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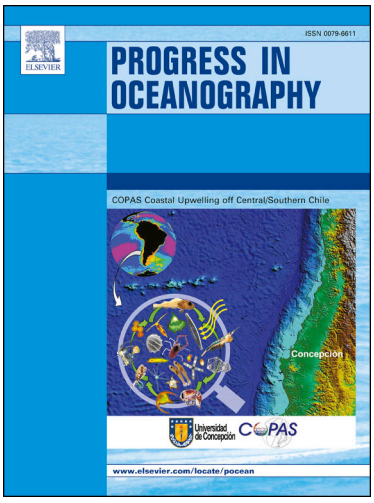

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Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic

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ABSTRACT

Species of the family Sternoptychidae (hatchetfishes) occur worldwide and play critical roles by sequestering carbon, recycling nutrients, and acting as a key trophic link between epipelagic primary consumers and higher trophic levels in marine ecosystems. Nevertheless, basic knowledge on their ecology is still lacking and their functional ecology remains understudied with respect to composition, organization, functions and environment interactions. Here we integrated comprehensive information collected in the western Tropical Atlantic on the diversity, abundance, distribution and trophic ecology of hatchetfishes, including physicochemical features of their habitats and extensive carbon and nitrogen stable isotope data on its main prey groups. On this basis we defined five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks and reveal a possible high resource partitioning. Additionally, these species might have a different feeding tie chronology. Hence, hatchetfishes segregate in different ecological groups responding differently to environmental constraints including oxygen concentration and presenting diverse functional roles. As deep-sea species that migrate to epipelagic waters, hatchetfishes may play a key role in the transfer of sub-surface photoassimilated carbon to deeper waters, a pathway through which the effects of climate change at the surface are transferred to the deep ocean. Moreover, as consumers of gelatinous organisms, these species convert "gelatinous energy" into "fish energy" readily usable by higher trophic levels, including endangered and commercially important species. This is a crucial trophic relationship that has been historically underestimated due to methodology limitations (e.g., quickly digested gelatinous organisms were probably underestimated in previous studies, based solely on stomach contents). Considering in ecosystem models this trophic relationship, as well as the functional organization of hatchetfishes, is important to properly answer important ecological questions including resource use, carbon transportation, and influence of mesopelagic community in climate change process.

Keywords: Brazil; diet; gelatinous organisms; mesopelagic; stable isotope composition; dissolved Oxygen; Mixing Model

INTRODUCTION

Mesopelagic fishes, distributed from surface to approximately 1000 m, are numerically the most important vertebrate component of all temperate and tropical oceanic waters (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014). Most part of these communities forms high-density biological layers at around 500 m in search of predator refuge during daytime (Sutton, 2013), and ascend to epipelagic layers (0–100 m) at night for feeding, following the diel vertical migration of zooplankton (Merrett and Roe, 1974). This "largest daily migration of animals on earth" (Hays, 2003) represents a major mechanism for transporting organic matter below the euphotic zone (Heath et al., 2016). Mesopelagic fishes play a critical role in marine ecosystems

by sequestering carbon, recycling nutrients, and acting as a key trophic link between primary consumers and higher trophic levels (e.g. larger fish, mammals and sea-birds) (Hedd and Montevecchi, 2006; Cherel et al., 2010; Drazen and Sutton, 2017).

In terms of abundance and biomass, representatives of the family Sternoptychidae (hatchetfishes) are one of the most conspicuous components of the mesopelagic ichthyofauna (Gjøsaeter and Kawaguchi, 1980). In the eastern tropical Atlantic, for example, hatchetfishes are amongst the most abundant and diverse mesopelagic fish group (Olivar et al., 2017, Olivar et al., 2018). This family, which occurs in all oceans, includes 78 valid species that usually present small bodies size (<100 mm of standard length, SL), numerous photophores and a highly variable intergeneric body morphology (Nelson et al., 2016). Previous studies on hatchetfishes provided important knowledge on biodiversity, abundance, vertical migration and feeding habits (e.g. Hopkins and Baird, 1985; Olivar et al., 2012; Carmo et al., 2015). Hatchetfishes are classified as a complex midwater group presenting a variety of migration patterns and feeding behaviour (Hopkins and Baird, 1985; Carmo et al., 2015). For instance, while vertical migration patterns are observed in some species (Hopkins and Baird, 1985; Kinzer and Schulz, 1985), it seems to be absent in others (Olivar et al., 2017). Hence, this taxonomic group may be constituted by different functional groups with diverse spatiotemporal distribution, responding differently to environmental constraints, and having distinct ecological roles.

Characteristics in terms of trophic ecology, habitat, distribution and migration patterns allow classifying species by functional group, which is a powerful approach to investigate effect of species on ecosystem functions, functional equivalence among species, and organisms adaptation to changing environmental conditions (McGill et al., 2006; Villéger et al., 2017). However, this approach requires integrated knowledge on biophysical and ecological aspects of the species that is often lacking in mesopelagic ecosystems. As an example, the ecology of hatchetfishes and how they interact with their environment remains poorly know worldwide and unexplored in many large oceanic areas, such as in the western Tropical Atlantic Ocean. Additionally, although knowledge on mesopelagic trophic ecology has progressively improved in the last decades, comprehensive food web studies considering multiple approaches are still scarce. Indeed, previous studies on the trophic ecology of hatchetfishes were mostly based on gut content analyses (GCA) (e.g. Hopkins and Baird, 1981; Sutton and Hopkins, 1996b; Carmo et al., 2015). Whilst GCA may provide high taxonomic resolution of the diet, the approach is

restricted by its short temporal representation and includes biases due to prey misidentification (Hyslop, 1980). Furthermore, the importance of key prey groups that are quickly digested (e.g. gelatinous organisms) remains underestimated, hampering a more complete understanding of pelagic food webs (Hopkins and Baird, 1985; Hidalgo and Browman, 2019). Alternatively, stable isotope analysis (SIA) is a useful tool to study food web structure, as it provides time-integrated information on all the material assimilated by organisms, including prey that are usually not accounted on GCA (Cherel et al., 2008; Post, 2002). Hence, combining both GCA and SIA allows for a more comprehensive picture of the flows of biomass across trophic compartments.

Here, we propose a comprehensive study on hatchetfishes by taking advantage of a set of data combining information on their abundance, distribution, diversity, trophic ecology and physical and chemical habitat. We combined gut content analyses with stable isotope data carried out on particulate organic matter, hatchetfishes and on their most likely prey, including zooplankton, crustaceans, fish larvae, and gelatinous organisms. Data were acquired around oceanic islands and seamounts in the western Tropical Atlantic, a poorly studied area of high biodiversity where Marine Protected Areas and Ecologically or Biologically Significant Marine Areas have been established (EBSAs; CBD, 2014). Specifically, we aim at answering the following questions: (i) what are the main species and functional groups of hatchetfishes, (ii) where are they distributed, (iii) what are the features of their diel vertical migration, (iv) what are their main prey and trophic relationships, and (v) how are they related with physical-chemical oceanographic conditions? Finally, as a synthesis, we propose a conceptual model describing the use of the environmental and trophic habitat of functional groups of hatchetfishes.

Material and Methods

Study area

The study area comprises the surround area of Rocas Atoll (3°52′S, 33°49′W), Fernando de Noronha Archipelago (3°50′S, 32°25′W) and adjacent seamounts (Fig. 1). Located in the western tropical Atlantic, an oligotrophic area, these islands cause eddies and turbulences that drive subsurface enriched waters to the surface, increasing primary production and therefore enhancing mass and energy fluxes throughout the food web (Travassos et al., 1999; Tchamabi et al., 2017). As a consequence, this large biogeographic unit has been referred to as an "oasis of life in an oceanic desert" (Hazin, 1993) and classified as 'EBSA - Banks Chain of Northern

Brazil and Fernando de Noronha', a special area in the ocean of fundamental importance for biodiversity and life cycles of several marine species (CBD, 2014).

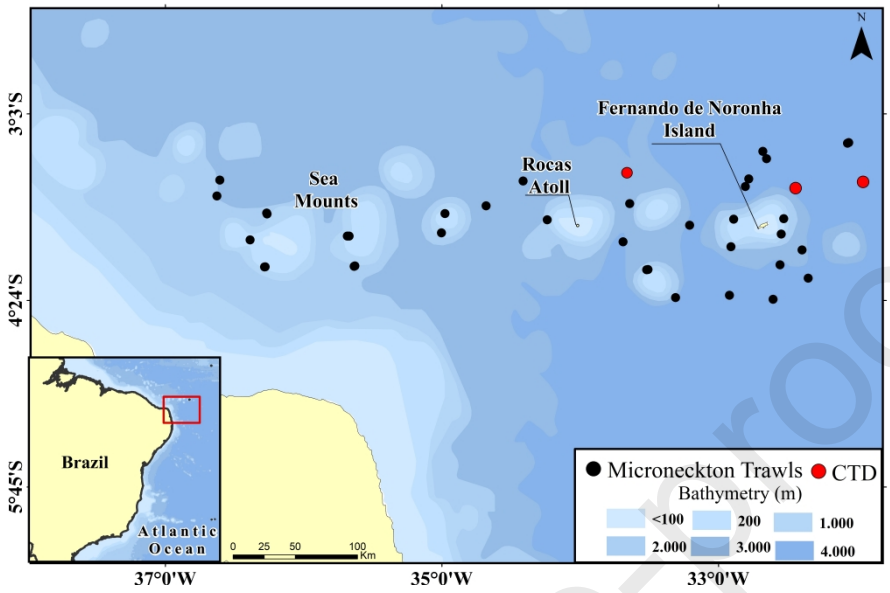

Figure 1. Study area with the CTD and micronekton-trawl sampling stations.

