ARTICLE

Marine Mammal Science

Diet and foraging opportunism of the Guiana dolphin (*Sotalia guianensis*) in the Abrolhos Bank, Brazil

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Abstract

Diet analysis allows exploring how coastal dolphins interact with the environment and their role in the marine food webs. We studied the diet and feeding ecology of the Guiana dolphin, *Sotalia guianensis*, through analysis of stomach content from 42 animals stranded on the eastern coast of Brazil. A total of 1,336 semidigested prey items (fish, otoliths, cephalopod beaks, and crustaceans) were identified. Teleost fish comprised the most frequent food item (92% of the total), followed by cephalopods, and crustaceans. Prey belonged to 34 taxa and richness in individual stomachs varied from 1 to 15 prey taxa. Prey were generally small, but showed a significant trend to increase in size with dolphin length. The main prey of Guiana dolphins were demersal, estuarine, and sound-making fish such as catfish and sciaenids. No sex-related differences in diet were found. Diet composition varied seasonally and occurrence of prey items was coherent with breeding or high abundance periods of some fish species and squids. Our study shows the importance of demersal prey from estuarine and soft-sediment habitats to Guiana dolphin in the Abrolhos Bank and reveals that feeding habits are generalist and opportunistic, with diet reflecting the seasonal abundance and availability of prey.

1 | INTRODUCTION

Cetaceans often regulate prey populations of fish, cephalopods, and crustaceans due to the high rate of food consumption, wide distribution, and high longevity (Katona & Whitehead, 1988; Trites, Cristensen, & Pauly, 1997). Thus, describing the diet of cetaceans is necessary to unravel the ecology of the aquatic environment and their trophic interactions, as well as the role of these top predators to ecosystems. Nevertheless, the knowledge about prey consumed by cetaceans is essential to understand important ecological processes, such as habitat use and movement patterns of this group.

The collection of information about the diet of cetaceans usually relies on indirect methods, such as stomach content analysis, stable isotope, and fatty acid signatures or molecular examination of prey (Bowen & Iverson, 2013; Pierce & Boyle, 1991; Tollit et al., 2009). Each method has strengths and weaknesses, but the identification of stomach contents is a low-cost method and allows the description of the diet with high taxonomic resolution and quantification of size and biomass of prey ingested (Barros & Clarke, 2009). This technique consists of the visual identification of semidigested prey or hard structure remains (e.g., otoliths, cephalopod beaks, crustacean carapaces) extracted from stomach contents.

The Guiana dolphin, *Sotalia guianensis* (van Bénéden, 1864), is a coastal dolphin endemic to the tropical and subtropical waters of the western Atlantic Ocean (Borobia, Siciliano, Lodi, & Hoek, 1991). The species is common throughout most of its distribution, inhabiting shallow waters close to the coast (Borobia et al., 1991). Feeding behavior of Guiana dolphins is diverse and includes individual and cooperative strategies (Rossi-Santos & Flores, 2009). Observation of interactions with muddy sea bottoms (Rossi-Santos & Wedekin, 2006) and the use of human-made structures to capture prey have been described (Monteiro-Filho, 1995). Unfortunately, the Guiana dolphins commonly get fatally entangled in fishing gear (Siciliano, 1994) and may compete with humans for limited resources.

Previous studies have described the diet of Guiana dolphins along southeastern and northeastern Brazilian coast (e.g., Borobia & Barros 1989; Carvalho, 1963; Gurjão, Furtado-Neto, Santos, & Cascon, 2003; Santos, Rosso, Aguiar, & Bassoi, 2002) and revealed the importance of demersal fish species and neritic cephalopods in the diet. More recently, studies have explored subjects such as feeding habitats (Daura-Jorge, Wedekin, & Simões-Lopes, 2011), dietary overlap between sympatric dolphins (Cremer, Pinheiro, & Simões-Lopes, 2012), nutritional composition of prey (Di Beneditto, Santos, & Vidal, 2009), and position in the trophic web (Di Beneditto, Souza, Kerigh, & Rezende, 2011). However, many fundamental questions still require answering, such as how diet varies seasonally and geographically, or whether there are dietary differences related to size and sex.

Here, we present valuable information about the diet and feeding ecology of the Guiana dolphin from samples collected during a 10-year period of a long-term monitoring program of stranded cetaceans along the eastern coast of Brazil. Our objectives were to answer the following questions regarding the Guiana dolphin in the Abrolhos Bank: (1) What are the prey and their relative contribution to the diet? (2) Are the feeding habits of the species generalist or specialist? (3) How does the diet vary seasonally, with size, or sex of individuals?

