

Eating catch of the day: the diet of porbeagle shark *Lamna nasus* (Bonnaterre 1788) based on stomach content analysis, and the interaction with trawl fisheries in the south-western Atlantic (52° S–56° S)

Mauro Belleggia^{1,2,3}  | Jorge Colonello¹  | Federico Cortés¹  | Daniel Enrique Figueroa⁴ 

¹Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

³Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMdP-CONICET, Mar del Plata, Argentina

⁴Biología de Peces, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata (UNMdP), Mar del Plata, Argentina

Correspondence

Mauro Belleggia, Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo S/N – Casilla de Correo 175 – CP 7600, Mar del Plata, Argentina.
Email: belleggia@inidep.edu.ar

ABSTRACT

This work examined the diet of the porbeagle shark *Lamna nasus* in the south-west Atlantic Ocean (SWAO, Argentina, 52° S–56° S) by analysing the stomach content information obtained by scientific observers who sampled specimens captured as by-catch on-board commercial fishing vessels from 2010 to 2020. A total of 148 fishing sites were analysed, in which the estimated catch was composed mainly of hoki *Macruronus magellanicus* (56.00%) and southern blue whiting *Micromesistius australis* (33.13%). From 413 porbeagle sharks sampled (292 females and 121 males) ranging from 71 to 241 cm total length (L_T) (mean: 179.76 ± 26.74 cm), 310 (75.06%) contained food in the stomachs. The forage fish were mainly hoki *M. magellanicus* (23.53%) and southern blue whiting *M. australis* (19.05%), followed by the Patagonian sprat *Sprattus fuegensis* (4.48%) and nototheniids (1.4%). Cephalopods and crustaceans accounted for 10% of the diet. The estimated trophic level was 4.35. Generalized linear models revealed that the consumption of hoki *M. magellanicus* and southern blue whiting *M. australis* increased with the L_T of the porbeagle shark. Moreover, smaller porbeagle sharks preyed upon both small and large teleost fish, whereas larger porbeagle sharks predated exclusively upon large fish. The diet of porbeagle shark involved interactions with fisheries as it fed upon the fish species that constituted the main catch in the analysed fishing sites, as well as the main catches of the austral trawl fisheries. The ecological role of porbeagle shark observed in the SWAO exposed implications for fisheries management from a multispecies perspective.

KEYWORDS

fishery interaction, Lamnidae, pelagic shark, trophic ecology

1 | INTRODUCTION

The family Lamnidae contains three genera and five species of mackerel sharks: *Carcharodon carcharias* (L. 1758), *Isurus oxyrinchus* Rafinesque 1810, *Isurus paucus* Guitart Manday 1966, *Lamna ditropis*

Hubbs & Follett 1947 and *Lamna nasus* (Bonnaterre 1788) (Compagno, 2008; Nelson *et al.*, 2016; Weigmann, 2016). These species are considered endothermic or heterothermic sharks that maintain elevated body core temperatures (and specifically stomach temperatures) compared to the surrounding sea water (Bernal

et al., 2005; Leigh et al., 2017; Lowe & Goldman, 2001). Both species of *Lamna* are epi and mesopelagic/neritic top predators distributed in cold temperate and polar seas (Ebert & Winton, 2010). The porbeagle shark *L. nasus* is one of the few known shark species that occurs in both the Arctic and Antarctic circumpolar regions, except the North Pacific inhabited by *L. ditropis* (Ebert & Winton, 2010; Figueroa, 1997). The porbeagle shark *L. nasus* showed horizontal (up to 10,000 km) and vertical (up to 1,300 m depth) movements in open oceans (Francis et al., 2015; Pade et al., 2009; Skomal et al., 2021) and have also sporadically been reported in rivers (Matheson, 1928) and coastal waters (Lucifora & Menni, 1998; Mabrugaña et al., 2015).

The genus *Lamna* is known for feeding on economically important species such as Pacific salmon, mackerels, Ray's bream and cephalopods (Ebert & Winton, 2010; Horn et al., 2013; Nagasawa, 1998; Yatsu, 1995). The porbeagle *L. nasus* with their pointed, grasping teeth feed predominantly on teleost fishes and cephalopod (Stevens, 2010), probably with minimal handling and rapid swallowing (Lucifora et al., 2009). The interaction of porbeagle shark with commercial fisheries would be associated with their prey (ICCAT, 2020). For instance, the porbeagle *L. nasus* is a common by-catch in the Chilean longline swordfish fishery in the south-eastern Pacific Ocean (Hoyle et al., 2017a; Torres-Florez & Reyes, 2007), as well as in the Uruguayan tuna longline fishery from the south-west Atlantic Ocean (SWAO, Domingo et al., 2008; Cortés et al., 2010; Forselledo, 2012; Mas, 2012). In New Zealand it is a common by-catch in tuna longline, mid-water trawl and coastal set net fisheries (Duffy, 2015). In Argentina they are subjected to incidental by-catch but mainly in trawling vessels operating south of 50° S (austral trawl fisheries), targeting hoki *Macruronus magellanicus* Lönnberg 1907, southern blue whiting *Micromesistius australis* Norman 1937, Patagonian toothfish *Dissostichus eleginoides* Smitt 1898 and austral hake *Merluccius australis* (Hutton 1872) (Cortés & Waessle, 2017; Waessle & Cortés, 2011). In Argentina, up to 90% of the reported porbeagle shark by-catch corresponds to the austral trawl fisheries (Cortés et al., 2017; Waessle & Cortés, 2011).

The removal of sharks by fishing has direct and indirect implications on the structure and function of marine ecosystems (Stevens et al., 2000). The direct effects of fishing through the capture of individual species include changes in abundance, size structure, life-history parameters and, at the extreme, could lead to extinction (Stevens et al., 2000). The indirect effects involve trophic interactions at the community level through a selective removal of key species (predator, prey or competitors), species replacement and enhancement of food supply through discards (Stevens et al., 2000) or depredation (Mitchell et al., 2018). The porbeagle shark *L. nasus* is classified as vulnerable globally in the IUCN Red List, but the categories differ regionally (Dulvy et al., 2014). In the SWAO, porbeagle shark was categorized as data deficient (Cuevas et al., 2020); therefore, biological and ecological studies focused on this species are a priority. The impact of fishing exploitation on the North Atlantic stock and the lack of data on the stocks of *L. nasus* in the Southern Hemisphere were the main reasons for its inclusion in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora

(CITES, 2013). Nonetheless, recent analyses on the status of the *L. nasus* stock in the Southern Hemisphere have concluded that there is a very low risk that the stock is subjected to overfishing (Hoyle et al., 2017b).

In SWAO, the seasonality and length frequency distributions of porbeagle shark registered in commercial fleet indicated that the nursery areas are located in northern and temperate regions (Forselledo, 2012; Soto & Montealegre-Quijano, 2012), whereas the adult feeding grounds are in southern and colder areas (Cortés et al., 2017; Waessle & Cortés, 2011). Similar migratory behaviour was observed in North Pacific for *L. ditropis*, from optimal thermal habitat (warmer temperatures at lower latitudes) to an optimal foraging habitat (Pacific salmon and Pacific herring aggregation in the Gulf of Alaska) (Hulbert et al., 2005). Nonetheless, the diet of porbeagle shark in the supposed feeding ground area in the austral region of the SWAO (52° S–56° S) has not been investigated to date. In this context, the general objective of the present work was to examine the diet of the porbeagle shark by analysing the stomach content information obtained by scientific observers who sampled specimens captured as by-catch in austral trawl fisheries from 2010 to 2020. The specific objectives were as follows: (a) to quantify the diet composition of the porbeagle shark in the SWAO (52° S–56° S), (b) to determine the trophic level, (c) to evaluate the effect of total length (L_T), sex, main species caught (MSC) in the fishing site, latitude, depth and hour on the diet and (d) to investigate the relationships between the L_T of predator and L_T of prey.

