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Key prey indicates high resilience on marine soft bottom habitats

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ABSTRACT

The key prey was determined based on the diet and spatial patterns of the Nektonic community in southern Brazil. The proposed tool to discriminate key prey was based on simple probabilistic methods and analytical procedures that integrate freely available software on the web. To avoid using arbitrary criteria in key prey determination it was used an indicator based on an adapted outlier analysis including a run of principal component analysis (PCA) and then the choice of prey that fall out of the 99% concentration ellipse. The results showed three key prey identified at species level: the shrimp *Artemesia longinaris* in the coastal habitats and euphausid *Euphausia similis* and anchovy *Engraulis anchoita* in the continental shelf habitats (warm and cold). The analysis of the diets of the indicator species of three necktonic assemblages showed that all of them had both pelagic and detritus as primary sources of energy. However, in shallow coastal waters prevailed access to benthic food web key prey. In deeper areas, the Warm shelf assemblage accessed more evenly the epifauna, infauna and the pelagic compartments, while the Cold shelf assemblage was more dependent on planktonic production and had a prevalence of pelagic key prey. Is demonstrated the importance of the identification of key prey, since it may indicate greater or lesser stability of predator populations depending on whether they come from compartments with more or less dynamic primary production processes, including climate-related changes that may affect the predator prey interactions. This study confirmed the prediction that demersal nekton has high disturbance recovery capacity, which may mask for decades the growing impact of fishing.

1. Introduction

Fishing in marine ecosystems may have profound effects on food webs and lead to trophic cascades or even ecological regime shifts (Österblom et al., 2006; Baum and Worm, 2009; Hayden et al., 2019). Demersal fisheries have been identified as the greatest threat to marine ecosystems by marine scientists worldwide with evident impacts on the food webs (Halpern et al., 2007). Both bottom-up and top-down controls are common in marine ecosystems and natural or human-induced removal of predators may increase the abundance of non-targeted predators or prey species (Worm and Myers, 2003). Additionally, prey abundance fluctuations or changes reflect in the abundance of their predators (Ware and Thomson, 2005; Edgar and Shaw, 1995).

In many ecosystems some prey species are important pathways of energy in the food webs. These species are called key prey and may have a main role by transferring energy from plankton or the detritus food web to the top predators (Frederiksen et al., 2006; Smith et al., 2011). According to Holt (1984), a key prey is a preferred prey that is able to maintain its abundance in the face of predation (through high reproductive rate) and may affect the community structure by sustaining a predator and reducing the density of other prey. Decreases of key prey abundance can have deep effects in food webs, leading to trophic cascades or changes in the ecological regime of marine ecosystems (Chiaradia et al., 2010). Furthermore, changes in the abundance of key prey may result in population changes and in the reproductive success of top predators (Seyboth et al., 2016). The identification of key prey species and their trophic links may help to evaluate the resilience of food webs to fluctuations or changes in their abundance. In practical terms, the identification of key prey species in marine ecosystems may contribute to evaluate the consequences of their fluctuation on the higher trophic levels, that include many target species of fisheries.

The wide soft bottom shelf of southern Brazil (29°–34°S) yields a significant part of the country's demersal and pelagic fish landings (Haimovici, 1998; Haimovici et al., 2006a). The region is affected by

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seasonal hydrographic shifts since it is influenced by the subtropical convergence, which involves the Brazil Current and the seasonal input of colder waters from southern regions (Peterson and Stramma, 1991).

The understanding of the trophic processeses involving the different biological compartment along the continental shelf of Southern Brazil can provide insights on the resilience to human impacts, especially by commercial fishing. The demersal nekton is an important link between the lower trophic levels of the detritus food web and the biological communities of the water column. Thus, the understanding of the trophic processes involving this biological compartment can provide insights on the resilience of marine ecosystems to human impacts, especially by commercial fishing.

The bony fish species composition in a series of research bottom trawls surveys along the contiental shelf (an upper slope) of Southern Brazil in the 1980s (Haimovici et al. 1994, 1996) was analyzed to identify three assemblages, and their indicator species and to relate their distribution to the seasonal hydrographic shifts (Martins and Haimovici, 2017) (Fig. 1). A large number of stomach contents of many species were collected in the surveys and the prey of many species were identified (Martins, 2000; Santos and Haimovici, 2001). These data were used to identfy the main sources of food itens and the key prey for the demersal nekton in the continental shelf of Southern Brazil. We present a simple and innovative approach based on probabilistic methods and analytical procedures (available in free software packages) for the identification of key prey. The importance of the key prey and its changes in their abundance is demonstrated and discussed to provide some insight on the resilience of demersal fisheries in the region and demersal nekton in general.

