Population variance in prey, diets and their macronutrient composition in an endangered marine predator, the Franciscana dolphin

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ABSTRACT

Disentangling the intricacies governing dietary breadth in wild predators is important for understanding their role in structuring ecological communities and provides critical information for the management and conservation of ecologically threatened species. Here we combined dietary analysis, nutritional composition analysis of prey, literature data and nutritional geometry (right-angled mixture triangle models -RMT-) to examine the diet of the most threatened small cetacean in the western South Atlantic Ocean, the Franciscana dolphin (*Pontoporia blainvillei*). We applied a recently developed extension of niche theory based on the RMT to help understand the dietary strategies of this species. Our results showed that across their range the Franciscanas consumed prey with variable protein-to-lipid energy ratios (LMM, p < 0.001). In an intensive study of one area, FMA IV, we found that dolphins sub-populations, which recent genetic evidence suggest should be differentiated into three management units, have diets with different protein energy and water mass compositions, but similar protein-to-lipid energy ratios. Furthermore, dolphins from the three areas mixed different combinations of prey in their diets to achieve the observed macronutrient ratios. These results suggest that the different habitats that each sub-population occupies (estuarine, north marine area and south marine) might be associated with different prey composition niches, but similar realized nutritional niches. Future priorities are to better comprehend possible geographical and long-term seasonal effects on prey consumption and dietary breadth of the different Franciscana populations to identify potential impacts (environmental and human-related), enhance the current management strategies to protect this endangered marine predator.

1. Introduction

Diets are most commonly considered in terms of foods eaten rather than complex mixtures of nutrients and other compounds they contain (Machovsky-Capuska et al., 2016a). In the case of predators, it is widely believed that the prey species they consume are fairly uniform in their nutritional and energetic content (Stephens and Krebs 1986; Stephens et al., 2006). However, evidence suggests that prey species can vary significantly in their nutrient composition, and predators selectively combine prey in their diets to balance their gain of macronutrients (Kohl et al., 2015; Toft and Wise, 1999).

Disentangling the intricacies governing prey selection and dietary breadth in wild predators can be extremely challenging, yet it is important for understanding the role of predators in structuring ecological communities, as well as habitat and species conservation, including the potential impacts of human pressures (e.g. fisheries) (Machovsky-Capuska et al., 2016b). An approach called Nutritional Geometry (NG) was developed to simplify the complexities of linking nutrients to prey quality, foraging behaviour, environmental parameters and geographic location, thus providing a nutritional framework for ecology

(Raubenheimer et al., 2009; Simpson and Raubenheimer 2012). However, field-based research has several logistical constraints that challenge the ability of researchers to collect data necessary for NG analyses, especially on the cumulative (e.g. daily) intakes of different foods and nutrients eaten (Machovsky-Capuska et al., 2016c; Rothman et al., 2012; Tait et al., 2014). To overcome this challenge, a proportions-based approach (right-angled mixture triangle-RMT) was developed to represent foods, diets and macronutrients as nested mixtures (Raubenheimer 2011). Data collected using a wide range of field-based techniques are appropriate for analysing in RMTs, including gut content and regurgitations analyses (Hyslop, 1980; Machovsky-Capuska et al., 2011), faecal analyses (Panthi et al., 2012) and bite rates (Paddack et al., 2006). RMTs are increasingly used in field-based nutritional ecology, covering a wide range of research disciplines including wildlife conservation (Raubenheimer et al., 2015), movement ecology (Nie et al., 2014), human-wildlife interactions (Coogan and Raubenheimer, 2016) and biological invasions (Machovsky-Capuska et al., 2016a; Machovsky-Capuska et al., 2016d). However, to date their use has been limited to a select group of wild predatory species, including Australasian gannets (*Morus serrator*, Machovsky-Capuska et al., 2016b; Tait et al., 2014); pine martens (*Martes martes*, Remonti et al., 2015); masked boobies (*Sula dactylatra tasmani*, Machovsky-Capuska et al., 2016c) and grizzly bears (*Ursus arctos*, Coogan et al., 2014, Coogan and Raubenheimer, 2016).

Recently, the RMT approach was used to develop models that integrate nutrients with foods and diets in the context of ecological niche theory to provide fresh insights into the dietary generalist-specialist distinction and help to understand the ecological distributions of species (Machovsky-Capuska et al., 2016a). This multi-nutrient framework enables researchers to define the dietary niche of species across three functional levels: i) the dietary macronutrient compositions on which the species is physiologically able to persist and thrive is known as the "fundamental macronutrient niche"; ii) the subset of the fundamental macronutrient niche that a species actually occupies given ecological constraints (e.g. high level of competition, reduced prey availability and environmental and human pressures) comprises the "realized macronutrient niche", and iii) the range of ecological and physical attributes of foods that the species is able to exploit provides the "food composition niche". This set of concepts provides a powerful framework for understanding dietary adaptations of animals, including their nutritional needs, and relating these across different scales from individuals to populations and species (Machovsky-Capuska et al., 2016a).

Marine predators are long-lived species that live in complex nutritional environments and represent an emerging model group for developing the study of macronutrient selection in wild predators (Malinowski and Herzing, 2015; Tait et al., 2014). Cetaceans, in particular, are highly-specialized marine top predators that have been extensively studied as "bio-monitors" of prey availability and pollutants, providing valuable information on the health of aquatic environments (Perrin and Würsig, 2009). Their aquatic lifestyle often limits direct observations in the wild making it difficult to collect reliable data on their foraging behaviour, except in shallow waters in geographical areas where water visibility is good (Barros and Clarke, 2009). As a consequence, several indirect techniques including analysing prey remains from stomachs and intestines of stranded and by-caught animals, are commonly used to assess prey consumption and diet (Barros and Clarke, 2009).

Franciscana dolphins (*Pontoporia blainvillei*; hereafter Franciscanas) are small (35.0–55.0 kg) carnivorous cetaceans endemic to the Southwestern Atlantic Ocean that live in coastal waters from Itaúnas (Brazil) to Peninsula Valdés (Argentina) (Bastida et al., 2007; Crespo et al., 1998). This species is considered the most threatened small cetacean in the western South Atlantic Ocean due to high incidental by-catch rates in artisanal gillnets (Crespo et al., 2010; Reeves et al., 2012). For conservation and management of this species, four "Franciscana

Management Areas (FMA)" have been created based on ecological and biological information on the species (e.g. geographic distribution, contaminants and parasite loads, vital rates, phenotype and genotype information) (Secchi et al., 2003): FMA I Rio de Janeiro and Espirito Santo in Brazil; FMA II São Paulo, Parana and North of Santa Catarina in Brazil; FMA III Rio Grande do Sul north and south and Uruguay; and FMA IV Buenos Aires and Rio Negro in Argentina.

Gaining a better understanding of food (hereafter referred as prey) and nutritional components of Franciscana diets, and how they vary across time and habitats, is important for unravelling the dietary niche in which the species is able to survive. Also, and most importantly, assessing the extent of overlap with coastal fisheries will provide a new dimension to management strategies. Here, we combined dietary analysis, proximate composition analysis of prey and nutritional geometry RMT models to examine at the levels of foods, nutrients and diets the foraging niche of Franciscanas from the different FMAs, with particular focus on FMA IV. We addressed three specific questions to better understand the diet of these endangered predators and its relationship with their geographical distribution: i) Do Franciscanas target similar prey species across the different FMAs and throughout FMA IV? ii) Do Franciscanas from different management areas have similar nutritional compositions in their diets across FMAs and across regions within FMA IV? iii) How does the prey composition consumed by Franciscanas vary between FMAs and within the FMA IV?

2. Materials and methods

2.1. Study area

The coastal waters of northern Argentina (35°–41° S) include two major, shallow estuaries formed by the Rio de la Plata and El Rincón System that influence the hydrography of the coastal zone (Fig. 1) (Guerrero et al., 2010). Our study area included most of the area between 34° and 40°S from the Bahía Samborombón, influenced by discharge from the Rio de la Plata to Monte Hermoso, but excluding the El Rincon System (Fig. 1) (Freije et al., 1981; Guerrero et al., 2010).

