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Diet of longnose stingray *Hypanus guttatus* (Myliobatiformes: Dasyatidae) in tropical coastal waters of Brazil

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Abstract

This study investigated the diet of longnose stingray *Hypanus guttatus* in the tropical waters of north-eastern Brazil. Samples were obtained from monthly sampling of artisanal fisheries from August 2007 to July 2008. A total of 258 specimens were examined, 127 females and 131 males, and stomach contents analysis suggested *H. guttatus* to be a generalist and opportunistic predator feeding on the most available prey in the environment. There was no significant difference in the diet composition of males and females, or between seasons. However, an ontogenetic dietary shift was observed with larger individuals having an increased proportion of molluscs in the diet, whilst smaller individuals predated primarily on small crustaceans.

Introduction

The longnose stingray *Hypanus guttatus* (Block & Schneider, 1801) is a demersal ray belonging to the Dasyatidae (stingray) family, which comprises 81 species (Last *et al.*, 2016). It is a marine and brackish-water stingray distributed along the western coast of the Atlantic Ocean, from the southern Gulf of Mexico to south-eastern Brazil (Bigelow & Schroeder, 1953; McEachran & Carvalho, 2002; Rosa & Furtado, 2016), attaining 180–200 cm disc width (DW; Stehmann *et al.*, 1978; Cervigón & Alcalá, 1999; Tagliafico *et al.*, 2013). This is the most common ray in artisanal and industrial fisheries along the northern (Lessa, 1997; Frédou & Asano-Filho, 2006) and north-eastern Brazilian coasts (Gadig *et al.*, 2000; Silva *et al.*, 2007; Lessa *et al.*, 2015), and has traditionally been a by-catch in shrimp trawl, bottom longline and gillnet fisheries. However, the species can be a frequent by-catch species in some areas (Frédou & Asano-Filho, 2006; Silva *et al.*, 2007; Paiva *et al.*, 2009) and, over the last decade, has become a target species for some artisanal fisheries in Pernambuco, Sergipe and Bahia states, where it is taken in large mesh ray-nets (Melo, 2016).

Throughout the species' distribution range in Brazil over the last decades, there has been a higher fishing pressure due to: (a) an increase in the number of fishing gears; (b) an increase in length of nets (ICMBio, 2011; Lessa *et al.*, 2016); (c) the specific targeting of rays; and (d) a recent uncontrolled increase in bottom longlines by fishers, the latter two by artisanal fleets in the study area. In addition, throughout the species' habitat there has been environmental degradation due to mangrove deforestation and the release of sewage to an extent which is hard to ascertain (Instituto Trata Brasil, 2013).

Most of the published information on *H. guttatus* is from occurrence records, limited data on catch rates, mass–length relationships (Teixeira *et al.*, 2017) and aspects of their diet and reproduction (Menni & Lessa, 1998; Silva *et al.*, 2007) with age and growth parameters estimated using multi-model inference (Gianeti *et al.*, 2019). Typical of Myliobatiformes, the species displays matrotrophic viviparity (with lipidic histotrophy) and gives birth to 2–4 embryos each year, with the young 14–17 cm disc width. Males are known to mature at 41–46 cm DW, females at 50–56 cm DW (Menni & Lessa, 1998; Yokota & Lessa, 2007; Gianeti, 2011). The age-at-maturity in males and females is 5 years and 7 years, respectively (Gianeti *et al.*, 2019). The most recent IUCN Red List Assessment for *H. guttatus* was Data Deficient (Rosa & Furtado, 2016).

Hypanus guttatus uses the coastal waters of north-east Brazil for parturition and for the development of young, and these waters provide similar nursery ground habitats for a range of other elasmobranchs, including *Rhizoprionodon porosus* (Poey, 1861), *Carcharhinus acronotus* (Poey, 1860), *Carcharhinus limbatus* (Valenciennes, 1839), *Carcharhinus falciformis* (Müller & Henle, 1839), *Pseudobatos percellens* (Walbaum 1792), *Narcine brasiliensis* (Olfers, 1831), *Aetobatus narinari* (Euphrasen, 1890), *Rhinoptera bonasus* (Mitchill 1815), *Hypanus marianae* (Gomes, Rosa & Gadig, 2000) and *Hypanus americanus* (Hildebrand &

Schroeder, 1928). The area is part of an ecologically and biologically significant area (EBSA; Convention on Biological Diversity, 2018), benefitting from micro-scale enrichment (Vital *et al.*, 2008), which provides environmental conditions that contribute to the high fishery production (Aragão, 2008) by the artisanal fleet, considered the largest in the north-east region of Brazil (Yokota & Lessa, 2006).

The few studies on the diet of *H. guttatus* from tropical Brazilian waters did not provide detailed identification of the prey composition, and the diet was either described by major taxonomic groups (Carvalho-Neta & Almeida, 2001; Silva *et al.*, 2001) or from studies on a specific prey taxon (Carqueija *et al.*, 1995).

