Original Article

Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil

Hugo Bornatowski1,2*, Andrés Felipe Navia3, Raul Rennó Braga1,2, Vinícius Abilhoa1,2, and Marco Fábio Maia Corrêa1

1Universidade Federal do Paraná, Caixa Postal 19020, CEP 81531–980 Curitiba, PR, Brazil
2GPIc – Grupo de Pesquisas em Ictiofauna. Museu de História Natural Capão da Imbuia, Rua Prof. Benedito Conceição, 407, 82810–080, Curitiba, PR, Brazil
3Fundación colombiana para la investigación y conservación de tiburones y rayas, Carrera 60A No 11 – 39, Cali, Colombia

*Corresponding author: tel/fax: +55 41 3229 6734; e-mail: anequim.bio@gmail.com


Understanding the trophic interactions and the position of species within a foodweb is crucial if we want to understand the dynamics of marine communities and the impact individual components of the community have on trophic network compartments. Recent studies have indicated sharks and rays are important elements within foodwebs. In this study, we evaluated the ecological importance of sharks and rays in a subtropical ecosystem off the coast of southern Brazil by using topological analyses. We tested the hypotheses that some elasmobranchs can be considered key elements within the foodweb, and that large predators have topological importance (act as keystones), so that, when large predators are excluded, mesopredator elasmobranchs occupy higher topological positions. Our results indicate that Galeocerdo cuvier, Carcharhinus obscurus, Carcharias taurus, Sphyrna lewini and S. zygaena are species with large ecological function values and may exert a powerful influence over lower levels. These issues need to be considered by conservation and fishery management groups since it appears that ecosystem integrity may be compromised by reductions in the populations of large predators.

Carcharhinus obscurus, S. zygaena and Zapteryx brevirostris were found to be the elasmobranchs with largest values of centrality, and can, therefore, be considered key elements in the topological structure.

Keywords: Elasmobranchs, keystone species, mesopredators, topological importance, top predators.

Introduction

Understanding the ecological role of a species within an ecosystem depends largely on knowledge of its trophic relations (Pimm, 2002; Montoya et al., 2006; Braga et al., 2012). Comprehending these trophic interactions and the position of species within a foodweb is a crucial step in clarifying the dynamics of marine communities and the impacts individual components (i.e. species) have on trophic network compartments (Lucifora et al., 2009; Heithaus et al., 2013). Failure to recognize the importance of direct and indirect effects can lead to serious gaps in our understanding of the causes and consequences of disturbances in foodwebs (Montoya et al., 2005).

The effects of changes in one or more components within a foodweb may propagate intensely through the system, resulting in changes in the abundance and web connectivity of other species (Paine, 1969; Soule et al., 1988; Heithaus et al., 2008; Baum and Worm, 2009; Dunne, 2009). Local extinctions can trigger secondary extinctions or otherwise considerably influence populations of coexisting species through direct and indirect effects in the trophic network (Pimm and Lawton, 1980). An example of this is a trophic cascade, in which the reduction of a predator population changes the relative abundance of prey populations as they are freed from direct (predation) and indirect effects (e.g. apparent competition, exclusion competition, behaviour effects). This process occurs when populations of large predators decline, resulting in increases in populations of intermediate components (called “mesopredators”, see Ritchie and Johnson, 2009), consequently leading to reduction in the populations of the mesopredators’ prey (Paine 1969; Terborgh and Winter, 1980; Soule et al., 1988; Heithaus et al., 2008). However, increases in mesopredator populations have
primarily been documented in cold and temperate waters or in other low diversity environments. There are only a few studies reporting this effect in tropical trophic networks (Navia et al., 2012).

Recent studies suggest that sharks and rays are important elements within their foodwebs, and that reductions in the size of populations of large sharks can initiate trophic cascades through top-down effects (e.g. Stevens et al. 2000; Myers et al. 2007; Ferretti et al. 2010). However, regulation of populations in the lower levels of a food chain is not always directly related to predation on one or more specific prey species. Therefore, understanding the role of indirect effects is crucial for our complete understanding of energy flow through a foodweb (Stevens et al., 2000; Navia et al., 2010).