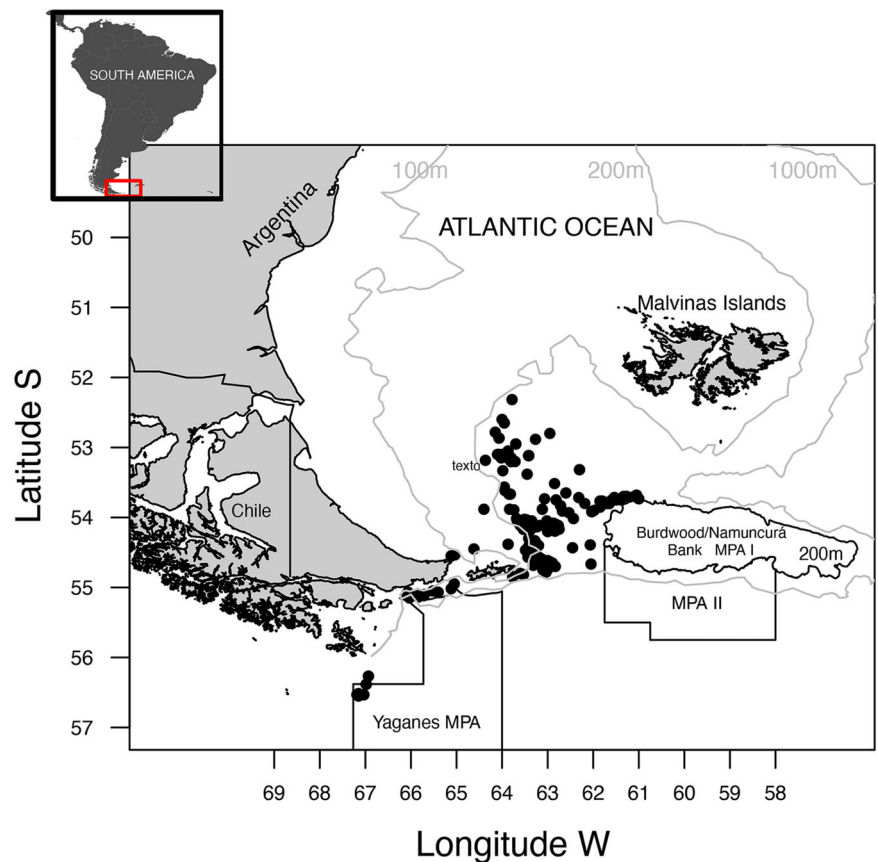
2 | MATERIALS AND METHODS

2.1 | Study area

The study area was located at the south-east of the southern tip of South America and at the west of Burdwood Bank/Namuncurá (52.19–56.33° S, 60.03–67.11° W, 94–816 m depth; Figure 1). The top of Burdwood/Namuncurá Bank is a large plateau of 80–150 m depth, situated at the east of Argentinean continental shelf break and Beagle Chanel, separated from them by deep water of 500–2,000 m depth (Van Mieghem & Van Oye, 1965). The study area was situated between three marine protected areas (MPA): the Burdwood/Namuncurá Bank has two MPA (Namuncurá MPA I and II, c. 60,000 km²) created in 2013 and 2018, considered an oceanic hotspot of benthic and nekton biodiversity (Figure 1) (Delpiani et al., 2020; Schejter et al., 2016; Schejter & Bremec, 2019). The Yaganes MPA encompass 68,834 km², which was created in 2018 with Namuncurá MPA II for biodiversity conservation and protection of structure and functioning of ecosystems (Figure 1).

Based on the assemblage of marine species, the study area is located in an ecoregion within the Magellanic and Patagonian slope biogeographic provinces (Menni et al., 2010; Perillo et al., 2006; Sabadin et al., 2020). The assemblage of species of this ecoregion extends its distribution towards northern, outer and deeper areas of the Argentinean continental shelf and slope, following the cold waters of

FIGURE 1 Map of the study area showing the fishing sites (solid circles) where specimens of porbeagle shark *Lamna nasus* were collected from 2010 to 2020, aboard the commercial fishing vessels to study the diet in the south-west Atlantic Ocean. MPA I: marine protected area at Burdwood/Namuncurá Bank delimited by the 200 m isobath (28,000 km²). MPA II: marine protected area at southern Burdwood/Namuncurá Bank (32,000 km²). Yaganes MPA (68,834 km²) partially shown



the Malvinas Current which ranges from 3.5 to 5° C at its origin (Guerrero *et al.*, 1999; Perillo *et al.*, 2006; Piola & Gordon, 1989). The Magellanic Province covers the slope (200–1,000 m) along the continental margin from 36° S to 43° S, and southward of 43° S from the coastline to 500 m depth, including the Malvinas Islands and the Burdwood/Namuncurá Bank (Menni *et al.*, 2010; Sabadin *et al.*, 2020). The Patagonian slope province ranged from 41° S to 57° S, between 500 and 2,500 m depth (Sabadin *et al.*, 2020). The mean surface temperature of this ecoregion ranges from 4 to 13° C (Balech & Ehrlich, 2008; Guerrero *et al.*, 1999).

2.2 | Data source

The comprehensive data set herein analysed was obtained from commercial fishing vessels by 15 scientific observers of the National Institute of Fisheries Research and Development (INIDEP, Argentina). The information was collected from 2010 to 2020 (Figure 1), and consisted of date, geographic coordinates and depth of the fishing sites. In each fishing site, the scientific observer made a reliable estimate of total catch composition in tons, following FAO observer programme operations manual (van Helvoort, 1986). A total of 148 fishing sites carried out during January (5), February (22), March (24), April (32), May (45), June (15) and July (5) were included in the analysis (Figure 1). The species that constituted more than 50% of the catch was established as the MSC at each fishing site. The MSC was hoki

M. magellanicus in 91 fishing sites, southern blue whiting *M. australis* in 48 fishing sites and other species in 9 fishing sites. The specimens of porbeagle shark *L. nasus* captured that could not be released alive were analysed (Figure 2a). These sharks were measured in L_T , sexed, their stomachs excised and opened, and prey items identified to the lowest possible taxonomic level. The L_T of fish consumed by porbeagle shark was recorded when gut contents were not highly digested (Figure 2b).

2.3 | Data analyses

The vacuity index of the porbeagle shark *L. nasus* was estimated to evaluate the rate of feeding activity as the percentage of empty stomachs (Moura *et al.*, 2008). The importance of each prey in the diet of the porbeagle shark *L. nasus* was assessed by calculating the percentage frequency of occurrence (%F, the total number of stomachs in which a given prey was found expressed as a percentage of the total number of stomachs with food). The presence-absence data were used to account the %F that provides an adequate and interpretable measure of diet composition (Baker *et al.*, 2014). Moreover, the %F approach provided a rapid, unambiguous and reliable account of diet composition, not affected by the condition of prey (Buckland *et al.*, 2017). Nonetheless, %F values are not additive because different prey usually occur together within a single stomach, meaning that they usually sum more than 100% for all different prey items of the

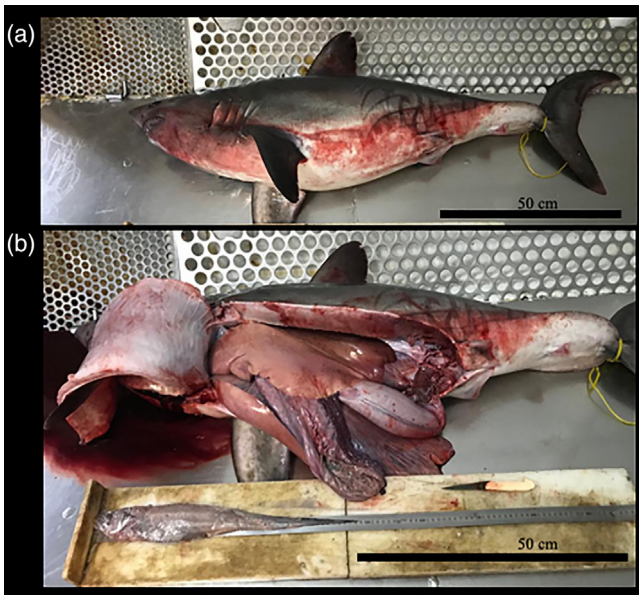


FIGURE 2 (a) Porbeagle shark *Lamna nasus* specimen caught as by-catch during May 2020 in the south-west Atlantic Ocean (53.54° S to 62.40° W, 488 m depth), sampled by observer to study the diet, juvenile female 147 cm total length (L_T). (b) The stomach content not highly digested allowed the measurement of their prey hoki *Macrurus magellanicus* (49 cm L_T)

predator. To resolve this disadvantage, the %F was expressed on a per cent basis, as the percentage of the percentage of the frequency of occurrence (%F) of each prey, as follows: $\%F = 100 \times \%F / \sum \%F$. The %F sum 100% and could be used as an alternative index to facilitate comparisons among diet studies. This index representative of the diet accurately describes the trophic spectrum and allows the estimation of other parameters such as the trophic level of the porbeagle shark, following the formula proposed by Cortés (1999) as follows:

$$\text{TROPH} = 1 + \sum_{i=1}^n P_i \text{Troph}_i$$

where TROPH is the trophic level of *L. nasus*, Troph_i is the trophic level of each prey item “i,” P_i is the %FF of each prey item “i” in the diet and “n” is the total number of prey items. The Troph_i was obtained from the literature (Cortés, 1999; Froese & Pauly, 2019; Troccoli et al., 2020).