The aim of the current study was to characterize the diet composition of *H. guttatus*, providing a detailed description of the food items found in the stomach contents, with the feeding habits analysed in relation to sex, size class and season.

Materials and methods

Specimens were obtained from monthly sampling of the by-catch of *Hypanus guttatus* landed by artisanal fisheries in Caiçara do Norte – RN (05°04′S 36°03′W), from August 2007 to July 2008. These fisheries employ beach seines (25 mm mesh size: <3 m water depth), shrimp otter trawls (30 mm mesh size: 8–10 m water depth, from January to April), hand lines (about 6 m deep) and bottom longlines (100 hooks, 3–4 m deep). The bottom sediment of this inner shelf fishing area is mainly composed of sand and clay, with the presence of carbonate enriched sands and mud increasing with depth (Tabosa, 2006; Vital *et al.*, 2010).

After collection the sex, disc width (DW cm) and total weight (TW g) were recorded for each specimen. The stomach of each stingray was removed, fixed in a 10% buffered formalin seawater solution and then preserved in 70% ethanol 72 h after fixation. The pieces of the fish used as bait, when found in the stomach, were removed and discarded before fixation, so as not to bias stomach content analysis or indices of vacuity. The percentage of empty stomachs was calculated and the weight of the stomach contents from each specimen was recorded after fixation. Prey types were identified to the lowest possible taxonomic level.

A randomized cumulative prey curve was plotted to assess if the sample size was satisfactory to describe the diet of *H. guttatus* in the sampled period (Ferry & Cailliet, 1996). The order in which stomach contents were analysed was randomized through a rarefaction of the sample using the PAST 3.24 statistical software (Hammer *et al.*, 2001) and the mean (± standard deviation) number of new prey observed was plotted for each consecutive stomach. To estimate the maximum number of prey that would have to be sampled to ideally describe the diet, we calculated the Jackknife1 estimator (Colwell & Coddigton, 1994; Colwell, 2004).

The frequency of occurrence (FO%), numerical frequency (N%) and percentage of weight (W%) of each prey type was calculated according to Hyslop (1980). To identify the most important prey species in the diet, the per cent index of relative importance (IRI%) (Pinkas *et al.*, 1971) was calculated, using the following formula: $\%IRI = FO\% \times (N\% + W\%)$. To examine the ontogenetic variation in diet, rays were divided into two size-classes (<40 cm DW; ≥40 cm DW). Because the Caiçara do Norte region has no clearly defined seasons based on temperature, seasonal variation was examined in terms of precipitation using two periods: a dry season (September–February) and a rainy season (March to August), based on Rao *et al.* (1993) and INMET (2010).

For evaluation of the feeding strategy (generalist or specialist), niche breadth and the importance of prey to the diet (dominant or rare), the graphical method proposed by Amundsen *et al.* (1996) was used, which consists of plotting a prey-specific abundance graph ($P_i\%$) (which is defined as the frequency calculated for a prey taxon from only the stomachs in which that prey taxon occurs) in relation to the prey item's FO%. The abundance percentage – relationship between prey-specific abundance and FO% that increases along a diagonal line from the lower left to the upper right side – illustrates the importance of prey items. Thus, the most important prey items are positioned on the upper right, while rare or non-important prey items are situated on the lower left side. The vertical axis represents the feeding strategy of the predator – generalist (lower part) or specialist (upper part). Prey plots situated near the upper left corner indicate the specialization of individual predators and plots situated in the upper right corner (restricted to one or just a few points) indicate population specialization (narrow feeding niche).

As a measure of the feeding niche breadth, the Levins Index (B_p) was used: $B_p = (B-1) / (n-1)$, where B_p is the Levins Index standardized by the number of prey item categories (n) and B is equal to $1/\Sigma\, p_i^2$, with p_i being the percentage weight of each prey category i in the sample (Krebs, 2014). Feeding niche breadth values range from 0 (a narrow niche) to 1 (a broad niche). To calculate $p_i\%$, B_p and the similarity in the diet, only the percentage weight (W%) of each taxon was considered due to the difficulty in counting the exact number of certain stomach prey types, such as bivalve molluscs, which are often found in pieces, as it was only possible to measure the weight of these items.

Similarities in diet composition (as a function of W%) between the groups defined by season (dry and rainy) and size class (<40 cm, ≥40 cm DW) were evaluated using multivariate statistical analysis according to Clarke & Warwick (2001) (PRIMER-E). Similarity matrixes were obtained using the Bray–Curtis similarity coefficient after square root transformation. A one-way analysis of similarity test (ANOSIM), using the seasons as factors, was used for the two size classes to evaluate whether diet composition was significantly influenced by season. To test for possible significant differences in diet composition between the two size classes, the same ANOSIM analysis was used, with size classes as the factor. To identify prey categories that contributed the most to the dissimilarity between groups SIMPER (similarity percentages) was performed. The Chi-square test was used to verify differences in W% of each item consumed by males and females in the sample (StatSoft, 2007).

