Journal of the Marine Biological Association of the United Kingdom

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Feeding habits of the franciscana dolphin (*Pontoporia blainvillei*) in south-eastern Brazil

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Original Article

Cite this article: Campos LB, Lopes XM, da Silva E, Santos MCO (2020). Feeding habits of the franciscana dolphin (*Pontoporia blainvillei*) in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* **100**, 301–313. https://doi.org/10.1017/S0025315420000120

Received: 31 August 2019
Revised: 14 January 2020
Accepted: 17 January 2020
First published online: 27 February 2020

Key words:
Feeding habit; *Pontoporia blainvillei*; South-western Atlantic; stomach content analysis

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Abstract

This study evaluated the feeding habits of the franciscana dolphin (*Pontoporia blainvillei*) in south-eastern Brazil. Stomach contents were collected from a total of 145 dead specimens found incidentally caught by fishing vessels or stranded between 2005 and 2015. Fish otoliths, cephalopod beaks and whole non-digested prey were used for prey species identification. A total of 9337 prey items were identified, including 26 species of teleost fishes and three species of cephalopods. The most important prey families were Sciaenidae among fish and Loliginidae among cephalopods. Franciscana dolphins tended to feed on small fish (mean = 5.25 cm) and cephalopods (mean = 8.57 cm). The index of relative importance (IRI) showed that *Pellona harroweri* and *Doryteuthis plei* were the most important prey for both males and females. The PERMANOVA test confirmed that there is no significant difference between the feeding habits of different sexes, but detected a significant difference among seasons. Overall, our results show that franciscana dolphins are predominantly ichthyophagous and non-selective in relation to the type of prey, feeding on pelagic, demersal and pelagic-demersal prey.

Introduction

Cetaceans play several important ecological roles in aquatic ecosystems, such as predation in trophic webs, resuspension of sediment and conveying nutrients both vertically and horizontally (Katona & Whitehead, 1988; Roman *et al.*, 2014). Understanding how cetaceans interact with the biotic and abiotic environment can lead to increasingly refined knowledge of these ecological roles. One of the tools to achieve this goal is to investigate their feeding habits.

There are several ways of studying cetacean feeding habits. It is possible to study them from *in situ* observations of feeding activities, using modern cameras attached to individuals (e.g. Calambokidis *et al.*, 2007) or acoustic recording tags in free-ranging individuals (e.g. Parks *et al.*, 2014). Alternatively, multiple laboratory methodologies could be applied, using samples from dead and live individuals for analyses of stable isotopes (e.g. Herman *et al.*, 2005; Newsome *et al.*, 2010), fatty acids (e.g. Herman *et al.*, 2005; Budge *et al.*, 2008), molecular identification of prey (e.g. Marshall *et al.*, 2010), and prey remains present in stomach contents (Barros & Clarke, 2009). The latter is a more traditional method, yet still considered cheaper and more accessible in comparison to the former quoted methods.

The franciscana dolphin, *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844), also known as toninha (Committee on Taxonomy, 2018), is a small cetacean and sole member of the Pontoporiidae family (Rodriguez *et al.*, 2002). It is endemic to the coastal shallow waters of the South-western Atlantic ocean, occurring from the northern coast of the state of Espírito Santo (18°25′S 30°42′W), south-east of Brazil (Siciliano, 1994), to the northern Gulf of San Matias (42°35′S 64°48′W), central Argentina (Crespo *et al.*, 1998). It is usually found in turbid waters within the 30 m isobath of the continental shelf (Pinedo *et al.*, 1989; Bordino *et al.*, 2002), generally near rivers and estuary mouths (Siciliano *et al.*, 2002). Two previously described populations dwell in estuarine habitats in the Babitonga (26°S) (Cremer *et al.*, 2012) and Laranjeiras (24°S) (Santos *et al.*, 2009) basins in Brazil. Interactions with fishery gillnets have been reported in several areas (see Ott *et al.*, 2002; Rosas *et al.*, 2002; Netto & Di Beneditto, 2008), representing one of the main threats that lead to the classification as a species 'vulnerable to extinction' by the International Union for the Conservation of Nature Red List of Endangered Species (Zerbini *et al.*, 2017). The incidental capture of ∼2900 franciscanas per year in the early 2000s was estimated over its entire distribution area (Secchi *et al.*, 2003). In the Cananéia region, south-eastern Brazil, a previous study estimated that the potential annual mortality of franciscana may be ∼330 specimens (Rosas *et al.*, 2002). Due to the alarming numbers of incidental catches in fishing operations and an imbalance in the degree of knowledge of the species throughout its distribution, Secchi *et al.* (2003) separated their range into four 'Franciscana Management Areas (FMAs)', defined as: FMA I: from Espírito Santo to Rio de Janeiro, Brazil; FMA II: from São Paulo to Santa Catarina, Brazil;

FMA III: from Rio Grande do Sul, Brazil, to Uruguay; and FMA IV: northern Argentina. After evaluating the main gaps in species knowledge by area based on Secchi *et al.* (2003) and the national franciscana dolphin action plan in Brazilian waters (Di Beneditto *et al.*, 2010), investigating the feeding habits of this species in the FMA II was listed as one of the priorities for further investigation.

For *P. blainvillei* in general, piscivorous and teuthophagous feeding habits have been described in the past few decades (e.g. Fitch & Brownell, 1971; Di Beneditto & Ramos, 2001; Rodriguez *et al.*, 2002; Bittar & Di Beneditto, 2009; Cremer *et al.*, 2012; Paso-Viola *et al.*, 2014). Most of the prey consumed by franciscanas throughout most of its distribution are of low commercial value or are usually considered as bycatch for the fishery market (Di Beneditto & Ramos, 2001; Bittar & Di beneditto, 2009). On the other hand, in specific sectors of its distribution, the main prey of franciscana dolphins were listed as the main targets of fishing operations (Rodríguez *et al.*, 2002; Paso-Viola *et al.*, 2014).

Over almost five decades, only 12 studies were published on feeding habits of franciscana dolphins. So far, 707 stomach contents were evaluated throughout the distribution range of the species. The samples were not evenly distributed among all FMAs. Within FMA II specifically, there are only two available studies based on the analyses of stomach contents of 66 individuals (Cremer *et al.*, 2012, N = 8; and Henning *et al.*, 2018, N = 58). Furthermore, at least 10 other unpublished studies were conducted for academic degree purposes, evaluating ∼600 additional samples.

Based on the described scenario, the objective of the present study was to more comprehensively evaluate the feeding habits of franciscana dolphins in FMA II using individuals found dead between 2005 and 2015, comparing present results to previous published studies conducted in all FMAs.

Materials and methods

Study area

The study area encompassed a large part of the southern Marine Protected Area of São Paulo state (São Paulo State Decree No. 53.526, 2008), Brazil (between 24°20′S and 25°30′S; e.g. Figure 1). The main economic activity in this region is commercial fisheries that involve more than 3000 fishermen (Mendonça *et al.*, 2003). The main exploited fish species in 2018 were *Macrodon atricauda*, *Micropogoninas furnieri*, *Mugil liza*, *Larimus breviceps*, in addition to the shrimp *Xiphopenaeus kroyeri*. These resources were mainly caught with bottom-set gillnets and double-trawl. Cananéia is the second county that most contributed to fish catches in the state of São Paulo (Ávila-da-Silva *et al.*, 2019). Due to the presence of a large number of vessels, cetacean bycatch has been occurring frequently in the area (Rosas *et al.*, 2002).