2 | MATERIALS AND METHODS

2.1 | Study area

The continental shelf of the eastern and northeastern coast of Brazil is generally narrow and has a steep slope (Ekau & Knoppers, 1999). The shelf off the southern coast of the state of Bahia and northern state of Espírito Santo
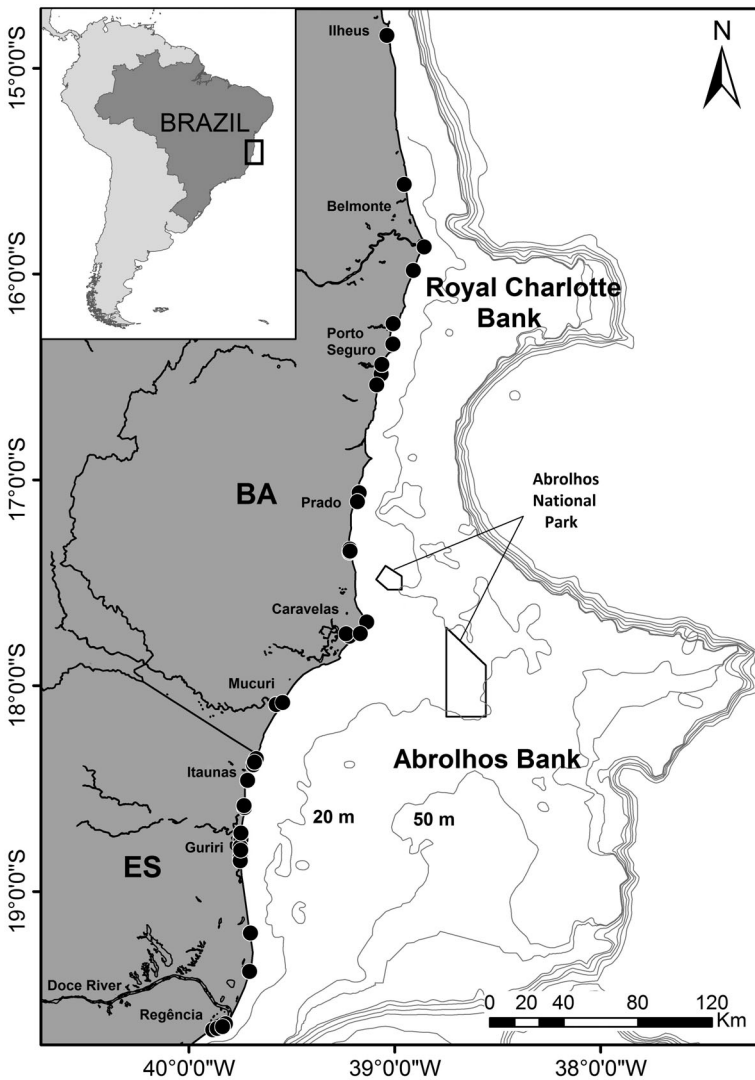
FIGURE 1 Map of Abrolhos and Royal Charlotte Banks showing the location (black dots) where the stranded Guiana dolphin individuals were collected (*n* = 40).

widens to form two large banks of tropical and warm waters: Royal Charlotte and Abrolhos Banks. These banks cover an area of 56,000 km^2 (Muehe, 2001), with mean sea surface temperatures ranging from 23°C to 28°C. The region is composed of different marine habitats, including large coralline algae banks (rhodoliths), coral reefs, sandstone barriers, and muddy/sandy bottoms (Dominguez, Martin, & Bittencourt, 2002). This mosaic is a "hotspot" of marine biodiversity in the western South Atlantic Ocean (Dutra, Allen, Werner, & Mckenna, 2006). Coastal areas receive the discharge of many rivers, which may form estuarine-mangrove complexes and sand banks. Carcasses of stranded Guiana dolphins were collected along the coast of the City of Ilheus (14°53′S, 39°02′W) to near the mouth of the Doce River (19°40′S, 39°53′W) (Figure 1).

2.2 | Sample preparation and identification

The sample consisted of stomach contents of 40 Guiana dolphins collected between 2003 and 2012 (Supplementary Material). The stomach of each carcass was extracted during necropsy and stored (−20°C). Carcasses were classified

by sex and body length. Dolphins with total body length >170 cm were considered adults; smaller ones were considered immatures (juveniles and calves) (according to Rosas & Monteiro-Filho, 2002).

Stomach contents were washed using a 1.0 mm mesh sieve and relevant items such as semidigested prey (fish and crustaceans), fish sagittal otoliths, and cephalopod beaks were separated after careful examination by the naked eye. All otoliths were washed with water-diluted neutral detergent and then dried for 48 hr at 60°C for storage. Cephalopod beaks were preserved in a 2:1 alcohol:glycerin solution. Semidigested prey were stored in 70% alcohol.

Otoliths were sprinkled with powdered graphite for better visualization (Pansard, Gurgel, Andrade, & Yamamoto, 2010). Fish species identification through sagittal otolith followed Abilhôa and Corrêa (1992), Corrêa and Vianna (1992/1993), Lemos et al. (1992, 1995a, 1995b) and the virtual base AFORO (Lombarte et al., 2006). All prey were identified at the lowest possible taxon (LPT) level. Cephalopod beaks were identified by Dr. Roberta Aguiar dos Santos with the aid of the reference collection from CEPSUL of ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade).

2.3 | Diet description and feeding strategy

The total number of preys consumed by each dolphin was calculated from the highest number of right or left fish otoliths (defined by the position of the sagittal sulcus) and the highest number of upper or lower cephalopod beaks. Size and mass of each fish prey were obtained from the otolith length measured from the tip of the rostrum to the posterior edge, parallel to the ridge. Only otoliths with well-preserved features (i.e., otoliths with both *sulcus acusticus* and morphology preserved) were considered for identification. The lower and upper rostral lengths of beaks were measured. Otolith and beak lengths were then used as predictor variables to estimate the total length and biomass of each prey, using regression equations from the literature (Di Beneditto, Ramos, & Lima, 2001; Lopes, Silva, Bassoi, Santos, & Santos, 2012; Santos, 1999). Whenever no regression equation was available, size and biomass were estimated using the equation for a congeneric or confamiliar species (Supplementary Material).

