



## Geographical and intrapopulation variation in the diet of a threatened marine predator, *Pontoporia blainvillei* (Cetacea)

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### ABSTRACT

Understanding diet variation is a major concern when developing conservation guidelines for threatened species, especially for marine predators whose prey availability can be reduced by commercial fisheries. Diet can vary in geographically structured populations due to variation in prey availability and within a location due to the effects of season, sex, age, and individual. However, these sources of variation are seldom considered together in dietary studies. We analyzed diet variation at the geographical and intrapopulation levels in the franciscana dolphin (*Pontoporia blainvillei*) by analyzing samples of stomach contents from individuals incidentally caught by artisanal fisheries. We investigated the geographical (Northern, Central, and Southern regions of the São Paulo State coast, Brazil) and intrapopulation effects of season, sex, and age. We used the leave-one-out cross-validation method to test for significance of the proportional similarity index, which measures the overlap between diet compositions. We found that diet varied across different levels, from the geographical to the individual level, including the effects of season, sex, and age. Diet variation as a function of age suggests an ontogenetic diet shift. Our findings indicate that ecological processes within local stocks should inform management at the local geographic scale. Evidence for ecological differences between franciscana stocks is of great significance for the conservation of this threatened species.

Abstract in Portuguese is available with online material.

*Key words:* conservation; franciscana dolphin; Index of Relative Importance; interindividual variation; ontogenetic diet shift; proportional similarity index; stomach contents.

VARIATION IN DIET HAS BEEN DOCUMENTED AMONG AND WITHIN GEOGRAPHICAL LOCATIONS, BUT THE FACTORS UNDERLYING THIS VARIATION ARE POORLY UNDERSTOOD (Rendell & Whitehead 2001, Nowacek 2002, Mann & Sargeant 2003). Diet is expected to vary by location because foraging success, as well as prey selection and availability, is affected by habitat structure and patterns of prey distribution (Heithaus & Dill 2002, Sargeant *et al.* 2007). Diet is also expected to vary within geographical locations due to the effects of season, sex, morphology, and age (Schoener 1968, Bolnick *et al.* 2003, Martins *et al.* 2008, Pires *et al.* 2013). Residual diet variation that is not attributable to factors such as sex or age class, defined as interindividual variation (Bolnick *et al.* 2003), can be associated with phenotypic and behavioral differences among individuals. Defining how each source contributes to variation in diet is crucial for assessing species' ecological patterns and their role in communities (Estes *et al.* 2003). However, all of these sources of variation in diet are rarely considered together. The potential sources should be addressed using a hierarchical

approach, from the most general factor to the most specific, to fully understand the feeding ecology in a system.

Dietary studies on marine predators are particularly relevant because they provide information on the diving and foraging behaviors, distribution, and ecological role of the species (Pauly *et al.* 1998, Santos *et al.* 2001, Fernández *et al.* 2011, Troina *et al.* 2016). Furthermore, dietary studies also contribute information about available biomass of the prey populations, competition between predators, interactions between predators and species targeted by commercial fisheries, and fluctuations in community structure (Santos *et al.* 2001). In addition to its important contribution to dynamic models of community and ecosystem function (Santos *et al.* 2001), dietary information is crucial for establishing conservation guidelines for threatened species, especially marine predators whose prey is often targeted by commercial fisheries (Heithaus *et al.* 2008).

The overlap between the diets of marine predators and prey targeted by commercial fisheries not only reduces their prey availability, but it also leads to their incidental capture, i.e., bycatch (Secchi *et al.* 1997, Santos *et al.* 2001). Bycatch is more likely to occur when there is great overlap between the diet of the

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predator and the commercial fisheries (Secchi *et al.* 2003). Indeed, the increase in frequency and intensity of interactions between marine predators and commercial fisheries makes bycatch a major threat to marine predators worldwide (Secchi *et al.* 1997, Bowen & Siniff 1999, Lewison *et al.* 2004, Reeves *et al.* 2012). Although the loss of a predator often results in dramatic changes in community structure (Terborgh *et al.* 2010), marine predators have poorly described diets due to the logistical challenges in studying these organisms (McPeck 1998, Denno & Lewis 2009).

Historical catch records from southern Brazil have demonstrated a shift in yearly landings of fish species in this region, with a reduction in the occurrence of some species and an increase in others (Haimovici *et al.* 1997, Haimovici 1998). This shift has occurred due to differential fishing pressure on species by commercial fisheries, with potential consequences for a highly threatened marine predator, the franciscana dolphin (*Pontoporia blainvillei*). A shift in the diet of the franciscana dolphin did occur after these changes in prey availability (Secchi *et al.* 2003, b), which may have been caused by a reduction in prey species due to over-exploitation by commercial fisheries. A study suggested that this shift in diet could reduce the reproductive success of this dolphin species (Secchi *et al.* 2003b).

The highly threatened franciscana dolphin is endemic to southwestern Atlantic coastal waters, occurring from Itaúnas in Brazil to Golfo San Matías in Argentina (Crespo *et al.* 1998, Siciliano *et al.* 2002). The effect of bycatch on the franciscana dolphin makes it the most endangered cetacean in the South Atlantic Ocean, and it is designated as vulnerable throughout its distribution area by the International Union for Conservation of Nature (Reeves *et al.* 2012). At least 2900 franciscana dolphins undergo bycatch each year throughout their distribution area (Ott 2002, Secchi *et al.* 2003, b). Furthermore, this number is thought to be underestimated due to unreported captures by non-monitored fisheries, under-reporting of bycatch by fishermen, and captured dolphins falling from the net before or during haul-out (Secchi *et al.* 2003b).

Major efforts have been undertaken to investigate geographical variation in the franciscana dolphin across its distribution range because the level of threat differs by locale (Ramos *et al.* 2002, Secchi *et al.* 2003, Mendez *et al.* 2008, 2010, Cunha *et al.* 2014). Evidence of geographical variation in the franciscana dolphin comes from phylogeographic analysis of mtDNA sequences combined with data on geographical distribution, life-history traits, and morphological variation (Rosas 2000, Ramos *et al.* 2002, Secchi *et al.* 2003, Mendez *et al.* 2010, Cunha *et al.* 2014). Four Franciscana Management Areas (FMAs) have been established to accommodate the already known geographical variation and to improve conservation and management actions at the local level (Secchi *et al.* 2003). FMA I includes Rio de Janeiro and Espírito Santo States (Brazil); FMA II includes São Paulo, Paraná, and Santa Catarina States (Brazil); FMA III includes Rio Grande do Sul State (Brazil) and Uruguay; and FMA IV covers the range of franciscana dolphins in Argentine waters (Fig. S1A).

