |                         |              |              |              |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| Unidentified Penaeidae         | 6.20                    | 0.02         | 23.53        | 5.93         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| <i>Litopenaeus schmitti</i>    | 0.78                    | 0.01         | 2.94         | 0.09         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| <i>Acetes</i> sp.              | 3.10                    | <0.01        | 8.82         | 1.11         |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| Unidentified Dendrobranchiata  |                         |              |              |              | 0.93                         | 1.14         | 2.02         | 0.08         | 3.46                         | 0.50         | 7.41         | 0.75         |                           |              |              |              |
| <i>Pleoticus muelleri</i>      |                         |              |              |              | 2.80                         | 2.28         | 5.05         | 0.49         | 7.79                         | 1.10         | 10.19        | 2.31         |                           |              |              |              |
| <i>Sicyonia dorsalis</i>       |                         |              |              |              | 1.40                         | 0.69         | 3.03         | 0.12         |                              |              |              |              |                           |              |              |              |
| <i>Xiphopenaeus kroyeri</i>    |                         |              |              |              |                              |              |              |              | 2.16                         | 0.66         | 4.63         | 0.33         |                           |              |              |              |
| Hippidae                       |                         |              |              |              | 0.93                         | 3.03         | 2.02         | 0.15         |                              |              |              |              |                           |              |              |              |
| Isopoda                        |                         |              |              |              | 3.27                         | 0.41         | 7.07         | 0.50         |                              |              |              |              |                           |              |              |              |
| Cladocera                      |                         |              |              |              | 0.47                         | 0.04         | 1.01         | 0.01         |                              |              |              |              |                           |              |              |              |
| Callianassidae                 |                         |              |              |              | 0.93                         | 6.36         | 2.02         | 0.28         |                              |              |              |              |                           |              |              |              |
| <i>Callinectes</i> sp.         |                         |              |              |              | 0.93                         | 1.25         | 2.02         | 0.09         | 30.30                        | 25.45        | 46.30        | 65.98        |                           |              |              |              |
| <i>Arenaeus cribrarius</i>     |                         |              |              |              |                              |              |              |              | 1.73                         | 3.17         | 3.70         | 0.46         |                           |              |              |              |
| Stomatopoda                    |                         |              |              |              |                              |              |              |              | 0.87                         | 0.11         | 1.85         | 0.05         |                           |              |              |              |
| <b>POLYCHAETA</b>              | <b>4.65</b>             | <b>0.61</b>  | <b>11.76</b> | <b>0.49</b>  | <b>41.58</b>                 | <b>24.71</b> | <b>52.52</b> | <b>35.08</b> |                              |              |              |              | <b>12.39</b>              | <b>4.27</b>  | <b>20.83</b> | <b>4.86</b>  |
| Unidentified                   | 4.65                    | <0.01        | 11.76        | 2.22         | 41.58                        | 24.53        | 51.51        | 65.65        |                              |              |              |              | 12.39                     | 4.27         | 20.83        | 5.69         |
| <b>CEPHACHORDATA</b>           |                         |              |              |              |                              |              |              |              |                              |              |              |              |                           |              |              |              |
| Amphioxus                      |                         |              |              |              | <b>7.48</b>                  | <b>16.99</b> | <b>11.11</b> | <b>2.73</b>  |                              |              |              |              |                           |              |              |              |
| <b>MOLLUSCA</b>                |                         |              |              |              |                              |              |              |              |                              |              |              |              | <b>49.55</b>              | <b>21.68</b> | <b>41.66</b> | <b>41.60</b> |

