Original Article

Intrapopulation variation in the diet of franciscana dolphin (*Pontoporia blainvillei*) off southern Brazil

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Abstract

The franciscana dolphin (*Pontoporia blainvillei*) is a coastal dolphin endemic to the western South Atlantic Ocean. The dolphin is listed as vulnerable in the IUCN Red List, with incidental catches in gillnet fisheries the greatest conservation concern for this species. Insights into the feeding habits of this dolphin are essential to understand its distribution, movements and use of habitat, which are fundamental for effective management of the species. The feeding habits of franciscana dolphins were investigated from analyses of stomach contents of animals incidentally caught by two fishing operations from southern and northern regions of the southern Brazilian coast. In this study we investigate the existence of intrapopulation (sexual maturity and sex-related) variation in the diet of the franciscana dolphin, evaluating the spatial (northern and southern geographic areas) and seasonal influences. The analyses were based on Linear and Generalized Linear Models (LM and GLM). The majority of identified prey species were bottom-dwelling teleosts and the squid *Doryteuthis sanpaulensis*. The most important prey differed spatially and seasonally between northern and southern regions of the study area, and our results revealed significant differences between sexes and sexual maturity stages, mainly related to prey species sizes. This variation might indicate differences in prey selection, availability or habitat use patterns among these groups. In any case, these dietary differences are likely to minimize intraspecific competition for food resources, and/or indicate spatio-temporal variation in prey availability.

Introduction

The franciscana dolphin *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) is a small cetacean endemic to the western South Atlantic Ocean, with a distribution ranging from south-eastern Brazil (Siciliano *et al.*, 2002) to Golfo Nuevo, Argentina (Crespo *et al.*, 1998). Franciscana dolphins are primarily coastal, inhabiting waters beyond the surf zone and out to the 30 or 50 m isobath, depending on the region (Crespo, 2009; Secchi, 2014). Furthermore, diet seems to play an important factor for franciscana dolphin distribution. For example, Gomez & Cassini (2015) when analysing different variables (e.g. sea surface temperature, salinity, prey availability) to estimate their effect on the species distribution, found that the prey *Cynoscion guatucupa* represented the most important variable. There is strong evidence that franciscana dolphin is not continuously present throughout its distribution in Brazil (Siciliano *et al.*, 2002; Danilewicz *et al.*, 2012), and there are two hiatuses proposed on the south-eastern Brazilian coast (Amaral *et al.*, 2018). Due to considerable population level differences (both genetic and morphological), Secchi *et al.* (2003) divided the franciscana dolphin area of distribution into four Franciscana Management Areas (FMAs). The species is classified as 'Vulnerable' in the IUCN Red List of Threatened Species throughout its range (Zerbini *et al.*, 2017), principally as a consequence of incidental mortality in fisheries. Within the study area (Franciscana Management Area III), along the Rio Grande do Sul (RS) state coast – southern Brazil, this species has been experiencing unsustainable rates of bycatch in gillnets for at least four decades (Moreno *et al.*, 1997; Ott *et al.*, 2002; Secchi *et al.*, 2003; Secchi & Fletcher, 2004; Prado *et al.*, 2013, 2016, 2021). At a regional level, franciscana dolphins are listed as 'Critically Endangered' in the study region (Rio Grande do Sul State, Decree No. 51.797/2014).

Franciscana dolphin females are larger than males and lactation lasts for around nine months (Danilewicz *et al.*, 2002), with calves taking solid food from around their third month of age (Pinedo *et al.*, 1989; Danilewicz *et al.*, 2002; Secchi, 2014). The majority of franciscana dolphin prey belong to three main taxonomic groups: fish (~80%), crustaceans

(∼10%) and molluscs (∼10%) (Brownell, 1975; Pinedo, 1982; Rivero *et al.*, 2000; Rupil *et al.*, 2019). Previous dietary studies indicate that this dolphin preys predominantly upon bottom-dwelling juvenile teleosts, squid and shrimp (Ott, 1994; Bassoi, 1997; Oliveira *et al.*, 1998; Di Beneditto, 2000; Campos *et al.*, 2020), and several studies suggest that the species is a generalist and opportunistic predator (e.g. Danilewicz *et al.*, 2002; Cremer *et al.*, 2012; Paso-Viola *et al.*, 2014). Nevertheless, there are few inferences about intrapopulation prey preferences or diet specialization for franciscana dolphins (e.g. Bassoi, 1997; Troina *et al.*, 2016; Henning *et al.*, 2017).

Intrapopulation foraging preferences can be attributed to differences between sexes (e.g. ecological sexual dimorphism; Shine, 1989) and/or age groups (e.g. ontogenetic niche shifts; Polis, 1984). Sexual differences in body size, as in the case of franciscana dolphins, distinct physiological demands e.g. pregnancy and lactation, and parental guidance of juveniles could lead to differences in diet among males and females. A common inference about age group (mature and immature individuals) or size class specificity in diet is that this separation may reduce exploitation competition for food (Polis, 1984), and increase individual fitness by avoidance of competitive selection (Wrona *et al.*, 1979). Thus, differences in body size and resource use may allow competitive coexistence both between gender and age groups (Keast, 1977; Maiorana, 1978), or increasing niche width of a species (Polis, 1984). Investigating franciscana dolphin diet composition, preference and variation is crucial to fully understand its dietary requirements and foraging, dietary niche characterization and its role in community and ecosystem functioning (Bearhop *et al.*, 2004; Secchi, 2010).

The aim of this research was to investigate spatio-temporal diet variation with emphasis on assessing if intraspecific differences in feeding regimes exist between sexes and sexual maturity stages of franciscana dolphins for two distinct geographic areas off the southern Brazilian coast.

Materials and methods

Franciscana dolphin data

Samples were collected from dolphins incidentally killed in coastal gillnet fishing operations from Rio Grande (32°08′S 52°05′W; N = 172) and from Tramandaí (29°58′S 50°07′W; N = 98) southern Brazil, between 1994 and 2000 (Figure 1). The division of the study region into southern and northern coastal sites was based on the fishing grounds used by the vessels from Rio Grande and Tramandaí, respectively (see Moreno *et al.*, 2018 and Boffo & Reis, 2003). Data on location, date of capture event, sex, total body length and weight were recorded. Individuals were categorized as sexually mature or immature based on gross and histological examination of gonads (N = 102; Botta *et al.*, 2010), or inferred from total body length (sexually mature female >138.9 cm and sexually mature male >128.2 cm; N = 168; Danilewicz *et al.*, 2000).

Sample data

The stomachs (including the main and pyloric chambers) were excised and opened for the diet analysis. The main contents analysed were otoliths, cephalopod beaks and crustacean remains (mainly cephalothorax). Otoliths and cephalopod beaks were measured with a microscope equipped with an ocular micrometer (0.1 mm scale). The total otolith length (LO) was considered as an estimate of the original size of fish prey species (total fish length). To estimate the original size of cephalopod species (mantle length), we measured the upper rostral beak length (URL) and

lower rostral beak length (LRL) for squids and sepiolids; and upper hood beak length (UHL) and lower hood beak length (LHL) for octopuses. Reference collections of fish otoliths (Lucato, unpubl. data) and cephalopod beaks (Santos, 1999) for the study area were available in the Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, Universidade Federal do Rio Grande (FURG). The collections allowed correct prey identification and reliable regression equations to estimate the original length (mm) and weight (g) of the prey species at time of ingestion. The reconstructed size (mm) and weight (g) were calculated for 31 prey species. Specialists from FURG and Universidade Católica do Rio Grande do Sul identified crustacean specimens, but we were not able to reconstruct their size and weight data.

To assess the importance of prey items in the diet of franciscana dolphin we calculated the Index of Relative Importance using the formula: IRI = (% N + % W) * % O (Pinkas *et al.*, 1971). Here, % N is the percentage of numerical abundance of a particular prey recovered from all stomachs; % W is the percentage of reconstructed weight by a particular prey; and % O the proportion of stomachs that contained this particular prey species, regardless of weight or abundance. IRI values considering all the prey ingested were calculated for the southern and the northern areas separately (see Table 1).