Four metrics described prey importance in the diet of Guiana dolphins: (1) occurrence frequency (%O), (2) percentage number (%N), (3) percentage of biomass (%B), and (4) percentage Index of Relative Importance (%IRI). The latter is a measure of contribution to the diet based on the combination of its occurrence frequency and numerical and biomass prevalence (Cortés, 1997).

To evaluate the feeding strategy of the Guiana dolphins we used the Costello plot adapted by Amundsen, Glaber, and Staldvik (1996), that consists of the specific abundance (P_i; plotted on the coordinate) vs. occurrence (in percent on the abscissa). Specific abundance is obtained through: $P_i = (\sum N_i / \sum N_t) \times 100$, where N_i is the numeric abundance of prey i, and N_t is total number of items in the stomachs in which the prey i was present. We pooled prey species into families to evaluate whether feeding specialization on prey of similar ecological niche occurred.

In order to understand the feeding preferences of Guiana dolphins, each prey was classified according to some ecological traits (vertical guild, trophic guild, bottom type preference, relationship with estuary, schooling behavior, and sound production) (see Supplementary Material for further details). A presence/absence matrix was constructed to further apply a cluster analysis, where rows correspond to species and columns correspond to ecological traits.

2.4 | Statistical analyses

The Spearman correlation coefficient was used to determine the strength of predator–prey size/mass relationship. *T*-tests were used to detect possible differences in total biomass consumption between sexes and among size/maturity categories. Because several specimens of the same prey taxon found in a stomach cannot be considered independent samples, the specimens' median size was used to avoid pseudo-replication.

A nonparametric MANOVA (NPMANOVA) (Anderson, 2001) with 9,999 permutations was used to assess differences in diet between sexes and among austral seasons of the year. Autumn and winter data were pooled due to

small sample size. Prey abundance was used to construct a dissimilarity matrix using the Bray-Curtis index. To minimize diet variation bias, rare prey (%O < 10) were not included in this analysis.

Dolphin niche width was expressed by the Simpson index of evenness (E); the index ranges from 0 to 1 and maximum evenness is obtained when all abundances are equal. This index is relatively unaffected by rare species (Krebs, 1999).

Prey were grouped through the unweighted pair group method with arithmetic mean (UPGMA) clustering method using the Jaccard index. This binary index is suitable for presence/absence matrices. The contribution of ecological traits to the formation of groups was assessed a posteriori through a similarity percentage analysis (SIMPER) using the Bray-Curtis index (Clarke, 1993).

3 | RESULTS

3.1 | Sample

Forty-two stomachs were available, of which two were empty and excluded from further analyses. The mean length of the 40 dolphins analyzed was 172 cm (SD = 21.06, range = 108–208 cm). Most dolphins were males (n = 22); 15 were females. Due to the high degree of decomposition of the carcasses, three dolphins could not be sexed and two others measured. During necropsy, most dolphins were diagnosed as victims of incidental entanglement in gill nets (n = 26, 65%).

A total of 1,370 prey were found, of which 1,258 were teleost fish (91.8%), 100 cephalopods (7.3%), and 12 crustaceans (<1%) (Table 1). Teleost fish occurred in all stomachs (100% of occurrence), cephalopods in 21 stomachs (52.5%), and crustaceans in only four stomachs (10%). Thirty-six taxa were identified, representing 17 families, 29 genera, and 27 species of teleost fish (otoliths of another 167 teleost specimens were too highly digested to be identifiable), two Loliginidae squid species and Dendrobranchiata shrimps that could not be identified due to the absence of rostrum (Table 1).

The cumulative species curve did not reach an asymptote (see Supplementary Material). We, however, estimated that only six new, rare prey species would be added, doubling the sample size. Thus, the sample size was sufficient to describe the diet of the Guiana dolphin in the study area.

3.2 | Prey importance

The total prey biomass ingested by the 40 Guiana dolphins before their death was estimated to be almost 43 kg (mean = 1,067.2, SD = 2,092.9, range = 7.6–12,647.1 g). Per dolphin, the mean number of prey was 33.2 (SD = 39.6, range = 2–211) and the mean number of taxa was 4.4 (SD = 2.4, range = 1–14). The mean size and weight of prey fish were, respectively, 9.9 cm (SD = 9.8, range = 1–70 cm) and 33.7 g (SD = 87.1, range = 1.2–835.0 g). The mean size and weight of cephalopod preys were, respectively, 8.4 cm (SD = 4.4, range = 3.6–25.8 cm) and 24.3 g (SD = 30.1, range = 3.4–166.1 g).

Teleost fish were the main prey of the Guiana dolphin (%N = 90.7, %O = 100, %B = 94.2, %IRI = 97.4). Cephalopods were relatively important in terms of occurrence (%O = 56.4), however, their numbers, weight, and relative importance were low (%N = 7.2; %B = 3.6; %IRI = 2.3). Crustaceans were consumed sporadically and had a negligible contribution to the diet of the species in the study area (%O = 10.0; %N = 1.0; %B = 0.2; %IRI = 0.3).