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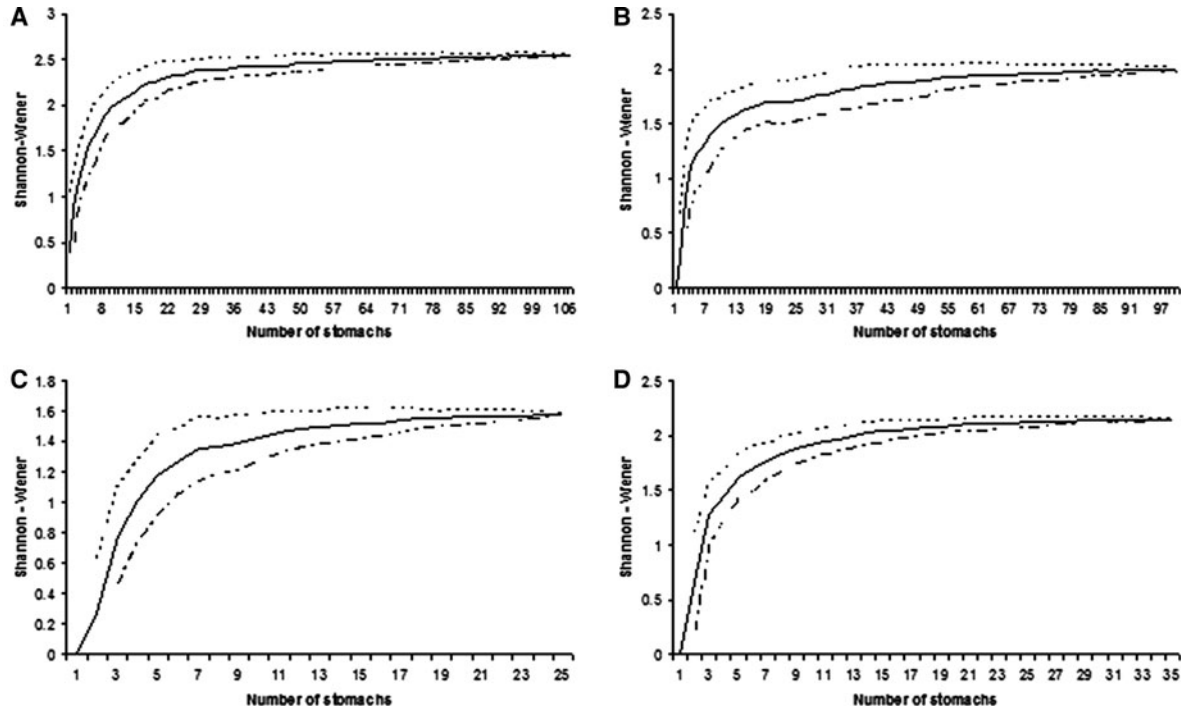


Fig. 2. Cumulative average (solid line) and standard deviation (dotted lines) of Shannon – Wiener diversity index for samples of studied batoid species in southern Brazil: (A) *Rhinobatos percellens*; (B) *Zapteryx brevirostris*; (C) *Rhinoptera bonasus*; (D) *Rioraja agassizi*.

