
Assessing trophic interactions between pelagic predatory fish by gut content and stable isotopes analysis around Fernando de Noronha Archipelago (Brazil), Equatorial West Atlantic

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Abstract :

The objective of this study was to analyse the feeding habits and trophic interactions between four oceanic predatory fish around the Fernando de Noronha Archipelago (FNA), Brazil, in the western equatorial Atlantic (3.86°S/32.42°W), internationally recognised as an environment of high economic and ecological value. For this purpose, biological samples of yellowfin tuna (*Thunnus albacares*), wahoo (*Acanthocybium solandri*), barracuda (*Sphyraena barracuda*) and dolphinfish (*Coryphaena hippurus*) were collected for stomach contents and stable isotopes analysis. Values of the Index of relative importance (IRI) revealed varied diets, with a strong presence of teleost fishes (Diodontidae and Exocoetidae) for all species, with yellowfin tuna having a greater diversity of food items. Despite being generalists/opportunists, the feeding strategy of these predators showed a tendency towards a specialised diet in the use of the available resources around the FNA. They presented a narrow trophic niche width (Levins index, $Bi < 0.6$) and low overlap between species, except between barracuda and wahoo (MacArthur and Levin's, $R0 = 0.72$). Isotopic compositions had broad values of $\delta^{13}C$ and $\delta^{15}N$ and were significantly different between species. Our results provide information about the four species' trophic organisation and suggest that the predators avoid competition by preying on different prey, thus allowing their coexistence.

Keywords : Western Equatorial Atlantic, Trophic ecology, Tuna, Stomach content, Stable isotope

1 INTRODUCTION

Trophic studies are essential for ecosystem conservation and integrated assessment of living marine resources (Zavala-Camin, 1996; Bornatowski, 2010). Top predators such as tuna and tuna-like species are essential for food-web stability and marine ecosystems sustainability. They can regulate the abundance of prey, and the removal of predators can cause changes in the habitat and the populations of subsequent trophic levels (top-down control) (Hunsicker et al., 2012). A better understanding of fish diet, offshore marine community structure and ecological function are needed to quantify the type of food and distribution of resources among predators.

Trophic ecology through analysis of stomach contents constitutes the most widespread and used method for understanding the demersal and pelagic fish diets (Braga et al., 2012). In addition, the use of stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) enabled to bring important insights into networks (Peterson and Fry, 1987). Indeed, $\delta^{15}\text{N}$ can be considered a proxy for an organism's trophic position since it increases significantly with trophic level (Post, 2002; Caut et al., 2009). In contrast, $\delta^{13}\text{C}$ differs considerably between primary producers (Post, 2002; Herzka et al., 2009), providing information on the origin of the organic matter (Fry, 2006). The spaces formed by the δ -space composed of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes are comparable to the dimensions established by ecological niches ("n-dimensional-hypervolume") and help to assess community structure (Bearhop et al., 2004). The combination of the two methods is therefore essential to expand our knowledge of energy flows in marine food webs (Manetta and Cecilio, 2003) and, for this reason, they have been used globally (Tripp-Valdez et al., 2014; Li et al., 2015; Torres-Chávez et al., 2018).

Inserted in a Marine Protected Area (MPA Fernando de Noronha - Atol das Rocas - São Pedro and São Paulo Archipelago) and including a National Marine Park (PARNAMAR), the Fernando de Noronha Archipelago (FNA) is located in an oceanic region with oligotrophic characteristics. However, this archipelago has unique importance for its surroundings, generating, attracting and aggregating marine life, among them important fishery resources (Travassos et al., 1999; Lima et al., 2016). For these characteristics, the FNA is recognised as an EBSA ("Ecologically or Biologically Significant Areas") (SCBD, 2014), an environment with special conditions, with particular biodiversity, which is part of the migratory route of several species that find shelter, feeding and reproduction areas (Vaske-Jr et al., 2004).

Among the fishery resources that occurs around the FNA, four species of oceanic predators, *Thunnus albacares* (Yellowfin tuna - YFT), *Sphyraena barracuda* (Barracuda - BAR), *Acanthocybium solandri* (Wahoo - WAH) and *Coryphaena hippurus* (Dolphinfish - DOL) are caught by local artisanal and recreational fisheries (Dominguez et al., 2013) reflecting a relevant ecological, social and economic link. They are agile species, capable of large movements, but they use the habitat in different ways. Three species are highly migratory (*A. solandri*, *T. albacares*, *C. hippurus*); meanwhile, *S. barracuda* is classified as more resident. *Sphyraena barracuda* is the species that shows the most significant capacity to inhabit different environments like nearshore reefs, deeper marine environments, along with sharks and grouper, is considered as top predator of estuaries and reefs (O'Toole et al., 2011).

Several studies on the feeding ecology of these oceanic predators have been carried out in the Atlantic, Pacific and Indian oceans to investigate their dietary compositions. These predators are mainly generalists-opportunists, mainly feeding on fish, crustaceans and cephalopods (Dragovich, 1969; Zavala-Camin, 1981; Vaske-Jr Castello, 1998, 2004; Oxenford and Hunte, 1999; Oxenford et al., 2003; Allain, 2003; Menoscal et al., 2012; DeSylva, 1963; Schmidt, 1989; Grubich et al., 2008). However, all these earlier studies were restricted to the analysis of stomach contents to describe diets. In this context, to observe if predators exhibit a similar ecological pattern in the FNA region, we combine two approaches for the first time.

The present study access and describe the feeding habits of these four oceanic predators through stomach content analysis, and observe some aspects of their trophic relationships and partitioning of food resources with stable isotope data. We also aim at describing the differential

role that this island plays in the trophic ecology of the studied species, filling an important gap on trophic aspects of essential fishery resources around the FNA.

2 MATERIALS AND METHODS

Study area

The FNA (03°51.3'S and 32°25.6'W) consists of 21 islands and islets 540 km from the city of Recife, capital of Pernambuco state, on the northeast coast of Brazil (Figure 1). The climate is tropical warm, characterised by oceanic domain, with well-defined seasons, with the rainy season occurring between March and July and the dry season between August and February (Almeida, 2006; Teixeira et al., 2003). As regards the sea surface temperature, the seasonal variation gradient is minimal, with the lowest values occurring in the months of August-September-October (mean of 26.3°C) and the highest in the months of March-April-May (mean of 28.3°C) (Tchamabi et al., 2018).

The main island has particular characteristics, such as a sharp relief and two distinct sides. The “inside sea” is the most protected face from winds and currents, facing northwest, with characteristics of the calm sea during most of the year. The “outside sea”, facing southeast, presents traces of a more agitated sea under the action of the southeast trade winds and the South Equatorial current, with a westward flow, characterised by low nutrient content and low concentration of suspended particulate matter (Stramma and England, 1999; Serafini et al., 2010). According to Lessa et al. (1998), it is in the outside sea that fishing areas are located, close to the “wall” (Shelf break region), where the depth drops sharply (50 to 1.000 m), and the primary fishery resources are concentrated being the target of artisanal and sport fishing.

Ethical Statement

The collection of the scientific purpose material was approved and complied with the laws, guidelines and policies on animal welfare of the Ethics Committee on the use of animals of the Federal Rural University of Pernambuco CEUA-UFRPE (Process Nb. 23082.008290/2018-18), and the Chico Mendes Institute for Biodiversity Conservation (ICMBio) through the Biodiversity Authorization and Information System (SISBIO; Process Nb. 62915-6).

Sample collection and data analysis

Biological samples (stomachs and muscle tissue) were carried out onboard a recreational fishing vessel using a rod and reel in the island's proximity. Occasionally, samples of artisanal fishing boats were obtained during fish landings at the local port. The collections took place during expeditions of about 8 to 10 days carried out during July and October 2018 and January, March, April, May, and September 2019. All biological material was collected during fish evisceration at the end of each fishing cruise, recording data regarding the species caught and its total length (cm). The muscle tissues (~ 5g) were removed from the anterior dorsal region of the fish with a scalpel, immersed in 5 ml cryovials and store in plastic bags with the stomach.