Sampling

Samples came from cetaceans incidentally caught by fishing gillnets or found stranded along ∼115 km of coastline. Beach surveys for dead cetaceans were conducted opportunistically from 2005 to 2016, providing a total of six freshly dead franciscana dolphins for this study. Fishing operations based out of Cananéia port were monitored from 2004 to 2007, and from 2011 to 2016, supplying 139 additional specimens for this investigation. From the 145 sampled stomachs, 86 belonged to males and 59 to females; 33 were sampled in summer, 36 in autumn, 51 in winter, 20 in spring. Five individuals had no precise sampling date/season. No stomach contents were added from previous studies and thus, the data presented here are derived from stomach contents analysed solely from this study.

Stomach contents were screened using a fine mesh sieve (200 μm). The whole and degraded items were stored in alcohol (70%). The otoliths were dry preserved. Cephalopod beaks were stored in a 1:1 solution of alcohol (70%) and glycerin.

Identification of food items

The *sagitta* otoliths and cephalopod beaks were identified to the lowest possible taxonomic level using a stereomicroscope, a reference otolith collection of fish collected in the study area, and published catalogues (Corrêa & Vianna, 1992/93; Lemos *et al.*, 1992/93, 1995*a*, 1995*b*; Vaske-Junior, 2006; Rossi-Wongtschowski *et al.*, 2014; Siliprandi *et al.*, 2016; Santificetur *et al.*, 2017). Otoliths and beaks were then classified into two categories each: right or left otoliths and lower or upper beaks. The higher value between these two categories was used to determine the total number of individuals of each prey species per stomach to avoid counting the same organism twice.

Estimating prey size and weight

The micrometre scale on a stereomicroscope was used for measurements with precision of up to 0.1 mm for all non-digested otoliths and beaks. The total length of each otolith was considered to be the longest longitudinal distance from the anterior tip to the most posterior projection (Kimura *et al.*, 1979). The upper and lower rostral length was used for cephalopods, according to Clarke (1986). Regression equations from previous studies (Supplementary Table S1) were used to determine the biomass and total length or mantle length of each identified prey. When otoliths and beaks were broken or eroded, the mean of the calculated weights and lengths for the specific prey species in all analysed stomachs was used as quoted by Marçalo *et al.* (2018).

Index of relative importance

The numerical frequency (%N), the biomass (%W), the frequency of occurrence percentage (%O) and the index of relative importance (IRI) were calculated according to Pinkas *et al.* (1971). Fish and cephalopods were analysed separately, as cephalopod beaks remain longer than fish otoliths within the cetacean stomach due to their different digestion times (Clarke, 1986). The IRI were calculated separately for each gender and season. Three species ingested by the analysed dolphins had no regression equations, so an adaptation proposed by Cremer *et al.* (2012) was used considering IRI = %N × %O. Diagrams similar to those presented by Pinkas *et al.* (1971) were produced using R-3.4.4 software (R Core Team, 2018) to help visualization. In the IRI Diagrams the relative importance of each prey species in the diet is depicted by a rectangle with horizontal axes representing the numerical frequency (%N) and biomass percentage (%W), and with the vertical axis representing frequency of occurrence percentage values (%O).

Amundsen diagram

Feeding strategy and the size of the feeding niche were evaluated using the Costello graphical method (Costello, 1990) modified by Amundsen *et al.* (1996). This graphical representation is constructed from the relation between the frequency of occurrence (O) and the specific abundance (%P; equation (1) below) of a taxonomic group of prey. The specific abundance is defined as the percentage of a taxonomic group of prey taking into account

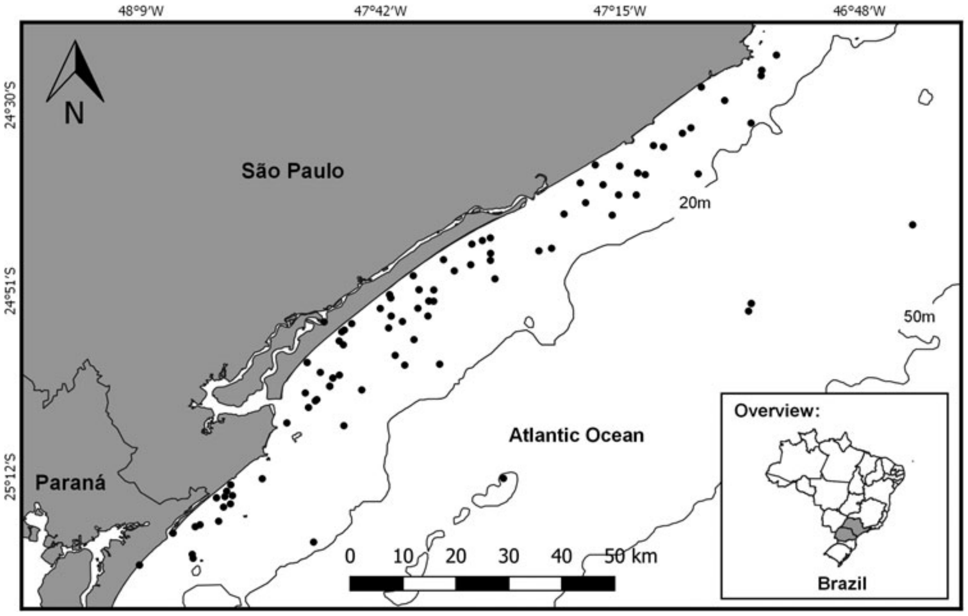

Fig. 1. Map of the study area showing the southern coastal region of São Paulo state and the northern coast of Paraná state, south-eastern Brazil. Beach surveys were conducted along a 115 km stretch of coastline and dots indicate the exact locations where incidentally captured dolphins were collected.

only the stomachs in which this taxon occurred.

$$\%P_i = \left(\frac{\sum_i S_i}{\sum_{ti} S_{ti}}\right) \times 100 \qquad (1)$$

where S_i is the contribution (by biomass in this study) of prey i to the stomach contents and S_{ti} is the total biomass of stomach contents in which prey i occurred.

Ecological indices

The feeding habits of the analysed franciscana dolphins were evaluated for each gender and season using the Simpson diversity index, which gives more importance to the most common species rather than to the rare ones, and is less sensitive to their richness (Magurran, 1988). To investigate the existence of possible overlap between feeding habits of males and females, Jaccard (qualitative) and Bray–Curtis (quantitative) ecological indices of similarity were employed.

Statistical analysis

Total weight and length of identified prey ingested by males and females were compared using the Wilcoxon–Mann–Whitney test (referred to as MW from here on). The difference in prey numerical abundance in stomach contents between different sexes and seasons were assessed employing a PERMANOVA (permutation multivariate analysis of variance) test. It was performed considering 9999 permutations using the Bray–Curtis distance. For any PERMANOVA significant P-values, a pairwise comparison was made between all pairs of groups to detect the origin of the difference. These non-parametric tests were used due to non-normality of the data. All statistical analyses were conducted using R-3.4.4 software (R Core Team, 2018), considering a significance level of 0.05.

