

Trophic overlap between marine mammals and fisheries in subtropical waters in the western South Atlantic

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ABSTRACT: Marine mammals and humans are apex predators and both may compete for fish in ecosystems under continuous fishing pressure. We assessed the degree of trophic overlap between prey species found in the diet of 5 marine mammals (39 specimens of sea lion *Otaria flavescens*, 61 fur seals *Arctocephalus australis*, 76 franciscana dolphins *Pontoporia blainvillei*, 25 bottlenose dolphins *Tursiops truncatus* and 28 Lahille's bottlenose dolphins *T. gephyreus*) and the catches of the 6 main commercial fishing gears used in southern Brazil (coastal gillnets, oceanic gillnets, purse seine, demersal pair trawling, bottom [single] trawl and double-rig trawling) between 1993 and 2016. An adjusted general overlap index indicated an overall moderate to high overlap. Specific overlap analysis showed that *O. flavescens* and *T. truncatus* presented high trophic relationships with fisheries, followed by *T. gephyreus*. Smaller interactions were observed for *A. australis* and *P. blainvillei*, even though they also exploit commercial fishing resources. Coastal gillnet and pair bottom trawling are the fisheries that most target the fish species favoured by *O. flavescens*, *T. gephyreus* and *T. truncatus*. The information presented in this study on trophic interactions may assist decision making for both fishery management and conservation measures for these apex predators. Commercial fishing activities are a major threat to marine mammals both regionally and globally. Current levels of fishing or its intensification may lead to dramatic changes in the coastal marine food web, including additional threats to coastal marine mammal populations in southern Brazil.

KEY WORDS: Trophic interactions · Feeding ecology · Marine mammals · Fisheries · Marine conservation

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1. INTRODUCTION

Marine mammals are an informal group which contains representatives of 3 orders, Cetartiodactyla, Sirenia and Carnivora (Gatesy et al. 2013, Würsig et al. 2018). They exhibit complex and heterogeneous distributions throughout the ocean, between polar and equatorial regions, and coastal and estuary zones, as well in freshwater environments (Forcada 2018). While some marine mammals have mostly monotypic diets (e.g. sea otters specializing on benthic invertebrates and baleen whales specializing on large zooplankton), others (e.g. pinnipeds and toothed whales) consume a variety of prey species including mainly benthic invertebrates, fish and cephalopods (e.g. Pauly et al. 1998, Trites & Spitz 2018). However, in general, pinnipeds and toothed whales are mostly opportunistic and generalist, whereas fish contribute roughly to 50% of their diets (e.g. Pauly et al. 1998, Trites & Spitz 2018). The differences and similarities in the diets of the species reflect their evolutionary adaptations to marine life, both morphologically and behaviourally (Trites & Spitz 2018), which are associated with different feeding strategies and habitats used by marine mammals while foraging (Heithaus et al. 2018). This foraging behaviour can sometimes lead to interactions with humans.

Interactions between marine mammals and human activities occur when feeding, breeding, and resting areas overlap with areas used or impacted by humans. In this context, the main threats to marine mammals arising from interactions with human activities are linked to habitat loss from coastal development, water pollution, noise pollution from military and seismic sonar, boat strikes, direct harvesting, marine debris, effects of climate change, entanglement in fishing gear and loss of prey or other food sources due to poor fisheries management (Polidoro et al. 2008, Schipper et al. 2008).

Interactions with fisheries are currently the main conservation problem of most marine mammal species (Schipper et al. 2008, Northridge 2018), and this conflict generally constitutes a global problem resulting in negative consequences for both parties. While this competition could lead to a decrease in the relative abundance of the marine mammals or changes in their diet composition, the production yield for fishermen could also decrease (Wickens 1995, Lavigne 2003). Globally, the fishing industry has been experiencing an unprecedented crisis since the late 1990s. A number of natural populations of fishery resources have collapsed as a result of increased fishing effort, overfishing of important stocks, impacts of fisheries

on natural ecosystems and a lack of proper fishing management (e.g. Haimovici 1998, Froese et al. 2012, Pauly & Zeller 2016). Another factor that also potentiates this scenario is habitat loss in continental and estuarine aquatic systems related to water pollution, deforestation, disordered urban development and improper management practices (e.g. Barletta et al. 2010).

All of these factors can exacerbate the conflict between marine mammals and fisheries, and the interactions between them can be either operational or biological. Biological (or ecological) interactions refer to the indirect effects of competition for fish or food resources, while operational interactions include direct contact between marine mammals and fisheries. As a result of interactions with fisheries, marine mammals can impact commercial fish stocks and damage commercial fishing gears. They may also get entangled in discarded material, harassed by fishing vessels or even attacked by fishermen (Wickens 1995, Lavigne 2003, Northridge 2018).

Trophic relationships (biological interactions) between marine mammals and fisheries are complex and little studied despite their importance for understanding how top predators coexist in an ecosystem under continuous and growing human pressures (Trites et al. 1997, Yodzis 1998). Although not a measure of competition, trophic overlap indices may be used to provide an approximation of the levels of biological interaction between marine mammals and fisheries. This approach has been successfully used in the western South Atlantic Ocean (e.g. Dans et al. 2003, Szteren et al. 2004, Romero et al. 2011, Machado et al. 2018).

In the subtropical region of the western South Atlantic, the industrial fishery targeting coastal demersal fish species began with bottom trawling in the 1950s followed by the introduction of bottom gillnets in the 1980s (Yesaki & Bager 1975, Vasconcellos et al. 2014). Coastal pelagic fish species, mainly bluefish *Pomatomus saltatrix* (Linnaeus, 1766), began to be explored as a potential commercial species by purse seiners in the 1960s (Yesaki & Bager 1975) and by pelagic gillnetters in the 1980s (Haimovici & Krug 1996). In southern Brazil, fisheries removal is estimated to account for about one-quarter of the total primary production of continental shelf ecosystems (Vasconcellos & Gasalla 2001). This value is typical of intensely fished coastal mid-latitude regions (Pauly & Christensen 1995). Since the 1970s, when Brazilian trawlers were banned from fishing in Argentinian and Uruguayan waters, coastal demersal fishing in southern Brazil intensified (Haimovici

et al. 2014). Intense fishing in the region led to the decrease in the abundance of the main species in the coastal demersal fisheries in the following decades, including *Micropogonias furnieri* (Vasconcellos & Haimovici 2006), *Cynoscion guatucupa* (de Miranda & Haimovici 2007), *Macrodon atricuada* (Cardoso & Haimovici 2015) and *Umbrina canosai* (Haimovici & Cardoso 2016). Since these fisheries began, there has been no indication of a reduction in fishing effort, and the current overall scenario is the overexploitation of coastal fishing resources (Haimovici et al. 2006, Haimovici & Cardoso 2017).

In the last decades, in the subtropical region of the western South Atlantic, studies evaluated the trophic ecology of marine mammals, focussing on describing the main prey consumed by these predators through the analysis of the stomach contents (Santos & Haimovici 2001, Oliveira et al. 2008, Milnham et al. 2016, Secchi et al. 2017, Machado et al. 2018) and faecal analysis (Naya et al. 2000, 2002). Recently, similar studies were conducted using stable isotopes in this region (e.g. Vales et al. 2014, Drago et al. 2015, Troina et al. 2016, Secchi et al. 2017). However, only a few studies have assessed the trophic overlap between marine mammals and fisheries in this region (Szteren et al. 2004, Bergamino et al. 2012, Riet-Sapirza et al. 2013, Machado et al. 2018). In this context, Machado et al. (2018) evaluated the trophic overlap between the South American sea lions *Otaria flavescens* (Shaw, 1800) and commercial fishing in southern Brazil. Similar studies were conducted in Uruguay with *O. flavescens*, South American fur seals *Arctocephalus australis* (Zimmermann, 1783), franciscana dolphins *Pontoporia blainvillei* (Gervais and D'Orbigny, 1844) and common bottlenose dolphins *Tursiops truncatus* (Montagu, 1821) (Szteren et al. 2004, Bergamino et al. 2012, Riet-Sapirza et al. 2013). Studies of trophic overlap between marine mammals and fisheries have already been conducted in other regions of the world (e.g. Kaschner et al. 2001, Dans et al. 2003, Kaschner & Pauly 2005, Romero 2011). Understanding the potential effects of stock overexploitation on top predator populations is only possible with knowledge of the trophic interactions between marine mammals and industrial fisheries. Understanding these interactions is therefore a priority, especially in areas with intense fishing effort, such as the southern region of Brazil. Thus, management measures put in place to reduce the conflicts between marine mammals and commercial fishing activities should consider the feeding habits of the species and their interactions with fishing activities.