Then, the samples were frozen at -18°C and kept in freezers until the moment of the laboratory analysis.

Feeding habits

The food items found in the stomachs were separated into large groups (teleosteans, molluscs, crustaceans and others) and identified at the lowest possible taxonomic level with the aid of specialised literature for fish (Barletta and Corrêa, 1992; Human and Deloach, 2002), crustaceans (Bowman and Gruner, 1974) and cephalopods (Clarke, 1986; Vaske-Jr, 2006). Organic matter that cannot be identified was grouped into the category “digested organic matter” and weighed in the same group. However, when the food item was considered partially digested, they were weighed, identified and grouped into the most general group (*e.g.*, fish).

To determine the contribution of each prey to the diet composition, three relative metrics of prey quantity were used: numerical abundance (%N), weight percentage (%W), and frequency of occurrence (%FO) (Hyslop, 1980). These measures combining with the index of relative importance (IRI) (Pinkas et al. 1971), provides a more accurate description of the importance of the diet. The IRI provides the ordering of a preferential scale of food items (essential, secondary and occasional foods) (Fonteles Filho, 2011) using the formula: $IRI = (\% N + \% W) \times \% FO$, where: %N = Percentage in the number of prey, %W = weight percentage, %FO = Percentage in the frequency of occurrence of prey. In addition, to assist comparisons between food categories and their diets, the IRI was expressed on a percentage basis (% IRI): $\% IRI = 100 \times IRI_i \div \sum IRI_i$; the IRI_i represents the IRI value for each category of prey *i*. To determine dietary differences in species with a large size range, we grouped them into three size classes to analyse possible dietary changes associated with the size.

The graphic method proposed by Costello (1990) and modified by Amundsen et al. (1996) was applied to describe dietary strategies. The concepts refer to a two-dimensional representation of the strategy used by predators, plotting the values of the frequency of occurrence and abundance of prey. The proposed formula for this method is $P_i = (\sum S_i \div \sum St_i) \times 100$ in which: P_i = abundance of specific prey *i*, S_i = stomach content (volume, weight or number) composed of prey *i*, St_i = total stomach content of the predators that contained only prey *i* in the stomach.

The range of trophic niche (diet range) was calculated for each species with the standardised index of Levin's (Hurlbert, 1978), with the % N of prey. Values <0.6 indicate that the predator is selecting some groups of prey and values close to 1 (> 0.6) indicate that the predator is a generalist (Krebs, 1999). The index is given by the formula: $B = 1 \div \sum_{i=1}^n P_i^2$ where: B = amplitude of trophic niche, n = total number of prey consumed by the predator, P_i = proportion of food item *i*.

The diet overlap among predators was investigated using the MacArthur and Levins's Index modified by Pianka (Krebs, 1989), using the formula $O_{jk} = \sum p_{ij} p_{ik} \div \sqrt{(\sum p_{ij}^2 \times \sum p_{ik}^2)}$, where: O_{jk} = overlapping diets, p_{ij} = proportion of item *i* in the total of items of species *j*, and p_{ik} = proportion of the item *i* in the total of items of species *k*. The index ranges from 0, with diets having no common items (no overlap), to 1, with identical diets (total overlap).

For the stable isotope analysis (SIA), small samples of muscle tissue extracted from each predator were washed with distilled water and oven-dried at 60°C for 48 h (Garcia et al.,

2007). After that, the samples were ground until the formation of a fine and homogeneous powder and stored in cryotubes. Stable isotope analyses were performed on a continuous flow mass spectrometer (Delta V + with an IV interface) linked to an elemental analyser (Flash EA 2000) at the Ocean Spectrometry Center (Plouzané, France). The results were expressed in δ based on international standards (Pee Dee Belemnite for $\delta^{13}\text{C}$ and N_2 in the air for $\delta^{15}\text{N}$) (Peterson and Fry, 1987), following the formula: $X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$ (in ‰), where X is ^{13}C or ^{15}N and R the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The experimental precision, based on the standard deviation of repeated measurements from an internal laboratory standard (Thermo-Acetanilide), was <0.11 ‰ for $\delta^{15}\text{N}$ and <0.04 ‰ for $\delta^{13}\text{C}$. As the C/N of all individuals was between 3.2 and 3.4, it was not necessary to perform the delipidation process, which avoids bias in isotopic results when lipid content is high (C/N>4) or when comparing species with varying lipid contents (Post et al., 2002). The isotopic composition of the species was investigated by biplots of the average values of the stable isotopes of carbon and nitrogen (Layman et al., 2012). Kruskal-Wallis tests were used to test possible differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between species. Carbon and nitrogen relationships as a function of fish size were examined using Spearman's correlation coefficient. Then, to assess trophic interactions in the total isotopic niche area occupied by the species, the metric established by Layman et al. (2007) was performed, in which the total area is an indication of the width of the isotopic niche of a population or community in an isotopic space (biplot).

Bayesian ellipses were used to characterise the isotopic niche area (95% prediction ellipse area) and evaluate the differences between the isotopic niche widths of the four predators (Jackson et al., 2011). The isotopic niche width was assessed based on the standard ellipse area corrected for small samples (SEAc). This correction provides a consistent comparison of the degree of isotopic niche overlap between the four predators (Jackson et al., 2011, 2012). Moreover, isotopic niche analysis was applied only for individuals within a similar size range (between 72 cm - 130 cm).

The potential niche overlap among species was estimated by calculating the maximum likelihood fitted standard ellipses using the function `maxLikOverlap` based on 95% prediction ellipse area (Jackson et al., 2011). The significance level of $\alpha = 0.05$ was considered for all statistical tests, and all analyses were performed using the software R 3.4.4 (R Core Team, 2018 - Rstudio), with the SIBER package ("Stable Isotope Bayesian Ellipses in R" (Jackson and Parnell, 2016)).

3 RESULTS

Stomach Content Analysis (SCA)

A total of 235 stomachs were analysed, of which 202 (85.95%) presented food content, distributed among the four species studied as follows: *S. barracuda* - BAR (n = 125), *A. solandri* - WAH (n = 29), *T. albacares* - YFT (n = 34) and *C. hippurus* - DOL (n = 14).

The length of *S. barracuda* ranged from 54 to 102 cm in total length (TL), mostly composed of adult individuals ($L_{50} = 66.0$ cm, DeSylva, 1963) (Figure 2). A total of 23 categories of prey were identified, with 10 of them at the species level (Table 1). According to the IRI values, the diet was composed mainly of fish, particularly representatives of the families

Diodontidae (% N = 28.23; % IRI = 20.95) and Exocoetidae, which presented considerable values for all metrics (% N = 18.18; % P = 46.27; % FO = 7.50; % IRI = 45.70). Crustaceans were its secondary prey, and cephalopods were occasionally ingested (Table 1).

For *A. solandri*, the specimens measured from 72 and 160 cm TL, with a high presence of adult individuals ($L_{50} = 110$ cm, Viana et al., 2013) (Figure 2). A total of 15 different prey were identified, among teleosts, crustaceans and cephalopods, with fish (% IRI = 46.04) being the most important category (essential items), with emphasis on the families Diodontidae (% IRI = 20.09) and Exocoetidae (% IRI = 14.08) (Table 1). The food items occasionally consumed were Ommastrephidae squids (*Ornitotheuthis antillarum*, % IRI = 4.43) and euphausiids (% IRI = 0.20), respectively (Table 1). In addition, for this species, a high degree of parasitism by *Hirudinella ventricosa* (79.5%) was observed in most stomachs analysed.