To test the hypothesis that the consumption of the main identifiable prey of porbeagle shark (hoki and southern blue whiting) was influenced by L_T , sex, MSC in the fishing site and depth, the authors fitted generalized linear models (GLMs) and used the information theory selection criteria (Burnham & Anderson, 2002). The presence/absence data of the most important prey of the porbeagle shark were used as dependent variables. This kind of binary response variable has a binomial error distribution and allows to fit GLMs with a logit link (Crawley, 2005). The explanatory variable MSC (levels: hoki, southern blue whiting and others) was treated as dichotomous due to the low

number of fishing sites with MSC others (9 of 148 fishing sites). The levels of the variable MSC were hoki, and southern blue whiting combined with others to fit the consumption of hoki, whereas to fit the consumption of southern blue whiting the levels of the MSC were southern blue whiting, and hoki combined with others. The GLMs with all possible combination of two independent variables were also fitted. A null model was included in the model selection approach to test the hypothesis that none of the independent selected variables influenced the consumption of modelled prey. The AIC and Akaike's weight (w) were estimated for each model and used as an indicator of the probability that a model is that best explained the variability in the data (Burnham et al., 2011; Burnham & Anderson, 2002). The models with the highest w (and the lowest AIC) were considered the best in explaining the variations in the consumption of porbeagle shark prey and were plotted with the function *invlogit*. When two or more models had similar AIC values and did not provide strong support to select any particular GLM, the authors applied model averaging function to the top models that added $w > 0.6$, using *MuMIn* package (Johnson & Omland, 2004; Symonds & Moussalli, 2011). All analyses were performed using R version 4.0.3 (<http://www.R-project.org>).

The relationships between predator L_T and fish prey L_T were evaluated by fitting quantile regression models (Cade & Noon, 2003). This tool allows the interpretation of more than a single slope of the response variable, by fitting regressions of 20%, 50% and 80% quantiles to test the minimum, medium and maximum increase in size of fish prey consumed with the increase in the porbeagle shark body size, respectively (Cade & Noon, 2003). These analyses were performed with quantreg R-package Version 5.73 (Koenker, 2020).

2.4 | Ethical statement

The porbeagle shark specimens were sampled when they could not be returned alive to the sea, respecting the welfare of animals, following international, national and institutional guidelines for the care and use of animals, in accordance with the ethical standards of the institution where the study was conducted. This study was carried out with the consent of INIDEP (National Institute for Fisheries Research and Development, Argentina) and the fishing companies, following the Argentinean regulations regarding shark management and conservation (CFP, 2021).

3 | RESULTS

The most abundant species on the estimated catch from the 148 fishing sites analysed were bony fish, mainly hoki *M. magellanicus* (56.00%) and southern blue whiting *M. australis* (33.13%) (Figure 3). Other species represented 9.81% of the catch composition and consisted mainly of the morid cods *Notophycis marginata* and *Salilota australis*, rattails *Macrurus holotrachys* and *Coelorinchus fasciatus*, Patagonian toothfish *D. eleginoides*, notothenids *Patagonotothen ramsayi*, austral hake *M. australis*, pink cusk-eel *Genypterus blacodes*,

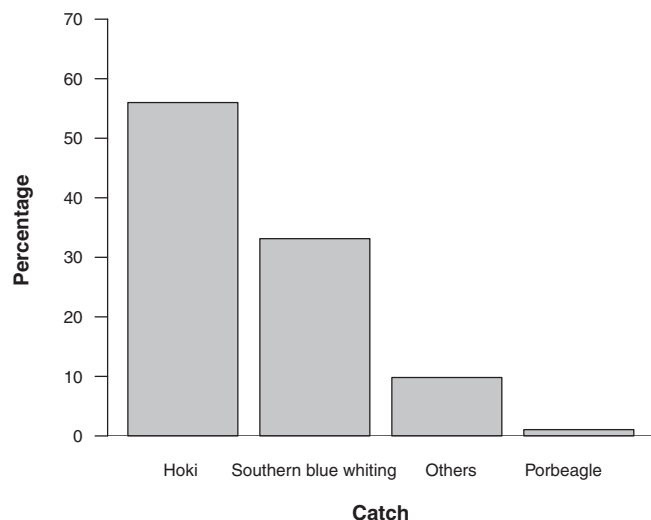


FIGURE 3 Percentage composition of the total catch from the 148 fishing sites analysed in the south-west Atlantic Ocean to study the diet of the porbeagle shark *Lamna nasus*

medusafishes (*Seriotelella* spp.) and Rajidae skates (mainly *Bathyraja* spp., *Dipturus* spp.) (Figure 3). The porbeagle shark represented 1.06% of the catch composition (Figure 3).

A total of 413 porbeagle sharks (292 females and 121 males) ranging from 71 to 241 cm L_T were sampled (Figure 4). The L_T distributions were significantly different between sexes (Kolmogorov-Smirnov test: $D = 0.28$, $P < 0.001$) (Figure 3). The mean L_T of females (range 71–241 cm, mean 183.74 cm, s.d. 27.02) were larger (t -test, $t = -5.11$, $P < 0.001$) than males (ranged 87–218 cm, mean 170.16 cm, s.d. 23.49) (Figure 4). A total of 103 stomachs were empty, resulting in a vacuity index of 24.94%. The vacuity indices of females and males were 27.24% and 18.18%, respectively. The porbeagle shark fed mainly on fish (88.34%), followed by cephalopods (5.85%) and crustaceans (4.29%). The most important identifiable fish prey were hoki *M. magellanicus* and southern blue whiting *M. australis*, followed by the Patagonian sprat *Sprattus fuegensis*, notothenids and the southern hake *M. australis* (Table 1). Cephalopods were represented by the families Octopodidae, Ommastrephidae and Onychoteuthidae (Table 1). Crustaceans occurred in the stomachs in less frequency than cephalopods and included lithodids, shrimps, lobster crabs and euphausiids. The estimated trophic level of porbeagle shark in this region was 4.35 (Table 1).

The consumption of hoki *M. magellanicus* increased with the L_T of the porbeagle shark and was higher when hoki was the main capture of the fishing site [Figure 5a; intercept = $-8.56 (\pm 1.26)$, parameters = $0.034 (\pm 0.006) L_T + 1.88 (\pm 0.39)$ Hoki MSC, AIC = 316.6, $w = 0.99$, deviance explained = 14.25%]. The consumption of southern blue whiting *M. australis* also increased with the L_T of the porbeagle shark and was the more important prey when it was the main species captured in the fishing site [Figure 5b; intercept = $-3.41 (\pm 1.31)$, parameters = $0.010 (\pm 0.007) L_T + 3.00 (\pm 0.36)$ southern blue whiting MSC, AIC = 230.4, $w = 0.66$ (model averaged), deviance explained = 30.87%].