Statistical analysis

To investigate prey species abundance according to franciscana dolphin diet groups (sex and sexual maturity stage), we used GLM as it is a flexible generalization of ordinary linear regression that allows for response variables that have error distribution models other than a normal distribution (Venables & Dichmont, 2004). The response variables prey species number (non-normal counts) were analysed based on a Poisson error structure. The explanatory categorical data 'sex' with two-level factor (male and female), 'sexual maturity stage' with two-level factor (mature and immature), 'area' with two-level factor (northern and southern) and 'season' with a four-level factor, used the log-link function and a linear variance-mean relationship (Graphen & Hails, 2002). Final models' selection was based on a stepwise procedure using the Akaike Information Criterion (AIC) (Crawley, 2012). Analysis of deviance was performed to obtain the values of degrees of freedom, residuals, and *P*, to identify significant relationships from the models.

We assessed the relationships between reconstructed prey length and weight (response variables) and franciscana dolphin sex, maturity stage, season and area (northern and southern) using linear models (LMs). Log-transformations were performed when the residuals contravened the assumption of normality, and model selection was based on stepwise procedure using the AIC (Crawley, 2012). From the LMs, analysis of variance tables were used to obtain the values of degrees of freedom, residuals, F, and *P*, to identify significant relationships.

Rényi diversity profiles was chosen to rank prey species comparing franciscana dolphin groups according to diversity (Kindt & Coe, 2005), since these profiles by the Rényi series provide different diversity measures to compare equivalently the group's diet. This index was calculated using the vegan package (Oksanen *et al.*, 2019).

Results

Franciscana dolphin and stomach contents data

The number of franciscana dolphin sampled for each area, season and ontogenetic groups are shown in Table 1 (for 26 dolphins in the northern area, sexual maturity and/or gender could not be
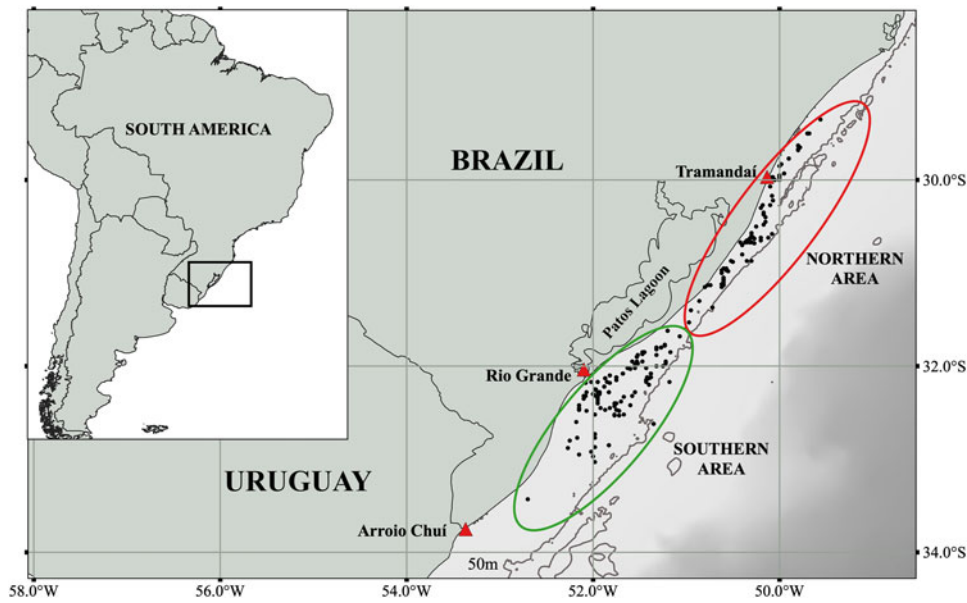
Fig. 1. Locations of franciscana dolphin (*Pontoporia blainvillei*) incidental by-catch events along the southern Brazilian coast (N = 270). The division of the study region into the northern (red ellipsoid) and southern (green ellipsoid) areas was based on the areas fished by the fishing vessels operating from Tramandaí and Rio Grande cities, respectively.

Table 1. Numbers of franciscana dolphin analysed in this study

Southern area	Summer	Autumn	Winter	Spring	Total
Male	12	28	33	27	100
Female	12	20	23	17	72
Immature	14	22	35	29	100
Mature	10	26	21	15	72
Total	24	48	56	44	
Northern area	Summer	Autumn	Winter	Spring	**Total**
Male	10	2	12	20	44
Female	9	3	7	9	28
Immature	12	2	16	16	46
Mature	9	4	4	27	44
Total	25	8	22	43	

achieved). Only nine of the analysed stomachs were empty, including eight stomachs from lactating calves. A total of 13,354 otoliths, 12,248 cephalopod beaks and 182 remains of crustaceans (mainly cephalothorax) were identified. Fish and cephalopods were the most important prey groups in the diet of franciscana dolphin (see Table 2). Bottom-dwelling teleosts (26 species) were the most numerous among the fishes, whereas shelf-demersal squid (3 species) and shelf-benthic octopus (2 species) were the predominant cephalopods (Table 2).

Analysis of reconstructed prey lengths, discriminated by species, show considerable variation (Table 3), with some ingested fish (e.g. *Trichiurus lepturus*) much larger than the mean fish size consumed by franciscana dolphin. Some species minimum sizes are only 4–6 mm in length, which could be part of the diet of the prey itself rather than direct intake by the dolphin. Nevertheless, this is still doubtful as in some events we could find many of these tiny otoliths and no bigger otoliths or any remains of bigger prey which would indicate the predator of these small fishes. The mean and median reconstructed fish lengths are estimated to be 96.37 and 59.98 mm, respectively (N = 4443), which represents juvenile fish (Haimovici, 1997a). The range of lengths was similar for both the northern and southern study areas. In contrast, the reconstructed cephalopod

mantle lengths represent adult individuals (Santos, 1999) (mean = 105.48 mm, median = 105.77 mm, N = 6192), within 97% of the beaks from the common squid (*Doryteuthis sanpaulensis*).

GLMs and LMs

GLM revealed most of the highly significant differences of prey species number were related to spatial and temporal explanatory variables (Table 4). Hence, the comparisons of intrapopulation groups (i.e. sex, sexual maturity stage) were made only within each study site (northern or southern), mitigating potential biases resulting from spatial differences. Moreover, season has a very important influence on diet variation (see Table 4). There were few significant differences between sexual maturity stages, and no significant differences in prey species numbers ingested between males and females in both study areas. Contrariwise, the linear models for reconstructed prey length and weights between the study areas, sex and sexual maturity showed significant differences for 86% of the analyses (Table 5). A detailed description of the significant results according to each explanatory variable (geographic, temporal and ontogenetic) is presented below.

Table 2. A summary of the prey species composition and relative importance of prey items (% N, % W, % O and IRI) of franciscana dolphin diet from southern and northern coastal regions of the study area