Results

Stomachs were examined from 258 *Hypanus guttatus* specimens (127 females, 12.7–88.5 cm DW, 62.2–22,000 g TW; and 131 males, 12.7–57.0 cm DW, 23.1–5750 g TW). The sex ratio was not significantly different from 1:1 ($\chi^2 = 0.031$, $P > 0.05$). From these stomachs, 49 (19%) were empty. The non-stabilization of the randomized cumulative prey curve in an asymptote (Figure 1) indicates that, despite the significant number of analysed stomachs, this was not sufficient to characterize the *H. guttatus* diet in its fullness in the sampled region. The Jackknife1 estimator was calculated as 100.86 (Figure 1), suggesting that about 30 items could still be found in the *H. guttatus* diet.

Overall, 209 individuals had stomachs containing food (n = 79 females <40 cm; n = 27 females ≥40 cm; n = 87 males <40 cm and n = 16 males ≥40 cm DW); (Table 1). The percentage of empty stomachs varied significantly throughout the months ($\chi^2 = 207.48$, $P < 0.05$), with the highest observed value in July 2008. During the months of August, September, October and December 2007 and April 2008, none of the examined stomachs were empty (Table 1). The proportion of empty stomachs did not differ between males and females ($\chi^2 = 2.47$, $P = 0.12$). No significant difference was found in the proportions of empty stomachs between fish <40 cm or ≥40 cm DW ($\chi^2 = 1.65$, $P = 0.20$).

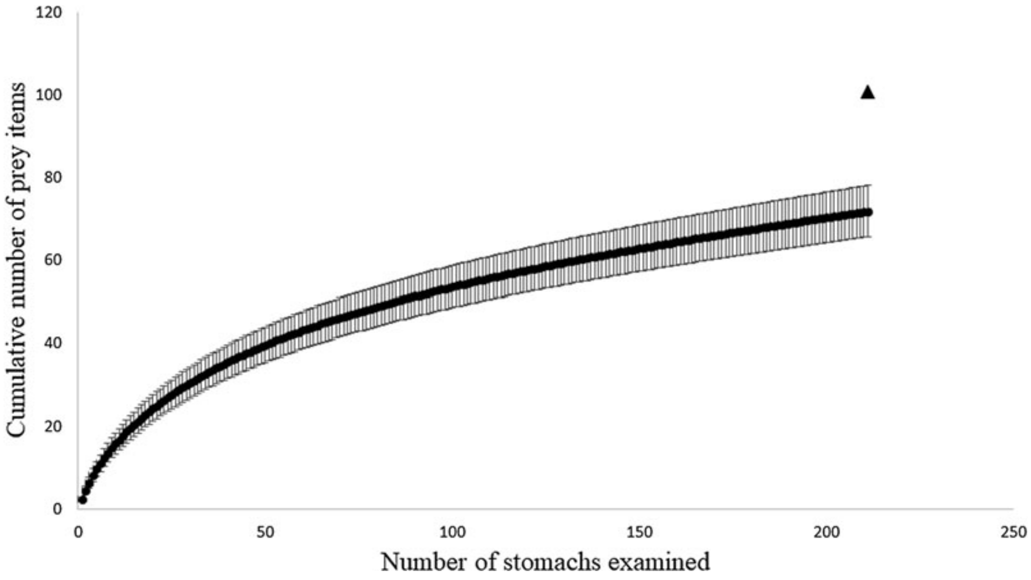

Fig. 1. Randomized cumulative prey curve for stomachs of *Hypanus guttatus* collected in Caiçara do Norte (north-eastern Brazil). Error bars represent standard deviations. Jackknife 1 estimator = black triangle.

Table 1. Number of sampled stomachs (n) of *H. guttatus* size classes in Caiçara do Norte between August 2007 and July 2008

	Smaller size class (n)				Larger size class (*n*)			
Months	Male	Female	Empty	Total	Male	Female	Empty	Total
Aug/07	15	17	0	32	0	0	0	0
Sep/07	5	6	0	11	1	0	0	1
Oct/07	3	5	0	8	0	7	0	7
Nov/07	4	2	2	8	1	0	0	1
Dec/07	6	4	0	10	0	2	0	2
Jan/08	5	7	0	12	0	1	1	2
Feb/08	4	6	3	13	2	1	0	3
Mar/08	6	5	6	17	1	1	0	2
Apr/08	5	3	0	8	1	0	0	1
May/08	17	9	10	36	2	4	0	6
Jun/08	11	11	4	26	2	3	2	7
Jul/08	6	5	4	15	5	8	17	30

Smaller size class is <40 cm disc width and larger size class is ≥40 cm disc width.