Data

Data were collected over 31 sampling stations (Fig. 1, Suppl. material 1) during the scientific survey ABRACOS 2 (Acoustics along the BRAzilian COaSt 2), conducted onboard the R/V *Antea* from 9th April to 6th May 2017 (Bertrand, 2017). Conductivity, Temperature, Depth and Oxygen hydrographic profiles were collected using a CTDO SeaBird911+. Particulate organic matter (POM) was sampled by filtering seawater from the maximum fluorescence depth through GF/F filters (47 mm), followed by a dry proceeding of 36 hours (40°C). Zooplankton samples were collected using a Bongo net (60 cm of mouth diameter and mesh size of 300 µm) that was obliquely towed from 200 m depth up to the surface.

Mesopelagic fishes, crustaceans and gelatinous organisms were collected during day and night with a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm) from 10 to 1113 m depth for about 30 min at 2–3 knots (Fig. 1). Targeted depth was defined for each tow according

to the presence of acoustic scattered layers or patches, as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder operating at 38, 70, 120 and 200 kHz. Except the layers 200–300 and 700–800 at night, where no aggregation of organism was observed through acoustics, all depth strata were sampled at least once (Suppl. Material 1). Tow duration was considered as the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded by means of a SCANMAR system. Targeted depth was defined for each tow according to the presence of acoustic scattered layer or patches as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120 and 200 kHz. The net geometry was monitored using SCANMAR sensors providing headline height, depth, and distance of wings and doors. As the trawl did not have any opening or closing mechanism, the collection of specimens during the lowering or hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed.

Hatchetfishes and their potential food were sorted to the lowest taxonomic level and frozen or, in the case of rarity or taxonomic uncertainty, fixed in a 4% formalin solution for one month and then preserved in a 70% alcohol solution. At the laboratory, individuals were identified, measured (nearest 0.1 cm of standard length, SL) and weighed (nearest 0.01 g of total weight, TW). Voucher specimens were deposited in the Fish Collection of the "Instituto de Biodiversidade e Sustentabilidadae" (NPM), Universidade Federal do Rio de Janeiro (UFRJ).

Hatchetfishes catch composition, abundance and vertical migration

The relative index of fish abundance (Catch Per Unit of Effort–CPUE) was calculated considering the number of specimens per hour, standardized to a similar mouth area of 120 m^2 (estimated through SCANMAR sensors). These values were obtained for each species considering the period of the day (day/night), depth strata (10–1000 m, intervals of 100 m) and sample stations. Daytime was considered to the extend from one hour after sunrise to one hour before sunset, while the night was from one hour after sunset to one hour before sunrise. Dawn or dusk samples were discarded when studying day/night vertical distributions. Migration patterns were classified as synchronous migrant (entire population responds synchronously to daily light variation), asynchronous migrant (only part of the population responds synchronously to diel daily light variation), and non-migrant (no evidence of vertical migration) (Sutton and Hopkins, 1996a). Patterns of interaction among hatchetfishes and their environment were

analysed by combining data on vertical distributions and mean profiles of temperature and oxygen.

Trophic ecology

Two approaches were implemented to assess the trophic ecology of hatchetfishes: Gut Content Analyses (GCA) and Stable Isotopes (SI) analyses. The GCA was applied for four species with at least 15 non-empty stomachs, following the method developed by Sutton and Hopkins (1996b): *Argyropelecus aculeatus, A. affinis, Sternoptyx diaphana,* and *S. pseudobscura*. Each specimen was dissected for removal of the digestive apparatus and only stomachs were analysed, with contents being removed and sorted into major taxa under a stereoscope.

Wherever is possible, consumed prey size measurements to the nearest 0.1 mm were carried out with a binocular stereoscope using an ocular micrometric scale. We measured the standard length of fishes; back of eye socket to tip of telson (excluding terminal spines) of decapods; tip of rostrum to tip of telson (excluding terminal spines) of euphausiids; anterior end of eyes to tip of uropods or telson (depending which was longer) of amphipods; valve length of ostracods; prosome length of copepods; maximum shell length of pteropods (Carmo et al., 2015). For very small-sized prey, food items were fixed in a labelled glass slide and measured using a microscope to the nearest 0.1 mm.

The contribution of each prey taxon to the composition of the diet was assessed using three metrics computed by pooled stomachs: frequency of occurrence (%FO), numerical abundance (%N) and weight percentage (%W) (Hyslop, 1980). The vacuity index (VI, %) was calculated as follows: $VI = \frac{Nv}{Ne} x\ 100$, where *Nv* is the number of empty stomachs and *Ne* the total number of examined stomachs. This index was calculated for each species considering day, night, and pooled periods. The feeding strategy was characterized through the modified Costello diagram (Amundsen et al., 1996), a graphic representation of prey items that allows the inference about the degree of the diet variability of a predator. Through this analysis, it is possible to plot the consumed prey specific importance of each consumed prey taxa against the frequency of occurrence in 2D diagram, with three axes representing the feeding strategy, prey importance, and niche width. For this analysis, the prey-specific abundance was calculated as follows: $P_i=(\Sigma S_i/\Sigma S_{ti}) * 100$, where P_i is the prey-specific abundance of prey i, S_i is the total abundance (in number) of prey i, and S_{ti} is the total stomach content in only those specimens with prey i in their

stomachs. Niche breadth was estimated by Levin's standardized index as follows (Levins, 1968) : $B_J = \frac{1}{n-1}(\frac{1}{\sum p_{ij}^2} - 1)$, where B_j is the Levin's standardized index for predator j, whereas ${p_i}^2{}_j$ is the proportion in weight of prey i in the diet of predator j and n is the number of prey categories. This index ranges between 0 and 1, indicating a generalist diet when a high value is obtained and a diet dominated by few prey items (specialist predator) when the index has a value close to zero.

The stable isotope analyses were conducted on five hatchetfishes species. Additionally, isotopic information on POM and on the following potential hatchetfishes prey were included: two fish larvae groups (Teleostei larvae 15–20 mm and Teleostei larvae 5–10 mm); five crustaceans; five gelatinous groups (divided into Siphonophorae and Thaliacea), and zooplankton (200–500 µm, mainly composed by copepods) (Table 1). Potential hatchetfishes prey were selected based on stomach contents analyses and literature (e.g. Hopkins and Baird, 1985; Bernal et al., 2015; Carmo et al., 2015). Despite not identified at species levels, fish larvae were grouped into size-classes, diminishing the isotopic variability within groups. The size of all prey groups was selected aiming to be size-adequate for hatchetfishes ingestion (based on prey size previously reported on literature). For isotopic analyses, the following soft tissues were extracted: white dorsal muscle for fishes, abdomen for crustaceans and body wall for larvae and gelatinous. After removal, soft tissues were cleaned with distilled water to remove exogenous material such as carapace, scales, and bones. Whole zooplankton samples have been stored in Eppendorf micro tubes. Samples were dried in an oven at 60°C for 48h and grounded into a fine powder with a mortar and pestle. In order to obtain unbiased values of $\delta^{13}C$, zooplankton and POM samples was separated to remove the carbonates. Zooplankton were acidified according to Cresson et al. (2012) by adding approximately 2 ml of 0.5 $mol.l^{-1}$ hydrochloric acid (HCl). POM filters were exposed to hydrochloric acid (HCl) vapour. After 4 hours, the filters and zooplankton were dried at 40ºC during 36h. Untreated sub-samples of POM and zooplankton were used to measure $\delta^{15}N$ and acidified one for $\delta\ ^{13}C$. Each sample was analysed for carbon and nitrogen isotope ratios through a mass spectrometer (Thermo Delta V+) coupled to an element analyser (Thermo Flash 2000, interface Thermo ConFio IV) in the Platform Spectrometry Ocean (PSO, IUEM), France. Results of stable isotope analysis for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are derived from the relation of the isotopic value from the sample and a known standard: $\delta^{13}C$ or $\delta^{15}N = [(Rsample/Rstandard) - 1] \times 10^3$; in which R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N. As differential lipid contents can bias the interpretation of $\delta^{13}C$ values, here we explored

the potential lipid bias by using % elemental by mass C:N ratios and the relationship between C:N (i.e., lipid content) and $\delta^{13}C$. As samples were not treated to remove lipids before analysis to prevent loss of material, the few prey groups that exhibited C:N dynamics consistent with high lipid content (C:N > 3.5) were normalized using the equation for aquatic animals provided by Post et al. (2007): $\Delta\delta^{13}C = -3.32 + 0.99 \times C:N$. $\Delta\delta^{13}C$ is the change in $\delta^{13}C$ caused by lipids and C:N is the carbon-to-nitrogen ratio (by mass) of the sample.

Table 1- List of hatchetfishes and potential prey groups analysed for stable carbon and nitrogen isotopic compositions.

Group	Category	Species	
Hatchetfishes	predator	*Argyropelecus aculeatus*	*Sternoptyx diaphana*
	predator	*Argyropelecus affinis*	*Sternoptyx pseudobscura*
	predator	*Argyropelecus hemigymnus*	-
Fish larvae	potential prey	Teleostei larvae 15–20 mm	Teleostei larvae 5–10 mm
Crustaceans	potential prey	*Euphausia gibboides*	*Pasiphaeidae* sp.
	potential prey	*Euphausia* sp.	*Phronima* sp.
Siphonophorae	potential prey	*Abylopsis tetragona*	Siphonophorae sp.
Thaliacea	potential prey	*Salpa* sp.	*Soestia zonaria*
	potential prey	*Pyrosoma altanticum*	-
Zooplankton	potential prey	200–500 µm, mainly composed by copepods	

Fish trophic position (TP_{SIA}) based on nitrogen stable isotopes was assessed based on the following equation (Post, 2002):

$$TP_{SIA} = \left[\left(\delta^{15}N_{consumer} - \delta^{15}N_{baseline}\right)/TDF\right] + TP_{baseline}$$

where $\delta^{15}Nc_{onsumer}$ and $\delta^{15}N_{baseline}$ are the $\delta^{15}N$ values of the target consumer and the baseline respectively; TDF is the trophic discrimination factor and $TP_{baseline}$ is the trophic position of the baseline. As POM may be influenced by the co-occurrence of detritus (Montoya et al., 2002) and microzooplankton in the water column (Post, 2002), primary consumers (TP2) are usually a better isotopic baseline to assess TP. Following the methodology of previous studies on the trophic position of mesopelagic fishes (Cherel et al., 2010; Ménard et al., 2014), the baseline utilized was the Salps, which are known to be filter-feeders primary consumers grazing on phytoplankton and other small food items. To account for uncertainty in TL estimation, a Bayesian model was incorporated in the calculation of TP_{SIA} using predict $\delta^{15}N$ values of hatchetfishes and a TDF of 3.15‰ ± 1.28‰ (McCutchan Jr. et al., 2003). For comparison,

trophic positions were also estimated using stomach content data (TP_g) (Adams et al., 1983), applying the equation:

$$TP_{SCA} = \sum(W_i T_i) + 1$$

where, W_i and T_i are the relative weight and the trophic position of the *i*th prey item respectively (adapted from Winemiller, 1990). W_i is the weight of prey *i* divided by the total weight of prey items.