The present study evaluates the trophic relationships of 5 species of marine mammals along with 6 important commercial fisheries in the southern region of Brazil. In addition, we assessed the potential trophic impacts caused by fisheries via the exploitation of the food resources of marine mammals and discuss how fisheries management could minimize these impacts.

2. MATERIALS AND METHODS

2.1. Study area

The southernmost region of Brazil is under the influence of the Subtropical Convergence Zone of the Atlantic Ocean which usually extends 950 km along the coast from Santa Marta Grande Cape (28° 40' S) to Uruguay (34° 40' S) (Seeliger & Odebrecht 1997) comprising an area of nearly 100 000 km². The region is an important breeding and feeding area for several marine vertebrates (e.g. Secchi et al. 2003, 2017, Colabuono & Vooren 2007, Oliveira et al. 2008, Milmann et al. 2016, 2018, Machado et al. 2018), due to the interaction of different water masses such as the Brazil Current, the Malvinas Current and fresh water from the large hydrographic basins of the La Plata River and the Patos–Mirim system (Seeliger & Odebrecht 1997). Because of the high levels of marine productivity, the region is also important for its high commercial fishing potential (Haimovici 1998). Conflicts between marine mammals and fishing activities through operational interaction are known in the area (e.g. Rosas et al. 1994, Secchi et al. 2003, Engel et al. 2014, Machado et al. 2016, Pont et al. 2016).

2.2. Selection and sampling of marine mammals

In order to evaluate the trophic relationship between marine mammals and their relationship with the local fisheries, the diets of the most common and abundant coastal species in southern Brazil were analysed (Oliveira 2013, Ott et al. 2013, Prado et al. 2016). Five species presented a sufficient sample number for the analysis of trophic relationships with fisheries: South American sea lions, South American fur seals, franciscana dolphins, common bottlenose dolphins and Lahille's bottlenose dolphins *Tursiops gephyreus* Lahille, 1908. The name *T. gephyreus* was recently resurrected and applied to the morphologically distinct form of *Tursiops* found along the coast of southern Brazil, Uruguay and Argentina (Wickert

et al. 2016). Despite the recent revalidation, the recognition of Lahille's bottlenose dolphins as a full species is still a matter of debate. It has been alternatively considered a subspecies (Costa et al. 2016) or ecotype (Oliveira et al. 2019) of *T. truncatus*. Regardless of the nomenclature applied, most studies suggest that the 2 forms may have distinct ecological and distributional attributes. Therefore, we judged it appropriate to analyse the 2 forms of *Tursiops* as different entities and for nomenclatural consistency with morphological identification we followed the taxonomy of Wickert et al. (2016).

For the analysis of the diet of local marine mammals, the stomachs of individuals found dead on the beach between Torres (29° 20' S, 49° 43' W) and the Lagoa do Peixe National Park (31° 21' S, 51° 02' W; Fig. 1) were collected and analysed. The sampling occurred between January 1993 and December 2014, being well represented in all months and years of the study, and a total of 285 expeditions were carried out, covering 27 194 km of surveyed beaches. In addition to the regular expeditions, specimens were also occasionally collected after the reporting of stranded animals by the local community until 2016. The voucher specimens (skull and eventually entire skeleton)

were deposited in the scientific collection of the Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS). Some specimens of common bottlenose dolphin previously analysed by Milmann et al. (2016) were also included in the present study.

2.3. Commercial fisheries landings

Catch data (kg) from coastal and oceanic gillnets, purse seine, pair trawl, bottom (single) trawl and double-rig trawl (Fig. 1) between 1993 and 2011 were extracted from landing reports of the Federal Fishery Research Centre in Rio Grande (Ibama/ICMBio/Ceperg 1993–2012), and these fisheries took place seasonally every year. A detailed description of fisheries can be found in Haimovici et al. (2006). Length data of the fish caught by commercial fishing activities were collected during the fishing landings and onboard surveys at the harbor of Rio Grande (32° 08' S, 52° 05' W), Imbé (29° 58' S, 50° 07' W) and Passo de Torres' (29° 19' S, 49° 43' W). The average length of mullet *Mugil liza* (Valenciennes, 1836), was extracted from the literature, and is related to land-

ings of artisanal (unknown fishing gear) and industrial (purse seine) fisheries carried out along the coast of the states of Rio Grande do Sul and Santa Catarina, southern Brazil (Lemos et al. 2014).

2.4. Diet analysis

Marine mammal stomachs were collected, and the contents were washed using a 0.5 mm mesh sieve to separate the remains of food items which were categorized into higher taxonomic groups (cephalopods, crustaceans and fish). Otoliths and fish bones (e.g. supraoccipital bone, mandible, maxilla) were stored dry, and cephalopod beaks and exoskeletons of crustaceans were stored in 70% ethanol. These items were identified as far as possible to the species level, using local reference collections (Costa et al. 2003, Rossi-Wongtschowski et al. 2014) and the cephalopod beak collection of the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul (CEPSUL).

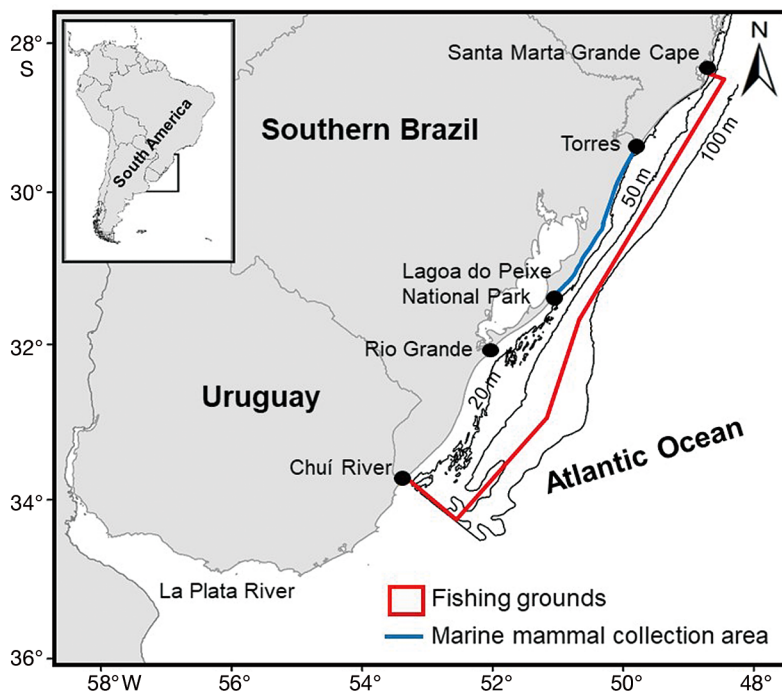


Fig. 1 Study area, indicating the stretch of the sandy beaches (ca. 270 km) where dead specimens of marine mammals (*Otaria flavescens*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops geophysus* and *Tursiops truncatus*) were collected (blue line). The main commercial fishing area used by the local fleet is indicated by the red line. The fishing harbour of Rio Grande, where the fish landing statistics were collected, is also shown

The minimum number of teleosts ingested was estimated by taking the higher number of fish bones or sagittal otoliths of the most representative side (left or right) for each species in each stomach. The same was done for cephalopod beaks, where the higher number of inferior or superior beaks of each specimen was considered. Finally, the total number of crustaceans was estimated by the absolute number of cephalothoraxes found.

Otoliths that were in good condition (see Recchia & Read 1989), fish bones (e.g. supraoccipital bone, mandible, maxilla) and cephalopod beaks were measured under a stereoscopic microscope with an ocular micrometer and a precision of 0.1 mm, or with digital callipers with 0.01 mm precision. Total length (mm) and biomass (g) of the prey were back-calculated using the size of these structures and published allometric regression equations (see compilation in Machado et al. 2018). Mean general biomass of a given prey item found in the predator's stomach was used to estimate fish biomass from damaged otoliths. A more detailed description of the dietary analysis is presented in Machado et al. (2018).

2.5. Statistical analysis

The importance of different prey species in the diet of marine mammals was estimated by the percentage of index of relative importance (%IRI = [%NF + %M] × [%FO]) (Pinkas et al. 1971, Hyslop 1980, Cortés 1997), which takes into account the numerical frequency (%NF = [estimated total number of prey *i* / total number of prey of all species] × 100); the frequency of occurrence (%FO = [O = number of stomachs with prey *i* / total number of stomachs] × 100); and the percentage of biomass contribution (%M = [estimated biomass of prey *i* / estimated total biomass] × 100).