2.2. Nutritional composition of diets

Since carbohydrates are an insignificant nutritional component of most marine prey (Craig et al. 1978) and fresh water is only available to many cetaceans from food moisture (Malinowski and Herzing, 2015), our comparisons are based on three essential nutrients: protein (P), lipid (L), and water (W). Following Senior et al. (2016), we used linear-mixed models (LMMs) to compare the log energy ratio of protein-to-lipid (lnPL) in prey species and diets between FMAs; and 2) used LMMs to investigate the proportion (as a percentage of wet weight) of logit transformed P and L in prey and diets. To estimate the energy value of each macronutrient, we converted macronutrient masses to energy (E) using the following coefficients: $P = 17$ kj/g and $L = 37$ kj/g (N.R.C., 1989). The statistical significance of the random component was assessed using a likelihood ratio test with the 'rand' function in the package *lmerTest* (Kuznetsova et al., 2015). Linear-mixed models (LMMs) were implemented using the 'lmer' function in the package *lme4* (Bates et al., 2015). All analyses were performed using the software R3.3.1 (R Development Core Team, 2015).

Right-angled mixture triangles (Raubenheimer, 2011) were used to explore in three dimensions the relationships between the wet weight proportions of W, P, and L in prey species and diets of different Franciscana populations and geographic areas. To improve our estimates of the realized nutritional niche for Franciscanas we combined our original data collected from FMA IV (Buenos Aires Province) with re-analyzed published data on the diet of this species collected from stomach contents from the other FMAs (Rio de Janeiro from the FMA I (Bittar, 2007), Sao Pablo from the FMA II (Henning, 2012), and Rio Grande do Sul north and south from the FMA III (Bassoi, 2005)) (Fig. 1,
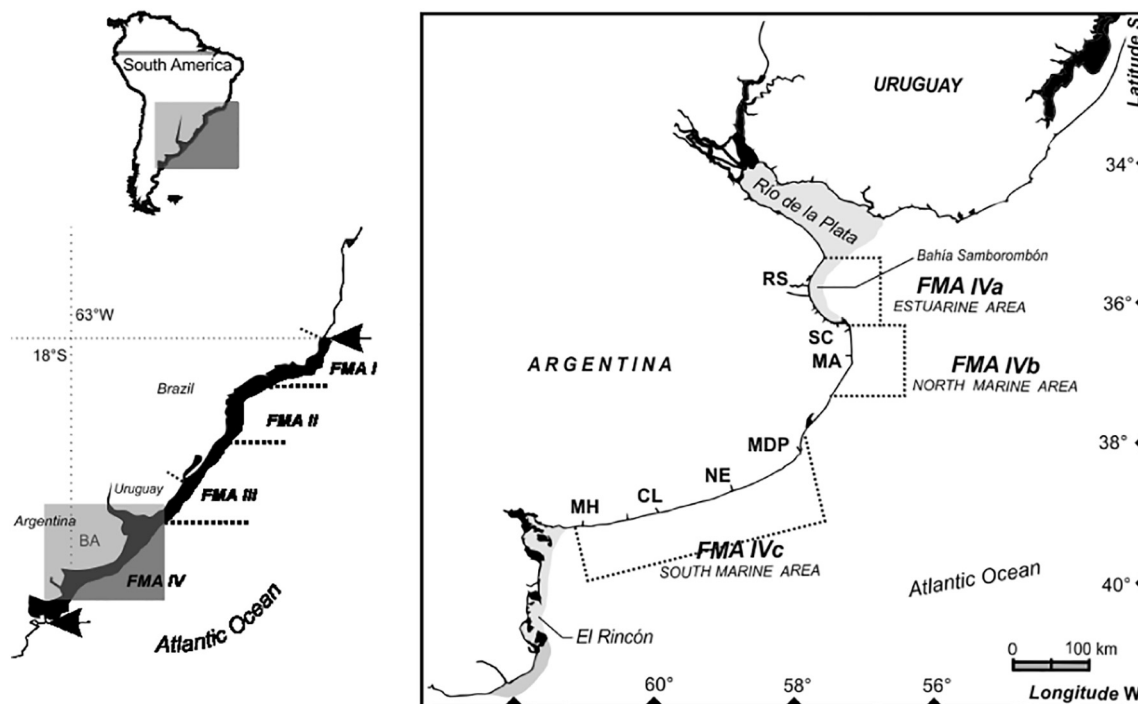
Fig. 1. Geographical distribution of Franciscanas (shaded in black) in South American waters. The four management areas (FMAs, adapted from Secchi et al. 2003) are shown on the left. A map of the study area (FMA IV and sub-FMAs - Argentina) is presented on the right, showing the three areas into which it was divided and the localities from which Franciscana dolphin carcasses were collected: Rio Salado, (RS), San Clemente del Tuyú (SC), Mar de Ajó (MA), Mar del Plata (MDP), Necochea (NE), Claromecó (CL) and Monte Hermoso (MH).

see supplementary information Table S1and S2). We have only used studies that provided a robust sample size with complete information (e.g. M % used in the RMTs) for each FMA and we only used prey species that contributed > 1.0% of wet mass (M %) to the overall diets. For the prey species consumed by Franciscanas we obtained the proximate nutrient composition from the available literature and estimated the diet for each of the seven geographic locations (see supplementary information Table S2 and S3). Following Tait et al. (2014), when possible we aimed to collect nutritional data from similar spatiotemporal proximity to the study (see supplementary information Table S3). These data on the proportion of prey species enabled us to estimate the nutritional composition of prey species constituting (in wet mass) 100.0% of the diet of Franciscanas from FMA I, 76.7% of the diet in FMA II, 89.3% of the diet in FMA III north, 95.9% of the diet in FMA III south, 98.6% of the diet in FMA IVa, 97.9%of the diet in FMA IVb and 98.6% of the diet in FMA IVc.

2.3. Stomach contents analysis of diet within FMA IV

Between 2000 and 2010, the diet of Franciscanas within FMA IV was studied through 173 stomach contents analysis of carcasses opportunistically collected from by-caught dolphins provided by artisanal fishermen from coastal waters of northern Argentina (see supplementary information Table S1). During post-mortem examination, sex and standard morphological measurements were recorded (Norris, 1961), and stomachs were excised and frozen at − 20 °C for later laboratory analysis. Prey items were individually weighed to 0.1 g, and stomach contents were washed through a 0.25-mm-mesh sieve to examine for otoliths and cephalopod beaks (following Meynier et al., 2008). Almost all prey items (99.6% of fish otoliths, 99.8% of cephalopod beaks and 100% of the crustacean remains) were identified to the lowest taxonomic level using the reference collection at the Marine Mammal Laboratory of the Universidad Nacional de Mar del Plata, Argentina.

2.4. Data analysis of prey and diets within FMA IV

For each prey item (fish and cephalopods) we estimated individual mass and total length using published length and weight regressions (Bassoi, 2005; Rodriguez et al., 2002) to later estimate the percentage of total prey weight that the species contributed to the overall diet (M %, wet weight). Two utilization indexes were assigned to each prey species: the frequency of occurrence percentage (FO%, calculated as the number of stomachs in which prey items were encountered), and the numerical abundance percentage (N%, calculated as the number of individuals of each prey type divided by the total number of individuals of all prey types).

The diet variability of Franciscanas was analyzed in relation to sex, standard length (SL), and geographic areas that the dolphins inhabited within the FMA IV. Following the latest genetic evidence of the population structure of Franciscanas (Méndez et al., 2008; Cunha et al., 2014; Negri et al., 2016), we divided the study area into three sub-FMA also characterized by oceanographic features (Guerrero et al., 2010): i) FMAIVa or the estuarine area of the *Bahia Samborombón*; ii) FMAIVb or northern marine area; and iii) FMAIVc or southern marine area (Fig. 1). The analyses were performed grouping prey into the four categories: i) pelagic fishes; ii) non-pelagic fishes (demersal, demersal-benthic and benthic species) following published records on the habitats of teleosts (Olivier et al., 1968; Bassoi, 2005); iii) cephalopods; and iv) crustaceans.