Prey	Common name	Southern area				Northern area			
		% N	% O	% W	IRI*	% N	% O	% W	IRI*
Fish		**46.95**	**95.93**	**12.29**		**64.43**	**89.80**	**29.79**	
Cynoscion guatucupa	Striped weakfish	23.05	65.12	2.18	1643.07	3.86	26.53	0.06	104.15
Trichiurus lepturus	Cutlass fish	2.38	36.63	3.78	225.64	5.39	54.08	10.69	869.70
Paralonchurus brasiliensis	Banded croacker	3.23	34.30	1.26	154.25	6.08	36.73	4.06	372.29
Urophycis brasiliensis	Squirrel codling	2.04	28.49	1.58	103.17	7.37	36.73	4.51	436.22
Anchoa marinii	Anchovy	4.84	28.49	0.17	142.76	1.56	14.29	0.12	23.96
Porichthys porosissimus	Lantern midshipman	1.62	21.51	0.61	48.10	2.60	22.45	1.42	90.30
Umbrina canosai	Argentine croaker	2.25	12.79	0.75	38.29	2.84	18.37	0.82	67.28
Peprilus paru	American harvestfish	0.66	7.56	0.02	5.14	0.09	3.06	0.02	0.33
Engraulis anchoita	Anchoita	0.54	7.56	0.09	4.76	0.69	7.14	0.22	6.49
Micropogonias furnieri	White croaker	0.51	5.23	0.33	4.42	0.72	5.10	0.51	6.27
Macrodon ancylodon	King weakfish	0.29	4.65	0.63	4.25	0.42	4.08	0.71	4.59
Cynoscion jamaicensis	Jamaica weakfish	0.22	3.49	0.27	1.70	2.93	10.20	0.80	38.08
Pomatomus saltator	Bluefish	0.24	3.49	0.05	1.01	0.03	1.02	0.32	0.35
Menticirrhus sp.	Southern kingcroacker	0.07	2.91	0.06	0.38	0.84	8.16	2.71	28.97
Trachurus lathami	Rough scad	0.03	1.74	0.002	0.06	0.63	8.16	0.12	6.09
Stellifer rastrifer	Rake stardrum	0.01	0.58	0.003	0.01	18.98	44.90	2.58	968.20
Stromateus brasiliensis	Butterfish	0.08	0.58	0.01	0.05	0.03	1.02	0.04	0.07
Pagrus pagrus	Red porgy					0.06	1.02	0.06	0.12
Ctenosciena gracilicirrhus	Barbel drum					0.18	4.08	0.04	0.88
Licengraulis grossidens	Atlantic sabretooth anchovy					0.03	1.02		0.03
Merluccius hubbsi	Argentine hake	0.27	4.65	0.01	1.29				
Prionotus sp.	Searobins	0.26	2.91	0.07	0.95				
Syacium papillosum	Dusky flounder	0.21	1.74	0.12	0.57				
Raneya fluminensis	Cuskeels	0.05	1.74	0.21	0.46				
Mugil sp.	Mullet	0.02	1.16	0.08	0.12				
Paralichthys isoceles	Sand flounder	0.01	0.58	0.002	0.01				
Scianidae		0.08	3.49			0.57	11.22		
Engraulidae		0.69	12.21			0.78	12.24		
Unidentified		3.29	64.53			7.78	58.16		

Cephalopod		**51.65**	**81.98**	**87.71**		**34.19**	**73.47**	**70.21**	
Doryteuthis sanpaulensis	Common long-finned squid	50.65	81.98	87.14	11,295.73	32.37	73.47	67.27	7319.91
Doryteuthis plei	Arrow squid	0.25	8.72	0.47	6.28	0.90	8.16	2.81	30.26
Argonauta nodosa	Knobby argonaut	0.68	11.63	0.09	8.93	0.90	8.16	0.05	7.71
Octopus tehuelchus	Tehuelche octopus	0.04	1.74	0.01	0.08	0.03	1.02	0.09	0.12
Semirossia tenera	Lesser bobtail squid	0.02	1.16	0.002	0.03				
Eledone sp.	Octopus	0.01	0.58		0.01				
Crustacean		**1.41**	**40.12**			**1.35**	**39.80**		
Pleoticus muelleri	Patagonian red shrimp	0.23	7.56						
Artemesia longinaris	Marine shrimp	0.28	4.65						
Loxopagurus loxocheles	Hermit crab	0.06	3.49						
Dardanus insignis	Hermit crab	0.01	0.58						
Penaeidae	'shrimps'	0.20	8.14						
Brachiura	'crabs'	0.02	1.16						
Pleocyemata	'crabs'	0.08	4.07						
Dendrobranchiata	'shrimps'	0.01	0.58						
Penaeoidea	'shrimps'	0.12	6.98			0.36	12.24		
Isopoda**	'bugs'	0.33	5.81			0.96	32.65		
Unidentified		0.07	3.49			0.03	1.02		
Total		9643	172	281,662.37 g		3351	98	71,469.44 g	

(% N + % W)(% O), Pinkas *et al.* (1971). **Could be also considered as secondary ingestion or post-mortem invasion.

Table 3. Analysis of prey species reconstructed lengths (mm) and weights (g) ingested by franciscana dolphins off the southern Brazilian coast (SE = standard error of the mean, SD = standard variation)

Species	Reconstructed prey lengths (mm)					Reconstructed prey weights (g)					
	Mean	Min.	Max.	SE	SD	Mean	Min.	Max.	SE	SD	*n*
Fishes											
Anchoa marinii	69.66	31.08	112.12	0.78	13.85	1.75	0.29	8.50	0.05	1.03	317
Ctenosciena gracilicirrhus	67.58	49.97	86.35	5.96	14.60	4.37	1.44	8.45	1.16	2.85	6
Cynoscion guatucupa	55.22	12.16	356.44	0.72	29.99	3.53	0.01	464.68	0.39	16.50	1753
Cynoscion jamaicensis	73.69	18.80	312.73	8.61	66.10	22.67	0.05	378.98	9.25	71.05	59
Engraulis anchoita	108.07	54.70	151.65	3.44	23.60	8.46	0.87	21.18	0.76	5.23	47
Macrodon ancylodon	200.15	60.61	359.63	12.39	66.71	78.17	1.65	479.57	17.67	95.14	29
Menticirrhus spp.	148.93	64.42	342.56	11.70	69.20	60.13	1.71	472.55	19.07	112.84	35
Merluccius hubbsi	25.46	5.82	95.12	6.63	30.39	1.40	0.24	7.50	0.49	2.22	21
Micropogonias furnieri	103.96	26.90	240.37	9.25	62.77	28.25	0.13	167.74	6.67	45.30	46
Mugil spp.	207.40	100.00	314.70			118.40	10.00	226.80			2
Pagrus pagrus	49.22	27.01	80.22	4.87	18.86	2.62	0.30	7.88	0.70	2.73	15
Paralichthys isosceles	96.31					4.89					1
Paralonchurus brasiliensis	102.43	6.47	228.72	2.78	53.82	17.18	0.01	130.69	1.28	24.85	376
Peprilus paru	36.88	12.45	86.59	2.20	15.23	1.61	0.08	12.61	0.29	2.04	48
Pomatomus saltator	119.17	44.34	290.93	16.81	60.61	29.01	0.68	225.98	16.69	60.20	13
Porichthys porosissimus	92.77	19.30	270.44	5.02	60.19	19.05	0.04	199.92	3.07	36.89	144
Prionotus spp.	54.58	19.62	248.38	12.69	52.31	11.71	0.06	182.18	10.65	43.95	17
Raneya fluminensis	63.07	28.66	119.77	1.60	3.57	11.90	9.85	14.57	0.32	8.19	5
Stellifer rastrifer	53.37	3.62	206.71	1.19	27.86	3.36	0.01	127.06	0.37	8.62	551
Stromateus brasiliensis	128.70	117.08	140.32			21.91	16.00	27.83	5.92	8.37	2
Syacium papillosum	104.49	63.50	177.16	6.19	27.67	17.03	6.79	56.43	2.56	11.45	20
Trachurus lathami	64.94	28.49	129.33	6.99	33.51	3.86	0.15	16.64	1.12	5.35	23
Trichiurus lepturus	402.05	84.38	888.97	10.31	194.81	51.22	0.11	392.12	3.31	62.67	357
Umbrina canosai	67.02	12.52	193.57	3.17	48.76	11.38	0.02	100.25	1.22	18.79	236
Urophycis brasiliensis	103.70	52.31	454.24	3.86	69.04	23.97	0.56	831.93	4.50	80.60	320
Cephalopods											
Argonauta nodosa	20.62	4.30	71.14	1.23	12.09	3.00	0.03	15.84	0.34	3.39	96
Eledone spp.	31.72					18.60					1
Doryteuthis plei	155.72	50.56	256.64	6.00	44.06	61.91	4.66	166.81	4.85	35.67	54
Doryteuthis sanpaulensis	106.47	22.75	250.21	0.47	36.36	48.64	1.10	283.21	0.46	36.03	6034
Octopus tehuelchus	32.08	19.62	62.78	7.82	17.47	17.18	2.60	65.95	12.22	27.31	5
Semirrosia tenera	16.90	13.99	19.79			2.48	1.47	3.49			2

Dietary variation by area

The main fish species in the diet of franciscana dolphin differed between the areas, with *Stellifer rastrifer* being the most important fish for northern and *Cynosion guatucupa* for the southern diet (see Tables 2 and 4). Southern animals had eaten larger and heavier cephalopods than northern franciscana dolphins, while the opposite was the case for fish (Table 5).

