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PRIMARY RESEARCH PAPER

Changes in the feeding ecology of South American sea lions on the southern Brazilian coast over the last two decades of excessive fishing exploration

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Abstract In the last decades, an increasing fishing effort and a decreasing trend in fish catches have been observed in southern Brazil. Considering that marine mammals and fisheries usually compete for the same resources, it is reasonable to presume that the feeding ecology of these predators is affected by the current scenario. To evaluate this hypothesis, long-term variation in the diet of the South American sea lion (*Otaria flavescens*) relative to fisheries exploitation was analyzed for two periods (1993–2003 versus 2004–2014). The degree of overlap between the relative biomass of the sea lions' diet and the target species of six types of local fishery was analyzed. An increase in prey overlap between sea lions and fisheries was observed in the more recent sampling period, along with an increase in prey diversity, richness, and niche breadth of the sea lions' diet. These results suggest that the overfishing scenario could partly explain the modified feeding ecology of the sea lions. In this context, we recommend a review and better regulation of the current fishing effort in the region, which we believe will be an important step to maintain the fish stocks and minimize the impact of fishing on marine top predators.

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Introduction

Feeding habits determine the range of food resources that a predator can exploit in the environment and, therefore, defines the position of the predator in the food web and its ecological role in the ecosystem (Pauly et al., 1998; Cortés, 1999; Jaksic, 2001). Predators differ in respect to the level of diversity and selectivity of prey and may range from highly selective to broadly opportunistic (Stephens & Krebs, 1986). Opportunistic predators consume different prey species relative to their respective abundance in the environment. On the other hand, selective predators select specific prey species regardless of their abundance (MacArthur, 1972; Pianka, 1999). With regard to the diversity of prey species consumed, generalist predators tend to have a more diverse diet, preying upon a large range of food types and displaying a large repertoire of feeding behaviors. In contrast, specialists have a less diverse diet, exploiting few resources or exhibiting a diet dominated by a specific and limited range of prey types (Schoener, 1972; Szteren, 2006). Selective predators are more vulnerable to changes in the availability of resources than opportunists, whereas opportunistic predators are more likely to adjust their habits and diets under similar changes in resource availability. Interspecific competition for resources can affect the breadth of the dietary niche of predators, which may expand (under reduced prey availability) or contract (under increased or uneven prey availability) depending on competitor characteristics (MacArthur, 1972; Pianka, 1999).

Within this theoretical framework, human activities, such as fishing, can compete for resources in the same way as other marine predators. The intense overfishing of species, which are also used as a food resource by marine mammals, can lead to changes in predators' body size (e.g., Drago et al., 2010) and diet composition (e.g., Secchi et al., 2003, 2016), and in some cases even to a decrease in a predators' relative abundance (e.g., Trites & Donnelly, 2003). Therefore, information on the feeding habits of a marine predator can reveal several aspects of its natural history and additionally makes it possible to predict human–wildlife conflicts.

Globally, fishing is an extremely important commercial activity. Since the late 1990s, the world has observed the collapse of several fish populations, mainly because of an increasing fishing effort, and the lack of adequate fishery management (Haimovici, 1998; Froese et al., 2012; Pauly & Zeller, 2016). The impact of this overfishing scenario can be observed in marine habitats off the southern Brazilian coast. Over the last decades, fishing areas as well as fishing effort have increased in this region (Boffo & Reis, 2003; Moreno et al., 2009; Cardoso & Haimovici, 2011; Machado et al., 2016), while the capture rates and the size of captured fish have declined (e.g., Haimovici & Miranda, 2005; Haimovici & Ignácio, 2005; Cardoso & Haimovici, 2011). Due to this intense pressure on fish stocks in southern Brazil, landed catches in the region have gradually declined since the 1970s (e.g., Haimovici & Cardoso, 2017). The pelagic fish species *Mugil liza* (Valenciennes, 1836) and *Pomatomus saltatrix* (Linnaeus, 1766) are at the limit of their capacity for exploitation, whereas the sciaenids *Cynoscion guatucupa* (Cuvier, 1830), *Macrodon atricauda* (Günther, 1880), *Micropogonias furnieri* (Desmarest, 1823), and *Umbrina canosai* (Berg, 1895), which together represent more than half of the landings of local marine fish, are overexploited (MMA, 2004; Haimovici & Cardoso, 2017). Some of these species are very important prey for several top predators in the region (e.g., Secchi et al., 2003; Bugoni & Vooren, 2004; Colabuono & Vooren, 2007;

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Oliveira et al., 2008, Milmann et al., 2016), and the effects of reducing the availability of food resources for such predators have been poorly evaluated and are not well understood.

The South American sea lion, *Otaria flavescens* (Shaw, 1800), is a marine carnivore predator distributed along the coast of South America from Torres, southern Brazil (29°20′S; 49°43′W) in the Atlantic Ocean, to Zorritos, northern Peru (03°40′S; 80°39′W) in the Pacific Ocean (Vaz-Ferreira, 1982; Bastida et al., 2007). In southern Brazil, as in many other areas, South American sea lions face serious conflicts with fishing activities (Rosas et al., 1994; Machado et al., 2015, 2016, Pont et al., 2016). Sea lions frequently consume fish caught in fishing nets (e.g., Machado et al., 2015, 2016, Pont et al., 2016), and can damage the fishing gear and the captured fish (Machado et al., 2016), potentially decreasing the production yield for fishermen (Machado et al., 2016; Pont et al., 2016). Moreover, the distribution of the South American sea lion overlaps greatly with important fishing areas along the South American coast (Crespo et al., 2012; Machado et al., 2016). However, despite the frequent claims of the fishermen (Pont et al., 2016), there is no strong evidence that South American sea lions have a significant impact on the profitability of the fisheries (e.g., Machado et al., 2016).

Diet analyses, mainly based on stomach contents, have revealed that South American sea lions primarily consume fish, cephalopods, and crustaceans (e.g., George-Nascimento et al., 1985; Thompson et al., 1998; Koen-Alonso et al., 2000; Oliveira et al., 2008). Analyses based on stable isotopes have indicated ontogenetic variations in the diet of South American sea lions associated with changes in their preferred prey species, and the habitats in which these prey species are found. The consumption of benthic and demersal prey increases when individuals approach adulthood. Furthermore, these stable isotope analyses did not show evidence of substantial variations in the relative contribution of demersal and pelagic prey in diet composition over the last decades (Zenteno et al., 2015). Nevertheless, historical changes in the isotopic baseline may hinder the interpretation of retrospective studies, and the interpretation of isotopic signals without relevant ecological data can be challenging (Zenteno et al., 2015). Although prey selectivity has never been strictly evaluated for South American sea lions, most authors have considered the species to be an opportunistic and generalist predator, because it feeds on a wide variety of prey species which are abundant in the environment (e.g., George-Nascimento et al., 1985; Thompson et al., 1998; Naya et al., 2000; Suarez et al., 2005; Oliveira et al., 2008; Romero et al., 2011; Bustos et al., 2012).

Considering the frequent interactions between the South American sea lion and fisheries, and the current overfishing along the southern Brazilian coast, it is important to quantify possible effects of this competition on this top predator's ecology. Moreover, since the species is thought to have a generalist feeding habit, the South American sea lion is a valuable model for investigating possible signals of dietary change related to fish stock depletion. Our working hypothesis is that the intense overfishing along the southern Brazilian coast has altered the feeding behavior of the South American sea lion due to changes in resource availability. Here we analyze the diet of South American sea lions along the southern Brazilian coast during two periods (1993–2003 versus 2004–2014). We compare dietary data with local fisheries productivity to quantify prey overlap and to look for potential evidence of temporal variation in fish consumption and alteration in the breadth of the dietary niche of sea lions due to current overfishing along the southern Brazilian coast over the last decades.

Materials and methods

Study area and data collection

The study area is located in the southernmost region of Brazil. This region is in the northwestern area of influence of the Subtropical Convergence Zone of the Atlantic Ocean, which usually extends from Santa Marta Grande Cape (Lat 28°40′S), in southern Brazil, to Uruguay (Lat 34°40′S) (Seeliger & Odebrecht, 1998). The Subtropical Convergence Zone of the Atlantic Ocean extends for about 950 km along the coast and comprises nearly 100,000 km^2 from the shoreline to the slope regions of the continental shelf. The interaction between the Brazil Current and the Malvinas Current, and the contribution of freshwater from the large hydrographic basins of the La Plata River and the Patos–Mirim system, makes this region an important breeding and feeding area for several marine organisms (Seeliger & Odebrecht, 1998).

Consequently, this region has a high fishing potential (Haimovici, 1998) and is of great importance as a feeding ground for several top predators (e.g., Secchi et al., 2003; Bugoni & Vooren, 2004; Colabuono & Vooren, 2007; Oliveira et al., 2008; Milmann et al., 2016).

For the diet analysis of the South American sea lion, the stomachs of animals found dead on beaches were collected. Specimens were collected during surveys covering 270 km of beaches on the northern coast of the state of Rio Grande do Sul, southern Brazil, between the municipality of Torres and the Lagoa do Peixe National Park (31°21′S, 51°02′W), at the municipality of Tavares (Fig. 1). From January 1993 to December 2014, 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. Geographic coordinates, sex, and total length were recorded for each specimen during the sampling activity and the following items were collected according to the American Society of Mammalogists (Norris, 1961): skull, stomach, and other tissue samples for biological analyses. Vouchers of this material were deposited in the marine mammals' scientific collection of the *Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul* (GEMARS), in Brazil.

Biomass data from six different types of local fishing activities (Fig. 1), coastal gillnet, oceanic gillnet, purse seine, pair trawl, bottom trawl and double-rig trawl (see Supplementary S1, for a detailed description of the fishing in this area), were extracted from pertinent landing reports of the federal fishery research center in Rio Grande from 1993 to 2011 (Ibama/Ceperg, 1993–2011). Therefore, comprehensive statistics on all fish landings were obtained from the commercial fleet harbored in this locality. A detailed description of this fishery can be found in Haimovici et al. (2006).