The %IRIs were calculated by grouping all species of marine mammals, separately by predator species, and by ecological grouping of prey species. The ecological groups were defined according to the habitat of the prey species: species exclusively associated with the bottom (demersal and benthic), species that swim free in the water column (pelagic) and species that use both the bottom and the water column (benthic–pelagic and demersal–pelagic) (Haimovici & Perez 1991, Carvalho-Filho 1999, Romero et al. 2011).

The trophic niche amplitude of each local marine mammal species was estimated through the Levins trophic niche amplitude index (*B*) (Krebs 1999), de-

fined by: $B = 1 / \sum p_i^2$, where *p* is the proportion of individuals of the *i*th resource found in the diet. This index was standardized (*B_s*), according to the following equation: $B_s = (B - 1) / (n - 1)$, where *n* represents the number of food items. This index is expressed on a scale from 0 to 1, with higher values indicating a greater niche amplitude and generalist habit of the predator (Krebs 1999). Shannon and Simpson species diversity indexes were calculated and compared using the software PAST 3.0, taking 95 % confidence intervals into account.

Shannon diversity index (*H*) was calculated as:

$$H = - \sum_{i=1}^S P_i \ln P_i \quad (1)$$

and Simpson's diversity (*D*) as:

$$D = \frac{1}{\sum_{i=1}^S P_i^2} \quad (2)$$

where *S* is the total number of species in the community (i.e. species richness found in all samples) and *P_i* is the proportion for the *i*th species.

The sampling coverage approach was completely standardized based on entropy (*q* statistic, Chao & Jost 2012) to assess the richness of prey species in the stomachs of marine mammals with abundance data in the online iNEXT software (<https://chao.shinyapps.io/iNEXTOnline/>; Chao et al. 2016). The estimate of sample coverage used for this analysis was suggested by Chao et al. (2013).

We used 'test G' in BioEstat 5.0 software to compare the size frequencies of fish consumed by marine mammals to the size of fish caught by commercial fishing activities. To visualize trophic interactions between fisheries, marine mammals and prey, a quantitative interaction network was constructed using the software 'Food Web Designer' (version 3.0.0.0) (Sint & Traugott 2016). Food webs were constructed using the percentage of biomass contribution of the different fish species to the total fisheries landings and to the diets of marine mammals. A correspondence analysis (CA) was used to evaluate associations between marine mammal species and fisheries. For this, the %M of the most important prey species for mammals and the main catches landed by the fisheries were used. CA was tested using PAST software version 3.0.

The general overlap (GO) index and the specific (SO) overlap index (Petraitis 1979, Ludwig & Reynolds 1988) were used to compare the potential trophic overlap between the prey species targeted by different marine mammals and the target species

caught by 6 types of local commercial fishery. The data used for the trophic overlap analysis (GO and SO) were the mass of the prey of the marine mammals and catches of the fisheries of all species that presented a %M > 1% in at least 1 of the 2 groups compared. When a species was not present in the diet of a particular marine mammal or in the catches of a particular fishery, a value of 0.00001 was used.

The GO is a symmetric index ($GO_{BA} = GO_{AB}$) that represents the probability that the trophic niche utilization curve of each predator stems from the common use curve of all predators. Thus, the null hypothesis of a complete trophic overlap between all marine mammals and fisheries (H_0 : $GO = 1$ versus H_a : $GO \neq 1$) was tested using V analysis (Ludwig & Reynolds 1988), which follows a distribution $X^2 (S - 1) (r - 1)$, where S is the number of predator categories (marine mammals and fisheries), and r is the number of prey categories. At the level of comparison, the GO generates an adjusted index (GO_a), which varies from 0 to 1 (Ludwig & Reynolds 1988). The adjusted index of this calculation (GO_a) was used because the GO index only allows for the evaluation of the hypothesis of complete trophic overlap between both predators (marine mammals and fisheries).

We also calculated and tested the SO index, which represents the probability of the niche amplitude curve of a predator (e.g. marine mammal) completely overlapping with that of the other predator (e.g. fishery). This index shows that the amplitude curve of a predator i may explain that of predator m (SO_{im}), but the reverse does not necessarily occur (Petratis 1979). SO_{im} also varies from 0 to 1, and the null hypothesis of a complete specific trophic overlap between both predators (H_0 : $SO_{im} = 1$ versus H_a : $SO_{im} \neq 1$) was tested through U analysis (Ludwig & Reynolds 1988), which follows a distribution $X^2 (r - 1)$, where r represents the number of prey categories.

3. RESULTS

3.1. Feeding ecology of marine mammals

A total of 229 stomachs were analysed: 76 of *Pontoporia blainvillei*, 61 of *Arctocephalus australis*, 39 of *Otaria flavescens*, 28 of *Tursiops gephyreus* and 25 of *T. truncatus*. From the combined analysis of the stomach contents of these marine mammals, it was possible to identify a total of 36 prey species (Table 1). Teleost fish were the most representative group with 26 species, followed by 6 species of cephalopod, 3 species of elasmobranch and at least 1 crustacean.

Sciaenidae was the most well represented fish family, with 9 species identified, corresponding to 48.9% of the relative importance for all marine mammals (pooled analysis). *Trichiurus lepturus* Linnaeus, 1758, *Paralichthys brasiliensis* (Steindachner, 1875) and *Doryteuthis sanpaulensis* (Brakonietcki, 1984) were the most important prey species, respectively, representing >75% of relative importance. *P. brasiliensis* was the most important prey for *O. flavescens*, whereas *T. lepturus* was the most important prey species for *A. australis*, *T. gephyreus* and *T. truncatus*; and *D. sanpaulensis* was the most important prey species for *P. blainvillei* (Table 1).

The highest trophic diversity was observed for *P. blainvillei*, followed by *T. gephyreus* (Table 2). The diversity of prey species consumed by *T. truncatus* indicates that this species has a rich diet when compared to other species studied here, while *O. flavescens*, *P. blainvillei* and *T. gephyreus* presented a very similar level of prey richness in their diets (Fig. 2). On the other hand, *A. australis* was the species with the lowest trophic richness in its diet (Fig. 2), but it was the marine mammal with the highest trophic niche amplitude index ($Bs = 0.31$), followed by *P. blainvillei* ($Bs = 0.19$), *T. gephyreus* ($Bs = 0.17$), *T. truncatus* ($Bs = 0.13$) and *O. flavescens* ($Bs = 0.09$). The results also showed that *O. flavescens* preferred demersal prey, while *A. australis* and *T. truncatus* consumed mainly benthic–pelagic and demersal–pelagic prey. *P. blainvillei* and *T. gephyreus* preyed both demersal and/or benthic and benthic–pelagic and/or demersal–pelagic prey (Fig. 3).

3.2. Trophic relationships of marine mammals with fisheries

Based on the analysis of commercial fishing landings from 1993 to 2011, 84 fishery resources were identified, of which 18 had a mass importance >1% for at least 1 fishery. These 18 resources, added to 16 that had a mass importance >1% for at least 1 of the marine mammal species, were included in the 26 taxa which were used in the analysis of trophic overlap (GO and SO index; Table 3). The results of total overlap ($GO = 0.67$, $V = 347081630$, $p < 0.001$) indicated that there was no complete overlap in the utilization of the same resources based on the curve of marine mammal and local fishery activity. However, the GO measures only whether there was total overlap or not. When overlap is not total, it can still be high. In this case, the adjusted total overlap value indicated a moderate to high overlap in resource

Table 1. Diet composition of the marine mammals *Otaria flavescens*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops gephyreus* and *Tursiops truncatus* on the southern Brazilian coast. EG: ecological group; D/B: demersal and benthic; P: pelagic; BP/DP: benthic–pelagic and demersal–pelagic; %FO: frequency of occurrence; %NF: numeric frequency; %M: percentage of biomass contribution; %IRI: percentage of index of relative importance. **Bold** values: most important prey for each species of marine mammal. *Important commercial fishing resources exploited in the southern region of Brazil