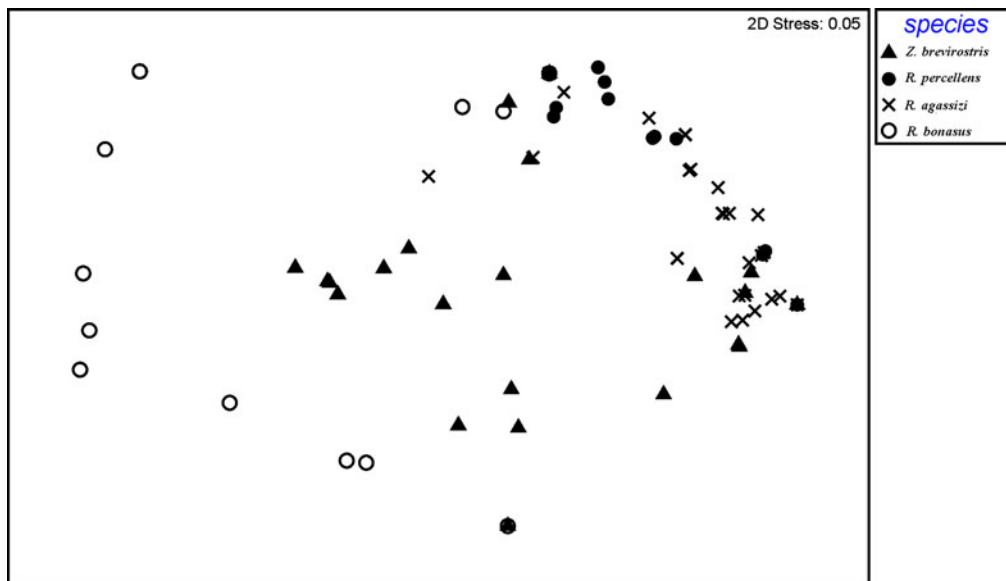


Fig. 3. Non-metric multidimensional scaling between the four studied species of batoids in southern Brazil.

Table 2. Analysis of similarities pairwise tests for all four species of batoids on the southern coast of Brazil.

| Species × species                             | R significance |       |
|---|----------------|-------|
|   | Statistics     | P     |
| <i>Z. brevirostris</i> × <i>R. percellens</i> | 0.435          | 0.001 |
| <i>Z. brevirostris</i> × <i>R. agassizi</i>   | 0.408          | 0.001 |
| <i>Z. brevirostris</i> × <i>R. bonasus</i>    | 0.311          | 0.001 |
| <i>R. percellens</i> × <i>R. agassizi</i>     | 0.111          | 0.001 |
| <i>R. percellens</i> × <i>R. bonasus</i>      | 0.423          | 0.001 |
| <i>R. agassizi</i> × <i>R. bonasus</i>        | 0.660          | 0.001 |

(Table 3). The most-observed prey items that contributed to the dissimilarity were Polychaeta (48.5%) and Caridea (45.6%) in *Z. brevirostris*, Brachyura (48.7%) and fish (46.7%) in *R. percellens*, Dendrobranchiata (53.5%) and fish (42.3%) in *R. agassizi*, and Ophiuroidea (48.2%), Gastropoda (18.2%), Bivalvia (13.5%), Polychaeta (9.3%), and fish (9.2%) in *R. bonasus*.

There was no feeding overlap among species (Table 4). The trophic levels of the batoids in this study are <4.0, placing them in intermediate trophic levels. The values were 3.4, 3.5, 3.6, and 3.7 for *R. bonasus*, *Z. brevirostris*, *R. percellens*, and *R. agassizi*, respectively.



**Table 3.** Items that contributed most to the dissimilarity between groups (> 10%). Dissimilarity percentages are expressed in bold in the column headings. Zb, *Zapteryx brevirostris*; Rp, *Rhinobatos percellens*; Ra, *Rioraja agassizi*; Rb, *Rhinoptera bonasus*.

|                  | <b>Zb × Rp(91%)</b> | <b>Zb × Ra(91%)</b> | <b>Rp × Ra(75%)</b> | <b>Zb × Rb(90%)</b> | <b>Rp × Rb(93%)</b> | <b>Ra × Rb(93%)</b> |
|------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| Fish             | 22.7                | 21.9                | 30.7                | –                   | 23.1                | 22.5                |
| Dendrobranchiata | –                   | 24.9                | 29.9                | –                   | –                   | 24.4                |
| Brachyura        | 22.7                | –                   | 27.6                | –                   | 22.2                | –                   |
| Polychaeta       | 20.2                | 20.2                | –                   | 21.9                | –                   | –                   |
| Caridea          | 20.8                | 19.5                | –                   | 20.4                | –                   | –                   |
| Ophiuroidea      | –                   | –                   | –                   | –                   | 16.0                | 16.0                |
| Gastropoda       | –                   | –                   | –                   | –                   | 10.0                | 10.0                |