Evidence for genetic geographical variation within FMAs associated with environmentally distinct areas comes from

analyses combining mtDNA sequences, microsatellite markers, and environmental data (Mendez *et al.* 2010, Costa-Urrutia *et al.* 2012). Specifically, the mitochondrial DNA control region in the franciscana dolphin differs among the Northern, Central, and Southern regions of São Paulo State (Cunha *et al.* 2014). In addition, contaminant profiles in franciscana dolphin tissues suggest the existence of stocks within São Paulo State (Alonso 2008, Lailson-Brito *et al.* 2011). São Paulo State has a heterogeneous geomorphologic formation throughout its coastal plain and is divided into three marked regions: Northern, Central, and Southern (Fig. S1B). The Northern region has the roughest shape, with hills close to the sea forming bays and coves (IPT 1981, Ab'Saber 2000, Souza & Cunha 2011). The Central region has long sandspit lines, and its coastal plain has a smoother shape (IPT 1981, Ab'Saber 2000, Souza & Cunha 2011). The Southern region has restinga areas separated by brackish water lagoons with mangroves along the restinga borders, the hills are far from the ocean, and the coastal plain is large with a smooth shape (IPT 1981, Ab'Saber 2000, Souza & Cunha 2011).

The diet of most marine mammals is expected to vary geographically (Pierce & Boyle 1991, Basso & Secchi 1999, Danilewicz *et al.* 2002). The diet of the franciscana dolphin has been described mainly by qualitative studies, and diet composition was reported to vary throughout the species distribution (Pinedo 1982, Rodríguez *et al.* 2002, Bittar & Di Benedetto 2009, Cremer *et al.* 2012). Therefore, we expected geographical variation in diet among the Northern, Central, and Southern regions of the São Paulo State coast. Variations in the diet of the franciscana dolphin also appear to be associated with seasonal variation in the abundance of prey (Danilewicz *et al.* 2002), which varies seasonally throughout the coast of São Paulo State (Ávila-da-Silva *et al.* 2005, Muto *et al.* 2014, Mendonça 2015). Other than one study within Rio Grande do Sul State coast (Basso 2005), quantitative studies on the effects of seasonality, sex, age class, or individual as sources of variation in the diet of the franciscana dolphin are lacking.

Franciscana dolphins are sexually dimorphic, with females larger than males, which might be associated with reproductive strategies and differential access to food resources (Pinedo 1991, Ramos *et al.* 2002, Troina *et al.* 2016). Preliminary, qualitative analyses indicate that female and male franciscana dolphins differ in the most important prey species in their diets (Danilewicz *et al.* 2000). Furthermore, analyses of ontogenetic diet variation in the franciscana dolphin revealed that the number of prey species consumed increases markedly with age, probably due to the learning process of prey search and capture (Rodríguez *et al.* 2002, Troina *et al.* 2016). Finally, individual variation in the diet of the franciscana dolphin has not previously been investigated, although this variation has been convincingly demonstrated in marine predators such as the bottlenose dolphin (*Tursiops* sp.; Sargeant *et al.* 2007) and sea otters (*Enhydra lutris*; Estes *et al.* 2003).

Here, we used a hierarchical statistical framework to decompose the factors that influence the diet of *P. blainvillei*. First, we evaluated the effects of space and time on the diet by examining dietary data for individuals sampled throughout the study area.

We then focused on a larger sample from a single region to evaluate the effects of sex, age, and individual variation.

## METHODS

**SAMPLE COLLECTION.**—We analyzed samples of franciscana dolphins ( $N = 58$ ) incidentally caught by artisanal gillnet fisheries from the Northern ( $N = 11$ , municipalities of Ubatuba, Ilhabela, Caraguatatuba, and São Sebastião), Central ( $N = 40$ , municipalities of Bertioga, Guarujá, Santos, São Vicente, Praia Grande, Mongaguá, Itanhaém, and Peruíbe), and Southern regions ( $N = 7$ , Iguape, Ilha Comprida, and Cananéia) of the São Paulo State coast in Brazil (Fig. S1B).

In most cetacean species, postnatal growth comprises three stages. Growth is exponential during the first year of life (Bryden 1972). Subsequently, growth slows and tends to be linear until sexual maturity, after which it approaches an asymptote (Bryden 1972). We classified franciscana dolphins into juveniles ( $N = 8$ ), subadults ( $N = 18$ ), or adults ( $N = 32$ ) according to total length. For females ( $N = 34$ ), juveniles were  $<90$  cm, subadults were  $>90$  cm and  $<119$  cm, and adults were  $>119$  cm. For males ( $N = 24$ ), juveniles were  $<90$  cm, subadults were  $>90$  cm and  $<107$  cm, and adults were  $>107$  cm (Ramos & Di Benedetto 2005, Bertozzi *et al.* 2010). The detailed distribution of specimens of franciscana dolphin bycaught according to region, season, sex, and age is shown in Table 1.

We kept bycaught specimens on ice for transport from the fishery to the laboratory, and we performed autopsies within 24 h after death. We excised stomachs, including all of the chambers, and froze them for later analysis. To collect prey remains, we unfroze the stomachs, washed stomach contents through a 0.5-mm sieve, and inspected the sieve for fish otoliths (*sagittal*), cephalopod beaks, and crustacean exoskeletons. We identified prey remains to the lowest possible taxon; remains that were excessively eroded or broken were not identified or measured. We estimated the number of fish ingested based on the total number of left or right otoliths (whichever was more numerous) plus half the number of eroded otoliths. We estimated the number of cephalopods ingested based on the total number of upper or lower beaks (whichever was more numerous) plus half the number of broken beaks.

**DATA DESCRIPTION.**—We identified fish otoliths via comparison with a reference collection from Laboratório de Ictiofauna e Crescimento (LABIC from Instituto Oceanográfico of the Universidade de São Paulo) and by using published guides (Figueiredo & Menezes 1980, Corrêa & Vianna 1992, Lêmos *et al.* 1992, Chao 2001, Di Benedetto *et al.* 2001, Waessle *et al.* 2003, Monteiro *et al.* 2005, Tuset *et al.* 2008, Volpedo *et al.* 2008, Pansard 2009). Specialists on respective taxa identified, quantified, and measured cephalopod beaks and crustaceans. Because most of the crustacean species identified are isopods that behave like fish parasites (Ana Setúbal Pires Vanin, personal communication), we did not consider them as franciscana dolphin prey. All of the taxa identified are listed in Table 2.