Prey taxon	EG	<i>O. flavescens</i> %IRI	<i>P. blainvillei</i> %IRI	<i>A. australis</i> %IRI	<i>T. gephyreus</i> %IRI	<i>T. truncatus</i> %IRI	All marine mammals			
							%FO	%NF	%M	%IRI
Scianidae										
<i>Paralanchurus brasiliensis</i>	D/B	51.8	5.9	0.00	28.0	0.07	32.2	27.9	9.8	23.06
<i>Macrodon atricauda</i> *	D/B	15.1	0.02	0.00	0.9	0.05	13.2	4.9	5.7	2.66
<i>Micropogonias furnieri</i> *	D/B	10.8	0.03	0.01	3.1	0.3	11.9	2.7	9.2	2.68
<i>Cynoscion guatucupa</i> *	BP/DP	5.9	0.5	0.00	0.3	9.5	18.5	3.5	5.5	3.16
<i>Cynoscion jamaicensis</i> *	D/B	0.01	0.3	0.00	0.1	0.00	4.8	0.8	0.24	0.09
<i>Umbrina canosai</i> *	D/B	2.2	0.7	0.00	0.1	0.6	10.1	4.0	2.4	1.25
<i>Menticirrhus</i> sp.*	D/B	0.8	0.5	0.03	2.6	0.1	10.6	1.3	3.2	0.90
<i>Stellifer rastrifer</i>	D/B	0.3	12.4	0.6	0.1	0.00	20.7	10.5	0.6	4.39
<i>Stellifer brasiliensis</i>	D/B	0.002	0.001	0.00	0.00	0.00	0.88	0.04	0.02	0.001
Phycidae										
<i>Urophycis brasiliensis</i> *	D/B	5.8	5.5	0.1	3.3	0.4	26.9	6.4	4.8	5.76
Trichiuridae										
<i>Trichiurus lepturus</i>	BP/DP	3.8	8.4	66.5	46.9	78.0	45.8	12.2	27.6	34.73
Pomatomidae										
<i>Pomatomus saltatrix</i> *	P	3.0	0.00	0.7	0.1	0.1	4.4	0.7	7.4	0.68
Paralichthyidae										
<i>Paralichthys</i> sp.*	D/B	0.2	0.00	0.00	0.01	0.00	2.6	0.3	0.3	0.03
Batrachoididae										
<i>Porichthys porosissimus</i>	D/B	0.2	1.7	0.00	0.2	2.7	12.8	2.0	2.4	1.06
Clupeidae										
<i>Brevoortia pectinata</i>	P	0.04	0.00	0.00	0.00	0.00	0.9	0.1	0.1	0.003
Stromateidae										
<i>Pepilus paru</i>	BP/DP	0.03	0.003	0.00	0.00	0.00	1.8	0.1	0.1	0.01
<i>Stromateus brasiliensis</i>	BP/DP	0.02	0.00	0.00	0.00	0.00	0.4	0.1	0.1	0.001
Engraulidae										
<i>Anchoa marinii</i>	P	0.004	0.2	1.2	0.00	0.00	5	1.6	0.1	0.17
<i>Engraulis anchoita</i>	P	0.00	0.1	0.00	0.00	0.00	2.6	0.2	0.0	0.01
<i>Lycengraulis grossidens</i>	P	0.00	0.001	0.00	3.1	0.6	4.4	2.1	0.8	0.24
Sparidae										
<i>Pagrus pagrus</i>	BP/DP	0.00	0.001	0.00	0.00	0.00	0.4	0.0	0.001	0.0002
Carangidae										
<i>Trachurus lathami</i>	BP/DP	0.00	0.1	0.00	0.00	0.2	2.64	0.19	0.258	0.02
Congridae										
<i>Conger orbignianus</i>	D/B	0.00	0.02	0.00	0.00	0.00	0.9	0.04	0.1	0.002
Mugilidae										
<i>Mugil liza</i> *	BP/DP	0.00	0.00	0.00	10.1	5.8	6.6	1.6	7.8	1.19
Ariidae										
<i>Genidens</i> sp.	D/B	0.00	0.00	0.00	0.3	0.00	1.3	0.2	0.3	0.01
Tetraodontiformes^a										
<i>Tetraodon lineatus</i>	BP/DP	0.01	0.00	0.00	0.6	0.0	2.2	0.4	0.78	0.05
Arhynchobatidae										
<i>Sympterygia bonaparti</i>	D/B	0.02	0.00	0.00	0.00	0.00	0.4	0.1	0.10	0.002
<i>Atlantoraja</i> sp. or <i>Rioraja</i> sp.	D/B	0.01	0.00	0.00	0.00	0.00	0.4	0.04	0.04	0.0006
<i>Sympterygia acuta</i>	D/B	0.003	0.00	0.00	0.00	0.00	0.4	0.02	0.02	0.0003
Loliginidae										
<i>Doryteuthis sanpaulensis</i>	BP/DP	0.03	62.1	30.2	0.2	0.4	40.5	13.8	8.64	17.33
<i>Doryteuthis plei</i>	BP/DP	0.00	1.5	0.01	0.1	0.7	8.8	1.5	1.08	0.43
Argonautidae										
<i>Argonauta nodosa</i>	BP/DP	0.00	0.06	0.1	0.00	0.6	5.3	0.5	0.14	0.07
Thysanoteuthidae										
<i>Thysanoteuthis rhombus</i>	P	0.00	0.00	0.00	0.00	0.1	0.4	0.04	0.06	0.001
Octopodidae										
<i>Octopus vulgaris</i>	D/B	0.003	0.00	0.00	0.00	0.00	0.44	0.02	0.011	0.0002
<i>Octopus tehuelchus</i>	D/B	0.04	0.00	0.00	0.00	0.00	0.4	0.02	0.4	0.004
Penaeidae										
Unidentified prawns		0.05	0.001	0.00	0.06	0.02	3.52	0.3	0.02	0.02

^aTwo fish preyed by *Otaria flavescens* and *Tursiops truncatus* as *Balistes* sp.

Table 2. Simpson and Shannon indexes for the diets of different marine mammal species estimated from samples collected on the southern Brazilian coast

Species	Diversity index	
	Simpson (CI)	Shannon (CI)
<i>Otaria flavescens</i>	0.690 (0.669, 0.709)	1.732 (1.669, 1.788)
<i>Arctocephalus australis</i>	0.736 (0.711, 0.761)	1.522 (1.441, 1.631)
<i>Pontoporia blainvillei</i>	0.808 (0.798, 0.818)	2.048 (2.002, 2.096)
<i>Tursiops gephyreus</i>	0.759 (0.739, 0.777)	1.882 (1.801, 1.951)
<i>Tursiops truncatus</i>	0.698 (0.646, 0.748)	1.793 (1.648, 1.943)

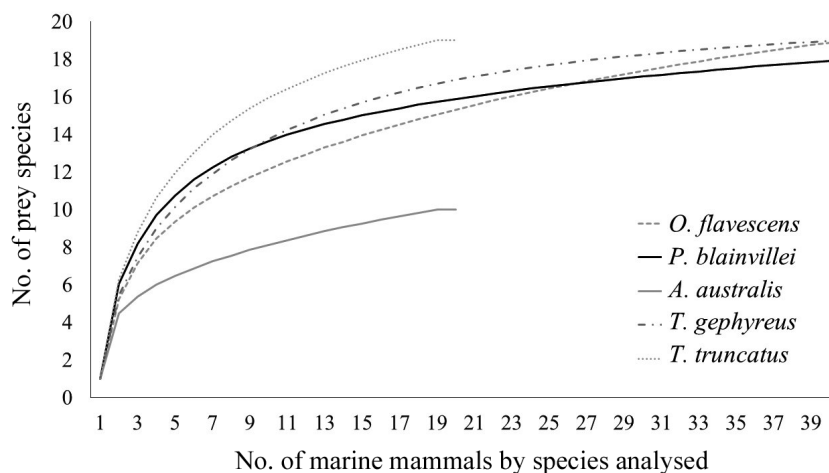


Fig. 2. Cumulative number of species preyed on by marine mammals (*Otaria flavescens*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops gephyreus* and *Tursiops truncatus*) along the southern Brazilian coast

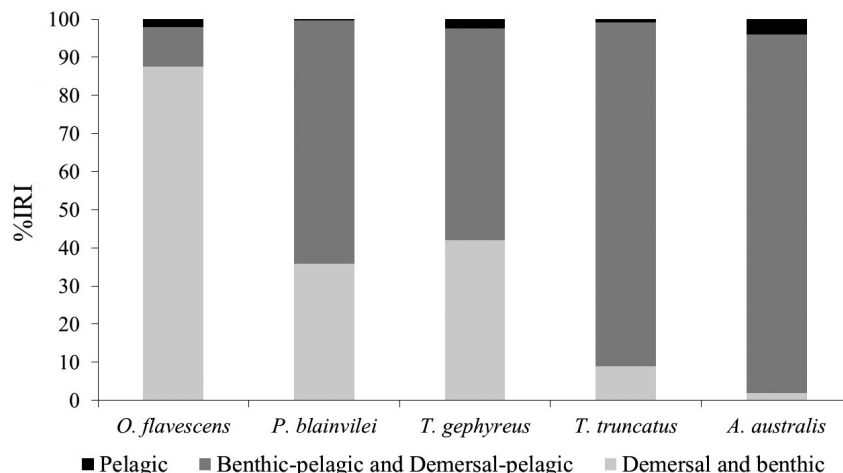


Fig. 3. Index of relative importance (%IRI) according to the ecological prey groups present in the diet of 5 marine mammal species (*Otaria flavescens*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops gephyreus* and *Tursiops truncatus*) along the southern Brazilian coast

sharing ($GO_a = 0.59$, $V = 347081630$, $p < 0.001$).