2. Methods

2.1. The study area

The Southern Brazilian continental shelf has a width of approximately 140 km in the border with Uruguay (34°35′S) and narrows northward (30°30′S) to less than 50 km. The dominant sediments on the inner shelf are sandy and shift gradually to mud with silts, clay and biodetrites on the outer shelf (Martins et al., 1972). This region is characterized by opposite flows: warm southward flowing Brazil Current, cold northward flowing of the coastal branch of the Malvinas Current and the runoff of the La Plata River (Piola et al., 2000; Moller et al., 2008). The confluence zone between the two currents along the continental shelf of Argentina, Uruguay and Southern Brazil form the western edge of the Subtropical Convergence. This highly variable mesoscale oceanographic feature oscillates seasonally along a latitudinal gradient between 30° and 46°S, with an alternate southward displacement of the warm and saltier Brazil Current from north and a northward penetration of the Malvinas Current from south (Emílsson 1961; Peterson and Stramma, 1991). The seasonal variation of water temperature and stratification over the shelf is strong in summer and weak or non-existent in winter (Castro and Miranda, 1998). These changes result in a displacement of the Shelf Subtropical Front (SSTF) perpendicular to the coastline, separating the nutrient-rich, colder, and less salty waters resulting from the mixture with Subantarctic Shelf Waters along the Argentinean shelf from the Rio de la Plata waters. The SSTF reaches up to 30°S in winter and retreats southward to around 34°S during the warmer months (Piola et al., 2000; Moller et al., 2008). A wind-induced intrusion of the nutrient-rich South Atlantic Central Water over the shelf break and outer shelf occurs mainly in spring and summer, when northeast winds are dominant (Garcia and Garcia, 2008).

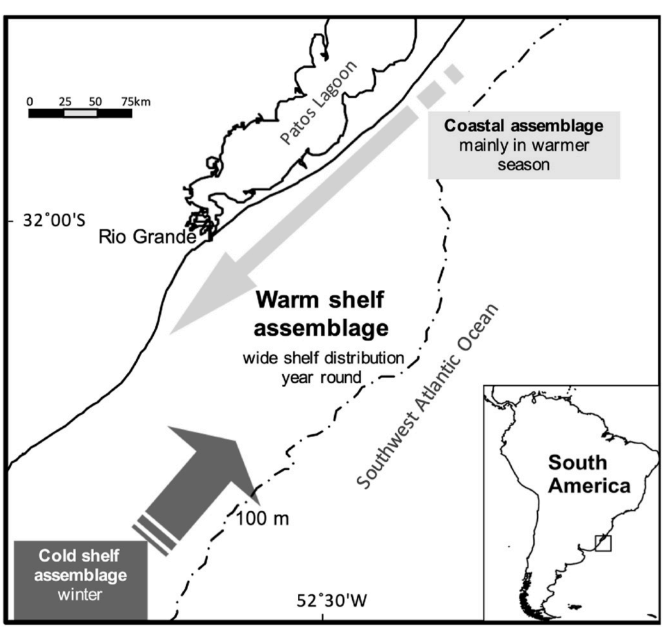

Fig. 1. Study area showing the position of the three demersal assemblages and its spatial dynamics (Source: Martins and Haimovici, 2017).

Because of its extension and high productivity associated to the Malvinas Current and the runoff the la Plata River and the Patos Lagoon, the large soft bottom continental shelf of southern Brazil has a relatively high primary productivity and is among the most important fishery grounds along the Brazilian coast (Ciotti et al., 1995; Haimovici et al., 2006b).

2.2. Demersal assemblages and main predators

In a previous study (Martins and Haimovici, 2017) three consistent groups of demersal nektonic species with similar spatial and seasonal distribution and named "assemblages" (Fig. 1) were determined upon data from 225 hauls in eight demersal trawl cruises on the continental shelf and upper slope of southern Brazil from 1981 to 1987. The net used had between 49.3 and 52.9 m ground-rope. The codend, stretched between opposite knots, had a mesh size of 40–50 mm and was covered by a second codend of the same mesh size. The trawling speed was around 5.5 km/h (3 knots). The hauls were usually 1 h long and were performed during daytime, beginning after sunrise and finishing before sunset. A detailed description of the sampling design and catches are given by Haimovici et al. (1994) and Haimovici et al. (1996).