**Table 4.** Feeding overlap using the Pianka index for all four species of batoids on the southern coast of Brazil.

|                        | <i>Z. brevirostris</i> | <i>R. percellens</i> | <i>R. agassizi</i> | <i>R. bonasus</i> |
|------------------------|------------------------|----------------------|--------------------|-------------------|
| <i>Z. brevirostris</i> | 1                      | 0.049                | 0.049              | 0.351             |
| <i>R. percellens</i>   |                        | 1                    | 0.469              | 0.061             |
| <i>R. agassizi</i>     |                        |                      | 1                  | 0.003             |
| <i>R. bonasus</i>      |                        |                      |                    | 1                 |

## DISCUSSION

In this study, *R. percellens* fed mainly on blue crabs *Callinectes* sp., and, to a lesser extent, on benthic teleost fish (e.g. flatfish). A study conducted more to the south of the Paraná coast found a similar diet for *R. percellens*, which ate shrimps, Brachyura crustaceans and teleost fish (Bornatowski *et al.*, 2010). However, studies in estuarine regions have found *R. percellens* diet to lack significant quantities of Brachyura crustaceans and teleost fish (Carmo *et al.*, unpublished data). It is possible that *R. percellens* present ontogenetic variation in their diet, because specimens studied by Carmo *et al.* (unpublished data) were smaller than those analysed in this paper and in comparison to animals analysed in the border region between Paraná and Santa Catarina (Bornatowski *et al.*, 2010). However, other hypotheses are that individuals use different food resources in areas occupied by other species, thereby avoiding interspecific competition or also could be due to different food availability in different locations.

In contrast to the present work, a study conducted on the São Paulo coast showed that *Z. brevirostris* exhibited a preference for Decapoda, followed by Polychaeta, Amphipoda, Isopoda and Cumacea (Soares *et al.*, 1992; Marion *et al.*, 2011). In another study on the coast of Argentina, Amphipoda, Polychaeta and Cephalochordata were the most abundant items in the diet (Barbini *et al.*, 2011), corroborating the results of the present study mainly by the considerable presence of Cephalochordata. As both regions are located further south in the Atlantic, it is possible that variation in prey abundance occurs, thus forcing this species to feed on different items exhibiting different behaviour between regions to avoid competition among species.

Studies conducted with *R. agassizi* on the coast of São Paulo have revealed a diet consisting mainly of crustaceans, teleost fish and Polychaeta (Soares *et al.*, 1999; Muto *et al.*, 2001). On the coast of Argentina, crustaceans were also the most abundant items (shrimps, crabs and amphipods), followed by teleost fish (Barbini *et al.*, 2011). These results support the analysis of the present study, where crustaceans and fish have similar importance in the diet of *R. agassizi*.

Other studies have suggested that *R. bonasus* feeds on Mollusca, influencing the abundance of these prey and affecting the commercial bivalve industry (Orth 1975; Krauter & Castagna, 1980; Smith & Merriner, 1985; Peterson *et al.*, 2001). However, some studies have shown that high consumption of molluscs is not common to all locations where the species is observed. In the present study, *R. bonasus* demonstrated a preference for Echinodermata (Ophiuroidea), followed by gastropods and bivalves. In a study conducted in the Gulf of Mexico, polychaete worms dominated the stomach contents of *R. bonasus*, with low numbers of bivalve molluscs (Craig *et al.*, 2010). In an estuarine area of Port Charlotte, Florida, USA, another study found high consumption of crustaceans by *R. bonasus*, followed by polychaete worms and, finally, bivalve molluscs (Collins *et al.*, 2007). The high consumption of Ophiuroidea by *R. bonasus* in the present study was also reported for a congener, *R. steindachneri*, on the Colombian coast (Navarro-González *et al.*, 2012).