The Bayesian mixing model, MixSIAR (Stock and Semmens, 2013), provides the most accurate estimations of source or prey contributions when tissue and species-specific discrimination factors are used (Caut et al., 2008). We applied this analysis to estimate the relative contribution of specific prey of hatchetfishes to their diet. Potential dietary endpoints applicable to hatchetfishes included in SIAR analysis were derived from stomach contents analyses and published information(e.g. Bernal et al., 2015; Carmo et al., 2015; Hopkins and Baird, 1985). The following prey groups were included (Table 1): i) Zooplankton; ii) *Abylopsis tetragona* (Siphonophorae); iii) *Euphausia gibboides* (Euphausiacea); iv) *Phronima* sp. (Amphipoda); v) *Salpa* sp. (Thaliacea); vi) *Soestia zonaria* (Thaliacea); vi) Teleostei larvae 15-20 mm (Teleostei), and vi) Teleostei larvae 5-10 mm (Teleostei). As trophic discrimination factors for mesopelagic fishes are poorly known, according to previous studies (Richards et al., 2018; Valls et al., 2014) we run mixing models using discrimination factors of 3.15‰ ± 1.28‰ and 0.97‰ ± 1.08‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Sweeting et al., 2007; Cherel et al., 2010; Menard et al., 2014).

All statistical analyses were performed with R version 3.4.4 (R Core Team, 2018), using the packages *SIAR* ("Stable Isotope Analysis in R"; Parnell et al., 2010) and *SIBER* ("Stable Isotope Bayesian Ellipses in R"; Jackson and Parnell, 2016) for the estimation of isotopic niche areas and overlaps and Mixing models respectively. The package *tRophicPosition* ("tRophicPosition: Bayesian Trophic Position Calculation with Stable Isotopes) (Quezada-Romegialli et al., 2017)) was used for trophic positions calculations.

RESULTS

Oceanographic conditions

Throughout the study area, the surface layer was characterized by warm waters (28°C) within a shallow (~50 m) and homogeneous mixed layer (Figure 2). The temperature profile was characterized by a sharp thermocline extending from 86 m to 132 m, presenting a thermal difference of 12.3ºC from the upper to the lower limit of the thermocline. The vertical profile of salinity was quasi-homogeneous, with the highest gradient located between 80 and 120 m. The profile of dissolved oxygen concentration was homogeneous within the mixing layer, decreasing at the upper limit of the thermocline and usually presenting three minima, at depths of 100 m, 300 m, and 450 m. In contrast to the decreasing temperature and salinity, the dissolved oxygen slowly increased below 550 m. Within our study area, the vertical profiles of temperature, salinity and oxygen were very homogeneous.

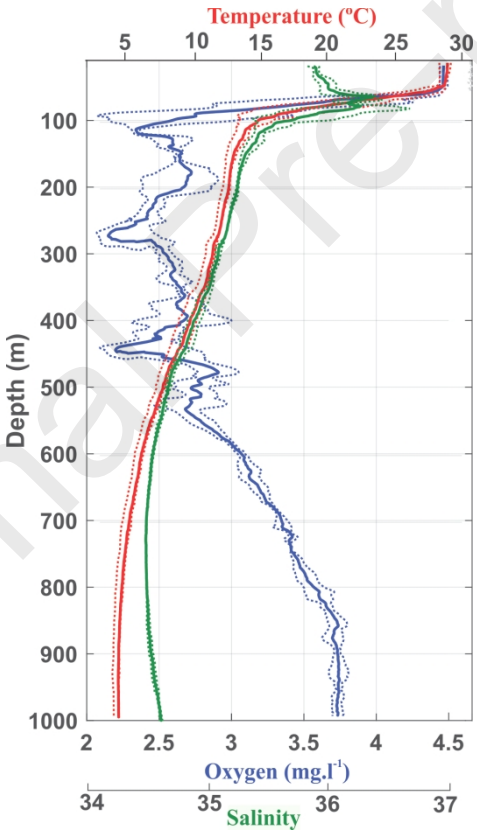

Figure 2. Mean and standard deviation of vertical profiles of temperature (red), salinity (green) and dissolved oxygen (blue) off oceanic islands of the western Tropical Atlantic between April and May 2017.

Hatchetfishes catch composition, abundance and vertical migration

The thirty-one hauls conducted off the northeast Brazilian oceanic islands corresponded to an effort of 695 min and 76 km of trawled distance. A total of 1756 specimens of hatchetfishes have been collected, comprising the following genera and species: *Argyropelecus* (*A. aculeatus, A. affinis*, *A. gigas*, *A. hemigymnus, A. sladeni*), *Sternoptyx* (*S. diaphana*, *S. pseudobscura*, and *S. pseudodiaphana*), and *Valenciennellus* (*V. tripunctulatus*) (Table 2). The most abundant species were *S. diaphana* and *A. affinis*, representing together 85% of individuals by number. *Argyropelecus gigas, S. pseudodiaphana,* and *V. tripunctulatus* were relatively rare, representing together less than 1% of all specimens (Table 2). Overall, standard length of sampled specimens ranged from 2.2 cm (*S. diaphana*) to 8.6 cm (*A. gigas*) (Table 2, Suppl. Material 2).

Argyropelecus aculeatus abundance peaked from 500–600 m at daytime, with its distribution ranging from 300 to 1000 m (Fig. 3). At night, the vertical distribution of this species expanded to 100–1000 m depth and was polymodal, possibly indicating that only part of the population performed diel vertical migration. Temperature range of this species varied from 4.5 to 12°C, with no occurrence above the thermocline or within the zones of minimum oxygen concentrations (Table 2). *Argyropelecus affinis* and *A. sladeni*, presented very similar vertical distribution and migration patterns, with a peak in abundance at 400–500 m during daytime and at 0–100 m at night (Fig. 3). Both species presented a broad polymodal distribution (0–1000 m) and temperature range (5–29°C), being, however, able to swim close/above the upper thermocline layer (50 m). In addition, at daytime, the peak of abundance for both species coincided with the layer of lowest oxygen concentration (1.9 $ml.l^{-1}$) (Table 2). *Argyropelecus hemigymnus* presented two peaks of abundance during daytime (300–400 m, 700–800 m), being found between 4.5–12°C and in oxygen minimum layers (300–400 m) (Fig. 3).

Sternoptyx diaphana was the only species of the genus presenting vertical migration. It was mostly distributed in the range 700–900 m during both day and night, but a small portion of the population was observed migrating up to 100–200 m at night. This species was found between 4.5 and 15°C and showed no clear relationship with oxygen minimum layers. *Sternoptyx pseudobscura* did not present diel vertical migration patterns, being more frequent at 800–1000 m (4.5–5°C). Finally, only a short size range and few specimens of *Argyropelecus gigas*, *Valenciennellus tripunctulatus*, and *S. pseudodiaphana* were sampled, precluding inferences about the vertical distribution or migration of these species (Fig. 3).

Horizontally, *A. aculeatus* and *A. affinis* were collected along the entire latitudinal range, showing the highest values of abundance in the seamount areas (Fig. 4). *Argyropelecus hemigymnus, A. sladeni, Sternoptyx diaphana*, and *S. pseudobscura* were also found in a relatively broad latitudinal range, but highest values of abundance were located at the east side of Fernando de Noronha. *Sternoptyx pseudodiaphana* and *V. tripunctulatus* were only captured on the east side of Fernando de Noronha and off Rocas Atoll. Finally, *Argyropelecus gigas* were sampled at two locations around the seamount areas and one close to Rocas Atoll.

Table 2 – Absolute number of specimens (*n*), frequency of occurrence in relation to overall samples (FO%), depth range, observed migration pattern (AM: asynchronous migrant; NM: non-migrant), standard length [mean ± standard deviation (range)], total weight [mean ± standard deviation (range)] , and temperature (T) and dissolved oxygen (DO) range of hatchetfishes occurrence from oceanic islands and seamounts of the western Tropical Atlantic. *Pattern derived from a very small number of specimens.

