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Feeding Habits of Franciscana Dolphins (*Pontoporia blainvillei*): Echolocation or Passive Listening?

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Abstract

Research on the feeding habits of Franciscana dolphins (*Pontoporia blainvillei*) in waters along the Uruguayan coast was carried out using stomach contents from 41 individuals that were incidentally entangled in artisanal fishing nets or were stranded on the beach. A total of nine prey species were identified: eight teleosts and one squid. Teleosts were identified in 99.8% of the 37 stomach samples, corresponding to a total of 342 individuals. The striped weakfish (*Cynoscion guatucupa*) was the most important teleost by index of relative importance (IRI) (*n* = 127; IRI = 49.4%), followed by the toadfish (*Porichthys porosissimus*) (*n* = 90; IRI = 26.6%) and the whitemouth croaker (*Micropogonias furnieri*) (*n* = 66; IRI = 17.3%); whereas the remaining fish species represented less than 6.5% IRI. From eight species of fish found in stomach contents, four of them (striped weakfish, toadfish, whitemouth croaker, and Argentine croaker [*Umbrina canossai*]) actively produce sound. Fish, particularly those emitting sound, were the most important food content, representing 97.4% IRI. The Levin's index of niche breadth shows a specialist feeding strategy, and data indicated that the Franciscana chooses soniferous prey along the Uruguayan coast. Therefore, we suggest that Franciscana dolphins find their prey in the low visibility waters of the Rio de la Plata estuary and the murky waters of the Uruguayan ocean coast through passive listening. However, this behavior may also lead Franciscana dolphins to be attracted to artisanal fishing nets because of the sounds produced by the fish caught in nets, which puts them in danger of becoming entangled.

Key Words: Franciscana dolphins, *Pontoporia blainvillei*, diet, Uruguay coast, passive listening, soniferous fishes

Introduction

Understanding predator–prey relationships is one of the main goals of animal ecology. Information on prey selection is often used to provide the foundation for dietary niche characterization (Bearhop et al., 2004); and along with diet composition, this is one of the most important input parameters in food web models (Christensen & Pauly, 1992; Berens-McCabe et al., 2010).

Cetacean diets are commonly quantified through stomach content analyses from stranded, bycaught, or harvested animals (e.g., Fitch & Brownell, 1971; Gannon et al., 1997; Barros & Wells, 1998). The Franciscana dolphin (*Pontoporia blainvillei,* Gervais & d'Orbigny 1844) is an endemic dolphin from the southwestern Atlantic Ocean that is caught incidentally in coastal fishing nets all along its geographical distribution—from Itaúnas, Brazil (18° 25' S, 30° 42' W) to Península Valdés, Argentina (42° 35' S, 64° 48' W) (Praderi et al., 1989; Secchi et al., 1997; Crespo et al., 1998; Bordino et al., 2002; Rodríguez et al., 2002; Franco-Trecu et al., 2009). Due to their continued incidental mortality throughout most of its distribution, it is considered the most endangered small cetacean of the southwestern Atlantic Ocean (Secchi & Wang, 2003). Consequently, the Franciscana dolphin is classified as "Vulnerable" (A3d) by the International Union for Conservation of Nature (IUCN) (Reeves et al., 2008). However, little is known about the behavior of this endemic dolphin in the wild (Bordino et al., 2002; Melcón et al., 2012; Wells et al., 2013; Tellechea & Norbis, 2014; Tellechea et al., 2016; Cremer et al., 2017).

Many studies on the trophic ecology of the Franciscana dolphin have been performed in the southwestern Atlantic Ocean region (Fitch & Brownell, 1971; Pinedo, 1982; Brownell, 1989; Ott, 1994; Rodríguez et al., 2002; Bassoi, 2005; Cremer et al., 2012; Paso-Viola et al., 2014;

Baptista et al., 2016; Troina et al., 2016). Studies of feeding habits have found that this dolphin exhibits opportunistic feeding behavior and is a prey generalist, consuming fish, cephalopods, and crustaceans as the most common prey (Rodríguez et al., 2002; Bassoi, 2005; Paso-Viola et al., 2014). These earlier studies show that the Franciscan dolphin feed on soniferous (i.e., noise-producing) fish species, particularly sciaenids. So far, dietary studies have not contemplated that this dolphin may prefer sound-producing fish, nor has it been studied what percentage of these sound-producing fish are components of their diet. The Franciscana dolphin could be using passive listening to catch prey as has been documented in the case of bottlenose dolphin (*Tursiops truncatus,* Montagu 1821) (Barros & Odell, 1990; Barros, 1993).