Dietary variation by season

The southern area showed twice as many significantly different prey species frequencies through seasons as the northern area (Table 4). Not surprisingly, the importance of warm water related fish and cephalopod species (e.g. *Trichiurus lepturus*, *Peprilus paru*, *Argonauta nodosa*) and cold water species (e.g. *Anchoa marinii*, Family Engraulidae, *Doryteuthis sanpaulensis*) were different through the seasons. The biggest fish (lengths and weights) ingested were found in the summer season, and the smallest fish were from winter months in both areas. This finding is mainly influenced by the bigger fish prey *T. lepturus* (see Table 3), with higher occurrence in summer and autumn, decreasing considerably in the winter. Additionally, the biggest cephalopods were consumed during spring and summer months equally between the areas. Hence, seasonal results of prey species sizes for both areas

Table 4. List of generalized linear models (GLMs) and the analysis of deviance according to study area (northern, southern), sex (male, female), sexual maturity stage (mature, immature), and seasonality (summer, autumn, winter and spring) for the numerical abundance of prey species recovered from the stomach contents of franciscana dolphins by-caught on the southern Brazilian coast

Generalized linear model formula (family = Poisson, link = log)	df	res. df	*P*	Means (log)	Estimated effects
Northern and Southern areas = explanatory					
Anchoa marinii	1	259	0.002	N = 0.2 S = 0.5	N = −0.2 S = 0.1
Cynoscion guatucupa	1	259	<0.001	N = 0.4 S = 1.5	N = −0.7 S = 0.4
Cynoscion jamaicensis	1	259	0.006	N = 0.2 S = 0.0	N = 0.1 S = −0.1
Menticirrhus sp.	1	259	0.015	N = 0.1 S = 0.0	N = 0.1 S = 0.0
Merluccius hubbsi	1	259	0.025	N = 0.0 S = 0.1	N = −0.1 S = 0.0
Peprilus paru	1	259	0.049	N = 0.0 S = 0.1	N = −0.1 S = 0.0
Stellifer rastrifer	1	259	<0.001	N = 0.8 S = 0.0	N = 0.5 S = −0.3
Trachurus lathami	1	259	0.004	N = 0.1 S = 0.0	N = 0.1 S = 0.0
Urophycis brasiliensis	1	259	0.018	N = 0.6 S = 0.4	N = 0.2 S = −0.1
Doryteuthis sanpaulensis	1	259	<0.001	N = 1.7 S = 2.3	N = −0.4 S = 0.2
Total shrimp specimens	1	259	0.013	N = 0.1 S = 0.2	N = −0.1 S = 0.1
Male and Female of northern area = explanatory	NS				
Male and Female of southern area = explanatory	NS				
Mature and Immature of northern area = explanatory					
Stellifer rastrifer	1	91	0.024	M = 0.2 I = 1.4	M = −0.6 I = 0.6
Total fish specimens	1	91	0.003	M = 2.1 I = 2.9	M = −0.4 I = 0.4
Total shrimp specimens	1	91	<0.001	M = 0.0 I = 0.2	M = −0.1 I = 0.1
Mature and Immature of southern area = explanatory					
Cynoscion guatucupa	1	167	0.043	M = 1.2 I = 1.6	M = −0.2 I = 0.2
Total fish specimens	1	167	0.023	M = 2.6 I = 2.8	M = −0.1 I = 0.1
Total shrimp specimens	1	167	0.003	M = 0.1 I = 0.3	M = −0.1 I = 0.1
Seasonality of northern area = explanatory				Sum | Aut | Win | Spr	Sum | Aut | Win | Spr
Anchoa marinii	3	91	<0.001	0.0 | 0.3 | 0.7 | 0.1	−0.2 | 0.1 | 0.4 | −0.1
Stellifer rastrifer	3	91	0.036	1.0 | 0.7 | 1.5 | 0.4	0.1 | −0.1 | 0.7 | −0.4
Trichiurus lepturus	3	91	<0.001	1.1 | 0.5 | 0.2 | 0.9	0.3 | −0.3 | −0.6 | 0.1
Family Engraulidae	3	91	0.020	0.0 | 0.0 | 0.4 | 0.1	−0.1 | −0.1 | 0.2 | −0.1
Doryteuthis plei	3	91	<0.001	0.3 | 0.5 | 0.0 | 0.0	0.2 | 0.4 | −0.1 | −0.1
Argonauta nodosa	3	91	0.009	0.3 | 0.2 | 0.0 | 0.1	0.2 | 0.1 | −0.1 | −0.1
Seasonality of southern area = explanatory					
Anchoa marinii	3	167	<0.001	0.1 | 0.6 | 1.0 | 0.2	−0.5 | 0.0 | 0.5 | −0.4
Cynoscion guatucupa	3	167	<0.001	0.5 | 1.1 | 2.5 | 1.0	−1.0 | −0.4 | 1.0 | −0.5
Macrodon ancylodon	3	167	0.008	0.0 | 0.0 | 0.2 | 0.0	−0.1 | 0.0 | 0.1 | 0.0
Paralonchurus brasiliensis	3	167	<0.001	0.3 | 0.2 | 0.7 | 0.8	−0.2 | −0.4 | 0.2 | 0.3
Peprilus paru	3	167	<0.001	0.3 | 0.2 | 0.0 | 0.0	0.2 | 0.1 | −0.1 | −0.1
Porichthys porosissimus	3	167	0.001	0.4 | 0.6 | 0.1 | 0.1	0.1 | 0.3 | −0.2 | −0.2
Trichiurus lepturus	3	167	<0.001	0.8 | 0.9 | 0.1 | 0.5	0.3 | 0.4 | −0.4 | 0.0
Umbrina canosai	3	167	<0.001	0.4 | 0.2 | 0.1 | 0.4	0.2 | 0.0 | −0.2 | 0.2
Family Engraulidae	3	167	0.001	0.0 | 0.1 | 0.3 | 0.1	−0.1 | −0.1 | 0.1 | 0.0
Total fish specimens	3	167	<0.001	2.2 | 2.6 | 3.2 | 2.4	−0.5 | −0.1 | 0.5 | −0.3
Doryteuthis sanpaulensis	3	167	<0.001	1.8 | 1.5 | 2.6 | 3.1	−0.5 | −0.8 | 0.3 | 0.8
Argonauta nodosa	3	167	<0.001	0.4 | 0.2 | 0.0 | 0.0	0.3 | 0.1 | −0.1 | −0.1
Total shrimp specimens	3	167	0.012	0.2 | 0.3 | 0.1 | 0.4	0.0 | 0.0 | −0.1 | 0.1

Table 5. List of linear models (LM) and the analysis of variance according to study area (northern, southern), sex (male, female), sexual maturity (mature, immature), and seasonality (summer, autumn, winter and spring) for reconstructed fish and cephalopod prey lengths (mm) and weights (g)