Species	***n***	**FO%**	**Depth (m)**	**Migration pattern**	**Standard length (cm)**	**Total weight (g)**	**T (°C)**	**DO (ml.l^{-1})**
Argyropelecus aculeatus	53	26	200–1000	AM	5.2±1.3(3.0–8.2)	6.0±4.8(0.89–20.99)	4.5–12.0	1.9–3.6
Argyropelecus affinis	427	31	50–800	AM	5.2±0.8(2.7–8.2)	2.6±1.3(0.31–6.96)	5.0–29.0	1.9–4.5
Argyropelecus gigas	9	9	600–700	NM*	8.6±0.4(7.8–9.1)	14.2±2.4(10.49–17.00)	5.0–6.0	2.8–2.9
Argyropelecus hemigymnus	49	34	300–1000	NM	2.4±0.4(1.4–3.6)	0.3±0.1(0.10–0.66)	4.5–12.0	1.9–3.6
Argyropelecus sladeni	26	23	50–800	AM	5.1±0.9(3.2–6.6)	3.7±1.7(0.71–7.20)	5.0–29.0	1.9–4.5
Sternoptyx diaphana	1076	43	130–1000	AM	2.2±0.4(1.1–4.3)	0.6±0.4(0.05–4.30)	4.5–15.0	1.9–3.6
Sternoptyx pseudobscura	118	23	520–1000	NM	3.5±1.1(1.3–5.9)	2.4±1.7(0.24–7.60)	4.5–7.0	2.3–3.6
Sternoptyx pseudodiaphana	3	6	850–1000	NM*	4.9±0.8(4.2–5.9)	6.9±2.5(5.29–9.94)	4.5–5.0	2.3–3.6
Valenciennellus tripunctulatus	4	9	400–430	NM*	3.1±0.1(3.1–3.2)	0.2 ±0.0(0.19–0.22)	9.0–9.0	1.9–2.5

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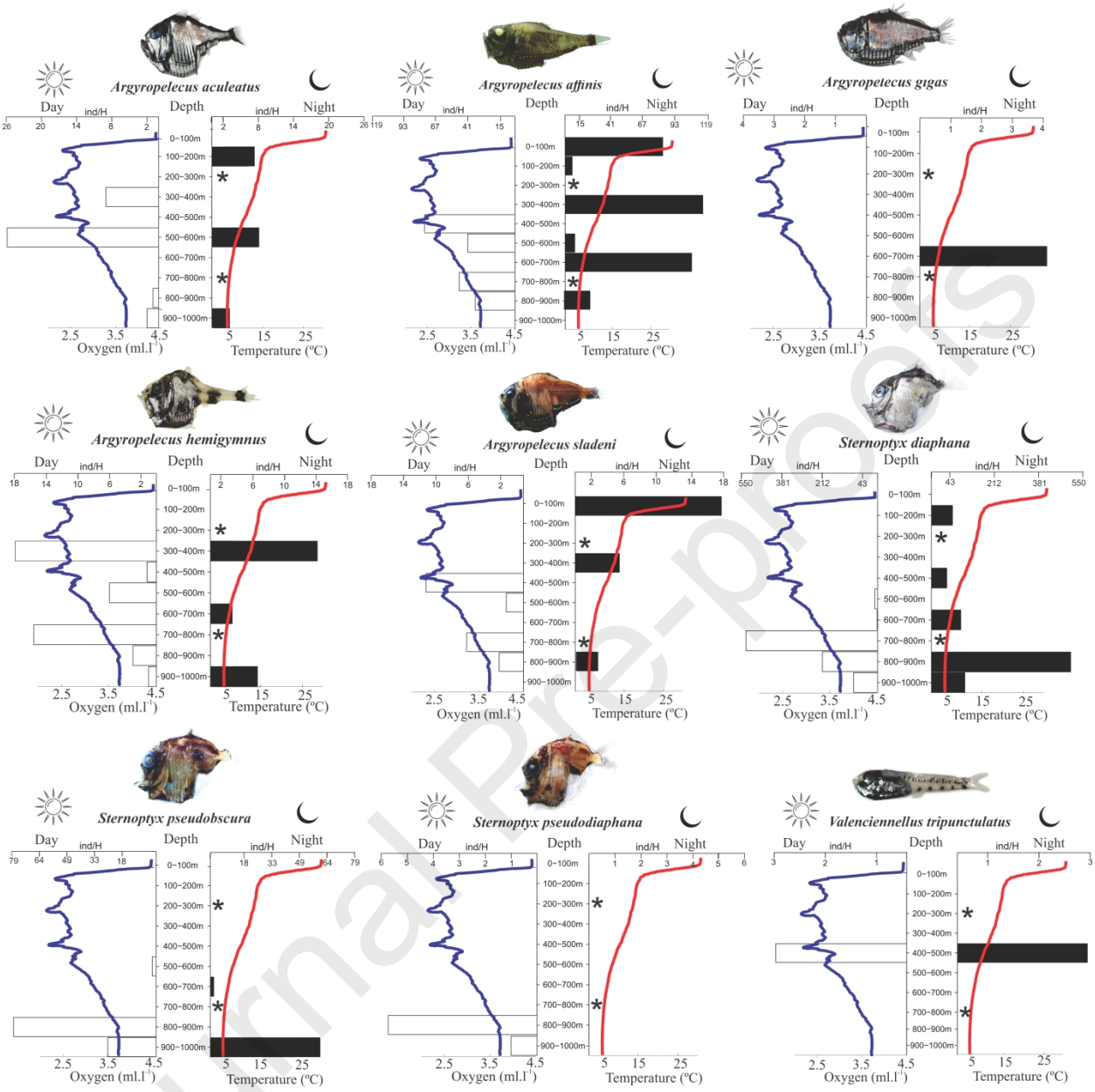

Figure 3. Average relative abundance (individuals.hour^{-1}) per depth strata and day period of hatchetfishes species from oceanic islands and seamounts of the western Tropical Atlantic. Coloured lines represent the average vertical profile of temperature (red) and dissolved oxygen (blue). * Depth strata not sampled.

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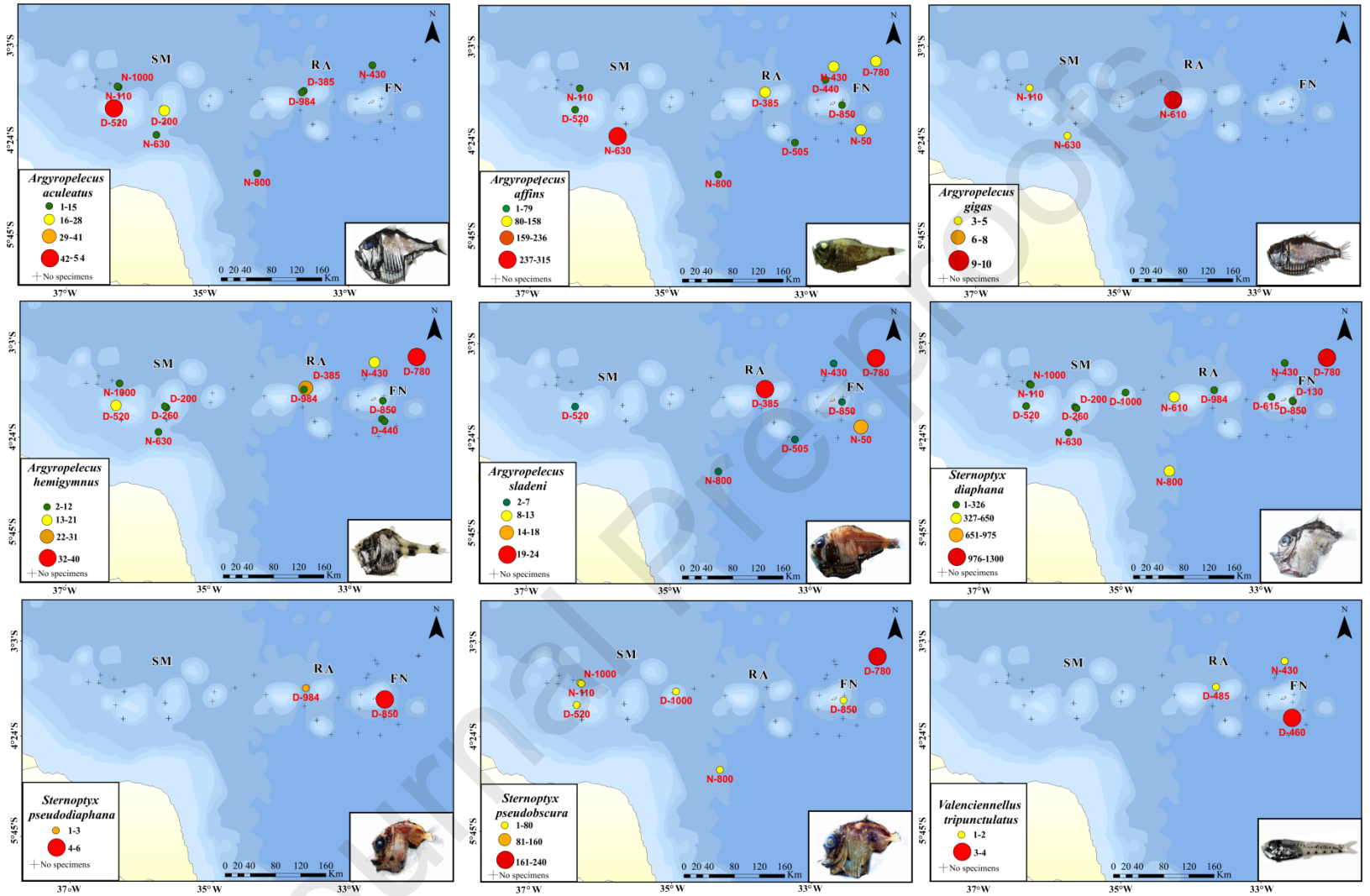

Figure 4. Catch per unit of effort (CPUE; individuals/hour) of hatchetfishes from oceanic islands and seamounts of the western Tropical Atlantic. SM-seamounts; RA–Rocas Atoll; FN–Fernando de Noronha Archipelago; D–day; N–night; Red Numbers–depth.