Some researchers have hypothesized that coastal bottlenose dolphins use passive listening to locate noise-producing prey (Barros & Odell, 1990; Barros, 1993; Barros & Wells, 1998). In a novel experiment in Sarasota Bay, Gannon et al. (2005) found that bottlenose dolphins indeed responded to the playback of fish sounds. These dolphins changed their direction of travel, turning towards the sound source when fish noises were played. In addition, dolphins significantly increased their rate of echolocation immediately following playback of fish sounds. Gannon et al. concluded that bottlenose dolphins use passive listening extensively during the search phase of foraging. By listening passively, dolphins may obtain useful information regarding the identity, number, size, and location of soniferous prey. Berens-McCabe et al. (2010) indicated that at the population level, resident bottlenose dolphins of Sarasota Bay also preferred soniferous fish prey.

The aim of this work was to analyze if the wild resident Franciscana dolphin from the Uruguayan coast relies more on passive listening than on echolocation as suspected for individuals in the southwestern Atlantic Ocean region. This was achieved by analyzing their feeding habits and assessing if sound-producing fish are important prey of the dolphins in this area. For this purpose, stomach contents of dolphins entangled in artisanal fishing nets and stranded on the beach were examined. A second objective was to determine the overall diet composition of the Franciscana dolphin.

Methods

Stomach Contents Analysis

A total of 41 Franciscana dolphin stomachs were analyzed, which were taken from animals between 84 to 165 cm in total length (FTL)—24 females (mean = 119.7 cm; SD = 26.4) and 17 males (mean = 121.8 cm; SD = 18.1). These lengths indicate that stomach contents were likely sampled from calves (78 to 94 cm), juveniles, and adults (105 to 169.5 cm) (Kasuya & Brownell, 1979; Rodríguez et al., 2002). Each dolphin specimen's FTL (cm) was recorded according to Norris (1961), and intact stomachs were carefully removed. All died as a result of being incidentally entangled in artisanal fishing nets or from being stranded on the beach off the Uruguayan coast during 2013 and 2016 (Figure 1). They were kept in freezers at -20° C until necropsies were performed. Undigested or partially digested fish were removed for identification, and then the stomach contents were washed using a 0.3 mm sieve and preserved in 70% ethanol to recover bones and otoliths if present. Food items were identified to

Figure 1. Map of the study area off the Uruguayan coast; positions of entangled and stranded dolphins included in this study are shown as grey dots.

the lowest possible taxon using laboratory catalogs from fish in the area. The total number of empty stomachs was also recorded. Total lengths (cm) for all prey (PTL) species were measured and total mass (g) of each species estimated using length–weight relationships previously described (Ehrhardt et al., 1977; Haimovici, 1982; Bugoni & Vooren, 2004; Rodríguez & Gasalla, 2008; Segura et al., 2012).

The frequency of occurrence (FO) was calculated as the number of stomachs in which prey occurred, the numerical abundance (*N*) as the number of individuals of each prey type/total number of individuals of all prey types, and the reconstructed biomass (W) as the biomass of each prey type/total biomass represented by all prey (Hyslop, 1980; Castley et al., 1991; Cortés, 1997). The relative importance of prey species was evaluated using the index of relative importance calculated as IRI = $[N + W] * FO$ and then transformed as a percentage (% IRI) (Pinkas et al., 1971; Hyslop, 1980). The IRI is a proper metric used to characterize the type and abundance of prey ingested, and it could reveal if the fish that produce sound are important in the diet of this dolphin (Hyslop, 1980).