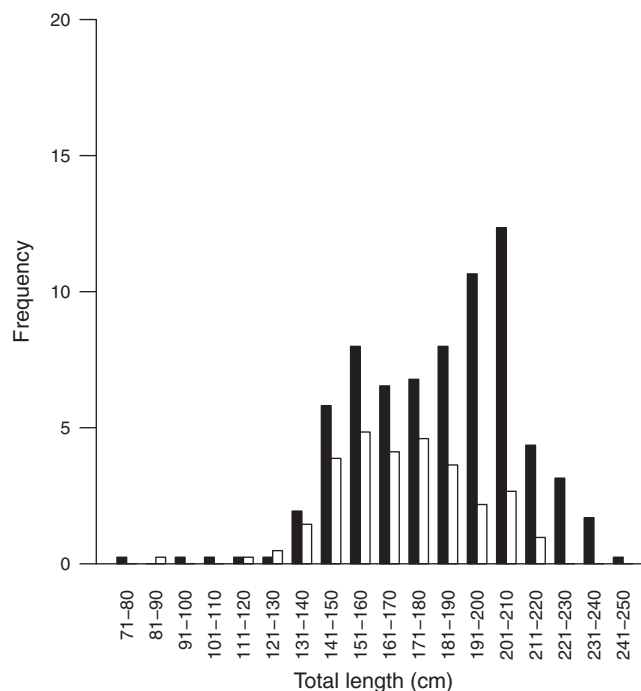


FIGURE 4 Total length frequency distribution of the porbeagle shark *Lamna nasus* by sex, collected to study their diet in the south-west Atlantic Ocean (■) Female, (□) Male

A total of 61 fish prey could be measured in L_T . The medium and maximum values of the L_T of the fish consumed by the porbeagle shark were independent of the L_T of the predator (slope of the quantile 50% = 0.01; $P = 0.80$; slope of the quantile 80% = -0.02 ; $P = 0.51$; Figure 6). On the contrary, minimum values of the L_T of the fish consumed by the porbeagle shark were positively correlated with the L_T of the predator (slope of the quantile 20% = 0.13; $P = 0.03$; Figure 6).

4 | DISCUSSION

The stomach content information obtained by scientific observers on-board commercial fishing vessels during 2010 and 2020 revealed that the porbeagle shark *L. nasus* in the SWAO foraged predominantly on teleost fish. The diet also included cephalopods and crustaceans, but in less proportion than what was reported in previous studies from the north-west Atlantic (Joyce *et al.*, 2002), New Zealand (Horn *et al.*, 2013), Kerguelen Islands (Cherel & Duhamel, 2004), south Pacific (Yatsu, 1995) or Antarctic Peninsula (Rodhouse, 2013). The other species of the genus, *L. ditropis*, also feeds mainly on teleost fish (Hulbert *et al.*, 2005; Nagasawa, 1998), and the diet of the majority of the pelagic shark species that have been investigated consisted of teleost fish, followed by cephalopods (Crooks, 2020). The porbeagle shark fed mainly on hoki *M. magellanicus* and the southern blue whiting *M. australis*, two large planktivorous fishes from the SWAO (Brickle *et al.*, 2009). As was also noted by Joyce *et al.* (2002), unidentified teleosts formed an important part of the stomach contents

Prey	F	%F	%%F	Troph	
Fish	288	92.90	88.34		
Macruronidae – <i>Macruronus magellanicus</i>	84	27.10	23.53	3.9	(a)
Gadidae – <i>Micromesistius australis</i>	68	21.94	19.05	3.3	(a)
Clupeidae – <i>Sprattus fuegensis</i>	16	5.16	4.48	2.6	(a)
Nototheniidae – <i>Patagonotothen</i> spp.	5	1.61	1.40	3.5	(a)
Merlucciidae – <i>Merluccius australis</i>	3	0.97	0.84	4.5	(a)
Rajidae	1	0.32	0.28	3.65	(b)
Nototheniidae – <i>Dissostichus eleginoides</i>	1	0.32	0.28	4.57	(c)
Fish not identified	140	45.16	39.22	3.24	(b)
Cephalopods	19	6.13	5.83		
Ommastrephidae – <i>Illex argentinus</i>	6	1.94	1.68	3.2	(b)
Octopodidae – <i>Octopus</i> spp.	7	2.26	1.96	3.2	(b)
Onychoteuthidae – <i>Moroteuthopsis ingens</i>	5	1.61	1.40	3.2	(b)
Cephalopods not identified	1	0.32	0.28	3.2	(b)
Crustaceans	14	4.52	4.29		
Natantia	2	0.65	0.56	2.52	(b)
Lithodidae – <i>Lithodes santolla</i>	1	0.32	0.28	2.52	(b)
Euphausiidae <i>Euphausia</i> spp.	1	0.32	0.28	2.2	(b)
Munididae – <i>Munida gregaria</i>	1	0.32	0.28	2.52	(b)
Crustaceans not identified	10	3.23	2.80	2.52	(b)
Others prey	5	1.61	1.53		
Gasteropoda	1	0.32	0.28	2.5	(b)
Polychaeta	1	0.32	0.28	2.5	(b)
Not identified remains	3	0.97	0.84	2.5	(b)

Trophic level *L. nasus* 4.35

Note. The trophic level of each prey item (Troph) was obtained from: (a) Froese & Pauly, 2019; (b) Cortés, 1999; (c) Troccoli *et al.*, 2020.

(39.22%). Assuming that these heavily digested and therefore unrecognizable fish have the same distribution as the identifiable prey items, hoki and southern blue whiting would be even more important on the diet of the porbeagle shark. The stomach temperature c. 16°C above ambient reported for *L. ditropis* (Bernal *et al.*, 2005; Goldman *et al.*, 2004) might account for the high degree of digestion and the high proportion of unidentified fish observed in this study, as well as in those works focused on other lamnoids species.

The percentage of empty stomachs (24.94%) was lower than in other diet studies on porbeagle sharks, which ranged from 51.31% in north-west Atlantic (Joyce *et al.*, 2002) to 38.78% in New Zealand (Horn *et al.*, 2013). Although the aforementioned works were carried out on commercial longline vessels and it could lead on an over-estimation of the number of empty stomachs, the results of this study suggested a relatively high feeding activity for the species in this region, like in Kerguelen waters where from 26 porbeagles dissected, 25 contained prey items (Cherel & Duhamel, 2004). Similarly, in South Pacific Ocean from 63 porbeagles analysed, 57 had prey (Yatsu, 1995). In addition, sharks may regurgitate because of capture stress, which increases the number of animals with empty stomachs (Shiffman *et al.*, 2014). These results also suggested that the hotspot

of this species at the east of the southern tip of South America and between three MPA (Burdwood/Namuncurá Bank MPA I, MPA II and Yaganes) (Cortés & Waesle, 2017) would be associated with a critical feeding ground area. Seasonal foraging migrations into these prey-rich waters might be a key feature of the life history of the porbeagle shark in the SWAO. With the thermoregulatory ability (Bernal *et al.*, 2012), Lamnids sharks can feed in cold waters where prey are more abundant (Campana & Joyce, 2004).

The migration and aggregation of porbeagle sharks during summer and fall into austral region of SWAO seem to coincide with non-reproductive aggregation of hoki *M. magellanicus* (Giussi *et al.*, 2016) and southern blue whiting *M. australis* (Wöhler *et al.*, 2004), the forage fish of *L. nasus* in this area (this study). A comparable pattern was observed for *L. ditropis*, as their aggregations in north-east Pacific were associated with reproductive migrations of their main prey, the Pacific salmon (*Oncorhynchus* spp.) (Hulbert *et al.*, 2005; Williams *et al.*, 2010). In general, female shark species in pregnant condition move to warmer waters during the cooler months of the year, increasing the rate of embryonic development (Economakis & Lobel, 1998). The 2,000 km pupping migration of porbeagle females to an unproductive region of the ocean, followed by a return migration

TABLE 1 Diet composition of the porbeagle shark *Lamna nasus* off south-western Atlantic Ocean expressed in frequency of occurrence (F), in percentage of the frequency of occurrence (%F) and the new percentage of the percentage of the frequency of occurrence (%%F)

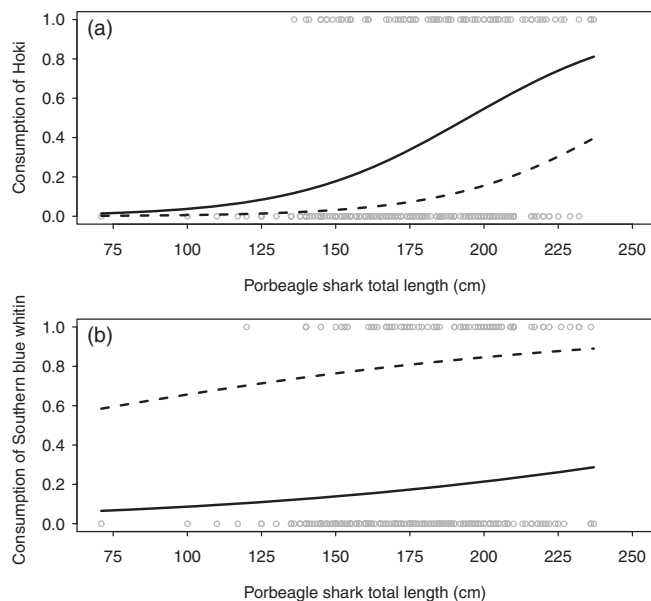


FIGURE 5 Generalized linear models (GLMs), selected using Akaike's weights, fitted for the presence/absence data of the main prey of the porbeagle shark *Lamna nasus* off south-west Atlantic Ocean, that explain changes in the consumption of: (a) hoki *Macrurus magellanicus* and (b) southern blue whiting *Micromesistius australis*. The GLMs have binomial error distribution and a logit link, and were plotted using inverse logit function. The diet was influenced by total length and MSC (main species caught) in the fishing site (—) Hoki, (---) Southern blue whiting and others, (—) Hoki and others, (---) Southern blue whiting