One approach for analysing trophic networks and determining the importance of indirect effects is to use a structural method that evaluates the position of individual species and identifies which species play key roles in the ecosystem (Jordán and Scheuring, 2002; Dambacher et al., 2010; Navia et al., 2010). Following this approach, we evaluate the importance of sharks and rays in a subtropical ecosystem off southern Brazil. In spite of population and ecosystem dynamics (e.g. functional response, density dependence, length and weight of organisms), the method applied in this study is static, however, it provides a realistic overview of the importance of elasmobranchs in foodwebs. We tested the hypothesis that sharks and rays can be considered key elements within the foodweb, and sought to answer two main questions. (i) Are sharks and rays important components in a foodweb to the extent that reductions in their populations could result in the disruption of connections within the web? (ii) Do large predators have topological importance (act as keystones), so that, when excluded, mesopredator elasmobranchs occupy higher positions?

**Material and methods**

### Data and trophic network

A predator–prey matrix was constructed from an analysis of the stomach contents of species in southern Brazil. To construct this matrix, we gathered information on 820 stomach contents of 15 elasmobranchs (see Appendix A) from artisanal fishery landings along the central coast of the state of Paraná, southern Brazil (Figure 1), from April 2010 to March 2012. Mesh sizes used by the gillnet fishery include 7-, 9-, 11-, 16-, 18- and 45-cm stretch mesh. Gillnets were set a maximum of 20 km from the coast in water depths up to 30 m. The 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. However, to reduce bias caused by different levels of prey quantification or inconsistency in the use of numerical indices among all studies examined, we considered only the presence/absence of prey species in predator diets.

Additional data concerning elasmobranchs, teleostean fishes, reptiles, birds and invertebrates were obtained through the grey literature and published articles from 1980–2012. Data for 23 027 stomachs was obtained from the literature for 132 predators, corresponding to 10 elasmobranchs, one bird category, one reptile, 56 teleosts and 64 invertebrates (See Supplementary data, Appendix A). When dietary information was unavailable for some species in the study zone, information from similar ecosystems was used to complete foodweb. To construct the foodweb, the information on stomach contents was compiled to the species taxonomic level when possible. When this information was not available, genera, families or orders were used.

![Figure 1. Central coast of the state of Paraná (black bar), southern Brazil.](https://academic.oup.com/icesjms/article-abstract/71/7/1586/671404)

These data were used to construct a quadratic matrix of presence/absence ("who eats whom") in predator diets, in which rows represent predator species and columns represent prey species. A “1” in entry $a_{ij}$ indicates that the predator on row $i$ preys on the species in column $j$ (Dunne et al., 2002a; Abarca-Arenas et al., 2007; Gaichas and Francis, 2008; Navia et al., 2010, 2012). We then used the network analysis software NetDraw 2.075 (Borgatti, 2002) to visualize the matrix as a trophic network, and calculated density ($D = S/L$) and connectance ($C = L/(S^2)$), where $S$ is the number of species, and $L$ is the number of links (Martinez, 1992); these measures are used to characterize foodwebs. Cannibalism was considered in the connectance calculation because some shark species shows this characteristic.

### Topological analysis

The node degree and “mesoscale” indices were used in the topological analysis, as suggested by several authors (Jordán and Scheuring, 2002; Jordán et al., 2006; Abarca-Arenas et al., 2007; Navia et al., 2010). The node degree ($D_i$) takes into account the number of nodes connected directly to node $i$. The degree of node $i$ ($D_i$) is the sum of its prey (in-degree, $D_{in,i}$) and its predators (out-degree, $D_{out,i}$): $D_i = D_{in,i} + D_{out,i}$. It was computed using NetDraw software (Borgatti, 2002).

After calculating the node degree ($D_i$) for all nodes in the network, we applied centrality indices to determine which nodes contribute most rapidly to the spread of effects in the web. The Betweenness Centrality ($BC$) index quantifies how often node $i$ is on the shortest path between each pair of nodes $j$ and $k$; the index was computed using the NetDraw software (Borgatti, 2002). The standardized index for node $i$ ($BC_i$) is given by:

$$BC_i = \frac{2 \times \sum_{j \leq k} g_{j,k}(i)/g_{j,k}}{(N-1)(N-2)}.$$
where $i \neq j$ and $k$, $g_{ij}$ is the number of equally shortest paths between nodes $j$ and $k$, and $g_a(i)$ is the number of these shortest paths that include node $i$ ($g_a$ could be equal to 1); the denominator represents the reciprocal of the number of pairs of nodes not including node $i$. This index thus measures how central a given node is in terms of being included in many of the shortest paths in the network. If $BC_i$ is large for trophic group $i$, it indicates that the loss of this node will have many rapidly spreading effects in the web.