TABLE 1. Distribution of specimens of franciscana dolphin (*Pontoporia blainvillei*) bycaught along São Paulo state coast according to region of the bycatch, season, sex, and age.

	Spring	Summer	Fall	Winter	Total
<b>Northern region</b> ( $n = 11$ )					
Female	1	3	1	1	6
Male	0	2	0	3	5
	1	5	1	4	
Adult	0	5	1	2	8
Subadult	1	0	0	2	3
Juvenile	0	0	0	0	0
	1	5	1	4	
<b>Central region</b> ( $n = 40$ )					
Female	8	8	5	5	26
Male	3	3	2	6	14
	11	11	7	11	
Adult	2	4	6	6	18
Subadult	7	1	1	5	14
Juvenile	2	6	0	0	8
	11	11	7	11	
<b>Southern region</b> ( $n = 7$ )					
Female	0	1	1	0	2
Male	1	3	1	0	5
	1	4	2	0	
Adult	1	3	2	0	6
Subadult	0	1	0	0	1
Juvenile	0	0	0	0	0
	1	4	2	0	
<b>São Paulo State Coast</b> ( $n = 58$ )					
Female	9	12	7	6	34
Male	4	8	3	9	24
	13	20	10	15	
Adult	3	12	9	8	32
Subadult	8	2	1	7	18
Juvenile	2	6	0	0	8
	13	20	10	15	

We estimated the original length and mass of prey items based on their remains using power equations (Table 2). Power equations are derived from differential equations that model growth in the dimensions of two body parts under the assumption that the body parts grow exponentially (Huxley & Teissier 1936, Nijhout & German 2012). For fish, we used power equations that we developed, whereas for cephalopods, we followed Santos (2009) and Santos and Haimovic (1997). We measured otolith length and width using photographs (Auto Montage software with precision of 0.01 mm) taken with a digital camera coupled to a stereomicroscope. For each species in each sample, we used the left or right otolith measurement (whichever was more numerous) as input for the equations to estimate the original prey size. Similarly, we estimated squid size based on the size of the

TABLE 2. Taxa identified in stomachs of *Pontoporia blainvillei* bycaught along São Paulo state coast. Fish length–weight power equations estimated from the LABIC database.

Prey species	Ln (TL)	<i>n</i>	R <sup>2</sup>	Ln (Weight)	<i>n</i>	R <sup>2</sup>
Teleostei						
<i>Anchoa filifera</i>	4.128 + 0.843*ln(OL)	4	0.997	0.303 + 2.784*ln(OL)	4	1.000
<i>Cetengraulis edentulus</i>	3.510 + 1.076*ln(OL)	232	0.805	−1.679 + 3.485*ln(OL)	106	0.893
<i>Chirocentrodon bleekermanus</i>	3.916 + 0.878*ln(OL)	82	0.827	1.577 + 3.551*ln(OL)	119	0.946
<i>Ctenosciaena gracilicirrhus</i>	3.286 + 0.877*ln(OL)	22	0.814	636 + 0.785*ln(OL)	21	0.852
<i>Cynoscion guatucupa</i>	3.691 + 0.759*ln(OL)	40	0.971	−0.578 + 2.357*ln(OL)	40	0.958
<i>Cynoscion jamaicensis</i>	3.738 + 0.660*ln(OL)	45	0.981	−0.530 + 2.135*ln(OL)	45	0.939
<i>Cynoscion virescens</i>	3.718 + 0.696*ln(OL)	86	0.968	−0.541 + 2.216*ln(OL)	86	0.940
<i>Isopisthus parvipinnis</i>	3.642 + 1.045*ln(OL)	75	0.949	−0.853 + 3.433*ln(OL)	81	0.944
<i>Larimus breviceps</i>	3.383 + 1.073*ln(OL)	38	0.955	−1.256 + 3.553*ln(OL)	37	0.970
<i>Lycengraulis grossidens</i>	TL = (2.549*OL)+ 1.646 <sup>a</sup>	8	0.655	W = 0.344*OL <sup>3.108a</sup>	8	0.715
<i>Menticirrhus americanus</i>	3.665 + 1.223*ln(OL)	12	0.968	−0.791 + 3.780*ln(OL)	12	0.991
<i>Micropogonias furnieri</i>	3.986 + 0.667*ln(OL)	23	0.941	0.157 + 2.207*ln(OL)	25	0.947
<i>Orthopristis ruber</i>	3.718 + 0.696*ln(OL)	86	0.968	−0.541 + 2.216*ln(OL)	86	0.940
<i>Pagrus pagrus</i>	TL = 16.272*LO <sup>1.229a</sup>	27	0.989	W = 0.067*OL <sup>3.675a</sup>	27	0.986
<i>Paralanchurnus brasiliensis</i>	3.556 + 1.191*ln(OL)	43	0.975	−1.551 + 3.979*ln(OL)	43	0.979
<i>Pellona barroweri</i>	4.029 + 0.608*ln(OL)	88	0.974	0.552 + 1.842*ln(OL)	88	0.979
<i>Peprilus paru</i>	3.305 + 0.955*ln(OL)§	33	0.812	−0.661 + 2.639*ln(OL)	32	0.822
<i>Pogonias cromis</i>	3.718 + 0.696*ln(OL)	86	0.968	−0.541 + 2.216*ln(OL)	86	0.940
<i>Serranus auriga</i>	3.578 + 0.756*ln(OL)	8	0.870	−0.631 + 2.552*ln(OL)	8	0.865
<i>Stellifer brasiliensis</i>	3.568 + 1.213*ln(OL)	51	0.843	−0.746 + 3.719*ln(OL)	31	0.901
<i>Stellifer rastrifer</i>	3.730 + 1.127*ln(OL)	118	0.861	−0.292 + 3.555*ln(OL)	118	0.875
<i>Trichiurus lepturus</i>	5.193 + 0.898*ln(OL)	172	0.989	0.627 + 2.952*ln(OL)	180	0.977
<i>Umbrina canosai</i>	2.846 + 1.194*ln(OL)	135	0.896	−2.629 + 3.623*ln(OL)	135	0.897
Cephalopods						
<i>Doryteuthis plei</i>						
<i>Doryteuthis sanpaulensis</i>						
<i>Loliguncula brevis</i>						
Crustacea						
<i>Aegatboa</i> sp.						
<i>Ceratotboa</i> sp.						
<i>Cymothoa</i> sp.						