Since the shapes of relationships relating response variables to explanatory variables were unknown, generalized additive models (GAMs) (Hastie and Tibshirani, 1990; Zuur et al., 2007) were used. The response variable of models (prey number) had a large variance because of the large number of zero values in the samples; therefore a negative binomial error distribution was specified (Crawley, 2005). A log link was used in the models because response variables could only take zero or positive values (Crawley, 2005). For each model fitted within a prey category, we calculated the Akaike information criterion (AIC) and selected the model with the lowest AIC. Where two models had very similar AIC values the more parsimonious model was

Table 1
Franciscana Management Areas (FMAs) comparison and standard deviation (SD) of the energy logit-transformed proportion of protein (P), lipid (L) and protein-to-lipid ratio (lnPL) estimated using linear-mixed models. Significance of variance components was assessed by likelihood ratio test (d.f. = 1).

Macronutrient	Effect	Variance	SD	χ^2	p
P	FMA	< 0.001	< 0.001	0.00	1.00
	Residual	0.03	0.19		
L	FMA	0.04	0.19	2.75	< 0.05
	Residual	0.05	0.22		
W		0.02	0.15	1.3	< 0.001
	FMA				
	Residual	0.04	0.35		
LnP:L	FMA	0.11	0.34	6.22	< 0.01
	Residual	0.00	0.08		

preferred (Table S4) (Luque et al., 2009). Prey categories were also fitted against a null model (i.e. a model without any of the independent variables) to test the hypothesis that none of the variables had an effect on the consumption of any prey (Lucifora et al., 2009).

3. Results

3.1. Minimal realized nutritional niche of Franciscanas

An overall comparison of the macronutrient composition of the diets confirmed a high degree of variation between-FMA in the proportion of lipid energy and the lnPL energy ratio of the observed diets of all the populations studied (Table 1). The RMT showed the differences in P:L wet mass ratios in the diets of the different Franciscanas' populations; these range from a P:L ratio of 8.9:1 (FMA IVa) to 20.1:1 (FMA II) and provide an estimate of the minimal realized macronutrient niche of the species (Fig. 2).

The RMTs presented in Fig. 3 show that Franciscanas from the FMA III mainly preyed upon long-finned squid (FMA III north = 69.8% and

Fig. 2. Right-angled mixture triangle showing the average macronutrient composition (hollow symbols) of the diet consumed by Franciscana dolphins from the Franciscana Management Areas (FMAs): FMA I (pentagon), FMA II (diamond), FMA III north (star), FMA III south (ellipse), FMA IVa (triangle), FMA IVb (circle) and FMA IVc (square). Solid diamonds show the composition of all prey species retrieved from dolphin guts across all FMAs. The grey area contains all the prey consumed by Franciscanas providing an estimate of the prey composition niche, whereas the dark grey area contains the diets from all the populations and represents the minimal realized nutritional niche of Franciscanas.

FMA III south = 88.2% in mass, wet weight) (Fig. 3a, b). The northern Franciscanas (FMA I and FMA II) mostly consumed slender inshore squid (40.9%), which was combined with two other species in FMA II (Fig. 3c) and six species in FMA I (Fig. 3d).

3.2. Diet composition and prey size in FMA IV

From 173 carcasses examined, 151 (87.3%) of the stomachs contained prey (FMA IVa, n = 45; FMA IVb, n = 74 and FMA IVc, n = 54) and 9587 prey were identified representing 27 species, including fish (n = 21), crustaceans (n = 4) and cephalopods (n = 2). Non-pelagic species (n = 20) dominated the prey list in the diet of Franciscanas (Table 2).

In FMA IV, fish were the most frequent (FO% in the table) prey followed by cephalopods, whereas the latter was the most abundant prey (N%). The most frequent prey in the diet of Franciscanas in FMA IV was the striped weakfish, whereas the most abundant was the long-finned squid, also contributing almost 80% of total mass (M %, Table 2).

The SL of fish consumed ranged from 31 to 283 mm (mean length 70 ± 37 mm, n = 3641), but the modal size of consumed fish was 55 mm. Cephalopods consumed by Franciscanas were slightly larger than fishes (mantle mean 106 ± 36 mm, n = 2026). The shortest cephalopod mantle was 38 mm and the longest was 183 mm, but the most common size consumed was 130 mm.

3.3. Variability of diet within FMA IV

Franciscanas from the FMA IVa fed on a total of 18 prey species; only seven contributed > 1% mass of the diet and white croaker had the greatest mass percentage. From the 23 prey species consumed in FMA IVb, five contributed > 1% of mass and striped weakfish and the long-finned squid were the most important prey in mass. Finally, in FMA IVc, Franciscanas preyed upon nine species; only three contributed > 1% mass and long-finned squid was the most relevant prey in mass (Table 2).

Results from the generalized additive models showed a significant effect of geographic area and SL on the numbers of prey consumed, but no effect of dolphin sex (Table 3). Fewer fish (pelagic and non-pelagic) were consumed in the FMA IVc than in the other two regions, whereas significantly more cephalopods were consumed in the FMA IVc than FMA IVb (absent in FMA IVa) (Table 3). A significant increase with SL of predator was observed in the consumption of non-pelagic fishes, the dominant teleosts (Fig. S5a). In contrast, the consumption of pelagic fishes increased significantly with SL up to ca. 110 cm, after which the effect leveled off (Fig. S5b). The number of crustaceans eaten decreased with SL and more were eaten in the FMA IVb than in the other two areas (Table 3, Fig. S5c).

3.4. Nutrient composition of prey and diet of Franciscanas from FMA IV

To consistently assess the nutritional composition of diets, we used a total of 67 stomach contents from three consecutive years (2008, n = 39; 2009, n = 18 and 2010, n = 10). A comparison of the nutrient composition of the different prey consumed by Franciscanas in FMA IV showed differences in the energy proportions of P (estimated between-prey SD = 75.25, χ^2 = 15.9, d.f. = 1, p < 0.0001), L (estimated between-prey SD = 14.6, χ^2 = 10.1, d.f. = 1, p < 0.001), the lnPL ratios (SD = 5.6, χ^2 = 1.5, d.f. = 1, p < 0.0001) and the mass contribution of W (estimated between-prey SD = 1.7, χ^2 = 227.0, d.f. = 1, p < 0.0001). Franciscanas consumed prey with a wide range of P:L (mass, wet weight) from 3.6:1.0 (argentine anchovy) to 32:1.0 (silverside), with a higher variability in lipids than in proteins (Coefficient of Variation, CV: L = 82.9; P = 20.6).