Diet analysis

The stomachs of South American sea lions (Table S1) collected were washed with a 0.5-mm mesh sieve and food items found were separated into higher taxonomic groups (fish, cephalopods, and crustaceans). Whenever an entire prey item was found, its total length and mass were taken. Otoliths and bone structure characteristic of the sincranium (e.g., supraoccipital bone, mandible, maxilla) were stored dry. Entire and/or fragments of elasmobranchs, beaks of cephalopods, and the exoskeleton of crustaceans were preserved in 70% ethanol. Diagnostic items were identified by comparison with the fish otolith reference collection of GEMARS, the cephalopod beak collection of *Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul* (CEPSUL), and identification guides (Costa et al., 2003; Rossi-Wongtschowski et al., 2014).

The minimum number of ingested teleosts was estimated as a function of the total number of *saggita* otoliths of the most representative side (left or right) for each species in each stomach. Additionally, for *Pomatomus saltatrix* and *Trichiurus lepturus* Linnaeus, 1758, the total numbers of mandibles or maxillae (always the most representative side) and supraoccipital bones were also used (respectively). Elasmobranch numbers were estimated by direct count of the partially digested specimens in the stomachs. Cephalopod numbers were estimated based on the maximum number of superior or inferior beaks of each specimen found, while crustacean numbers were estimated by the total number of cephalothorax.

Otoliths that were not highly damaged (according to Recchia & Read, 1989) and cephalopod beaks were measured under a stereoscopic microscope with 10 × millimetric ocular and 0.8 × to 3.5 × objective lenses. Sincranium bones were measured with a digital caliper with 0.01 mm precision. Total length (mm) and biomass (g) of bony fish were estimated from the total length of the otoliths. In the case of *P. saltatrix* and *T. lepturus,* the sizes of the mandibles and maxillae, as well as the supraoccipital bone, were also considered. The rostral length and hood length of the beaks were used to estimate size and mass of cephalopods. Specific regression equations found in the literature were used for each taxon (Table S2). To estimate fish biomass from severely damaged otoliths, the mean general biomass of a given prey found in the predator's stomach was used.

Statistical analysis

South American sea lions' diet composition and importance of prey were estimated through appropriate indexes following Pinkas et al. (1971), Hyslop (1980), Cortés (1997), and Chambellant et al. (2013):

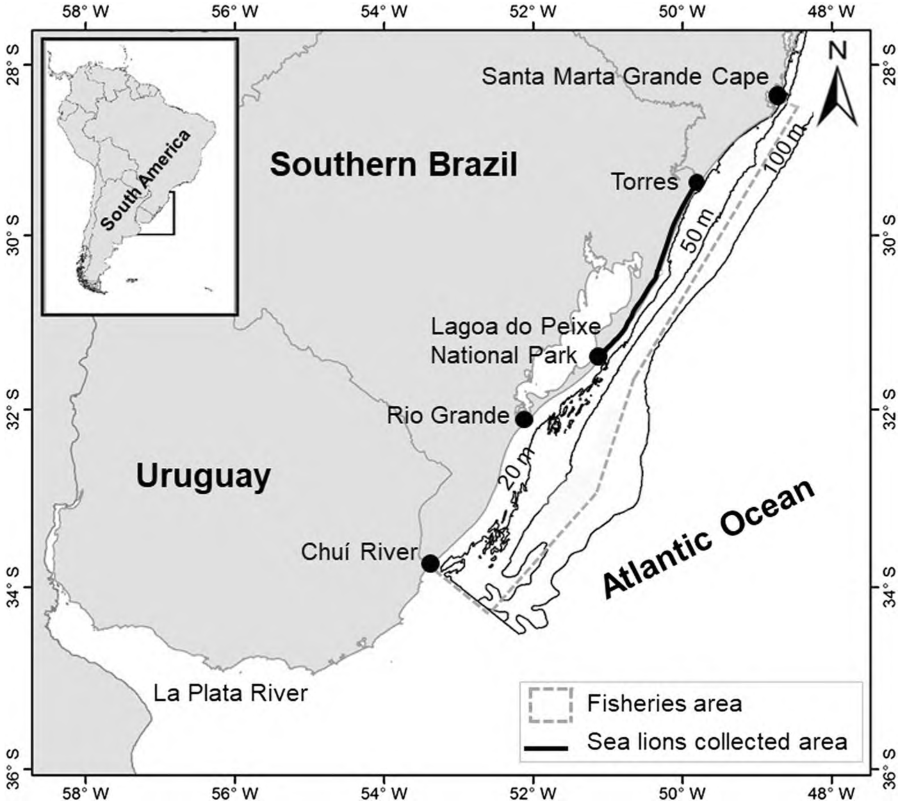

Fig. 1 Study area indicating the stretch of the sandy beaches (ca. 270 km) where the dead specimens of South American sea lion (*Otaria flavescens*) were collected. Main fishing area used by the local fleet is indicated by gray dashed line. The fishing harbor of Rio Grande, where the fish landing statistics were collected, is also shown

(1) numeric frequency ($\%N = [N =$ total number estimated for prey i/total number of prey of all species] * 100); (2) frequency of occurrence ($\%O = [O =$ number of stomachs containing prey i/total number of stomachs] * 100); (3) percentage of biomass contribution ($\%M = [M =$ estimated biomass of prey i/total estimate of biomass] * 100); (4) percentage of energy contribution ($\%E =$ [energy of prey i/total of energy of prey] * 100); index of relative importance (IRI $(\%N + \%M) \times (\%O)$—this index was expressed on a percent basis (%IRI). The energetic contribution of each prey species was estimated so that the percentage of energetic contribution could be calculated (E = energy of prey i in kj g^{1} * estimated total biomass of prey i in g). The energetic value (kj g^{-1}) of each prey was obtained through information available in the literature (Table S3).

The indexes were calculated for prey species, zoological and ecological groups. Zoological groups considered were teleosts, elasmobranchs, mollusks (cephalopods), and crustaceans. Ecological groups were defined according to the prey's vertical distribution: demersal/benthic (species exclusively associated with the bottom), pelagic (species exclusively using the water column), and benthic/pelagic or demersal/pelagic (species that use both the bottom and the water column) (Haimovici & Perez, 1991; Carvalho-Filho, 1999; Romero et al., 2011).

Additionally, the percentage of the relative importance index (%IRI) was compared to evaluate potential differences in a temporal and ontogenetic scale. For the temporal analysis, data were grouped in two periods (1993–2003 versus 2004–2014). Since there are variations in fish species abundance related to seasonal patterns and marine currents in southern Brazil (Martins & Haimovici, 2017), the data used for seasonality analysis were divided into two seasons: summer/autumn (November to April) and winter/spring (May to October).

For the analysis of ontogenetic variation in the diet, males of the South American sea lion were grouped into two age categories, juveniles (from 1 to 8 years) and adults (nine or more years) (Drago et al., 2009a; Grandi et al., 2010; Zenteno et al., 2015). The age of each individual was estimated through the analysis of growth layer groups (GLGs) in the teeth, and a detailed description of the method is presented by Audibert et al. (2017). Whenever teeth were not present when the skull was collected, the age category was estimated by the condyle-basal length (Drago et al., 2009a) and/or total length of the animal (Grandi et al., 2010).

Potential variations in the diet composition of South American sea lions regarding the interdecadal scale (1993–2003 versus 2004–2014) were tested by generalized linear models (GLM). Moreover, a *G test* was used to compare frequencies of the diet's %IRI, niche breadth index, indexes of species diversity and richness, and the composition of the total lengths of fish preyed on by South American sea lions during both periods. GLMs were also used to evaluate potential variations in a seasonal scale (summer/autumn and winter/spring) and age class (juveniles and adults).

Generalized linear models using numerical abundances as response variables were constructed for the main prey and ecological groups. Interdecadal periods, seasons, and ontogenetic categories were the explanatory variables tested. Models combining these variables were also tested (e.g., period + seasons + ontogenetic classes and all combinations). Null models were used to test the hypothesis that no independent variable affected prey abundance. Due to a high number of empty stomachs, models incorporating the number of prey found in the stomachs were tested with a negative binomial error distribution (Crawley, 2005). A *log link* was used on the models because response variables could only be either zero or have positive values (Crawley, 2005). The Akaike Information Criterion (AIC) and AIC weight (w) were calculated for each adjusted model. The AIC is a statistical tool of model identification and selection and represents the amount of information lost when adjusting a given model (Franklin et al., 2001). Therefore, the model with the lower AIC is the one that better explains the data observed. The *G test* was used to compare %IRI frequencies of the prey of South American sea lions for both periods in the software BioEstat 5.0.

The niche breadth was estimated by the Levins Niche Breadth Index (B) (Krebs, 1999). This index is defined by $B = 1/\Sigma pi^2$, where P means the proportion of individuals of a given i resource found in the diet. The index has a minimum of 1 when only one prey type is found in the diet and a maximum of n, where n is the total number of prey categories, each representing an equal proportion of the diet. This index was then standardized (Bs) to limit it to a 0–1 scale according to the following equation: $Bs = (B - 1)/(n - 1)$, where n means the number of food items. In the zero to one scale, higher numbers mean greater niche breadth and, therefore, characterize a generalist predator (Krebs, 1999). The species diversity indexes of Simpson (D) and Shannon were calculated based on the number of prey of a given species found in the stomachs of South American sea lions in both periods (see the diversity indexes bellow); further they were compared through a rarefaction based on 95% confidence intervals in the software PAST 3.0.

Simpson's diversity (D):

$$D = \frac{1}{\sum_{i=1}^{S} P_i^2}.$$

Shannon diversity index (H):

$$H = -\sum_{i=1}^{S} P_i \ln P_i,$$

where Pi is the proportion for the ith species, and S is the total number of species in the community (i.e., species richness found in all samples).

To evaluate the richness of prey species found in the stomach contents of South American sea lions in both periods, the sampling coverage approach was completely standardized based on entropy (q statistics, Chao & Jost, 2012) with abundance data in the online software iNEXT (https://chao.shinyapps.io/iNEXTOnline/—Chao et al., 2016). This analysis used an estimate of the sampling coverage suggested by Chao et al. (2013).

In order to avoid individual effects in the comparison of means of the estimated total lengths of fish predated by South American sea lions in the two different periods (1993–2003 versus 2004–2014), a mean was calculated for each prey species found in each stomach. Afterwards, these means for each prey species and per period analyzed were compared by paired t test in the software PAST 3.0.