To estimate the diversity of the dolphin diet, the Shannon diversity index H ($H = -\Sigma\, pi * ln(pi)$, where $pi = ni/N$, ni = number of individuals of the species in a sample, and N = total number of individuals registered in the sample) and the Berger-Parker species richness index ($d = Nmax/N$, where Nmax is the number of individuals in the most abundant species and N is the total number of individuals in the sample) were calculated (Magurran, 2004). The Shannon diversity index is widely used in aquatic ecology (Washington, 1984; Krebs, 1989). This index is a nonparametric measure that implies no assumption about the prey's abundance or distribution, reflects both evenness and richness (Krebs, 1989), falls between 0 (indicating the stomach contents consist of only one prey) and 3.5, but rarely exceeds 4.0 (Washington, 1984). The Berger-Parker dominance measure expresses the proportional importance of the most abundant species (prey) (Magurran, 2004) and can take values between 0 and 1. Low values indicate lowered dominance by any one species (prey) in a diet (Magurran, 2004).

Specialization in the diet was analyzed using Levin's index of niche breadth (with 9,999 bootstrap resampling), standardized by the Hulbert (1978) method. This index varies between 0 and 1, and the predator is considered a specialist when the value is close to zero and a generalist when it is close to 1 (Ludwig & Reynolds, 1988).

To test for no significant differences between the stomach contents of stranded and entangled dolphins, and between dolphins obtained off the Rio de la Plata and Atlantic Ocean coast, a permutation multivariate analysis of variance (PERMANOVA) test (N = 9,999 permutations) using Bray-Curtis distances (Anderson, 2001; Legendre & Legendre, 2012) and the numerical abundance data (number of individuals of each prey type by predator) were calculated. In all cases, the significance level considered was $p = 0.05$. The statistical software *PAST* (Hammer et al., 2001) was used for all statistical analyses and diversity indices.

Results

Prey Consumption: Stomach Contents Analysis

From the 41 stomachs sampled, only four were empty; these stomachs were not included in the analysis. A total of nine food species in fresh condition, or in the beginning of digestion, were identified: striped weakfish (*Cynoscion guatucupa,* Cuvier 1830), whitemouth croaker (*Micropogonias furnieri,* Desmarest 1823), Argentine croaker (*Umbrina canossai,* Berg 1895), banded croaker (*Paralonchorus brasiliensis,* Steindachner 1875), and southern king weakfish (*Macrodon articauda,* Günther 1880)—all species belonging to the family Sciaenidae; toadfish (*Porichthys porosissimus,* Valenciennes 1837; Family Batrachoididae); Atlantic anchovy (*Engraulis anchoita,* Hubbs & Marini 1935; Family Engraulidae); and Brazilian codling (*Urophycis brasiliensis*, Kaup 1858; Family Phycidae). The Sao Paulo squid (*Loligo sanpaulensis,* Brakoniecki 1984; Family Loligindae) (Table 1) was only detected in one stomach. Unidentified individuals (UI) were found in eight stomachs (Table 1). The UI were not taken into account in the quantitative analysis since they were only found in small quantities and, hence, the contribution was considered to be insignificant overall. No otoliths and bones were found. Teleosts were recorded in 99.8% of the 37 stomachs and corresponded to a total of 342 individuals. The striped weakfish was the most important teleost (n = 127; IRI = 49.4%), followed by toadfish (n = 90; IRI = 26.6%) and whitemouth croaker (n = 66; IRI = 17.3%); whereas the remaining fish species represented less than 6.5% IRI (Table 1). The five species of fish that produce sound represented 97.4% IRI of total prey.

Length composition of all species eaten ranged from 7 to 24 cm PTL, with modal and median length at 13 cm PTL and a mean length of 13.1 ± 0.1 cm (Table 1). The cumulative frequency at 50% of prey was 13 cm PTL.

The estimate of Shannon diversity index was 1.633 (lower value [25%] = 1.532, upper value [75%] = 1.705), and the Berger-Parker species richness index was 0.363 (lower value [25%] =

Table 1. Diet composition of the Franciscana dolphins collected off the Uruguayan coast, 2013 to 2016; frequency of occurrence (FO), numerical abundance (*N*), biomass (W), percentage Index of Relative Importance (IRI), and prey length characteristics: max, min, and mean length with standard error (SE).

