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Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic

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Abstract :

Lanternfishes (Myctophidae) are among the most abundant, widespread, and diverse fish groups in the world ocean. They account for a significant part of oceanic fish biomass and play crucial roles in various ecosystem processes, including carbon sequestration and nutrient recycling. However, despite the increasing risks they face (e.g. global warming, plastic pollution, and exploitation of deep-sea resources), many aspects of the lanternfishes ecology still remain poorly known. Here, we investigate the species composition, vertical migration, and trophic ecology of lanternfishes in the Southwestern Tropical Atlantic (SWTA) and the influence of physicochemical factors on their horizontal structuring. We show that lanternfishes are a highly diverse and an abundant fish family of the SWTA, comprising at least 33 species and contributing 40% of all fish collected (in number). We reveal that some of these species may differ in their patterns of prey composition and migratory behaviour, leading to multidimensional niches, underestimated trophic links (e.g. gelatinous organisms), and several mechanisms to avoid competitive exclusion. At least 73% of the lanternfish species reported here seem to migrate to the surface to feed at night. Additionally, they are a central food source for mesopelagic and bathypelagic predators, thereby connecting shallow and deep-sea ecosystems. Finally, we show that the structure of lanternfish assemblages is not strongly affected by environmental conditions analysed here (i.e., throughout the thermohaline structure and current systems), leading to weak horizontal assemblage separation.

Highlights

► Lanternfishes are a highly diverse and abundant fish family of the Southwestern Tropical Atlantic. ► Lanternfishes presented a high variability of prey composition and migratory behaviour. ► At least 73% of lanternfishes observed here vertically migrate to the surface to feed at night. ► Lanternfishes act as a secondary prey for epipelagic predators and a central food source for deep-sea species. ► Lanternfish assemblages are not strongly affected by the thermohaline structure and current systems of the region.

Keywords : Mesopelagic Zone, Seamounts, Oceanic Islands, Stable Isotopes, Deep-sea, Diel Vertical Migration, Niche Partitioning, Trophodynamics.

Introduction

Lanternfishes (Myctophidae) are amongst the most abundant, widespread, and diverse fish groups in the world ocean (Gjøsaeter and Kawaguchi, 1980; Catul et al., 2011). This family includes 254 species that are generally small (mean maximum length of 90 mm) and are dominant in pelagic environments (Poulsen et al., 2013; Priede, 2017; Fricke et al., 2020; Cherel et al., 2020). Most myctophid species migrate vertically to the surface to feed at night and actively transport the carbon they ingest to deep waters during the day (Catul et al., 2011). Moreover, they play a significant role in energetic pathways by consuming zooplankton and providing forage for numerous epipelagic (e.g. tuna, mammals, squids, and diving seabirds) and deep-sea (e.g. viperfish, lancetfish, and moonfish) predators (Sutton and Hopkins, 1996; Cherel et al., 2010; Choy et al., 2013; Rosas-Luis et al., 2014; Eduardo et al., 2020b). These traits are crucial for connecting epipelagic and deep-sea ecosystems and oceanic carbon storage (Catul et al., 2011; Sutton, 2013; Cavan et al., 2019).

Many species of this notable fish group remain poorly known despite facing increasing risks of several kinds (St. John et al., 2016; Martin et al., 2020). While there is a lack of scientific information on the diversity and ecology of lanternfishes in most oceanic basins, the side effects of global warming (Levin et al., 2019), plastic pollution (Davison and Asch, 2011), and exploitation of deep-sea resources are accelerating (Hidalgo and Browman, 2019; Drazen et al., 2020). Further investigations on the ecology and conservation of lanternfishes are recommended. Research has already addressed important aspects of their taxonomy (e.g., Wisner 1976; Nafpaktitis et al., 1977; Hulley, 1992; Martin et al., 2018), distribution (e.g. Braga and Costa, 2014; Olivar et al., 2017; Cherel et al., 2020; Sutton et al., 2020), morphometry (Tuset et al., 2018; Eduardo et al., 2020c; López-Pérez et al., 2020), vertical migration (Watanabe et al., 1999; Olivar et al., 2012, 2017; Annasawmy et al., 2018; Wang et al., 2019) and trophic ecology (e.g. Hudson et al., 2014; Bernal et al., 2015; Olivar et al., 2018; Annasawmy et al., 2020; Czudaj et al., 2020; Contreras et al., 2020; Bode et al., 2021). These studies demonstrated that lanternfishes present a broad range of vertical and feeding behaviours (Hopkins and Gartner, 1992; Watanabe et al., 1999; Catul et al., 2011). However, less attention has been given on how lanternfish species are scattered over different patterns of resource use (niche partitioning), as a means to avoid resource competition.