TL, total length.

<sup>a</sup>Equations for *L. grossidens* and *P. pagrus* are from Di Benedetto et al. (2001).

upper or lower squid beaks. Because there was no reference to fish length–weight estimation curves for the São Paulo State coast, we estimated the parameters of the power equations using the LABIC collection and data base containing the length and wet mass of fish together with the length of their otoliths.

STATISTICAL ANALYSIS.—We calculated the Index of Relative Importance, IRI (Pinkas et al. 1971), for each prey species to describe the diet of the franciscana dolphin as follows:

$$\text{IRI} = (N + W) \cdot \text{FO}, \quad (1)$$

where *N* is the percentage of numerical abundance of prey, *W* is the percentage of prey estimated biomass, and FO is the percentage of stomach content samples in which a prey taxon occurred.

We assigned individuals to each of the three regions—Northern, Central, and Southern—according to where they were bycaught. To test for a geographical effect on the diet of the franciscana dolphin, we first calculated the pairwise overlap between the pooled diets representing each of the three regions using Schoener's (1968) proportional similarity index (*PS*), which varies from zero (no overlap) to 1 (total overlap). We then calculated the average overlap between regions ( $\overline{PS}$ ). Because we wanted a measure of diet variation (as opposed to overlap) among regions, we computed  $V = 1 - \overline{PS}$ , so that larger values of *V* indicate stronger diet variation among regions. To test the significance of *V*, we performed a resampling procedure under the assumption that individuals from different regions sample their diets randomly from a common pool of resources (the average of the proportional contributions of each resources in each of the three regions). We assigned *M<sub>k</sub>* items drawn from the



common pool of resources via multinomial sampling to the dietary profiles of each subpopulation, where  $M_k$  is the empirical number of items found in the stomachs of all individuals from each region. We then calculated  $V$  for each of the resampled diets (10,000) to generate a null distribution of  $V$  values. The observed  $V$ -value was considered significant if  $\geq$  95th percentile of null values.

Because the number of observations for each region varied, we also tested sensitivity to sample size. We performed a rarefaction analysis by randomly removing individuals (5%–75%) from our original dataset, recalculating the diet of rarefied regions, and computing  $V$  (1000 random combinations per percentage of individuals removed). If  $V$  is sensitive to sample size, it should vary widely, as the dataset was resampled (Araújo *et al.* 2010).

To further investigate intrapopulational variation, we subsampled our dataset including only individuals from the Central region, for which we had data for all seasons, sexes, and age classes. We calculated the pairwise diet overlap between individuals using the  $PS$  index and then fitted a linear regression model of  $PS$  as a function of sex, age, and season. We then obtained the distribution of the model parameters from the leave-one-out cross-validation method. We tested the significance of the parameters using the  $\chi$ -test for the pairwise comparisons between all levels of each factor, that is, season (winter  $\times$  fall  $\times$  spring  $\times$  summer), sex (female  $\times$  male), and age (juvenile  $\times$  subadult  $\times$  adult). We adjusted the  $P$ -values for multiple testing using the Bonferroni correction.

Because we found that season, sex, and age are structuring factors of the franciscana dolphin diet, we further examined if residual diet variation could be attributed to individual variation within each age category. We calculated the average pairwise diet overlap ( $\overline{PS}$ ) between individuals within each age category and calculated  $V = 1 - \overline{PS}$ , which estimates the average interindividual diet dissimilarity. We tested the significance of  $V$  values using null distributions (10,000 null  $V$  values) generated by multinomial sampling of the dietary proportions corresponding to each age category while preserving the original number of individuals and the number of prey items per individual. We considered observed  $V$  values significant if  $\geq$  the 95th percentile of null distribution of values.

## RESULTS

We identified 25 fish and four squid species in the diet of franciscana dolphin throughout the São Paulo State coast. Most of the franciscana prey species were from demersal or estuarine habitats. The most important species in the diet, according to the IRI values, were *Pellona barroweri*, *Doryteuthis plei*, *Paralanchurus brasiliensis*, *Isopisthus parvipinnis*, *Stellifer rastriifer*, *Cynoscion jamaicensis*, *Doryteuthis sanpaulensis*, and *Larimus breviceps* (Table 3), comprising six fish and two cephalopods (*Doryteuthis* sp.). These eight species were present in more than 25 percent of the stomachs. The fish species *Umbrina canosai*, albeit not having a high IRI value, also had a frequency of occurrence higher than 25 percent. Although diet composition studies based on stomach contents using IRI values

usually compare the importance of fish and cephalopods, otoliths tend to be digested more quickly than squid beaks (Pierce & Boyle 1991, Bowen & Siniff 1999), biasing estimates in favor of more slowly digested prey (Pierce & Boyle 1991, Bowen & Siniff 1999, Bassoi 2005, Troina *et al.* 2016).

The sequences of importance of prey obtained using IRI or numeric abundance statistics were similar (Table 3 and Fig. 1A). According to the IRI values (Table 3), fish are more important than cephalopods in the diet of the franciscana dolphin. The fish species *P. barroweri* was the most important, with an IRI value much higher than the second-ranked species, a cephalopod (Fig. 1A). The importance of *P. barroweri* can be explained not only because it had the highest numeric percentage (31.1%) of all prey species (Fig. 1A) but also because it had the highest frequency of occurrence (78%). By contrast, the second most important species, the cephalopod species *D. plei*, had a numeric percentage of 18.2 percent and a frequency of occurrence of 46 percent.

We found evidence of diet variation between Northern, Central, and Southern regions ( $V = 0.4290$ ;  $P < 0.001$ ; Fig. 1B-C).

TABLE 3. Index of Relative Importance values of teleostei and cephalopods identified in stomachs of *Pontoporia blainvillei* bycaught along São Paulo state coast.