For *T. albacares*, total length ranged from 47 to 128 cm, indicating a predominance of juvenile individuals below the size at first maturity ($L_{50} = 99.2$ cm, Diaha et al., 2016) (Figure 2). A total of 24 prey were identified, and according to IRI (Table 1), teleosts (% IRI = 33.24) represented the most notable taxonomic group, followed by crustaceans, especially Phyllosoma larvae (% IRI = 32.98) and Ommastrephid cephalopods, such as *Ornitotheuthis antillarum* (% IRI = 7.64).

Only adult specimens of *C. hippurus* were captured, ranging from 72 to 130 cm TL ($L_{50} = 50.0$ cm, Dos Santos et al., 2014) (Figure 2). Ten prey items were identified; the fish group was the most representative (% IRI = 8.25), in particular, the family Exocoetidae (% IRI = 4.14) and *Dactylopterus volitans* (% IRI = 1.59), followed by specimens of Hemiramphidae (% IRI = 0.33). A single specimen of a gelatinous organism was found (% IRI = 0.09) (Table 1).

The predatory feeding strategies revealed that, in general, there was a higher concentration of prey with a low frequency of occurrence (F_i) and low prey-specific abundance (P_i) (Fig. 3). *Acanthocybium solandri* exhibited the highest concentration of prey with intermediate abundance (Acanthuridae, Gempylidae, Ommastrephidae, Crustaceans), and *S. barracuda*, *C. hippurus* and *T. albacares* showed a tendency towards specialisation in the consumption of dominant groups (Diodontidae, Exocoetidae, Teleostei), with the last species showing the greatest amount of rare prey among the four predators. Although the predators are considered to be generalists, it was observed a tendency to be specialised in the use of resources, where the behaviour can be evidenced by a low amplitude of trophic niche (Levins Index, $B_i < 0.6$) (Table 2), as well as low diet overlap between species, except between *S. barracuda* and *A. solandri* (MacArthur and Levin's, $R = 0.72$) (Table 3).

Stable Isotope Analysis (SIA)

Stable isotopes analysis was performed on 213 muscle tissues of the four species of different sizes (Table 4). Results revealed a relatively wider isotopic range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ presented in a bivariate diagram (Figure 4). The adult of *A. solandri* reached the highest average of $\delta^{15}\text{N}$, while the *C. hippurus* exhibited the lowest average. The $\delta^{13}\text{C}$ ratios were more enriched for juvenile *S. barracuda* and adult *A. solandri*, while juvenile *T. albacares* and *C. hippurus* adults showed the lowest and similar $\delta^{13}\text{C}$ ratios. Significant differences were found for carbon (Kruskal-Wallis, p-value <0.001) and nitrogen (Kruskal-Wallis, p-value <0.001) isotope ratios between the four studied species. The results of Spearman's correlation for the four predators

revealed a significant positive effect of $\delta^{15}\text{N}$ concerning the body length only for the *S. barracuda* ($p < 0.05$, $\rho = 0.53$); the other species showed no significant tendency (Figure 5). Regarding the interactions between $\delta^{13}\text{C}$ and body size, a significant correlation was observed for *T. albacares* ($p < 0.05$, $\rho = 0.80$) and *A. solandri* ($p < 0.05$, $\rho = 0.52$) (Figure 6). *Acanthocybium solandri* exhibited the highest SEAc value (6.3) while *T. albacares* showed the lowest (2.2). *Coryphaena hippurus* and *S. barracuda* had similar SEAc values (4.2 and 4.6 respectively) (TABLE 5). A high overlap was observed between *A. solandri* and *S. barracuda* (3.39); the other overlap values were more moderate, in a small range between 1.25 and 1.84 (TABLE 5).

4 DISCUSSION

Fernando de Noronha archipelago (FNA) is a relevant area for the conservation of marine biodiversity. In general, oceanographic processes transform the low-productive waters from tropical oceans into high-productivity environments around the oceanic islands (Travassos et al., 1999; Lima et al., 2016). Processes such as the island effect favour the maintenance of an important trophic web, influencing all surrounding fauna that find in this environment an opportune place for the development of their biological functions (Aquino, 2016, Tchamabi et al., 2017). High migratory capacity fish face the challenge of food spatio-temporal variability, and their survival depends on the efficiency in locating areas with greater resources availability (Rohit et al., 2010). Research that assesses how predators organise and interact in sharing food resources is crucial to understand the functioning of the ecosystem and the connections between ecological processes of energy transfer (McCauley et al., 2012; Schroeder et al., 2020). However, combining ecological methodologies such as stomach content analysis and stable isotopes has been increasingly used as a tool in these trophic evaluations, being unprecedented in the study area.

In equatorial regions, seasonal variation gradients are not very marked. We note that although we have samples from different periods (4 in the rainy season and 3 in the dry season), no significant environmental changes were observed that could indicate any influence on the trophic ecology of the species studied. The feeding activity of *S. barracuda* was very similar to the results obtained in the North Atlantic (Bahamas) (DeSylva, 1963), the Indian Ocean (Blaber, 1982) and the Western Caribbean (Torres-Chávez et al. 2018), showing a piscivorous behaviour for the specie, with a small contribution of invertebrates. The ichthyophagous behaviour reflected by the *A. solandri* is compatible with that found by Vaske-Jr et al. (2004) and Albuquerque et al. (2019), both in the region of the São Pedro and São Paulo Archipelago SPSPA (Equatorial Atlantic), closest location and with similar environmental characteristics to the FNA, where it was observed significant predation upon the flyingfish *Cheilopogon cyanopterus*, relatively abundant in the vicinity of this archipelago. The diet of predators can vary closely according to the level of abundance and availability of prey in each region (Mendoza-Ávila et al., 2016). Some authors consider that *T. albacares* has a very comprehensive diet describing the predator as an opportunistic species that does not distinguish the type or size of prey (Magnuson and Heitz, 1971; Vaske-Jr and Castello, 1998; Silva et al., 2019). The results obtained here corroborate this trophic behaviour of this species around the FNA, being the predator with a greater diversity of food items among the species studied.

Despite the reduced sample size of *C. hippurus*, the results are congruous to those obtained by Oxenford and Hunte (1999) in the Eastern Caribbean, which observed the dolphinfish's piscivorous behaviour. The diet was composed of a wide variety of fish species, including small pelagic similar to those found in this study, also observed by Vaske-Jr and Lessa (2004) in the Exclusive Economic Zone (ZEE) in Northeast Brazil, which described 23 taxa of fish and, Pimenta et al. (2014) in the north coast of Rio de Janeiro, determining a preference for fish in all analysed dolphinfish stomachs.

Some biological aspects (hydrodynamic forms, ontogeny, positioning of the mouth and types of teeth) affect the diets of the species and allow the use of different strategies by carnivorous fish, including the consumption of the same prey by different species when the resource is abundant (DeResende et al., 1996; Grubich et al., 2008). Our study showed a tendency towards individual specialisation. This tendency was observed among individuals of the same species by the high BPC (Costello's method), where only a limited fraction of predators consumed specific food categories, as well as by the narrow trophic niche (Levins <0.6), indicating diets dominated by a few prey groups. Hence, generalist or opportunistic species (Silva et al., 2019; Tripp-Valdez et al., 2014; Torrez-Chávez et al., 2018) can be composed of individuals specialised in resource use available around the FNA. Although predators have broad trophic spectra, the tendency to specialise on a select number of prey species, which may vary according to space and time, characterises these predators as plastic specialists (Baque-Menoscal et al., 2012). Ecologically or biologically significant areas such as FNA are important feeding points for oceanic predators, providing diversity and abundance of prey (Assunção, 2017; Serafini et al., 2010). Oceanic islands are important environments for maintaining local biodiversity and non-resident species since in their surroundings, physical processes trigger an increase in primary biomass and consequently develop the entire adjacent food web. Larvae of Dactylopteridae, Diodontidae, Hemihamphidae, Exocoetidae, and invertebrates were identified in the stomachs of the pelagic oceanic predators studied, reflecting the wide dispersal of these larvae, which are known to inhabit coastal waters and adjacent islands. This phenomenon is essential to attract predators such as tuna and tuna-like species that prey on these abundant resources in FNA waters (Vaske-Jr and Lessa, 2004).