A three year comparison of the nutritional composition of diets of the different sub-populations within FMA IV showed significant
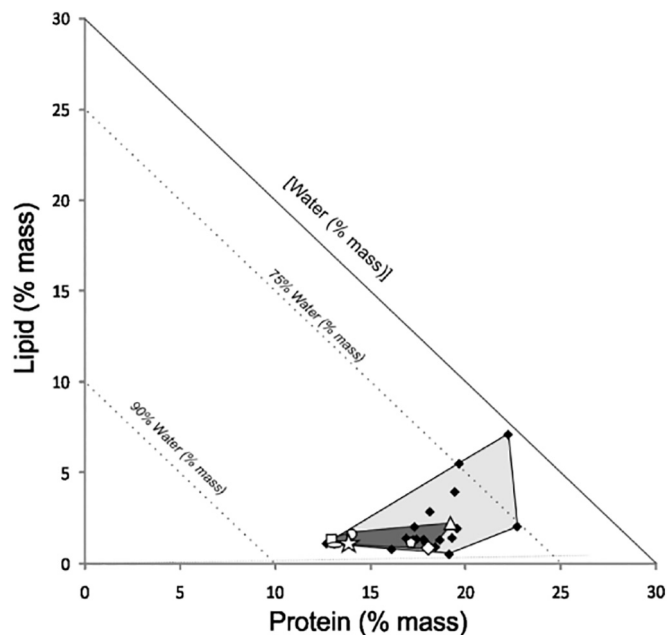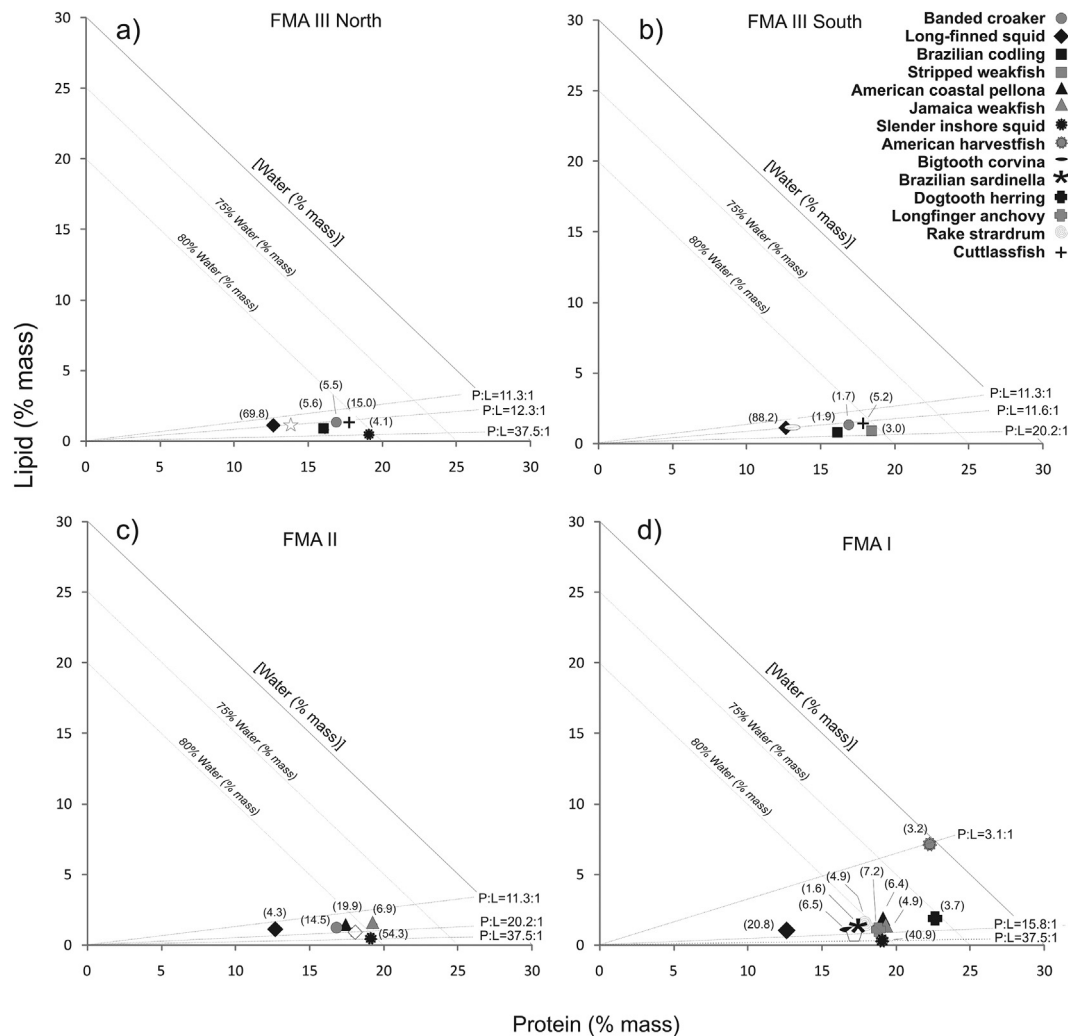
Fig. 3. Right-angled mixture triangle showing the protein, lipid and water composition (as % wet mass) of prey and diets from different Franciscanas Management Areas (FMA) a) FMA III north, b) FMA III south, c) FMA II, and d) FMA I. Black and grey symbols represent compositions of individual prey species. Open symbols represent the average nutritional composition of the diet consumed by dolphin populations in FMA I (pentagon), FMA II (diamond), FMA III north (star) and FMA III south (ellipse).

differences in proportional composition of P energy over the three years (2008, SD = 0.2, χ^2 = 49.3, d.f. = 1, p < 0.0001; 2009, SD = 0.2, χ^2 = 7.18, d.f. = 1, p < 0.001 and 2010, SD = 0.15, χ^2 = 3.6, d.f. = 1, p < 0.05) and also the W mass contribution (2008, SD = 3.4, χ^2 = 38.2, d.f. = 1, p < 0.0001; 2009, SD = 3.4, χ^2 = 6.19, d.f. = 1, p < 0.001 and 2010SD = 2.6, χ^2 = 1.95, d.f. = 1, p < 0.05). However, no significant differences were observed in L energy (2008, SD = 0.22, χ^2 = 3.3, d.f. = 1, p = 0.08; 2009, SD = 0.3, χ^2 = 1.4, d.f. = 1, p = 0.20 and 2010, SD = 0.07, χ^2 = 0.8, d.f. = 1, p = 1.00) and lnPL energy of the diets (2008, SD = 0.06, χ^2 = 0.3, d.f. = 1, p = 1.00; 2009, SD = 0.11, χ^2 = 0.11, d.f. = 1, p = 0.70 and 2010, SD = 0.0002, χ^2 = 0.5, d.f. = 1, p = 1.00).

The RMT showed differences in M % contribution of each prey towards the diet in each sub-population in the FMA IV. Long-finned squid provided most of the macronutrients to the diet of Franciscanas in the marine areas: FMA IVc (wet mass, 2008, 95.2%; 2009, 96.5% and 2010, 98.2%) and in FMA IVb (2009, 91.9% and 2010, 94.6%, whereas in 2008 they mainly combined long-finned squid (47.4%) with striped weakfish (47.4%), (Fig. 4). However, white croaker was the main prey (2008, 35.0%; 2009, 66.3% and 2010, 70.9%) in the estuarine area (FMA IVa) (Fig. 4).

Within FMA IVb, significant differences were observed in the proportional composition of P energy (SD = 4.5, χ^2 = 1.2, d.f. = 1, p < 0.05) and lnPL energy (SD = 2.4, χ^2 = 6.1, d.f. = 1, p < 0.05) of the diets across the three different years, whereas L energy

(SD = 0.02, χ^2 = 1.1, d.f. = 1, p = 0.97) and W mass contribution (SD = 0.2, χ^2 = 1.2, d.f. = 1, p = 0.82) were not significant. In FMA IVa, no differences were observed in the nutritional composition of the diets (energy proportional composition of P (SD = 0.05, χ^2 = 3.5, d.f. = 1, p = 0.86)), L (SD = 0.08, χ^2 = 1.9, d.f. = 1, p = 0.90), lnPL (SD = 0.06, χ^2 = 2.1, d.f. = 1, p = 0.96) and mass contribution of W (SD = 0.4, χ^2 = 1.6, d.f. = 1, p = 0.88). Likewise, no significant differences were observed in FMA IVc in the dietary energy proportional composition of P (SD = 0.03, χ^2 = 1.1, d.f. = 1, p = 0.80), L (SD = 0.03, χ^2 = 1.3, d.f. = 1, p = 0.90), lnPL (SD = 0.01, χ^2 = 1.4, d.f. = 1, p = 0.95) and mass contribution of W (SD = 0.3, χ^2 = 1.1, d.f. = 1, p = 0.73).

4. Discussion

Marine predators forage in complex environments and face nutritional challenges due to accelerating environmental change and human pressures (Machovsky-Capuska et al., 2016b; Tait et al., 2014). Understanding the foraging and nutritional goals and diet breadth of predators provides critical information for the management and conservation of ecologically threatened species (Machovsky-Capuska et al., 2016a; Raubenheimer et al., 2012; Rothman, 2015). Nutritional geometry has been used to link feeding strategies, nutrition and demography in wild endangered species including kakapo (*Strigops habroptilus*, Raubenheimer and Simpson, 2006), gorillas (*Gorilla beringei*,

Table 2

Composition of the diet of franciscana dolphins in the fourth Franciscana Management Area (FMA IV) and sub-FMAs (FMA IVa = estuarine area; FMA IVb = north marine and FMA IVc = south marine) from Argentinean waters. Relative prey importance is shown using several metrics: N (total number of individuals); N% (numerical abundance percentage); M%, (wet mass percentage) and FO% (frequency of occurrence percentage). Following Olivier et al. (1968) and Bassoi (2005), prey were also classified into P = pelagic and NP = non-pelagic.