Prey species	N	W	O	IRI
<i>Pellona barroweri</i>	31.05	15.61	77.97	3638.08
<i>Doryteuthis plei</i>	18.2	40.21	45.76	2672.84
<i>Paralanchurus brasiliensis</i>	3.89	11.6	40.68	630.13
<i>Isopisthus parvipinnis</i>	6.70	4.59	54.24	612.37
<i>Stellifer rastriifer</i>	8.94	4.21	30.51	401.21
<i>Cynoscion jamaicensis</i>	4.44	4.79	30.51	281.61
<i>Doryteuthis sanpaulensis</i>	6.41	4.52	25.42	277.84
<i>Larimus breviceps</i>	3.40	2.49	30.51	179.70
<i>Stellifer brasiliensis</i>	2.47	1.15	18.64	67.48
<i>Anchoa filifera</i>	1.31	2.58	15.25	59.32
<i>Umbrina canosai</i>	1.63	0.16	25.42	45.50
<i>Trichiurus lepturus</i>	0.61	1.93	13.56	34.44
<i>Lycengraulis grossidens</i>	2.29	0.73	10.17	30.71
<i>Loliguncula brevis</i>	1.33	0.55	15.25	28.67
<i>Cynoscion guatucupa</i>	0.84	0.78	16.95	27.46
<i>Ctenoscaena gracilicirrhus</i>	1.19	0.53	6.78	11.66
<i>Chirocentrodon bleekermanus</i>	0.12	0.38	5.08	2.54
<i>Micropogonias furnieri</i>	0.26	0.37	1.69	1.06
<i>Menticirrhus americanus</i>	0.09	0.17	3.39	0.88
<i>Serranus auriga</i>	0.32	0.08	1.69	0.68
<i>Pagrus pagrus</i>	0.23	0.04	1.69	0.46
<i>Cetengraulis edentulus</i>	0.09	0.02	3.39	0.37
<i>Cynoscion virescens</i>	0.03	0.08	1.69	0.19
<i>Chloroscombrus chrysurus</i>	0.03	0.02	1.69	0.08
<i>Engraulis anchoita</i>	0.03	0.02	1.69	0.08
<i>Pogonias cromis</i>	0.03	0.02	1.69	0.08
<i>Orthopristis ruber</i>	0.03	0.01	1.69	0.07
<i>Peprilus paru</i>	0.03	0.02	1.69	0.05

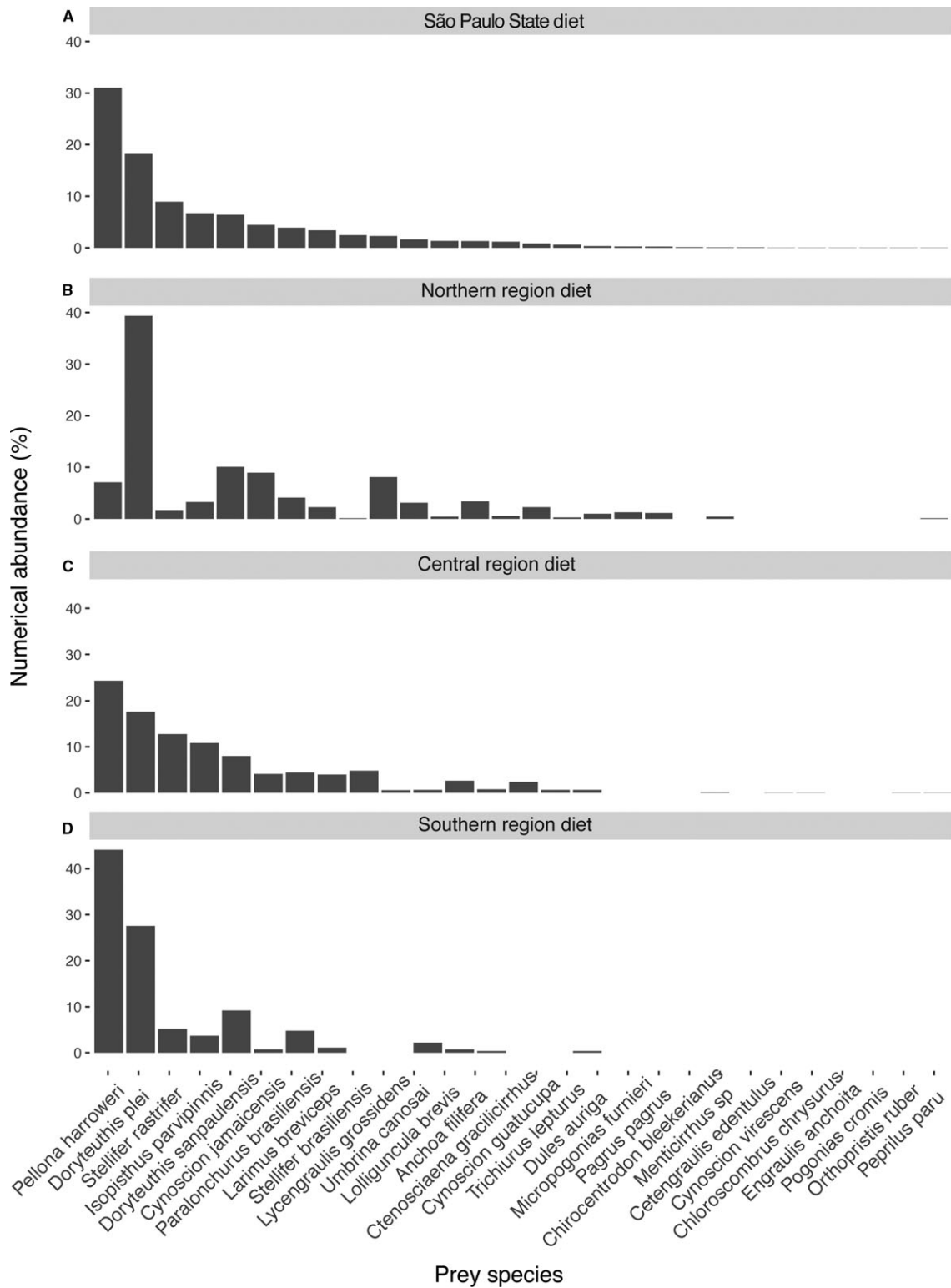


FIGURE 1. Distribution of prey species in the diet of the franciscana dolphin according to numerical abundance for (A) the entire São Paulo State coast and by region: (B) Northern, (C) Central, and (D) Southern.