The isotopic compositions were different between the species studied, reinforcing the dietary analysis composed of prey of different trophic levels and different feeding strategies (Li et al., 2016). The more enriched values of $\delta^{13}\text{C}$ for *S. barracuda* and more impoverished for *A. solandri*, *C. hippurus* and *T. albacares* indicate contributions from different compartments of the ecosystem in animal feeding (Hobson et al., 1994). It is known that in the marine environment, coastal food webs are more enriched in $\delta^{13}\text{C}$ than pelagic food webs (Cherel and Hobson, 2007). Oceanic islands can be areas of higher primary productivity and zooplankton abundance than the enclosing oceanic waters (Macedo-Soares et al., 2012; Lima et al., 2016). As the case of FNA, which has many sources of $\delta^{13}\text{C}$ originating from the biological activity in the island (Silva et al., 2019). Indeed, the high productivity in the island shallower waters attracts a diversity of marine species that serve as energy sources for predators, as we observed in our study. *Sphyræna barracuda* is a species with less displacement capacity and more resident character in the shallow waters, and their feeding strategy included organisms associated with the coastal environment as *Decapterus sp.*, *S. crumenophthalmus*, and *O. micropterus*. However, the stomach content analysis of *A. solandri*, *C. hippurus* and *T.*

albacares indicated that these species remain longer in the oceanic pelagic food web or consuming more depleted prey in $\delta^{13}\text{C}$ (Li et al. 2016).

The more significant variation of $\delta^{15}\text{N}$ observed in *A. solandri* may reflect ontogenic diet shifts, since the species becomes more enriched in nitrogen increases with trophic position and thus, with size (Cherel and Hobson, 2007). Larger and faster-swimming animals have a broad home range, interacting with more species, crossing vast areas with different isotopic compositions, and feeding upon varied isotopic baselines (Luckhurst, 2015). These factors, associated with the turnover time to incorporate food information into tissues, contribute to the variation of the elements analysed (O'Reilly et al., 2003). The largest isotopic niche area presented (SEAc) was observed for *A. solandri*; this species also exhibited the more generalist/opportunist behaviour (highest concentration of intermediate abundance). Moreover, *A. solandri* can inhabit the epipelagic, mesopelagic and bathypelagic areas, showing preferences to some regions (Allain, 2003). This behaviour might be related to the prey abundance available in the area (Sepulveda et al., 2011), corroborating the species plasticity diet. In addition, physiological differences in fish, such as nutritional stress generated by poor diet quality or starvation, can also affect $\delta^{15}\text{N}$ enrichment (Vanderklift and Ponsard, 2003). In this study, *A. solandri* exhibited a high degree of parasitism (79.5%) caused mainly by the trematode *Hirudinella ventricosa*, which may have affected its nutritional status, limiting the range of prey that could be ingested. The proportion of excreted and assimilated nitrogen is higher during periods of starvation and in animals that withstand frequent periods of fasting (Román-Reyes, 2005).

A moderate correlation of $\delta^{15}\text{N}$ in relation to size was only observed for *S. barracuda*, indicating a possible increase in nitrogen concentration as the individual grows. The positive relationship may be associated with the decreasing dietary importance of small invertebrates and with the increased consumption of larger prey with high nutritional value, such as fish, which is a strategy to supply energy needs throughout the life cycle of the *S. barracuda*. These results are similar to those obtained by De la Morinière et al. (2003) and Torres-Chavez et al. (2018) in the Caribbean, which studied the movement between habitats determined by trophic approaches by *S. barracuda*. The significant relationship between $\delta^{13}\text{C}$ and body size in *T. albacares* and *A. solandri* may indicate an increasing proportion of invertebrates in the diets since crustaceans and cephalopods have less depleted values compared to fish (Li et al., 2015). Also, juvenile individuals continue to feed constantly on smaller prey (Ménard et al., 2006), especially *T. albacares*, a species that presented greater diversity of food resources and a large portion of invertebrate organisms. For example, Moore (2014) studied trophic dynamics between tunas and sympatric species in southeastern Florida and concluded that $\delta^{13}\text{C}$ enrichment could be explained by trophic enrichment in relation to body size.

High overlap between *A. solandri* and *S. barracuda* was observed by both isotope and gut content analysis showing that the species seem to share common resources in FNA. Similar results were obtained in the North Atlantic with dolphinfish and two tuna species presented high overlap indicating that predators use compatible resources and occupy similar niches (Teffer et al., 2015). The other species showed different isotopic niche sizes and little overlap between ellipses, indicating the ability of predators to adapt to environments (Gonzalez et al., 2019), possibly recurring to alternative individual feeding strategies, consuming prey of distinct isotopic compositions. This niche segregation was also corroborated by analysing diet overlap

(MacArthur and Levin's Levin's Index; $R0 > 0.6$). Resource sharing is suggested when an overlap of isotopic niches occurs in a scenario where sources are abundant (Alley, 1982).

The isotopic values and the piscivorous diet of predators highlight the use of shallow water resources by *S. barracuda*, *T. albacares*, *A. solandri* and *C. hippurus* species that spend most of their time in the most superficial layer of the ocean, in continuous feeding activity on abundant and appreciate epipelagic organisms in their diets (Vaske-Jr and Lessa, 2004). Variations can occur due to the morphology and bioecology of each animal, allowing these fish to occupy the habitat in different ways (Magnunson and Heitz, 1971; Bertrand et al., 2002) and with different trophic behaviours, according to the availability of prey from each geographic region. The different distributions in the water column by predators can also be associated with differences in trophic spectra (Baque-Menoscal et al., 2012); for example, *T. albacares* can dive into deeper waters accessing other prey. These behaviours can be an adaptive response through the differential use of habitat, a tactic adopted to reduce competition between species (Costa et al., 2020) and optimise the biomass gain in sympatric situations. The similarity between diets can often point to overlap levels, representing food resources shared between fish species or size classes of a single species, not necessarily indicating competition (Lucena et al., 2000). According to Li et al. (2015), in marine ecosystems, segregation in feeding habits has been described as a common mechanism to allow the coexistence of several sympatric predators.

The two complementary methodologies employed in this study (stomach content and stable isotopes) reflect a trend towards trophic plasticity regarding the use and sharing of food resources available around FNA, where predators occupying a similar trophic niche share and divide common resources. According to the availability and abundance of prey, they adapt to improve the capacity for exploration and survival using resources shared by several species and/or used by a single one in different ontogenetic stages, reducing competition, coexisting in the same area and maximising energy gain. Also, it is important to note that the high concentration of organisms (Exocoetidae, Diodontidae) in oceanic environments make these isolated areas important points of energy storage during the migration processes of predators turning this environment into an oasis for marine life. Another important result obtained in this study is that the sardine (*Harengula clupei*), of known local abundance and much used as bait by the artisanal fishery (Travassos, 2003; Dominguez et al., 2016), does not seem to be an important food item for the four species studied during their trophic activities around the FNA.