Understanding niche partitioning among lanternfishes is central to resolving the paradox between ecological theories demonstrating competitive exclusion and the fact that many of these species are morphologically and ecologically similar but do not drive one another to extinction (Schoener, 1974; Hopkins and Gartner, 1992; Finke and Snyder, 2008). Additionally, understanding niche partitioning helps clarify the coexistence of sympatric species and how resource use shapes their contribution to ecological processes (i.e., fluxes of carbon and nutrients; Brandl et al., 2020). Examining the use of resources in the unified framework of niche segregation, however, requires simultaneous information on biophysical and ecological aspects that are usually lacking. As an example, niche segregation typically occurs along three axes: diet (feeding ecology), space (habitat), and time (feeding chronology; Schoener, 1974). For lanternfishes, this information is sparse and restricted to just a few locations (Hopkins and Gartner, 1992; Hopkins et al., 1996; Hopkins and Sutton, 1998; Catul et al., 2011). Moreover, most previous studies addressing the trophodynamics of these species did not include predators and were based solely on stomach contents. Further approaches (e.g., stable isotopes, fatty acids, and genetics) should be included to provide a comprehensive picture of resource uses. Additional data on the trophic ecology of lanternfishes would help to clarify their trophic links and thus niche differentiation.

Another key point in the study of lanternfishes is how physical drivers shape their diversity and community structure. Variations in temperature, oxygen, and upper circulation processes play important roles in the ecology and movement of deep-pelagic species (Bertrand et al., 2010; Proud et al., 2017; Boswell et al., 2020). However, only a few studies, focusing on restricted locations, have been performed addressing the influence of these oceanographic variables in lanternfishes (Olivar et al., 2017; Milligan and Sutton, 2020). Oceanic islands and seamounts of the Southwestern Tropical Atlantic (SWTA), for instance, are interesting locations to study the influence of physical drivers on biological communities, as they sustain distinctive biodiversity and are considered as Ecologically or Biologically Significant Marine Areas (EBSAs; CBD, 2014). Additionally, this region includes different biogeographic provinces with contrasting thermohaline features, current systems, and water-mass properties, leading to diversification of biodiversity and ecosystems (Bourlès et al., 1999; Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021; Tosetto et al., 2021).

We conducted an integrative study of the ecology of lanternfishes, taking advantage of a comprehensive dataset collected in the SWTA. First, we assessed their vertical migration and trophic ecology by coupling information on their abundance, vertical distribution, habitat (oxygen, temperature and fluorescence), and trophodynamics. We did this by exploring the main trophic links of lanternfishes through the analysis of stable isotopes (carbon and nitrogen) of size fractions of zooplankton, gelatinous organisms, crustaceans, fish larvae, and epipelagic and deep-sea fish predators. Second, we assessed the importance of the influence of oceanographic features on lanternfishes by comparing their species composition, spatial distribution, and assemblage structuring under two different physicochemical scenarios. Finally, we discuss the functional roles of lanternfishes.

Material and Methods

Study area

The study area is located off northeastern Brazil and includes the Fernando de Noronha Archipelago (03°50′S, 32°25′W), Rocas Atoll (03°52′S, 33°49′W), and seamounts of the Fernando de Noronha Ridge (Fig. 1). This region is divided into two areas with significant differences in currents and thermohaline structures (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021). The first region, here named as Area 1, is mainly located along the Brazilian continental slope and encompasses the seamounts off northern Rio Grande do Norte State (Fig. 1). This area is under the western boundary current system, characterised by the North Brazil Undercurrent (NBUC) and the North Brazil Current (NBC) (Dossa et al., 2021). The second region, here named as Area 2, encompasses the Fernando de Noronha Archipelago, Rocas Atoll, and seamounts around and between these islands (Fig. 1). This second area is mainly under the influence of the central branch of the South Equatorial Current (cSEC) at the surface and South Equatorial Undercurrent (SEUC) at the subsurface (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021).