The following eight species/genera comprised 89.2% of the Guiana dolphin diet (based on %IRI): *Stellifer* spp., *Isopisthus parvipinnis*, *Macrodon* sp., *Bagre* sp., *Dorytheuthis plei*, *Trichiurus lepturus*, *Mugil* sp., and *Loliguncula brevis* (Table 1). Most taxa (n = 23) had a negligible contribution to the diet of the species (IRI < 1%). The Guiana dolphin had large dietary plasticity in the size of prey, consuming fish of up to 70 cm (Figure 2). Despite consuming a wide range of prey sizes, 90% of items were smaller than 20 cm.

TABLE 1 Prey consumed by Guiana dolphins in the Abrolhos Bank. Taxa code, number (N) and size range (S, in cm, from otolith/beak lengths) of specimens, occurrence in stomachs (O, number out of 40 stomachs), estimated total biomass (B, in grams, from otolith/beak lengths). Indexes present the same statistics (N, O, and B) expressed in percentage and the percentage index of Relative Importance (%IRI). Taxa highlighted in bold comprise approximately 90% of the diet according to %IRI. ni = not identified.

Taxa	Descriptive parameters					Indexes			
	Code	N	S	O	B	%N	%O	%B	%IRI
Teleostei	Tel								
Achiriidae	Ach								
Achirid ni	Ach ni	14	5.1–11.7	3	454.3	1.2	7.5	1.1	<0.1
Albulidae	Alb								
Albula vulpes	Alb vul	10	5.9–24.2	3	714.7	0.8	7.5	1.7	<0.1
Ariidae	Ari								
Aspistor luniscutis	Asp lun	18	2.8–25.1	4	553.0	1.5	10.0	1.3	<0.1
Bagre sp.	**Bag sp.**	**61**	**4.8–26.4**	**8**	**4,214.7**	**5.1**	**20.0**	**9.9**	**7.38**
Clupeidae	Clu								
Opisthonema oglinum	Opi ogl	8	3.9–17.1	3	183.2	0.7	7.5	0.4	<0.1
Chirocentrodon bleekerianus	Chi ble	41	6.9–9.4	2	251.1	3.4	5.0	0.6	<0.1
Engraulidae	Eng								
Anchoa sp.	Anc	94	4.0–12.1	4	472.9		10.0	1.1	0.27
Lycengraulis grossidens	Lyc gro	9	5.9–15.4	3	115.3	0.8	7.5	0.3	<0.1
Cetengraulis edentulus	Cet ede	1	6.8	1	9.1	—	—	—	—
Engraulid ni	Eng ni	13	3.1–7.5	3	39.3	1.1	7.5	0.1	<0.1
Hemirhamphidae	Hem								
Hemirhamphus brasiliensis	Hem bra	8	20.6–30.0	3	601.3	0.7	7.5	1.4	<0.1
Pristigasteridae	Pri								
Pellona harroweri	Pel har	40	6.3–12.3	7	581.8	3.3	17.5	1.4	2.03
Centropomidae	Cen								
Centropomus undecimallis	Cen und	5	37.9–51.1	1	1,760.0	0.4	2.5	4.1	0.28
Carangidae	Car								
Chloroscombrus chrysurus	Clo chr	10	12.1–15.9	2	256.7	0.8	5.0	0.6	<0.1
Carangid ni	Car ni	13	12.5–20.4	2	674.6	1.1	5.0	1.6	0.33
Gerreidae	Ger								
Diapterus auratus	Dia aur	29	6.0–9.7	5	410.8	2.4	12.5	1.0	1.04
Eucinostomus sp.	Euc sp.	4	6.8–10.9	1	75.1	0.3	2.5	0.2	<0.1
Haemulidae	Hae								
Conodon nobilis	Con nob	2	12.4–17.7	1	192.4	—	—	—	—
Haemulon aurolineatum	Hae aur	1	8.6	1	10.0	—	—	—	—
Haemulon steindachneri	Hae ste	8	6.8–9.2	3	57.3	0.7	7.5	0.1	<0.1
Pomadasys corvinaeformis	Pom cor	5	10.2–13.9	2	106.8	0.4	5.0	0.3	<0.1
Haemulid ni	Hae ni	1	5.8	1	5.1	—	—	—	—
Lutjanidae	Lut								
Lutjanid ni	Lut ni	3	5.9–16.8	3	134.6	0.3	7.5	0.3	0.10

(Continues)