The Warm shelf Assemblage was present year round at depths from 20 m to 100 m. The Cold shelf Assemblage occurred almost exclusively in the cold season and between 40 m and 80 m. The Coastal Assemblage was found at dephs below 20 in the northern part of the study area in the cold season and expanded southward in the warm season. The species or size categories of more abundant and frequent species witch represented over 80% of their total biomass in any of the three assemblages was considered as an Indicator Species (*sensu* Dufrene and Legendre, 1997). The 17 indicator species or size categories within a species accounted more than 52% of the total catches in biomass in the six demersal surveys carried out in the study area are showed on Table 1. The indicator species of the nektonic assemblages combine both spatial and sesonal distribution pattern and were considered to be more representative of the food webs of the nektonic demersal compartments of ecosystem of southern Brazilian shelf than either spatial or temporal independent approaches.

2.3. Identification of food items

The dietary studies of predators were based on information extracted from 4601 stomach contents from 14 species, three of which were subdivided into two categories (juveniles and adults) totaling 17 different types of predators (Table 1). From this total, 2669 stomachs from nine types of predators were obtained specifically for this study and five had their primary data reprocessed (Haimovici et al., 1989, 1993;

Table 1
Number of stomach contents, percent of total biomass in the surveys and the percent in weight of each prey categories of the indicator species of three nektonic shelf assemblages in Southern Brazilian continental shelf.

Assemblage	Predator	Analyzed stomachs	% Cont. Shelf biomass	Prey category			
				Benthic Infauna	Benthic Epifauna	Nekton	Plankton
Coastal	*Macrodon atricauda* (Günther, 1880) (adult)	850	3.9	0.2	23.4	76.4	–
	Macrodon atricauda (Günther, 1880) (juvenile)	541	1.1	0.5	65.5	34.0	–
	Menticirrhus littoralis (Holbrook, 1860)	94	0.1	71.0	23.5	5.0	0.5
	Micropogonias furnieri (Desmarest, 1823) (juvenile)	59	0.2	39.6	56.2	4.1	0.1
	Paralonchurus brasiliensis (Steindachner, 1875)	311	2.7	53.3	45.3	1.2	0.2
	Pogonias cromis (Linnaeus, 1766)	127	0.2	78.2	20.2	1.6	
Cold shelf	*Cynoscion guatucupa* (Cuvier, 1830) (adult)	146	9.9	0.2	12.7	75.6	11.4
	Engraulis anchoita Hubbs and Marini, 1935	541	0.3	2.4	–	–	97.6
	Merluccius hubbsi Marini, 1933(adult)	102	5.7	–	–	100.0	
	Merluccius hubbsi Marini, 1933 (juvenile)	124	0.8	<0.1	–	84.6	15.4
	Trachurus lathami Nichols, 1920	106	1.1	–	–	–	100.0
	Umbrina canosai Berg, 1895 (adult)	213	8.9	80.2	9.9	9.6	0.4
	Umbrina canosai Berg, 1895 (juvenile)	385	6.1	88.4	5.4	2.2	3.9
Warm Shelf	*Ctenosciaena gracilicirrhus* (Metzelaar, 1919)	68	4.0	40.0	11.1	30.0	18.9
	Cynoscion jamaicensis (m)	63	1.9	–	33.3	62.1	4.6
	Prionotus punctatus (Bloch, 1797)	555	2.8	0.6	82.5	16.9	–
	Trichiurus lepturus Linnaeus, 1758 (juvenile)	316	2.7	–	0.7	38.7	60.6
	Total	4601	52.4				

Martins et al., 2005; Teixeira and Haimovici, 1989). Data from the remaining 1932 stomachs (41%) of three types of predators were obtained from published data (Schwingel, 1991; Baptista Metri, 2007; Juras, 1979). Stomachs were obtained from scientific cruises and commercial fish sampling.

A sample of at least 30 stomachs of each species of predator was analyzed. Stomachs were fixed in 10% formalin and subsequently preserved in 70% alcohol. The food items in the stomach contents processed in the laboratory were identified at the lowest possible taxonomic level and weighed with a 0.1 g precision. Decapod crustaceans and fish were mostly identified at family to species level depending of the degree of digestion. Other benthic and planktonic invertebrates were usually identified only to class or, at most, order levels.

2.4. Food item classification

Food items were grouped as proposed in Lowe-McConnell (1962) and Froese and Pauly (1998) in four categories in which both taxonomic ecological and criteria were taken in account: Plankton, composed mainly of copepods, euphausiids and hyperidae of the macro and mesozooplankton, cnidarians, ctenophores, salps and appendiculars; Benthic Infauna, that included organisms with low locomotion power, permanently associated to the substrate and composed mainly of polychaetes, benthic molluscs, ophiuroids and amphipods; Benthic Epifauna, of organisms with higher power of locomotion, composed mainly of prawns, crabs and lobsters, and Nekton, that included squids, octopuses and fish.