Comparison to previous studies

In the current study, the authors opted to consider only the data from peer reviewed studies published in scientific journals (Supplementary Table S2). Unpublished studies comprise mostly theses required for Masters and PhD degrees and they are not easily accessible by the scientific community, written in Portuguese or Spanish, and lacking a robust scientific review before becoming available.

Results

Composition of food items

A total of 11,188 otoliths and 2343 cephalopod beaks were found in the 145 surveyed stomachs. Otoliths were present in 143 stomachs (99%) and cephalopod beaks in 111 (77%). A total of 109 stomach contents (75%) had both fish and cephalopods. None of the 145 stomachs analysed was empty. Due to the high degree of digestion, it was not possible to identify 347 otoliths. The prey total estimates comprised 7406 fishes and 1931 cephalopods in the analysed stomachs. Franciscana dolphins preyed on at least 26 different species of bony fish (Table 1), belonging to seven distinct families: Engraulidae, Sciaenidae, Pristigasteridae, Trichiuridae, Clupeidae, Paralichthyidae and Phycidae, the first two being the most represented. At least three distinct species of cephalopods were consumed (Table 1), all belonging to the family Loliginidae.

The studied females preyed on at least 19 taxonomic groups of bony fish from five distinct families (Engraulidae, Sciaenidae, Pristigasteridae, Trichiuridae and Clupeidae), while males preyed on 24 groups from six different families (Engraulidae, Sciaenidae, Trichiuridae, Pristigasteridae, Paralichthyidae and Phycidae). Seven taxonomic groups were ingested only by males and two only by females. Both sexes preyed on the same three species of cephalopods.

Franciscana dolphins preyed on a larger number of fish taxonomic groups in winter (21, from six families), followed by summer (19, from four families), autumn (14, from five families) and spring (13, from four families). The same three species of cephalopods were ingested all year round.

Estimates of prey size and weight

The reconstructed fish size ranged between 0.85 cm (*L. breviceps*) and 52.49 cm (*T. lepturus*), with a mean size of 5.25 cm. The

Table 1. List of prey species identified after evaluating the stomach contents of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil between 2005 and 2015

Prey items	%N	%O	%W	IRI	%IRI	Ranking
TELEOSTS						
Sciaenidae						
Ctenosciaena gracilicirrhus	1.69	6.90	0.77	16.95	0.15	10
Cynoscion guatucupa	1.23	13.79	0.51	23.95	0.21	9
Cynoscion jamaicensis	0.51	6.21	0.57	6.75	0.06	14
Cynoscion striatus	0.01	0.69	0.01	0.01	0.00	25
Isopisthus parvipinnis	15.87	62.07	27.70	2704.72	24.13	2
Larimus breviceps	5.70	31.72	4.72	330.50	2.95	5
Menticirrhus sp.	0.69	11.03	0.42	12.13	0.11	13
Micropogonias furnieri	1.53	7.59	0.30	13.83	0.12	12
Paralonchurus brasiliensis	2.90	24.14	5.28	197.52	1.76	6
Pogonias cromis	0.03	0.69	0.01	0.03	0.00	22
Stellifer sp.	19.83	58.62	26.16	2695.75	24.05	3
Umbrina sp.	6.05	15.86	1.23	115.51	1.03	7
Engraulidae						
Anchoa filifera	0.01	0.69	0.02	0.03	0.00	24
Anchoa lyolepis[a]	0.09	2.76		0.24	0.00	16
Anchoa sp.	8.17	28.97	5.97	409.58	3.66	4
Anchoa tricolor	0.01	0.69	0.02	0.03	0.00	23
Anchoviella lepidentostole	0.07	1.38	0.06	0.17	0.00	17
Cetengraulis edentulus[a]	0.04	1.38		0.06	0.00	20
Engraulis anchoita	0.16	4.83	0.20	1.73	0.02	15
Pristigasteridae						
Chirocentrodon bleekerianus	2.53	9.66	2.76	51.01	0.46	8
Pellona harroweri	32.23	85.52	21.69	4611.42	41.15	1
Clupeidae						
Opisthonema oglinum[a]	0.01	0.69		0.01	0.00	26
Sardinella brasiliensis	0.03	0.69	0.14	0.12	0.00	18
Trichiuridae						
Trichiurus lepturus	0.46	8.28	1.39	15.26	0.14	11
Phycidae						
Urophycis sp.	0.14	0.69	0.03	0.12	0.00	19
Paralichthyidae						
Syacium sp.	0.01	0.69	0.04	0.04	0.00	21
CEPHALOPODS						
Loliginidae						
Doryteuthis plei	59.44	62.76	88.03	9254.94	77.85	1
Doryteuthis sanpaulensis	1.82	11.03	1.91	41.17	0.35	3
Lolliguncula brevis	38.75	53.10	10.06	2591.53	21.80	2

Numerical frequency (%N), frequency of occurrence percentage (%O), biomass (%W), the Index of Relative Importance (IRI), the IRI percentage and ranking are presented. Males and females were pooled together

[a] An adaptation of the IRI was used because of the absence of regression equations.

reconstructed fish weight ranged from 0.03 g (*I. parvipinnis*) to 118.87 g (*C. guatucupa*), with a mean of 4.42 g (Table 2). The reconstructed size of cephalopods ranged between 1.57 cm (*L. brevis*) and 30.88 cm (*D. plei*), with a mean of 8.57 cm. The reconstructed weight of cephalopods ranged from 0.31 g (*L. brevis*) to 255.72 g (*D. plei*), with a mean of 22.64 g (Table 2).

Among the 15 fish species consumed by both sexes (Table 3), 10 presented significant different sizes and weights when comparing males and females (*Anchoa* sp. – MW = 12,613.5 and $P = 2.8 \times 10^{-3}$; *C. bleekerianus* – MW = 3659.5 and $P = 2.4 \times 10^{-3}$; *C. gracilicirrhus* – MW = 307.5 and $P = 6.5 \times 10^{-6}$; *I. parvipinnis* – MW = 37,837.5 and $P = 1 \times 10^{-4}$; *L. breviceps* – MW = 5156.5

Table 2. List of identified prey items after evaluating the stomach contents of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil between 2005 and 2015