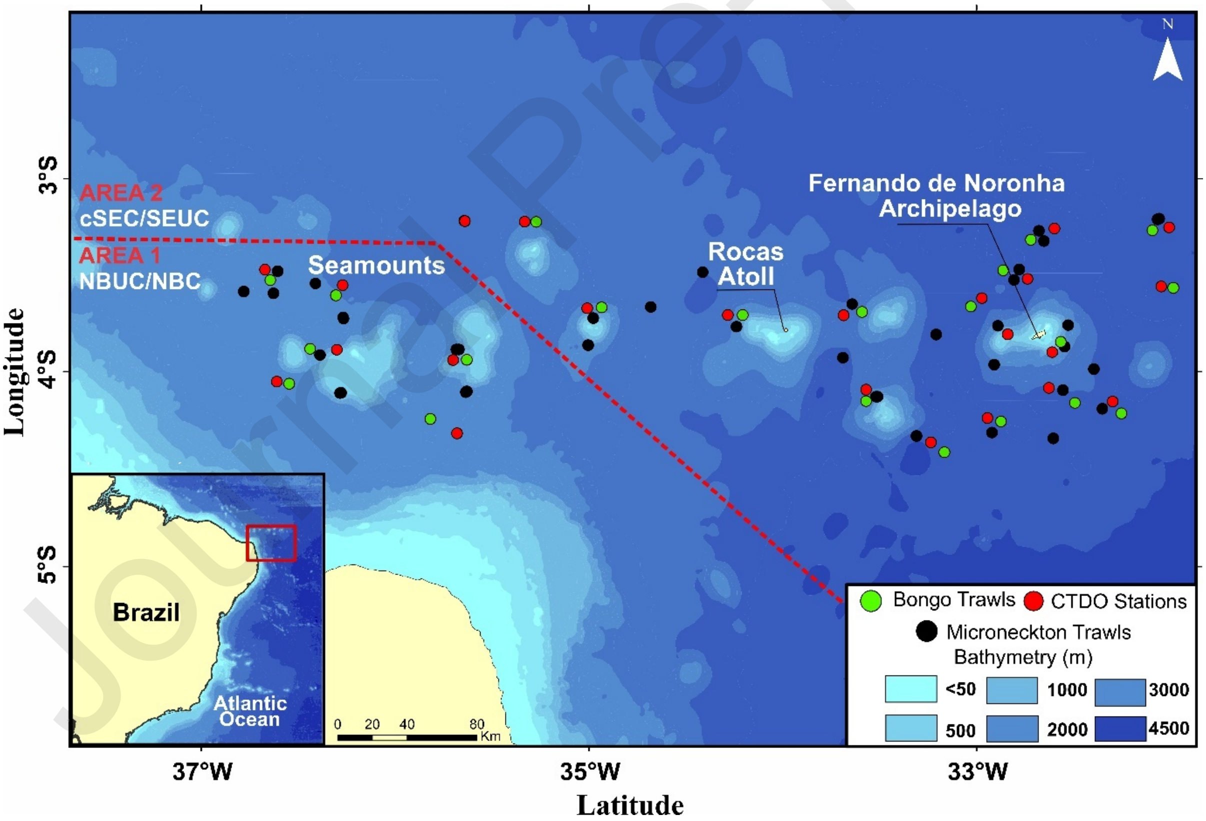

Figure 1. Study area (Fernando de Noronha Ridge) with CTD, bongo, and micronekton-trawl sampling stations. Red dashed line divides the study area according to current systems: cSEC– central branch of the South Equatorial Current; SEUC– South Equatorial Undercurrent; NBC– North Brazil Current; NBUC– North Brazil Undercurrent (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021) .

Collection of specimens and data

Specimens and data were collected off northeastern Brazil during a research cruise (Acoustics along the BRAzilian COaSt 2; ABRACOS2) carried out from 9th April to 6th May 2017, aboard the French RV *Antea* (Bertrand, 2017). Sampling of mesopelagic fishes, crustaceans, and gelatinous organisms was conducted during day and night at 33 stations using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm, estimated opening area: 120 m^2) from 10 to 1,113 m depth (Fig. 1; Eduardo et al., 2020a). Targeted depth was defined for each tow according to the presence of acoustic scattering layers or patches as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120, and 200 kHz. Each trawl was performed for about 30 min at 2–3 knots. Tow duration was considered to begin at the moment of the arrival of the net at the pre-set depth and last until the lift-off time, recorded with a SCANMAR system (Eduardo et al., 2020a). The net geometry was also monitored, using SCANMAR sensors to give headline height, depth, and distance of wings and doors to ensure the net was opened and therefore fishing. As the trawl was not fitted with an opening or closing mechanism, the collection of specimens during the lowering and hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed; see Eduardo et al. (2020a,b) for more information on field procedures.