Commonname	Scientificname	Habitat	Overall FMA IV				FMA IVa			FMA IVb			FMA IVc		
			N	FO %	N %	M%	FO %	N %	M%	FO %	N %	M%	FO %	N %	M%
TELEOSTS			4359	82.08	45.49										
Strippedweakfish	*Cynoscion guatucupa*	NP	2698	57.8	28.17	6.98	46.67	28.63	7.31	54.05	42.40	15.13	72.22	17.61	2.28
White croaker	*Micropogonias furnieri*	NP	504	23.12	5.26	5.24	60.00	28.91	55.44	14.86	2.12	0.48	3.70	0.28	0.00
Brazilian codling	*Urophysis brasiliensis*	NP	116	9.25	1.21	0.98	11.11	0.41	4.40	14.86	3.20	4.05			
Argentine anchovy	*Engraulis anchoita*	P	259	28.9	2.70	1.59	22.22	4.50	2.75	29.73	3.93	2.08	33.33	1.26	1.33
Banded croaker	*Paralonchurus brasiliensis*	NP	147	10.4	1.53	0.93	17.78	4.84	6.31	13.51	2.24	1.09			
Rough scad	*Trachurus lathami*	P	137	14.45	1.43	1.31	13.33	4.56	0.41	5.41	3.29	0.27			
Silverside	*Odontesthes bonariensis*	P	179	5.78	1.87	1.85	13.33	6.71	13.38	5.41	0.52	0.49			
Argentine croaker	*Umbrina canosai*	NP	115	5.78	1.20	0.05	13.33	5.12	8.98	8.11	0.35	0.00			
King weakfish	*Macrodon ancylodon*	NP	86	6.94	0.90	0.1	4.44	0.21	0.60	4.05	0.17	0.01			
Cuskeds	*Raneya fluminensis*	NP	12	2.89	0.13	0.48				5.41	0.17	0.00			
Mullet	*Mugil platanus*	P	9	2.89	0.09		4.44	0.35	0.13	1.35	0.03	0.00			
Lantern midshipman	*Porichthys porosissimus*	NP	3	0.58	0.03					4.05	0.12	0.00			
Butterfish	*Stromateus brasiliensis*	P	7	1.16	0.07	0.03	4.44	0.55	0.29	8.11	1.60	0.12	31.48	1.58	0.70
Anchovy	*Anchoa marinii*	P	1	0.58	0.01					4.05	0.41	0.00			
Flatfish	*Etropus longimanus*	NP	30	0.58	0.31					2.70	0.20	0.02			
Deep-bodied pipe fish	*Leptonotus blainvillanus*	NP	1	0.58	0.01					2.70	0.06	0.01	5.56	0.21	0.00
Atlantic anchovy	*Lysengraulis olidus*	P	4	1.73	0.04	0.22	4.44	0.35	0.00	1.35	0.03	0.00			
Brazilian flathead	*Percophis brasiliensis*	NP	6	1.73	0.06					1.35	0.03	0.00			
Bluefish	*Pomatomus saltatrix*	NP	6	1.73	0.06					1.35	0.09	0.69			
Jenyns'ssprat	*Ramnogaster arcuata*	NP	14	1.73	0.15		2.22	2.07	0.00						
Red porgy	*Pagrus pagrus*	NP	6	2.31	0.06		2.22	0.07	0.00						
	Unidentified teleosts		19												
CEPHALOPODS			4762	49.13	49.71										
Long finned-squid	*Loligo sanpaulensis*	NP	4746	48.55	49.55	79.8				45.95	32.77	75.57	92.59	77.09	95.03
Tehuelche octopus	*Octopus tehuelchus*	NP	8	1.16	0.08	0.27				1.35	0.06	0.00	1.85	0.13	0.48
	Unidentified cephalopods		8												
CRUSTACEANS			456	25.43	4.73										
marine shrimp	*Artemesia longinaris*	NP	261	16.18	2.72		15.56	1.04		21.62	5.38		9.26	1.30	
marine shrimp	*Pleoticus muelleri*	NP	40	1.73	0.41		2.22	1.24		1.35	0.12		1.85	0.38	
Oppossum shrimp	*Neomysis americana*	NP	135	1.16	1.4		4.44	9.34							
Small white shrimp	*Peisos petrunkevitchi*	NP	9	0.58	0.09		2.22	0.62							
	Unidentified crustaceans		11												

NP: non-pelagic species, P: pelagic species

Table 3

Summary of generalized additive models for the prey consumption of franciscanas in coastal Argentinean waters. For categorical explanatory variables, the effect given for each level is relative to a reference level (for the variable area, all comparisons are in relation to the estuarine area -FMA IVa- with the exception for cephalopods referred to the north marine area -FMA IVb-). For each model, all significant explanatory variables are listed with their associated probability (P) value and the overall % deviance explained by the model. For categorical and linear explanatory variables, the direction of the effect is indicated as + or −; for smoothers (s), the degrees of freedom are indicated in parentheses.

		Significant variables			% Deviance explained
		SL	FMA IVb	FMA IVc	
Pelagic teleosts	Smoothers	4,28			14.8
	Effect			−	
	P value	P < 0,01		P = 0.05	
Non pelagic teleosts	Smoothers	1			6.36
	Effect			−	
	P value	P = 0.289		P = 0.05	
Cephalopods	Smoothers				9,76
	Effect			+	
	P value			P < 0,01	
Crustaceans	Smoothers	1,96			34,1
	Effect		+		
	P value	P < 0,01	P < 0,01		

Rothman et al., 2012), giant pandas (*Ailuropoda melanoleuca*, Nie et al., 2014) and masked boobies (*Sula dactylatra tasmani*, Machovsky-Capuska et al., 2016b). The present study provides novel insights into the nutritional relationships between prey and dietary macronutrient composition of a wild endangered marine mammal, and compares them between different populations.

4.1. Overview of the nutritional strategies in the different management units

Understanding the nutritional composition of the different prey sources and dietary breadth of a population is the first step to comprehend the scope of the prey composition, realized and fundamental niches that plays a vital role for implementing conservation strategies (Machovsky-Capuska et al., 2016a). Marine environments are complex and involve a highly heterogeneous group of biogeographic regions with well-established ecological and oceanographic features that influence the distribution of populations (Spalding et al., 2007). We found nutritional differences in the range of prey compositions consumed between the different Franciscana populations. Our nutritional models (RMT) showed that Franciscanas from FMA III (north and south) obtained most of their dietary macronutrients from long-finned squid (69.8 M % and 88.2 M %), consistent with the marine sub-FMA from Argentina (FMA IVb and c), demonstrating that this prey species plays an important nutritional role in the diet of these populations (Fig. 3).