For each food item, the percentage in weight relative to the total weight of all food items in the stomach contents was calculated. The complete list of the 178 food items is presented in the Supporting Information and the standardized percentage in weight in each of the four prey categories in the stomach contens of each of the 17 types of predators is presented in Table 1.

2.5. Key prey determination

Key prey of the indicator species in each assemblage were those present in large number of stomachs and represented a high proportion of the weight in relation to the other prey.

Two approaches have been proposed for the quantitative identification of key prey, one based on importance ratios of predators for each prey (i.e. Plaganyi and Essington, 2014) and a second through numerical modeling of ecosystems. (i.e. Libralato et al., 2006), both based on biomass balance of functional groups and contrary to what is proposed in the present study, involves a complex analyzes that are not accessible to many research groups and managers or do not take in account the spatial and temporal variability of predators.

The method used in this study to identify key prey was based in an outlier analysis. In a first step, a principal component analysis (PCA) was run in the PAST program (Hammer et al., 2001) from a variance-covariance matrix where each cell corresponded to the percent weight of each prey in each predator. In a second step, the ellipse of concentration in which 99% of population of points are expected to fall was plotted (Hammer et al., 2001; Husson et al., 2004). The highest scores in either axis fell out of the ellipse and were of prey present in a large number of predators and/or a large proportion in weight. Those outliers, corresponding to frequent and or abundant prey were considered the key prey. This method included easy to apply non-parametric comparative tests and multivariate analyzes widely available in statistical packages what makes it more accessible to use as a management tool. It is applicable to environments for which there is an intermediate to high level of knowledge on the distribution and diet of the most abundant species, which is frequently the case of intensely fished ecosystems.

2.6. Statistical analysis

The differences in the contribution in weight of different categories of prey on different assemblages of predators was verified with the Mann-Whitney test for independent samples and performed in the PAST program (Hammer et al., 2001). Significative differences were considered whose probability associated with the paired tests was equal to or less than 5% ($p < 0,05$).

3. Results

3.1. Trophic patterns by assemblage

The percent in weight in the stomach contents of the indicator species of each of the three nektonic assemblages identified on the Southern Brazilian continental shelf are presented in Table 1 and summarized in Fig. 2. In the Coastal Assemblage, benthic epifauna was the main food source followed by nekton, benthic infauna and almost no plankton. In the Cold shelf Assemblage stomach contents there was no significant differences in the percentages between benthic infauna, nekton and plankton and the percentage of benthic infauna was very low. Warm