The fisheries data analyses were also segregated according to sea lions diet periods. The overlap of target species between the prey consumed by South

American sea lions and those captured by six types of local fisheries activities, regarding the interdecadal scale (1993–2003 versus 2004–2014), was tested by the Schoener trophic overlap index (*C*) (Schoener, 1970). This index is defined as $C = 1 - 0.5\ (\Sigma|Wxi - Wyi|)$, where *Wxi* is the weight proportion of item *i* used by South American sea lions (Table 1), and *Wyi* is the weight proportion of item *i* used by a given fishery (Table 2). The value of the Schoener index varies between zero and one, where zero means no overlap and one means total overlap. For each of the periods, the mean values of the trophic overlap indexes between South American sea lions and the six fisheries were calculated, and then compared by t test in the software PAST 3.0.

Results

General diet composition

Fifty stomachs of male South American sea lions were analyzed; 39 of those contained items that could be identified and used in the analyses (20 from 1993 to 2003 and 19 from 2004 to 2014). A total of 1,950 prey from 27 species were identified (Table 1), with an estimated biomass of 144,850 g. The prey species richness per stomach varied from one to 10 (median = 4). The amount of ingested prey varied from one to 495 (median = 19), while biomass varied from 9 to 18,660 g (median = 2,394 g).

Teleosts were dominant, with 20 identified species representing 10 families, followed by elasmobranchs, cephalopods, and crustaceans (Table 1). Sciaenidae was the most important fish family represented by nine species, which corresponds to 86.2% of the prey. Considering the entire study period, *Paralonchurus brasiliensis* (Steindachner, 1875) was the most important species (%IRI = 51.8), followed by *Macrodon atricauda* (%IRI = 15.1) and *Micropogonias furnieri* (%IRI = 10.8). In addition, *Cynoscion guatucupa, Urophycis brasiliensis* (Kaup, 1858), *Trichiurus lepturus, Pomatomus saltatrix* and *Umbrina canosai* presented %IRI values between 2 and 6, assuming a secondary importance on the species' diet (Table 1). With regards to the energetic contribution, approximately 70% was provided by *P. brasiliensis, M. furnieri, M. atricauda*, and *P. saltatrix* (Table 1).

Diet variation

Seasonal variation: no significant difference was observed in the total number of prey consumed between summer/autumn months (*n* = 574, median = 17.5) and winter/spring months (*n* = 1382, median = 14.5; $U = 168.5$; $n_1 = 12$, $n_2 = 30$, $P = 0.749$) by South American sea lions on the southern Brazilian coast. In the summer/autumn, only *P. brasiliensis* and *M. furnieri* presented a relative importance higher than 15%, while in the winter/spring only *P. brasiliensis* presented a relative importance higher than 15% (Table S4). The GLM analyses (Table 3) indicated a reduction in the consumption of *U. brasiliensis* and *M. furnieri* in summer/autumn months, whereas winter/spring was the only period of the year when *P. saltatrix* was consumed (Supplement – SVI). Moreover, in the winter/spring, *P. brasiliensis, M. furnieri, M. atricauda*, and *P. saltatrix* were important sources of energy, while *P. brasiliensis* and *M. furnieri* were important in the summer/autumn (Table S4).

Ontogenetic variation: in general, South American sea lion adult males (*n* = 25) consumed 25 species of prey, and the number of ingested prey ranged from one to 495 (median = 39), while the biomass ranged from 170 to 18,660 g (median = 2,659 g). *Paralonchurus brasiliensis* (%IRI = 55.11) was the most important species, followed by *M. atricauda* and *M. furnieri* (Table S5). Juvenile males (*n* = 14) preyed on 14 species, and the number of ingested prey ranged from one to 61 (median = 6), while the biomass ranged from 9 to 7,961 g (median = 1.721 g). The greatest energetic contribution was provided by the consumption of *M. furnieri* (%E = 23.05) (Table S5), although *P. brasiliensis* (%IRI = 25.95) and *T. lepturus* (%IRI = 24.23) also had a high importance in the diet composition of this age class. The trophic overlap index showed a high overlap between the diets of juveniles and adults of South American sea lions (*C* = 0.66). The GLM analyses showed a greater consumption of *P. brasiliensis*, *M. furnieri*, *U. brasiliensis*, and *C. guatucupa* by adults than juveniles (Table 3).

Prey habitat variation: demersal and benthic prey had a greater importance than other ecological groups in the diet of South American sea lions (%IRI = 88.9). Species with benthic-pelagic and demersal-pelagic habitats had a low %IRI (9.5), despite the high frequency of occurrence (%O = 69.0). Pelagic species

Table 1 Diet composition of the South American sea lion (*Otaria flavescens*) at southern Brazilian coast

Prey Taxon		Total period 1993–2014						Decade 1993–2003						Decade 2004-2014					
		N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI
Teleosts	EG	1920	98.46	100.00	98.01	97.66	99.80	1020	99.71	100.00	99.75	99.67	99.98	900	96.77	100.00	96.27	95.65	99.52
Scieanidae		1680	86.15	89.74	61.95	66.19	92.60	919	89.83	85.00	65.85	69.37	90.93	761	81.83	94.74	58.06	62.96	93.37
Paralonchurus brasiliensis	D/B	1011	51.85	56.41	21.42	21.57	51.72	641	62.66	60.00	25.51	25.64	60.04	370	39.78	52.63	17.34	17.46	39.80
Macrodon atricauda	D/B	253	12.97	43.59	14.68	14.78	15.08	163	15.93	35.00	17.73	17.82	13.37	90	9.68	52.63	11.63	11.71	14.84
Micropogonias furnieri	D/B	121	6.21	41.03	14.83	18.07	10.80	53	5.18	25.00	9.98	12.14	4.30	68	7.31	57.89	19.66	23.98	20.68
Cynoscion guatucupa	BP/DP	95	4.87	51.28	4.28	3.99	5.87	34	3.32	55.00	6.10	5.68	5.88	61	6.56	47.37	2.46	2.30	5.66
Umbrina canosai	D/B	168	8.62	15.38	2.86	2.80	2.21	10	0.98	10.00	1.18	1.15	0.24	158	16.99	21.05	4.54	4.45	6.00
Menticirrhus littoralis (Holbrook, 1847)	D/B	13	0.67	15.38	3.41	4.50	0.79	7	0.68	15.00	4.91	6.47	0.95	6	0.65	15.79	1.92	2.54	0.54
Stellifer rastrifer (Jordan, 1889)	D/B	16	0.82	20.51	0.37	0.39	0.31	9	0.88	15.00	0.36	0.39	0.21	7	0.75	26.32	0.38	0.41	0.40
Cynoscion jamaicensis (Vaillant & Bocourt, 1883)	D/B	2	0.10	5.13	0.07	0.07	0.01	1	0.10	5.00	0.03	0.02	0.01	1	0.11	5.26	0.12	0.11	0.02
Stellifer brasiliensis (Schultz, 1945)	D/B	1	0.05	2.56	0.02	0.02	<0,00	1	0.10	5.00	0.05	0.05	0.01						
Phycidae		80	4.10	35.90	8.78	7.57	3.22	20	1.96	40.00	10.12	8.72	3.32	60	6.45	31.58	7.44	6.43	3.09
Urophycis brasiliensis	D/B	80	4.10	35.90	8.78	7.57	5.79	20	1.96	40.00	10.12	8.72	5.48	60	6.45	31.58	7.44	6.43	5.81
Trichiuridae		75	3.85	25.64	7.95	7.79	2.11	64	6.26	35.00	14.50	14.20	4.99	11	1.18	15.79	1.41	1.38	0.29
Trichiurus lepturus	BP/DP	75	3.85	25.64	7.95	7.79	3.78	64	6.26	35.00	14.50	14.20	8.24	11	1.18	15.79	1.41	1.38	0.54
Pomatomidae		31	1.59	12.82	16.90	13.48	1.65	10	0.98	10.00	8.83	7.04	0.67	21	2.26	10.53	24.94	19.91	2.02
Pomatomus saltatrix	P	31	1.59	12.82	16.90	13.48	2.97	10	0.98	10.00	8.83	7.04	1.11	21	2.26	10.53	24.94	19.91	3.79
Paralichthyidae		14	0.72	12.82	0.71	0.55	0.13	2	0.20	10.00	0.24	0.19	0.03	12	1.29	15.79	1.17	0.91	0.27
Paralichthys sp.	D/B	14	0.72	12.82	0.71	0.55	0.23	2	0.20	10.00	0.24	0.19	0.05	12	1.29	15.79	1.17	0.91	0.51
Batrachoididae		9	0.46	12.82	0.63	0.49	0.10	2	0.20	10.00	0.20	0.16	0.03	7	0.75	15.79	1.06	0.82	0.20
Porichthys porosissimus (Cuvier, 1829)	D/B	9	0.46	12.82	0.63	0.49	0.18	2	0.20	10.00	0.20	0.16	0.05	7	0.75	15.79	1.06	0.82	0.38