The Closeness Centrality index ($CC_i$) was also applied. This index is based on the proximity principle and quantifies how short the minimal paths from a given node to all other nodes are (Wassermann and Faust, 1994). This index was also computed using NetDraw software (Borgatti, 2002). In its standardized form the $CC_i$ is expressed as:

$$CC_i = \frac{N - 1}{\sum_{j=1}^{N} d_{ij}},$$

where $i \neq j$, and $d_{ij}$ is the length of the shortest path between nodes $i$ and $j$ in the network. This index thus measures how close a node is to the rest of the nodes. The smallest value of $CC_i$ will be for the trophic group that, if removed, would affect the most other groups.

**Keystone index**

The keystone index ($K_i$) is used to characterize the importance of a species within an ecosystem according to its position in the trophic network; it is also known as the index of topological importance. Whereas the previous indices are based solely on the topological links between nodes, the keystone index considers additional information, including predator–prey relationships. It was defined in detail by Jordán (2001) and Jordán et al. (2006), and is expressed as:

$$K_i = \sum_{i=1}^{n} \frac{1}{d_i} (1 + K_{bc}) + \sum_{i=1}^{n} \frac{1}{f_i} (1 + K_{eu}),$$

where $n$ is the number of predators eating species $i$, $d_i$ is the number of prey of the $e^{th}$ predator and $K_{bc}$ is the bottom-up keystone index of the $e^{th}$ predator. Symmetrically, $m$ is the number of prey eaten by species $i$, $f_i$ is the number of predators of the $e^{th}$ prey and $K_{eu}$ is the top-down keystone index of the $e^{th}$ prey. For node $i$, the first summation of the equation quantifies bottom-up effects ($K_{bu}$), while the second summation quantifies top-down effects ($K_{ad}$). After rearranging the above equation, the terms that contain the values of $K$, i.e. $\sum K_{bc}/d_i + \sum K_{ad}/f_i$, refer to indirect effects ($K_{ind}$), while those that do not contain $K_i$, i.e. $\Sigma 1/d_i$, refer to direct effects ($K_{dir}$). The sums of the various effects ($K_{bu} + K_{ad}$) and ($K_{ind} + K_{dir}$) equal:

$$K_i = K_{bu,i} + K_{ad,i} = K_{dir,i} + K_{ind,i}.$$  

In addition to providing information about the number of direct connections among nodes, the keystone index also provides information on how these neighbours are connected to one another ecologically (Jordán et al., 2006), emphasizing vertical interactions over horizontal interactions (e.g. trophic cascades vs. apparent competition). It also characterizes positional importance, separating direct from indirect effects, as well as bottom-up from top-down effects in the trophic network (Jordán, 2001).

This $K_i$ index, in principle, gives the number of species susceptible to secondary extinction after the removal of a particular species from the network (Jordán, 2001, 2005; Quince et al., 2005). Thus, the higher the value of $K_i$, the higher the probability of its removal triggering additional extinctions (Jordán and Scheuring, 2002). The keystone index was computed using the FLKS 1.1 software package (Jordán, 2005; provided by F. Jordán), which is designed for characterization of the vertical positional importance of species in foodwebs.

To answer the two central questions of this study we assessed the structural importance of the sharks considered to be the top predators in the trophic network under study by computing all indices with and without these species.

**Results**

A total of 139 species were considered, resulting in a matrix with 139 nodes and 837 interactions. Elasmobranch species considered were: “Top predators” (Carcharhinus obscurus, C. limbatus, Carcharias taurus, Sphyrna lewini, S. zygaena and Galeocerdo cuvier) and “mesopredators” (Squatina guggenheim, Rhizoprionodon lalandii, R. porosus, Mustelus schmitti, Zapteryx brevirostris, Rhinobatos perelegens, Dasyatis guttata, Narcine brasiliensis, Rioraja agassizi, Rhinoptera spp. (R. bonasus + R. brasiliensis) and Myliobatis goodei). The density of the network was $D = 0.18$, with a connectivity of $C = 0.043$.

**Results with top predators**

Based on the node degree ($D_i$), Polychaeta was the node with the largest value (38), followed by Portunidae (37), Trichiurus lepturus and Amphipoda (34), Paralichthys brasiliensis (32), Carcharhinus obscurus and Loligo sp. (30). Other elasmobranchs also scored large values for the node degree: Z. brevirostris (27), Rioraja agassizi (24), Sphyrna lewini (23), Galeocerdo cuvier and S. zygaena (22), Squatina guggenheim and Carcharias taurus (21), C. limbatus (20), and Rhizoprionodon lalandii and Mustelus schmitti (19) (Figure 2, Table 1).