TABLE 1 (Continued)

| Taxa	Code	N	S	O	B	%N	%O	%B	%IRI
Sciaenidae	Sci								
Ctenosciaena gracilicirrhus	Cte gra	1	2	1	1.2	—	—	—	—
Cynoscion virescens	Cyn vir	3	10.1–35.6	3	503.5	0.3	7.5	1.2	<0.1
Isopisthus parvipinnis	**Iso par**	213	1.1–17.9	14	3,005.5	17.8	35.0	7.0	**21.44**
Larimus breviceps	Lar bre	29	1.8–15.4	8	530.6	2.4	20.0	1.2	1.81
Menticirrhus americanus	Men ame	3	9.3–49.1	2	2,532.2	0.3	5.0	5.9	0.76
Paralonchurus brasiliensis	Par bra	16	1.7–17.1	5	391.0	1.3	12.5	0.9	<0.1
***Macrodon* sp.**	**Mac sp.**	64	4.9–37.9	7	14,004.3	5.3	17.5	32.8	**16.47**
Stellifer rastrifer	**Ste ras**	141	1.5–19.2	18	1,036.8	11.8	45.0	2.4	**15.77**
Stellifer brasiliensis	**Ste bra**	20	1.0–12.3	8	157.4	1.7	20.0	0.4	**1.01**
***Stellifer* sp.**	**Ste sp.**	150	1.1–8.0	13	97.7	12.5	32.5	0.2	**10.23**
Mugilidae	Mug								
***Mugil* sp.**	**Mug sp.**	16	10.8–41.0	6	2,644.8	1.3	15.0	6.2	**2.79**
Pomatomidae	Pom								
Pomatomus saltatrix	Pom sal	1	22	1	93.4	—	—	—	—
Sphyraenidae	Sph								
Sphyraena sp.	Sph sp.	6	24.1–33.3	3	1,094.9	0.5	7.5	2.6	0.57
Trichiuridae	Tri								
Trichiurus lepturus	**Tri lep**	30	8.7–70.2	8	2,293.6	2.5	20.0	5.4	**3.89**
Teleost ni	**Tel ni**	167	—	28	—	—	—	—	—
Cephalopoda	Cef								
Loliginidae	Lol								
Dorytheuthis plei	**Dor ple**	51	5.1–25.8	12	1,868.5	4.3	30.0	4.4	**6.39**
Loliguncula brevis	**Lol bre**	45	3.6–7.9	9	524.0	3.8	22.5	1.2	**2.77**
Loliginid ni		4	—	1	—	—	—	—	—
Crustacea	Cru								
Penaeidae	Pen	10	4.4–6.0	2	22.6	0.8	5.0	0.1	<0.1
Dendrobranchiata	Den	2	10.9–11.6	2	28.0	—	—	—	—

3.3 | Diet variation

A positive size-correlation was found between prey ($r = 0.53$, $p < .05$) and dolphins as shown in Figure 3. Larger prey (>20 cm) were only found in the gut contents of adults (>170 cm). A positive correlation was also found between mean prey biomass ($r = 0.39$, $p < .05$) and dolphin size. We failed to find a difference in niche width between adults (median = 0.61, $SD = 0.29$) and immature individuals (median = 0.54, $SD = 0.26$, $r = 0.15$, $p = .88$). The overall median niche amplitude for Guiana dolphins was 0.61 ($SD = 0.28$) and the higher and lower individual niche widths were 0.91 and 0 (only one prey ingested), respectively.

We failed to find a difference in the taxonomic composition of the diet between sexes (NPMANOVA: $F = 0.56$, $p = .91$) or maturity classes (NPMANOVA: $F = 1.24$, $p = .21$). Thus, all data were pooled for seasonal analyses.
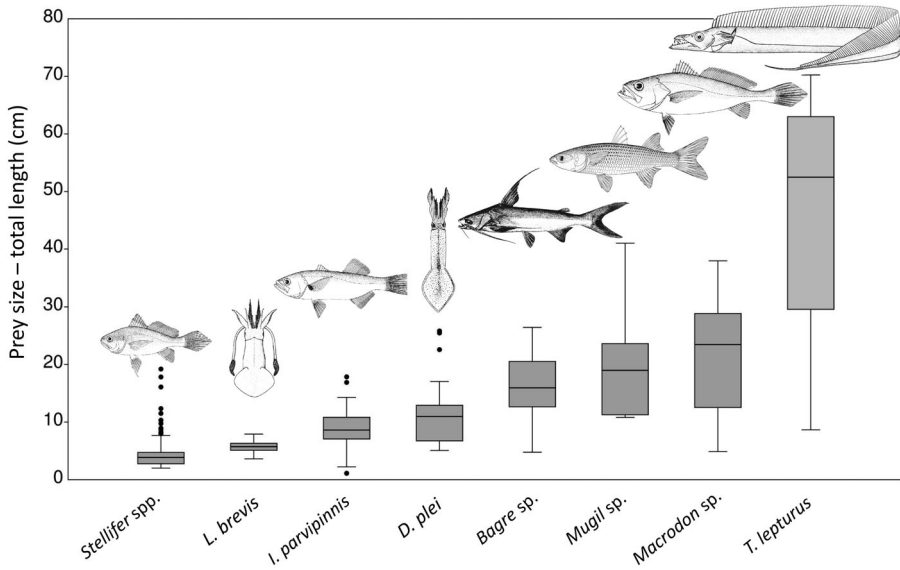
FIGURE 2 Size of the most important prey (%IRI) consumed by Guiana dolphins in the Abrolhos Bank. Boxes show the first and third quartiles (interquartile range) and median line; whiskers correspond to up to 1.5 times the interquartile range, and points denote outliers (>1.5 times the interquartile range). Drawings from Carpenter (2002).
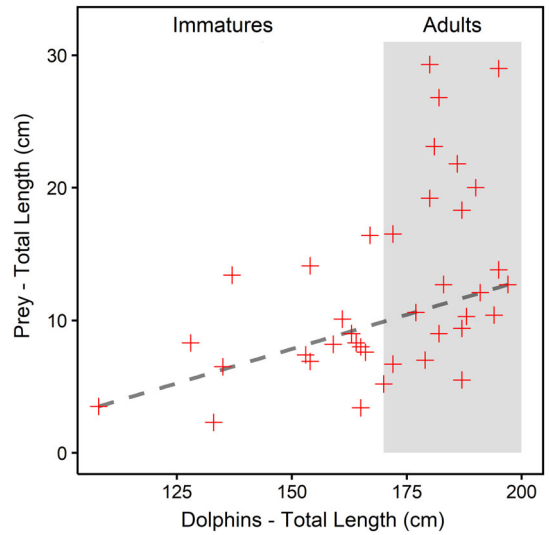
FIGURE 3 Median size of prey consumed according to Guiana dolphin size in the Abrolhos Bank. The gray dashed line shows the regression line.