However, there were months where the occurrence of empty stomachs coincided with the number (n) of neonates (assumed to be individuals of 12.7–17 cm DW with internal yolk reserves still present; November 2007, n = 2; February 2008, n = 2; March 2008, n = 8; May 2008, n = 12 and June 2008, n = 5) and adults that were reproductively active (males with sperm in the seminal vesicle and females presenting full-term embryos and/or mature ovarian follicles) (January 2008, n = 5; June 2008, n = 8 and July 2008, n = 30).

Diet composition

Seventy-two prey categories from five major groups (Polychaeta, Crustacea, Mollusca, Sipuncula and Teleostei) were identified in the diet of *H. guttatus* (Table 2). The caridean shrimp *Ogyrides alphaerostris* was the dominant prey type in terms of FO% (37%), N% (56%), W% (32%) and IRI% (32.51). Molluscs, mainly represented by Tellinidae bivalves (IRI% = 4.69), were the second main prey type, followed in order of importance by the opossum shrimp *Bowmaniella* sp. (IRI% = 2.69), the caridean shrimp *Leptochela serratorbita* (IRI% = 2.26) and Sipuncula (IRI% = 0.37). Polychaetes exhibited relatively high FO% values (FO% = 15.17), but the W% and N% were low. As there was no significant difference in W% of the items identified between males and females ($\chi^2 = 0.34$, $P = 1$), the genders were grouped to test seasonal and ontogenetic differences in diet composition.

Feeding strategy

As there were significant ontogenetic differences in the diet for *H. guttatus* of <40 cm and ≥40 cm DW, the graphical method for understanding the feeding strategy was performed separately for the two groups (Figure 2). According to the feeding strategy plots, most prey items consumed by both size classes of *H. guttatus* had low frequency of occurrence and low prey-specific abundance indicating these prey types were of low importance and

Table 2. Composition of *H. guttatus* diet in terms of frequency of occurrence (FO%), percentage weight (W%), numeric frequency (N%) and per cent index of relative importance (IRI%) (n.i. = not identified), evaluated in Caiçara do Norte between August 2007 and July 2008

Prey types	FO%	W%	N%	IRI%
Polychaeta				
Polychaeta n.i.	15.17	1.56	0.27	0.28
Goniadidae	3.79	0.31	0.58	0.03
Glyceridae	3.79	0.46	0.30	0.03
Onuphidae	0.95	0.37	0.05	<0.01
Sabellidae	0.47	0.01	0.05	<0.01
Crustacea				
Crustacea n.i.	9.00	3.16	0.52	0.33
Decapoda	2.37	0.42	0.14	0.01
Dendrobranchiata	0.95	0.26	0.05	<0.01
Penaeoidea	0.47	0.10	0.03	<0.01
Penaeidae	3.79	0.91	0.25	0.04
Litopenaeus schmitti	0.47	0.08	0.03	<0.01
Metapenaeopsis sp.	0.47	0.04	0.19	<0.01
Rimapenaeus constrictus	4.74	1.36	0.41	0.08
Xiphopenaeus kroyeri	1.42	0.11	0.08	<0.01
Sergestidae	0.95	0.05	0.05	<0.01
Sergestes sp.	0.47	0.09	0.03	<0.01
Acetes americanus	3.79	0.41	8.37	0.33
Pleocyemata				
Caridea	2.84	0.31	0.52	0.02
Ogyrididae	1.42	0.06	0.08	<0.01
Ogyrides alphaerostris	36.97	32.25	55.70	32.51
Processidae	0.47	0.01	0.03	<0.01
Processa hemphilli	0.47	0.02	0.05	<0.01
Palaemonidae				
Palaemonine	0.47	0.05	0.03	<0.01
Periclimenes sp.	2.84	0.12	0.36	0.01
Periclimenes longicaudatus	5.21	0.23	1.15	0.07
Disciadidae				
Discias sp.	0.95	0.01	0.05	<0.01
Pasiphaeidae	0.47	0.03	0.03	<0.01
Leptochela sp.	1.90	0.10	0.22	0.01
Leptochela serratorbita	24.64	3.48	5.68	2.26
Brachyura n.i.	6.64	0.91	0.36	0.08
Portunidae	3.79	1.20	0.25	0.05
Callinectes sp.	4.74	1.28	0.33	0.08
Calappidae	2.37	0.15	0.22	0.01
Pinnotheridae	2.37	0.04	0.14	<0.01
Parthenopidae	0.47	0.05	0.03	<0.01
Anomura				
Albuneidae				
Albunea sp.	0.47	0.06	0.03	<0.01
Albunea paretti	0.47	0.15	0.03	<0.01
Hippidae				
Emerita sp.	0.47	0.01	0.03	<0.01
Thalassinidea				
Thalassinidae	0.47	<0.01	0.03	<0.01
Callianassidae	0.47	0.01	0.03	<0.01
Upogebiidae				
Upogebia sp.	1.90	0.74	0.38	0.02
Mysidacea	3.79	13.47	0.47	0.53
Bowmaniella sp.	14.22	3.75	15.18	2.69
Palinura				
Palinuridae				
Panulirus sp.	1.90	0.22	0.11	0.01
Amphipoda	0.47	<0.01	0.03	<0.01
Gammaridea	0.47	0.01	0.05	<0.01
Ampelisca sp.	0.47	0.01	0.03	<0.01
Cumacea	2.84	0.06	0.58	0.02
Isopoda	0.47	0.02	0.05	<0.01
Flabelifera	1.42	0.24	0.11	<0.01
Stomatopoda				
Squilla sp.	0.47	0.05	0.16	<0.01
Mollusca				
Mollusca n.i.	0.47	0.03	0.03	<0.01
Bivalvia	11.85	4.66	0.22	0.58
Tellinidae	26.07	16.05	1.95	4.69
Tellina sp.	0.47	0.34	<0.01	<0.01
Gastropoda	0.47	0.01	0.03	<0.01
Rissoidae	0.47	0.01	0.03	<0.01
Sipuncula	8.53	2.23	2.11	0.37
Teleostei				
Teleostei n.i.	6.64	2.42	0.38	0.19
Dactylopterus volitans	1.90	0.34	0.19	0.01
Menticirrhus americanus	0.47	0.04	0.03	<0.01
Trichiurus lepturus	0.95	0.90	0.05	0.01
Symphurus sp.	0.47	0.10	0.03	<0.01
Engraulidae	1.90	1.11	0.14	0.02
Haemulidae	2.37	0.74	0.19	0.02
Haemulopsis corvinaeformis	1.42	0.31	0.11	0.01
Clupeidae	0,47	0.16	0.05	<0.01
Ariidae	1.90	0.84	0.47	0.02
Anguilliformes	0.47	0.02	0.05	<0.01
Digested material	0.47	0.09	<0.01	<0.01
Debris	1.42	0.68	<0.01	0.01
Plant remains	1.42	0.14	<0.01	<0.01