Understanding how these predators use the available food resources is essential to comprehend the environmental dynamics where changes may be caused by different sources (climate, pollution, fishing, and other impacts). In these regards, knowledge of the trophic interactions within and among fishery resources is fundamental to assess the ecological role of island regions that constitute high environmental and economic value spaces, especially in oligotrophic oceans, supporting the development of management policies based on an ecosystem approach. Furthermore, the integrated use of methods such as SCA and SIA can provide a good overview of food webs dynamics to carry out ecosystem models of energy flows, such as Ecopath and ECOSIM. Finally, due to the economic relevance of these predators, further studies that consider the ontogenetic patterns, the isotopic information of prey, and seasonality are necessary to understand better the spatiotemporal changes in feeding habits and trophic dynamics.

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Accepted Article

Table 1: Diet composition from the analysis of the stomach contents of four species of pelagic fish caught in the Fernando de Noronha Archipelago expressed in percentage contribution metrics in: % N = Number, % W = Weight, % FO = Frequency of Occurrence and % IRI = Relative Importance Index, N = number of total samples, NES = number of empty stomachs.

Prey (Group/Taxa)	<i>Sphyræna barracuda</i> N = 136; NES = 11				<i>Acanthocybium solandri</i> N = 49; NES = 20				<i>Thunnus albacares</i> N = 36; NES = 2				<i>Coryphaena hippurus</i> N = 14; NES = 0			
	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Teleostei (Not identified)	9.57	8.44	14.17	18.62	8.57	41.7	34.48	55.3	21.09	8.36	52.94	36.02	15.00	51.01	31.00	8.25
Acanthuridae	4.78	12.49	2.50	3.15	0.95	12.4	3.45	1.8	-	-	-	-	2.50	4.54	8.00	0.22
Acanthostracion sp.	-	-	-	-	-	-	-	-	0.26	0.36	2.94	0.04	-	-	-	-
<i>Balistes capriscus</i>	0.48	0.03	0.83	0.03	-	-	-	-	0.26	0.09	2.94	0.02	-	-	-	-
<i>Diretmus argenteus</i>	0.48	0.49	0.83	0.08	-	-	-	-	-	-	-	-	-	-	-	-
Decapterus sp.	0.48	0.02	0.83	0.03	-	-	-	-	0.78	0.01	8.82	0.17	-	-	-	-
Diodontidae	28.23	1.32	7.50	16.18	23.81	15.8	13.79	20.9	0.26	3.91	2.94	0.29	-	-	-	-
<i>Diodon holocanthus</i>	7.66	0.28	0.83	0.48	-	-	-	-	-	-	-	-	-	-	-	-
Chilomycterus sp.	-	-	-	-	-	-	-	-	-	-	-	-	2.50	0.87	7.69	0.11
Exocoetidae	18.18	46.27	11.67	54.89	17.14	5.8	20.69	14.8	2.86	0.19	11.76	0.86	42.50	1.61	23.01	4.14
<i>Exocoetus volitans</i>	0.48	0.02	0.83	0.06	-	-	-	-	0.52	0.01	2.94	0.04	2.50	1.43	7.69	0.12
<i>Dactilopterus volitans</i>	3.83	1.48	2.50	0.97	-	-	-	-	-	-	-	-	12.50	38.41	7.69	1.59
Cheilopogon sp.	3.83	0.02	1.67	0.47	-	-	-	-	-	-	-	-	12.50	0.06	7.69	0.39
Hemiramphidae	0.96	0.03	1.67	0.12	0.95	0.01	3.45	0.13	-	-	-	-	5.00	0.31	15.38	0.33
<i>Oxyporhamphus micropterus</i>	0.96	5.27	0.83	0.38	25.71	0.32	3.45	3.43	-	-	-	-	-	-	-	-
Gempylidae	2.39	1.11	0.83	0.21	1.90	12.2	3.45	1.9	-	-	-	-	-	-	-	-
<i>Gempylus serpens</i>	1.91	3.71	0.83	0.34	-	-	-	-	-	-	-	-	2.50	1.49	7.69	0.12
<i>Selar crumenophthalmus</i>	0.48	0.23	0.83	0.04	-	-	-	-	-	-	-	-	-	-	-	-
Cephalopod	5.74	0.39	2.50	1.12	-	-	-	-	0.78	0.04	0.94	0.06	-	-	-	-
Enoplotheutidae	0.96	0.51	0.83	0.09	1.90	1.13	6.90	0.80	3.91	0.71	5.88	0.65	-	-	-	-
<i>Enoplotheutis anapsis</i>	-	-	-	-	-	-	-	-	0.52	0.01	2.94	0.04	-	-	-	-
<i>Abralia veranyi</i>	-	-	-	-	-	-	-	-	0.26	0.02	2.94	0.02	-	-	-	-
Ommastrephidae	-	-	-	-	4.76	8.14	6.90	3.40	0.52	22.05	2.94	1.59	-	-	-	-
<i>Ornitotheutis antillarum</i>	1.91	0.25	0.83	0.13	7.62	0.79	13.79	4.43	8.85	3.19	26.47	7.64	-	-	-	-
<i>Ommastrephes bartramii</i>	-	-	-	-	2.86	0.25	10.34	1.23	1.04	0.14	5.88	0.17	-	-	-	-
<i>Ocythoe tuberculata</i>	-	-	-	-	0.95	0.11	3.45	0.14	-	-	-	-	-	-	-	-
Pteropod	-	-	-	-	-	-	-	-	0.52	0.12	5.88	0.09	-	-	-	-
Macrozooplankton	-	-	-	-	-	-	-	-	15.36	27.59	17.65	18.17	-	-	-	-
Portunidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Parribacus antarcticus</i>	0.48	2.01	0.83	0.15	-	-	-	-	-	-	-	-	-	-	-	-
Crustaceans (Not identified)	4.31	14.34	1.67	2.27	1.0	4.0	3.4	0.7	3.91	2.48	8.82	1.36	-	-	-	-
<i>Brachyscelus crusculum</i>	-	-	-	-	-	-	-	-	0.26	0.01	2.94	0.02	-	-	-	-
Phyllosoma	1.44	0.40	0.83	0.11	-	-	-	-	30.21	28.25	23.53	32.98	-	-	-	-
Lobster larvae	-	-	-	-	-	-	-	-	7.03	2.45	8.82	2.01	-	-	-	-
Eufausia sp.	-	-	-	-	0.95	0.58	3.45	0.20	0.26	0.01	2.94	0.02	-	-	-	-
Copepod (Penella)	0.48	0.89	0.83	0.08	1.90	1.4	3.45	0.4	-	-	-	-	-	-	-	-
Stenopodidae	-	-	-	-	-	-	-	-	0.26	0.02	2.94	0.02	-	-	-	-
<i>Oxycephalus piscatoris</i>	-	-	-	-	-	-	-	-	0.26	0.02	2.94	0.02	-	-	-	-
Brachyura (Megalopa larvae)	-	-	-	-	-	-	-	-	0.52	0.05	5.88	0.08	-	-	-	-
Gelatinous Oceanic cnidarian	-	-	-	-	-	-	-	-	-	-	-	-	2.50	0.25	7.69	0.09

Table 2: Representative values of niche amplitudes calculated for each predator species using the standardized Levin's index (B_i). The numbers in parentheses correspond to the number of prey found for each species.

Species	B_i
<i>Sphyraena barracuda</i>	0.17 (23)
<i>Acanthocybium solandri</i>	0.13 (15)
<i>Thunnus albacares</i>	0.21 (24)
<i>Coryphaena hippurus</i>	0.04 (10)

Table 3: Food overlap values through combinations between species obtained by the MacArthur and Levin's Index. Values above 0.6 are considered evidence of a diet with high similarity.

	A	B	C	D
A. <i>Sphyraena barracuda</i>	-	0.72*	0.22	0.56
B. <i>Acanthocybium solandri</i>	-	-	0.18	0.42
C. <i>Thunnus albacares</i>	-	-	-	0.21
D. <i>Coryphaena hippurus</i>	-	-	-	-

Table 4: Amplitude of the total lengths of the species, number of samples, values of Minimum, Maximum, Mean \pm Standard deviation of stable isotopic composition of carbon and nitrogen (values given in ‰) and the total number of samples analysed by species.