The SO analysis showed that even at low intensity, *O. flavescens* and *T. truncatus* are the 2 marine mammals whose resource use most overlaps with the exploitation curve of the resources exploited by fisheries (Fig. 4; Table S1 in the Supplement at www.int-res.com/articles/suppl/m639p215_supp.pdf). However, the fisheries exploited the resources with greater intensity than these 2 marine mammal species, with the exception of the double-rig trawl and oceanic gillnet fishery (Fig. 4). The diet of *O. flavescens* was less related to one type of bottom trawl, and the diet of *T. truncatus* was less related to double-rig trawl. In contrast, *A. australis* and *P. blainvillei* were the 2 marine mammals that least exploited the same prey species targeted by the local commercial fisheries (Fig. 4; Table S1). In the same way, *P. blainvillei* and *A. australis* were the predators that least overlapped with fisheries in their preferred prey species (Fig. 4, Table S1). *T. gephyreus* presented intermediate trophic interactions with the local fisheries, in comparison with other local marine mammals. Coastal gillnet and pair trawling were the fishery activities that most exploited the same food resources used by *O. flavescens*, *T. gephyreus* and *T. truncatus* (Fig. 4; Table S1).

Although some overlap was detected in resource use, in general marine mammals consumed smaller fish than the commercial size caught by local fisheries (Figs. S1–S3). Nevertheless, South American sea lions showed the greatest overlap with fisheries in terms of the size of fish they consumed, including species caught by pair trawling (*Micropogonias furnieri* and *Macrodon atricauda*), bottom trawl (*M. furnieri*) and coastal gillnet (*Pomatomus saltatrix*). South American sea lions also consumed 2 prey species of similar size to the discards from pair trawling (*Cynoscion guatucupa* and *Umbrina canosai*) and consumed *M.*

Table 3. Marine fisheries landings (in kg) in Rio Grande harbour captured by 6 different types of industrial fisheries (1993–2011), and stomach contents (kg) of 5 stranded marine mammal species (*Otaria flavescens*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops gephyreus* and *Tursiops truncatus*) collected during the study on the southern Brazilian coast. Only those species that presented a mass (kg) >1 % of the biomass of at least one of the groups (predators and fisheries) and that were used in the analysis of trophic niche overlap (general overlap [GO], adjusted GO [GO_a] and specific overlap [SO] are listed)

Resource	Industrial fishing gears (total mass landings, kg)				Marine mammals (total mass consumption, kg)						
	Pair trawl	Bottom trawl	Double-rig trawl	Purse seine	Coastal gillnet	Oceanic gillnet	<i>O. flavescens</i>	<i>P. blainvillei</i>	<i>A. australis</i>	<i>T. geophyreus</i>	<i>T. truncatus</i>
<i>Artemesia longinaris</i>	360.0	44712.0	15032585.0	0.00001	62756.0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Cynoscion guatucupa</i>	44971512.0	10325549.0	2747521.0	1190191.0	20391223.0	11059816.0	6.2	0.09	0.00001	2.2	13.1
<i>Cynoscion jamaicensis</i>	2477949.0	79597.0	98516.0	23072.0	68795.0	57068.0	0.1	0.5	0.00001	0.3	0.00001
<i>Genidens spp.</i>	751813.0	91600.0	128461.0	352648.0	779017.0	962759.0	0.00001	0.00001	0.00001	1.2	0.00001
<i>Loligo spp.</i>	2808.0	480.0	96532.0	12620.0	6380.0	63229.0	0.2	34.7	2.3	0.4	0.6
<i>Macrodon ancylodon</i>	30401387.0	73823.0	1221442.0	665448.0	1500407.0	757387.0	21.3	0.2	0.00001	0.8	0.2
<i>Menticirrhus spp.</i>	1418149.0	13934.0	367206.0	17927.0	561397.0	209416.0	4.9	1.7	0.1	5.0	0.7
<i>Merluccius hubbsi</i>	334152.0	333187.0	442744.0	24933.0	715055.0	1000780.0	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Micropogonias furnieri</i>	28443464.0	1782199.0	2661256.0	6916481.0	45631488.0	12927026.0	21.5	0.09	0.01	11.0	3.4
<i>Mugil liza</i>	704703.0	5427.0	120864.0	7641964.0	4704227.0	340124.0	0.00001	0.00001	0.00001	15.0	15.9
<i>Octopus spp.</i>	55347.0	0.00001	147082.0	3791.0	5020.0	14346.0	1.6	0.00001	0.00001	0.00001	0.00001
<i>Paralichthys brasiliensis</i>	996159.0	142205.0	3930243.0	38801.0	350868.0	224602.0	1.0	0.00001	0.00001	0.2	0.00001
<i>Paralanchurus brasiliensis</i>	757601.0	0.00001	90080.0	320.0	3940.0	80036.0	31.0	3.5	0.00001	3.9	0.02
<i>Pleoticus muelleri</i>	11022.0	9288.0	7152461.0	0.00001	33558.0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Pogonias cromis</i>	364948.0	46.0	195987.0	659824.0	151658.0	1960.0	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Pomatomus saltatrix</i>	455533.0	8583.0	223831.0	10766796.0	5269581.0	1467813.0	24.5	0.00001	3.3	0.7	0.9
<i>Porichthys porosissimus</i>	34562.0	4446.0	49378.0	10600.0	12838.0	27429.0	0.9	2.2	0.00001	0.8	5.4
<i>Prionotus spp.</i>	3575244.0	944879.0	2356556.0	107421.0	3413747.0	2702339.0	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Scomber japonicus</i>	540.0	0.00001	3600.0	1936913.0	242180.0	3454.0	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Squatina spp.</i>	902965.0	288858.0	779327.0	32277.0	707869.0	3538657.0	0.00001	0.00001	0.00001	0.00001	0.00001
<i>Stellifer spp.</i>	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.6	1.7	0.04	0.1	0.00000
<i>Tetraodon</i> spp.	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.2	0.00001	0.00001	2.7	0.2
<i>Trachurus lathami</i>	23840.0	17628.0	0.00001	3686111.0	260.0	134335.0	0.00001	0.5	0.00001	0.00001	0.5
<i>Trichiurus lepturus</i>	1101591.0	16665.0	77906.0	56214.0	354090.0	329884.0	11.5	5.4	25.3	38.7	27.7
<i>Umbina canosai</i>	41456413.0	11784463.0	2798720.0	1212843.0	20785809.0	18126123.0	4.1	0.8	0.00001	2.1	2.6
<i>Urophycis brasiliensis</i>	2112590.0	568554.0	3726073.0	70368.0	2089000.0	3256474.0	12.7	1.2	0.2	3.7	1.2
Other species	5857495.0	973215.0	1669370.0	2290451.0	2662935.0	3669994.0	1.4	0.9	0.6	2.7	0.5
Total	167212147.0	27509338.0	46117741.0	37718014.0	110504098.0	60955051.0	143.8	53.4	31.9	91.5	72.9

furnieri larger than those discarded in pair trawling (Fig. S1). Although 17 analyses indicated that *O. flavescens* prey on smaller fish than the fish caught by local fisheries, in 47 % of these analyses, it was possible to identify a high degree of overlap ranging from 43.79 to 86.56 % (Fig. S1).

T. gephyreus preyed upon *U. brasiliensis* smaller than those caught by coastal gillnet fishing, pair trawling, bottom trawling and those discarded by trawling. It also predated *M. liza* smaller than the catches of local industrial and artisanal fisheries, with no size overlap with industrial fishing and a 33.30 % overlap with artisanal fisheries (Fig. S3). Although *T. truncatus* predated *M. liza*, which is highly targeted by the local artisanal (100 %) and industrial fisheries (91.67 %), the proportion of the distribution in the size frequency was not similar. *T. truncatus* also preyed on *C. guatucupa*, with a large overlap in size with fish of this species caught by coastal gillnet fishing (73.68 %), pair trawling (81.58 %), double-rig trawling (79.95 %) and single trawling (57.89 %) and also predated fish larger than those discarded in pair trawling (Fig. S3).