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Gut content analyses

Among the 361 individuals analysed, 305 (84%) had stomachs with content. Stomachs with content represented 90% and 57% of those sampled at night and at daytime, respectively (Table 3). For *Argyropelecus aculeatus,* 14 stomachs had content and few prey items were identified. All stomachs analysed for this species came from fish caught during the day. *Argyropelecus aculeatus* fed largely on juveniles of hatchetfishes (63%W) and *Euphausia* spp. (36% W), occasionally complementing its diet with amphipods (6% FO) (Fig. 5; Table 3). *Sternoptyx pseudobscura* presented the highest percentage of stomachs with content and high prey diversity. The vacuity index for this species was 2.8% and 0% during the day and at night, respectively. *Sternoptyx pseudobscura* fed predominantly on unidentified teleostei (32% W), *Euphausia* spp. (24%W), and gelatinous organisms belonging to the class Thaliacea (12%W). Likewise, *S. diaphana* presented a high percentage of stomachs with content, high prey diversity, and relatively low vacuity index (17% day; 14% night). This species fed predominantly on *Euphausia* spp. (21% W), Teleostei larvae (17%W), and amphipods (15% W). Finally, *A. affinis* diet was essentially composed of unidentified teleostei (32%W), teleostei larvae (24%W), Gonostomatidae (13%W), and *Euphausia* spp. (9%W). For this species, the vacuity index was 100% and 9% during the day and at night, respectively (Fig. 5; Table 3).

The Costello diagrams of all species showed a high proportion of points positioned towards the lower and upper portion of the vertical y-axis of the graph, indicating a generalist habit with some prime prey groups (euphausiids, Teleostei and Thaliacea). This generalist behaviour, with main prey groups, is confirmed by the intermediary-high values of Levins standardized index for *A. affinis* (B*i*=0.88), *S. pseudobscura* (B*i*=0.69), and *S. diaphana* (Bi=0.47), which indicate a moderate-broad trophic niche breadth. *Argyropelecus aculeatus,* however, presented a restricted niche breadth (Bi=0.29).

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Table 3 - Diet composition of hatchetfishes based on gut content analyses and dietary indexes calculated for each prey item: Standard Length (SL), number of stomachs analysed (N), number of stomachs with content (NSC), abundance percentage (%N), weight percentage (%W), frequency of occurrence (%F), percentage index of relative abundance (%IRI), vacuity index total (%VI), vacuity index day (%VD), vacuity index Night (%VN) , mean and range of prey size (PS, mm).

Prey		*Argyropelecus aculeatus* **SL:** 7.6 ±0.9 **N:**19 **NSC:**14 **VI**:26 V**D**: 26 V**N**: -				*Argyropelecus affinis* **SL:** 5.5 ±0.6 **N:**36 **NSC:**21 **VI**:41 V**D:**9 V**N:**100				*Sternoptyx diaphana* **SL:** 2.3 ±0.4 **N:**216 **NSC:**181 **VI**:16 V**D**:17 V**N**:14				*Sternoptyx pseudobscura* **SL:** 3. ±0.9 **N:**90 **NSC:**89 **VI**:1.1 V**D:2.8** V**N:**0			
Group/taxa		%N	%W	%Fo	PS	%N	%W	%Fo	PS	%N	%W	%Fo	PS	%N	%W	%Fo	PS
Fish	Teleostei larvae	-	-	-	-	14.3	24.1	9.5	12.3	4.5	17.2	1.7	15.0	1.1	2.0	2.5	17.0(9.0–25.0)
	Teleostei	-	-	-	-	9.5	31.1	9.5	13.0	1.3	6.0	4.2	18.0(13.0–22.0)	12.6	32.1	6.2	20.5(19.0–22.0)
	Myctophidae larvae	-	-	-	-	-	-	-	-	0.4	1.8	1.7	-	-	-	-	-
	Gonostomatidae	-	-	-	-	4.8	13.1	4.8	19.0	-	-	-	-	-	-	-	-
	Sternoptychidae	1.1	63.4	5.6	12.6	-	-	-	-	-	-	-	-	-	-	-	-
Crustaceans	Amphipoda	1.1	0.7	5.6	8.2	4.8	6.9	4.8	1.2(0.3–2.2)	30.8	15.4	33.1	3.6(1.5–8.2)	8.2	7.2	11.1	4.0
	Ostracoda	-	-	-	-	19.0	2.8	14.3	4.2(3.3–4.5)	24.5	11.0	20.3	4.3(3.6–5.1)	6.6	2.6	3.7	4.0(3.0–5.0)
	Copepoda	-	-	-	-	-	-	-	-	11.4	2.1	5.1	2.4(1.2–3.0)	1.6	3.2	2.5	-
	Decapoda	-	-	-	-	9.5	7.0	9.5	-	8.2	11.2	9.3	25.0(20.0–28.9)	1.6	3.2	2.5	13.0(10.0–16.0)
	Euphausia spp.	97.7	36.0	38.9	9.2 (8.4–10.2)	9.5	9.0	9.5	9.7 (9.5–10.0)	14.2	20.7	7.7	21.0	34.1	23.7	9.9	10.5(9.0–12.0)
Mollusc	Gastropod	-	-	-	-	-	-	-	-	1.5	0.1	0.8	-	-	-	-	-
	Pteropoda	-	-	-	-	-	-	-	-	1.1	0.4	4.2	7.4	0.5	0.6	1.2	-
	Cephalopod	-	-	-	-	-	-	-	-	0.4	1.0	1.7	-	0.5	6.7	1.2	-
Gelatinous	Thaliacea	-	-	-	-	4.8	2.2	4.8	6.2	0.9	11.2	2.5	-	9.3	12.4	6.2	6.1
	Cnidaria	-	-	-	-	4.8	4.0	9.5	-	0.9	2.0	3.4	-	0.5	7.7	9.9	-

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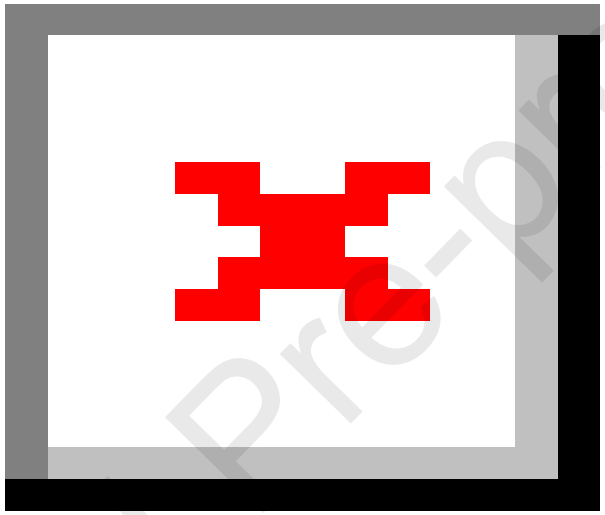

Figure 5. Costello graph showing the relationships between prey-specific abundance and frequency of occurrence (%FO) of prey items in the diet of hatchetfishes. The explanatory Costello diagram and its interpretation of feeding strategy (BPC = between-phenotype component, WPC=within-phenotype component) are shown in the background of the graphs.

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Stable isotope analysis

Mean $\delta^{13}C$ values for hatchetfishes were similar among species, with a difference of only 1‰ separating the most depleted (*S. pseudobscura*: -19.08±0.11‰) and the most enriched species (*A. aculeatus*: -17.98±0.35‰) (Table 4; Fig. 6). However, a much higher range was found between $\delta^{15}N$ mean values, with 3.9‰ separating the most enriched (*A. affinis*: 11.85±0.27‰) and the most depleted species (*A. aculeatus*: 7.95±1.29‰) (Table 4; Fig. 6). Considering prey groups, crustaceans included the most $\delta^{13}C$ and $\delta^{15}N$ enriched taxa, with mean isotopic values raging from 7.31±0.5‰ and -19.47±0.51‰ (*Euphausia* sp.) to 5.88±0.28‰ and -19.03±0.18‰ (*Phronima* sp.) for $\delta^{15}N$ and $\delta^{13}C$ respectively. Gelatinous organisms (Siphonophorae and Thaliacea) showed a wide range of stable isotopic values, ranging from 2.99±0.68‰ (*Pyrosoma altanticum)* and -20.27±0.25‰ (*Soestia zonaria*) to 9.10±0.25‰ and -19.25±0.04‰ (Siphonophorae sp.) for $\delta^{15}N$ and $\delta^{13}C$ respectively. The zooplankton presented mean isotopic values of 3.04±0.60‰ for $\delta^{15}N$ and - 19.45±0.31‰ for $\delta^{13}C$. Lastly, the POM had the mean isotopic values of 2.82±1.19‰ and - 22.41±0.69‰. Based on the TEF assumed for $\delta^{15}N$ (3.15±1.28‰), the zooplankton and Thaliacea species mostly represented primary consumers, while crustaceans, Siphonophorae and fish larvae were secondary consumers. Hatchetfishes are thus a mixing of secondary and tertiary consumers.

Table 4. Number of samples, standard length (cm) and stable isotope values of hatchetfishes (predator), potential prey and POM analysed for isotopic composition.*Lipid corrected species.