Species	TL (cm)	n	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)		
			Min.	Max.	Mean \pm SD	Min.	Max.	Mean \pm SD
<i>Sphyraena barracuda</i> (BAR)	54-102	121	-17.97	-15.17	-16.03 \pm 0.53	9.32	12.17	10.58 \pm 0.55
<i>Acanthocybium solandri</i> (WAH)	72-147	43	-18.51	-16.09	-16.71 \pm 0.48	8.54	13.33	11.18 \pm 1.04
<i>Thunnus albacares</i> (YFT)	47-128	34	-18.91	-16.44	-17.06 \pm 0.34	8.62	11.79	10.46 \pm 0.34
<i>Coryphaena hippurus</i> (DOL)	72-130	12	-18.18	-16.38	-17.19 \pm 0.50	9.56	11.19	10.13 \pm 0.50

Table 5: Area of the standard ellipse (SEAc) adjusted for small sample sizes and values of the probability of overlap from Bayesian analysis of four pelagic species: *S. barracuda* (A), *C. hippurus* (B), *A. solandri* (C) and *T. albacares* (D).

Species	SEAc (‰ ²)	B	C	D
A. <i>Sphyraena barracuda</i> (BAR)	4.6	3.39	1.25	1.27
B. <i>Acanthocybium solandri</i> (WAH)	6.3			
C. <i>Thunnus albacares</i> (YFT)	2.2	1.75		1.85
D. <i>Coryphaena hippurus</i> (DOL)	4.2	1.84		

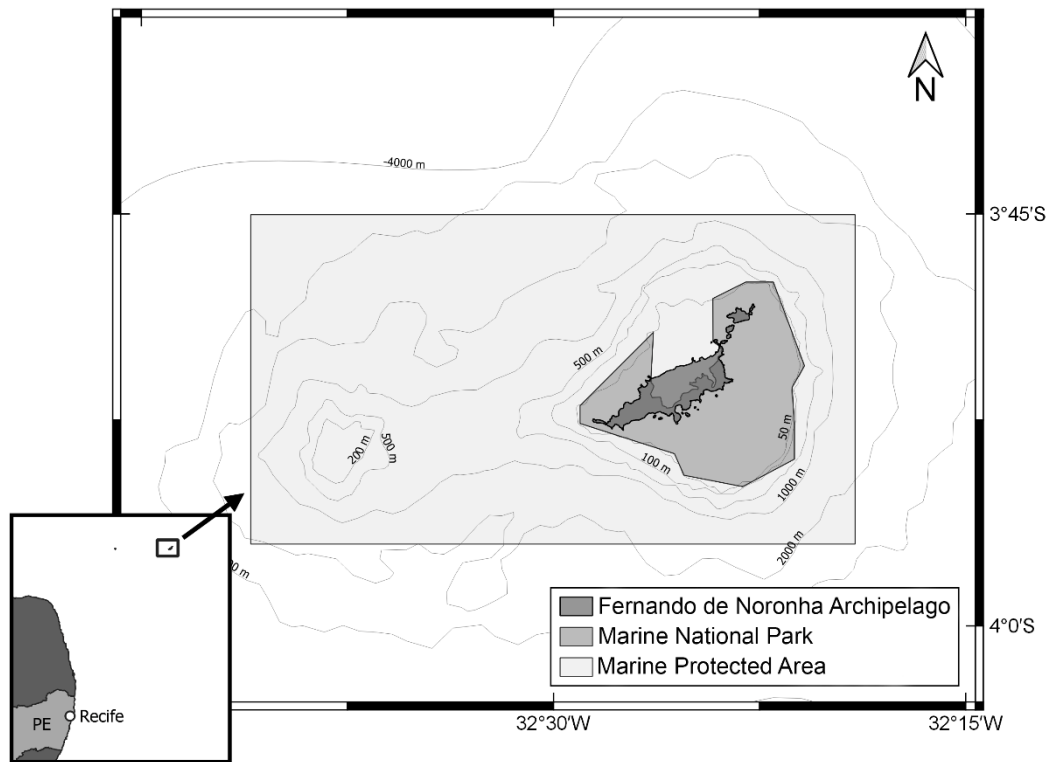


Figure 1: Fernando de Noronha Archipelago and protected areas on the northeast coast of Brazil.

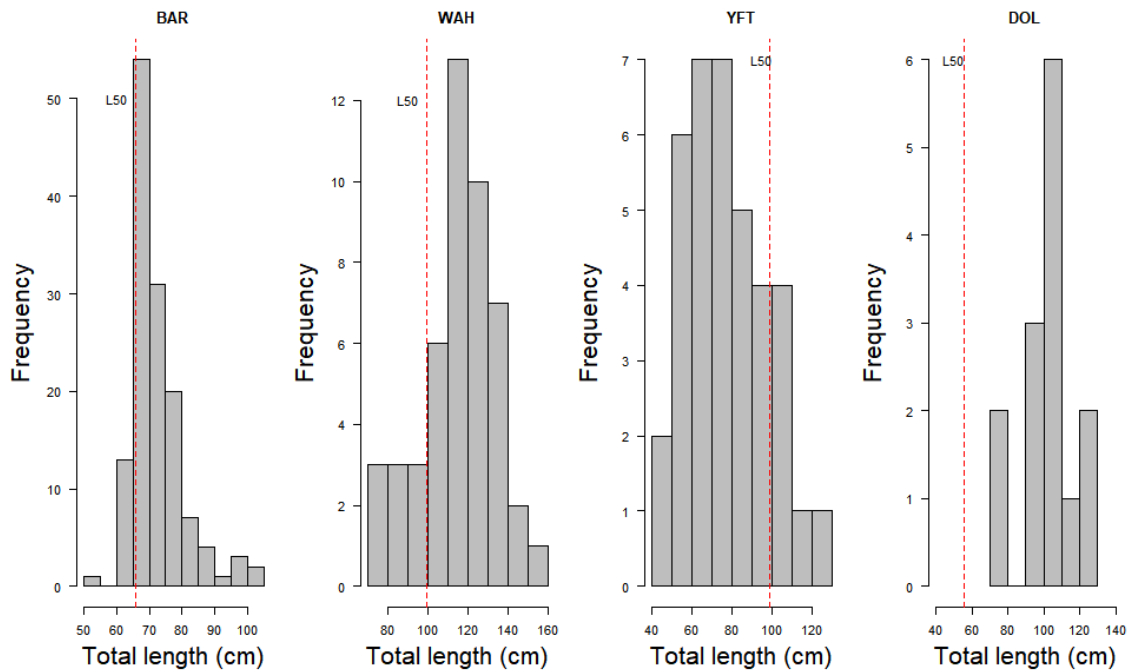


Figure 2: Distribution of length frequencies for a) *S. barracuda* (BAR), b) *A. solandri* (WAH), c) *T. albacares* (YFT), d) *C. hippurus* (DOL). The vertical dotted red line indicates the size at first maturity (L_{50}) for each species.