In the CA used to evaluate associations between marine mammal species and fisheries, 6 main clusters were observed (Fig. 5). *O. flavescens* formed the largest cluster, with close association with the coastal gillnet, oceanic gillnet, pair trawl and simple trawl (red ellipse) fisheries. The other marine mammal species showed associations with different taxa (e.g. *P. blainvillei* with the cephalopods), but not with

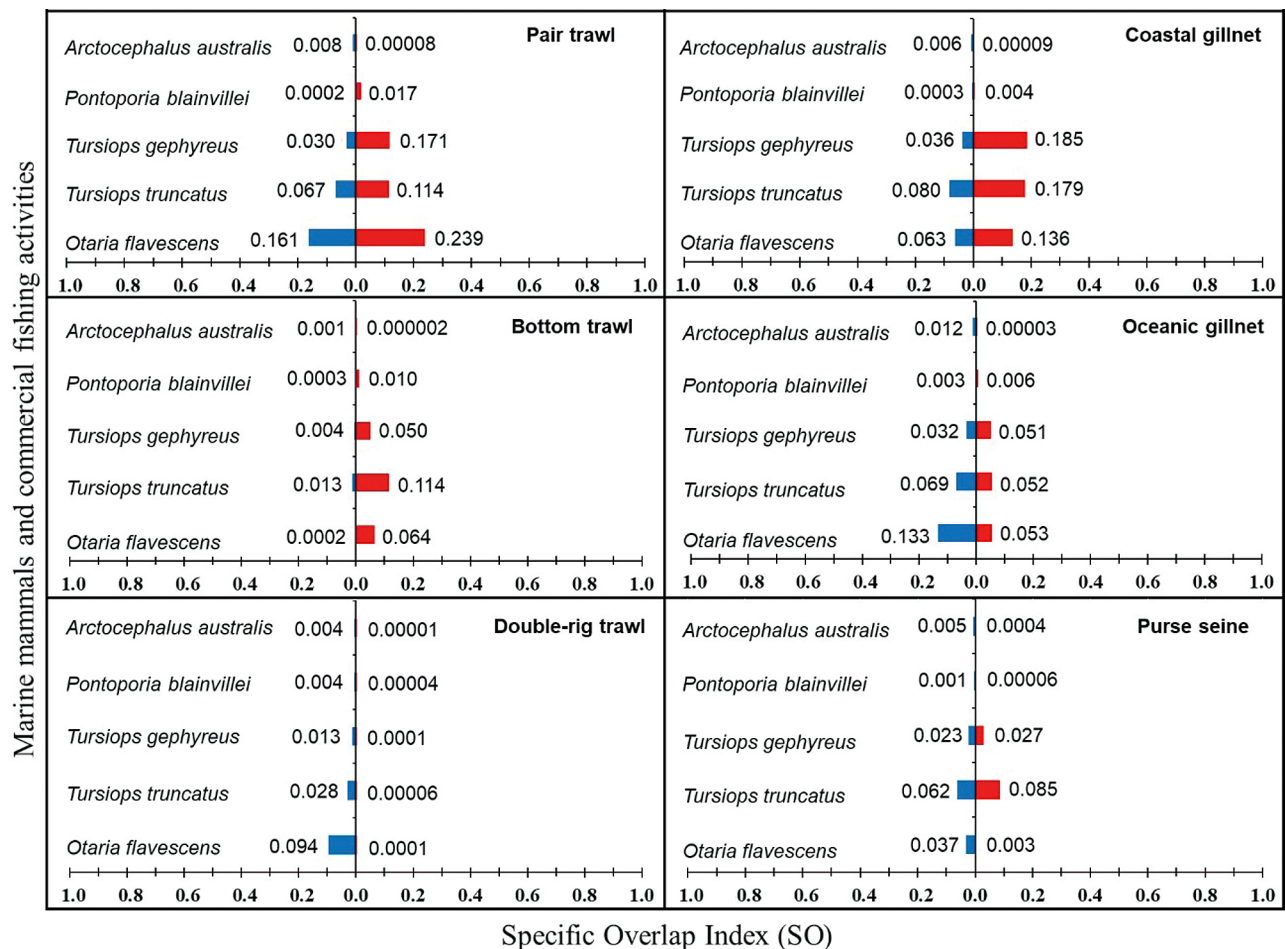


Fig. 4. Specific overlap index (SO) between the stomach contents of 5 stranded marine mammal species (*Otaria flavesceus*, *Pontoporia blainvillei*, *Arctocephalus australis*, *Tursiops geophysus* and *Tursiops truncatus*) and the 6 commercial fishing activities analysed in the present study on the southern Brazilian coast. Values on the left (blue) represent the utilization curve of marine mammal food resources that overlap the curves of exploitation of resources by fisheries. Values on the right (red) represent the utilization curve of resources by fisheries that overlap the utilization curve of marine mammal food resources

any specific fishery (Fig. 5). Fig. 6 shows the connections of each species of marine mammal with their main prey, as well as the relationships of the fisheries with the main catches landed.

4. DISCUSSION

Resource overlap between fisheries and marine mammals has been quantified in different ways around the world (e.g. Kaschner et al. 2001, Dans et al. 2003, Kaschner & Pauly 2005, Romero 2011, Bergamino et al. 2012). However, this is the first broad study about the relationships between marine mammal trophic ecology and fishing catches and how they interact in Brazil. Usually, the degree of overlap of prey species targeted by marine mammals with those

targeted by fisheries varies greatly among species, with the pinnipeds being one of the groups with the greatest fisheries overlap (e.g. Kaschner et al. 2001, Romero 2011).

In the present study, however, the 2 species of pinnipeds showed a very distinct pattern. Whereas *Otaria flavesceus* showed the greatest dietary overlap with species targeted by fisheries, *Arctocephalus australis* had the lowest. The high overlap of *O. flavesceus* with fisheries seems to be directly related to its behaviour. It is noteworthy that *O. flavesceus* interacts directly with the fisheries in southern Brazil, including the predation of fish caught in gillnets (e.g. Machado et al. 2016, 2018), as well as the incidental catch of *O. flavesceus* in pair trawls (Machado et al. 2015).

Therefore, it is not surprising that the coastal gillnet and pair trawling fisheries were those that most