According to the $BC_i$, six elasmobranch species were among those with the 20 largest values (see Table 1). Zapteryx brevirostris showed the largest value of $BC_i$ followed by Paralichthys sp., Polychaeta and Portunidae (Table 1). Carcharhinus obscurus, S. zygaena, and S. guggenheim were among the 20 species with largest values (5th, 6th and 16th respectively), the rest being teleost fish and/or invertebrates.

*Carcharhinus obscurus* was the elasmobranch species with the largest value for Closeness Centrality ($CC_i$); only Portunidae, Polychaeta, T. lepturus, Amphipoda, and P. brasiliensis had larger values. Five additional elasmobranchs were also among the 20 components with the largest values for the index: S. guggenheim, C. taurus, Z. brevirostris, S. zygaena and M. schmittii appeared at positions 12, 15, 17, 18 and 19, respectively (Table 1). Species with large values of $CC_i$ are considered to be components whose removal will affect the majority of other groups.

Five large sharks (G. cuvier, C. obscurus, C. taurus, S. lewini and S. zygaena) showed the largest values of the $K_i$; being considered as keystone species in the network leads to powerful top-down effects (Table 2). Another large shark (C. limbatus) appeared in the 10th position of importance. Five other elasmobranch species in the mesopredator group were among the 20 species with the highest values of $K_i$ (see Table 2). Besides the strong top-down control by large sharks cited above, bivalves and macroalgae scored the largest values for $K_i$ and important bottom-up values (Table 2).
The indirect effects values of *G. cuvier*, *C. oscurus*, *C. taurus*, *S. lewini* and *S. zygaena* are much larger than the values of their direct effects. Therefore, reductions of their populations can lead to secondary extinctions in the trophic network through top-down effects (Table 2). Elasmobranch mesopredators also showed large values of $K_i$, however they were smaller than those of other components (i.e. bivalves, seabirds, macroalgae, *T. lepturus*) (see Table 2).

### Results without top predators

When large predators were excluded from the analysis, small changes were observed. Polychaeta continued to have the largest node degree (37), followed by Amphipoda (34) and Portunidae (32). *Zapteryx brevirostris* also maintained the same node degree (27). Similarly, *Z. brevirostris* still maintained the largest value of $BC_i$, however *S. guggenheim* rose to the 13th position (Table 1). According to $CC_i$, only two elasmobranchs were among the 20

---

**Table 1.** The top 20 compartments of the foodweb off the coast of southern Brazil in terms of the two centrality indexes (*Betweenness* and *Closeness*); the node degree for each compartment is also given.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Degree</th>
<th>Complete network, with top predators</th>
<th>Network without top predators</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>Z. brevirostris</em></td>
<td>Portunidae</td>
</tr>
<tr>
<td>1</td>
<td>27</td>
<td>27</td>
<td>27</td>
</tr>
<tr>
<td>2</td>
<td>17</td>
<td><em>Paralichthys</em> sp.</td>
<td>Polychaeta</td>
</tr>
<tr>
<td>3</td>
<td>38</td>
<td><em>Polychaeta</em></td>
<td><em>T. lepturus</em></td>
</tr>
<tr>
<td>4</td>
<td>37</td>
<td>Portunidae</td>
<td><em>Amphipoda</em></td>
</tr>
<tr>
<td>5</td>
<td>30</td>
<td><em>C. oscurus</em></td>
<td><em>P. brasiliensis</em></td>
</tr>
<tr>
<td>6</td>
<td>22</td>
<td><em>S. zygaena</em></td>
<td><em>C. oscurus</em></td>
</tr>
<tr>
<td>7</td>
<td>25</td>
<td><em>Bivalve</em></td>
<td>Loligo sp.</td>
</tr>
<tr>
<td>8</td>
<td>34</td>
<td>Amphipoda</td>
<td><em>Cynoscion</em> sp.</td>
</tr>
<tr>
<td>9</td>
<td>32</td>
<td><em>P. brasiliensis</em></td>
<td><em>P. muelleri</em></td>
</tr>
<tr>
<td>10</td>
<td>34</td>
<td><em>T. lepturus</em></td>
<td><em>Gastropoda</em></td>
</tr>
<tr>
<td>11</td>
<td>14</td>
<td><em>L. synagris</em></td>
<td>Brachyura</td>
</tr>
<tr>
<td>12</td>
<td>19</td>
<td><em>Anchoa</em> sp.</td>
<td><em>S. guggenheim</em></td>
</tr>
<tr>
<td>13</td>
<td>28</td>
<td><em>M. americanus</em></td>
<td><em>Anchoa</em> sp.</td>
</tr>
<tr>
<td>14</td>
<td>20</td>
<td><em>S. brasiliensis</em></td>
<td><em>Bivalve</em></td>
</tr>
<tr>
<td>15</td>
<td>21</td>
<td><em>P. muelleri</em></td>
<td><em>C. taurus</em></td>
</tr>
<tr>
<td>16</td>
<td>21</td>
<td><em>S. guggenheim</em></td>
<td>Ophiuroidea</td>
</tr>
<tr>
<td>17</td>
<td>26</td>
<td><em>Gastropoda</em></td>
<td><em>Z. brevirostris</em></td>
</tr>
<tr>
<td>18</td>
<td>30</td>
<td>Loligo sp.</td>
<td><em>S. zygaena</em></td>
</tr>
<tr>
<td>19</td>
<td>27</td>
<td><em>Cynoscion</em> sp.</td>
<td><em>M. schmitti</em></td>
</tr>
<tr>
<td>20</td>
<td>21</td>
<td><em>Copepoda</em></td>
<td>Mysidacea</td>
</tr>
</tbody>
</table>