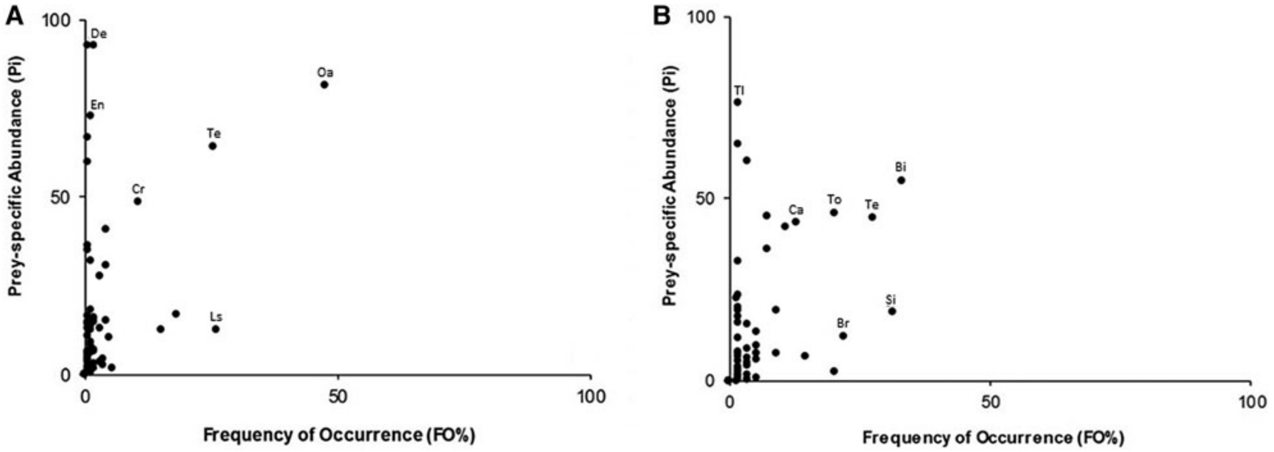

Fig. 2. Representation of the diet pattern of *H. guttatus* using all identified stomach content items for smaller size class (<40 cm disc width) (A) and larger size class (≥40 cm disc width) (B). Oa, *Ogyrides alphaerostris*; Te, Tellinidae n.i.; De, Dendrobranchiata; Ti, *Trichiurus lepturus*; En, Engraulidae; Cr, Crustacea n.i.; Ls, *Leptochela serratorbita*; Bi, Bivalvia n.i.; To, Teleostei n.i.; Si, Sipuncula n.i.; Br, Brachyura n.i.; Ca, *Callinectes* sp.

were only eaten occasionally, indicating a generalist diet and thus a broad niche width. However, the caridean shrimp *O. alphaerostris* and bivalves (including Tellinidae) were located more superiorly and right on the graph, which would indicate a certain specialization on these items by *H. guttatus* <40 cm DW and *H. guttatus* ≥40 cm DW, respectively. Items as Dendrobranchiata and Engraulidae (Figure 2A), and *Trichiurus lepturus* (Figure 2B) were located in the upper left corner on the graph, which would suggest the specialization of a few individuals of the population on these items. The Levins Index was low for both size-classes (<40 cm DW, $B_p = 0.07$; ≥40 cm DW, $B_p = 0.2$).