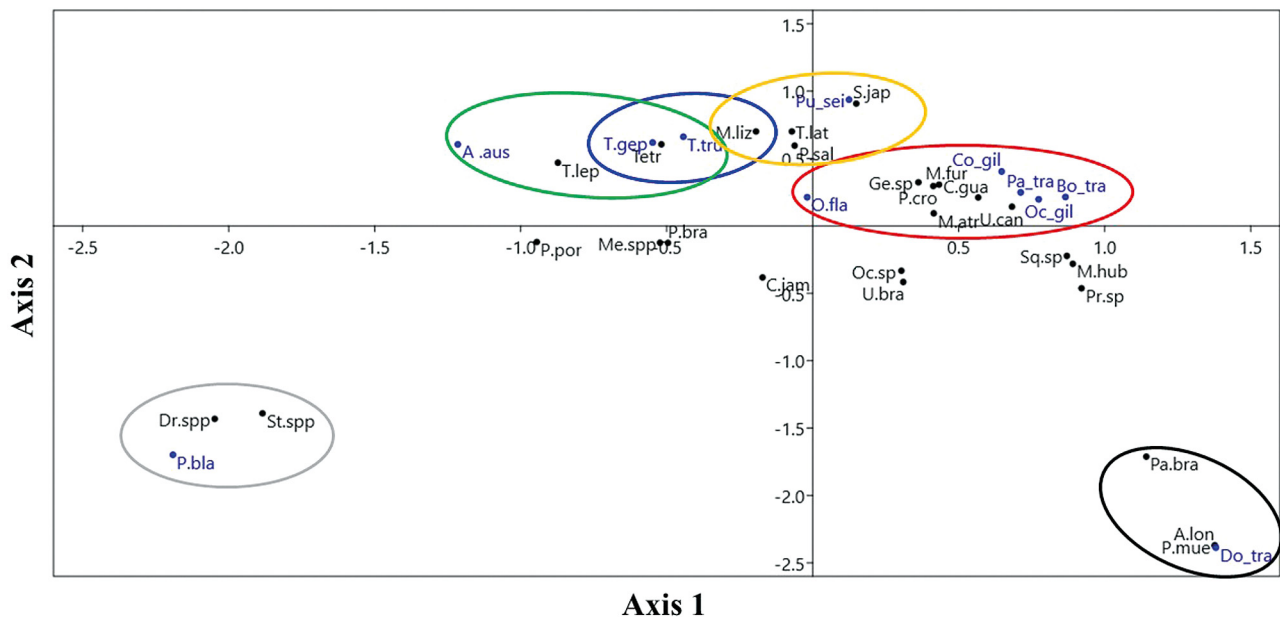


Fig. 5. Correspondence analysis (CA) for interactions between resources, marine mammals and commercial fishing activities. Association of *Pontoporia blainvillei* (P.bla) with *Doryteuthis* spp. (Dr.spp.) and *Stelifer* spp. (S.spp) (gray ellipse); *Arctocephalus australis* (A.aus), *Tursiops geophyreus* (T.gep) and *Tursiops truncatus* (T.tru) with *Trichiurus lepturus* (T.lep) (green ellipse); *Tursiops geophyreus* and *Tursiops truncatus* with *Mugil liza* (M.liz) and Tetraodontiformes (Tetr) (blue ellipse); *Otaria flavescens* (O fla), coastal gillnet (Co_gil), oceanic gillnet (Oc_gil), pair trawling (Pa_tra) and single trawl (Bo_tra) with *Cynoscion guatucupa* (C.gua), *Micropogonia furnieri* (M.fur), *Macrodon atricauda* (M.atri) and *Umbrina canosai* (U.can) (red ellipse); double-rig trawl (Do_tra) with *Artemesia longinaris* (A.lon), *Pleoticus muelleri* (P.mue) and *Paralichthys* spp. (Pa.spp) (black ellipse); purse seine (Pu_sei) with *Mugil liza*, *Pomatomus saltatrix* (P.sal), *Scomber japonicus* (S.jap) and *Trachurus lathami* (T.lat) (yellow ellipse). *Paralorchurus brasiliensis* (P.bra), *Menticirrhus* sp. (Me.sp), *Cynoscion jamaicensis* (C.jam), *Pogonias cromis* (P.cro), *Urophycis brasiliensis* (U.bra), *Genidens* sp. (Ge.sp), *Prionotus* sp. (Pr.sp), *Squatina* sp. (Sq.sp), *Porichthys porosissimus* (P.por), *Merluccius hubbsi* (M.hub), *Octopus* sp. (Oc.sp)

utilized the same food resources used by *O. flavescens*. These 2 fisheries also target food resources used by *Tursiops truncatus*. Due to the higher values of the specific trophic overlap indexes and the overlap between the sizes of the predated fish and those captured/discarded by the fisheries, *O. flavescens* and *T. truncatus* were the species of marine mammals that presented the highest trophic relationship with these fisheries. In contrast, *T. geophyreus* has an intermediate level of overlap between its preferred prey species and those targeted by fisheries, while *A. australis* and *Pontoporia blainvillei* seem to have a very low level of biological interaction with fisheries.

The bottom pair trawl and gillnet fisheries are the main coastal commercial fishing activities in southern Brazil (e.g. Klippel et al. 2005, Haimovici et al. 2006). The main resources exploited by these fisheries (e.g. *Macrodon atricauda*, *Micropogonias furnieri*, *Umbrina canosai*, *Cynoscion guatucupa*, *Urophycis brasiliensis* and *Pomatomus saltatrix*) accounted for 16% of the IRI of the prey of marine mammals. Some of these resources, such as *M. furnieri*, *M. atricauda*, *U. canosai* and *C. guatucupa*, which together

account for more than half of the landings of marine fish in southern Brazil, are overexploited while others such as *P. saltatrix* and *Mugil liza* are at the limit of sustainable exploitation (MMA 2004, Haimovici & Cardoso 2017).

Nevertheless, the most important fish prey (*Paralorchurus brasiliensis* and *Trichiurus lepturus*) of the marine mammals in this study are not important fishery resources in the region, and they are mostly rejected in large quantities, mainly by bottom trawl fisheries (e.g. Haimovici & Mendonça 1996, Haimovici & Fischer 2007). In terms of biomass, the discards of these 2 fish species represented approximately one-third (31.3%) of the species discarded by bottom pair trawling (L. G. Cardoso & M. Haimovici unpubl. data). They were also among the most abundant species in the bottom trawl surveys performed along southern Brazil and are indicator species of the warm-water coastal fish assemblage (Haimovici et al. 1996, Martins & Haimovici 2017). Therefore, although these species are not fishing targets, the fish mortality caused by the bottom trawling fleet may result in negative impacts on their stocks, as was

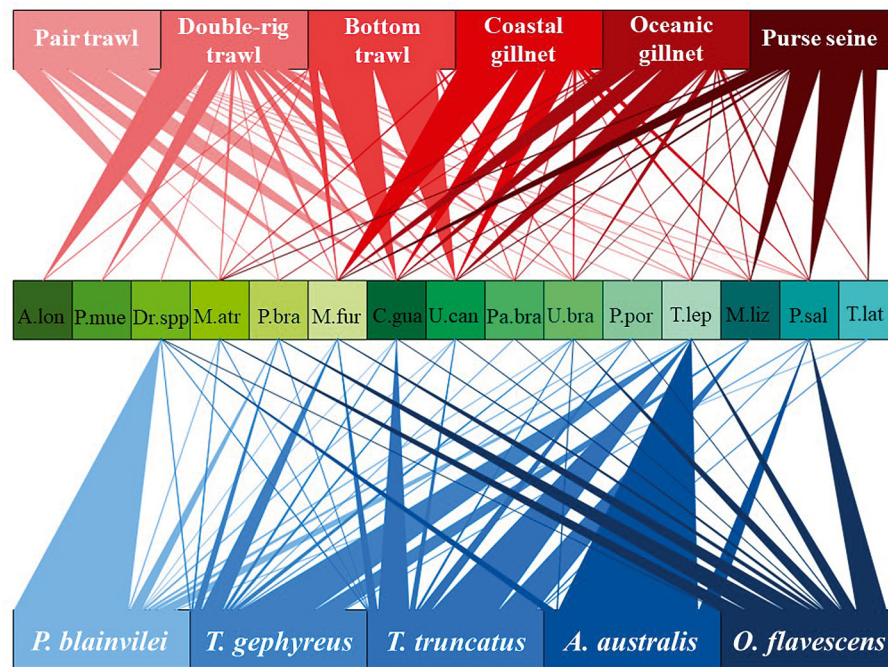


Fig. 6. Trophic interaction networks between fisheries, marine mammals and prey species along the southern Brazilian coast. The bars show the different types of fishing gear (top), fish species (middle) and marine mammal predators (bottom). Triangles represent the observed trophic links of fisheries landings (upwards) and marine mammal diet (downwards). The width of the triangles indicates the percentage of each fish species contributing to the relative diet composition of the predators and fishery landings. *Artemesia longinaris* (A.lon), *Pleoticus muelleri* (P.mue), *Doryteuthis* spp. (Dr.spp.), *Macrodon atricauda* (M.atr), *Paralichthys brasiliensis* (P.bra), *Micropogonias furnieri* (M.fur), *Cynoscion guatucupa* (C.gua), *Umbrina canosai* (U.can), *Paralichthys brasiliensis* (Pa.bra), *Urophycis brasiliensis* (U.bra), *Porichthys porosissimus* (P.por), *Trichiurus lepturus* (T.lep), *Mugil liza* (M.liz), *Pomatomus saltatrix* (P.sal), *Trachurus lathami* (T.lat)

observed for *Dules auriga* Cuvier, 1829, which is a component of bottom trawling bycatch and saw its spawning potential reduced by 50 % (Rovani & Cardoso 2017). It is also worth mentioning that *T. lepturus* is already caught in high numbers in southeast Brazil (e.g. Ávila-da-Silva et al. 2014, FIPERJ 2014), and its fishery in southern Brazil may intensify if the demand increases. *T. lepturus* has a demersal-pelagic habit, performing vertical migration whereby it goes to deeper waters during daytime to feed, thus becoming available for consumption by demersal and pelagic predators. A voracious species with large jaws, its diet varies ontogenetically (Martins et al. 2005) and it occupies a wide range of trophic levels (Chiou et al. 2006). Because of its abundance and presence in the water column, *T. lepturus* is a key resource for *T. truncatus*, *T. gephyreus* and *A. australis*. It is also an important prey for *O. flavescens* and *P. blainvillei* in subtropical waters in the western South Atlantic, and has been reported in diets of other marine mammal species in the region, such as *A. tropicalis* (Gray, 1872), *A. gazella* (Peters, 1875) (Oliveira et al. 2008), *Lagenodelphis hosei* Fraser, 1956 (Moreno et al. 2003), *Kogia breviceps* (Blain-