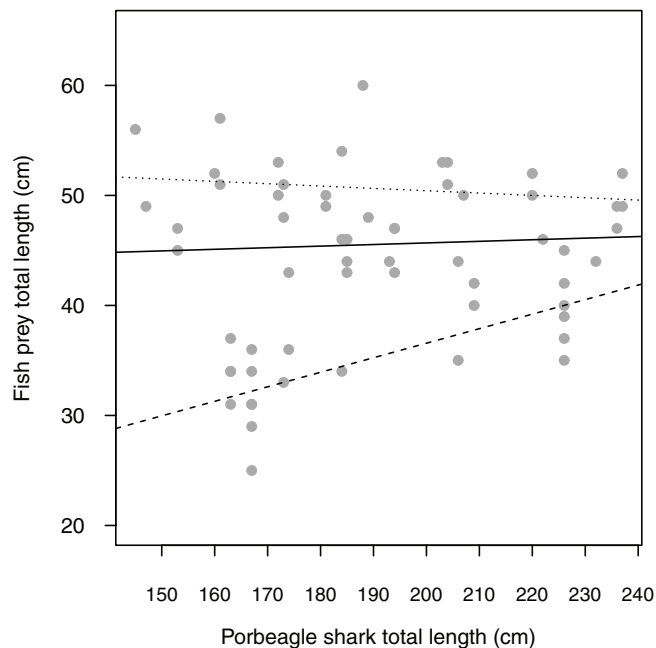


FIGURE 6 Quantile regressions of the total length (L_T) of fish consumed and the L_T of the porbeagle shark *Lamna nasus* predator off south-west Atlantic Ocean. The dotted, solid and dashed lines represent 20%, 50% and 80% quantile regressions, respectively

within several months by both females and pups, remains the subject of discussion in the north Atlantic (Biais *et al.*, 2017; Campana *et al.*, 2010). This migratory pattern appears to be similar in the SWAO (Cortés *et al.*, 2010; Domingo *et al.*, 2008; Forselledo, 2012; Mas, 2012). The ability to maintain body temperature above sea temperature (Bernal *et al.*, 2012) allows adult females to access feeding areas with high abundance of prey, unavailable to other ectothermic predators. Seasonal migration of porbeagle sharks, particularly adult females, from northern area with optimal conditions for gestation, to foraging area in austral region of SWAO, may be related with avoiding competition for resources and their thermoregulatory adaptation. The presence of prey in large schools and shoals (Giussi *et al.*, 2016; Wöhler *et al.*, 2004) with a high energetic value (Ciancio *et al.*, 2007; Eder & Lewis, 2005) would compensate the cost of the extensive southward migration in SWAO.

The horizontal (up to 10,000 km) and vertical (up to 1,300 m depth) movements indicated that porbeagle sharks exhibited a considerable plasticity across coastal, shelf and shelf-edge habitats (Francis *et al.*, 2015; Pade *et al.*, 2009; Skomal *et al.*, 2021) and has the ability to occupy different trophic niches across habitats and seasons, as was noted in north Atlantic (Joyce *et al.*, 2002). In western north Atlantic, the porbeagle shark was associated with the continental shelf moving between the surface and the bottom remaining less than 200 m depth during summer, whereas they moved into mesopelagic depths (200–1,000 m) during winter, possibly allowing the exploitation of prey not available to other predators (Skomal *et al.*, 2021). In the present study, prey items of porbeagle shark were associated mainly with demersal and mesopelagic habitat, because prey items from benthic and deep habits (*e.g.*, *D. eleginoides*, *Patagonotothen* spp. and benthic invertebrates) were scarce. Nonetheless, these sharks are known to feed both on the surface and at the bottom (Stevens, 1973). Information about feeding habits of porbeagle shark is unknown in temperate latitudes of SWAO, but if mesopelagic resources are limited, the porbeagle shark with their capacity to remain at colder depths for longer periods (Bernal *et al.*, 2012; Pade *et al.*, 2009), and their characteristics lunate caudal fin and hunting capabilities (Stevens, 1973), could exhibit a vertical trophic niche expansion in northern areas of the SWAO, exploiting more frequently benthic prey in cold-deep waters.

The consumption of hoki *M. magellanicus* and southern blue whiting *M. australis* increased with the body size of the porbeagle shark. Moreover, small porbeagle sharks preyed upon both small and large teleost fish, whereas bigger porbeagle sharks appear to be more selective, predated mainly only on large fish, maximizing energy intake per prey eaten and avoiding lower trophic levels. Similar behaviour was observed in north Atlantic, as juveniles tended to consume a less diverse range of prey species, comprising mostly of small pelagic fish and cephalopods, whereas larger sharks appear to become more piscivorous capable of capturing large teleosts (Joyce *et al.*, 2002). Ontogenetic change in feeding habits is a general pattern observed in marine fishes (Dalponti *et al.*, 2018) and specially in elasmobranchs, because increase in length, swimming speed, size of jaws, teeth, energy requirements and experience with prey result in improving the ability to capture different species (Wetherbee & Cortés, 2004).

Although the diet of elasmobranchs usually varied predictably with predator size (Heithaus, 2004), ontogenetic changes in diet have not been previously reported for the porbeagle shark *L. nasus* in SWAO.

The present paper applied the percentage of the percentage of the frequency of occurrence (%F) that sums 100% among all prey items, instead of the traditional percentage of the frequency of occurrence (%F), which sums more than 100% when two different prey are found in a single stomach. The %F is a robust and interpretable index in diet studies, especially with large sample sizes, and it is known by quantifying the diet with a minor loss of information in comparison to more intensive and meticulous methods, with far less effort and low cost than more detailed methods (Baker *et al.*, 2014). Moreover, the simple presence/absence or frequency of occurrence approach (%F) provided a rapid, unambiguous and reliable account of diet composition, not affected by the condition of prey (Buckland *et al.*, 2017). Nonetheless, as the total sum of the %F gives more than 100%, it does not allow the estimation of other parameters such as the trophic level. The new %F provided a solution to these weaknesses avoiding bias in the estimation of the trophic level of the porbeagle shark, which resulted higher than four indicating that it was a tertiary consumer in the SWAO. As in general fish have trophic levels ranging between 2 and 4.7 (Stergiou & Karpouzi, 2005), the porbeagle shark occupied the upper trophic positions. These results are in accordance with the trophic level estimated by Cortés (1999) for the porbeagle shark and other 148 shark species belonging to 23 families. Cortés (1999) concluded that sharks as a group are tertiary consumers (trophic level >4) that occupy trophic positions similar to those of marine mammals and higher than those of seabirds (Wetherbee & Cortés, 2004). On the contrary, small sharks (*i.e.*, scyliorhinids, squatinids and triakids) exhibited lower trophic levels similar to many skates (Ebert & Bizzarro, 2007). In the study region, the porbeagle shark has a higher trophic position than coastal dolphins, porpoises, seabirds (cormorans, penguins) and oceanic whales, but a lower trophic position than offshore cetaceans such as long-finned pilot whales (Ricciardelli *et al.*, 2020). The effects of predation of *L. nasus* over the main prey (hoki *M. magellanicus* and the southern blue whiting *M. australis*), still unknown, could be low because of their high abundances (Giussi *et al.*, 2016; Wöhler *et al.*, 2004). The abundance of hoki was estimated to be more than 1 million tons, being the most abundant finfish in the SWAO, 45° S (Giussi *et al.*, 2016). On the contrary, the abundance of southern blue whiting *M. australis* is 500,000 tons, but exhibited decreasing trends (Wöhler *et al.*, 2004). Similarly, mako sharks consume 4%–14% of bluefish populations in the north-western Atlantic, but the impact on population size appears not to be significant (Stillwell & Kohler, 1982).