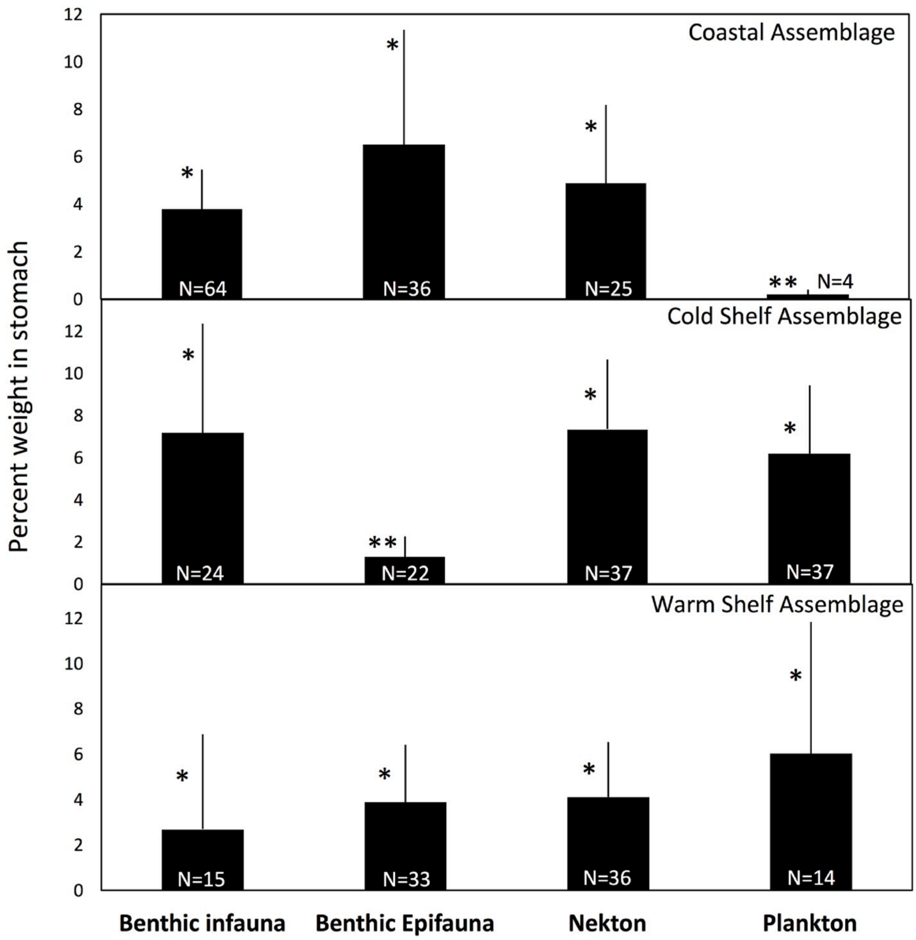

Fig. 2. Mean percent weight of four prey categories and on three assemblages of demersal fishes of southern Brazilian continental shelf. Vertical bars represent standard deviation. Different number of asterisks represent significant differences in the Mann-Whitney test ($p < 0.05$).

shelf assemblage presented plankton as more abundant prey followed by nekton, benthic epifauna and benthic infauna without significative differences between categories but, when pooled, pelagic prey (nekton and plankton) summed 10% compared with 7% of benthic prey (infauna and epifauna).

The main prey responsible by the trophic patterns of each assemblage are presented in Fig. 3. The Coastal assemblage, characterized by benthic prey, showed the dominance of the epifaunal shrimp *Artemesia longinaris* (32%) and the importance of juveniles of the fishes *Paralonchurus brasiliensis* (9%) and *Macrodon atricauda* (6%) as nektonic prey. In the Cold shelf assemblage, the pelagic prey were more relevant, highlighting the small engraulid fish *Engraulis anchoita* (14%) and the krill *Euphausia similis* (10%). In the Warm shelf assemblage, both benthic epifaunal *Artemesia longinaris* (8%) and *Portunus spinicarpus* (8%) and infaunal (undetermined Gammaridea (8%), as well as the planktonic *Euphausia similis (9%)*, pelagic nektonic *Engraulis anchoíta* (5%) and juvenile *Cynoscion guatucupa* (5%) were important component of the indicator species diets.

3.2. Key prey

The discrimination of the main key prey based in the scatterplot of the two principal components of the PCA analysis of variance covariance matrix of 178 prey (lines) versus 17 predators (columns) (Mode Q) (Supporting Information) is shown on Fig. 4. The components 1 and 2 accounted 45,7% of the total variance and most of the points corresponding to the prey are concentered inside the 99% variation ellipse. Only three species (*Engraulis anchoita, Euphausia similis, Artemesia longinaris*) and two categories (undetermine Teleostei and undetermined Polychaete) were out of the ellipse. From these five categories, Undetermined Teleostei and Polychaete are pools of species, in many cases too much digested for a more precise identification. Although polychaetes and fish are collectively recognized as relevant food, only three species have been defined as key prey.

The coastal shrimp *Artemesia longinaris* was far the dominant prey in the Coastal assemblage and also important in the Warm shelf assemblage. The forage fish *Engraulis anchoita* was the dominant prey in Cold shelf assemblage and also important in the Warm shelf assemblage. The krill *Euphausia similis* was dominant among planktonic prey in both Warm and Cold shelf assemblages but had irrelevant presence in Coastal assemblage (Fig. 3), therefore it can concluded that the key prey in coastal waters was *A. longinaris* year round and in deeper shelf water, the key prey was *E.anchoita* and *E. similis*. A schematic diagram showing the three key prey identified and the demersal nekton indicator species for which they were most important is presented in Fig. 5.

4. Discussion

The analysis of the diets of the indicator species of three necktonic assemblages showed that all of them had both pelagic and detritus as primary sources of energy. However, in shallow coastal waters prevailed access to benthic food web key prey. In deeper areas, the Warm shelf assemblage accessed more evenly the epifauna, infauna and the pelagic compartments, while the Cold shelf assemblage was more dependent on planktonic production and had a prevalence of pelagic key prey.