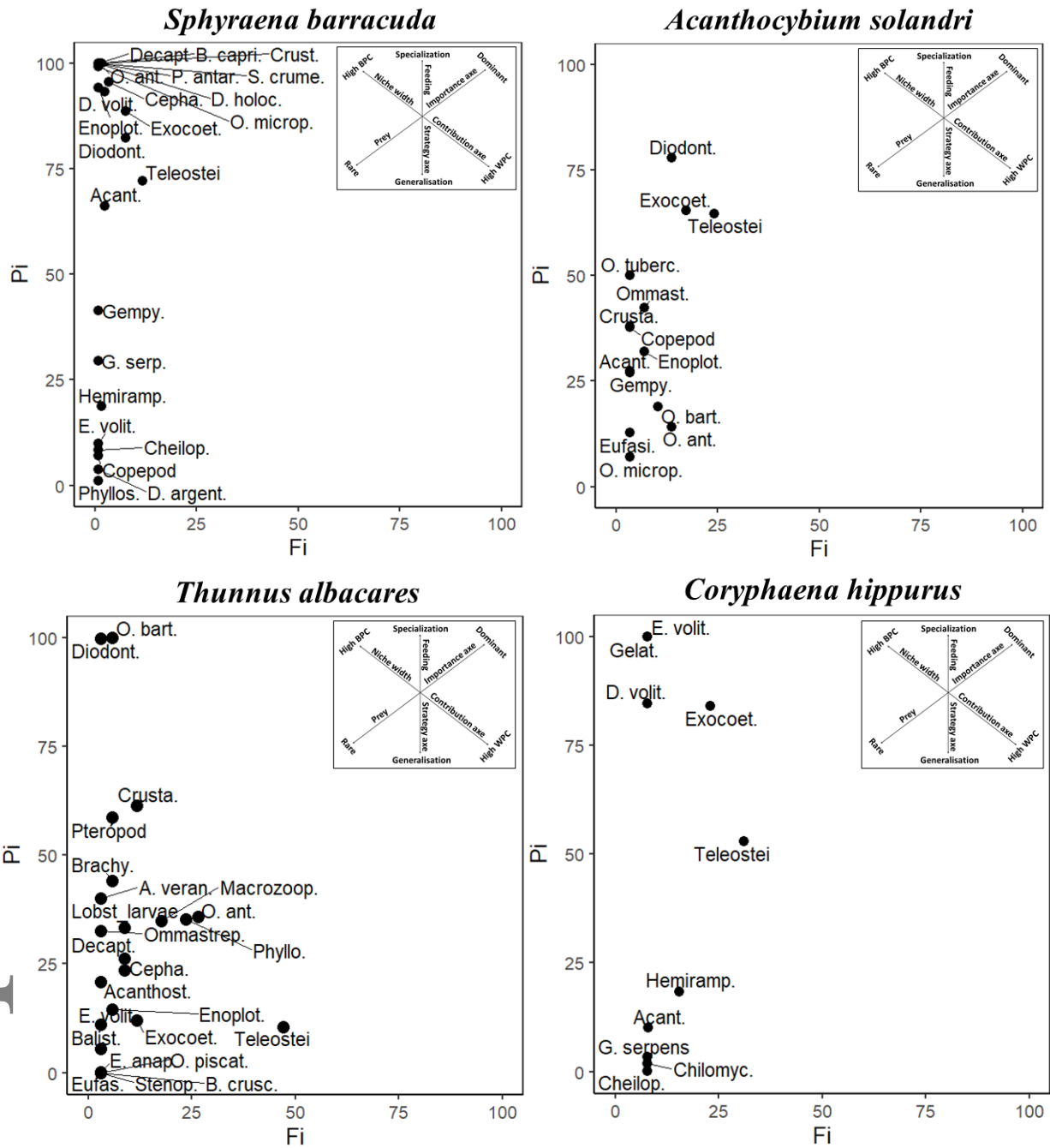


Figure 3: Relationship between the relative Prey-specific abundance (P_i , %) and the Frequency of occurrence (F_i , %) of prey items in the diet of four pelagic predators (*S. barracuda*, *A. solandri*, *T. albacares*, *C. hippurus*) captured along the Fernando de Noronha Archipelago. The arrows in the background of Costello's graphs denote the interpretation of the species feeding (Costello diagram (1990) modified by Amundsen et al., (1996)).

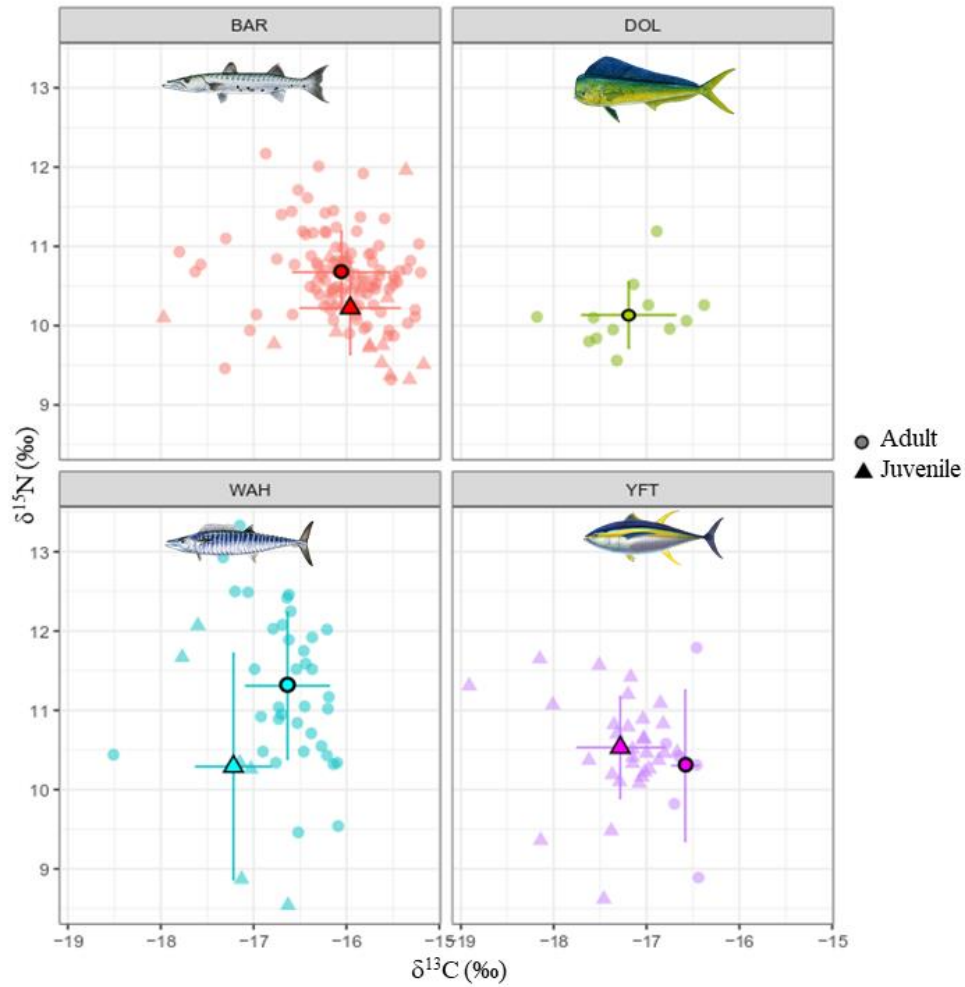


Figure 4: Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *S. barracuda* (BAR), *C. hippurus* (DOL), *A. solandri* (WAH) e *T. albacares* (YFT), circle and triangle are the mean \pm standard deviation for juveniles and adults.