Group	Species	Category	*n*	Standard Length mean ± SD	$\delta^{13}C$ (‰) mean ± SD	$\delta^{15}N$ (‰) mean ± SD	C:N mean ± SD
Fish	*Argyropelecus aculeatus*	predator	5	5.80±0.63	- 17.98±0.35	7.95±1.29	3.33± 0.05
	Argyropelecus affinis	predator	10	5.34±0.25	- 18.36±0.13	11.85±0.27	3.31±0.04
	Argyropelecus hemigymnus	predator	10	2.98±0.53	- 18.83±0.23	11.46±0.53	3.40±0.90
	Sternoptyx diaphana	predator	5	2.87±0.22	- 18.88±0.12	10.94±0.50	3.34±0.05
	Sternoptyx pseudobscura	predator	5	4.08±0.38	- 19.08±0.11	10.11±0.20	3.58±0.01
Fish larvae	Teleostei larvae 15–20 mm	potential prey	6	-	- 18.51±0.40	7.16±0.66	3.23±0.01
	Teleostei larvae 5–10 mm	potential prey	10	-	- 19.69±0.11	5.92±0.20	3.24±0.01
Crustaceans	*Euphausia gibboides*	potential prey	6	1.50±0.11	-19.30±1.01	6.93±0.09	3.28±0.04
	Euphausia sp.	potential prey	3	1.43±0.13	-19.47± 0.51	7.31±0.88	3.26±0.09
	Pasiphaeidae sp.	potential prey	3	-	-19.11±0.05	6.06±0.09	3.14±0.02
	Phronima sp.	potential prey	3	-	-19.03±0.18	5.88±0.28	3.60±0.20
Siphonophorae	*Abylopsis tetragona*	potential prey	3	-	-17.84±0.29	7.25±1.00	3.31±0.09
	Siphonophorae sp.	potential prey	3	-	-19.25±0.04	9.10±0.25	3.48±0.11
Thaliacea	*Pyrosoma altanticum**	potential prey	11	-	-18.50±0.20	2.99±0.68	5.34±0.24
	Salpa sp.*	potential prey	6	-	-19.82±0.53	5.47±0.54	4.50±0.77
	Soestia zonaria	potential prey	6	-	-20.27±0.25	3.77±0.58	3.35±0.19
Zooplanckton		potential prey	19	-	-19.45±0.31	3.04±0.60	4.52±0.51
POM		-	17	-	-22.41±0.69	2.82±1.19	-

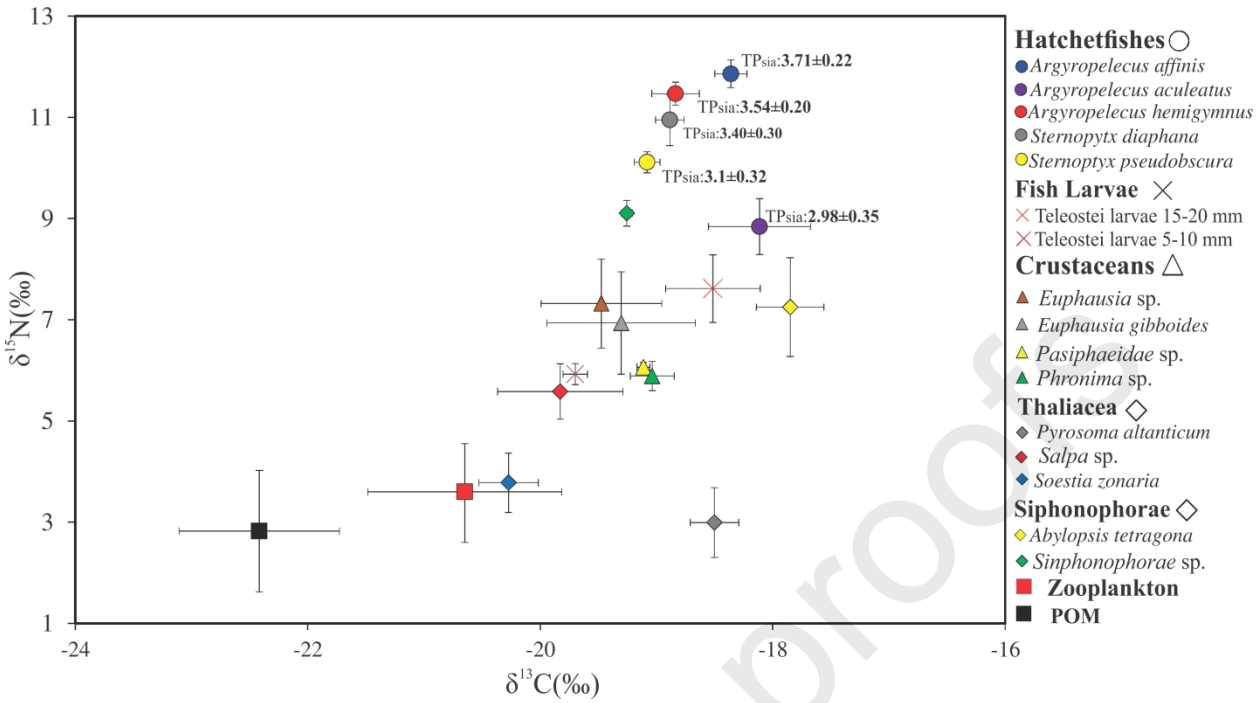

Figure 6 –Stable carbon and nitrogen isotope values of particulate organic matter (POM), zooplankton, gelatinous organisms, crustaceans and hatchetfishes. TPsia– Trophic position based on stable isotope analyses.

The mean trophic levels calculated by isotopic analyses (TP_{sia}) ranged from 2.9±0.3 (*A. aculeatus*) to 3.7±0.2 (*A. affinis*) (Fig. 6). Compared with TP_{sia}, the gut content trophic levels (TP_g) were higher in all cases: *A. aculeatus* (3.8 *vs*. 2.9±0.3), *S. pseudobscura* (3.7 *vs*. 3.1±0.3), *A. affinis* (3.8 *vs*. 3.7±0.2) and *S. diaphana* (3.6 *vs.* 3.4±0.3).

The mixing model is in general agreement with the stomach content analyses (SCA) (Table 5). However, in comparison with SCA, the isotopic analyses showed a much higher contribution (up to 40%) of gelatinous prey (Thaliacea and Siphonophorae). Overall, *Abylopsis tetragona*, *Euphausia gibboides*, *Phronima* sp., and Teleostei larvae 15–20 mm were the most important prey for all species of the genus *Argyropelecus*. For *S. diaphana,* the most important prey was *Soestia zonaria*, *Phronima* sp. and Teleostei larvae 5–10 mm. Lastly, the major prey for *S. pseudobscura* were *Euphausia gibboides, Soestia zonaria*, and Teleostei larvae 5–10 mm.

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Table 5 – Isotopic mixing-model estimates of prey contribution (mean ± SD) for hatchetfishes species from oceanic islands and seamounts of the western Tropical Atlantic.

	Species/prey	*Argyropelecus aculeatus*	*Argyropelecus affinis*	*Argyropelecus hemigymnus*	*Sternoptyx diaphana*	*Sternoptyx pseudobscura*
Crustacean	Zooplanckton (Copepods)	0.25 ± 0.15%	8.56 ± 5.90%	9.98 ± 6.95%	6.36 ± 5.00%	9.65 ± 7.00%
	Euphausia gibboides	14.42 ± 8.17%	14.14 ± 7.00%	13.74 ± 7.86%	10.35 ± 7.00%	13.31 ± 7.23%
	Amphipoda (*Phronima* sp.)	17.07 ± 8.4%	13.24 ± 6.55%	13.68 ± 7.55%	19.68 ± 6.83%	11.99 ± 6.66%
Siphonophorae	*Abylopsis tetragona*	19.47 ± 7.98%	18.40 ± 6.21%	16.55 ± 7.51%	12.35 ± 7.00%	12.90 ± 6.83%
Thaliacea	*Salpa* sp.	13.48 ± 1.00%	8.81 ± 6.16%	10.25 ± 6.68%	12.56 ± 6.82%	11.45 ± 7.00%
	Soestia zonaria	11.95 ± 7.67%	9.83 ± 6.45%	11.14 ± 6.82%	15.79 ± 7.31%	14.47 ± 6.77%
Fish Larvae	Teleostei larvae 15─20 mm	16.26 ± 7.35%	17.64 ± 7.30%	16.34 ± 8.15%	10.49 ± 7.23%	11.12 ± 7.19%
	Teleostei larvae 5─10 mm	7.00 ± 6.00%	9.38 ± 5.33%	8.32 ± 5.00%	13.74 ± 7.36%	15.21 ± 6.13%

DISCUSSION

In the present study, we define functional groups based on the use of the vertical habitat and the trophic ecology to provide a novel vision of hatchetfishes ecology. Indeed, we reveal an important environmental and ecological niche partitioning among groups with further consequences in terms of ecological processes in pelagic ecosystems, including predator-prey relationships. Among other, we show that Hatchetfishes forage more on gelatinous than previously considered, with important consequences for the energetic transfer in the food web but also vertically in the water column. Additionally, for the first time we describe the habitat, vertical migration and trophic ecology of hatchetfishes along the western Tropical Atlantic.

Before interpreting our data some considerations should be made regarding our methodology. First, mesopelagic fishes usually present efficient net avoidance behaviour (Kaartvedt et al., 2012) and, as in all studies based on trawls, the micronekton net we used might not be equally selective for all species. Thus, the diversity of hatchetfishes observed here may not be only a consequence of biogeographic patterns of this group, but also reflects the gear selectivity. Further, despite we took precautions to avoid collection of specimens during the lowering or hoisting (see methodology), our gear did not have an opening or closing mechanism. For that reason, we focused on the major patterns of vertical migration, avoiding a precise quantification of standing stocks in different depth strata. Finally, the trophic analyses might be influenced by sample number, fish size, season, depth, geographic location, taxonomic identification of prey,

and species utilized to run mixing models. Due to the rarity and low sample number of some of the studied species (e.g. *A. gigas*, *S. pseudodiaphana*, and *V. tripunctulatus*), it was not possible to test all these variables in our study. The analyses were conducted by coupling stomachs and mixing several size classes (e.g. juveniles and adults), which may lead to loss of information on ontogenetic variation of both vertical behaviour and trophodynamics patterns (Olivar et al., 2017; Olivar et al., 2018; Silveira et al., 2020). Therefore, we do not aim at exhaustively describe the trophic ecology and vertical behaviour of all hatchetfishes but at providing new valuable information for an important understudied group worldwide.