Not surprisingly, ecologically equivalent species to the three key

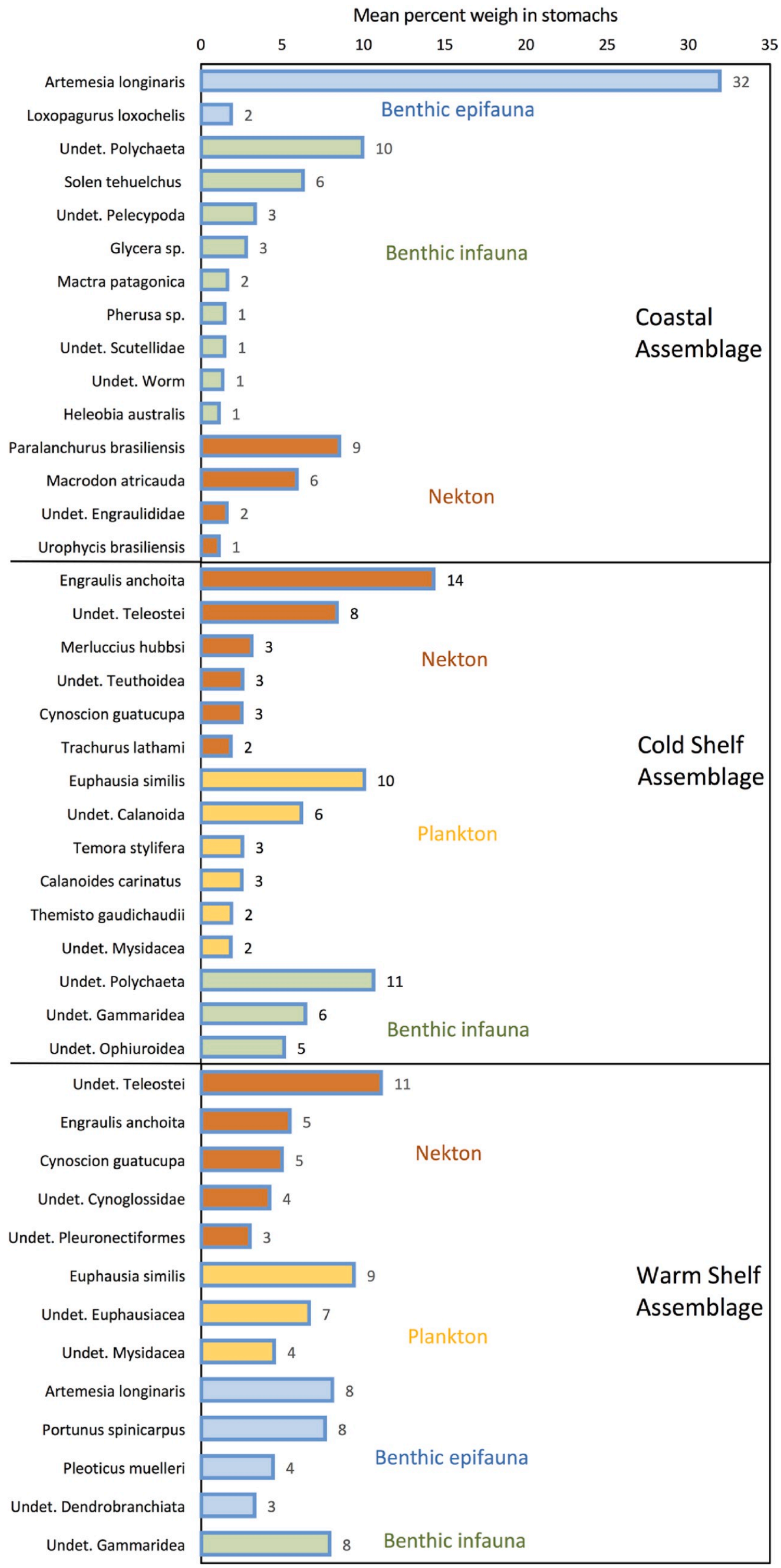

Fig. 3. Mean percent weight of 80% most dominant four prey categories (color bars) in three assemblages of demersal nekton of southern Brazilian continental shelf (Coastal, Cold shelf and Warm shelf assemblages). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