Franciscana dolphins from the Northern region fed mainly on the cephalopod *D. plei* (38% in numerical abundance), whereas most other prey species had a numerical abundance smaller than 10 percent. In the Central region, franciscana dolphin fed mainly on the fish *P. barroweri* (22% in numerical abundance, less than the value observed for the main prey species in the Northern region). In addition, in the Central region, a higher number of prey species had numerical abundances greater than 10 percent. In the Southern region, franciscana dolphins also fed mainly on the fish *P. barroweri* (42% in numerical abundance), although the cephalopod *D. plei* had a high numerical abundance (28%) and all of the other prey species had a numerical abundance smaller than 10 percent. Therefore, geographical location is a factor structuring the diet of the franciscana dolphin along the São Paulo State coast.

Based on the analysis performed on the sample from the Central region, we found that season, sex, and age are structuring factors of the franciscana dolphin diet (Table 4), explaining approximately 16, 3, and 16 percent of the variance, respectively. The effect of season on the diet of the franciscana dolphin is demonstrated by the differences between the species consumed in winter and in spring (Table 4). Females and males feed mainly on the cephalopod species *D. plei* and on the fish species *P. barroweri*. However, these species had a higher numerical abundance in the diet of females compared with males (Fig. 2A-B). The species ranked third in numerical abundance in the diet of females is the cephalopod species *D. sanpaulensis*, and the remaining prey species had numerical abundances lower than 10 percent. In the diet of males, the fish species *S. rastrifer* and *I. parvipinnis* and the cephalopod species *D. sanpaulensis* had numerical abundances higher than 10 percent. In addition, we found that age affects the franciscana dolphin diet. Specifically, juveniles had a different diet compared with adults in terms of the number of prey species consumed and the most consumed prey species (Fig. 3A-C).

Because we found that season, sex, and age structure the franciscana dolphin diet, we further examined if residual diet variation could be attributed to individual variation within each age category. Even considering the three age classes separately, individual variation in the diet of the franciscana dolphin in the Central region was high (juvenile:  $V = 0.9561$ ;  $P < 0.001$ ; subadult:  $V = 0.6576$ ;  $P < 0.001$ ; adult:  $V = 0.7017$ ;  $P < 0.001$ ).

## DISCUSSION

Marine predators such as the franciscana dolphin strongly influence the structure, function, and dynamics of marine communities (Heithaus *et al.* 2008, Estes *et al.* 2011). Gathering information on marine mammals is particularly challenging owing to the difficulty of observing their feeding habits and behavior. It is seldom possible to determine these habits by direct observation in the field. In this study, we used stomach content data to investigate population structure. Stomach content analysis is proven to be a valid method for assessing population-scale diets of cetaceans restricted to inshore waters (Dunshea *et al.* 2013), such as the franciscana dolphin.

TABLE 4. Pairwise diet overlap between franciscana dolphin individuals from the Central region of São Paulo State coast. Linear regression model of PS index as a function of season (winter  $\times$  fall  $\times$  spring  $\times$  summer), sex (female  $\times$  male), and age (juvenile  $\times$  subadult  $\times$  adult). Z-score represents the distance from the sample mean to the population mean in units of standard error. P-values are the significance levels of each comparison and adjusted P-values are the significance levels of each comparison corrected for multiple testing using Bonferroni correction.

Comparison	z	P-value	Adjusted P-value
<i>Sex</i>			
Female $\times$ Male	-3.504	$4.586 \times 10^{-4}$ *	0.005*
<i>Age</i>			
Adult $\times$ Subadult	2.041	0.041*	0.412
Adult $\times$ Juvenile	-9.344	$9.236 \times 10^{-21}$ *	$9.236 \times 10^{-20}$ *
Juvenile $\times$ Subadult	-1.150	0.250	1.000
<i>Season</i>			
Winter $\times$ Summer	-2.432	0.015*	0.150
Winter $\times$ Spring	-4.307	$1.658 \times 10^{-5}$ *	$1.658 \times 10^{-4}$ *
Winter $\times$ Fall	-1.603	0.109	1.000
Spring $\times$ Summer	-0.598	0.549	1.000
Spring $\times$ Fall	0.875	0.381	1.000
Fall $\times$ Summer	-0.062	0.950	1.000

\* Statistically significant comparison.

The feeding habits of the franciscana dolphin have mainly been studied in its southern range, from the coast of Rio Grande do Sul in Brazil to the coast of Argentina, using a sample size of around 36 stomachs (Rodríguez *et al.* 2002, Bassoi 2005, Cremer *et al.* 2012). However, the São Paulo State coast has been poorly investigated, with a single study based on a sample of two stomachs (Schmiegelow 1990). We combined a reasonable sample size (63 stomachs) with an analytical approach to investigate geographical and intrapopulation variation in the franciscana diet.

We used a quantitative approach to decompose variation at different levels, from the regional to the individual. Specifically, we found that the franciscana dolphin diet varied with geography, season, sex, age, and individual. Thus, management actions must be focused in an area-specific manner (Sharples *et al.* 2012). Data analysis detected trends in individual variation, which are difficult to observe directly in aquatic species with cryptic habits such as the franciscana dolphin (Secchi *et al.* 2003). Our work provides important information about a declining species, and our analysis may be applicable to studies of the diets of other marine mammals.

Similarly to previous studies, we identified bottom-dwelling species as the main prey of the franciscana dolphin. However, our results differ in terms of the importance of squids in the diet of the franciscana dolphin. Previously, *D. sanpaulensis* was considered to be the main squid prey consumed by the franciscana dolphin (Bassoi 2005, Cremer *et al.* 2012), whereas we found that *D. plei* is more important throughout São Paulo State. Both squid species are abundant in coastal waters of São Paulo State, but *D. sanpaulensis* is more abundant in southern Brazil (Alvarez Perez