							Prey length			
Prey item	Soniferous	%FO	*N*	%N	%W	%IRI	Min	Max	Mean	SE
Teleosts			349							
Cynoscion guatucupa	Yes	23.1	127	36.3	50.7	49.4	11	24	14.6	0.2
Porichthys porosissimus	Yes	25.2	90	25.7	17.2	26.6	7	16	11.1	0.2
Micropogonias furnieri	Yes	21.0	66	18.9	14.7	17.3	10	21	13.1	0.2
Umbrina canosai	Yes	9.4	26	7.4	9.5	3.9	10	16	13.5	0.3
Engraulis anchoita	No	8.4	19	5.4	3.9	1.9	10	17	12.9	0.4
Paralonchurus brasiliensis	No	4.2	7	2	1.1	0.3	11	13	12.1	0.3
Macrodon articauda	Yes	2.1	3	0.8	1	0.09	9	16	12.8	0.8
Urophisis brasiliensis	No	4.2	4	1.1	0.4	0.1	15	18	16.3	0.8
Cephalopods			7							
Loligo sanpaulensis	No	2.1	7	2	1.1	0.1	12	15	13.5	0.6
Unidentified species (UI)		8	12							

0.315, upper value [75%] = 0.415). The two estimate indexes showed a low diversity and specific richness in the diet of this dolphin. Levin's standardized index of niche breadth was 0.078, which indicates the Franciscana dolphin utilizes a specialist feeding strategy off the Uruguayan coast.

The PERMANOVA test confirmed that there were no significant differences between the stranded and entangled dolphin diets ($F = 1.28$; $p = 0.26$) and between Rio de la Plata and the Atlantic Ocean coast dolphin diets ($F = 0.12$; $p = 0.92$).

Discussion

Eight fish species were found in Franciscana dolphin stomachs in this study. The most important prey were striped weakfish, toadfish, and whitemouth croaker. Five of the eight fish species actively produce sound: (1) whitemouth croaker (Tellechea et al., 2010, 2011a), (2) striped weakfish (Tellechea & Norbis, 2012), (3) Argentine croaker (Tellechea et al., 2017), (4) southern king weakfish (W. Norbis, pers. comm., 10 July 2007), and (5) toadfish (W. Norbis, pers. comm., 10 July 2007). In terms of IRI, striped weakfish was the most important prey identified off the Brazilian and Argentinean coasts, followed by other sciaenids, including whitemouth croaker and southern king weakfish (Bassoi & Secchi, 1999; Di Beneditto & Ramos, 2001; Rodríguez et al., 2002; Bassoi, 2005; Paso-Viola et al., 2014; Troina et al., 2016).

No significant differences were found between the stomach contents of stranded and entangled dolphins or between dolphins of the Rio de la Plata and the Atlantic Ocean coast. The Rio de la Plata estuary and the Atlantic Ocean coast of Uruguay, a very dynamic area, are both influenced by the "run-off" of the Parana and Uruguay Rivers and the effect of winds that mix the waters and establish turbidity conditions (Nagy et al., 1997). These regions also have persistent fish assemblages and a reciprocal flow of species between adjacent associations, principally between external estuarine and inner continental shelf assemblages where the sciaenids constitute the more abundant fish species (Lorenzo et al., 2011). These dynamics between the estuary and the ocean could explain why the diet found in dolphins from different areas was not different. Throughout their distribution, Franciscana dolphins are classified as opportunistic in their feeding habits (Rodríguez et al., 2002; Bassoi, 2005; Paso-Viola et al., 2014); however, the Levin's standardized index of niche breadth indicates a specialist feeding strategy for the Franciscana dolphin population investigated in this study. The diversity indexes show a low diversity and specific richness in the diet of this dolphin in the Uruguayan coast, supporting the hypothesis that the Franciscana dolphin in this area is a specialist, preying principally on sound-producing fish.

Throughout its distribution, the Franciscana dolphin diet is composed of at least 76 prey species, with the majority of prey belonging to three main zoological groups: (1) fish (82.8%), (2) crustaceans (9.2%), and (3) molluscs (7.9%) (Fitch & Brownell, 1971; Pinedo, 1982; Brownell, 1989; Bassoi & Secchi, 1999; Rodríguez et al., 2002; Bassoi, 2005; Paso-Viola et al., 2014). In stomach content analysis studies throughout Brazil, a total of 25 prey species were found in dolphins collected north of Rio de Janeiro (Di Beneditto & Ramos, 2001); 36 prey species were identified in a study performed in Rio Grande do Sul (Bassoi, 2005); a total of 24 different prey were found along the northern coast of Buenos Aires (Rodríguez et al., 2002); and, finally, 11 prey were identified from the southern Buenos Aires coast (Pazo-Viola et al., 2014). The number of prey species in this study (nine) is considerably lower compared with these Brazilian studies; however, the species reported in this study are consistent with those found by Fitch & Brownell (1971) and Brownell (1989) who also conducted diet studies only in the Uruguayan Atlantic coastal area.