Linear model formula	df	res. df	F	P	Means (log)	Estimated effects
Northern and Southern areas = explanatory						
log (Fish reconstructed length)	1	4441	6.6	0.010	N = 4.3 S = 4.2	N = 0.1 S = 0.0
log (Fish reconstructed mass)	1	4441	6.3	0.012	N = 1.4 S = 1.3	N = 0.1 S = 0.0
log (Cephalopod reconstructed length)	1	6190	32.8	<0.001	N = 4.5 S = 4.6	N = −0.1 S = 0.0
log (Cephalopod reconstructed mass)	1	6190	37.2	<0.001	N = 3.3 S = 3.5	N = −0.2 S = 0.0
Male and Female of northern area = explanatory						
log (Fish reconstructed length)	1	1272	51.0	<0.001	F = 4.6 M = 4.1	F = 0.4 M = −0.1
log (Fish reconstructed mass)	1	1272	48.7	<0.001	F = 2.0 M = 1.2	F = 0.7 M = −0.2
log (Cephalopod reconstructed length)	1	932	14.1	<0.001	F = 4.6 M = 4.4	F = 0.1 M = −0.1
log (Cephalopod reconstructed mass)	1	932	14.3	<0.001	F = 3.4 M = 3.1	F = 0.2 M = −0.2
Male and Female of southern area = explanatory						
log (Fish reconstructed length)	1	2920	2.8	0.094	F = 4.2 M = 4.2	F = 0.0 M = 0.0
log (Fish reconstructed mass)	1	2920	0.0	0.878	F = 1.3 M = 1.3	F = 0.0 M = 0.0
log (Cephalopod reconstructed length)	1	5056	28.2	<0.001	F = 4.5 M = 4.6	F = −0.1 M = 0.0
log (Cephalopod reconstructed mass)	1	5056	52.6	<0.001	F = 3.3 M = 3.6	F = −0.2 M = 0.1
Mature and Immature of northern area = explanatory						
log (Fish reconstructed length)	1	1472	93.4	<0.001	M = 4.8 I = 4.0	M = 0.5 I = −0.2
log (Fish reconstructed mass)	1	1472	97.2	<0.001	M = 2.4 I = 1.1	M = 1.0 I = −0.3
log (Cephalopod reconstructed length)	1	1038	8.8	0.003	M = 4.5 I = 4.4	M = 0.1 I = −0.1
log (Cephalopod reconstructed mass)	1	1038	9.4	0.002	M = 3.4 I = 3.1	M = 0.1 I = −0.1
Mature and Immature of southern area = explanatory						
log (Fish reconstructed length)	1	2920	54.4	<0.001	M = 4.5 I = 4.0	M = 0.3 I = −0.1
log (Fish reconstructed mass)	1	2920	55.5	<0.001	M = 1.8 I = 1.1	M = 0.5 I = −0.2
log (Cephalopod reconstructed length)	1	5056	0.0	0.925	M = 4.6 I = 4.6	M = 0.0 I = 0.0
log (Cephalopod reconstructed mass)	1	5056	0.5	0.489	M = 3.5 I = 3.5	M = 0.0 I = 0.0
Seasonality of northern area = explanatory					Sum | Aut | Win | Spr	Sum | Aut | Win | Spr
log (Fish reconstructed length)	3	1517	24.1	<0.001	4.0 | 4.7 | 4.2 | 4.5	−0.2 | 0.4 | 0.0 | 0.2
log (Fish reconstructed mass)	3	1517	16.1	<0.001	1.1 | 2.0 | 1.5 | 1.7	−0.3 | 0.5 | 0.0 | 0.2
log (Cephalopod reconstructed length)	3	1130	9.0	<0.001	4.5 | 4.3 | 4.5 | 4.5	0.0 | −0.2 | −0.1 | 0.0
log (Cephalopod reconstructed mass)	3	1130	3.3	0.020	3.4 | 2.8 | 3.2 | 3.4	0.1 | −0.6 | −0.2 | 0.1
Seasonality of southern area = explanatory						
log (Fish reconstructed length)	3	2918	56.7	<0.001	4.5 | 4.4 | 4.0 | 4.2	0.3 | 0.2 | −0.1 | 0.0
log (Fish reconstructed mass)	3	2918	46.4	<0.001	2.1 | 1.5 | 1.1 | 1.5	0.7 | 0.1 | −0.2 | 0.2
log (Cephalopod reconstructed length)	3	5054	57.2	<0.001	4.5 | 4.4 | 4.5 | 4.7	−0.1 | −0.2 | −0.1 | 0.1
log (Cephalopod reconstructed mass)	3	5054	46.2	<0.001	3.4 | 3.0 | 3.4 | 3.8	−0.2 | −0.5 | −0.1 | 0.3

The estimated effects are average responses due to the given treatment combinations, having adjusted for all model terms. For instance, the interaction effects are changes in response after adjusting for the grand mean and both main effects.

are similar, with bigger prey being consumed by franciscana dolphins during warmer months.

Dietary variation by sex

GLM analyses revealed that there were no differences in prey species preferences between male and female individuals for each site (Table 4), and Rényi index profiles exhibited high diversity similarity (Figure 2). Nevertheless, there were differences in reconstructed lengths and weights of cephalopod and fish specimens consumed by males *vs* females (Table 5). Females had consumed longer and heavier cephalopods and fish in the northern area than

males, while the males had ingested longer and heavier cephalopods in the south (Figure 3). Moreover, considering males and females for the whole study area, there were no significant differences in the estimated mass of prey ingested (all samples, $P < 0.001$).

Dietary variation by sexual maturity stage

Variation in the diet between sexually immature and mature franciscana dolphins was observed. The main fish species (*C. guatucupa* and *S. rastrifer*) and shrimp specimens ingested differed significantly between maturity stages in both the northern

and southern areas (Tables 4 and 6). Prey species richness is higher for immature dolphins, as the importance of the main prey species ingested (Figure 2). Although sexually mature dolphins consumed a lower diversity of species (Figure 2), the ingested prey specimens had greater reconstructed lengths and weights (all prey, df = 4394, $F = 457.9$, $P < 0.001$, see Figure 3). For cephalopods, it was only in the north that sexually mature animals consumed larger prey than immature animals (Figure 3).

Discussion

Dietary variation by area

The study region is influenced by the Brazil–Malvinas Confluence (BMC), an important confluence of two distinct cold (Malvinas/ Falklands) and warm (Brazil) currents, as well as variability in freshwater discharges from Patos Lagoon and subsurface upwellings (Piola et al., 2000; Möller et al., 2008). An important feature of the BMC is that its position oscillates seasonally and geographically along the study area, affecting the north and south coastal regions differently, which in turn influences the distribution and abundance of many franciscana dolphin prey species (Haimovici, 1997a, 1997b). Consequently, the most important prey of franciscana dolphin differed between the northern and southern regions of the study area, which was also reported in other studies comparing neighbourhood sites and franciscana sub-populations distributed in marine and estuarine areas in Argentina (Rodrígues et al., 2002; Denuncio et al., 2017). Despite the fact that these are adjacent areas and some diet differences also include cephalopod beak presence and absence (and these structures can remain months in the stomach), it seems that the animals are not swimming to distant areas. However, these dietary geographic differences have been discussed before suggesting that franciscana dolphin may occupy, and possibly for long periods, small spatial ranges (Bordino et al., 2002, 2008; Bassoi et al., 2020), suggesting some degree of residency (Crespo et al., 2010).

Seasonal diet variation

The demersal ichthyofauna of the southern Brazilian shelf is transitional between tropical and temperate zones and variation of species richness and relative abundance follows seasonal temperature variations in coastal waters (>10°C) (Haimovici et al., 1996). The results of this study confirm this seasonal variation, and it is possible that the southern region could be more influenced by colder water masses than the northern area (see Table 4). Warmer seasons seem favourable for franciscana dolphins to feed upon bigger prey such as T. lepturus and cephalopods that were clearly the items that had contributed most to their diet during this period. The greater ingestion of prey biomass in warmer seasons could be explained by the needs to increase fat reserves (blubber), as energy storage for colder seasons. These diet results corroborate studies on the concentration of total lipid in the blubber of franciscana dolphins, being higher for summer/spring, 357.4 mg g^{-1}, than in autumn/winter, 318.6 mg g^{-1} (Caon & Kucharski, 2000).