Table 1 continued

Prey Taxon		Total period 1993–2014						Decade 1993–2003						Decade 2004-2014					
		N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI
Teleosts	EG	1920	98.46	100.00	98.01	97.66	99.80	1020	99.71	100.00	99.75	99.67	99.98	900	96.77	100.00	96.27	95.65	99.52
Clupeidae		4	0.21	5.13	0.35	0.25	0.02							4	0.43	10.53	0.69	0.49	0.08
Brevoortia pectinata (Jenyns, 1842)	P	4	0.21	5.13	0.35	0.25	0.04							4	0.43	10.53	0.69	0.49	0.16
Stromateidae		9	0.46	7.69	0.58	1.20	0.06							9	0.97	15.79	1.16	2.39	0.24
Peprilus paru (Linnaeus, 1758)	BP/DP	4	0.21	5.13	0.34	0.70	0.03							4	0.43	10.53	0.68	1.40	0.15
Stromateus brasiliensis Fowler, 1906	BP/DP	5	0.26	2.56	0.24	0.50	0.02							5	0.54	5.26	0.48	0.99	0.07
Cynoglossidae		1	0.05	2.56	0.14	0.11	< 0.00							1	0.11	5.26	0.28	0.28	0.01
Balistes sp.	BP/DP	1	0.05	2.56	0.14	0.11	0.01							1	0.11	5.26	0.28	0.28	0.03
Engraulidae		2	0.10	2.56	0.03	0.03	< 0.00							2	0.22	5.26	0.06	0.06	0.01
Anchoa marinii Hildebrand, 1943	P	2	0.10	2.56	0.03	0.03	< 0.00							2	0.22	5.26	0.06	0.06	0.02
Unidentified Family		15	0.77	28.21	…	…	…	3	0.29	10.00	…	…	…	12	1.29	47.37	…	…	…
Sp.1		3	0.15	2.56	…	…	…							3	0.32	5.26	…	…	…
Unidentified teleosts		12	0.62	25.64	…	…	…	3	0.29	10.00	…	…	…	9	0.97	42.11	…	…	…
Elasmobranchs		15	0.77	7.69	0.71	0.65	0.06	1	0.10	5.00				14	1.83	21.05	1.42	1.29	0.35
Arhynchobatidae		13	0.67	2.56	0.71	0.65	0.02							13	1.40	5.26	1.42	1.29	0.10
Sympterygia bonapartii Müller & Henle, 1841	D/B	5	0.26	2.56	0.27	0.25	0.02							5	0.54	5.26	0.55	0.50	0.08
Atlantoraja platana (Günther, 1880) or *Rioraja agassizii* (Müller & Henle, 1841)	D/B	2	0.10	2.56	0.11	0.10	0.01							2	0.22	5.26	0.22	0.20	0.03
Sympterygia acuta Garman, 1877	D/B	1	0.05	2.56	0.05	0.05	< 0,00							1	0.11	5.26	0.11	0.10	0.02
Unidentified elasmobranchs		5	0.26	2.56	0.27	0.25	0.02							5	0.54	5.26	0.55	0.50	0.08
Unidentified Family		2	0.10	5.13	…	…	…	1	0.10	5.00	…	….	…	4	0.43	21.05	…	….	…

Table 1 continued

Prey Taxon	EG	Total period 1993–2014						Decade 1993–2003						Decade 2004-2014					
		N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI	N	%FN	%FO	%M	%E	%IRI
Teleosts		1920	98.46	100.00	98.01	97.66	99.80	1020	99.71	100.00	99.75	99.67	99.98	900	96.77	100.00	96.27	95.65	99.52
Unidentified elasmobranchs		2	0.10	5.13	…	…	…	1	0.10	5.00	…	….	…	4	0.43	21.05	…	….	…
Cephalopods		6	0.31	15.38	1.27	1.69	0.12	2	0.20	10.00	0.25	0.33	0.02	4	0.43	21.05	0.03	0.04	0.05
Octopodidae		2	0.10	5.13	1.13	1.50	0.04							2	0.22	10.53	2.26	3.01	0.18
Octopus vulgaris Cuvier, 1797	D/B	1	0.05	2.56	1.10	1.46	0.04							1	0.11	5.26	2.20	2.93	0.16
Octopus tehuelchus d'Orbigny, 1834	D/B	1	0.05	2.56	0.03	0.04	< 0.00							1	0.11	5.26	0.06	0.08	0.01
Loliginidae		4	0.21	10.26	0.14	0.18	0.02	2	0.20	10.00	0.25	0.33	0.03	2	0.22	10.53	0.03	0.04	0.02
Doryteuthis sanpaulensis (Brakoniecki, 1984)	BP/DP	4	0.21	10.26	0.14	0.18	0.04	2	0.20	10.00	0.25	0.33	0.05	2	0.22	10.53	0.03	0.04	0.03
Crustaceans		9	0.46	7.69	0.01	0.01	0.02							9	0.97	15.79	0.02	0.02	0.08
Penaeidae		9	0.46	7.69	0.01	0.01	0.03							9	0.97	15.79	0.02	0.02	0.11
Artemesia longinaris (Spence Bate, 1888)	D/B	9	0.46	7.69	0.01	0.01	0.05							9	0.97	15.79	0.02	0.02	0.21

Ecological groups (EG): *D/B* demersal and benthic, *P* pelagic, *BP/DP* benthic-pelagic and demersal-pelagic, *N* total number of prey. *%FN* Numeric frequency, *%FO* Frequency of occurrence, *%M* Percentage of biomass contribution, *%E* Percentage of energetic contribution, *%IRI* Percentage of index of relative importance

Table 2 Models that better explain the consumption (response variable) of the main prey species South American sea lion (*Otaria flavescens*) at southern Brazilian coast

	Intersection	Coefficient	AIC	*W*
Prey species				
Cynoscion guatucupa	0.916 (0.403)	– 1.167 (0.710) juveniles	162.110	0.240
Macrodon atricauda	1.621 (0.556)		183.520	0.315
Micropogonias furnieri	1.739 (0.483)	– 1.665 (0.728) summer/autumn; – 2.626 (0.732) juveniles	147.490	0.322
Paralonchurus brasiliensis	3.397 (0.467)	– 2.280 (0.780) juveniles	255.870	0.344
Pomatomus saltatrix	– 0.092 (0.531)	– 20.699 (288.189) summer/autumn	60.065	0.321
Trichiurus lepturus	0.900 (0.564)	– 1.680 (0.841) period 2004–2014	112.151	0.251
Umbrina canosai	1.307 (0.537)		91.505	0.973
Urophycis brasiliensis	1.379 (0.549)	– 2.258 (0.871) summer/autumn; – 2.798 (0.873) juveniles	119.270	0.390
Ecological groups				
Benthic-pelagic and Demersal-pelagic	1.302 (0.257)		227.940	0.341
Demersal and Benthic	– 3.898 (0.335)	– 1.905 (0.563) juveniles	377.560	0.395
Pelagic	– 0.301 (0.617)		76.310	0.267
Zoological groups				
Crustaceans	– 32.790 (4.089)	21.890 (489.201) period 2004–2014	27.306	0.183
Elasmobranchs	– 3.258 (1.079)	2.913 (1.292) period 2004–2014	55.706	0.295
Mollusks (cephalopods)	– 1.966 (0.354)		43.652	0.259
Teleosts	4.955 (0.740)		426.360	0.324

Standard errors are between parentheses. Explanatory categorical variables: "periods" with two levels, 1993–2003 and 2004–2014; "seasons" with two levels, summer/autumn and winter/spring; and "ontogenetic categories" also with two levels, Juveniles and Adults

AIC Akaike information criteria for selection of the best model, *W* Akaike weights (a measure of explained information of the model)

were the less important ecological group (%IRI = 1.9). Overall, benthic-pelagic and demersal-pelagic preys were more important for juveniles (%IRI = 26.6) than for adults (%IRI = 7.8); however, the difference was not significant (Table 3). On the other hand, adult males consumed significantly more demersal prey than juveniles (Table 3).

Interdecadal variation: the GLMs analysis demonstrated little difference in the importance of the main prey consumed by the South American sea lions between both periods analyzed (1993–2003 versus 2004–2014), with the exception of *T. lepturus* that was consumed more often in the first period than in the second one (Tables 1, 3). Another interesting result was the increase of elasmobranchs and crustaceans in the period 2004–2014 (Tables 1, 3). In accordance with the results of the GLM analyses, the *G test* also did not show a significant difference in the comparative analysis of IRI frequencies ($G = 34.423$; gl = 25; $P = 0.099$) between the two periods. However, the ecological indexes used to evaluate potential temporal alterations in the diet of South American sea lions showed a broadening exploitation of feeding resources from the first decade to the second. The richness index (Chao & Jost, 2012) (Fig. 2), Simpson's diversity index (D) (first decade $D = 0.570$; CI = 0.537/0.6001 – second decade $D = 0.780$; CI = 0.758/0.800) and Shannon's diversity index (H) (first decade $H = 1.320$; CI = 1.238/1.395 – second decade $H = 2.003$; CI = 1.916/2.079), showed that South American sea lions had a more rich and diverse diet in the second decade of the study. The results of Levins niche breadth analysis indicated that South American sea lions from Southern Brazil have broadened their trophic niche in the last decade from $Bs = 0.09$ in 1993–2003 to $Bs = 0.14$ in 2004–2014,

Table 3 Marine fisheries landings in Rio Grande harbor (in southern Brazilian coast) in metric tons captured by six different types of industrial fisheries during the two periods of the study (i.e., 1993–2003 and 2004–2011)

Industrial fishing gears	Pair trawl		Bottom trawl		Double-rig trawl		Purse seine	
Periods Fishing resources	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011
Artemesia longinaris	0.4	0.0	0.0	44.7	12,734.1	2298.5	0.0	0.0
Chloroscombrus chrysurus (Linnaeus, 1766)	0.02	0.4	0.02	0.0	0.0	0.0	0.0	0.0
Conger orbignyanus Valenciennes, 1837	471.8	179.0	256.5	12.6	130.2	34.3	1.6	3.6
*Cynoscion guatucupa**	32,535.0	12,436.6	9683.8	641.7	1638.4	1109.1	739.4	450.8
Cynoscion jamaicensis	1513.9	964.0	79.5	0.1	75.0	23.5	1.2	21.9
Hyporthodus niveatus (Valenciennes, 1828)	16.9	0.03	10.0	25.0	26.5	0.8	11.6	0.0
*Macrodon ancylodon**	18,720.5	11,680.9	59.8	14.1	1039.0	182.4	21.8	643.7
Menticirrhus spp.	836.0	582.1	12.5	1.5	296.8	70.4	1.0	16.9
Merluccius hubbsi	258.5	75.7	322.8	10.4	246.4	196.4	7.1	17.8
*Micropogonias furnieri**	15,746.4	12,697.0	1596.8	185.4	1704.0	957.3	4026.7	2889.8
Mugil liza	229.2	475.5	4.0	1.4	44.5	76.3	2343.0	5299.0
Paralichthys brasiliensis (Ranzani, 1842)	577.6	418.6	121.9	20.3	3364.7	565.5	6.0	32.8
*Paralonchurus brasiliensis**	64.5	693.1	0.0	0.0	8.5	81.6	0.0	0.3
Pleoticus muelleri (Spence Bate, 1888)	11.0	0.0	0.0	9.3	6601.0	551.5	0.0	0.00
Pogonias cromis (Linnaeus, 1766)	175.8	189.1	0.05	0.0	13.3	182.7	372.8	287.1
*Pomatomus saltatrix**	366.6	89.0	8.4	0.2	54.2	169.7	7783.8	2983.0
Prionotus spp.	1885.8	1689.4	875.1	69.8	1715.2	641.4	13.7	93.7
Scomber japonicus Houttuyn, 1782	0.5	0.0	0.0	0.0	0.9	2.7	8.5	1928.4
Seriola lalandi Valenciennes, 1833	8.0	39.8	1.4	0.0	2.3	12.6	610.2	958.2
Sphyrna spp.	15.9	16.1	7.0	0.1	12.2	4.4	3.4	1.6
Squatina spp.	882.1	20.9	287.3	1.5	747.1	32.3	32.3	0.02
Trachurus lathami Nichols, 1920	18.7	5.2	15.8	1.8	0.0	0.0	3685.8	0.4
*Trichiurus lepturus**	39.4	1062.2	1.1	15.6	4.8	73.1	2.9	53.3
*Umbrina canosai**	23,915.6	17,540.8	10,962.9	821.6	1202.1	1596.6	176.0	1036.9
*Urophycis brasiliensis**	1529.1	583.5	511.0	57.5	2822.6	903.4	26.2	44.2
Other species	2973.9	2981.0	717.1	40.0	1284.3	583.2	824.8	255.0
Total landings	102,792.9	64,420.1	25,534.6	1974.7	35,768.2	10,349.5	20,699.7	17,018.3