The composition and importance of prey (%IRI) consumed by Guiana dolphins varied seasonally (Figure 4). In summer the most important prey were shortfin corvine (*Isopisthus parvipinnis*, 34.5%), slender inshore squid (*Doritheuthis plei*, 33.3%), and cutlassfish (*Trichiurus lepturus*, 16.5%). The diet in autumn/winter was mainly composed of catfish (*Bagre* sp., 33.7%), mullet (*Mugil* sp., 29.4%), and little croaker (*Stellifer* spp., 27.5%). In spring the main prey were little croaker (*Stellifer* spp., 27.5%) and weakfish (*Macrodon* sp., 34.8%). The dietary composition varied among the three seasons (NPMANOVA: $F = 3.32$, $p < .05$). A post hoc pairwise comparison showed that all seasons differed from each other at $p < .05$.
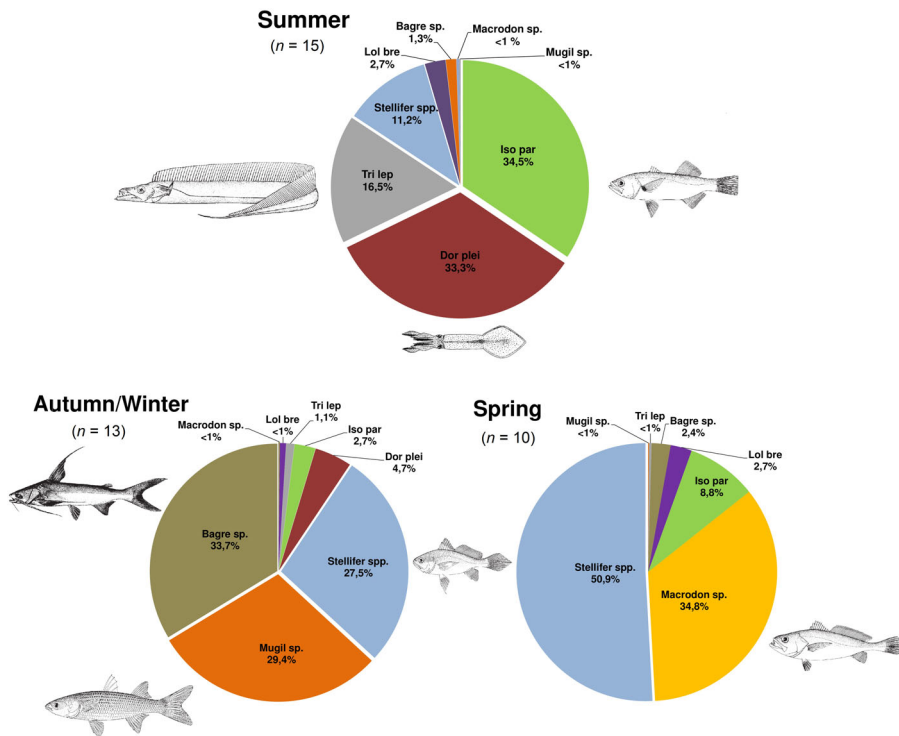
FIGURE 4   Seasonal variation in the composition (%IRI) of the Guiana dolphin diet in the Abrolhos Bank, Brazil. Taxa codes are given in Table 1. Drawings from Carpenter (2002).

3.4 | Feeding strategy

At the family (or higher) level, most prey of the Guiana dolphin had low frequency of occurrence and low specific abundance. The following four groups could be built: rare prey (%O < 10), common prey (10 < %O < 50), frequent prey (%O > 50), and dominant prey (%O > 50; %Pi > 50) (Figure 5).

Rare prey included Achiriidae, Albulidae, Carangidae, Centropomidae, Hemiramphidae, Lutjanidae, Pomatomidae, Sphyraenidae and Dendrobranchiata. Common prey included Ariidae, Clupeidae, Gerreidae, Haemulidae, Mugilidae and Pristigasteridae. Frequent prey comprised Scianidae and Loliginidae. The only taxon that could be considered dominant was Scianidae, which had percentage frequency of occurrence, specific abundance, and %IRI higher than 50%.