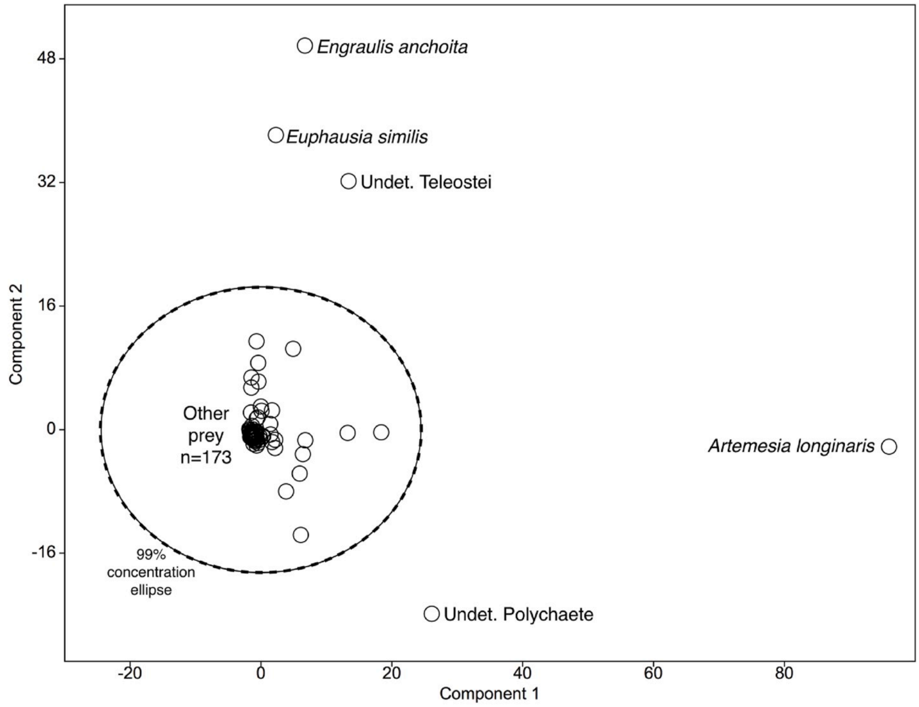

Fig. 4. Scatter plot of the two main components of PCA analysis of 178 prey items in relation to 17 predator species/categories and 99% concentration ellipse. The nominated food items outside of the ellipse represents key prey.

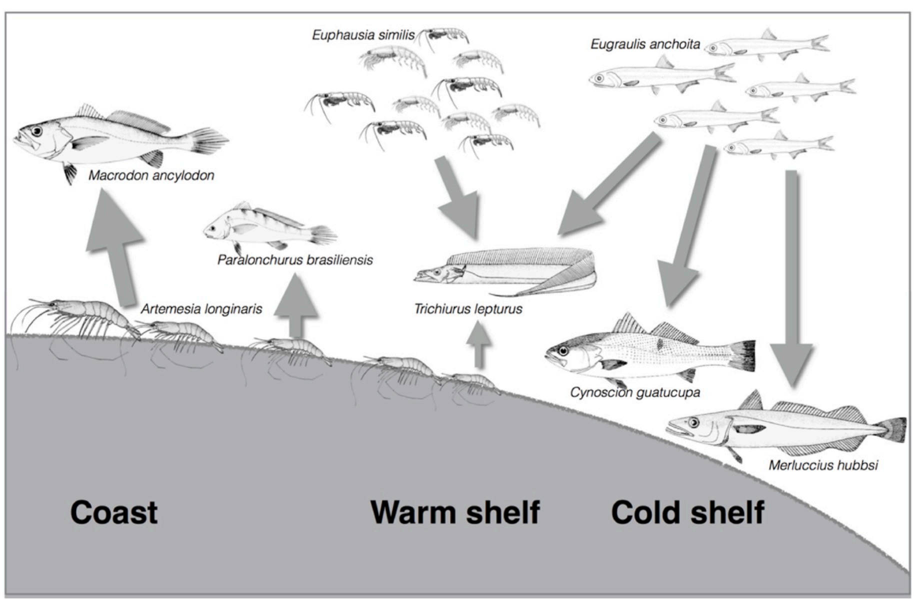

Fig. 5. Schematic diagram of a profile of continental shelf of southern Brazil with view from south to north showing the distribution of the key prey of demersal shelf assemblages, its main predators and trophic relationships.

prey identified in this study are also important in structuring subtropical and temperate coastal marine ecosystems in various parts of the world, indicating that a small number of prey species can play key roles in similar marine habitats.

Small pelagic fish represent an important link between plankton and top predators and are important as a food source for several demersal species (Frederiksen et al., 2006; Preciado et al., 2008). The anchovy *E. anchoita* has been identified as an essential species to the pelagic ecosystem of the Western South Atlantic (Lima and Castello, 1995; Costa et al., 2016). Velasco and Castello (2005) showed through numerical ecosystem modeling that the anchovy *Engraulis anchoita*, was prominent in coupling demersal and pelagic sub-systems being prey of large fish predators, both demersal and pelagic cold-season migrants as *Pomatomus saltatrix* (Haimovici and Krug, 1992), *Cynoscion guatucupa* (Martins, 2000), *Pagrus pagrus* (Capitoli and Haimovici, 1993) and the main prey for the penguin *Spheniscus Mageallanicus* (Marques et al., 2018).