Franciscanas from FMA II had the highest dietary P:L ratio by mass in comparison with the other FMA populations. The dolphins from this population obtained most of their dietary macronutrients from slender inshore squid (54.3 M %), which had the lowest overall energy content of all prey species. The macronutrient composition of the diet of the FMA I population was also heavily influenced by slender inshore squid (40.9 M %), in combination with other prey that had higher energy content. The differences in the prey composition niche, the macronutrient composition of the diets and the realized nutritional niches of
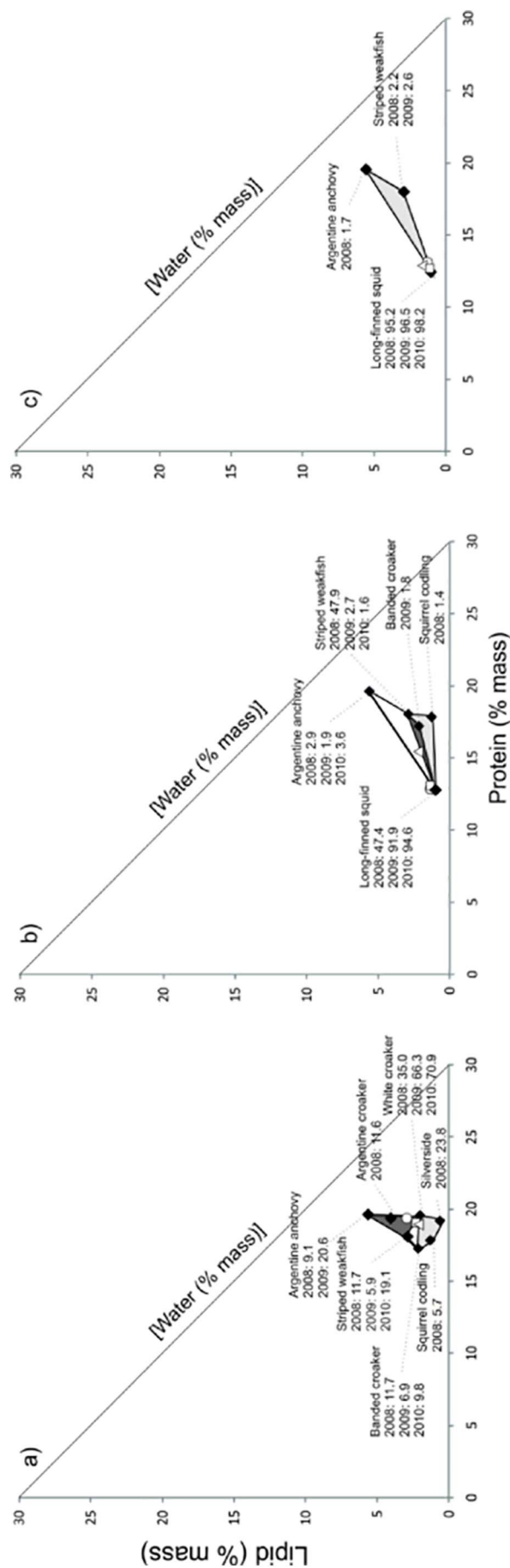
Fig. 4. Right-angled mixture triangle showing the nutrient composition of prey and diets (as % wet weight) of Franciscanas within the fourth unit of management (FMA IV): a) FMA IVa, b) FMA IVb and c) FMA IVc. Prey composition and realized nutritional niches of the Franciscanas in three consecutive years are in different colors: 2008 = *light grey polygon*, 2009 = *dark grey polygon* and 2010 = *white polygon*. White symbols represent the nutrient composition of the diet consumed by dolphin populations in 2008 (triangle), 2009 (circle) and 2010 (square). Black symbols represent prey species that are labelled with their common name and their nutritional contribution to the diets (wet mass %) in the different proposed sub-FMA IV (a, b and c).

these populations are likely to be related to several non-exclusive factors. First, recent genetic evidence suggested that Franciscanas in FMA I and FMA II should be considered to be evolutionary distinct compared to the southern Franciscanas (FMA III and FMA IV) (Cunha et al., 2014). Second abiotic and biotic factors are well known to influence the abundance, distribution and nutritional quality of marine prey (Österblom et al., 2008; Spitz et al., 2010; Wanless et al., 2005). Third, both geographic areas are well known for the impacts that commercial fisheries have on prey stocks that Franciscanas' consumed (Cunha et al., 2014). Fourth, Guiana dolphins (*Sotalia guianensis*) in the FMA I and II have similar foraging strategies to Franciscanas and are likely to compete for similar prey sources (Cremer et al., 2012; Lopes et al., 2012). However, the relevance of these factors remains to be explored.

4.2. Prey and macronutrient composition of diets in FMA IV

Although some morphological similarities supported the maintenance of the existing management areas (Barbato et al., 2012), recent genetic evidence of the population structure of Franciscanas suggested that the current format of four FMA is insufficient to manage and protect the different populations (Cunha et al., 2014). In the FMA IV, evidence of growth (Denuncio, 2012), pollutant concentrations (Polizzi et al., 2013), fisheries impact (Bordino and Albareda, 2004; Negri et al., 2012) and diet (Rodriguez et al., 2002; this study) support the need for a reassessment of the extent of the FMA IV.

Nutrition plays a prominent role in intra- and inter-specific interactions, population composition and evolution (Simpson and Raubenheimer, 2012). Our results demonstrate that Franciscanas that inhabit the FMA IV consumed prey species that differ in their protein-to-lipid ratios (mass, wet weight) (Tables 2) from 3.6:1.0 (argentine anchovy) to 32.3:1.0 (silverside), supporting previous findings that marine predators feed on nutritionally diverse prey (Machovsky-Capuska et al., 2016b, Machovsky-Capuska et al., 2016c).

Franciscanas in different sub-regions within FMA IV have diets with similar P:L energy ratios, but mixed different combinations of prey in their diets. In the south marine habitat (FMA IVc) they mainly preyed upon long-finned squid that provide almost all the macronutrients (94.2 M %) in their diet, whereas in north marine habitat (FMA IVb) long-finned squid (69.2 M %) provided the majority of the macronutrients in the diet in combination with four other species (Brazilian codling, striped weakfish, Argentine anchovy and banded croaker). In the absence of long-finned squid in the estuarine area (FMA IVa), Franciscanas obtained most of their macronutrients from the white croaker (56.6 M %), which was combined with six other prey species (silverside, argentine croaker, striped weakfish, argentine anchovy, banded croaker and Brazilian codling). The differences provided above suggest that Franciscanas within the FMA IV forage in three different habitats that might constitute similar realized nutritional niches: estuarine, north marine area and south marine habitats (Fig. 4). These differences are likely to be influenced by primary production, prey assemblages availability, pollution and oceanographic conditions (e.g. bathymetry, hydrography, etc.) within these distinct ecoregions (Guerrero et al., 2010; Jaureguizar et al., 2006; Spalding et al., 2007). These results are consistent with recent genetic evidence that suggested the consideration of a sub-division of FMA IV management unit into three new populations: the sub-FMA IVa, IVb and IVc (Cunha et al., 2014; Méndez et al., 2008; Negri et al., 2016).

Little is known about the lives of wild Franciscanas, due to their elusive behaviour (Bastida et al., 2007). Field-based information on these marine predators has been collected from by-caught animals provided by artisanal fishermen, and the dietary information has been mostly obtained from the analyses of stomach contents (Rodriguez et al., 2002). Although the present dataset provides an exceptional opportunity to build an integrated measure of the dietary niche breadth and population differences within this species, the interpretation of the results presented in here is subject to potential caveats. Sample sizes

may not ideal due to the unpredictability of fatal entanglements, or due to difficulties in accessing remote areas (Bilgmann et al., 2011). The use of published data to estimate the nutritional composition of prey also has clear limitations, because of uncertainties around consistency and validation of the methods used (Tait et al., 2014; Remonti et al., 2015). However, these data also provide a unique opportunity to integrate spatiotemporal scales that could lead to novel insights into the ecology of animals that are difficult to study (either because they are too large to be handled, or are cryptic, protected, or even extinct) (Spitz et al., 2012).

Here, for the first time, we combined dietary analyses and nutritional geometry to better understand the nutritional ecology of Franciscana dolphins at multiple levels. First, we showed that Franciscanas are able to consumed prey that differ in their P:L energy ratios. Second, we estimated the minimal range of prey that contributes to the food composition niche and dietary compositions that contributes to the realized nutritional niche of Franciscanas. Third, we provide evidence that the three Franciscana sub-populations suggested by genetic evidence are likely to occupy three different prey composition niches with similar realized nutritional niches within the FMA IV. There is a need for a sustainable collection of data on the nutritional composition of prey and dietary intake in Franciscanas from the different geographic locations and during different seasons, to clearly establish how anthropogenic impacts (e.g. fisheries interactions, pollutants, etc.) and environmental fluctuations influence the nutritional quality of prey available, and their food composition and realized nutritional niches of the different Franciscana populations. This information will be vital to further explore the population structure of this species. Future studies should also consider coupling animal-borne biologging techniques, including the recently tested cetacean-borne video camera and integrated sensor system (C-VISS, see more details in Pearson et al., 2017) with nutritional geometry and other indirect dietary analytic methods (e.g. stable isotopes, fatty acid signatures and others) to enhance our knowledge on the nutritional ecology of marine predators and improve conservation measures for endangered species (Machovsky-Capuska et al., 2016e).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2017.05.008.