		Weight (g)		Length (cm)	
Prey items	N	Mean ± SD	Min–Max	Mean ± SD	Min–Max
TELEOSTS					
A. filifera	1	5.77	–	7.73	–
Anchoa sp.	410	3.02 ± 1.24	0.8–7.12	6.16 ± 0.79	4.23–8.25
A. tricolor	1	5.8	–	7.71	–
A. lepidentostole	5	2.78 ± 1.54	1.41–4.62	5.84 ± 1.12	4.78–7.14
C. bleekerianus	151	4.32 ± 1.83	0.73–13.19	7.32 ± 1.11	4.02–11.17
C. gracilicirrhus	89	1.98 ± 1.35	0.57–10.55	3.9 ± 0.84	2.44–7.4
C. guatucupa	56	1.3 ± 2.59	0.03–14.19	4.64 ± 1.75	1.55–11.63
C. jamaicensis	28	4.25 ± 5.26	1.11–29	5.73 ± 1.68	3.85–11.76
C. striatus	1	1.8	–	6.06	–
E. anchoita	4	9.73 ± 4.69	5.85–16.55	11.64 ± 1.68	10.06–14.02
I. parvipinnis	645	9.65 ± 16.69	0.03–118.87	6.44 ± 3.86	0.93–19.3
L. breviceps	291	3.49 ± 4.63	0.14–30.02	3.85 ± 1.89	0.85–10.48
Menticirrhus sp.	41	2.34 ± 2.92	0.11–11.38	6.16 ± 2.29	2.81–11.32
M. furnieri	89	0.79 ± 0.45	0.17–2.2	2.43 ± 0.79	0.85–4.3
P. brasiliensis	162	7.78 ± 14.78	0.12–91.62	5.89 ± 3.32	1.33–16.65
P. harroweri	1694	2.99 ± 4.79	0.05–40.04	4.55 ± 2.2	0.94–12.87
P. cromis	2	1.62 ± 0.06	1.58–1.66	4.4 ± 0.02	4.38–4.41
S. brasiliensis	2	17.96 ± 0	17.96	9.7 ± 0	9.7
Stellifer sp.	1039	5.6 ± 7.08	0.11–82.93	5.4 ± 2.13	1.78–14.79
Syacium sp.	1	9.36	–	8.03	–
T. lepturus	29	12.15 ± 14.64	0.49–55.14	28.31 ± 11.58	8.66–52.49
Umbrina sp.	356	0.82 ± 1.19	0.04–12.9	3.82 ± 1.03	1.59–10.03
Urophycis sp.	10	0.89 ± 0.25	0.66–1.49	5.96 ± 0.46	5.5–6.99
Total	5107	4.42 ± 8.35	0.03–118.87	5.25 ± 3.17	0.85–52.49
CEPHALOPODS					
D. plei	1146	33.49 ± 26.16	1.8–255.72	11.48 ± 4.08	3.29–30.88
D. sanpaulensis	35	23.86 ± 19.52	4.11–86.1	7.98 ± 2.73	4.03–15.26
L. brevis	745	5.89 ± 5.55	0.31–70.47	4.13 ± 1.34	1.57–11.5
Total	1926	22.64 ± 24.59	0.31–255.72	8.57 ± 4.84	1.57–30.88

Number of prey measured (N), Mean value and Standard Deviation (SD), minimum and maximum values (Min-Max) of estimated total weight and length for each species are presented.

and $P = 2.1 \times 10^{-9}$; *Menticirrhus* sp. – MW = 38.0 and $P = 1.9 \times 10^{-3}$; *M. furnieri* – MW = 505.0 and $P = 4.8 \times 10^{-4}$; *P. brasiliensis* – MW = 1495.5 and $P = 4.2 \times 10^{-8}$; *P. harroweri* – MW = 238,240.5 and $P = 3.1 \times 10^{-26}$; *Umbrina* sp. – MW = 13,027.5 and $P = 3.3 \times 10^{-2}$). In all cases except for *C. bleekerianus*, females consumed larger prey than males. The slender inshore squid (*D. plei*) was the only cephalopod species that had a significant difference in the size and weight of individuals consumed by both sexes; males captured larger individuals than females (MW = 208,267, $P = 3.8 \times 10^{-16}$).

Index of relative importance

Pooling males and females, the highest values of %N and %O for fish were observed for the American coastal pellona (*P. harroweri*). Based on the IRI, the most important items were *P. harroweri*, *I. parvipinnis* and *Stellifer* sp. Together, these three items corresponded to ~90% of the IRI (Table 1), explained by their high value of %O (e.g. Figure 2). The most important cephalopod species found in all analysed stomachs was *D. plei* (77% of IRI). For this prey item, %N, %W and %O were above 50% (e.g. Figure 2), which explains the high IRI observed (e.g. Table 1). The six prey species with greatest importance in feeding habits were the same for both males and females, but the order of importance for both was different (e.g. Table 4).

Although the most representative species among prey organisms are the same in different seasons, differences in the order of importance of fish species were observed (e.g. Table 5 and Figure 3). The order of importance of the ingested cephalopods remained the same throughout all seasons; *D. plei* was the most important item throughout the year. However, in winter and spring the importance of *L. brevis* and *D. sanpaulensis* was slightly higher than in the other seasons (e.g. Table 5 and Figure 3).

Table 3. List of prey shared by males and females of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil between 2005 and 2015

	Male			Female		
Prey items	N	Weight (g)	Length (cm)	N	Weight (g)	Length (cm)
TELEOSTS						
Anchoa sp.	308	2.9 ± 1.1	6.1 ± 0.7	102	3.5 ± 1.6	6.4 ± 0.9
A. lepidentostole	3	1.7 ± 0.3	5 ± 0.3	2	4.4 ± 0.2	7 ± 0.1
C. bleekerianus	74	4.7 ± 1.6	7.6 ± 0.9	77	4 ± 2	7.1 ± 1.2
C. gracilicirrhus	25	1.3 ± 0.7	3.3 ± 0.7	64	2.3 ± 1.4	4.1 ± 0.8
C. guatucupa	39	1.3 ± 2.2	4.8 ± 1.5	17	1.4 ± 3.3	4.3 ± 2.2
C. jamaicensis	12	3.7 ± 2.3	5.7 ± 1.3	16	4.7 ± 6.7	5.7 ± 2
I. parvipinnis	427	8.6 ± 16.5	6 ± 3.8	218	11.7 ± 16.8	7.2 ± 3.9
L. breviceps	199	2.4 ± 2.8	3.4 ± 1.5	92	5.8 ± 6.5	4.9 ± 2.2
Menticirrhus sp.	33	1.5 ± 1.7	5.5 ± 1.9	8	5.8 ± 4.2	8.7 ± 2.2
M. furnieri	32	0.6 ± 0.4	2.1 ± 0.7	57	0.9 ± 0.4	2.6 ± 0.8
P. brasiliensis	101	5.1 ± 13.9	4.9 ± 2.9	61	12.2 ± 15.2	7.6 ± 3.3
P. harroweri	1028	2.2 ± 3.4	4.1 ± 1.9	666	4.3 ± 6.1	5.2 ± 2.4
Stellifer sp.	596	5.1 ± 5.5	5.3 ± 2	443	6.3 ± 8.7	5.5 ± 2.2
T. lepturus	12	10.9 ± 15.1	27.4 ± 11.3	17	13 ± 14.7	29 ± 12.1
Umbrina sp.	218	0.7 ± 0.9	3.7 ± 0.9	138	1 ± 1.5	4 ± 1.2
[a]Total sample	3127	3.75 ± 7.79	4.94 ± 2.85	1980	5.48 ± 9.06	5.73 ± 3.55
CEPHALOPODS						
D. plei	522	40.1 ± 28.9	12.6 ± 4.2	624	28 ± 22.2	10.6 ± 3.8
D. sanpaulensis	8	22.8 ± 26.8	7.6 ± 3.5	27	24.2 ± 17.5	8.1 ± 2.5
L. brevis	450	5.6 ± 4.8	4.1 ± 1.3	295	6.3 ± 6.6	4.2 ± 1.4
Total sample	980	24.12 ± 27.44	8.63 ± 5.28	946	21.1 ± 21.13	8.51 ± 4.34

Number of evaluated prey (N), mean value and standard deviation of total weight and length for each species are presented.