Sex-related diet variation

Prey species diversity identified from stomach contents of male and female franciscana dolphins were similar in both areas (see Figure 2), as observed using stable isotope analysis (Troina et al., 2016). We did not find significant differences of prey species abundance ingested by males and females (see Table 2), but there were disparities in some species occurrence (see Table 7). Males

from the northern coast appear to consume a higher number of species related to warm water masses from the Brazil Current (Haimovici, 1997a, 1997b), such as S. rastrifer and the cephalopods Doryteuthis plei and Argonauta nodosa. This is possibly related to the larger sample size of males, both in the northern and southern areas, during the warmer periods. This could also explain the ingestion of significantly larger cephalopods (by mantle length and weight) by males from the southern area (Haimovici & Perez, 1991; Santos, 1999). Females in both study areas also ingested shrimp species more frequently, which is in agreement with previous franciscana dolphin studies (Pinedo, 1982; Ott, 1994; Bassoi, 1997; Henning et al., 2017), and possibly related to parental guidance of juveniles/immature individuals, which show a high prevalence of shrimps in their diet (Bastida et al., 1992; Smith & Read, 1992; Danilewicz et al., 2002; Rupil et al., 2019; this study). Furthermore, crabs (e.g. Loxopagurus loxocheles, Dardanus insignis, Pleocyemata) occurred more frequently in females, all of which are benthic species abundant in shallow coastal waters (Capítoli, 1997). In terms of general prey numerical abundance, females consumed more fish than males, however, smaller fish specimens (recruits) were similar to the prey size ingested by immature dolphins. Overall, the findings of this study suggest that sexually mature females may be distributed closer to the coast than sexually mature males, at least in some periods (e.g. austral summer), as a result of juvenile guidance.

The reconstructed mass of all prey combined was similar for both males and females in the whole study area. Female dolphins have greater body lengths and extra demands for energy during pregnancy and lactation, but notably adult males had similar values of total prey biomass. This suggests that males, in spite of their smaller body mass, might be consuming more prey biomass than females. Swimming and travelling could be an extra demand for energy, as suggested previously for males. This finding is consistent with total lipid concentrations in franciscana dolphin blubber in southern Brazil, which are higher in males (369.3 mg g^{-1}) than females (296.9 mg g^{-1}) (Caon & Kucharski, 2000). Therefore, it might be possible that the males are using a different habitat for feeding than females, where males' movements would not be so restricted to the coast as females, or they could be swimming to deeper areas or further along the coast. These differences, however, should be further investigated.

Dietary variation by sexual maturity stage and prey size selection

Overall, sexually immature franciscana dolphins ingested smaller prey than sexually mature individuals (see Figure 3). The observed differences in reconstructed fish prey size (length and weight) at time of ingestion between maturity groups is likely to be a result of young animals consuming more juvenile fishes, and sexually mature animals consuming more of the subadult and adult size fishes. The majority of small teleosts consumed by immature dolphins were estimated to be the size typical of densely schooling demersal recruits (<50 mm) distributed throughout the coastal continental shelf off southern Brazil (Haimovici et al., 1996; Martins & Haimovici, 2016; Pio et al., 2016). Thus, it seems that immature franciscana dolphins are not only ingesting the most abundant and available resource in the area as well as easier prey to catch than marine shrimps, (Dall et al., 1990) one of the first prey consumed by immature dolphins.

In contrast, sexually mature franciscana dolphins appear to be feeding more selectively, consuming larger fish prey with greater biomass. Other studies demonstrated franciscana dolphin predation on a variety of teleosts with mean total length greater than 150 mm, representing the fish subadult sizes for many species
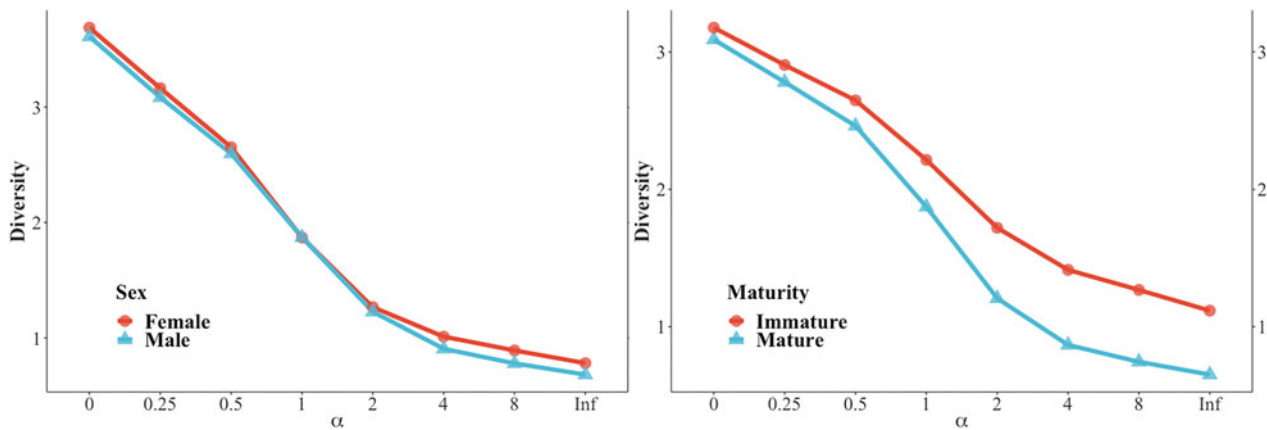
Fig. 2. Prey species richness and diversity profiles of Rényi comparing the franciscana dolphin groups (sex and sexual maturity). The Rényi diversity profile at scale 0 reflects species richness, at scale 1 the Shannon index, at scale 2 the Simpson index and at scale Inf the Berger–Parker index (the dominance of the most abundant prey species).
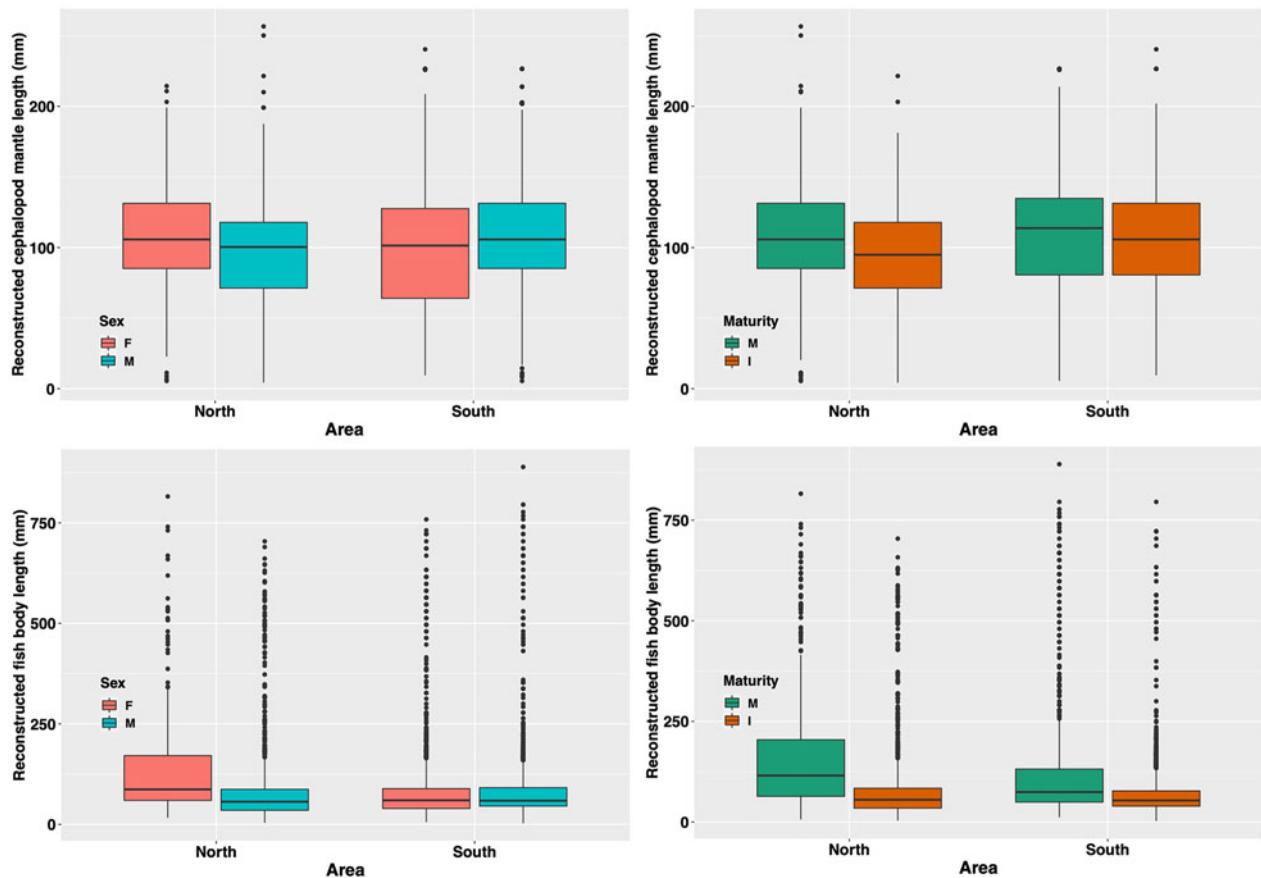
Fig. 3. Ontogenetic variation in reconstructed lengths of prey items (cephalopod beaks = 6192 and fish otoliths = 4443) recovered from the stomachs of by-caught franciscana dolphins from the two study areas (north = 98, south = 172) off the southern Brazilian coast. The horizontal line in the interior of the box is located at the median of the data. The height of the box is equal to the interquartile range, and the outliers are drawn individually, indicated as circles. All the points more than 1.5*(Inter-Quartile Range) are considered outliers.