References

Barbato, B.H.A., Secchi, E.R., Di Beneditto, A.P.M., Ramos, R.M.A., Bertozzi, C., Marigo,

J., Bordino, P., Kinas, P.G., 2012. Geographical variation in Franciscana (*Pontoporia blainvillei*) external morphology. J. Mar. Biol. Assoc. U. K. 92, 1645–1656.

Barros, N.B., Clarke, M.R., 2009. Diet. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals. Academic Press, San Diego, pp. 311–317.

Bassoi, M., 2005. Feeding ecology of *Pontoporia blainvillei* of southern Brazil. In: PhD Thesis. Southampton University, United Kingdom.

Bastida, R., Rodriguez, D., Secchi, E., da Silva, V., 2007. Mamíferos Acuáticos de Sudamérica y Antártida. Vázquez-Mazzini Editores, Buenos Aires.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J.Stat. Softw. 67, 1–48.

Bilgmann, K., Möller, L.M., Harcourt, R.G., Kemper, C.M., Beheregaray, L.B., 2011. The Use of Carcasses for the Analysis of Cetacean Population Genetic Structure: A Comparative Study in Two Dolphin Species. PLoS ONE 6 (5), e20103. http://dx.doi. org/10.1371/journal.pone.0020103.

Bittar, V.T., 2007. Relações tróficas entre *Trichiurus lepturus* (Osteichthyes, Perciformes) e *Pontoporia blainvillei* (Mammalia, Cetacea) na costa norte do Rio de Janeiro. In: Master Thesis. Universidade Estadual do Norte Fluminense Darcy Ribeiro, Rio do Janeiro.

Bordino, P., Albareda, D., 2004. Incidental mortality of Franciscana dolphin *Pontoporia blainvillei* in coastal gillnet fisheries in northern Buenos Aires, Argentina. In: Technical Paper SC/56/SM11 Presented at the International Whaling Commission Meeting, Sorrento, Italia.

Coogan, S.C.P., Raubenheimer, D., 2016. Might macronutrient requirements influence grizzly-bear human conflict? Insights from nutritional geometry. Ecosphere 7 (1), e01204. http://dx.doi.org/10.1002/ecs2.1204.

Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet Mixing in a large omnivore. the Grizzly Bear: a geometric analysis. PLoS One 9 (5), e97968. http://dx.doi.org/10.1371/journal.pone. 0097968.

Craig, J.F., Kenley, M.J., Talling, J.F., 1978. Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. Freshw. Biol. 8 (6), 585–590.

Crawley, M.J., 2005. Statistics: an Introduction Using R. Wiley, Chichester.

Cremer, M.J., Pinheiro, P.C., Simões-Lopes, P.C., 2012. Prey consumed by Guiana dolphin *Sotalia guianensis* (Cetacea, Delphinidae) and Franciscana dolphin *Pontoporia blainvillei* (Cetacea, Pontoporiidae) in an estuarine environment in southern Brazil Iheringia. Ser. Zool. 102 (2), 131–137.

Crespo, E.A., Harris, G., González, R., 1998. Group size and distributional range of the Franciscana *Pontoporia blainvillei*. Mar. Mamm. Sci. 14 (4), 845–849.

Crespo, E.A., Pedraza, S.N., Grandi, M.F., Dans, S.L., Garaffo, G.V., 2010. Abundance and distribution of endangered Franciscana dolphins in Argentine waters and conservation implications. Mar. Mamm. Sci. 26 (1), 17–35.

Cunha, H.A., Medeiros, B.V., Barbosa, L.A., Cremer, M.J., Marigo, J., 2014. Population structure of the endangered franciscana dolphin (*Pontoporia blainvillei*): reassessing management units. PLoS One 9 (1), e85633.19. http://dx.doi.org/10.1371/journal. pone.0085633.

Denuncio, P., 2012. Biología y conservación del delfín del Plata (*Pontoporia blainvillei*) en el sector costero bonaerense. In: PhD Thesis. Universidad Nacional de Mar Del Plata, Argentina.

Freije, R.H., Asteasuain, R.O., de Schmidt, A.S., Zavatti, J.R., 1981. Relación de la salinidad y temperatura del agua con las condiciones hidrometeorológicas en la porción interna del estuario de Bahía Blanca. In: Contribuciones Cientificas, IADO. Vol. 57. pp. 1–18.

Guerrero, R.A., Piola, A., Molinari, G., Osiroff, A., 2010. Climatología de temperatura y salinidad en el Río de la Plata y su Frente Marítimo, Argentina-Uruguay. Instituto Nacional de Investigación y desarrollo Pesquero INIDEP, Mar del Plata (95 pp).

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman and Hall, London.

Henning, B., 2012. Ecología alimentar da toninha *Pontoporia blainvillei*. In: Master Thesis. Universidade de Sao Paulo, Brazil.

Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. J. Fish Biol. 17 (4), 411–429.

Jaureguizar, J.A., Menni, R., Lasta, C., Guerrero, R., 2006. Fish assemblage of the Northern Argentine Coastal System: spatial patterns and their temporal variations. Fish. Oceanogr. 15, 326–344.

Kohl, K.D., Coogan, S.C.P., Raubenheimer, D., 2015. Do wild carnivores forage for prey or for nutrients? Evidence for nutrient-specific in vertebrate predators. BioEssays 37 (6), 701–709.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2015. lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). In: R Package Version 2.0-25, (http://CRAN.R-project.org/package = lmerTest (24.10.2015)).

Lopes, X.M., da Silva, E., Bassoi, M., Dos Santos, R.A., Santos, M.C.O., 2012. Feeding habits of Guiana dolphins, *Sotalia guianensis*, from south-eastern Brazil: new items and a knowledge review. J. Mar. Biol. Assoc. UK 92 (8), 1723–1733.

Lucifora, L.O., García, V.B., Escalante, A.H., 2009. How can the feeding habits of the sand tiger shark influence the success of conservation programs? Anim. Conserv. 12, 291–301.

Luque, P.L., Learmonth, J.A., Santos, M.B., Ieno, E., Pierce, G.J., 2009. Comparison of two histological techniques for age determination in small cetaceans. Mar. Mammal Sci. 25 (4), 902–919. http://dx.doi.org/10.1111/j.1748-7692.2009.00304.x.

Machovsky-Capuska, G.E., Dwyer, S.L., Alley, M.R., Stockin, K.A., Raubenheimer, D., 2011. Evidence for fatal collisions while plunge diving in Gannets. Ibis 153, 631–635.

Machovsky-Capuska, G.E., Coogan, S.C.P., Simpson, S.J., Raubenheimer, D., 2016e. Motive for killing: what drives prey choice in wild predators? Ethology. http://dx.

doi.org/10.1111/eth.12523.

Machovsky-Capuska, G.E., Priddel, D., Leong, P.H.W., Jones, P., Carlile, N., Shannon, L., Portelli, D., McEwan, A., Chaves, A., Raubenheimer, D., 2016b. Coupling bio-logging with nutritional geometry to reveal novel insights into the foraging behaviour of a plunge-diving marine predator. N. Z. J. Mar. Freshw. Res. http://dx.doi.org/10. 1080/00288330.2016.1152981.

Machovsky-Capuska, G.E., Senior, A., Zantis, S., Barna, K., Cowieson, A., Pandya, S., Pavard, C., Shiels, M., Raubenheimer, D., 2016d. Dietary protein selection in a freeranging urban population of common myna birds. Behav. Ecol. 27, 219–227. http:// dx.doi.org/10.1093/beheco/arv142.