We captured nine species of hatchetfishes along the oceanic islands of the Western Tropical Atlantic (WTA), being the second most important mesopelagic fish group in terms of biomass and abundance (40% of all specimens collected in micronekton trawls), after myctophids (L. N. Eduardo, unpublished data). Six additional species of Sternoptychidae have also been recorded in the western South Atlantic: *Argyripnus atlanticus*, *Maurolicus stehmanni*, *M. weitzmani*, *Polyipnus clarus*, *P. laternatus*, and *Sonoda megalophthalma* (Lima et al., 2011; Lins Oliveira et al., 2015). Hence, with a total of 15 valid species (our study and the literature), the richness of sternoptychids in the western South Atlantic is similar to those reported in the western (Harold, 2003) and eastern Central Atlantic (Harold and Angelis, 2016) and higher than those observed in the Mediterranean Sea (2 species; Olivar et al., 2012), China (9 species; Wang et al., 2019), California (7 species; Davison et al., 2015), and western Indian Ocean (5 species; Annasawmy et al., 2019). Controversially, the diversity of hatchetfishes along the WTA seems to be lower than that reported in the western Central Pacific (40 species; Harold, 2001), where a high diversification of the genus *Polyipnus* has been reported (22 species). However, in addition to the influence of intrinsic biogeographic differences among locations (e.g. oceanographic conditions and food availability), sampling strategy and effort were different among studies, which may also affect the observed picture of diversity (Eduardo et al., 2018).

At our spatial scale we did not observe clear pattern in the horizontal distribution of Hatchetfishes, but the presence of horizontal patterns could be hampered by the relatively low number of specimens by station. This is also the case of physicochemical conditions since no differences in vertical profiles were observed. Indeed, the study area was recently characterised as homogeneous in terms of thermohaline structure (Assunção et al., *in press*). On the other hand, clear differences were found in term of vertical space occupation and we could define five

functional groups based on the foraging ecology, diel vertical migration, space occupation, and relationship with physico-chemical conditions.

The first functional group (Group 1), composed by *A. affinis* and *A. sladeni*, presented the highest vertical range of distribution from more than 800 m deep to the surface layer, which correspond to a 23°C variation. During daytime these species were mostly distributed at 400-500 m in the layer presenting the minimum oxygen level. Oxygen concentration at this depth (1.9 $ml.l^{-1}$) may be classified as mild hypoxia, which is defined as low oxygen conditions where sensitive species show avoidance reactions (Hofmann et al., 2018). These species were previously reported inhabiting low oxygenated waters (classified as near to hypoxia) of the eastern tropical Atlantic (Olivar et al., 2017). Therefore, during the day, species from Group 1 are likely in search for predator refuge and/or saving energy by resting in a water mass with low temperature and dissolved oxygen concentration (Bertrand et al., 2006; Sutton, 2013). At night, they ascended to epipelagic waters (0–100 m) presumably to feed, following the nightly ascension of zooplankton (Sutton, 2013). Indeed, all stomach of *A. affinis* collected at night had food content, while those sampled at daytime were mostly empty. Additionally, the major prey taxa recovered in the stomachs of this species were fish larvae (13 mm) and ostracods (3.3–4.5 mm), organisms typically found in higher densities in epipelagic waters (especially at night) (Parra et al., 2019; Stefanoudis et al., 2019). The nightly ascension of these species has also been reported in the western Indian Ocean and central equatorial Atlantic (Kinzer and Schulz, 1988; Annasawmy, et al., 2019). However, this pattern was not observed along the eastern tropical Atlantic (Olivar et al., 2018). Additionally, this work is the first reporting *A. affinis* and *A. sladeni* in waters above 100 m. Differences on oceanographic features, food availability, species competition and/or sample methods may explain dissimilarities among locations.

The mixing model based on stable isotope data for species from the Group 1 revealed a relatively high contribution of *Abylopsis tetragona* (19%), a siphonophore that performs daily vertical migration and concentrate above 150 m depth at night (Andersen et al., 1992). *Argyropelecus affinis* also helds the highest trophic position. This could be an adaptation to overcome the high energetically demanding migrating diel behaviour. Finally, as reported for other hatchetfishes here and elsewhere (Kinzer and Schulz, 1985; Sutton and Hopkins, 1996a), this Group, as well as Groups 2 and 4, presented an asynchronous pattern of vertical migration, where the entire population apparently does not respond synchronously to diel variation in the light

intensities. This pattern of migration seems to be regulated by feeding, with only the hungry portion of the population migrating a given day (Sutton and Hopkins, 1996a).

The second functional group (Group 2) was composed by *A. aculeatus*, peaking at 500–600 m during daytime and 100–200 m at night. Whatever the diel period, this species was not found at the layers with minimum oxygen concentration (Fig. 3) or above the thermocline. This restricted vertical pattern (8°C of temperature range) seems to be reflected in the trophic ecology of *A. aculeatus,* since this species that cannot benefit from the epipelagic fish larvae, presented different prey preferences (euphausiids and sternoptychids) and a lower trophic level than the Group 1. *Argyropelecus aculeatus* also presented a relatively high isotopic contribution (20%) of the vertically migrating siphonophore *A. tetragona* (Andersen et al., 1992). A similar vertical distribution for this species was also observed along the eastern Gulf of Mexico and central equatorial Atlantic (Hopkins and Baird, 1985; Kinzer and Schulz, 1985).

The third functional group (Group 3), composed of *A. hemigymnus,* does not perform clear diel vertical migration. Whatever the time it presented a bimodal distribution with two peaks of abundance at 300–400 m and at 700–800 m. Interestingly, no exemplar was collected in shallow layers while studies performed in colder waters have registered a shallower distribution (150 m) (Merrett and Roe, 1974; Andersen et al., 1992). Hence, temperature might be an important factor regulating the upper distribution of this species. Although we did not analyse the stomach content of *A. hemigymnus*, our isotopic analyses and previous studies on stomach contents indicate that this species has a relatively high trophic level (3.5) and forage on euphausiids, copepods, chaetognaths, fish and gelatinous (Hopkins and Baird, 1973; Ikeda et al., 1994).

The fourth functional group (Group 4), composed by *S. diaphana*, presented the peak of abundance at 700–800 (day) and 800–900 (night), presenting no clear relationship with thermocline or minimum oxygen layers. In contrary to other functional groups, only a small part of *S. diaphana* seems to perform daily vertical migrations. Indeed, this species seem to forage both day and night (based on vacuity index). This pattern was found in previous studies, where this species was defined as a generalist predator with limited pursuit capability, whose feeding strategy consists of taking the nearest available prey within a very limited distance (Hopkins and Baird, 1973). In fact, the largest diversity of prey was found for this species. However, *S. diaphana* prey diversity seems vary according to the sampling locations (e.g. Hopkins and Baird, 1973; Sutton

and Hopkins, 1996a; Carmo et al., 2015), probably following the variation of food availability in different sites. As an example, while *S. diaphana* primarily ingests copepods and euphausiids along the Pacific Ocean (Hopkins and Baird, 1973), in the current study, however, among its main prey taxa were amphipods and teleostei larvae, despite euphausiids was also present.

The fifth functional group (Group 5) was composed by *S. pseudobscura*. This species presented no patterns of vertical migration or clear relationship with thermocline and minimum oxygen layers, being mostly found in the deeper waters (< 700 m). This same pattern was observed in the eastern Gulf of Mexico (Hopkins and Baird, 1985). The trophic level of this species was relatively low (3.1), which may be explained by the lower energy costs to feed and lower metabolism due to a colder water habitat. *Sternoptyx pseudobscura* presented a generalist behaviour with preferences on ostracods and euphausiids. As these prey groups usually perform daily vertical migration (Hays, 2003; Lira et al., 2014), it is likely that *S. pseudobscura* has daily feeding behaviour. According to our data, *A. gigas* and *S. pseudodiaphana* may have a similar migration and spatial pattern than *S. pseudobscura.* However, due to our low sample number (n < 9) and restricted sizes (e.g. only large size classes of *A. gigas* were caught) these species were not allocated to any functional group. Additional data and/or different sample methods may complement distribution patterns for these species. The last species, *V. tripunctulatus,* was also rare (6 specimens sampled), presented no pattern of vertical migration, and was only found at the layer of minimum oxygen values (400–500 m). Previous studies reported that, as other hatchetfishes, *V. tripunctulatus* usually feeds on copepods, ostracods, and euphausiids (Hopkins and Baird, 1981; Sutton and Hopkins, 1996a).

Finally, we observed two interesting patterns on mesopelagic trophodynamics. First, a high contribution of teleostei (based on stomach content and isotopes) was noted for all hatchetfishes species included in trophic analyses. This pattern diverges from those find for hatchetfishes in the northern Mid-Atlantic Ridge, eastern Gulf of Mexico, and western Mediterranean Sea (Hopkins and Baird, 1973; Bernal et al., 2015; Carmo et al., 2015). This variability in fish larvae consumption is likely driven by variation in food availability. Indeed, many teleostei larvae were caught during our trawling operations and a recent study addressing zooplankton communities in the same location, highlights a high biovolume of fish larvae on sample size fraction higher than 2000 μm (Figuereido et al., under review). This might be related with presence of islands and sea mounts within the study area. As an example, Fernando de Noronha Island and Rocas Atoll include

several coral reefs and have been referred to as an "oasis of life in an oceanic desert" (Hazin, 1993; CDB, 2014). Second, some of the potential prey included on isotopic analyses presented relatively high mean $\delta^{15}N$ values. For instance, mean $\delta^{15}N$ values for euphausiids (7.3) were higher than those reported on the western Mediterranean (2.8) (Valls et al., 2014). Moreover, *Siphonophorae* sp $\delta^{15}N$ mean (9.1) was relatively high (e.g. greater than those found for *A. aculeatus*). This pattern of high nitrogen values may be associated with differences on species size, feeding behavior, and variations on oceanographic features (e.g. low oxygenated areas facilitates denitrification) and nutrients availability (Montoya, 2008).