Diet comparisons

There were no significant differences in the diet composition (categorized by W%) between the dry and the rainy season for either the smaller size class (ANOSIM % W: global $R = -0.004$, $P = 0.49$) or larger size class (ANOSIM W%: global $R = 0.095$, $P = 0.097$) of *H. guttatus*. However, it was observed that the items consumed by the smaller size class from August to December 2007 were mostly crustaceans (*O. alphaerostris* and unidentified Crustacea) and from January to March 2018 the most consumed items were Tellinidae (Bivalvia) and the caridean shrimp *L. serratorbita* (Figure 3). In April 2008, there was an increase in the percentage of mysids *Bowmaniella* sp., alongside Tellinidae, until June 2008, when the marked presence of *O. alphaerostris* in the stomach contents was once again evident (Figure 3).

Unidentified bivalves and Tellinidae were the most consumed prey types by the larger size class in the sampled months, except in September 2007 and March 2008, when sipunculids became the most consumed prey taxon. In August 2007, teleost fish and polychaetes were more evident and in October 2007, there was an increased presence of brachyuran crabs *Callinectes* sp. together with sipunculids and teleosts (Figure 3).

Although some overlap was found, a significant difference was observed between the diet composition of the two size classes of *H. guttatus* (ANOSIM W%: global $R = 0.427$, $P = 0.001$). Through the SIMPER analysis it was estimated that the average dissimilarity in diet composition between the two size classes was 89.4% (Table 3). The prey types with a high contribution to the dissimilarity between these groups were *O. alphaerostris*, unidentified bivalves, tellinid bivalves, sipunculids, *L. serratorbita*, unidentified teleosts and unidentified brachyurans. The caridean shrimp *O. alphaerostris* was the prey item that contributed most to the similarity of diet composition of the smaller size class, while bivalves (mainly Tellinidae) were the prey items that contributed most to the similarity in the diet of the larger size class (Table 3). The prey types of the categories Sipuncula, unidentified teleosts, Brachyura and Polychaeta, were not recorded in the diet of the smaller size class, but they were important to the diet of the larger size class, and therefore contributed to the dissimilarity between these two groups (Table 3).

Discussion

The months with the highest proportion of empty stomachs coincided with the months in which neonates and reproductive adults were observed. Neonates still being nourished by the internal yolk reserves had no food content in their stomachs. Reproductive adults were also found with no stomach contents. In mating and/or parturition periods some elasmobranch species are known to cease feeding (Springer, 1960; Capapé, 1975; Olsen, 1984).

The diet of *H. guttatus* includes a varied range of benthic and benthopelagic organisms. A wide variety of prey items was also found in other studies on the diet of *H. guttatus*. Silva *et al.* (2001) found Echinodermata (Holothuroidae), Mollusca (Bivalvia and Gastropoda), various crustaceans (Pennaeidae, Portunidae, Stomatopoda, Isopoda and Amphipoda), Polychaeta, Sipuncula and Teleostei in the diet of *H. guttatus* from Ceará State, northeastern Brazil. Carvalho-Neta & Almeida (2001) studying the species in Maranhão State coast found the following prey items in order of frequency of occurrence: brachyuran crustaceans (54%; mainly *Callinectes* sp.), polychaetes (11%), teleosts (5%), decapod larvae (4%) and priapulids (4%). Both studies characterized the species as a generalist and opportunistic predator feeding on the most available prey items. Differences in the order of preference of food items between studies probably reflect differences in prey availability between sampling areas. Carqueija *et al.* (1995) focused their study only on crustacean decapods, but found nine different families of this group in the diet of *H. guttatus* from Bahia State coast.

The prey categories found, especially Bivalvia, Teleostei, Caridea, Brachyura, Polychaeta and Sipuncula, have also been found in the diet of other stingrays, such as *Hypanus say* (Snelson & Williams, 1981), *N. kuhlii* (Compagno *et al.*, 1989), *Dasyatis marmorata* (Capapé & Zaouali, 1992), *Hypanus americanus* (Gilliam & Sullivan, 1993), *Hemitrygon akajei* (Taniuchi & Shimizu, 1993), *Dasyatis chrysonota* (Ebert & Cowley, 2003),