The results of this study provided evidence that porbeagle shark feed on the fish species that constituted the main catches of the austral trawl fisheries in the region, like hoki *M. magellanicus* and the southern blue whiting *M. australis*. As the analysis of the stomach contents provided information on the last meal and not on the assimilated prey, other reliable and more informative methods such as stable isotope and fatty acid analysis are warranted to validate trophic relationships herein elucidated through stomach content analyses and to offer new information on

trophic flows and sources of primary productivity (Buckland *et al.*, 2017). Even if any of these prey had been consumed during capture, the porbeagle shark interacted with fisheries by depredating the catch, and it would have to be considered for the management and assessment of both predator and prey species. The spatial distribution of *L. nasus* is characterized by large aggregations during summer and autumn in the study area (Cortés & Waessle, 2017), in accordance with the by-catch that also showed a strong seasonality, and it was higher in austral trawl fisheries during this period (Cortés *et al.*, 2017; Cortés & Waessle, 2017). The interaction of fisheries with large marine fauna is also well documented worldwide (Afonso *et al.*, 2012; Gilman *et al.*, 2007; Montevecchi, 2001; Szteren & Páez, 2002). In New Zealand tuna longline fishery, the limitation of fishing operations to daylight hours when porbeagles are too deep to be caught seems to be a simple way of porbeagle by-catch mitigation (Francis *et al.*, 2015). Nonetheless, these management decisions are complex and subject to different trade-offs that could include the impact on other vulnerable species such as seabirds (Francis *et al.*, 2015). In SWAO, the close relationship of porbeagle shark with target species of the austral trawl fisheries determines that their interaction is inevitable. The design of selective devices to prevent retention porbeagle shark, without implicating the target species catch, as well as to avoid areas or seasons with high abundance of sharks (MPA) may contribute considerably to mitigate the fishery interaction and the incidental catch of porbeagle shark. As these alternatives appear to be difficult to be implemented, it is necessary at least to develop devices that avoid the entrance of shark into the fish bin with the entire capture (*i.e.*, bars), as well as to apply the best handling practices for the safe release of sharks.

The porbeagle shark is classified as vulnerable globally, critically endangered in the north-east Atlantic and Mediterranean Sea, and endangered in the north-west Atlantic (Dulvy *et al.*, 2014), but it was categorized as data deficient in the SWAO (Cuevas *et al.*, 2020). The available data and the stock assessment in the Southern Hemisphere indicated that there is a very low risk that the stock is subject to over-fishing (Hoyle *et al.*, 2017b). Nonetheless, by nature of their extreme K life-history strategies, and high position in trophic food webs, these large shark species are more vulnerable to intense fishing activity than other species (Stevens *et al.*, 2000). In Argentina, by-catch is mainly related to trawl fleet that operates at 50°S (Cortés & Waessle, 2017), but their commercialization is banned. Moreover, Argentina has adopted management measures to discourage the catch and trade of large sharks, and finning was banned (CFP, 2021). This work contributed to a better understanding of the trophic role of this data-deficient species and has important implications for the porbeagle shark conservation in SWAO.

ACKNOWLEDGEMENTS

We thank the 15 scientific observers on-board the commercial fishing vessels for the data collection: Aguilar, Bargas Peña, Cheverria, Coppa, Di Tullio, Flores, Freyre, Galluzo, Glavina, Irasola, Merlo, Moreno, Repetto, Romanelli and Terren. We are grateful to the librarians from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Silvoni, Lizondo and Navas, for providing the most helpful documentation. We are also grateful to Eduardo Aguilar (observer

from INIDEP) who took photographs of the porbeagle shark that illustrate the paper. Special thanks are given to the two journal referees for their constructive comments that improved the manuscript. This is INIDEP contribution N°2247.

ORCID

Mauro Belleggia  <https://orcid.org/0000-0003-1584-4743>

Jorge Colonello  <https://orcid.org/0000-0003-1159-4089>

Federico Cortés  <https://orcid.org/0000-0001-5142-2965>

Daniel Enrique Figueroa  <https://orcid.org/0000-0003-3258-1092>

REFERENCES

- Afonso, A. S., Santiago, R., Hazin, H., & Hazin, F. H. V. (2012). Shark bycatch and mortality and hook bite-offs in pelagic longlines: Interactions between hook types and leader materials. *Fisheries Research*, 131, 9–14.
- Baker, R., Buckland, A., & Sheaves, M. (2014). Fish gut analysis: Robust measures of diet composition. *Fish & Fisheries*, 15(1), 170–177.
- Balech, E., & Ehrlich, M. D. (2008). Esquema Biogeográfico del Mar Argentino. *Revista del Instituto Nacional de Investigación y Desarrollo Pesquero*, 19, 45–75.
- Bernal, D., Carlson, J. K., Goldman, K. J., & Lowe, C. G. (2012). Energetics, metabolism, and endothermy in sharks and rays. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (Vol. 2, pp. 211–237). Boca Raton, FL: Taylor and Francis Group, LLC.
- Bernal, D., Donley, J. M., Shadwick, R. E., & Syme, D. A. (2005). Mammal-like muscles power swimming in a cold-water shark. *Nature*, 437, 1349–1352.
- Biais, G., Coupeau, Y., Séret, B., Calmettes, B., Lopez, R., Hetherington, S., & Righton, D. (2017). Return migration patterns of porbeagle shark (*Lamna nasus*) in the northeast Atlantic: Implications for stock range and structure. *ICES Journal of Marine Science*, 68, 1354–1365.
- Buckland, A., Baker, R., Loneragan, N., & Sheaves, M. (2017). Standardising fish stomach content analysis: The importance of prey condition. *Fisheries Research*, 196, 126–140.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference*. New York, NY: Springer.
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.
- Brickle, P., Arkhipkin, A. I., Laptikhovskiy, V., Stocks, A., & Taylor, A. (2009). Resource partitioning by two large planktivorous fishes *Micromesistius australis* and *Macruronus magellanicus* in the southwest Atlantic. *Estuarine, Coastal and Shelf Science*, 84, 91–98.
- Cade, B., & Noon, B. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1, 412–420.
- Campana, S. E., & Joyce, W. (2004). Temperature and depth associations of porbeagle shark (*Lamna nasus*) in the northwest Atlantic. *Fisheries Oceanography*, 13, 52–64.
- Campana, S. E., Joyce, W., & Fowler, M. (2010). Subtropical pupping ground for a cold-water shark. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 769–773.
- CFP (2021). Consejo Federal Pesquero. Medidas de Manejo de Condrictios. CFP Resolution N°08/2021. Retrieved from [https://cfp.gob.ar/resoluciones/Resolucion%208%20\(3-06-21\)%20medidas%20de%20manejo%20de%20condrictios.pdf](https://cfp.gob.ar/resoluciones/Resolucion%208%20(3-06-21)%20medidas%20de%20manejo%20de%20condrictios.pdf)
- Cherel, Y., & Duhamel, G. (2004). Antarctic jaws: Cephalopod prey of sharks in Kerguelen waters. *Deep Sea Research Part I*, 51(1), 17–31.
- Ciancio, J., Pascual, M., & Beauchamp, D. (2007). Energy density of Patagonian aquatic organisms and empirical predictions based on water content. *Transactions of the American Fisheries Society*, 136, 1415–1422.
- CITES (2013). Convention on international trade in endangered species of wild fauna and flora. Inclusion of *Lamna nasus* (Bonnaterre, 1788) in Appendix II in accordance with Article II 2(a). CoP16 Prop. 44. Sixteenth meeting of the Conference of the Parties, Bangkok (Thailand), 3–14 March 2013. Retrieved from <https://cites.org/sites/default/files/eng/cop/16/prop/E-CoP16-Prop-44.pdf>
- Compagno, L. J. V. (2008). Pelagic elasmobranch diversity. In T. J. Pitcher, M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean* (pp. 14–23). Oxford, UK: Blackwell Publishing.
- Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, 56, 707–717.
- Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F., Domingo, A., Heupel, M., ... Simpfendorfer, C. (2010). Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquatic Living Resources*, 23, 25–34.
- Cortés, F., Waessle J. A., Massa A. M., & Hoyle, S. D. (2017). Aspects of porbeagle shark bycatch in the Argentinean surimi fleet operating in the southwestern Atlantic Ocean (50–57°S) during 2006–2014. Western and Central Pacific Fisheries Commission. Rarotonga, Cook Islands. 9–17 August 2017. Retrieved from <https://www.wcpfc.int/meetings/sc13>
- Cortés, F., & Waessle, J. A. (2017). Hotspots for porbeagle shark (*Lamna nasus*) bycatch in the southwestern Atlantic (51°S–57°S). *Canadian Journal of Fisheries and Aquatic Sciences*, 74(7), 1100–1110.
- Cuevas, J.M., García, V., Montealegre Quijano, S., Paesch, L., Estalles, M., Falabella, V., Santos, R., Bovcon, N., Chiamonte, G., Coller, M., Figueroa, D., García, M., Acuña, E., Bustamante, C., Pompert, J., & Campagna, C. (2020). Report of the IUCN regional red list workshop for species of the Patagonian Sea: Chondrichthyans. Forum for the conservation of the Patagonian Sea. Retrieved from <http://marpatagonico.org/descargas/Informe-Condrictios.pdf>
- Crawley, M. J. (2005). *Statistics: An introduction using R*. Chichester, UK: Wiley.
- Crooks, N. (2020). Chondrichthyes diet. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1–11). Cham, Switzerland: Springer International Publishing.
- Dalpointi, G., Guariento, R. D., & Caliman, A. (2018). Hunting high or low: Body size drives trophic position among and within marine predators. *Marine Ecology Progress Series*, 597, 39–46.
- Delpiani, S. M., Bruno, D. O., Vazquez, D. M., Llompert, F., Delpiani, G. E., Fernández, D. A., ... Díaz de Astarola, J. M. (2020). Structure and distribution of fish assemblages at Burdwood Bank, the first sub-Antarctic marine protected area “Namuncurá” in Argentina (southwestern Atlantic Ocean). *Polar Biology*, 43, 1783–1793.
- Domingo, A., Forselledo, R., Miller, P., & Passadore, C. (2008). *Plan de acción nacional para la conservación de condrictios en las pesquerías uruguayas. (PAN - Condrictios Uruguay)*. Montevideo, Uruguay: DINARA.
- Duffy, C. A. J. (2015). Family Lamnidae, mackerel sharks. In C. D. Roberts, A. L. Stewart, & C. D. Struthers (Eds.), *The fishes of New Zealand, vol. 2, systematic accounts* (pp. 70–73). Wellington, New Zealand: Te Papa Press.
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., ... White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590.
- Ebert, D. A., & Bizzarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fish*, 80, 221–237.
- Ebert, D. A., & Winton, M. V. (2010). Chondrichthyans of high latitude seas. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *The biology of sharks and their relatives* (Vol. 2, pp. 116–158). Boca Raton, FL: CRC Press.