Diversity of functional group reveals vertical niche partitioning and multiple ecosystem processes

The deep-sea is usually characterized by a relatively high environmental stability and a decrease of productivity and food availability with depth (Priede, 2017), which should promote the competition for limited resources (Kumar et al., 2017). Even so, mesopelagic ecosystems are one of the richest and diverse environments on earth (Heath et al., 2016). This implies that species are distributed unevenly throughout different multidimensional niches and thereby avoiding competitive exclusion (Drazen and Sutton, 2017; Kumar et al., 2017). Indeed, by defining five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks (Fig. 7), we reveal a possible high resource partitioning. Additionally, these species might have a different feeding tie chronology (Hopkins and Baird, 1985). Hence, hatchetfishes segregate in different ecological groups responding differently to environmental constraints and presenting diverse functional roles. Vertical segregation has also been described for euphausiids, copepods and gelatinous organisms (Siphonophorae and Thaliacea), main prey groups of hatchetfishes (Hu, 1978; Barange, 1990; Andersen et al., 1992; Stefanoudis et al., 2019), but without proposing a multidimentional description of their niche. Identifying, understanding, and considering the multidimensional functional groups structure of the mesopelagic environment is fundamental to answer important ecological questions such as resource use, carbon sequestration and associated role in climate regulation.

Groups 1, 2, and 4 are vertical migrants playing an important role in transporting organic matter between euphotic zone and deeper oceanic layers (Fig. 7). As epipelagic habitants at night, these groups may be more vulnerable to anthropogenic impacts including pollution, fisheries, sound and light pollution, and climate-related changes (e.g. alterations in temperature, pH,

stratification and oxygenation) (Steinberg et al., 2012). On the other hand, Group 5 is composed by a non-migrant species (*S. pseudobscura*) that occur in deeper waters and might be less vulnerable to human impacts. This species (and likely *A. gigas* and *S. pseudodiaphana*) also contributes indirectly to active transport of carbon, once they feed on zooplankton undertaking dial vertical migration (e.g. euphausiids and copepods). Thus, the actively vertically transported organic matter by zooplankton remains in the mesopelagic layer. This process will also sequester carbon and act as a sink in the global carbon cycle (Wang et al., 2019). These non-migrant species also interact with higher trophic levels that migrate to feed at the lower mesopelagic zone (500–1000 m) (Drazen and Sutton, 2017). This relationship also accelerates carbon sequestration in the mesopelagic layer.

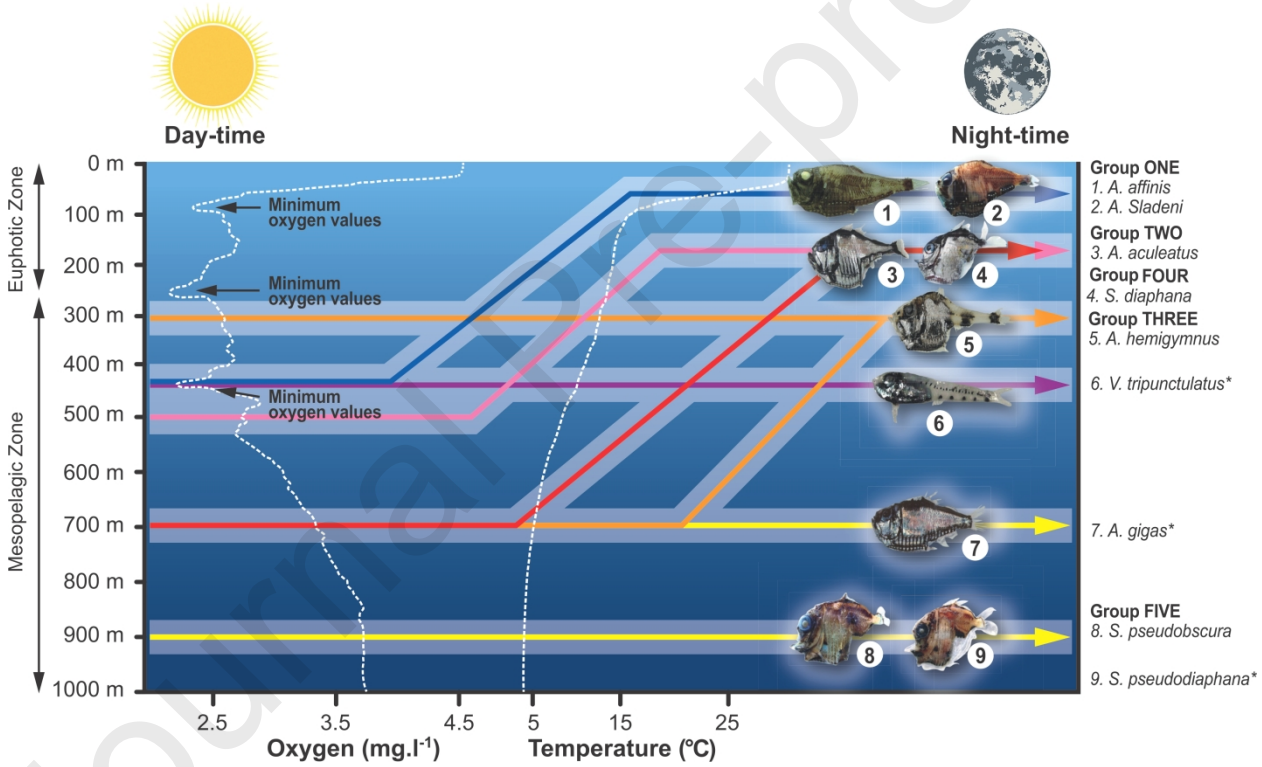

Figure 7 - Conceptual model exhibiting vertical niche partitioning of hatchetfishes from the western Tropical Atlantic. Coloured horizontal lines indicate the peak of abundance of each species at day and upper limit distribution at night. It does not necessarily mean that the species are totally partitioned, but rather that the centres of their distribution are different. The depth layers 200–300 m and 700–800m were not sampled at night. White vertical lines indicate the mean

vertical profile of temperature and dissolved oxygen along the study area. *Migration pattern based on very low-observed species ($n < 10$).

Gelatinous prey as an important underestimated trophic resource

Differences in digestibility may cause certain taxa to stand out more than others because their hard parts resist digestion (Robison, 2004; Carmo et al., 2015). For example, the exoskeletons of crustaceans usually resist digestion and conserve taxonomic characters. Gelatinous prey, on the other hand, are often unidentifiable in the stomachs, especially after chemical preservation (Henschke et al., 2016). As in previous studies on hatchetfishes, gelatinous prey was not significant in any diet index based on our gut content analyses. The mixing model, however, revealed that Thaliacea and Siphonophorae appeared to be important prey groups, as they may contribute up to 40% of the diet of some hatchetfishes. For example, *S. diaphana* and *S. pseudobscura* (mostly found in deeper waters) had a high diet contribution of *Soestia zonaria* (>20%), while *A. affinis*, *A. aculeatus* and *A. hemigymnus* (usually in shallower waters) showed a great contribution of *Abylopsis tetragona*. Indeed, gelatinous prey is a highly diverse group that may constitute up to 90% of the biomass of zooplankton community (Henschke et al., 2016), and zooplankton feeders likely take advantage of that. In the mixing model, we included three abundant gelatinous prey as study case. However, further isotopic information on gelatinous groups (e.g. larvaceans and other salps species) may provide more insightful information on the trophodynamics between hatchetfishes and gelatinous groups. These trophic relationships also reflect on trophic position, which may be overestimated when based solely on stomach contents. TPg were higher than TPsia in all cases. For instance, *A. aculeatus* that presented the highest contribution of gelatinous prey had the highest TPg but the lowest TPsia.

The high importance of gelatinous organisms for mesopelagic species has also been recently highlighted in other studies (McClain-Counts et al., 2017). In the same way, our results indicate that gelatinous organisms (mainly Thaliacea and Siphonophorae) are an important prey group for hatchetfishes. This feature has been historically underestimated due to methodological limitations, hampering the understanding of pelagic food webs, flows of biomass across compartments and, eventually, the influence of fishes in regulating climate in the coming decades (Hidalgo and Browman, 2019; Hopkins and Baird, 1985).

CONCLUSION: GENERAL PATTERNS AND ECOLOGICAL ROLES

Hatchetfishes comprise a diverse and abundant mesopelagic fish group acting as secondary and tertiary consumers. Based on their habitat and trophic ecology, five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks were defined. It revealed a possible high multidimensional resource partitioning (Fig. 7) linked with complex patterns of migration, feeding behaviour, and interactions with the environment. Hatchetfishes are species-specific in feeding habits and important predators on the zooplankton community, especially on amphipods, euphausiids, ostracods, copepods, fish larvae, and chaetognaths. Additionally, hatchetfishes species seems to be differently distributed in relation to minimum oxygen layers and the thermocline. As a result of climate changes, both oceanographic features may be changing in the next decades (Levin et al., 2019), affecting the distribution, feeding and ecological interactions of hatchetfishes.

As vertical migrators, hatchetfishes play a role by transferring material and energy from the subsurface waters to deeper layers, a pathway through which the effects of climate change are mitigated by a carbon transfer to the deep ocean. Moreover, as consumers of Thaliacea and Siphonophorae organisms, these species convert "gelatinous energy" into "fish energy" readably usable by higher trophic levels, including endangered and commercially important species (Ibáñez et al., 2004; Potier et al., 2007; Varghese and Somvanshi, 2016). This is a crucial trophic relationship that has been historically underestimated. As the density of gelatinous organisms might be highly increased upon intense anthropogenic impacts (e.g. eutrophication, overfishing, or climate change) (Henschke et al., 2016), it is likely that these organisms will have even higher importance for hatchetfishes in the Anthropocene. Despite the importance of hatchetfishes, challenges of sampling in the deep-sea hamper a complete assessment of the biodiversity, ecology and ecosystem roles of this group. As humans expand resource extraction and habitat impact in the deep ocean, the understanding of mesopelagic ecosystems, their processes, and functions is mandatory, especially when sustainability is intended to be achieved.

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Highlights

- Hatchetfishes were divided into five functional groups.
- Hatchetfishes have different diet, isotopic composition, and vertical distribution.
- Hatchetfishes are differently distributed in relation to oceanographic features.
- Hatchetfishes forage more on gelatinous organisms than previously thought.
- Hatchetfishes play a key role in the transfer of photoassimilated carbon to deeper waters.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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