The body pattern of batoids enables predation on benthic organisms (Moyle & Cech Jr, 1982) because these animals have a ventral mouth with high mandibular protrusion, making them capable of feeding on prey associated with the bottom. They also exhibit a high degree of interspecific variation in jaw and teeth morphology, showing different feeding performance and thereby allowing a widely varied diet (Goiten *et al.*, 1998; Wilga & Motta, 1998; Dean *et al.*, 2007). In fact, besides the anti-predatory tactics, abundance of prey in the environment, and interspecific competition, food ingestion is highly dependent on the morphology and behaviour of the predator (Moyle & Cech Jr, 1982; Heithaus 2004). The dietary differences observed between the studied species seem to be related to behavioural and mechanical versatility of feeding apparatus (mouth and jaws structure) of each species (Dean *et al.*, 2007). *Rhinobatos percellens*, for example, has relatively larger mouth, allowing the consumption of elusive larger prey such as blue crabs and flatfish (Dean *et al.*, 2007). *Rhinoptera bonasus*, in contrast, has large dental plates and functional specialization for durophagy, making possible the consumption of hard-shelled organisms (Smith & Merriner 1987; Summers 2000; Collins *et al.*, 2007). *Zapteryx brevirostris* has a smaller mouth, allowing the consumption of small prey such as small shrimps and Polychaeta. Despite the relatively smaller mouth in a V-shape (Dean *et al.*, 2007), *R. agassizi* feeds on small prey items such as Gammaridae, but also is capable of consuming larger preys such as teleost fish. Future studies on the feeding apparatus (jaw and teeth morphology) related to prey items are needed to evaluate with precision the feeding performance of batoid species.

The sharing of resources can be a facilitating mechanism in explaining the observed coexistence of species (Schoener, 1974; O'Shea *et al.*, 2013). In a study conducted off the coast of Tasmania, Australia, two sympatric rays coexisted in the absence of dietary overlap (Yick *et al.*, 2011). In contrast, a study of six species of rays on the Australian coast found some diet overlap, suggesting the presence of degrees of resource partitioning (Treloar *et al.*, 2007). On the coast of Argentina, two sympatric rays, *Psammobatis normani* and *P. rudis*, also showed dietary overlap, revealing a degree of competition for resources (Mabragaña & Gilberto, 2007). Despite marginal overlapping between *R. percellens* and *R. agassizi* studied here, the diets of the batoids indicate that feeding differs substantially among the four species, suggesting a partitioning of food resources available in the environment. Although results of the present study indicate feeding partitioning between the four batoid species, future studies on spatial and temporal distributions of species and the abundance of prey in the area of the present study are needed to determine the feeding strategies of each species. In addition, more comparisons with other benthic species (e.g. inshore lizardfish *Synodus foetens*, flatfish species, the Brazilian electric ray *Narcine brasiliensis*, stingrays *Dasyatis* spp., the Brazilian cownose ray *Rhinoptera brasiliensis* and others) are needed to verify the levels of competitions between all communities.

All four species had trophic levels <4.0, thus characterizing them as intermediate food chain predators (Cortés 1997; Ebert & Bizarro, 2007). The study of mesopredators is extremely important because the population decline of large predators (such as by fishing pressure) can lead to substantial increases in mesopredator populations, causing cascading trophic effects within the ecosystem (Ritchie & Johnson, 2009; Heithaus *et al.*, 2008; Navia *et al.*, 2010). For instance, the cownose ray, *R. bonasus*, has been the subject of studies regarding its population impact on bivalve molluscs in the North Atlantic (e.g. Orth, 1975; Kraeuter & Castagna, 1980; Smith & Merriner, 1987; Peterson *et al.*, 2001). Due to a high degree of feeding specialization, *R. bonasus* is a candidate to be a strong interactor (Paine, 1969), with a strong influence on cascading effects (Power *et al.*, 1996; Power, 1997; Myers *et al.*, 2007).