The cluster analysis of the ecological traits of Guiana dolphin prey revealed seven groups at 0.6 similarity (Figure 6). The upper two branches of the cluster loosely associate strictly benthic taxa living in/on soft bottoms, Penaeids and Dendrobranchiata (that could not be weighted) and achirid soles (<0.1 %IRI). The two groups, A and B, sum up 71.5 %IRI. The ecological traits that most distinguish group A from B were habitat and bottom type (SIMPER = 75%). The most important preys to the diet of Guiana dolphins, group B, were typically of soft bottoms and estuarine environments. Feeding guild and relationship with estuaries were the main factors that segregate group C from group D + E (SIMPER = 78.2%). Group C primarily consisted of prey that use estuaries and are piscivorous. Finally, groups D and E were separated by vertical and trophic guild (SIMPER = 84%). Group D was formed by piscivorous and pelagic species, while group D + E was formed by omnivorous and benthonic-pelagic prey.

FIGURE 5 Costello diagram showing the frequency of occurrence, specific abundance, and the Index of Relative Importance (%IRI) of Guiana dolphin's prey (grouped by family).
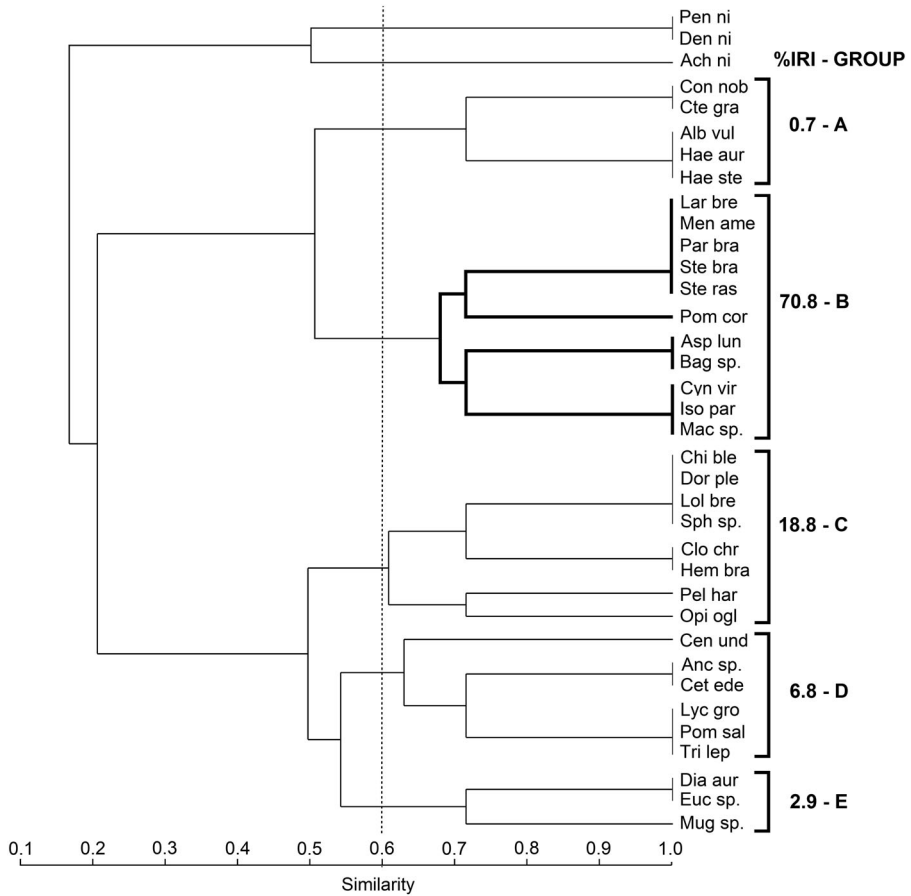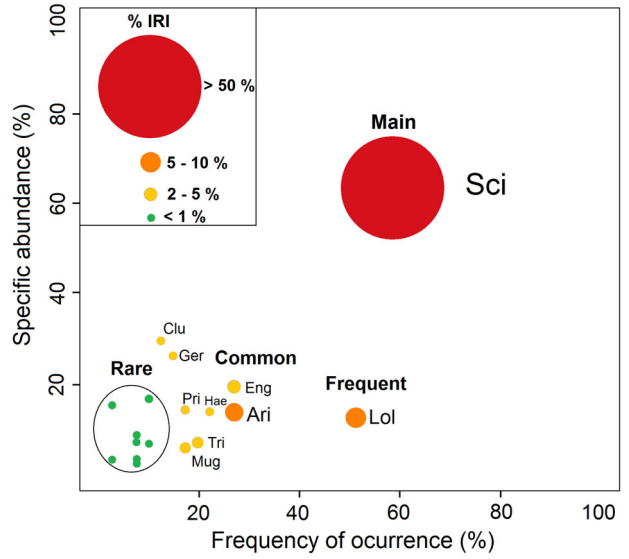
FIGURE 6 Cluster analysis of prey items of the Guiana dolphin along the coast of the Abrolhos Bank by the following ecological traits: vertical guild, trophic guild, bottom type, relationship with estuaries, schooling behavior, and sound production. Relative importance of each group (%IRI) for the Guiana dolphin diet is shown to the right of groups.