- Economakis, A. E., & Lobel, P. S. (1998). Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes*, 51, 129–139.
- Eder, E. B., & Lewis, M. N. (2005). Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *Marine Ecology Progress Series*, 291, 43–52.
- Figuerola, D. E. (1997). Un nuevo registro de *Lamna nasus* (Bonaterre, 1788) (Elasmobranchii: Lamnidae), en proximidades de las Islas Georgias del Sur. *Neotropica*, 43, 109–110.
- Forselledo, R. (2012). Distribución, estructura poblacional y aspectos reproductivos del tiburón pinocho *Lamna nasus* (Bonaterre, 1788) en el Atlántico Sudoccidental (Master thesis). Retrieved from <https://www.colibri.udelar.edu.uy/jspui/bitstream/20.500.12008/1411/1/uy24-15679.pdf>
- Francis, M. P., Holdsworth, J. C., & Block, B. A. (2015). Life in the open ocean: Seasonal migration and diel diving behaviour of southern hemisphere porbeagle sharks (*Lamna nasus*). *Marine Biology*, 162, 2305–2323.
- Froese, R., & Pauly, D. (2019). FishBase. World Wide Web electronic publication. Retrieved from www.fishbase.org
- Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P., & Kinan-Kelly, I. (2007). Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. *Biological Conservation*, 139, 19–28.
- Giussi, A. R., Zattereri, A., Di Marco, E., Gorini, F., Bernardele, J., & Marí, N. (2016). Biology and fishery of long tail hake (*Macrurus magellanicus*) in the southwest Atlantic Ocean. *Marine and Fishery Sciences*, 28, 55–82.
- Goldman, K. J., Anderson, S. D., Latour, R. J., & Musick, J. A. (2004). Homeothermy in adult salmon sharks, *Lamna ditropis*. *Environmental Biology of Fishes*, 71, 403–411.
- Guerrero, R. A., Baldoni, A., & Benavides, H. (1999). Oceanographic conditions at the southern end of the argentine continental slope. *INIDEP Scientific Documents*, 5, 7–22.
- Heithaus, M. R. (2004). Predator-prey interactions. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *The biology of sharks and their relatives* (pp. 487–521). Boca Raton, FL: CRC Press.
- Horn, P. L., Ballara, S. L., Sutton, P. J. H., & Griggs, L. H. (2013). Evaluation of the diets of highly migratory species in New Zealand waters. *New Zealand Aquatic Environment and Biodiversity Report*, 116, 1–141.
- Hoyle, S. D., Edwards, C. T. T., Roux, M. J., Clarke, S. C., & Francis, M. P. (2017b). Southern hemisphere porbeagle shark (*Lamna nasus*) stock status assessment. WCPFC-SC13-2017/SA-WP-12. Western and Central Pacific Fisheries Commission. Rarotonga, Cook Islands. 9–17 August 2017. Retrieved from <https://www.wcpfc.int/meetings/sc13>
- Hoyle, S. D., Quiroz, J. C., Zarate, P., Devia, D., & Azocar, J. (2017a). Population indicators for porbeagle sharks in the Chilean swordfish fishery. Western and Central Pacific Fisheries Commission. Rarotonga, Cook Islands. 9–17 August 2017. Retrieved from <https://www.wcpfc.int/meetings/sc13>
- Hulbert, L. B., Aires-da-Silva, A. M., Gallucci, V. F., & Rice, J. S. (2005). Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. *Journal of Fish Biology*, 67, 490–509.
- ICCAT (2020). Report of the 2020 porbeagle shark stock assessment meeting. Retrieved from https://www.iccat.int/Documents/Meetings/Docs/2020/REPORTS/2020_POR_SA_ENG.pdf
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19, 101–108.
- Joyce, W., Campana, S. E., Natanson, L. J., Kohler, N. E., Pratt, H. L., & Jensen, C. F. (2002). Analysis of stomach contents of the porbeagle shark (*Lamna nasus*) in the northwest Atlantic. *ICES Journal of Marine Science*, 59, 1263–1269.
- Koenker, R. (2020). Package ‘quantreg’, quantile regression, R package version 5.73. Retrieved from <https://cran.r-project.org/web/packages/quantreg/quantreg.pdf>
- Leigh, S. C., Papastamatiou, Y., & German, D. P. (2017). The nutritional physiology of sharks. *Reviews in Fish Biology and Fisheries*, 27, 561–585.
- Lowe, C. G., & Goldman, K. J. (2001). Thermal and bioenergetics of elasmobranchs: Bridging the gap. *Environmental Biology of Fishes*, 60, 251–266.
- Lucifora, L. O., & Menni, R. C. (1998). First record of a porbeagle shark, *Lamna nasus*, in brackish waters of Mar Chiquita lagoon, Argentina. *Cybius*, 22, 87–88.
- Lucifora, L. O., Garcia, V. B., & Escalante, A. H. (2009). How can the feeding habits of the sand tiger shark influence the success of conservation programs? *Animal Conservation*, 12, 291–301.
- Mabragaña, E., Lucifora, L. O., & Díaz de Astarloa, J. M. (2015). A record of the Porbeagle, *Lamna nasus*, in coastal waters of Buenos Aires (Argentina) confirmed by DNA barcoding. *DNA Barcodes*, 3, 139–143.
- Mas, F. (2012). Biodiversidad, abundancia relativa y estructura poblacional de los tiburones capturados por la flota de palangre pelágico en aguas uruguayas durante 1998-2009 (Master thesis). Retrieved from <https://www.colibri.udelar.edu.uy/jspui/bitstream/20.500.12008/1411/1/uy24-15679.pdf>
- Matheson, C. (1928). Porbeagle shark in the river tow. *Nature*, 3077, 608–609.
- Menni, R. C., Jaureguizar, A. J., Stehmann, M. F. W., & Lucifora, L. O. (2010). Marine biodiversity at the community level: Zoogeography of sharks, skates, rays and chimaeras in the southwestern Atlantic. *Biodiversity and Conservation*, 19, 775–796.
- Mitchell, J. D., McLean, D. L., Collin, S. P., & Langlois, T. J. (2018). Shark depredation in commercial and recreational fisheries. *Reviews in Fish Biology and Fisheries*, 28, 715–748.
- Montevecchi, W. A. (2001). Interactions between fisheries and seabirds. In E. A. Schreiber & J. Bugar (Eds.), *Biology of marine birds* (pp. 527–557). Boca Raton, FL: CRC Marine Biology Series.
- Moura, T., Figueiredo, I., Farias, I., Serra-Pereira, B., Neves, A., Gordo, L., & Borges, M. F. (2008). Ontogenetic dietary shift and feeding strategy of *Raja undulata* Lacepede, 1802 (Chondrichthyes: Rajidae) in the Portuguese continental shelf. *Scientia Marina*, 72, 311–318.
- Nagasawa, K. (1998). Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin*, 1, 419–433.
- Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the world* (5th ed.). Hoboken, NJ: John Wiley & Sons.
- Pade, N. G., Queiroz, N., Humphries, N. E., Witt, M. J., Jones, C. S., Noble, L. R., & Sims, D. W. (2009). First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wide-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology*, 370, 64–74.
- Perillo, G., Piccolo, M., & Marcovecchio, J. (2006). Coastal oceanography of the western south Atlantic continental shelf (33°S to 55°S). In A. A. Robinson & K. Brink (Eds.), *The sea. The global Coastal Ocean. Regional studies and syntheses* (pp. 295–327). Cambridge, MA: Harvard University Press.
- Piola, A. R., & Gordon, A. L. (1989). Intermediate waters in the southwest south Atlantic. *Deep-Sea Research*, 36(1), 1–16.
- Riccialdelli, L., Becker, Y. A., Fioramonti, N. E., Torres, M., Bruno, D. O., Raya Rey, A., & Fernández, D. A. (2020). Trophic structure of southern marine ecosystems: A comparative isotopic analysis from the Beagle channel to the oceanic Burdwood Bank area under a wasp-waist assumption. *Marine Ecology Progress Series*, 655, 1–27.
- Rodhouse, P. G. K. (2013). Role of squid in the southern Ocean pelagic ecosystem and the possible consequences of climate change. *Deep Sea Research Part II: Topical Studies in Oceanography*, 95, 129–138.
- Sabadin, D. E., Lucifora, L. O., Barbini, S. A., Figuerola, D. E., & Kittlein, M. (2020). Towards regionalization of the chondrichthyan fauna of the Southwest Atlantic: A spatial framework for conservation planning. *ICES Journal of Marine Science*, 77(5), 1893–1905.