Captured organisms were identified, sorted, and frozen (-20°C) 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, myctophids were identified according to Nafpaktitis et al. (1977), measured (to the nearest 0.1 cm for standard length, SL), and weighed (to the nearest 0.01 g for total weight, TW). Voucher specimens were deposited in the Fish Collection of the “Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro” (NUPEM/UFRJ).

Particulate organic matter (POM) was sampled at 22 stations by filtering seawater from the maximum fluorescence depth through pre-combusted GF/F filters (47 mm), followed by oven-drying for 36 hours (40°C). Zooplankton samples were collected using bongo nets (four nets with mesh sizes of 64, 120, 300, and 500 µm) that were towed from 200 m depth up to the surface at 22 stations (Fig. 1). After collection, these samples were pooled, sieved, and divided into six size fractions (<100; 100–200; 200–500; 500–1000; 1000–2000; >2000 µm). Potential epipelagic fish predators were collected with hook-and-line around the Fernando de Noronha Archipelago using a sport fishing boat.

Hydrographic profiles of conductivity, temperature, oxygen, and fluorescence with depth were collected using a CTDO SeaBird 911+ at 22 stations (Fig. 2). The upper (UTD) and lower (LTD) thermocline depths were defined using the criteria of Assunção et al. (2020). The UTD is the depth at which the temperature gradient is equal to 0.1°C/m, while the LTD corresponds to the last depth below the UTD where the Brunt Väisälä frequency (N^2, the buoyancy frequency squared) is up to four orders of magnitude ($N^2 \geq 10^{-4}$).

Catch composition and patterns of dominance for lanternfishes

The relative index of lanternfish abundance (catch per unit effort, CPUE) was calculated considering the number of specimens of a given species captured per hour in each trawl. Trawls were classified considering the period (day/night), depth strata (10–1,000 m, intervals of 100 m), and defined Area (Area 1 or Area 2). Except for the layers 200–300 m and 700–800 m at night, where no aggregations of organisms were observed by acoustics, all depth strata were sampled at least once (Table 1; Eduardo et al., 2020a). Day was defined as the time from one hour after sunrise to one hour before sunset, and night as the time from one hour after sunset to one hour before sunrise (Eduardo et al., 2020a). Dawn or dusk samples were thus discarded when studying day/night vertical distributions.

Table 1. Number of trawls per depth strata (m) and period of the day.

Depth Strata	Day	Night
10–100	3	3
100–200	3	1
200–300	3	–
300–400	1	1
400–500	3	1
500–600	1	1
600–700	1	1
700–800	2	–
800–900	1	1
900–1000	2	2

Patterns of dominance were obtained by calculating a relative importance index (RII; Garcia et al., 2006; Eduardo et al., 2018) based on the frequency of occurrence (%FO; the number of occurrences of a species divided by the total number of trawls) and CPUE in each pre-established area (Area 1, Area 2, and both areas combined). Species showing %FO > average %FO were considered frequent fishes, whereas those with %FO < average %FO were considered rare. A similar method was applied to %CPUE, resulting in highly abundant (%CPUE > average %CPUE) and scarce (%CPUE < average %CPUE) categories. Finally, based on these criteria, species were classified into four groups of relative importance: (1) highly abundant and frequent, (2) highly abundant and rare, (3) scarce and frequent, and (4) scarce and rare. Species were considered dominant when classified in the first of these categories.

Vertical migration and distribution

Vertical distribution patterns were investigated for the 18 species with a sample number higher than 30. Patterns of migration were categorised for each species based on their observed vertical distribution range, peak abundance during the day, and shallowest distribution at night. Despite the thermohaline structure and stratification at shallow layers (0–300 m) being different between Areas 1 and 2, the thermal gradients between surface and deeper layers were alike. Therefore, for the vertical migration analyses, the samples from the two areas were aggregated, allowing for an increase in the sample size and robustness of our analyses.

Trophic ecology

To investigate trophodynamics, stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were conducted on nine dominant lanternfishes (based on the RII indexes) and their most probable groups of prey (17) and predators (10) (Table 2). Potential prey and predators of myctophids were selected based on the literature and locally abundant species (Kinzer and Schulz, 1988; Bernal et al., 2015; Battaglia et al., 2016; McClain-Counts et al., 2017; ABRACOS unpubl. data). While the stable isotopes of carbon undergo small levels of fractionation (0.5–1‰) during trophic transfer and can be used to define energy pathways from primary producers to consumers, nitrogen stable isotopes undergo larger levels of fractionation (2–4‰) and can be used to make estimations of trophic position and food chain length (Post, 2002).