(Ott, 1994; Rivero *et al.*, 2000; Bittar & Di Beneditto, 2009; Machado *et al.*, 2020). An example is *T. lepturus*, which had a mean length of over 400 mm (subadults), and various specimens greater than 700 mm, categorized as adult size (Martins & Haimovici, 1997). Overall, it seems likely that franciscana dolphins eat more of the most available prey in the area (Bassoi & Secchi, 2000), in many cases recruit teleosts (Haimovici *et al.*, 1996), but when subadult and adult fish are also abundant (>100 mm, e.g. *T. lepturus*, *Urophycis brasiliensis*), adult dolphins appear to select such prey.

Additionally, franciscana dolphins do appear to select larger squid, because the average size of squid preyed on by this dolphin (106.5 mm, see Table 3) was higher than those found during research surveys in this area, especially in summer, where the mantle length average was 58.4 mm (Andriguetto & Haimovici, 1991; Santos, 1999). Paso-Viola *et al.* (2014) found that franciscana dolphin, mainly adult animals, do appear to select larger squid because most cephalopods consumed in southern Buenos Aires were mature individuals (>110 mm), and franciscana dolphins in the Babitonga Bay estuary (Brazil) ingested bigger

Table 6. A summary of the prey species composition and relative importance of prey items (N %, W %, O % and IRI) for sexual mature and immature individuals from southern and northern coastal regions of the study area

| | Southern area | | | | | | | | Northern area | | | | | | | |
| | Mature (N = 72) | | | | Immature (N = 100) | | | | Mature (N = 44) | | | | Immature (N = 46) | | | |
Prey items	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI
Fish																
Cynoscion guatucupa	45.4	65.3	14.0	3876.5	57.4	65.7	24.8	5393.7	5.2	15.9	0.0	127.2	8.0	39.1	0.5	224.8
Trichiurus lepturus	9.3	48.6	34.6	2132.8	3.9	28.3	23.6	778.4	12.3	56.8	34.2	2645.1	6.2	54.3	41.0	2564.0
Paralonchurus brasiliensis	11.7	40.3	7.7	781.1	5.7	30.3	15.1	632.0	22.0	38.6	15.2	1435.8	5.4	37.0	13.8	710.4
Urophycis brasiliensis	6.9	34.7	18.4	879.6	3.8	24.2	2.4	152.0	17.4	43.2	20.4	1632.3	9.6	32.6	3.4	422.9
Anchoa marinii	10.2	25.0	0.8	274.4	11.8	31.3	2.4	445.3	3.2	13.6	0.1	45.8	2.0	15.2	0.7	41.9
Porichthys porosissimus	4.1	20.8	5.9	208.0	3.6	22.2	3.4	155.9	5.5	15.9	5.8	180.4	3.6	30.4	3.4	213.4
Umbrina canosai	3.1	12.5	3.3	79.7	6.2	13.1	11.3	228.8	5.9	15.9	4.8	170.3	4.1	23.9	0.1	101.1
Peprilus paru	0.7	5.6	0.1	4.4	1.9	9.1	0.4	20.8					0.2	6.5		1.3
Engraulis anchoita	2.0	8.3	0.6	21.9	1.0	7.1	0.8	12.3	2.7	6.8	0.9	24.3	0.5	6.5	0.5	6.9
Micropogonias furnieri	0.8	4.2	2.7	14.7	1.4	6.1	2.7	24.4					1.5	10.9	4.6	67.2
Merluccius hubbsi	0.5	5.6	0.1	3.2	0.7	4.0	0.1	3.0								
Macrodon ancylodon	0.5	5.6	3.8	23.7	0.8	4.0	7.5	33.5	1.5	6.8	2.6	27.9				
Cynoscion jamaicensis	0.6	6.9	3.4	28.1	0.4	1.0	0.0	0.5	1.3	4.5	2.7	18.4	5.8	15.2	3.1	135.2
Pomatomus saltator	1.1	2.8	0.6	4.6	0.3	4.0	0.2	2.0								
Prionotus sp.	0.2	2.8	0.0	0.6	0.8	3.0	1.6	7.1								
Menticirrhus sp.	0.5	5.6	0.7	6.7	0.0	1.0	0.0	0.1	1.3	11.4	12.6	158.3	1.3	6.5	5.6	45.2
Raneya fluminensis	0.1	1.4	0.6	1.0	0.1	2.0	3.7	7.8								
Trachurus lathami	0.1	1.4	0.0	0.1	0.1	2.0	0.0	0.2	0.6	4.5	0.0	2.8	1.2	13.0	1.0	28.1
Syacium papillosum	1.6	4.2	1.5	12.9												
Mugil sp.	0.1	1.4	1.0	1.5	0.0	1.0	0.0	0.0								
Paralichthys isosceles	0.1	1.4	0.0	0.1												
Stellifer rastrifer					0.0	1.0	0.1	0.1	3.2	31.8	0.1	106.0	39.1	60.9	21.6	3697.0
Stromateus brasiliensis	0.6	1.4	0.1	1.0					0.2	2.3	0.2	1.0				
Pagrus pagrus													0.1	2.2	0.5	1.4
Ctenosciena gracilicirrhus									0.6	4.5	0.1	3.2	0.1	2.2	0.1	0.5
Licengraulis grossidens													0.1	2.2		0.1
Cephalopod																
Doryteuthis sanpaulensis	96.4	91.7	99.1	17,924.2	99.1	66.7	99.5	13,243.9	95.6	81.8	96.6	15,719.7	93.5	67.4	96.1	12,774.1

(Continued)

Table 6. (*Continued.*)

| | Southern area | | | | | | | | Northern area | | | | | | | |
| | Mature (N = 72) | | | | Immature (N = 100) | | | | Mature (N = 44) | | | | Immature (N = 46) | | | |
Prey items	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI
Doryteuthis plei	0.7	12.5	0.7	16.4	0.4	9.1	0.5	7.4	2.2	9.1	3.1	48.2	2.6	6.5	3.9	42.6
Argonauta nodosa	2.8	20.8	0.2	62.5	0.4	15.2	0.0	5.7	2.0	15.9	0.1	34.3	3.9	2.2	0.0	8.5
Octopus tehuelchus	0.1	1.4	0.0	0.1	0.1	1.0	0.0	0.1	0.2	2.3	0.2	0.9				
Semirossia tenera	0.1	1.4	0.0	0.1	0.0	1.0	0.0	0.0								
Eledone sp.	0.1	1.4	0.0	0.1												
Crustacean																
Pleoticus muelleri	7.3	4.2			20.4	10.1										
Artemesia longinaris	2.4	1.4			24.7	6.1										
Loxopagurus loxocheles	9.8	5.6			2.2	2.0										
Dardanus insignis	2.4	1.4														
Penaeidae	4.9	2.8			18.3	12.1										
Penaeoidea	9.8	5.6			8.6	8.1							54.5	26.1		
Brachiura	4.9	2.8														
Pleocyemata	14.6	6.9			2.2	2.0										
Dendrobranchiata					1.1	1.0										
Isopoda	39.0	8.3			17.2	4.0			100.0	45.5			40.9	19.6		