- Schejter, L., & Bremec, C. S. (2019). Stony corals (Anthozoa: Scleractinia) of Burdwood Bank and neighbouring areas, SW Atlantic Ocean. *Scientia Marina*, 83(3), 247–260.
- Schejter, L., Rimondino, C., Chiesa, I., Diaz de Astarloa, J. M., Doti, B., Elias, R., ... Bremec, C. (2016). Namuncurá marine protected area: An oceanic hot spot of benthic biodiversity at Burdwood Bank, Argentina. *Polar Biology*, 39, 2373–2386.
- Shiffman, D. S., Frazier, B., Kucklick, J., Abel, D., Brandes, J., & Sancho, G. (2014). Feeding ecology of the sandbar shark in south Carolina estuaries revealed through $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis. *Marine and Coastal Fisheries*, 6, 156–169.
- Skomal, G., Marshall, H., Galuardi, B., Natanson, L., Braun, C. D., & Bernal, D. (2021). Horizontal and vertical movement patterns and habitat use of juvenile porbeagles (*Lamna nasus*) in the Western North Atlantic. *Frontiers in Marine Science*, 8, 624158.
- Soto, J. M. R., & Montealegre-Quijano, S. (2012). Elevación de Río Grande, una importante área de cría del tiburón sardinero *Lamna nasus* en el Atlántico Sur. II Simposio Iberoamericano de ecología reproductiva, reclutamiento y pesquerías. 19–22 November 2012. Mar del Plata, Argentina. Retrieved from <http://info.inidep.edu.ar/wp-content/uploads/2014/12/libro-resumenes.pdf>
- Stergiou, K. I., & Karpouzi, V. K. (2005). The trophic position of fishes in the Hellenic marine ecosystems. In E. Papathanassiou & A. Zenetos (Eds.), *State of the Hellenic marine environment* (pp. 280–284). Athens, Greece: Hellenic Centre for Marine Research.
- Stevens, J. D. (1973). Stomach contents of the blue shark (*Prionace glauca* L.) off south-west England. *Journal of the Marine Biological Association of the United Kingdom*, 53, 357–361.
- Stevens, J. D. (2010). Epipelagic oceanic elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *The biology of sharks and their relatives* (Vol. 2, pp. 3–35). Boca Raton, FL: CRC Press.
- Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyan), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57, 476–494.
- Stillwell, C. E., & Kohler, N. E. (1982). Food, feeding habits, and estimates of daily ration of the shortfin Mako (*Isurus oxyrinchus*) in the North-west Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 407–414.
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21.
- Szteren, D., & Páez, E. (2002). Predation by southern sea lions (*Otaria flavescens*) on artisanal fishing catches in Uruguay. *Marine and Freshwater Research*, 53, 1161–1167.
- Torres-Florez, J. P., & Reyes, P. R. (2007). Tiburones Y Rayas Abisales Del Extremo Austral De Chile (Patagonia). XII Congreso Latino-Americano de Ciencias do Mar – XII COLACMAR, Florianópolis, 15–19 April 2007.
- Trocconi, G. H., Aguilar, E., Martinez, P., & Belleggia, M. (2020). The diet of the Patagonian toothfish *Dissostichus eleginoides*, a deep-sea top-predator off Southwest Atlantic Ocean. *Polar Biology*, 43(10), 1595–1604.
- van Helvoort, G. (1986). Observer program operations manual FAO. Technical paper 275, 1: 207. Retrieved from <http://www.fao.org/3/S8480E/s8480e00.HTM>
- Van Mieghem, J., & Van Oye, P. (1965). *Biogeography and ecology in Antarctica*. The Hague, The Netherlands: Dr. W. Junk Publishers.
- Waessle, J. A., & Cortés, F. (2011). Captura incidental, distribución y estructura de tallas de *Lamna nasus* en aguas Argentinas (período 2006–2010). *Informe Investigación INIDEP*, 84, 1–11.
- Weigmann, S. (2016). Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *Journal of Fish Biology*, 88, 837–1037.
- Wetherbee, B. M., & Cortés, E. (2004). Food consumption and feeding habits. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *The biology of sharks and their relatives* (pp. 223–244). Boca Raton, FL: CRC Press.
- Williams, R., Okey, T. A., Wallace, S. S., & Gallucci, V. F. (2010). Shark aggregation in coastal waters of British Columbia. *Marine Ecology Progress Series*, 414, 249–256.
- Wöhler, O. C., Cassia, M. C., & Hansen, J. E. (2004). Caracterización biológica y evaluación del estado de explotación de la polaca (*Micromesistius australis*). In R. Sánchez & S. Bezzi (Eds.), *El Mar Argentino y sus recursos pesqueros. Tomo IV. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado del estado de explotación* (pp. 283–305). Mar del Plata, Argentina: INIDEP.
- Yatsu, A. (1995). The role of slender tuna, *Allothunnus fallai*, in the pelagic ecosystems of the South Pacific Ocean. *Japanese Journal of Ichthyology*, 41, 367–377.

How to cite this article: Belleggia, M., Colonello, J., Cortés, F., & Figueroa, D. E. (2021). Eating catch of the day: the diet of porbeagle shark *Lamna nasus* (Bonnaterre 1788) based on stomach content analysis, and the interaction with trawl fisheries in the south-western Atlantic (52° S–56° S). *Journal of Fish Biology*, 1–11. <https://doi.org/10.1111/jfb.14864>