Industrial fishing gears	Coastal gillnet		Oceanic gillnet		Total fishing by periods	
Periods Fishing resources	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011
Artemesia longinaris	43.1	19.7	0.0	0.0	12,777.6	2362.9
Chloroscombrus chrysurus (Linnaeus, 1766)	0.0	14.7	0.0	0.02	0.04	15.2

Table 3 continued

Industrial fishing gears	Coastal gillnet		Oceanic gillnet		Total fishing by periods	
Periods Fishing resources	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011	1993–2003 Mass (tones)	2004–2011
Conger orbignyanus Valenciennes, 1837	10.5	8.5	69.5	36.1	940.2	274.2
*Cynoscion guatucupa**	10,259.1	10,132.1	5601.5	5458.3	60,457.2	30,228.6
Cynoscion jamaicensis	30.8	38.0	32.2	24.9	1732.6	1072.4
Hyporthodus niveatus (Valenciennes, 1828)	17.1	4.9	91.6	3.4	173.6	34.2
*Macrodon ancylodon**	383.3	1117.1	241.0	516.4	20,465.4	14,154.5
Menticirrhus spp.	227.6	333.8	50.0	159.5	1423.9	1164.1
Merluccius hubbsi	104.1	610.9	306.5	694.3	1245.3	1605.5
*Micropogonias furnieri**	24,932.1	20,699.3	5361.6	7565.4	53,367.6	44,994.3
Mugil liza	997.2	3707.0	149.3	190.9	3767.1	9750.2
Paralichthys brasiliensis (Ranzani, 1842)	77.1	273.8	119.0	105.6	4266.3	1416.6
*Paralonchurus brasiliensis**	1.7	2.2	2.5	77.6	77.1	854.9
Pleoticus muelleri (Spence Bate, 1888)	33.6	0.0	0.0	0.0	6645.6	560.7
Pogonias cromis (Linnaeus, 1766)	141.2	10.5	0.8	1.1	703.9	670.5
*Pomatomus saltatrix**	3825.0	1444.6	447.2	1020.6	12,485.1	5707.0
Prionotus spp.	764.2	2649.5	1292.7	1409.6	6546.7	6553.5
Scomber japonicus Houttuyn, 1782	2.6	239.6	0.6	2.8	13.1	2173.6
Seriola lalandi Valenciennes, 1833	17.1	78.9	69.3	129.6	708.3	1219.1
Sphyrna spp.	70.0	5.1	552.3	42.8	660.8	70.2
Squatina spp.	511.7	196.1	3392.9	145.7	5853.5	396.5
Trachurus lathami Nichols, 1920	0.3	0.0	124.2	10.2	3844.7	17.5
*Trichiurus lepturus**	75.9	278.2	7.2	322.7	131.3	1805.1
*Umbrina canosai**	6411.0	14,374.9	7680.1	10,446.0	50,347.7	45,816.7
*Urophycis brasiliensis**	658.3	1430.7	996.0	2260.5	6543.2	5279.9
Other species	1663.1	1832.6	2533.1	1210.0	9996.3	6901.8
Total landings	51,257.7	59,502.8	29,120.9	31,834.1	265,174.1	185,099.5

Only species representing at least 1% of the landings of a fishery type in each period were included in the list. The remaining species were grouped as "other species"

*Most important species for feeding of the South American sea lion

suggesting the species are consumed the same prey in both decades, with the exception of *T. lepturus* which decreased in the frequency of its consumption.

Fishing catch

A total of 90 species of fish were captured by the six types of local fishery, being 71 bony fishes, followed by elasmobranchs (11 species), crustaceans (five species), and cephalopods (three species). The biomass of the captures, represented about 450 million tons (1993–2003 = 265 million tons and 2004–2011 = 185 million tons; Table 2).

Niche overlap between the South American sea lions' diet and local fisheries

The Schoener index indicated an increase in niche overlap between South American sea lions and fisheries from 1993–2003 to 2004–2014 (Table 4). When we compared the means of the target species overlap of both periods, we found that the increase is significant ($P = 0.033$). The highest target species

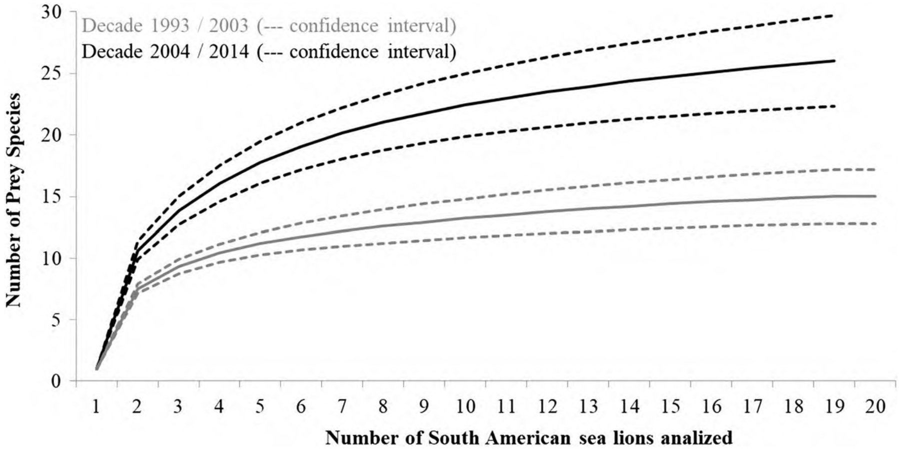

Fig. 2 Cumulative number of species preyed by the South American sea lion (*Otaria flavescens*) in Southern Brazil. Dotted lines indicated confidence interval of 95%

overlap index was recorded for the purse seine fishery in the second period (decade 2004–2014) of the study ($C = 0.466$), followed by the pair trawl ($C = 0.444$) and the oceanic gillnet ($C = 0.415$) fisheries. The fishery that had the lowest prey overlap with South American sea lions was the bottom trawl fishery ($C = 0.221$). The target species overlap with South American sea lions diet over the two decades was greater with purse seine followed by ocean gillnet fisheries along the southern Brazilian coast (Table 4).

The mean size of the four of the seven main fish prey species consumed by South American sea lions increased over the study period (but not significantly), while the four remaining species decreased in mean size (Table 5).

Discussion

General diet composition

South American sea lions consumed 27 prey species along the southern Brazilian coast over the last two decades. Of these, most were teleosts, with 20 identified species representing 10 families (Sciaenidae was the best represented family), followed by elasmobranchs, cephalopods, and crustaceans, revealing a predominant demersal and benthic feeding habit. Results also demonstrated little difference in the importance of the main prey consumed by the South American sea lions between both periods analyzed (1993–2003 versus 2004–2014). However, significant temporal alterations were observed indicating an

Table 4 The Schoener trophic niche overlap index (C) between the South American sea lion (*Otaria flavescens*) and six types of local fisheries over two decades (1993–2013 and 2004–2014) in southern Brazil

Fisheries	Schoener index (*C*)		Index value increase (%) between decades
	1993–2003	2004–2014	
Pair trawl	0.380	0.444	+ 0.064
Bottom trawl	0.161	0.221	+ 0.060
Double-rig trawl	0.228	0.317	+ 0.089
Purse seine	0.235	0.466	+ 0.231
Coastal gillnet	0.275	0.360	+ 0.085
Oceanic gillnet	0.236	0.415	+ 0.180
Mean*	0.253 (SD = 0.073)	0.371 (SD = 0.091)	+ 0.118

SD standard deviation

*The Schoener index increased significantly in mean combining all fisheries ($P = 0.033$)

increase in the trophic niche of South American sea lions in the last decade. Results also demonstrated an increase in the overlap between species consumed by sea lions and species targeted by fisheries in the analyzed time span.

Sciaenidae is the most abundant family of fish on the continental shelf of Southern Brazil (Haimovici et al., 1996; Martins & Haimovici, 2017) and is an important fish resource in the region (e.g., Haimovici et al., 2006; Moreno et al., 2009; Haimovici & Cardoso, 2017). This fish family is also an important resource for several top predators in the region, including marine mammals (e.g., *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844)—Secchi et al., 2003; *O. flavescens*—Oliveira et al., 2008; *Tursiops truncatus* (Montagu 1821)—Milmann et al., 2016; Secchi et al., 2016) and seabirds (e.g., *Sterna hirundo* Linnaeus, 1758 – Bugoni & Vooren, 2004; *Thalassarche melanophrys* (Temminck, 1828) and *T. chlororhynchos* (Gmelin, 1789)—Colabuono & Vooren, 2007). *Paralonchurus brasiliensis* is one of the most representative species of the family, both in number of individuals and in biomass in Southern Brazil (Martins & Haimovici, 2017) and is the predominant prey of the South American sea lion in Brazil.