The krill, *Euphausia similis* has a worldwide distribution, being more common in the southern oceans (RAMS, 2009). It has been identified as a main component of the zooplankton in Australia (Taylor et al., 2010; Williams et al., 2001) and southern Brazil (Montú et al., 1997). It has already been identified as a dominant item in the diet of cod and capelin in arctic waters (Dalpadado et al., 2016). As in southern Brazil, the species and another one similar (*E. pacifica*) has been associated with subtropical convergence systems such as in the Kuroshio current (RAMS, 2009; Okazaki et al., 2019) and Southern Indic Ocean (Pakhomov et al., 1994). Studies of the vertical migration of *E. similis* in Tasmania have shown that the species tends to be closer to the bottom during the day, unlike other species of krill studied (Harris et al., 2014) which explains their predominance as the main euphausiid present in the diet of demersal species in southern Brazil.

The shrimp *Artemesia longinaris* has been identified as a dominant component of the coastal inshore macroinvertebrate assemblage in southern Brazil. It is the main target of the double-rig trawl fishery in the region (Haimovici and Mendonça, 1996) with landings that reached two to seven thousand tons between 2001 and 2004 (Baptista Metri, 2007). The presence of the *A. longinaris* as key prey is due in part to their life strategy with early maturation, high fecundity and multiple spawning (Cardoso and Haimovici, 2016, Semensato and Di Beneditto, 2008) that are characteristics that fit them in the classic description of key prey given by Mills et al. (1993).

Polychaetes are dominant components of marine macrobenthos in terms of number of species and individuals and are food sources for a wide variety of epifauna and fish species (Hutchings, 1998) including the continental shelf of southern Brazil where they are dominant components of several assemblages of benthic invertebrates (Capítoli and Bemvenuti, 2006). Polychaetes in the soft bottoms in southern Brazil are important for the stability of the food source for many species, since, unlike pelagic prey, their seasonal biomass variability is low (Capítoli and Bemvenuti, 2006).

Low-trophic species such as small pelagic fish, krill and small shrimp accounting for about 30% of the marine fish landings (Smith et al., 2011). Although not largely consumed by humans, many of them may represent important role in the food chains by transferring energy from plankton or the detritus food web to the top predators (Frederiksen et al., 2006; Smith et al., 2011; Queiros et al., 2019). This is the case of the key prey identified in the continental shelf of southern Brazil.

However, the food webs of the southern Brazil continental shelf are quite diversified and, except for *Artemesia longinaris* in coastal waters, the other two key prey *Engraulis anchoita* and *Euphausia similis* represented only a relatively small fraction of the food sources of the four sciaenid fishes that have been intensely fished for 70 years and still represent around 70% of the landings of the demersal fishery on the region (Yesaki and Bager, 1975; Cardoso and Haimovici, 2016). As shown by Byron and Link (2010), the opportunistic habit of demersal species to simultaneously access various ecological compartments can explain this pattern that lead to a great resilience of demersal species.

In a study carried out in southeastern Brazil, it was demonstrated that demersal nekton also has a high omnivory, simultaneously accessing compartments of the detritus and pelagic food web, indicating a high capacity for recovery of disturbances as also showed by Nascimento et al. (2012). The theoretical consideration of this paper is consistent with what was observed in present study, with for example, the documented resilience of *M. atricauda* stock (Cardoso and Haimovici, 2016), even after suffering a high impact from fishing.

As concluding remarks, this study showed that it is possible to identify key prey in marine ecosystems using a simple method, but at the same time preserving essential information such as the abundance, seasonal and spatial variability of predators. It is also demonstrated the importance of the identification of key prey, since it may indicate greater or lesser stability of predator populations depending on whether they come from compartments with more or less dynamic primary production processes, including climate-related changes that may affect the predator prey interactions (As shown by Friedland et al., 2018). Finally, on one hand, this study confirmed the prediction that demersal nekton has high disturbance recovery capacity, which may mask for decades the growing impact of fishing. On the other hand, the identification of the key prey species may contribute to alert fishery managers to keep a low fishing pressure on them to decrease the risk of their collapse.

CRediT authorship contribution statement

Agnaldo Silva Martins: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Manuel Haimovici:** Conceptualization, Validation, Resources, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.104963.

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