All isotopic information was obtained from individuals collected in Area 2, where a greater number of species was captured. For each fish and crustacean, white muscular tissue was dissected and cleaned with distilled water to remove exogenous material such as carapaces, scales, and bones. The entire body without the head was used for fish larvae, while entire specimens were used for gelatinous organisms. Zooplankton was divided into six size fractions (see Table 2). For reference values of organic matter, stable isotopes of particulate organic matter (POM) were also included. 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. Stable isotope analysis results for $\delta^{13}C$ and $\delta^{15}N$ were derived from the relation of the isotopic value from the sample and a known standard according to:

$$\delta^{13}C \text{ or } \delta^{15}N = [(Rsample/Rstandard) - 1] \times 10^{3}$$

in which R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N. Accuracy of the measurement was checked by repeated analyses of internal samples of acetanilide.

As differing lipid contents can bias the interpretation of $\delta^{13}C$ values, we explored the potential lipid bias by using percentage elemental by mass C:N ratios and the relationship between C:N (i.e., lipid content) and $\delta^{13}C$. Since samples were not treated to remove lipids before analysis to prevent loss of material, the few prey groups that showed C:N dynamics consistent with high lipid content (C:N > 3.5) were normalised using the equation for aquatic animals provided by Post et al. (2007):

$$\Delta\delta^{13}C = -3.32 + 0.99 \times C:N$$

where $\Delta\delta^{13}C$ is the change in $\delta^{13}C$ caused by lipids and C:N is the carbon-to-nitrogen ratio (by mass) of the sample. Further information on the isotopic sample treatments is provided in Eduardo et al. (2020a).

Table 2. Lanternfishes and their potential prey and predator groups considered in carbon and nitrogen stable isotope analyses. Species were classified into deep-sea or epipelagic predator according to Harrison (2002) and Sutton et al. (2020).

Group	Category	Species		
Myctophidae	–	*Diaphus brachycephalus*	*Diaphus dumerilii*	*Diaphus fragilis*
	–	*Diaphus mollis*	*Diaphus perspicillatus*	*Electrona risso*
	–	*Hygophum taaningi*	*Lampanyctus nobilis*	*Lepidophanes guentheri*
Stomiidae	Deep-sea predator	*Borostomias elucens*	*Chauliodus sloani*	*Malacosteus niger*
Scorpaenidae	Deep-sea predator	*Ectreposebastes imus*	–	–
Sphyraenidae	Epipelagic predator	*Sphyraena barracuda*	–	–
Coryphaenidae	Epipelagic predator	*Coryphaena hippurus*	–	–
Carangidae	Epipelagic predator	*Elagatis bipinnulata*	–	–
Scombridae	Epipelagic predator	*Acanthocybium solandri*	*Katsuwonus pelamis*	*Thunnus albacares*
Fish larvae	Prey	Teleostei larvae 5–10 mm	Teleostei larvae 15–20 mm	–
Crustacea	Prey	*Euphausia gibboides*	*Euphausia* sp.	*Phronima* sp.
		Pasiphaeidae sp.	–	–
Siphonophorae	Prey	*Abylopsis tetragona*	Siphonophorae sp.	–
Thaliacea	Prey	*Pyrosoma atlanticum*	*Salpa* sp.	*Soestia zonaria*
Zooplankton	Prey	Zoo A (<100 µm)	Zoo B (100–200 µm)	Zoo C (200–500 µm)
		Zoo D (500–1000 µm)	Zoo E (1000–2000 µm)	Zoo F (>2000 µm)

The relationships between lanternfishes and their potential prey and predators were analysed through a bi-dimensional plot of carbon and nitrogen. Additionally, for each group (Table 2), we included corrected standard ellipse areas (SEAc), which allow inferences of isotopic niches (Jackson et al., 2011). The standard ellipses area (SEA) represents the mean core of the isotopic niche and covers approximately 40% of the available data (Jackson et al., 2011). This method is less sensitive to sample sizes than other conventional methods (e.g., convex hull area). To address biases that can emerge from comparisons drawn between groups of unequal sample sizes (i.e., underestimation of the population's SEA for small samples), we used a corrected standard ellipse area (SEAc) that maintains the same geometric features but with a slight increase in the ellipse area for smaller sample sizes (Jackson et al., 2011).