4 | DISCUSSION

4.1 | Diet description

The use of the cumulative curve of species richness was important to account for the number of samples while comparing the richness of species in the diet among studies. In this work, it was clear from the curve that the 40 stomachs used were sufficient for an accurate description of the diet, because the rate of discovery of new items decreased substantially after 20 stomachs. Furthermore, extrapolating with the cumulative curve suggests that doubling the sample to 80 stomachs would increase the diet richness described by only 12%.

The diet of Guiana dolphins in the Abrolhos Bank was essentially piscivorous, as elsewhere on the Brazilian coast (e.g., Daura-Jorge et al., 2011; Lopes et al., 2012). Many of the main prey we observed (*Stellifer* spp., *Isopisthus parvipinnis*, *Dorytheuthys plei*, *Trichiurus lepturus*, *Mugil* sp., and *Loliguncula brevis*) are important resources in other areas (Daura-Jorge et al., 2011; Lopes et al., 2012; Pansard et al., 2010). On the other hand, some prey dominates in particular regions such as *Bagre* sp. and *Macrodon* sp. in the Abrolhos Bank (present study) and *Micropogonias furnieri*, *Porichthys porossisimus* or *Haemulon plumieri* elsewhere (Cremer et al., 2012; Di Beneditto & Ramos, 2004; Pansard et al., 2010). This strongly suggests that Guiana dolphins diet changes spatially in accordance with prey availability.

When considering the exceptional biodiversity of Abrolhos Bank (Dominguez et al., 2002; Dutra et al., 2006; Vieira & Musick, 1993), diet plasticity would reflect in higher prey richness compared to other regions (Daura-Jorge et al., 2011; Lopes et al., 2012; Pansard et al., 2010). The sheer size of our study area, more than 450 km of coastline, may also have contributed to this richness.

4.2 | Diet variation

Guiana dolphin diet varies seasonally and the predominance of some prey matches with their breeding or high abundance period (Daura-Jorge, Rossi-Santos, Wedekin, & Simões-Lopes, 2007; present study). Thus, squids (Haimovici & Perez, 1991; Martins, Perez, & Schettini, 2006) and cutlass fish (Martins & Haimovici, 1997) mostly concentrate in Brazilian shallow-waters during summer months, while catfish (Pinheiro et al., 2006) spawning period is between summer and autumn.

A positive correlation between size of Guiana dolphins and prey biomass and size was also found. This suggests an opportunistic feeding strategy where, as expected from previous findings on bottlenose dolphin (Cockcroft & Ross, 1990; Milmann, Danilewicz, Machado, Santos, & Ott, 2016), larger predators feed upon larger prey (present study).

4.3 | Feeding strategy

Guiana dolphin in the Abrolhos Bank mostly feed on small fish (<20 cm) that inhabit soft bottoms and are associated with estuaries (e.g., Sciaenidae and Ariidae). This confirms the importance of these ecosystems (Bisi et al., 2013) and type of substrates (e.g., Rossi-Santos & Wedekin, 2006) to the species, including in aspects to its conservation. The dominance of Sciaenidae (Daura-Jorge et al., 2011; Lopes et al., 2012; present study) may be associated with their high abundance in coastal waters (Andrade-Tubino, Ribeiro, & Vianna, 2008; Pinheiro & Martins, 2009; Pinheiro, Martins, Araújo, & Pinto, 2009). Sciaenids also are active sound producers (Ramcharitar, Gannon, & Popper, 2006) that dolphins could locate through passive listening, especially in courtship and spawning periods (Gilmore, 2002). Such a feeding strategy for detecting and capturing prey has been already suggested for bottlenose dolphins (*Tursiops truncatus*) foraging in low visibility waters (Barros & Myrberg 1987; Gannon et al., 2005). A yet unexplored possibility would be that sound-producing gas bladders might be more reflexive to dolphin sonar. The importance of

squid in the diet (see Lopes et al., 2012) is probably linked to the high energetic gain that would be provided by semelparous reproducing adults that are both highly nutritious and, often, gregarious.

In opposition to the finding in northeastern Brazil, which suggests that the Guiana dolphin is a specialist predator (Pansard et al., 2010), in the Abrolhos Bank the species exhibits a mixed feeding strategy, with generalization on rare and common families. The apparent specialization on Sciaenidae is most likely a response to higher availability rather than a foraging specialization. It is also noteworthy that sciaenid otoliths are large and less susceptible to erosion and may be overrepresented in the stomach contents of this and other studies.

4.4 | Concluding remarks

The diet of Guiana dolphins in the Abrolhos Bank is mainly piscivorous, composed of small demersal-benthonic fish from estuaries and other soft-bottoms shallow waters. This reinforces the importance of such ecosystems heavily impacted by anthropogenic pressures, especially through destructive fishing with high bycatch/discards (e.g., trawling fishery). Guiana dolphins exploit an array of food items that have different ecological and behavioral characteristics, thus supporting a generalist and opportunistic feeding strategy to readily exploit available prey in the highly dynamic coastal and estuarine habitats along the Abrolhos Bank. Further studies should explore individual variation and latitudinal effects, how diet is coupled with prey availability and detection, and anthropogenic effects caused by competition.

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