It is noteworthy to mention that this study was conducted close to an important marine protected area, called the Wildlife Refuge of *Ilha dos Lobos*, which has been designed to protect the South American sea lions in Brazilian waters. This marine protected area encompasses a small island in front of the municipality of Torres, which is used as a haul-out site by South American sea lions and it is considered the northern limit of the species' distribution in the western South Atlantic Ocean (Vaz-Ferreira, 1982; Bastida et al., 2007). Although occurring at a relatively low population density in this area (probably less than 200 animals in total, e.g., Sanfelice et al., 1999; Pavanato et al., 2013), the species plays an important role in the local ecosystem and faces considerable conflicts with fishing activities (Engel et al., 2014; Machado et al., 2016; Pont et al., 2016). Despite being regularly present at *Ilha dos Lobos* and adjacent waters, only a small number of South American sea lions have been found dead on the beaches in the region (GEMARS, unpublished data). It is important to highlight that the size of our sample is the result of an intense sampling effort carried out over 22 years, which provides valuable information on the feeding ecology of South American sea lions and their overlap with fisheries along the southern Brazilian coast.

Our results indicated little variation in the composition of the main prey species of the South American sea lion throughout the interdecadal interval analyzed. However, it is important to mention that the consumption of crustaceans and elasmobranchs was observed only for the most recent decade (Table 3). Similar results were observed in traces of stable isotopes (^{13}C and ^{15}N) in the bones and teeth of South American sea lions between 1986 and 2009 in Southern Brazil (Zenteno et al., 2015). Moreover, the isotopic signal did not support evidence of substantial variation in diet composition over the last decades. Nevertheless, they

Table 5 Mean comparison of the total length (mm) of the main fish prey consumed by the South American sea lions (*Otaria flavescens*) between the two decades of study in southern Brazilian coast

Prey	1993–2003 (n = 20)				2004–2014 (n = 19)				Teste t
	No	No prey	Min/Max	Mean (SD)	No	No prey	Min/Max	Mean (SD)	*P*
Cynoscion guatucupa	7	14	73/425	209 (137.7)	6	15	89/261	167 (68.3)	0.515
Macrodon atricauda	6	96	171/253	201 (34.7)	10	77	88/299	229 (66.4)	0.357
Micropogonias furnieri	4	47	168/335	248 (89.8)	8	51	156/390	284 (87.2)	0.523
Paralonchurus brasiliensis	8	449	119/184	163 (21.5)	9	285	118/201	166 (31.4)	0.850
Pomatomus saltatrix	3	10	300/447	285 (58.8)	2	21	375/432	404 (40.3	0.729
Trichiurus lepturus	5	43	683/784	753 (41.2)	4	11	567/786	686 (90.4)	0.179
Umbrina canosai	2	7	141/187	164 (32.5)	3	94	111/134	120 (12.5)	0.108
Urophycis brasiliensis	5	12	274/420	357 (55.1)	3	37	186/405	297 (109.5)	0.331

No amount of analyzed stomachs. *No prey* amount of preys. *Min* minimum, *Max* maximum. *SD* standard deviation the authors acknowledge that historical changes in the isotopic baseline may hinder the interpretation of retrospective studies and the interpretation of isotopic signals without relevant ecological data can be challenging (Zenteno et al., 2015).

Diet variation

An increase in feeding activity is reported for the South American sea lions close to the breeding grounds as the breeding period approaches (in spring; e.g., George-Nascimento et al., 1984; Bustos et al., 2012). Adult male South American sea lions are able to travel long distances during foraging trips, which may be up to 300 nm and last for an average of 5.7 days (Campagna et al., 2001). Young males seem to make their feeding trips in coastal areas, reaching distances up to 33 nm from the coast and seldom exceeding depths of more than 50 m (Rodríguez et al., 2006). Although females are very rare in the study site (less than 5.7% of the carcasses collected in 22 years; GEMARS, unpublished data), information from the La Plata River Estuary (Argentina–Uruguay) indicates that during their foraging trips, which last for an average of 6.1 days, they travel up to 128.1 nm (Rodríguez et al., 2013).

In the present study, there was no increase in the consumption of prey between summer/autumn and winter/spring. This contrasting result could be related to the fact that no breeding activity of the species occurs in the study area (Sanfelice et al., 1999). In the present study, even though juveniles and adults of the South American sea lion exhibit a similar diet composition and a high trophic overlap, some differences observed (generalized linear models and ecological groups) indicate that each age class could be using different foraging strategies. A greater consumption of demersal and benthic prey suggests that adults feed on resources associated with the sea floor. The greater importance of benthic-pelagic and demersal-pelagic prey for juveniles is largely influenced by the consumption of *T. lepturus*. This corroborates previous assumptions that this ecological group could have a great importance to juvenile South American sea lions (Drago et al., 2009a; Zenteno et al., 2015).

Intra-population variation in foraging strategies and feeding habits could be beneficial for the population by minimizing effects of intraspecific competition (e.g., Breed et al., 2006; Lewis et al., 2006; Drago et al., 2015). Moreover, ontogenetic variations observed in the feeding habits of the South American sea lion could be associated with prey habitat. The consumption of benthic and demersal prey increases with the ontogenetic development of the predator (Drago et al., 2009a; Zenteno et al., 2015; this study). This could be a result of the progressive improvement of diving skills due to the development of physiological capacity with the gain of body mass and age (Le Boeuf et al., 1996; Horning & Trillmich, 1997).

The results of the present study show that the composition of the main prey species of South American sea lions did not change over the last decades, despite a decrease in the availability of fish and overexploitation of several important fish stocks in southern Brazil (e.g., *C. guatucupa*, *M. atricauda, M. furnieri*, *M. liza, P. saltatrix*, and *U. canosai*) (MMA, 2004; Haimovici & Cardoso, 2017). Similar results were observed in traces of stable isotopes (^{13}C and ^{15}N) in the bones and teeth of South American sea lions between 1986 and 2009 in Southern Brazil (Zenteno et al., 2015). However, it can be clearly observed that South American sea lions, as opportunistic predators, are broadening their trophic niche probably in response to the resource depletion in the region. This behavior is in accordance with the theory of optimal foraging and interspecific competition for resources which suggests that the dietary niche breadth of predators may expand under reduced prey availability (MacArthur, 1972; Pianka, 1999). In this context, opportunistic predators are more likely to adjust their eating habits than selective predators, and can withstand the pressure from competition.

Niche overlap between in South American sea lions' diet and local fisheries

Even though the target species overlap indices do not measure competition, it is becoming evident that South American sea lions and fisheries are sharing and potentially competing for the same fishing resources in Southern Brazil. The potential niche overlap between South American sea lions and commercial fisheries has been evaluated using different indices along the species range. Szteren et al. (2004), using Colwell and Futuyma's overlap index, found a low overlap ($C = 0.22$) between the South American sea lions from *Isla de Lobos* in Uruguay and artisanal gillnet fishing. However, Riet-Sapriza et al. (2013), using the

Morisita–Horn (M–H) niche overlap index, observed a higher trophic overlap between sea lions, artisanal fisheries (M–H = 0.84), and coastal trawling (M–H = 0.79) in the same regions a few years later. The discrepancy in the results observed by Szteren et al. (2004) and Riet-Sapriza et al. (2013) along the Uruguayan coast may indicate that the local population of South American sea lions is suffering from the same impacts from fishing as the population from southern Brazil. It is important to mention that the South American sea lion population that arrives every year on the Brazilian coast is composed of animals from Uruguay (Pinedo, 1990; Oliveira et al., 2017). Furthermore, many fish stocks exploited in Brazil are stocks shared with Uruguay and these are suffering with the same problem of depletion caused by fisheries (e.g., Haimovici & Cardoso, 2017). On the Patagonian coast of Argentina, analyses of trophic interactions between South American sea lions and trawling suggest that the potential competition for resources between these species may be low (Dans et al., 2003; Romero et al., 2011), and that the intense fishing of the *Merluccius hubbsi* Marini, 1933 in the region does not seem to be affecting the feeding of sea lions (Drago et al., 2009b).

Moreover, the occurrence of interdecadal changes in diet and/or feeding strategies of South American sea lions was also observed in the North of Argentinean Patagonia. Nevertheless, in this particular case, the modifications to the diet were apparently associated with an increase in the population density of the South American sea lions (Drago et al., 2009b) in the region, and not to a decline of fishing stocks due to fishing pressure (Drago et al., 2009b). This behavior would be expected for an opportunistic predator, which adapts its feeding strategies according to population density, thus minimizing intraspecific competition. Nonetheless, we do not believe that something similar occurred in Southern Brazil due the low density of the species in the region (Sanfelice et al., 1999; Pavanato et al., 2013). It is important to highlight that there is evidence to suggest that the Uruguayan population South American sea lions is declining at an annual rate of 1.6–2.0%. The estimates of the total number of the remaining individuals of the species along the Uruguayan coast range from 12,000 to 13,000 individuals (Páez, 2005; Crespo et al., 2012). Although the species occurs in low density in southern Brazil and its movements are not fully understood, we cannot rule out the possibility that part of this decline could be occurring in the study area due to the conflict with the local fisheries (Machado et al., 2015).

It is noteworthy that the South American sea lion and fishing activities are in constant conflict in several areas along the range of the species (e.g., Rosas et al. 1994; Szteren & Páez, 2002; Sepúlveda et al., 2007; Machado et al., 2016). These interactions may be direct, such as predation of fish caught in the fishing nets (e.g., Szteren & Páez, 2002; Sepúlveda et al., 2007; Machado et al., 2016) and mortality of animals as a result of retaliatory attacks by fishermen or bycatch (e.g., Rosas et al., 1994; Reyes et al., 2013; Machado et al., 2015), or indirect, as in the case of South American sea lions and fishing industry using the same resources (e.g., George-Nascimento et al., 1985; Szteren et al. 2004; Koen-Alonso et al., 2000; Romero et al., 2011). In view of this, Oliveira et al. (2008) suggest that any management measure to reduce this conflict in Southern Brazil must consider the food habits of the species, as well as its interaction with fishing activities.