[a] Calculated with all species, not only with those shared by males and females.

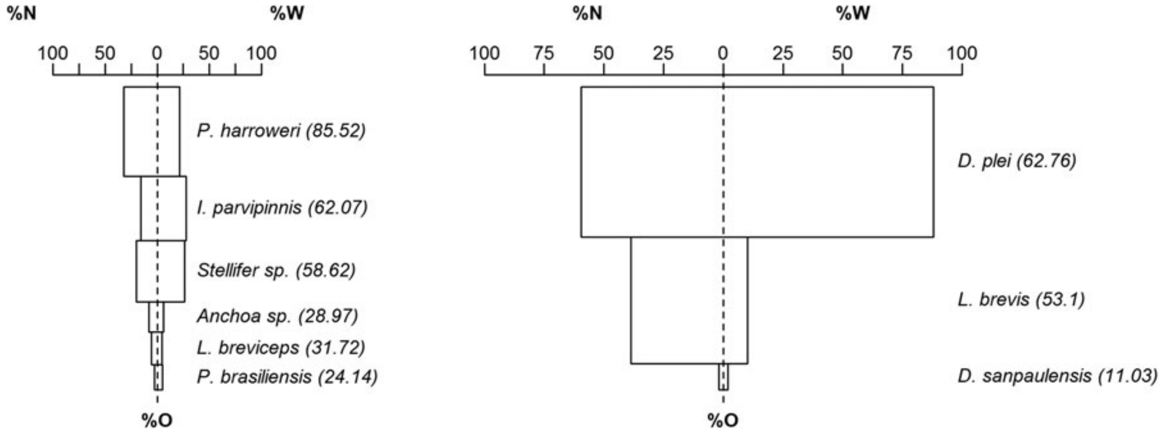

Fig. 2. Index of Relative Importance (IRI) diagram for the most important taxonomic groups of fish (left) and of cephalopods (right) found in the stomach contents of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil. The horizontal axis represents the numerical frequency (%N) and biomass (%W), the vertical axis represents the frequency of occurrence percentage (%O), also indicated in parentheses.

Amundsen diagram

From the total identified fish species, 21 occurred rarely ($O \leq 0.3$) and with a low specific abundance ($\%P \leq 20$). Two groups (*C. bleekerianus* and *Syacium* sp.) occurred very rarely ($O \leq 0.1$), but had a greater influence on the percentage of mass when ingested ($\%P \geq 27$). The three most dominant groups (*P. harroweri*, *I. parvipinnis* and *Stellifer* sp.) occurred frequently ($O \geq 0.58$) with higher specific abundance values ($\%P \geq 26$). All types of fish prey occurred at the bottom of the diagram, mostly in the lower left corner, characterizing a generalist feeding strategy for bony fish. For cephalopods, one species was dominant, *D. plei*, occurring in almost all the analysed stomachs ($O = 0.63$) with a high specific abundance ($\%P = 90$), characterizing a specialized

Table 4. List of the main prey species identified for males and females after evaluating the stomach contents of franciscana dolphins (*Pontoporia blainvillei*)

	Male					Female				
Prey items	%N	%O	%W	%IRI	Rk	%N	%O	%W	%IRI	Rk
TELEOSTS										
P. harroweri	32.17	86.05	18.47	37.56	1	32.33	84.75	25.25	45.40	1
I. parvipinnis	15.90	65.12	30.52	26.05	2	15.83	57.63	24.59	21.67	3
Stellifer sp.	19.08	61.63	27.13	24.54	3	21.01	54.24	25.09	23.26	2
Anchoa sp.	9.74	36.05	8.06	5.53	4	5.69	18.64	3.67	1.62	6
L. breviceps	6.23	32.56	4.06	2.89	5	4.85	30.51	5.45	2.92	4
P. brasiliensis	2.90	20.93	4.09	1.26	6	2.90	28.81	6.61	2.55	5
CEPHALOPODS										
D. plei	53.21	70.93	88.55	76.40	1	65.89	50.85	87.41	78.17	1
L. brevis	45.97	54.65	10.68	23.53	2	31.26	50.85	9.32	20.69	2
D. sanpaulensis	0.82	5.81	0.77	0.07	3	2.85	18.64	3.27	1.15	3

Numerical frequency (%N), frequency of occurrence percentage (%O), biomass (%W), the IRI percentage (%IRI) and the order of importance for each species of prey (Rk) are presented.

Table 5. List of the main prey species identified per sampling season after evaluating the stomach contents of franciscana dolphins (*Pontoporia blainvillei*)

	%IRI							
Prey items	Summer	Rk	Autumn	Rk	Winter	Rk	Spring	Rk
TELEOSTS								
P. harroweri	60.92	1	57.78	1	19.16	3	52.29	1
I. parvipinnis	22.52	2	27.80	2	24.39	2	13.25	3
Stellifer sp.	8.78	3	5.36	3	40.71	1	22.16	2
CEPHALOPODS								
D. plei	91.08	1	85.50	1	54.77	1	83.64	1
L. brevis	8.89	2	14.19	2	44.73	2	15.30	2
D. sanpaulensis	0.04	3	0.31	3	0.50	3	1.06	3

IRI percentage (%IRI) and the order of importance for each species of prey (Rk) are presented.

feeding habit in relation to cephalopods (e.g. Figure 4). The Amundsen diagram (e.g. Figure 4) suggests that males and females have similar dietary strategies as generalists in relation to fish and as specialists in relation to cephalopods.

Ecological indices

The diversity of prey species for both fish and cephalopods was similar between males and females. The similarity of feeding habits was 69% qualitatively (Jaccard index) and 77.5% quantitatively (Bray–Curtis index) in relation to the consumed prey (Table 6). Among seasons, winter and spring showed the highest diversity for both fish and cephalopods, with winter presenting the highest richness while spring showed the lowest richness for fish (Table 6).

Feeding habits between sexes and among seasons

The PERMANOVA test confirmed that there was no significant difference between the feeding habits of different sexes ($F = 0.67$, $P = 0.76$). However, a significant difference was observed ($F = 1.98$, $P = 2 \times 10^{-3}$) among seasons. This difference resulted from the comparisons between winter *vs* summer ($F = 2.92$, $P = 2 \times 10^{-3}$) and winter *vs* autumn ($F = 3.46$, $P = 5 \times 10^{-4}$).

Comparison to previous studies

In the present study, ichthyophagous and teutophagous feeding habits were clearly observed, with greater consumption of fish than cephalopods. Similar results were previously reported in 12 published studies considering all FMAs. The exception was the study from Santos & Haimovici (2001) that focused only on the consumption of cephalopods by marine mammals, including franciscana dolphins (Supplementary Table S2).