Three of the four species analysed, *R. percellens*, *R. agassizi* and *R. bonasus*, are found in the stomach contents of large predators in the study area (e.g. *Sphyrna lewini*, *Carcharias taurus*, *Carcharhinus obscurus*, *C. limbatus* and *Galeocerdo cuvier*) (Bornatowski, unpublished data). These data reveal the importance of these batoid species as a link between the higher and lower levels of the regional marine food chain. Thus, future studies on the diet and trophic relationships between large sharks and these and other species in the area are required to understand the real role of mesopredator elasmobranchs in food chains and ecosystem resource availability.

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## REFERENCES

- Barbini S.A. and Lucifora L.O. (2011) Feeding habits of the Rio skate, *Rioraja agassizi* (Chondrichthyes: Rajidae), from off Uruguay and north Argentina. *Journal of the Marine Biological Association of the United Kingdom* 91, 1175–1184.
- Barbini S.A., Lucifora L.O. and Hozbor N.M. (2011) Feeding habits and habitat selectivity of the shortnose guitarfish, *Zapteryx brevirostris* (Chondrichthyes, Rhinobatidae), off north Argentina and Uruguay. *Marine and Biological Research* 7, 365–377.
- Barausse A., Baremore I.E., Murie D.J. and Carlson J.K. (2010) Seasonal and size-related differences in diet of the Atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. *Aquatic Biology* 8, 125–136.
- Bornatowski H., Abilhoa V. and Charvet-Almeida P. (2009) Elasmobranchs of the Paraná Coast, southern Brazil, south-western Atlantic. *Marine Biodiversity Records* 2, e158. doi: <http://dx.doi.org/10.1017/S1755267209990868>.
- Bornatowski H., Robert M.C. and Costa L. (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.
- Bornatowski H., Heithaus M.R., Abilhoa V. and Corrêa M.F.M. (2012) Feeding of the Brazilian sharpnose shark *Rhizoprionodon lalandii* (Müller & Henle, 1839) from southern Brazil. *Journal of Applied Ichthyology* 28, 623–627.
- Braga R.R., Bornatowski H. and Vitule J.R.S. (2012) Feeding ecology of fishes: an overview of worldwide publications. *Reviews in Fish Biology and Fisheries* 22, 915–929.
- Bornatowski H., Navia A.F., Braga R.R., Abilhoa V. and Corrêa M.F.M. (2014) Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. *ICES Journal of Marine Science*. doi: [10.1093/icesjms/fsuo25](https://doi.org/10.1093/icesjms/fsuo25).
- Brickle P., Laptikhovskiy V.V., Pompert J. and Bishop A. (2003) Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Islands' shelf. *Journal of the Marine Biological Association of the United Kingdom* 83, 1119–1125.
- Clarke K.R. and Gorley R.N. (2006) *PRIMER v6: user manual*. Plymouth: PRIMER-E.
- Collins A.B., Heupel M.R. and Motta P.J. (2007) Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* 70, 1–20.
- Colwell R.K. (2005) *EstimateS version 7.5: Statistical estimation of species richness and shared species from samples*. Available from: <http://purl.oclc.org/estimates> (accessed 7 April 2014).
- 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.
- Cortés E. (1999) Standardized diet composition and trophic levels of sharks. *ICES Journal of Marine Science* 56, 707–717.
- Costa L. and Chaves P.T.C. (2006) Elasmobrânquios capturados pela pesca artesanal na costa sul do Paraná e norte de Santa Catarina,