However, the effect of fisheries on the feeding behavior of the South American sea lion has never previously been demonstrated. The results of the index of trophic overlap do not point to a total overlap between the diet of the South American sea lion and the catches of the fisheries in Southern Brazil. In this context, we can only speculate that fisheries are one of the factors that are probably modifying the feeding behavior of the sea lion along the southern Brazilian coast. This phenomenon can be expected and should be tested for other apex predators in the region. Moreover, excessive fishing pressure is a growing concern worldwide (e.g., Haimovici, 1998; Pauly et al., 2002; Froese et al., 2012; Pauly & Zeller, 2016 2017) and is having profound direct and indirect impacts on top predators. In the present study, five of the eight main fish species found in the diet of South American sea lions were already considered overexploited in Brazilian waters by the Brazilian Ministry of the Environment for more than a decade (MMA, 2004). Although competition, by definition, occurs only when a resource is scarce, it is reasonable to assume that this ecological interaction could increase in the future. The effects of these interactions are largely unpredictable, but could be harmful for many marine top predators (e.g., Secchi et al., 2003; Drago et al., 2010; Trites & Donnelly, 2003; Secchi et al., 2016). Therefore, the reduction in fishing effort and the establishment and/or increase of marine protected areas may be important measures to minimize the effects of fisheries. Within this context, it is imperative to ensure the long-term monitoring of the fishing effort and the population status of the species commercially exploited by the fishing fleet in Southern Brazil.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Audibert, P., C. J. Drehmer, D. Danilewicz & L. R. Oliveira, 2017. Do cranial suture age and growth layer groups correlate in South American pinnipeds? Journal of the Marine Biological Association of the UK. https://doi.org/10.1017/S0025315416001739.

Bastida, R., D. Rodríguez, E. Secchi & V. Silva, 2007. Mamiferos Acuaticos de Sudamerica y Antartida. Vazquez Mazzini Editores, Buenos Aires.

Boffo, M. S. & E. G. Reis, 2003. Atividade pesqueira da frota de média escala no extremo sul do Brasil. Atlântica 25: 171–178.

Breed, G. A., W. D. Bowen, J. I. McMillan & M. L. Leonard, 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proceedings of the Royal Society B: Biological Sciences 273: 2319–2326.

Bugoni, L. & C. M. Vooren, 2004. Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil. Ibis 146: 438–453.

Bustos, R., G. Daneri, A. Volpedo, A. Harrington & E. Varela, 2012. The diet of the South American sea lion *(Otaria flavescens)* at Río Negro, Patagonia, Argentina, during the winter–spring period. Iheringia. Série Zoologia 102: 394–400.

Campagna, C., R. Werner, W. Karesh, M. R. Marin, F. Koontz, F. Cook & C. Koontz, 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). Journal of Zoology 257: 205–220.

Cardoso, L. G. & M. Haimovici, 2011. Caracterização tecnológica, social, econômica e ecológica da atividade pesqueira sediada em Passo de Torres, Santa Catarina, Brasil. Boletim do Instituto de Pesca 37: 275–288.

Carvalho-Filho, A., 1999. Peixes: Costa Brasileira. Melro, São Paulo.

Chambellant, M., I. Stirling & S. H. Ferguson, 2013. Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment. Marine Ecology Progress Series 481: 269–287.

Chao, A. & L. Jost, 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533–2547.

Chao, A., Y. T. Wang & L. Jost, 2013. Entropy and the species accumulation curve: A novel estimator of entropy via discovery rates of new species. Methods in Ecology and Evolution 4: 1091–1110.

Chao, A., K. H. Ma, & T. C. Hsieh, 2016. iNEXT (iNterpolation and EXTrapolation) Online. Program and User's Guide [available on internet at http://chao.stat.nthu.edu.tw/wordpress/software_download/].

Colabuono, F. I. & C. M. Vooren, 2007. Diet of Black-browed *Thalassarche melanophris* and Atlantic Yellow-nosed *T. chlororhynchos* Albatrosses and White-chinned *Procellaria aequinoctialis* and Spectacled *P. conspicillata* Petrels off southern Brazil. Marine Ornithology 35: 9–20.

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

Cortés, E. A., 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56: 707–717.

Costa, R. C., C. A. Fransozo, G. A. S. Melo & F. A. M. Freire, 2003. Chave ilustrada para identificação dos camarões Dendrobranchiata do litoral norte do estado de São Paulo, Brasil. Biota Neotropica 3: 1–12.

Crawley, M. J., 2005. Statistics: an introduction using R. Wiley, Chichester.

Crespo, E. A., D. Oliva, S. L. Dans & M. Sepúlveda, 2012. Current status of the South American sea lion along the distribution range. Universidad de Valparaíso Press, Valparaíso.

Dans, S. L., M. Koen-Alonso, E. A. Crespo, S. N. Pedraza & N. A. García, 2003. Interactions between marine mammals and high seas fisheries in Patagonia: an integrated approach. In Gales, N., M. Hindell & R. Kirkwood (eds), Marine mammals: Fisheries; tourism and management issues. CSIRO Publishing, Victoria.

Drago, M., L. Cardona, E. A. Crespo & A. Aguilar, 2009a. Ontogenic dietary changes in South American sea lions. Journal of Zoology 279: 251–261.

Drago, M., E. A. Crespo, A. Aguilar, L. Cardona, N. García, S. L. Dans & N. Goodall, 2009b. Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. Marine Ecology Progress Series 384: 273–286.

Drago, M., L. Cardona, E. A. Crespo, M. F. Grandi & A. Aguilar, 2010. Reduction of skull size in South American sea lions reveals density-dependent growth during population recovery. Marine Ecology Progress Series 420: 253–261.

Drago, M., V. Franco-Trecu, L. Zenteno, D. Szteren, E. A. Crespo, F. G. R. Riet-Sapriza, L. Oliveira, R. Machado, P. Inchausti & L. Cardona, 2015. Sexual foraging segregation in South American sea lions increases during the pre-breeding period in the Río de la Plata plume. Marine Ecology Progress Series 525: 261–272.

Engel, M. T., S. Marchini, A. C. Pont, R. Machado & L. R. Oliveira, 2014. Perceptions and attitudes of stakeholders towards the wildlife refuge of Ilha dos Lobos, a marine protected area in Brazil. Marine Policy 45: 45–51.

Franklin, A. B., T. M. Shenk, D. R. Anderson & K. P. Burnham, 2001. Statistical model selection: an alternative to null hypothesis testing. In Shenk, T. M. & A. B. Franklin (eds), Modeling in natural resource management: Development, Interpretation, and application. Island Press, Washington: 75–90.

Froese, R., D. Zeller, K. Kleisner & D. Pauly, 2012. What catch data can tell us about the status of global fisheries. Marine Biology 159: 1283–1292.

George-Nascimento, M., R. Bustamante & N. C. Oyarzu, 1985. Feeding ecology of the South American sea lion *Otaria flavescens*: food contents and food selectivity. Marine Ecology Progress Series 21: 135–143.

Grandi, M. F., S. L. Dans, N. A. Gracia & E. A. Crespo, 2010. Growth and age at sexual maturity of South American sea lions. Mammalian Biology 75: 427–436.

Haimovici, M., 1998. Present state and perspectives for the southern Brazil shelf demersal fisheries. Fisheries Management and Ecology 5: 277–290.

Haimovici, M. & J. A. A. Perez, 1991. Coastal cephalopod fauna of Southern Brazil. Bulletin of Marine Science 49: 221–230.

Haimovici, M. & J. M. Ignácio, 2005. Pesca da corvina no sul do Brasil. In Rossi, C. L. W., M. C. Cergole & A. O. Ávila-da-Silva, (eds). Análise das principais pescarias comerciais da região sudeste-sul do Brasil: dinâmica populacional das espécies em exploração série documentos Revizee-Score sul, IOUSP: 101–107.

Haimovici, M. & L. V. Miranda, 2005. Pesca da pescada olhuda no sul do Brasil. In Rossi, C. L. W., M. C. Cergole & A. O. Ávila-da-Silva, (eds). Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Exploração Série Documentos Revizee-Score Sul, IOUSP: 40–45.

Haimovici, M. & L. G. Cardoso, 2017. Long-term changes in the fisheries in the Patos Lagoon estuary and adjacent coastal waters in Southern Brazil. Marine Biology Research 13: 135–150.

Haimovici, M., A. S. Martins & P. C. Vieira, 1996. Distribuição e abundancia de peixes teleósteos demersais sobre a plataforma continental do sul do Brasil. Revista Brasileira de Biologia 56: 27–50.

Haimovici, M., M. Vasconcellos, D. C. Kalikoski, P. Abdalah, J. P. Castello, & D. Hellebrandt, 2006. Diagnóstico da pesca no litoral do estado do Rio Grande do Sul. In Isaac, V. J., A. S. Martins, M. Haimovici, & J. M. Andriguetto Filho (eds). A pesca marinha e estuarina do Brasil no início do século XXI: recursos tecnologias, aspectos socioeconômicos e institucionais Belém: Universitária UFPA: 157–180.

Hyslop, E. J., 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17: 411–429.

Horning, M. & F. Trillmich, 1997. Ontogeny of diving behaviour in the Galápagos fur seal. Behaviour 134: 1211–1257.

Ibama/Ceperg, 1993–2011. Desembarque de pescados no Rio Grande do Sul. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Centro de Pesquisa e Gestão dos Recursos Pesqueiros Lagunares e Estuarinos. Projeto Estatística Pesqueira.[available on internet at http://www.demersais.furg.br/index.php/produção-pesqueira.html].

Jaksic, F. M., 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24: 241–250.

Koen-Alonso, M., E. A. Crespo & S. N. Pedraza, 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. Fishery Bulletin 98: 250–263.

Krebs, C. J., 1999. Ecological methodology. Benjamin/Cummings, Menlo Park.

Le Boeuf, B. J., P. A. Morris, S. B. Blackwell, D. E. Crocker & D. P. Costa, 1996. Diving behavior of juvenile northern elephant seals. Canadian Journal of Zoology 74: 1632–1644.

Lewis, R., T. C. O'Connell, M. Lewis, C. Campagna & A. R. Hoelzel, 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). Proceedings of the Royal Society B 273: 2901–2907.

Machado, R., L. R. Oliveira & S. Montealegre-Quijano, 2015. Incidental catch of South American sea lion in a pair trawl off southern Brazil. Neotropical Biological Conservation 10: 43–47.

Machado, R., P. H. Ott, I. B. Moreno, D. Danilewicz, M. Tavares, H. A. Crespo, S. Siciliano & L. R. Oliveira, 2016. Operational interactions between South American sea lions and gillnet fishing in southern Brazil. Aquatic Conservation: Marine and Freshwater Ecosystems 26: 108–120.

MacArthur, R. H., 1972. Geographical Ecology: patterns in the distribution of species. Harper & Row, New York.

Martins, A. S. & M. Haimovici, 2017. Seasonal mesoscale shifts of demersal nekton assemblages in the subtropical Southwestern Atlantic. Marine Biology Research 13: 88–97. https://doi.org/10.1080/17451000.2016.1217025.