Discussion

In the present study, fish of the families Sciaenidae and Engraulidae and squids of the family Loliginidae were the most representative prey. The Sciaenidae is the most representative family of fish in all four FMAs (Supplementary Table S2). Almost all members of this fish family have a well-developed swimming bladder that resonates with the vibrations produced by certain muscles, producing a rather peculiar sound (Menezes & Figueiredo, 1980). These sound emissions may help franciscana

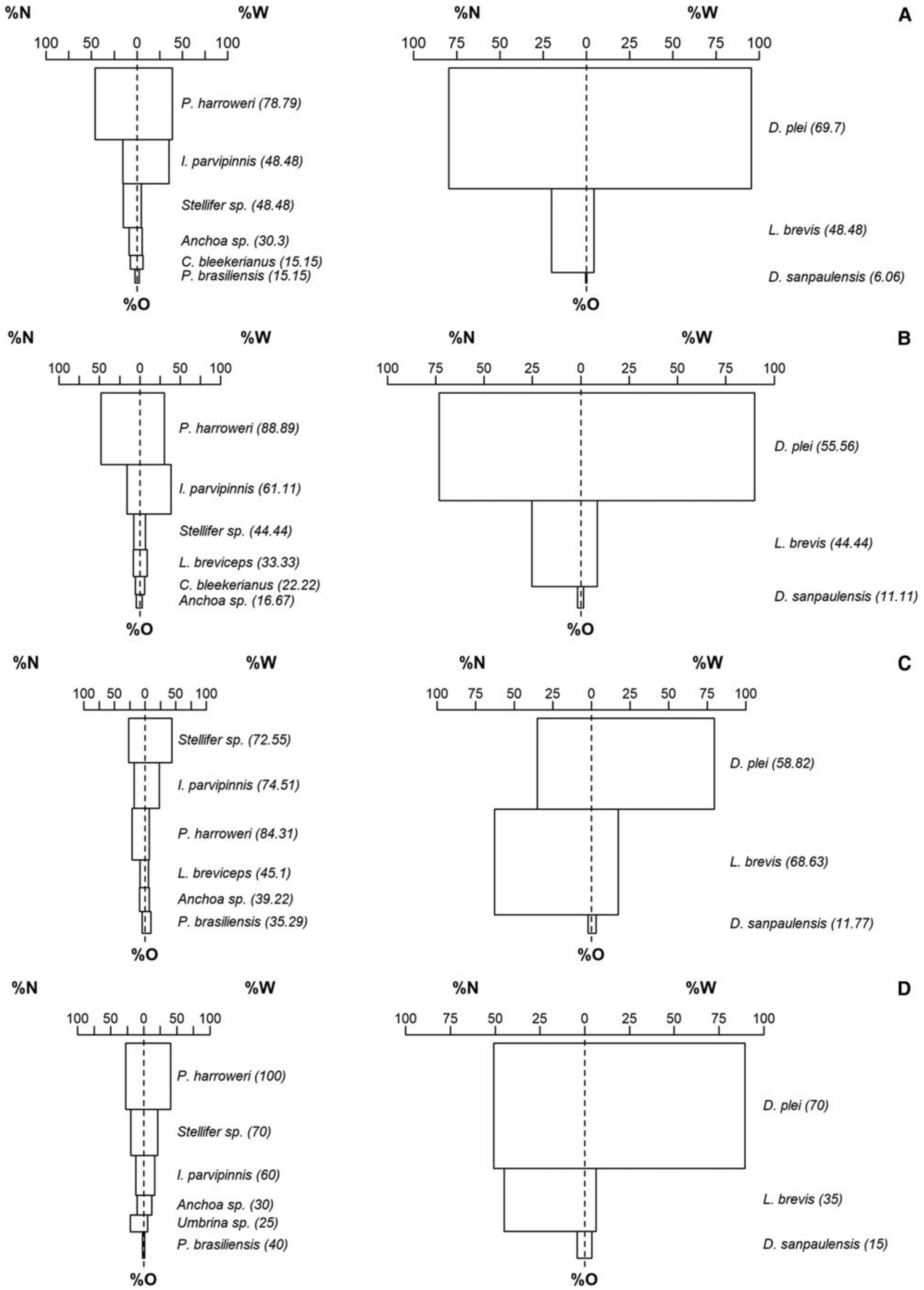

Fig. 3. Index of Relative Importance (IRI) diagram for the most important taxonomic groups of fish (left) and of cephalopods (right) found in the stomach contents of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil in summer (A), autumn (B), winter (C) and spring (D). The horizontal axis represents the numerical frequency (%N) and biomass (%W), the vertical axis represents the frequency of occurrence percentage (%O), also indicated in parentheses.

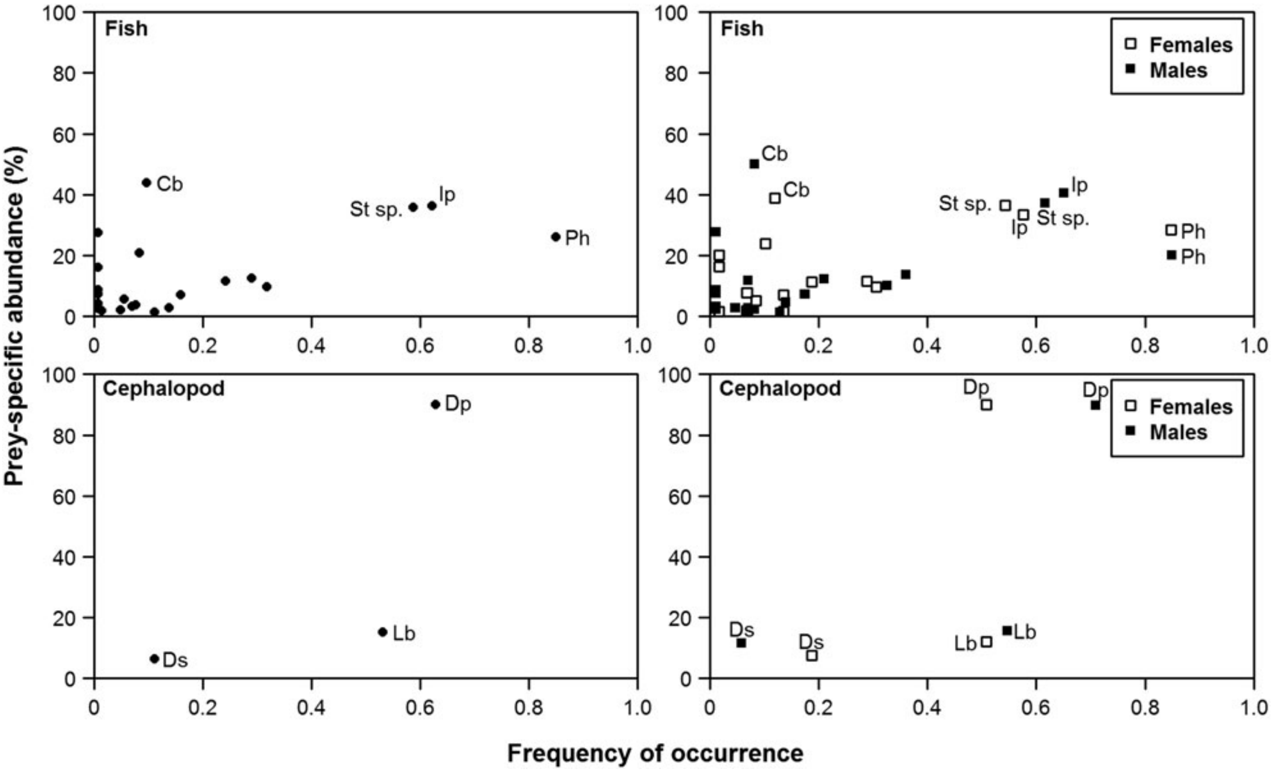

Fig. 4. Costello diagram (1990) modified by Amundsen *et al*. (1996) plotting the frequency of occurrence against the specific abundance of fish (top) and cephalopods (bottom) found as prey items in the stomach contents of franciscana dolphins, *Pontoporia blainvillei* bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil. Both sexes pooled together (left) and evaluated apart (right) are shown. Ph, *Pellona harroweri*; Ip, *Isopisthus parvippinis*; St. sp., *Stellifer* sp.; Cb, *Chirocentrodon bleekerianus*; Dp, *Doryteuthis plei*; Lb, *Loliguncula brevis*; Ds, *Doryteuthis sanpaulensis.*