Elasmobranchs are listed in bold.
largest values: *S. guggenheim* and *Z. brevirostris* in eighth and 13th position, respectively. The remaining positions were still occupied by teleost fish and invertebrates, with small changes in order, but not in composition.

On the other hand, after elimination of top predators from the system, the topological importance list was drastically changed. Two mesopredator sharks occupied the first positions in the ecosystem: *S. guggenheim* and *R. lalandii*, respectively (Table 2). They also had the largest top-down values. These results support the hypothesis that after the elimination of predators, mesopredators may play a major structural role in a subtropical trophic web. In addition to the two elasmobranch mesopredators (seabirds—*Sula leucogaster* and *Fregata magnificens*), *T. lepturus*, *Paralichthys* sp. and *Scomberomorus brasiliensis* now showed the largest $K_i$ values (top-down control) (Table 2).

**Discussion**

Structural foodwebs allow us to identify trophic relationships without grouping species into large groups (e.g. “sharks” or “rays”), as is common in mass balance studies (e.g. Kitchell et al., 2002; Sánchez et al., 2005; Freire et al., 2008). This allows us to evaluate the direct and indirect effects between components at different levels (Jordán, 2001; Jordán et al., 2008; Navia et al., 2010). The present study represents the first attempt to identify the structural relationships of elasmobranchs in a subtropical ecosystem using a topological approach. Trophic webs indicate that structural patterns are relatively constant in similar environments (Dunne, 2009), and our results on density and connectivity are consistent with other marine foodwebs (Dunne et al., 2002b; Gaichas and Francis, 2008; Navia, 2013), suggesting that this foodweb has a high structural complexity. This is observed in foodwebs with very low values of $C (= 0.03)$ (Dunne et al., 2002b). Hence, this study provides a reference for future comparisons of ecological importance and ecosystem control in subtropical environments.

$Zapteryx brevirostris$ was the main node in both scenarios (with and without top predators), according to the $B_{C_i}$ index. These results indicate that this elasmobranch plays a central role in the propagation of indirect effects (e.g. trophic cascade). This result contrasts with the findings of Navia et al. (2010), which did not indicate large $B_{C_i}$ values for small elasmobranchs (mesopredators) along the Pacific coast, a tropical ecosystem with high species richness. Instead, their results suggest that shrimp, brachyurans and stomatopods had higher $B_{C_i}$ index values and higher structural importance than elasmobranch mesopredators. In addition, in the present study, the large sharks *C. obscurus* and *S. zygaena* could also be considered as central components as a result of the trophic structure analysis. However, they did not have the highest $B_{C_i}$ index values in the system. Therefore, species in the medium trophic levels seem to control the propagation of trophic effects within the subtropical foodweb, in contrast to the findings of Navia et al. (2010) and Navia (2013) in a tropical foodweb.

According to the $CC_i$ index, six elasmobranchs were ranked among the top 20 positions (see Table 1). However, the highest rank of any of them was sixth place. When we excluded top predators from the analysis, only two elasmobranch species remained in the top 20 positions, and the highest ranked species dropped to eighth place. Invertebrates seemed to have higher structural importance than elasmobranchs, as found by Navia et al. (2010) and Navia (2013) on the Pacific coast. Elasmobranchs, like invertebrates, are closely connected with several species in the foodweb; as opportunistic predators with a wide trophic spectrum (Wetherbee et al., 2012), they are naturally linked to a wide variety of prey species.