Milmann, L., D. Danilewicz, R. Machado, R. A. Santos & P. H. Ott, 2016. Feeding ecology of the common bottlenose dolphin, *Tursiops truncatus*, in southern Brazil: analyzing its prey and the potential overlap with fisheries. Brazilian Journal of Oceanography 64: 415–422.

MMA - Ministério do Meio Ambiente. 2004. Instrução normativa IBAMA N° 05, de 21 de maio de 2004. Reconhece como espécies ameaçadas de extinção e espécies sobreexplotadas ou ameaçadas de sobreexplotação, os invertebrados aquáticos e peixes, constantes dos Anexos a esta Instrução Normativa. Diário Oficial da União, Brasília. No. 102.

Moreno, I. B., M. Tavares, D. Danilewicz, P. H. Ott & R. Machado, 2009. Descrição da pesca costeira de média escala no litoral norte do Rio Grande do Sul: comunidades pesqueiras de Imbé/Tramandaí e Passo de Torres/Torres. Boletim do Instituto de Pesca 35: 129–140.

Naya, D. E., R. Vargas & M. Arim, 2000. Análisis preliminar de la dieta del león marino del sur (*Otaria flavescens*) en Isla de Lobos, Uruguay. Boletín de la Sociedad Zoológica de Uruguay 12: 14–21.

Norris, K. S., 1961. Standardized methods for measuring and recording data on the smaller cetaceans. Journal of Mammal 42: 471–476.

Oliveira, L. R., P. H. Ott & L. R. Malabarba, 2008. Ecologia alimentar dos pinípedes do sul do Brasil e uma avaliação de suas interações com atividades pesqueiras. In Reis, N. R., A. L. Peracchi & G. A. S. D. Santos (eds), Ecologia de mamíferos. Technical Books Editora, Londrina: 93–109.

Oliveira, L. R., M. C. M. Gehara, L. D. Fraga, F. Lopes, J. I. Túnez, M. H. Cassini, P. Majluf, S. Cárdenas-Alayza, H. J. Pavés, E. A. Crespos, N. García, R. L. Castro, A. R. Hoelzel, M. Sepúlveda, C. Olavarría, V. H. Valiati, R. Quiñones, M. J. Pérez-Alvarez, P. H. Ott & S. L. Bonatto, 2017. Ancient female philopatry, asymmetric male gene flow, and synchronous population expansion support the influence of climatic oscillations on the evolution of South American sea lion (*Otaria flavescens*). PLoS ONE 12(6): e0179442. https://doi.org/10.1371/journal.pone.0179442.

Páez, H., 2005. Situación de la administración del recurso lobos y leones marinos en Uruguay. In Menafra, R., L. R. Gallgo, F. Scarabina & D. Conde (eds), Bases para la conservación y el manejo de la costa uruguaya. Sociedad Uruguaya para la Conservación de la Naturaleza, Vida Silvestre: 557–581.

Pauly, D. & D. Zeller, 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nature Compunction 7: 10244. https://doi.org/10.1038/ncomms10244.

Pauly, D. & D. Zeller, 2017. Comments on FAOs State of World Fisheries and Aquaculture (SOFIA 2016). Marine Policy 77(2017): 176–181.

Pauly, D., A. W. Trites, E. Capuli & V. Christensen, 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science 55: 467–481.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson & D. Zeller, 2002. Towards sustainability in world sheries. Nature 418: 689–695.

Pavanato, H., K. G. Silva, S. C. Estima, D. S. Monteiro & P. G. Kinas, 2013. Occupancy dynamics of South American Sea-Lions in Brazilian Haul-outs. Brazilian Journal of Biology 73: 855–862.

Pianka, E. R., 1999. Evolutionary ecology. Addison Wesley Longman, San Francisco.

Pinedo, M. C., 1990. Ocorrência de pinípedes na costa brasileira. Garcia de Orla Serie Zoologia 15: 37–48.

Pinkas, L., M. S. Oliphant & I. L. K. Iverson, 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fishery Bulletin 152: 1–105.

Pont, A. C., S. Marchini, M. T. Engel, R. Machado, P. H. Ott, E. A. Crespo, M. Coscarella, M. S. Dalzochio & L. R. Oliveira, 2016. The human dimension of the conflict between fishermen and South American sea lions in southern Brazil. Hydrobiologia 770: 89–104.

Recchia, C. A. & A. J. Read, 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Canadian Journal of Zoology 65: 2140–2145.

Reyes, P., R. Hucke-Gaete & J. P. Torres-Florez, 2013. First observation of operational interactions between bottom trawling fisheries and South American sea lion, *Otaria flavescens* in south-central Chile. Journal of the Marine Biological Association of the United Kingdom 93: 1–6.

Riet-Sapriza, F. G., D. P. Costa, V. Franco-Trecu, Y. Marín, J. Chocca, B. González, G. Beathyate, B. Louise Chilvers & L. A. Hückstadt, 2013. Foraging behavior of lactating South American sea lions, *Otaria flavescens* and spatial-resource overlap with the Uruguayan fisheries. Deep-Sea Research Part II: Topical Studies in Oceanography 88–89: 106–119.

Rodríguez, D., R. Bastida, D. G. Calkins & R. W. Davis, 2006. Movements of a juvenile southern sea lion in La Plata River Estuary (Argentina-Uruguay). In Trites, A. W., S. K. Atkinson, D. P. Demaster, L. W. Fritz, T. S. Gelatt, L. D. Rea & K. M. Wynne (eds), Sea Lions of the World. Alaska Sea Grant College Program, Fairbanks: 285–292.

Rodríguez, D. H., M. Dassis, A. Ponce de León, C. Barreiro, M. Farenga, R. O. Bastida & R. W. Davis, 2013. Foraging strategies of Southern sea lion females in the La Plata River Estuary (Argentina–Uruguay). Deep-Sea Res. Pt. II 88–89: 120–130.

Romero, M. A., S. Dans, R. Gonzalez, G. Svendsen, N. Garcia & E. Crespo, 2011. Solapamiento trofico entre el lobo marino de un pelo *Otaria flavescens* y la pesqueria de arrastre demersal del golfo San Matias, Patagonia, Argentina. Latin American Journal of Aquatic Research 39: 344–358.

Rosas, F. C. W., M. C. Pinedo, M. Marmontel & M. Haimovici, 1994. Seasonal movements of the South American sea lion (*Otaria flavescens*, Shaw) off the Rio Grande do Sul coast, Brazil. Mammalia 58: 51–59.

Rossi-Wongtschowski, C. L. B., C. C. Siliprandi, M. R. Brenha, S. A. Gonsales, C. Santificetur & A. M. Vaz-Dos-Santos, 2014. Atlas of marine bony fish otoliths (sagittae) of southeastern-southern Brazil Part I: Gadiformes (Macrouridae, Moridae, Bregmacerotidae, Phycidae and Merlucciidae); Part II: Perciformes (Carangidae, Sciaenidae, Scombridae and Serranidae). Brazilian Journal of Oceanography 62: 1–103.

Sanfelice, D., V. C. Vasques & E. A. Crespo, 1999. Ocupação sazonal por duas espécies de Otariidae (Mammalia, Carnivora) da Reserva Ecológica Ilha dos Lobos, Rio Grande do Sul, Brasil. Iheringia Série Zoologia 87: 101–110.

Schoener, T. W., 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408–418.

Schoener, T. W., 1972. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369–404.

Seeliger, U. & C. Odebrecht, 1998. Introdução e aspectos gerais. In Seeliger, U., C. Odebrecht & J. P. Castello (eds), Os Ecossistemas Costeiro e Marinho do Extremo Sul do Brasil. Ecoscientia, Rio Grande.

Secchi, E. R., P. H. Ott & D. S. Danilewicz, 2003. Effects of fishing by-catch and conservation status of the Franciscana dolphin, *Pontoporia blainvillei*. In Gales, N., M. Hindell & R. Kirkwood (eds), Marine Mammals: Fisheries, Tourism and Management Issues. CSIRO Publishing, Melbourne.

Secchi, E. R., S. Botta, M. M. Weigand, L. A. Lopes, P. F. Fruet, R. C. Genoves & J. Di Tullio, 2016. Long-term and gender-related variation in the feeding ecology of common bottlenose dolphins inhabiting a subtropical estuary and the adjacent marine coast in western South Atlantic. Marine Biology Research. https://doi.org/10.1080/17451000.2016.1213398.

Sepúlveda, M., M. J. Perez, W. Sielfed, D. Oliva, L. R. Durán, L. Rodríguez, V. Araos & M. Buscaglia, 2007. Operational interactions between South American sea lions *Otaria flavescens* and artisanal (small-scale) fishing in Chile: results from interview surveys and on-board observations. Fisheries Research 83: 332–340.

Stephens, D. W. & J. R. Krebs, 1986. Foraging Theory. Princeton Univ. Press, Princeton.

Szteren, D. & E. Páez, 2002. Predation by southern sea lions (*Otaria flavescens*) on artisanal fishing catches in Uruguay. Marine Freshwater Research 53: 1161–1167.

Szteren, D., D. Naya & M. Arims, 2004. Overlap between pinniped summer diet and artisanal fishery catches in Uruguay. The Latin American Journal of Aquatic Mammals 3: 119–125.

Szteren, D., 2006. Predation of *Otaria flavescens* over artisanal fisheries in Uruguay: opportunism or prey selectivity? The Latin American Journal of Aquatic Mammals 5: 29–38.

Thompson, D., C. D. Duck, B. J. McConnell & J. Garrett, 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. Journal of Zoology 246: 135–146.

Trites, A. W. & C. P. Donnelly, 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mammal Review 33: 3–28.

Vaz-Ferreira, R., 1982. *Otaria flavescens* (Shaw), South American sea lion. Mammals of the seas: small cetaceans, seals, sirenians and otters. FAO Fisheries Series 4: 477–495.

Zenteno, L., E. Crespo, D. Vales, L. Silva, F. Saporiti, L. R. Oliveira, E. R. Secchi, M. Drago, A. Aguilar & L. Cardona, 2015. Dietary consistency of male South American sea lions (*Otaria flavescens*) in southern Brazil during three decades inferred from stable isotope analysis. Marine Biology 162: 275–289.