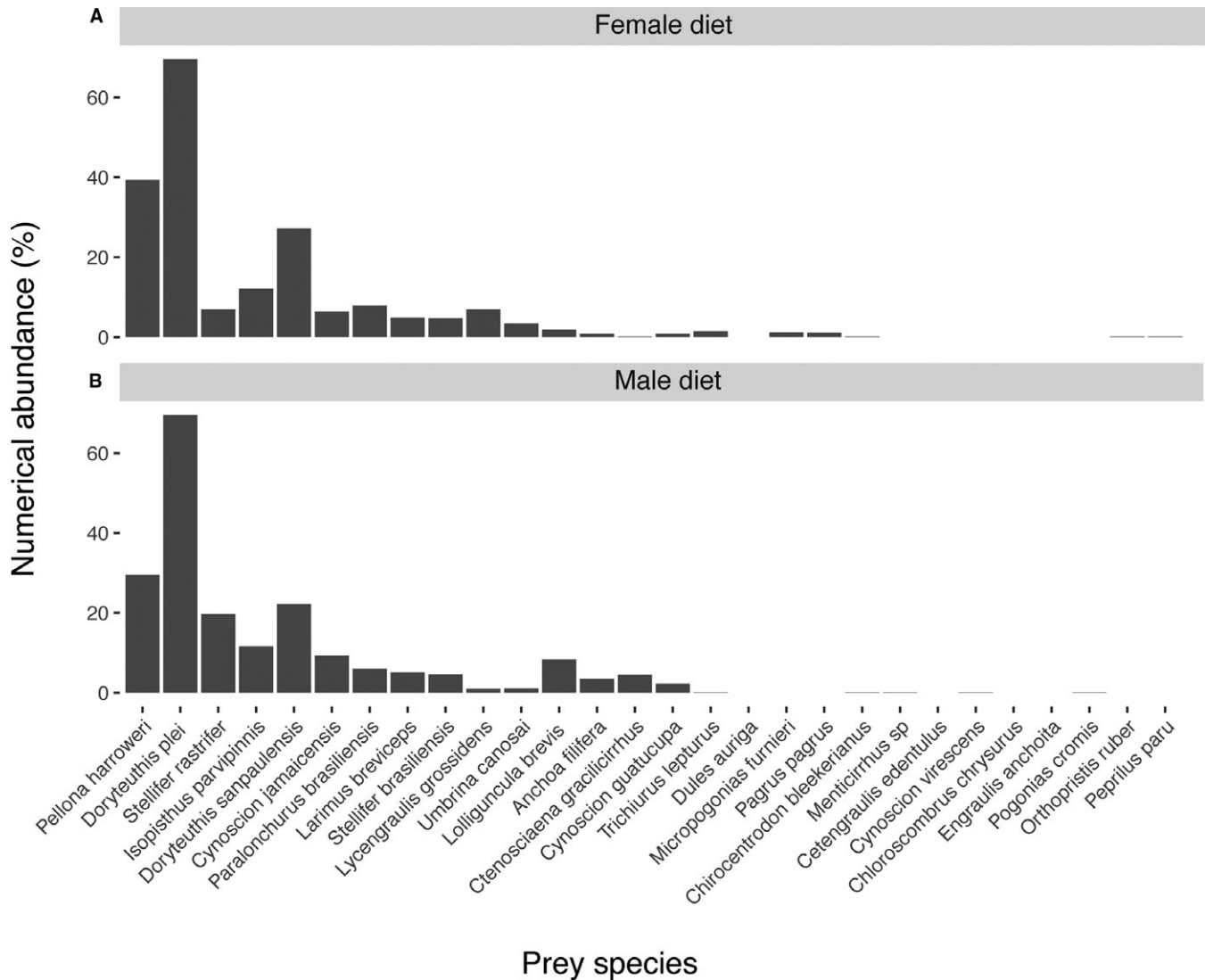


FIGURE 2. Distribution of prey species in the diet of the franciscana dolphin according to numerical abundance for (A) females and (B) males.

2002) where studies on the diet of the franciscana dolphins are common, whereas in the São Paulo State coast, *D. plei* is more abundant (Alvarez Perez 2002). Moreover, *D. plei* has a more elongated and cylindrical body shape (Santos & Haimovic 2001), which may facilitate its ingestion by the franciscana dolphin.

The regional variation found in the diet of the franciscana dolphin supports previous expectations for the existence of structure in FMAs. The geographical variation in diet that we observed suggests that the structure found using DNA sequence analysis might reflect ecological differences in diet (Secchi *et al.* 2003, Cunha *et al.* 2014), suggesting the need for further genetic investigations of franciscana population structure in São Paulo State. The geomorphological complexity of the São Paulo State coast may distinguish its regions ecologically and thereby influence the genetic structure of franciscana dolphins. Because the franciscana dolphin is a coastal cetacean rarely found more than 5 km from shore, it is most likely to move between neighboring regions in a stepwise fashion that restricts it to areas of

concentrated food resources (Rodríguez *et al.* 2002). This hypothesis is supported by the small home ranges measured for the franciscana dolphin in Argentina (Bordino *et al.* 2008, Wells *et al.* 2013). Because of this restricted movement, local subpopulations in São Paulo are likely limited by environmental discontinuities, as is the case along the coast of Argentina, where these coincide with genetically isolated populations of the franciscana dolphin (Mendez *et al.* 2010).

In addition to variation in diet between regions, we also found variation within a region. This variation may be associated with sexual dimorphism, as females are larger than males throughout the distribution region of the franciscana dolphin. Moreover, there are morphological differences in the anterior dimensions of the body between sexes, which might be related to changes in the oral apparatus and feeding habits (Barbato *et al.* 2012).

Intrapopulation variation is also partially related to dietary ontogenetic shifts, which affects the structure and dynamics of populations, communities, and ecosystems (Werner & Hall 1988,