Table 6. Richness (R), Simpson diversity index (Si), Jaccard similarity index (Jc) and Bray–Curtis coefficient (Bc) for fishes and cephalopods found in the stomachs of franciscana dolphins (*Pontoporia blainvillei*) bycaught (N = 139) or stranded (N = 6) in south-eastern Brazil between 2005 and 2015

Index	All	Male	Female	Summer	Autumn	Winter	Spring
R Fishes	26	24	19	19	14	21	13
R Cephalopods	3	3	3	3	3	3	3
Si Fishes	0.816	0.816	0.813	0.729	0.720	0.831	0.816
Si Cephalopods	0.496	0.502	0.462	0.329	0.401	0.483	0.538
Jc	–	0.690		–			
Bc	–	0.775		–			

Information on all the individuals (All), different gender and seasons are presented.

dolphins to locate prey in murky waters commonly present across this species range. Also, these sound emissions may increase the bycatch rate of this small cetacean, since in the search for food they may approach fishing nets in which the fish are clustered and emitting noise (Tellechea *et al*., 2017).

The great majority of ingested prey by the observed dolphins is found in a large proportion of the franciscana range, but in each FMA usually 2–4 species were predominant (e.g. Di Beneditto & Ramos, 2001; Paso-Viola *et al*., 2014; Tellechea *et al*., 2017). In the present study, ~90% of the IRI values for bony fish were related to three taxonomic groups, *P. harroweri* (42%), *I. parvipinnis* (24%) and *Stellifer* sp. (24%) (e.g. Figure 2), the former belonging to the Pristigasteridae family and the latter two belonging to the Sciaenidae family. All three species are highly abundant in Brazilian waters (Haimovici, 1998; Andrade-Tubino *et al*., 2008). The relevance of *P. harroweri* was also observed in previous studies conducted in south-eastern Brazil (FMAs I and II), listed among the four main taxonomic groups of bony fish in three of five previous investigations (Di Beneditto & Ramos, 2001; Bittar & Di Beneditto, 2009; Henning *et al*., 2018). The *P. harroweri* southern distribution limit is around the coast of Rio Grande do Sul, about 30°S (Di Dario *et al*., 2017). This species distribution was reflected in the absence of *P. harroweri* among the main prey items in FMAs III and IV (Paso-Viola *et al*., 2014; Denuncio *et al*., 2017; Franco-Trecu *et al*., 2017; Tellechea *et al*., 2017). *Pellona harroweri* is pelagic, contrasting with the demersal habits of *I. parvipinnis* and *Stellifer* sp.; the latter two are typically found close to unconsolidated substrates and usually found in coastal and estuarine waters in at least one stage of their life cycle (Fischer *et al*., 2011). None of the three main taxonomic groups of fish consumed by franciscana dolphins has great commercial value, but they are often secondary targets and one of the main byproducts in local shrimp fisheries (Mendonça & Miranda, 2008; Mendonça, 2015). The majority of fish species eaten by local franciscana dolphins are discarded by the shrimp trawl fishery or used as a by-product (e.g. fishmeal, bait) (Coelho *et al*., 1986; Fischer *et al*., 2011; Santos *et al*., 2016).

Among the cephalopods, the most important species in the analysed stomachs was *D. plei* followed by *L. brevis*. Previous studies have shown a greater importance of *D. sanpaulensis* and *D. plei* in franciscana dolphins feeding habits (Di Beneditto & Ramos, 2001; Bittar & Di Beneditto, 2009). These three species belong to the most abundant family (Loliginidae) along the south and south-east coast of Brazil (Santos & Haimovici, 2001). The three squid species found in the present study have pelagic and demersal habits. *Doryteuthis plei* and *L. brevis* are usually found in warm waters. *Doryteuthis plei* reaches deeper waters of up to 200 m on the continental shelf, while *L. brevis* is found in shallower waters of up to 40 m, typically in estuaries (Roper *et al.*, 1984). *Doryteuthis sanpaulensis* is also found on the continental shelf, but up to 60 m deep and in colder waters (Jereb & Roper, 2010). The preference for colder waters supports the frequent presence of *D. sanpaulensis* in the stomach contents of franciscana dolphins in FMAs III and IV (Supplementary Table S2). Cephalopod biota is influenced by the water masses and it would be expected that cold water masses from higher latitudes influence the diet of franciscanas in FMAs III and IV. Cephalopods may play an important role in the diet of *P. blainvillei* as it is a common item found throughout its distribution, with marked differences in specific local species observed by region. Both *D. plei* and *D. sanpaulensis* are important species for commercial and subsistence fishing in the surveyed area. However, the former appears to be the most important species of the Loliginidae family in the fishery activity of São Paulo and Santa Catarina states (FMA II) (Gasalla *et al.*, 2005*a*), while the latter appears as the main species in Rio de Janeiro (in an upwelling area) and Rio Grande do Sul states (FMAs I and III) (Gasalla *et al.*, 2005*b*). *Lolliguncula brevis* has no commercial relevance, and is usually by-caught in bottom trawling fisheries for shrimp and fish (Roper *et al.*, 1984).

The consumption of both pelagic (e.g. *D. plei*, *P. harroweri*) and demersal (e.g. *I. parvipinnis*, *Stellifer* sp.) prey, indicated a feeding habit based on captures made throughout the water column, from the surface waters to the substrate. Most species ingested by franciscana dolphins are caught by fishing, whether as primary or secondary targets, or as bycatch. Fishing activities, as well as franciscana dolphins feeding activities, occur throughout the water column. The overlap of human exploitation of living marine resources and the species foraging and feeding behaviour must also be listed as the main drivers to the high rates of incidental captures of this small cetacean.

Although the IRIs indicated the predominance of three fish species (*I. parvipinnis*, *Stellifer* sp. and *P. harroweri*), the opposite was suggested by the Amundsen diagram presented in Figure 4, showing that there was no dominant prey species in the franciscana dolphin diet. The estimated Simpson's diversity index indicated a high diversity of fish (0.82), suggesting this small cetacean showed a generalist fish feeding habit. On the other hand, the diversity of cephalopods in the diet of franciscana dolphins was not high (0.50), based on the dominance of one or two species (*D. plei* and *L. brevis*). *Doryteuthis plei* appeared as the dominant species among the cephalopods, while *L. brevis* was frequent, but with lesser importance among the available biomass, as a result of its much smaller size and weight (Roper *et al.*, 1984). The low variety among cephalopod prey in the diet of franciscana dolphins was possibly based on the low cephalopod richness in the surveyed area (Haimovici & Perez, 1991), which would not necessarily be distinguishable from a specialist feeding strategy. The abundance of cephalopod species, as well as a detailed evaluation of the main factors that ignite the capture of squids by franciscanas, should be evaluated to better understand the feeding strategy of these dolphins in the surveyed area.