- Brasil. *Biota Neotropica* 6, available at: <http://www.biotaneotropica.org.br/v6n3/pt/abstract/article+bno2706032006> (accessed 7 April 2014).
- Dean M.N., Bizzarro J.J. and Summers A.P. (2007) The evolution of cranial design, diet, and feeding mechanisms in batoid fishes. *Integrative and Comparative Biology* 47, 70–81.
- Ebert D.A. and Bizzarro J.J. (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* 80, 221–237.
- Ellis J.R., Pawson M.G. and Shackley S.E. (1996) The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 76, 89–106.
- Ferretti F., Worm B., Britten G.L., Heithaus M.R. and Lotze H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13, 1055–1071.
- Ferry L.A. and Caillet G.M. (1996) Sample size and data analysis: are we characterizing and comparing diet properly? In MacKinlay D. and Shearer K. (eds) *Feeding ecology and nutrition in fish. Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish*. International Congress on the Biology of Fishes. San Francisco, CA: American Fisheries Society, pp. 71–80.
- Goiten R., Torres F.S. and Signorini C.E. (1998) Morphological aspects related to feeding of two marine skates *Narcine brasiliensis* Olfers and *Rhinobatos horkelli* Müller & Henle. *Acta Scientiarum* 20, 165–169.
- Gotelli N.J. and Graves G.R. (1996) *Null models in ecology*. Washington, DC: Smithsonian Institution Press.
- Gotelli N.J. and Entsminger G.L. (2005) *EcoSim: Null models software for ecology, version 7.0*. Burlington: Kesity-Bear, Acquired Intelligence.
- Heithaus M.R. (2004) Predator–prey interactions. In Carrier J.C., Musick J.A. and Heithaus M.R. (eds) *Biology of sharks and their relatives*. Boca Raton, FL: CRC Press, pp. 487–521.
- Heithaus M.R., Frid A., Wirsing A.J. and Worm B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23, 202–210.
- Heithaus M.R., Frid A., Vaudo J.J., Worm B. and Wirsing A.J. (2010) Unraveling the ecological importance of elasmobranchs. In Carrier J.C., Musick J.A. and Heithaus M.R. (eds) *Biology of sharks and their relatives*. Boca Raton, FL: CRC Press, pp. 611–637.
- Hyslop E.J. (1980) Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17, 411–429.
- Krauter J.N. and Castagna M. (1980) Effects of large predators on the field culture of the hard clam *Mercenaria mercenaria*. *Fisheries Bulletin* 78, 538–540.
- Krebs C.J. (1999) *Ecological methodology*. Menlo Park, CA: Addison Wesley.
- Mabragaña E. and Gilberto D.A. (2007) Feeding ecology and abundance of two sympatric skates, the shortfin sand skate *Psammobatis normani* McEachran and the smallthorn sand skate *P. rudis* Gunther (Chondrichthyes, Rajidae), in the southwest Atlantic. *ICES Journal of Marine Science* 64, 1017–1027.
- Magurran A.E. (2004) *Measuring biological diversity*. Oxford: Blackwell Publishing.
- Marion C., Vaske-Junior T., Gadig O.B.F. and Martins I.A. (2011) Feeding habits of the shortnose guitarfish, *Zapteryx brevirostris* (Müller and Henle, 1841) (Elasmobranchii, Rhinobatidae) in south-eastern Brazil. *Brazilian Journal of Biology* 71, 83–89.
- Moyle P.B. and Cech Jr J.J. (1982) *Fishes: an introduction to ichthyology*. Englewood Cliffs, NJ: Prentice-Hall.
- Muto E.Y., Soares L.S.H. and Goitein R. (2001) Food resource utilization of the skates *Rioraja agassizii* (Müller & Henle, 1841) and *Psammobatis extenta* (Garman, 1913) on the continental Shelf off Ubatuba, south-eastern Brazil. *Revista Brasileira de Biologia* 61, 217–238.
- Myers R.A., Baum J.K., Shepherd T.D., Powers S.P. and Peterson C.H. (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846–1850.
- Myers R.A. and Worm B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Navarro-González J.A., Bohórquez-Herrera J., Navia A.F. and Cruz-Escalona V.H. (2012) Composición trófica de batoides en la plataforma continental frente a Nayarit y Sinaloa, México. *Ciencias Marinas* 38, 347–362.
- Navia A.F., Mejía-Falla P.A. and Giraldo A. (2007) Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. *BMC Ecology* 7, 8.
- Navia A.F., Cortés E. and Mejía-Falla P.A. (2010) Topological analysis of the ecological importance of elasmobranch fishes: a food web study on the Gulf of Tortugas, Colombia. *Ecological Modelling* 221, 2918–2926.
- Navia A.F., Torres A., Mejía-Falla P.A. and Giraldo A. (2011) Sexual, ontogenetic, temporal and spatial effects on the diet of *Urotrygon rogersi* (Elasmobranchii: Myliobatiformes). *Journal of Fish Biology* 78, 1213–1224.
- Orth R.J. (1975) Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. *Chesapeake Sciences* 16, 205–208.
- O’Shea O.R., Thums M., van Keulen M., Kempster R.M. and Meekan M.G. (2013) Dietary partitioning by five sympatric species of stingray (Dasyatidae) on coral reefs. *Journal of Fish Biology* 82, 1805–1820.
- Paine R.T. (1969) A note on trophic complexity and community stability. *American Naturalist* 103, 91–93.
- Peterson C.H., Fodrie F.J., Summerson H.C. and Powers S.P. (2001) Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129, 349–356.
- Pinkas L., Oliphant M.S. and Iverson I.L.K. (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. *California Fish and Game, Fisheries Bulletin* 152, 84 p.
- Power M.E. (1997) Estimating impacts of a dominant detritivore in a neotropical stream. *Trends in Ecology and Evolution* 12, 47–48.
- Power M.E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. and Paine R.T. (1996) Challenges in the quest for keystones. *BioScience* 46, 609–620.
- Ritchie E.G. and Johnson C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12, 982–998.
- Schoener T.W. (1974) Resource partitioning in ecological communities. *Science* 185, 27–39.
- Smith J.W. and Merriner J.V. (1985) Food habits and feeding behaviour of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries* 8, 305–310.
- Smith J.W. and Merriner J.V. (1987) Age and growth, movements and distribution of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Estuaries* 10, 153–164.
- Soares L.S.H., Rossi-Wongtschowski C.L.D.B., Álvares L.M.C., Muto E.Y. and Gasalla M.L.A. (1992) Grupos tróficos de peixes demersais da plataforma continental interna de Ubatuba, Brasil. I: Chondrichthyes. *Boletim do Instituto Oceanográfico* 40, 79–85.