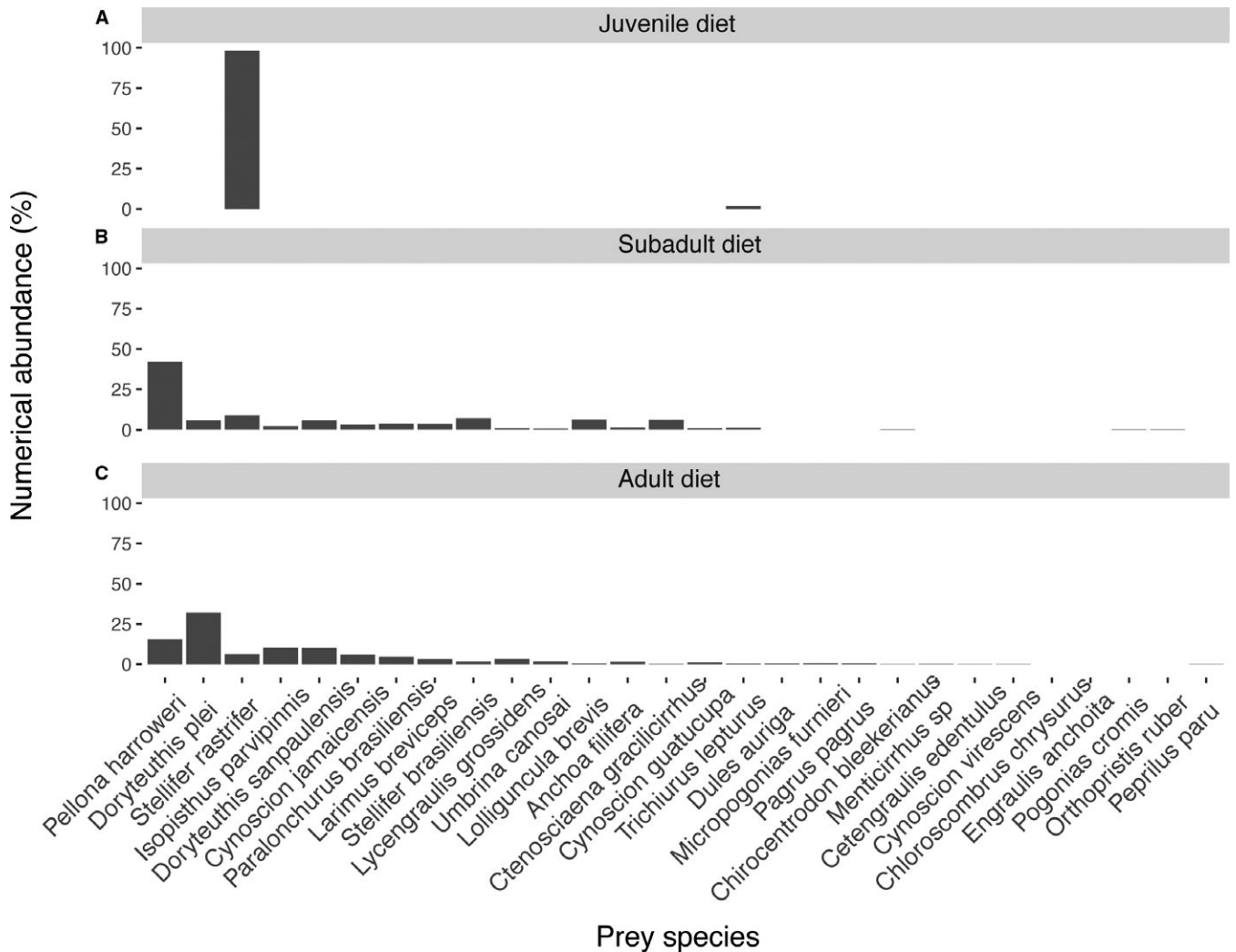


FIGURE 3. Distribution of prey species in the diet of the franciscana dolphin according to numerical abundance for (A) juveniles, (B) subadults, and (C) adults.

Polis & Strong 1996, Claessen *et al.* 2002, Hammerschlag-Peyer *et al.* 2011). Stomachs of juveniles in this study contained the remains of at least one otolith or squid beak, meaning that they had already started to feed (at least partially) on solid food. We found that juveniles fed primarily on one species of fish, whereas subadults fed on a larger number of species, and adults tended to feed on a smaller subset of species. The factors determining preference for a prey species are encounter rate, ease of capture, and handling time (Santos *et al.* 2013). Prey species that typically form dense schools are easier to find and for juveniles to capture (Haimovici *et al.* 1996) and were the type of prey consumed by franciscana dolphin juveniles. Subadults likely have better foraging tactics than juveniles, allowing them to explore a more diverse set of prey (Clarke 1996). The diet of adults tends to be more selective, likely resulting from improved foraging tactics due to their higher mobility (Santos 2009) and broader experience (Basso 2005).

Diet variation can be modeled as a function of sex, age, and morphotype, plus an error term, which represents the residual diet variation (Bolnick *et al.* 2003). Within this residual error term, there

can be important interindividual variation, which deserves a unique designation (Bolnick *et al.* 2003). Our analysis of individuals from the Central region showed that there is interindividual variation in the diet of the franciscana dolphin that could not be attributed to variation due to season, sex, or age. Individual variation in the diet has not been thoroughly investigated in dolphins, although it has been reported for the bottlenose dolphin *Tursiops* sp. (Sargeant *et al.* 2007). Diversity in foraging tactics in the bottlenose dolphin is strongly correlated with habitat use, ecology, and social learning.

Because we found evidence of intrapopulation variation in the diet of the franciscana dolphin, future studies should evaluate the long-term diet of individuals. Such long-term analysis should determine if individuals have diet habits (or niches) substantially narrower than the population's habits (or niches) throughout their lives. The occurrence of an individual niche substantially narrower than the population's niche would be evidence of individual specialization (Bolnick *et al.* 2003), with implications for the population ecology and evolutionary dynamics of the franciscana dolphin (Bolnick *et al.* 2011).

Bolnick *et al.* (2003) discussed the benefits of recognizing individual-level variation in ecological studies. First, this information provides a more complete description of a biological system (Bolnick *et al.* 2003). Second, information on individual variation is necessary if we are to make the transition from phenomenological models of population dynamics to mechanistic models in which the dynamics of a population is predicted based on the properties of its components (Bolnick *et al.* 2003). The development of a mechanistic model for predicting the dynamics of a population is of great relevance for the conservation of a species in decline, such as the franciscana dolphin. Third, population models that incorporate individual variation can result in profoundly different dynamical behavior due to the added capacity for frequency-dependent effects (Bolnick *et al.* 2003).

Finally, to improve conservation measurements and the design of management areas such as FMAs, managers must recognize that ecological systems are complex adaptive systems, in which large-scale patterns emerge in part from microscale processes, which then feed back to influence these processes in fundamental ways (Guichard *et al.* 2004). Improving the definition of boundaries of management areas further requires integrating complex biological information and understanding how their effects spread across diverse scales of space, time, and levels of biological organization (Guichard *et al.* 2004, Hagstrom & Levin 2017). In this sense, our main contribution to improving conservation management of marine mammals, particularly franciscana dolphins, is the recognition of both geographical and individual variation in their diet within São Paulo State. In summary, researchers and managers must integrate empirical and modeling approaches from the individual to the population and ecosystem levels to increase the success of conservation efforts (Guichard *et al.* 2004, Hagstrom & Levin 2017).

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## DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.5415m> (Henning *et al.* 2017), and at <https://sites.google.com/site/barbarahenning/research>.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Franciscana dolphin distribution with Franciscana Management Area (FMA) boundaries (A).

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