The average size of consumed fish was 5.25 cm (see Table 2), smaller than the average length (up to 11 cm) observed in other FMAs (e.g. Di Beneditto & Ramos, 2001; Rodriguez *et al.*, 2002; Bittar & Di Beneditto, 2009; Cremer *et al.*, 2012; Denuncio *et al.*, 2017; Tellechea *et al.*, 2017). The observed small prey sizes are often associated with younger development stages of the prey species (Cousseau & Perrota, 2000; Fischer *et al.*, 2011). Shallow coastal waters in close connection to estuaries and/or river discharges are used by local demersal teleosts as spawning areas (Menezes & Figueiredo, 1980), which explains the small size of the ingested fish by the observed franciscanas. Although the majority of prey sizes were smaller than 5 cm, prey larger than 20 cm were also found. Therefore, juvenile and adult individuals may also be important for the feeding habits of franciscana dolphins, especially due to their contribution to the ingested biomass. The consumed cephalopods were generally larger than fish (mean = 8.6 cm) as observed in previous studies (Rodriguez *et al.*, 2002; Paso-Viola *et al.*, 2014; Denuncio *et al.*, 2017).

The same taxonomic groups were consumed by both male and female *P. blainvillei*, despite the differences in the relevance order between both diets (Table 4). Some of the observed prey were previously reported among the four most important taxonomic groups by Henning *et al.* (2018). However, the order of importance differed when comparing this study to the previously quoted one. Males (N = 86) in the current study presented a greater richness of fish taxonomic groups than females (N = 59). However, that might be due to a larger male sample size.

Eleven of the 18 species consumed by both males and females showed a significant difference between their sizes and weights (Table 3). Of these, only two species (*D. plei* and *C. bleekerianus*) showed larger sizes and weights in the stomach contents of males. Female franciscana dolphins are generally larger than males (Crespo, 2009), possibly leading them to feed on larger prey. Fish diversity in the feeding habit of males and females was very similar (Simpson's diversity index of 0.82 and 0.81 respectively), even with the males showing a greater richness. Simpson's diversity index is not very sensitive to richness, and common species were in high abundance. The cephalopod diversity found in the stomachs of males and females was also very similar (0.50 and 0.46). Considering all the consumed prey, the Jaccard and Bray–Curtis similarity (0.69 and 0.78 respectively) were close to or above 70%, indicating there was a great overlap in the feeding habits of males and females of the analysed franciscana dolphins, confirmed by PERMANOVA. This similarity between prey consumed by *P. blainvillei* males and females may be associated with the use of similar habitats by both sexes, as previously reported by Danilewicz *et al.* (2009) for FMA III and by Wells *et al.* (2013) for FMA IV.

Although the composition of main prey species was similar among seasons, their order of importance varied throughout the year. This finding was also reported by a previous study conducted in FMA III (Franco-Trecu *et al.*, 2017). According to the PERMANOVA test, feeding habits of analysed franciscanas were significantly different when comparing winter *vs* summer and winter *vs* autumn, but it is important to remember that differences among sample size regarding seasons may be influencing this result. Differences in diets among seasons were also reported by Henning *et al.* (2018) in FMA II. However, in that study the significant difference was between prey ingested in winter *vs* spring. These differences may be related to the increase of fish body mass during the breeding season of different prey species, directly influencing the IRI. Reproduction of *P. harroweri* was reported in coastal waters on the northern coast of Santa Catarina (~27°S) in summer (Souza & Chaves, 2007), the season in which the highest IRI in the feeding habits of the analysed franciscanas was observed (e.g. Table 5 and Figure 3). Studies of *Stellifer stellifer* and *Stellifer rastrifer* on the coast of Santa Catarina and Paraná (~25°S) states, respectively, have found that the peak of the reproductive period occurs in winter and spring (Chaves & Vendel, 1997; Almeida & Branco, 2002), seasons in which the IRI appears to be larger for the taxonomic group *Stellifer* sp. (e.g. Table 5 and Figure 3).

Doryteuthis plei presented lower values of %N and consequently IRI mainly in winter and spring (e.g. Table 5 and Figure 3). In these two seasons many species of the Loliginidae family undergo seasonal migrations in response to changes in water temperature, in general moving to deeper areas (Roper *et al.*, 1984). Reinforcing this statement, aggregations of *D. plei* for reproductive purposes were observed in deeper waters in south-eastern Brazil in spring and winter (Rodrigues & Gasalla, 2008). As the franciscanas are found in coastal shallow waters, probably during this time, the area of occurrence of franciscanas and *D. plei* does not overlap.

There are some known biases in the analysis of stomach contents such as the different digestion status of each prey fragment, contamination by food items of the ingested prey, and being an instant rather than a long-term representation (Fitch & Brownell, 1968; Clarke, 1986; Michener & Kaufman, 2007). On the other hand, Dunshea *et al.* (2013) validated the use of this technique as an important representative of the diet of a coastal cetacean species on a population scale. Thus, the results presented here can be considered as relevant information about the diet of this small poorly known cetacean species which dwells in a restricted portion of the south-west coast of the Atlantic Ocean.

This study is one of the few aiming to describe the franciscanas' feeding habits in FMA II (Supplementary Table S2), and so far presents the largest sample size. According to the observed results, the franciscana dolphin is mostly teutophagous and ichthyophagous, not selective, probably feeding on what is most abundant in relation to species, prey size or season. It probably feeds along the water column on both pelagic and demersal resources. There may be an overlap between the resources caught by fishing as bycatch and prey ingested by local franciscanas.

Added to the present investigation, a total of 852 franciscana dolphins stomach contents were studied in almost 40 years throughout all FMAs. The results of these combined studies indicate an overlap of franciscana's restricted shallow and coastal distribution and the main fishery area from south-eastern Brazil to northern Argentina. This overlap, allied to their feeding habits, may be the main driver of franciscana dolphin high mortality rate in gillnets. Future fisheries management plans and conservation plans may consider the application of mitigation measures to reduce bycatch risk to franciscana dolphins in their distribution area.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315420000120

Acknowledgements. Logistical support was provided by the Instituto Oceanográfico – Universidade de São Paulo. The authors thank Linda Waters for reviewing English. The authors thank all fishermen who helped by collecting data. Samples were collected under permits SISBIO #15572-2 and #35635. The authors are thankful for all the efforts made by both reviewers to address very important comments to improve the original manuscript, and the very kind attention of the associated editor.

Financial support. The following institutions provided financial support to this study: Cetacean Society International (1995–2018), Earthwatch Institute (2003–2007), Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO) – Ministério do Meio Ambiente (BIRD/GEF/CNPq/ 2004–2005), and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP process number 2010/51323-6; 2011–2015). LBC had two fellowships from Conselho Nacional de Pesquisa e Desenvolvimento Tecnológico (CNPq Iniciação Científica process numbers: 159491/2013-4 and 146527/2014-3), XML had a fellowship (FAPESP process number 09/11545-2) and MCOS had a 30-month fellowship (CNPq Produtividade em Pesquisa process number 308331/2010-9), all related to the results presented in this study.

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