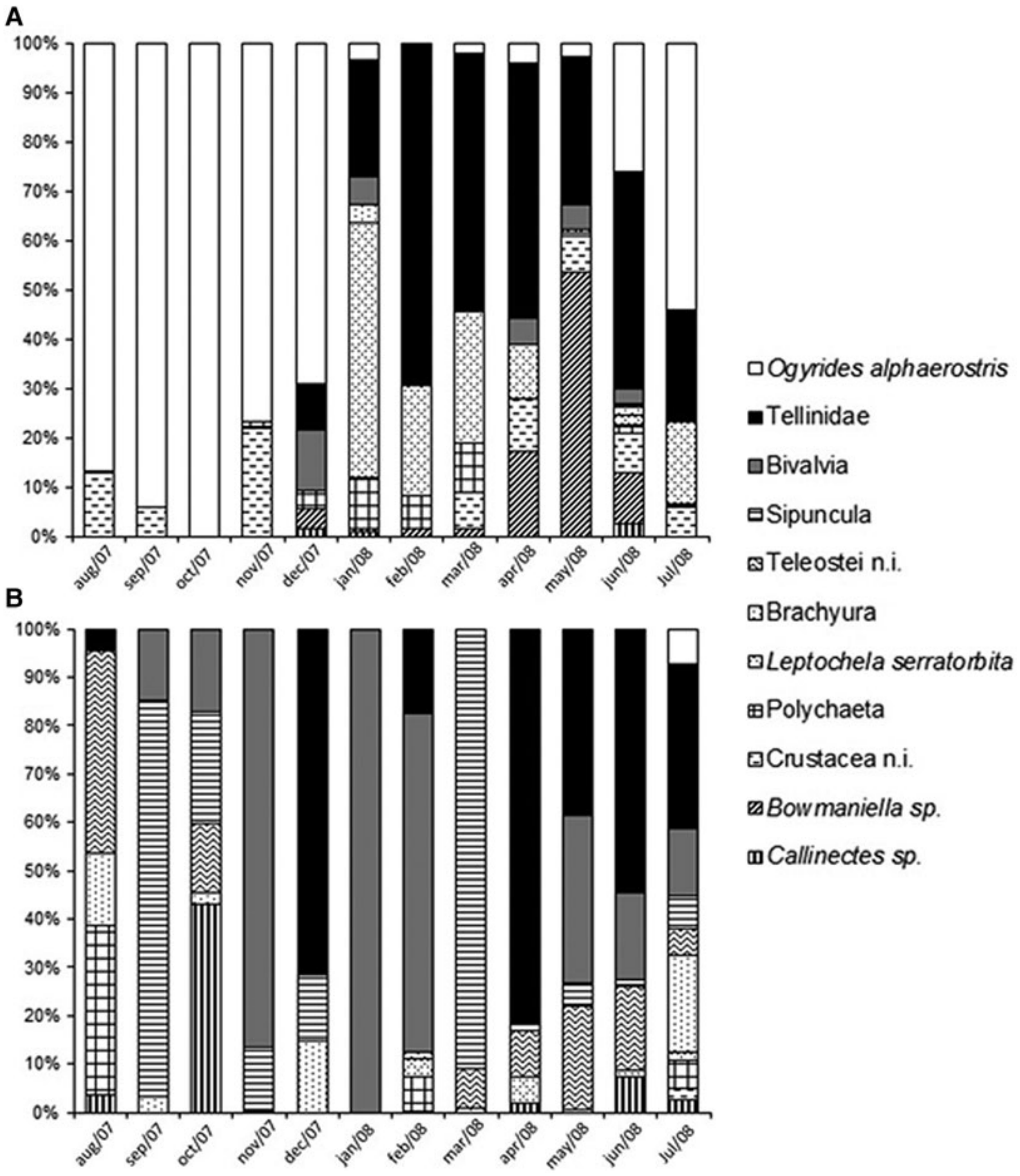

Fig. 3. Diet composition in terms of per cent weight (W%) of smaller size-class (A) and larger size-class (B) of *Hypanus guttatus* from the Caiçara do Norte region (north-eastern Brazil) between August 2007 and July 2008, by month.

Dasyatis pastinaca (Ismen, 2003; Yeldan *et al.*, 2009), *Himantura uarnak*, *Pastinachus sephen* (Raje, 2003) and *Urogymnus asperrimus* (Elston *et al.*, 2017).

The wide range of prey items found in the stomachs of *H. guttatus*, indicates this species to be a generalist and opportunist predator. Although the graphic method for feeding strategy suggests some specialization of the smaller size class on *O. alphaerostris* and of the larger size class on bivalves, this is probably more related to the greater availability of these prey in the environment in the sampling period, than to a preference for these prey. The same would apply to individuals of *H. guttatus* that presented the high p_i% value for the prey items Dendrobranchiata, Engraulidae and *Trichiurus lepturus* (points located in the upper left corner of the graph); these individuals probably encountered a greater abundance or large specimens of these prey, rather than being specialized predators on such prey species.