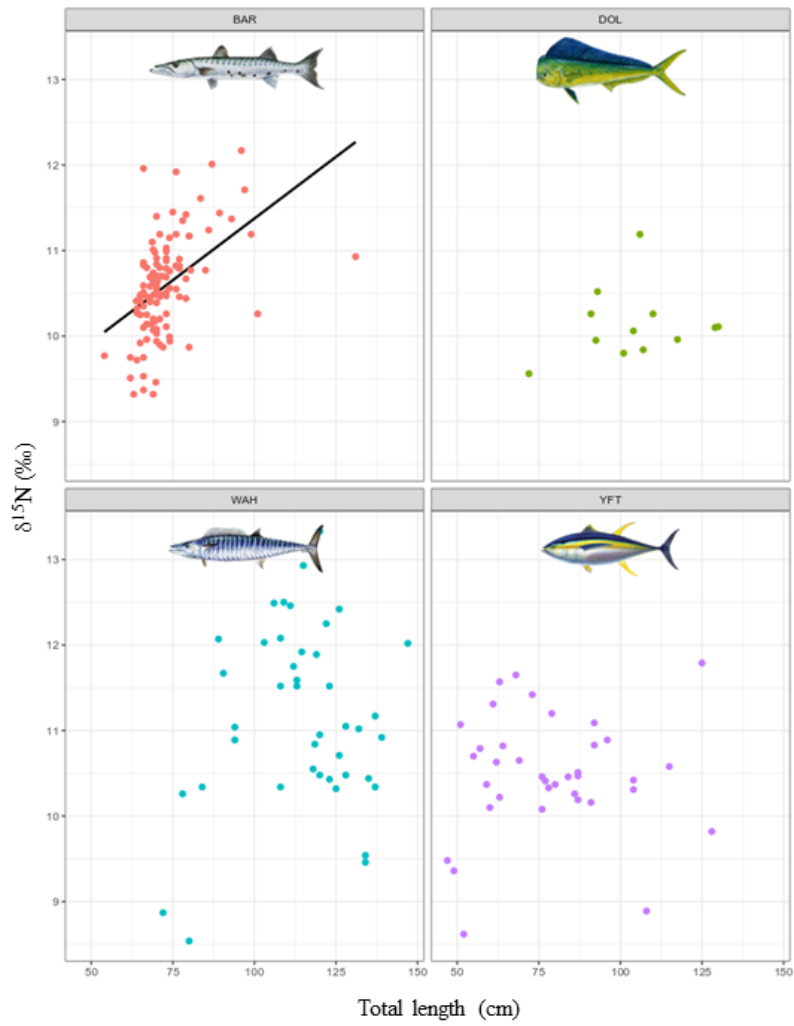


Figure 5: Distribution of $\delta^{15}\text{N}$ values by total length (cm) of *S. barracuda* (BAR), *C. hippurus* (DOL), *A. solandri* (WAH) e *T. albacares* (YFT). The line represents the significant relationship ($p < 0.05$).

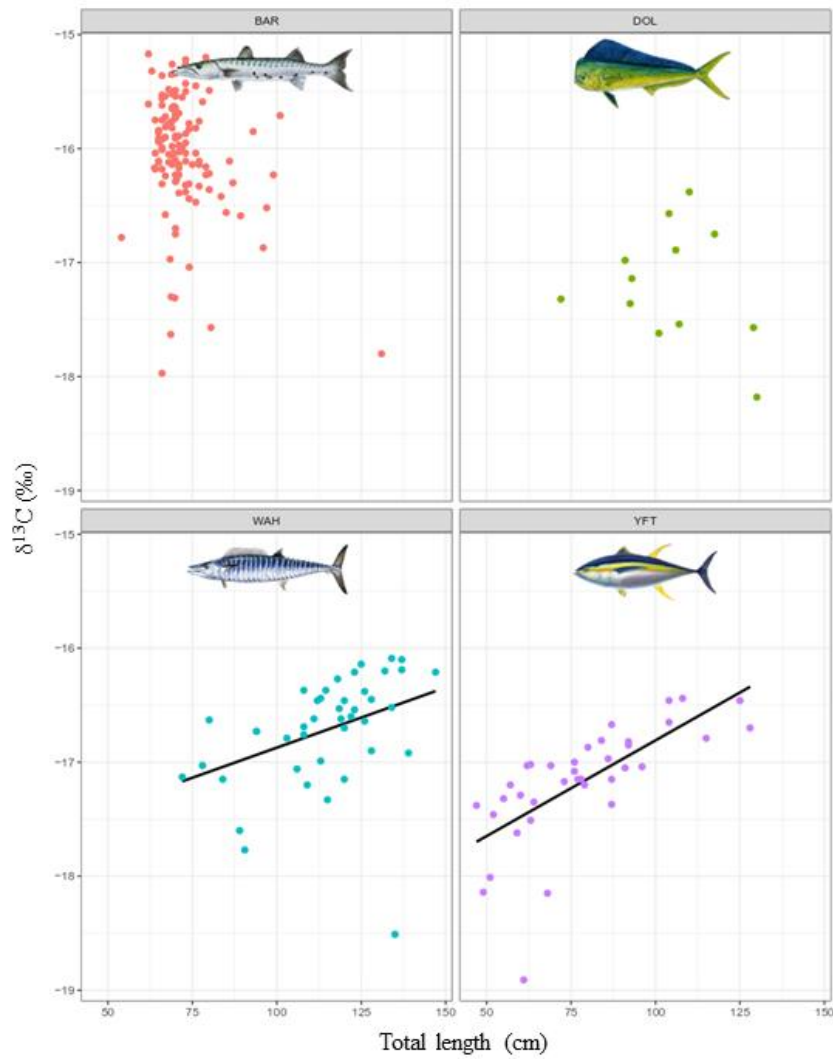


Figure 6: Distribution of $\delta^{13}\text{C}$ values by total length (cm) of *S. barracuda* (BAR), *C. hippurus* (DOL), *A. solandri* (WAH) e *T. albacares* (YFT). The line represents the significant relationship ($p < 0.05$).

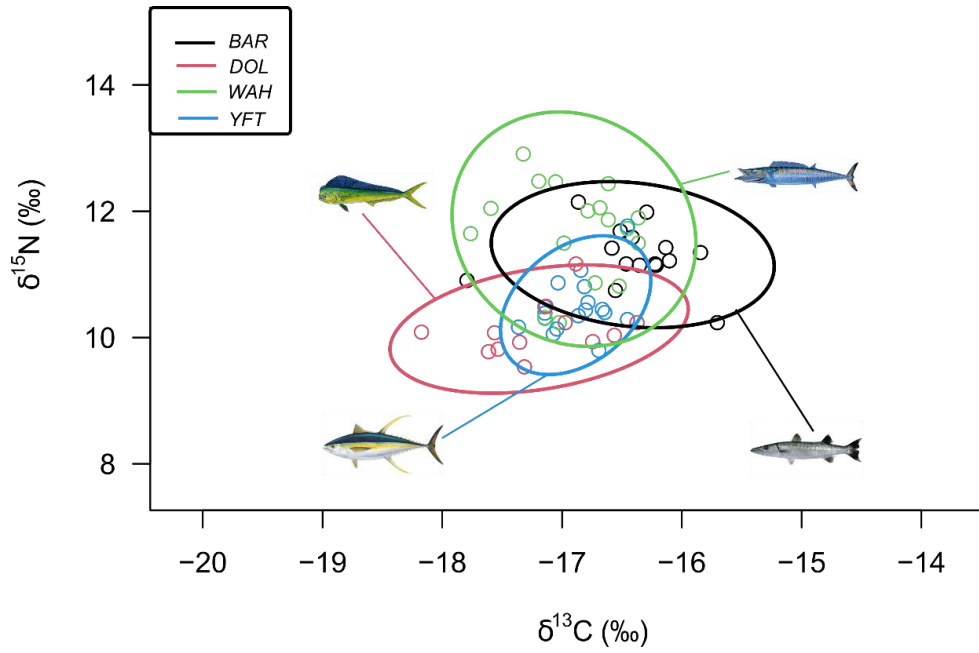


Figure 7: Isotopic niche (SIBER) for the species *S. barracuda* (BAR, black), *C. hippurus* (DOL, red), *A. solandri* (WAH, green) and *T. albacares* (YFT, blue). The lines represent the ellipse area for each species, with predicted values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The ellipses encompass 95% of the data.