Machovsky-Capuska, G.E., Senior, A.M., Benn, E., Tait, A.H., Schuckard, R., Stockin, K.A., Cook, W., Ogle, M., Barna, K., Melville, D., Wright, B., Purvin, C., Raubenheimer, D., 2016c. Sex-specific macronutrient foraging strategies in a successful marine predator: the Australasian gannet. Mar. Biol. 163, 75. http://dx.doi.org/10.1007/s00227-016- 2841-y.

Machovsky-Capuska, G.E., Senior, A.M., Simpson, S.J., Raubenheimer, D., 2016a. The multidimensional nutritional niche. Trends Ecol. Evol. 31, 355–365.

Malinowski, C.R., Herzing, D.L., 2015. Prey use and nutritional differences between reproductive states and age classes in Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. Mar. Mamm. Sci. 31, 1471–1493.

Méndez, M., Rosenbaum, H.C., Bordino, P., 2008. Conservation genetics of the Franciscana dolphin in Northern Argentina: population structure by-catch impacts and management implications. Conserv. Genet. 9 (2), 419–435.

Meynier, L., Stockin, K.A., Bando, M.K.H., Duignan, P.J., 2008. Stomach contents of common dolphin (Delphinus sp.) from New Zealand waters. N. Z. J. Mar. Freshw. Res. 42, 257–268.

Negri, M.F., Cappozzo, H.L., Túnez, J.I., 2016. Genetic diversity and population structure of the Franciscana dolphin, *Pontoporia blainvillei*, in Southern Buenos Aires, Argentina. N. Z. J. Mar. Freshw. Res. 50 (2), 326–338.

Negri, M.F., Denuncio, P., Panebianco, M.V., Cappozzo, H.L., 2012. Bycatch of Franciscana dolphins *Pontoporia blainvillei* and artisanal fisheries dynamic in the southernmost distribution of the species. Braz. J. Oceanogr. 60, 151–160.

Nie, Y., Zhang, Z., Raubenheimer, D., Elser, J.J., Wei, W., Wei, F., 2014. Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. Funct. Ecol. 29, 26–34.

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

N.R.C., 1989. Recommended dietary allowances, 10th ed. National Academy Press, Washington, DC.

Olivier, S.R., Bastida, R., Torti, M.R., 1968. Sobre el ecosistema de las aguas litorales de Mar del Plata: niveles tróficos. y cadenas tróficas pelágico-demersales y bentónicodemersales. In: Serie Contribuciones del Servicio de Hidrografía Naval. Vol. 58 (46pp).

Österblom, H., Olsson, O., Blenckner, T., Furness, R.W., 2008. Junk-food in marine ecosystems. Oikos 117, 967–977.

Paddack, M.J., Cowen, R.K., Sponaugle, S., 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25, 461–472.

Panthi, S., Aryal, A., Lord, J., Adhikari, B., Raubenheimer, D., 2012. Summer diet and habitat ecology of red panda (*Ailurus fulgens fulgens*) in Dhopatan hunting reserve. Nepal Zool. Stud. 51, 701–709.

Pearson, H.C., Jones, P.W., Srinivasan, M., Lundquist, D., Pearson, C.J., Stockin, K.A., Machovsky-Capuska, G.E., 2017. Testing and deployment of C-VISS (cetacean-borne video camera and integrated sensor system) on wild dolphins. Mar. Biol. 164, 42. http://dx.doi.org/10.1007/s00227-017-3079-z.

Polizzi, P., Chiodi Boudet, L., Romero, B., Denuncio, P., Rodriguez, D., Gerpe, M., 2013. Fine scale distribution constrains cadmium accumulation rates in two geographical groups of Franciscana dolphin from Argentina. Mar. Pollut. Bull. 72, 41–46.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. Version 3.3.1. R Foundation for Statistical Computing, Vienna, Austria (https://www.R-project.org/ (24.10.2015)).

Raubenheimer, D., Simpson, S.J., 2006. The challenge of supplementary feeding: Can geometric analysis help save the kakapo? Notornis. 53, 100–111.

Raubenheimer, D., 2011. Toward a quantitative nutritional ecology: the right-angled mixture triangle. Ecol. Monogr. 81, 407–427.

Raubenheimer, D., Simpson, S.J., Mayntz, D., 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Funct. Ecol. 23, 4–16.

Raubenheimer, D., Simpson, S.J., Tait, A.H., 2012. Match and mismatch: conservation physiology, nutritional ecology and the timescales of biological adaptation. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 367, 1628–1646.

Raubenheimer, D., Machovsky-Capuska, G.E., Chapman, C.A., Rothman, J.M., 2015. Geometry of nutrition in field studies: an illustration using wild primates. Oecologia 513 (177), 223–234.

Reeves, R., Dalebout, M., Jefferson, T.A., Karkzmarski, L., Laidre, K., O'Corry-Crowe, G., Rojas-Bracho, L., Secchi, E., Slooten, E., Smith, B.D., Wang, J.Y., Zerbini, A.N., Zhou, K., 2012. Pontoporia blainvillei. In: The IUCN Red List of Threatened Species 2012: e.T17978A17623386, http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS. T17978A17623386. (21.07.2016).

Remonti, L., Balestrieri, A., Raubenheimer, D., Saino, N., 2015. Functional implications of omnivory for dietary nutrient balance. Oikos. http://dx.doi.org/10.1111/oik.02801.

Rodriguez, D., Rivero, L., Bastida, R., 2002. Feeding ecology of the Franciscana (*Pontoporia blainvillei*) in estuarine and marine waters of northern Argentina. Lat. Am. J. Aquat. Mamm. 1 (1), 77–94.

Rothman, J.M., Chapman, C.A., Van Soest, P.J., 2012. Methods in primate nutritional ecology: a user's guide. Int. J. Primatol. 33 (3), 542–566.

Rothman, J.M., 2015. Nutritional geometry provides new insights into the interaction between food quality and demography in endangered wildlife. Funct. Ecol. 29

(1), 3–4.

Secchi, E.R., Danilewicz, D., Ott, P.H., 2003. Applying the phylogeographic concept to identify Franciscana dolphin stocks: implications to meet management objectives. J. Cetacean Res. Manag. 5, 61–68.

Senior, A.M., Grueber, C.E., Machovsky-Capuska, G.E., Simpson, S.J., Raubenheimer, D., 2016. Macronutritional consequences of food generalism in an invasive mammal, the wild boar. Mamm. Biol. doi. http://dx.doi.org/10.1016/j.mambio.2016.07.001.

Simpson, S.J., Raubenheimer, D., 2012. The Nature of Nutrition: an Integrative Framework from Animal Adaptation to Human Obesity. Princeton University Press, Princeton.

Spalding, M.D., Fox, H.E., Allen, G.R., Zach, N.D., Ferdaña, A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Edmund, K.D., McManus, M., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57, 573–583.

Spitz, J., Mourocq, E., Schoen, V., Ridoux, V., 2010. Proximate composition and energy content of forage species from the Bay of Biscay: high-or low-quality food? ICESJ. Mar. Sci. 67, 909–915.

Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., Ridoux, V., 2012. Cost of living dictates what whales, dolphins and porpoises eat: The importance of prey quality on predator foraging strategies. PLoS One 7 (11), e50096. http://dx.doi.org/10.1371/journal.pone.0050096.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University, Princeton.

Stephens, D.W., Brown, J.S., Ydenberg, R.C., 2006. Foraging: Behavior and Ecology. The University of Chicago Press, Chicago.

Tait, A.H., Raubenheimer, D., Stockin, K.A., Merriman, M., Machovsky-Capuska, G.E., 2014. Nutritional geometry and macronutrient variation in the diets of gannets: the challenges in marine field studies. Mar. Biol. 161, 2791–2801.

Toft, S., Wise, D.H., 1999. Growth, development, and survival of a generalist predator fed single-and mixed-species diets of different quality. Oecologia 119 (2), 191–197.

Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar. Ecol. Prog. Ser. 294, 1–8.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analyzing ecological data. Springer, New York.