The alternation and variation of prey items between the months sampled reinforce the idea that the species takes advantage of the prey availability in the environment at that moment. The substrate where the rays were captured, consisting mostly of clay, mud and sandy-mud, is the type of soft-bottom where crustaceans (one of the most important prey groups in the diet of *H. guttatus*) dominate the biomass of benthic macroinvertebrates (Abele, 1974; Virnstein, 1987). Tellinidae bivalves (another frequent prey) are also commonly found in this type of substrate (Simone & Wilkinson, 2008). Despite the wide variety of food items found, the randomized cumulative prey curve and Jackknife1 estimator indicated that at least 30 more items could still be found in the diet of *H. guttatus*, also supporting the hypothesis of a generalist diet.

The higher frequency of some prey in the stomachs may lead to a low calculated Levins Index value, suggesting narrow niche, when the width of the niche is more likely to be broad. The resource items in the stomach content of an individual should be counted only to provide an estimate of the dietary proportions for that individual (Krebs, 2014), which was done in the present study. On the other hand, the usage and importance of the resource ought to be scaled to their availability, because some resources are very abundant and common and other resources are uncommon or rare (Hurlbert, 1978), however, Levins' measure of niche width does not address the possibility that resources vary in abundance (Krebs, 2014).

Table 3. Per cent contribution of the most common prey in diet composition for the smaller size class and larger size class of *H. guttatus*, from Caiçara do Norte (north-eastern Brazil), captured between August 2007 and July 2008, and the most discriminant ones between these two groups

Smaller size class (<40 cm DW)		Larger size class (≥40 cm DW)	
Average similarity = 27.02%		Average similarity = 22.24%	
Prey categories	% Contrib.	Prey categories	% Contrib.
Ogyrides alphaerostris	58.8	Bivalvia n.i.	29.29
Tellinidae n.i.	12.08	Tellinidae n.i.	17.68
Leptochela serratorbita	9.47	Sipuncula	14.06
Bowmaniella sp.	5.20	Teleostei n.i.	8.94
Crustacea n.i.	5.19	Brachyura n.i.	8.12
		Leptochela serratorbita	5.59
		Polychaeta n.i.	3.60
		Callinectes sp.	3.28
Smaller size class × Larger size class			
Average Dissimilarity = 89.35%			
Prey categories	% Contrib.		
Ogyrides alphaerostris	11.83		
Bivalvia n.i.	8.66		
Tellinidae n.i.	7.91		
Sipuncula	5.57		
Leptochela serratorbita	4.81		
Teleostei n.i.	4.67		
Brachyura n.i.	4.38		
Polychaeta n.i.	4.30		
Crustacea n.i.	3.57		
Bowmaniella sp.	3.42		
Callinectes sp.	3.00		

%Contrib, per cent contribution; DW, disc width.

The observed difference in the diet between size classes is probably related to the greater physical capacity and experience of the larger stingrays to catch prey that smaller ones are not able to capture yet (e.g. Teleostei, Brachyura and Sipuncula). Silva *et al.* (2001) also found ontogenetic changes in the diet of this species and observed, as in the present study, an increase in the consumption of fish and molluscs among adults. Thorson (1983) analysed eight stomachs of *H. guttatus* from the Caribbean Sea and found only bony fishes and molluscs, but all stomachs analysed were from larger specimens (>581 mm DW).

In studies of *D. pastinaca* in Mediterranean waters, a similar diet shift to that observed for *H. guttatus* in the present study was also reported, with the preference for caridean shrimps decreasing, and teleosts and brachyuran crustaceans becoming dominant with increasing size (Capapé, 1975; Ismen, 2003; Yeldan *et al.*, 2009). The same pattern was observed for *D. marmorata* in Tunisian waters (Capapé & Zaouali, 1992), *Dasyatis chrysonota* in South Africa (Ebert & Cowley, 2003), *M. californica* in the northern coast of California (Gray *et al.*, 1997) and other batoids in coastal waters of Australia (Platell *et al.*, 1998).

There were no differences between the diets of *H. guttatus* males and females, probably because both sexes occupy the same habitat year-round and have access to the same prey types (Yokota & Lessa, 2006, 2007). Similar results were obtained for *H. guttatus* from the Maranhão State coast in north-eastern Brazil (Carvalho-Neta & Almeida, 2001) and for urolophid species off the coast of south-west Australia (Platell *et al.*, 1998). Sex differences in diet are more likely to occur in species that segregate sexually, such as the bat ray *Myliobatis californica* (Gray *et al.*, 1997). In the present study there were also no differences in the diet of *H. guttatus* in relation to dry and rainy seasons, a fact that is common in tropical coastal regions due to typical species richness and stability of the environmental conditions (Rohde, 1992; Willig *et al.*, 2003).

In conclusion, *H. guttatus* plays an important role as consumer of the benthonic and benthopelagic coastal communities from north-eastern Brazil, feeding on a wide range of most available prey on the environment. The species presents an ontogenetic change in the diet that is probably related to the greater physical capacity of larger individuals to catch different prey types.

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