ville, 1828) (Brentano & Petry 2020), *Stenella frontalis* (Cuvier, 1829) and *Delphinus delphis* Linnaeus, 1758 (GEMARS unpubl. data). Other top predators also use this resource, including the seabirds *Thalasarche melanophrys* (Temminck, 1828), *Procellaria aequinoctialis* Linnaeus, 1758 (Colabuono & Vooren 2007), the loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758) (A. J. Lenz pers. comm.) and pelagic fishes such as *Thunnus albacares* (Bonnaterre, 1788) (Vaske & Castello 1998), *Prionace glauca* (Linnaeus, 1758) and *Isurus oxyrinchus* Rafinesque, 1810 (Vaske & Rincón-Filho 1998). Ecosystem simulations suggest that populations of marine mammals could be reduced rapidly by decreasing the abundance of their prey (Trites et al. 2004). Reducing the availability of their main prey species can reduce the quantity and/or quality of the available food resources, and consequently cause nutritional stress for marine mammal populations. This situation may lead to reduced body size, reduced birth rates, increased infant and juvenile mortality, behavioural changes (e.g. longer foraging trips) and altered body condition (Trites & Donnelly 2003). The decline of some marine mammal populations has been attributed to

the overexploitation of some fish stocks (e.g. Notarbartolo di Sciara et al. 2002). In a review of the main impacts of human activities on cetacean populations in the Mediterranean Sea and Black Sea, Notarbartolo di Sciara et al. (2002) mentioned that at least 4 species (*D. delphis*, *Stenella coeruleoalba* [Meyen, 1833], *Phocoena phocoena* [Linnaeus, 1758] and *T. truncatus*) are strongly impacted by the overexploitation of their main prey stocks.

The effects of the decline of fishing stocks on the feeding ecology of some marine mammal populations in southern Brazil have already been reported. In the last decades, a shift in the diet of *P. blainvillei* and *T. truncatus* has been attributed to the overexploitation of *M. atricauda* and *M. furnieri* stocks (Secchi et al. 2003, 2017, Milmann et al. 2016). Changes in the diet of *O. flavescens* have also been reported as the species has expanded its trophic niche in response to the reduction in resource availability due to the overexploitation of fish stocks in southern Brazil (Machado et al. 2018).

A. australis could be the only marine mammal included in this study that would suffer fewer effects directly resulting from a continuous decrease of the fishing resources in the region. This species feeds mainly on benthic–pelagic and demersal–pelagic resources of minor importance to commercial fisheries. However, *A. australis* appears to be extremely dependent on *T. lepturus* as a prey species, so the targeting of this species by fisheries could, as previously mentioned, have a negative impact on *A. australis* populations. In fact, results from stable isotope analyses showed that overexploitation in fish stocks over the last 2 decades (1994–2011) did not alter the diet of adult males in southern Brazil (Vales et al. 2014). However, the total population of *A. australis*, including the breeding colonies in Uruguay, has been increasing steadily in recent decades (Franco-Trecu 2015, Cardenas-Alayza et al. 2016). This population increase together with heavy overexploitation in fish stocks may raise the chances of increased trophic interactions between this species and fisheries in southern Brazil.

After *A. australis*, *P. blainvillei* was the marine mammal species with the second lowest trophic relationship with fisheries, mainly due to its preference for smaller prey than those targeted by fisheries and the high importance of squid (*Doryteuthis sanpaulensis*) in its diet, as revealed in many studies across its distribution (e.g. Troina et al. 2016, Denuncio et al. 2017). In this context, it is worth mentioning that *D. sanpaulensis* is not an important commercial fishing resource in southern Brazil, and excessive

pressure on its stock does not seem likely in the coming years. However, as previously mentioned, the overexploitation of the *M. furnieri* stock clearly resulted in a decreased occurrence of this species in the diet of *P. blainvillei* from the 1970s to the 1990s (Secchi et al. 2003). In the present study, *M. furnieri* was virtually absent in the diet *P. blainvillei*, although this fish had a relatively high importance in the diet of *O. flavescens* and *T. geophyreus*.

The trophic relationships of *T. geophyreus* with the fisheries presented intermediate levels of importance when compared with the other species of marine mammals studied. However, resident populations of this species in estuarine regions in the south of Brazil showed a high level of interaction with the artisanal fisheries directed towards the capture of *M. liza* through cooperative fishing (e.g. Simões-Lopes et al. 1998, Zappes et al. 2011). This interaction occurs more intensely in the autumn (e.g. Simões-Lopes et al. 1998, Zappes et al. 2011, di Giacomo & Ott 2016) when *M. liza* migrates to the region (Lemos et al. 2014). According to Milmann et al. (2016), the autumn is a critical period for this resource, as it is the target of artisanal and industrial fishing, and the overexploitation of the *M. liza* stock could have negative consequences for *T. geophyreus* (Milmann et al. 2016). Autumn is an important period for the breeding of *T. geophyreus*, which are born in the summer and would be only a few months old at this time (Fruet et al. 2015), during which *M. liza* is an important food resource (Milmann et al. 2016, Secchi et al. 2017) for their lactating mothers. Currently, the *M. liza* stock from southern and southeastern Brazil is reported to be at the maximum limit of exploitation (MMA 2004, Haimovici & Cardoso 2017). The research on the diet of *T. truncatus* (Milmann et al. 2016, Secchi et al. 2017) in southern Brazil was published concomitantly with the revalidation of *T. geophyreus* as a species (Wickert et al. 2016). The study conducted by Milmann et al. (2016) (*T. truncatus* n = 3 and *T. geophyreus* n = 18) was performed in an area where both species of the genus *Tursiops* occur (Wickert et al. 2016). All animals in the study by Secchi et al. (2017) were initially identified as *T. truncatus*, but were later morphologically identified as *T. geophyreus* according to Wickert et al. (2016) (E. Secchi pers. comm.). Our results indicate that the 2 morphological forms of *Tursiops* occupy distinct ecological roles in the ecosystem, representing, at least, different ecotypes (see de Bruyn et al. 2013).

The incidental mortality or bycatch of marine mammals in fisheries is largely recognized as one of the

main problems for species conservation in many areas around the world. In southern Brazil, the 2 small cetaceans most affected by incidental capture by fisheries are *P. blainvillei* (e.g. Secchi et al. 2003) and *T. geophyreus* (e.g. Fruet et al. 2012). However, the impacts of the fisheries on marine mammals in the region could extend well beyond incidental mortality, as indicated by the shift in the diet of some species over the last decades (Milmann et al. 2016, Secchi et al. 2017, Machado et al. 2018). Therefore, further efforts are clearly needed to understand the real effects that major overexploitation in fish stocks may be causing in marine mammal populations and even other top predators in southern Brazil. In this context, further information from 2 areas is essential: (1) data on fishing effort, fishing areas and landing statistics, and (2) accurate estimates of population sizes of marine mammals. Unfortunately, both sets of data are currently very incomplete and mostly out of date. In fact, the last official landings data of marine resources in southern Brazil was published almost a decade ago (Ibama/ICMBio/Ceperg 1993–2012). Moreover, the only marine mammal for which an estimate of population size exists in the region is *P. blainvillei*, but this also needs to be updated (Danilewicz et al. 2010).

Finally, considering that fisheries management in Brazil has been historically ineffective (Haimovici & Cardoso 2017), it is likely that if no action is taken to modify the current scenario of overexploitation of the fishing stocks, the problems of bycatch and trophic overlap between marine mammals and fisheries may intensify, resulting in important changes to marine communities. In the context of a lack of enforcement or ineffective management or conservation strategies, Dowling et al. (2016) suggested that the most effective measures would be spatial and temporal approaches, such as the establishment of no-fishing zones or seasonal closures (e.g. Di Tullio et al. 2015). In this context, a recent rule prohibiting industrial bottom trawling all along the coast of the state of Rio Grande do Sul from the beach up to 12 nautical miles to the west (Rio Grande do Sul, 2018) can be considered a hope for the recovery of some fish stocks. However, the Brazilian government has recently proposed to remove species from the Brazilian Red List of threatened marine species (e.g. Lees 2015, Pinheiro et al. 2015), and has initiated discussions on ending the recent rule prohibiting industrial bottom trawling along the coast of Rio Grande do Sul. This development has revealed how fragile the situation in Brazil is with regards to achieving a sustainable management plan for fisheries.

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