Many studies have shown that the loss of large sharks causes changes in the intermediate levels of the foodweb (e.g. Stevens et al., 2000; Myers et al., 2007). Tropical marine regions, on the other hand, are known for their high diversity (e.g. Floeter and Gasparini, 2000; Joyeux et al., 2001; Heithaus et al., 2010). This high diversity leads to high structural complexity of foodwebs and
high topological redundancy, suggesting that trophic relationships could easily be readjusted if one or more of the components were lost (e.g. Dunne et al., 2002a, 2004; Frank et al., 2007; Navia et al., 2012; Navia, 2013). However, the BC analysis in the present study shows that some species of sharks and rays (e.g. Z. brevirostris, C. obscurus, S. zygaena) may act as key elements with high structural importance within the ecosystem, serving as important links between other compartments of the foodweb. This result highlights the importance of top-down control in the structuration of marine trophic webs, as observed in temperate ecosystems (e.g. Estes et al., 1998; Frank et al., 2007), and permits us to conclude that sharks and batoids are important components in the subtropical foodweb structure.

As proposed by some authors, sharks are key elements in the top-down control of marine ecosystems (see Heithaus et al., 2008); this conjecture is supported by the present study. Five large sharks (G. cuvier, C. obscurus, C. taurus, S. zygaena and S. levini) showed the highest values of $K_e$, suggesting that these species control lower levels in the food chain through predation (direct effects). Their major contributions, however, occurred through indirect effects (e.g. trophic cascades and apparent competition). This finding highlights the importance of large sharks in controlling the overall structure of the system. Stevens et al. (2000) proposed that the strongest responses to shark removals are not always seen in their effect on their main prey (direct effect), and that we need to focus on indirect effects on the foodweb as well. The results of the present study indicate that reductions in shark populations may lead to changes in other species through indirect effects on the foodweb (see values in Table 2), as recorded in tropical (Navia et al., 2010; Navia, 2013) and temperate environments (Coll et al., 2013).

The “mesopredator release” hypothesis for elasmobranchs (see Myers et al., 2007; Ritchie and Johnson, 2009) may be applicable in a structural context off the coast of Brazil, in contrast with the tropical system along the Pacific coast (Navia et al., 2010). When top predators were excluded from our analysis, two mesopredator sharks occupied the highest position in the foodweb and had the largest values of $K_e$ (see Table 2). This result suggests that, in this system, elasmobranch mesopredators will increase in structural importance if the populations of large sharks decline. This result contrasts with the findings of Navia (2013), which suggests that mesopredator release does not occur in tropical ecosystems because of their high species richness. In larger foodwebs with higher diversity, there is a greater chance that an excluded predator will be replaced by another species, thereby limiting the effects on the prey populations. In lower diversity systems, the exclusion of a single species has a higher chance of causing significant changes because there is a smaller set of species capable of replacing the lost species. In this way, our results provide additional evidence that latitude and species’ richness play a role in determining the structure of foodwebs, as has been suggested by other studies (Frank et al., 2007; Navia et al., 2012).

Despite the hypothesis that small elasmobranchs respond relatively rapidly to reductions in populations of their predators, the lower predation rate can be offset by fisheries-induced mortality on mesopredator populations (Bornatowski et al., 2012). For instance, Rhizoprionodon lalandii has a high recovery potential (Stevens et al., 2000; Lessa et al., 2009). However, this species is also an important economic resource in small-scale and artisanal fisheries, representing 60% of the total shark landings in south-eastern and southern Brazil (Motta et al., 2005; Andrade et al., 2008; Bornatowski et al., 2012). Squatina guggenheim, another shark that increases in topological importance with the exclusion of large sharks, lives up to 12 years, with first maturity at four years (Vooren and Klippel, 2005). However, because of the long generation times and low growth and reproductive rates, the size of the population of this species declined by 87% between 1980 and 2000 (Vooren and Klippel, 2005). Therefore, future studies on the effects of the loss of predators in foodwebs should be complemented with fisheries data, and also information on how the fishery affects mesopredator populations.

Acknowledgements
We thank Lida Teneva and James Nienow for English reviewing, as well as the two anonymous reviewers.

Supplementary data
Supplementary data are available at ICES Journal of Marine Science online.

Funding
We thank the CAPES for a scholarship to RRB, and CNPq for a scholarship to HB.

References