Table 7. A summary of the prey species composition and relative importance of prey items (% N, % W, % O and IRI) for male and female individuals from southern and northern coastal regions of the study area

Prey items	Southern area								Northern area							
	Male (N = 100)				Female (N = 72)				Male (N = 44)				Female (N = 28)			
	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI
Fish																
Cynoscion guatucupa	49.2	68.0	16.7	4478.6	59.5	61.1	18.7	4777.5	5.2	27.3	0.3	149.6	1.7	14.3	0.2	26.9
Trichiurus lepturus	5.7	38.0	37.2	1629.1	5.4	34.7	24.9	1051.8	6.5	59.1	37.6	2610.6	8.8	46.4	24.0	1525.9
Paralonchurus brasiliensis	7.4	35.0	12.9	708.1	7.7	33.3	7.9	522.9	6.1	34.1	13.3	659.3	20.9	46.4	19.9	1894.8
Urophycis brasiliensis	5.0	31.0	8.1	405.3	4.5	25.0	17.2	541.6	10.4	36.4	3.2	495.2	15.5	39.3	26.4	1645.4
Anchoa marinii	14.5	30.0	1.8	490.2	7.3	26.4	0.9	217.0	1.4	11.4	0.4	20.2	6.9	21.4	0.5	158.2
Porichthys porosissimus	4.9	19.0	1.2	115.1	2.4	25.0	8.5	272.2	2.3	25.0	4.3	166.3	6.9	28.6	4.7	330.1
Umbrina canosai	6.9	15.0	4.7	174.3	3.2	9.7	7.3	101.9	2.5	18.2	6.5	164.2	2.9	14.3	0.6	50.5
Peprilus paru	0.8	7.0	0.1	6.3	2.5	8.3	0.2	22.7	0.1	4.5		0.7				
Engraulis anchoita	1.7	9.0	1.2	26.3	0.7	5.6	0.2	5.2	1.0	6.8	1.3	15.5	2.2	10.7	0.5	29.4
Micropogonias furnieri	0.7	5.0	1.9	13.1	1.8	5.6	3.5	29.0	1.4	9.1	1.4	25.2	1.2	3.6	3.1	15.6
Merluccius hubbsi	0.6	6.0	0.1	4.0	0.7	2.8	0.1	2.1								
Macrodon ancylodon	0.4	4.0	6.0	25.6	1.0	5.6	4.2	29.3	0.1	2.3	2.4	5.7	0.2	3.6	0.4	2.3
Cynoscion jamaicensis	0.1	1.0	0.0	0.1	1.0	6.9	4.2	36.3	6.6	15.9	6.9	215.1	1.5	3.6	0.0	5.3
Pomatomus saltator	0.7	4.0	0.5	4.9	0.4	2.8	0.3	2.0								
Prionotus sp.	0.1	1.0	1.1	1.2	1.2	5.6	0.1	7.1								
Menticirrhus sp.	0.1	2.0	0.5	1.2	0.3	4.2	0.4	3.0	1.6	6.8	5.3	47.0	0.7	10.7	15.0	168.8
Raneya fluminensis	0.2	2.0	2.9	6.1	0.1	1.4	0.7	1.0								
Trachurus lathami	0.1	3.0	0.0	0.5					0.4	6.8	0.3	4.9	0.2	3.6	0.1	1.2
Syacium papillosus	0.6	2.0	1.5	4.2	0.4	1.4	0.5	1.2								
Mugil sp.	0.0	1.0	1.4	1.4	0.1	1.4	0.0	0.1								
Paralichthys isoceles					0.1	1.4	0.0	0.1								
Stellifer rastrifer	0.0	1.0	0.0	0.1					40.9	47.7	16.4	2733.0	15.0	42.9	4.5	836.6
Stromateus brasiliensis	0.3	1.0	0.1	0.4					0.1	2.3	0.3	0.9				
Pagrus pagrus									0.1	2.3	0.0	0.4				
Ctenosciena gracilicirrhus									0.1	4.5	0.1	0.9				
Licengraulis grossidens									0.1	2.3						
Cephalopod																
Doryteuthis sanpaulensis	98.4	82.0	99.6	16,376.0	97.4	81.9	98.6	16,055.8	91.5	63.6	94.4	11,831.3	97.1	78.6	97.7	15,309.0

Table 7. (*Continued.*)

Prey items	Southern area								Northern area							
	Male (N = 100)				Female (N = 72)				Male (N = 44)				Female (N = 28)			
	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI	% N	% O	% W	IRI
Doryteuthis plei	0.3	7.0	0.2	3.6	0.9	11.1	1.3	24.9	3.3	11.4	5.5	100.1	2.0	7.1	2.3	30.5
Argonauta nodosa	1.3	11.0	0.1	16.1	1.3	12.5	0.1	16.9	5.2	13.6	0.1	71.9	0.9	3.6	0.0	3.2
Octopus tehuelchus					0.3	4.2	0.0	1.2								
Semirossia tenera					0.1	2.8	0.0	0.4								
Eledone sp.					0.1	1.4	0.0	0.1								
Crustacean																
Pleoticus muelleri	7.7	6.0			27.1	9.7										
Artemesia longinaris	26.9	4.0			10.2	5.6										
Loxopagurus loxocheles	2.6	2.0			6.8	5.6										
Dardanus insignis					1.7	1.4										
Penaeidae	16.7	8.0			10.2	8.3										
Penaeoidea	10.3	8.0			6.8	5.6			33.3	13.6			29.4	17.9		
Brachiura	1.3	1.0			1.7	1.4										
Pleocyemata					13.6	9.7										
Dendrobranchiata					1.7	1.4										
Isopoda	26.9	6.0			18.6	5.6			61.1	25.0			70.6	42.9		

cephalopods than the larger co-occurring Guiana dolphins (Cremer *et al.*, 2012). In conclusion, franciscana dolphins have fairly opportunistic behaviour in terms of prey abundance and occurrence, although for some prey species the dolphin has a preference for bigger specimens, mainly selected from adult individuals.

Ontogenetic shifts in diet

Ontogenetic dietary differences may be the result of changing foraging or physiological abilities (Frainer *et al.*, 2015), the relative importance of energy intake (Hin *et al.*, 2019) or differences in experience (i.e. culture). The prey consumed by sexually mature individuals in this study suggest active foraging behaviour and high mobility (Clarke, 1997; Santos & Haimovici, 2001), and feeding on the larger individuals in the spawning grounds allows the predator to take protein at its maximum production and concentration (Clarke, 1997). Further, studies on caloric values of franciscana dolphin prey have shown that squid have greater gross energy content than fish (Di Beneditto *et al.*, 2009). Energy requirements are higher for larger individuals, but the variations of feeding regimes between sexual maturity categories could also indicate a degree of adaptation to minimize prey competition within the population (Nikolsky, 1963). Minimizing interspecific competition for prey is also suggested by Teixeira *et al.* (2020) showing lower niche overlap between franciscana dolphins and two other coastal dolphin species.

In terms of physiological ability, the maturation of the echolocation system of young individuals is likely to be related to their prey preferences (Frainer *et al.*, 2015), as well their experience in detecting prey. Passive listening would increase efficiency of capturing soniferous fish species, therefore, franciscana dolphins may obtain useful information by listening, such as prey identification and location, body size and number of fish present (Tellechea *et al.*, 2017), as was described for common bottlenose dolphins (*Tursiops truncatus*) in Florida (USA) (Barros & Wells, 1998; McCabe *et al.*, 2010). This foraging behaviour would likely increase in efficiency as the dolphin ages, with sexually mature individuals being more experienced in both tracking and capturing their prey.

In summary, dietary variations between sex and sexual maturity groups of franciscana dolphin could indicate that these groups select certain prey types over others, potentially as a result of (1) ability to capture particular prey, (2) a degree of adaptation to minimize prey competition within the population, (3) differential use of habitat and/or (4) other unknown pattern of niche segregation as described for other marine species (e.g. Phillips *et al.*, 2004).

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