- Summers A.P.** (2000) Stiffening the stingray skeleton—an investigation of durophagy in myliobatid stingrays (Chondrichthyes, Batoidea, Myliobatidae). *Journal of Morphology* 243, 113–126.
- Treloar M.A., Laurenson L.J.B. and Stevens J.D.** (2007) Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters. *Environmental Biology of Fishes* 80, 181–196.
- Valls M., Quetglas A., Ordines F. and Moranta J.** (2011) Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean). *Scientia Marina* 75, 633–639.
- Vaudo J.J. and Heithaus M.R.** (2009) Spatiotemporal variability in a sandflat elasmobranch fauna in Shark Bay, Australia. *Marine Biology* 156, 2579–2590.
- Vaudo J.J. and Heithaus M.R.** (2011) Dietary niche overlap in a near-shore elasmobranch mesopredator community. *Marine Ecology Progress Series* 425, 247–260.
- Vooren C.M. and Klippel S.** (2005) *Ações para a conservação de tubarões e raias no sul do Brasil*. Igaré, Porto Alegre, 262 pp.
- Wilga C.D. and Motta P.J.** (1998) Feeding mechanism of the Atlantic guitarfish *Rhinobatos lentiginosus*: modulation of kinematic and motor activity. *Journal of Experimental Biology* 201, 3167–3184.
- Yick J.L., Barnett A. and Tracey S.R.** (2011) Niche overlap and trophic resource partitioning of two sympatric batoids co-inhabiting an estuarine system in southeast Australia. *Journal of Applied Ichthyology* 27, 1272–1277.
- and
- Zares T.M. and Rand A.S.** (1971) Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52, 336–342.

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