It is noteworthy that the toadfish was the second most recurrent prey (25% FO) as previous studies off the Uruguayan coast have identified this species as the most consumed prey (Brownell, 1989). The contribution of toadfish between the diet of Franciscana dolphins from Uruguay and Argentina differs. It is one of the most important prey items in Uruguay as this and past studies have shown (Praderi, 1984; Brownell, 1989), while it is less common prey in Argentina (Rodríguez et al., 2002; Paso-Viola et al., 2014), although it is still a common species (Menni et al., 1984). This fish is hard to find; it inhabits caves in rocks or stays buried. This further suggests that the Franciscana dolphin may locate this fish in the dark waters of the Rio de la Plata estuary and the murky waters of the Uruguayan oceanic coast through passive listening. Recently, recordings of Franciscana dolphin echolocation in the wild on the Uruguayan coast with passive buoys were obtained (Tellechea et al., 2016); and in comparison with the records made on the Argentina coast (Melcón et al., 2012), it seems that in the latter place the use of echolocation is more frequent. Perhaps the comparatively fewer number of sounds recorded on the Uruguayan coast may be explained by the foraging/feeding behavior of the dolphins. As has been shown for the bottlenose dolphins, the same species may have different foraging behavior in different places (Gannon et al., 2005).

The technique of using passive listening to find prey is not new; this strategy has been already described for other cetaceans (Barros & Odell, 1990; Barros, 1993; Barrett-Lennard et al., 1996; Barros & Wells, 1998; Gannon et al., 2005; Berens-McCabe et al., 2010). Passive listening would increase the efficiency in capturing energetically rich prey (Barros & Wells, 1998; Gannon, 2003) as many soniferous fish species raise their frequency and intensity of calls during spawning periods (Tellechea et al., 2010, 2011a, 2011b; Tellechea & Norbis, 2012). In some specific species of sciaenid fishes, the sounds emitted are audible up to 630 m (Gannon, 2003), which is much further than the maximum echolocation detection range known for any dolphin, regardless of target strength (Au, 1993; Au et al., 2007). Given that fish sounds propagate more or less omnidirectionally (Barimo & Fine, 1998), passive listening would allow dolphins to keep a large area under surveillance without expending energy or advertising their presence. Therefore, the Franciscana dolphin may obtain useful information by listening such as prey identification and location, body size, and number of fish present. Using this information to assess the quality of prey from a distance would surely be advantageous for these predators (Gannon et al., 2005). Once the prey has been detected, the Franciscana dolphin could use echolocation to track and capture the prey (Au, 1993; Gannon et al., 2005; Ridgway et al., 2015).

Frainer et al. (2015) suggest that the poor development of the biosonar structures of the young Franciscana may be one of the causes in the increase in bycatch mortality. Due to improved motor skills and probably more experience with echolocation, adult Franciscana dolphins should be less likely to be caught in nets. However, the bycatch mortality of this species includes mostly adults with developed sonar as was shown here.

Passive listening could also contribute to Franciscana dolphins frequently ending up as bycatch as the sound-producing fish species are the target of some fisheries in this region, possibly causing dolphins to approach artisanal fishing nets to feed. These fish, whitemouth croaker, striped weakfish, and Argentine croaker, emit disturbance calls when they are entangled in nets (Tellechea et al., 2010, 2011a; Tellechea & Norbis, 2012). Bordino et al. (2002) show that even with the use of sonorous alarms to deter dolphins in fisheries focusing on those fishes, the Franciscana dolphin continued to get entangled in the nets. We therefore suggest that even with the use of acoustic alarms, this dolphin is attracted to the nets, possibly as a result of the fish sounds. As the Franciscana dolphin has been classified as "Vulnerable" throughout its distribution, principally as a consequence of the incidental mortality in artisanal fisheries, further studies are needed to clarify if this dolphin is attracted to fishing nets by soniferous fish and to identify ways to successfully prevent this from happening.

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