The relative contribution of each potential prey to the lanternfishes diet was estimated through the Bayesian mixing model MixSIAR (Stock and Semmens, 2013). This analysis can provide estimations of source or prey contributions when tissue- and species-specific discrimination factors are fixed (Caut et al., 2008). As diet determination from MixSIAR is closely related to the sources utilised in this analysis, the potential dietary endpoints applicable to lanternfishes were chosen based on a literature review and by picking the most abundant local species (Kinzer and Schulz, 1988; Bernal et al., 2015; Battaglia et al., 2016; McClain-Counts et al., 2017; ABRACOS, unpubl. data). The following prey groups were included: i) Zooplankton (200–500 µm), ii) *Abylopsis tetragona* (Siphonophorae), iii) *Euphausia gibboides* (Euphausiacea), iv) *Phronima* sp. (Amphipoda), v) *Salpa* sp. (Thaliacea); vi) *Soestia zonaria* (Thaliacea), vii) Teleostei larvae 5−10 mm, and viii) Teleostei larvae 15−20 mm. Trophic discrimination factors for mesopelagic fishes are poorly known. However, based on previous studies (Valls et al., 2014; Richards et al., 2019), we ran mixing models using discrimination factors of 3.15‰ ± 1.28‰ and 0.97‰ ± 1.08‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Cherel et al., 2008; Ménard et al., 2014; Eduardo et al., 2020a).

All statistical analyses were performed with R version 4.0.3, using the packages *SIBER* (Stable Isotope Bayesian Ellipses in R; version 2.1.6; Jackson et al., 2011) and *SIAR* (Stable Isotope Analysis in R; version 4.2; Parnell et al., 2010) for the estimation of isotopic SEAc and mixing models, respectively.

Horizontal distribution and assemblage structure

Fish assemblage structure and horizontal distribution were analysed through a complete linkage agglomerative clustering by calculating a Bray-Curtis similarity matrix based on log-transformed (log (x+1)) fish relative abundance. The non-parametric permutation procedure ANOSIM (Analysis of Similarity; Clarke and Warwick, 2001) was applied to test for differences between physicochemical scenarios (Area 1 *vs*. Area 2), period (day *vs*. night), and depth (epipelagic 0–200 m; upper mesopelagic 200–500 m; lower mesopelagic 500–1000 m). The similarity percentage routine (SIMPER) was applied to determine the species contribution to the similarity within a group of sampled sites and the dissimilarity between groups. The species that cumulatively contributed to over 70% of dissimilarity between groups were classified as discriminating species (Eduardo et al., 2018). All statistical analyses were performed with R version 4.0.3, using the *Vegan* package (version 2.5-7; Oksanen et al., 2019).

Results

Oceanographic data

The thermal difference between the surface (29°C) and 1000 m depth (4°C) was 25°C in both areas defined for the study. Area 1 was characterised by a weak thermal stratification, a deep thermocline (lower limit at 166 m), and a fluorescence maximum peaking at 100 m (Fig. 2). In this area, the water column was evenly oxygenated (Fig. 2) and subsurface salinity was high (>36.5). In contrast, Area 2 was characterised by a strong thermal stratification with a well-marked and shallow thermocline (60–120 m). This area encompassed a shallow fluorescence peak (60 m) and a layer with low oxygen concentration (minimum ~2.5 ml.l^{-1}) ranging between the base of the thermocline down to ~600 m depth.

In both Area 1 and Area 2, the mixed layer was formed by warm Tropical Surface Water (Fig. 3; TSW; $\sigma\theta > 24.5$ kg.m^{-3}; Stramma and England, 1999; Gasparin et al., 2014). Below, at the upper part of the thermocline, lies the Subtropical Underwater (SUW), which has the strongest core in Area 1 (Fig. 3). In the subsurface layer, below the thermocline and down to 500 m, lies the South Atlantic Central Water (SACW; $24.5 < \sigma\theta < 27$ kg.m^{-3}; Stramma and England, 1999). The oxygen minimum observed in Area 2 was located at the SACW level, indicating a weak renewal in this region (Stramma and Schott, 1999). Finally, the isopycnal $\sigma\theta = 27.1$ kg. m^{-3} marks the transition between SACW and Antarctic Intermediate Water (AAIW). The latter is characterised by a local salinity minimum of ~34.5 and a local oxygen maximum of ~3–3.5 ml.l^{-1}.

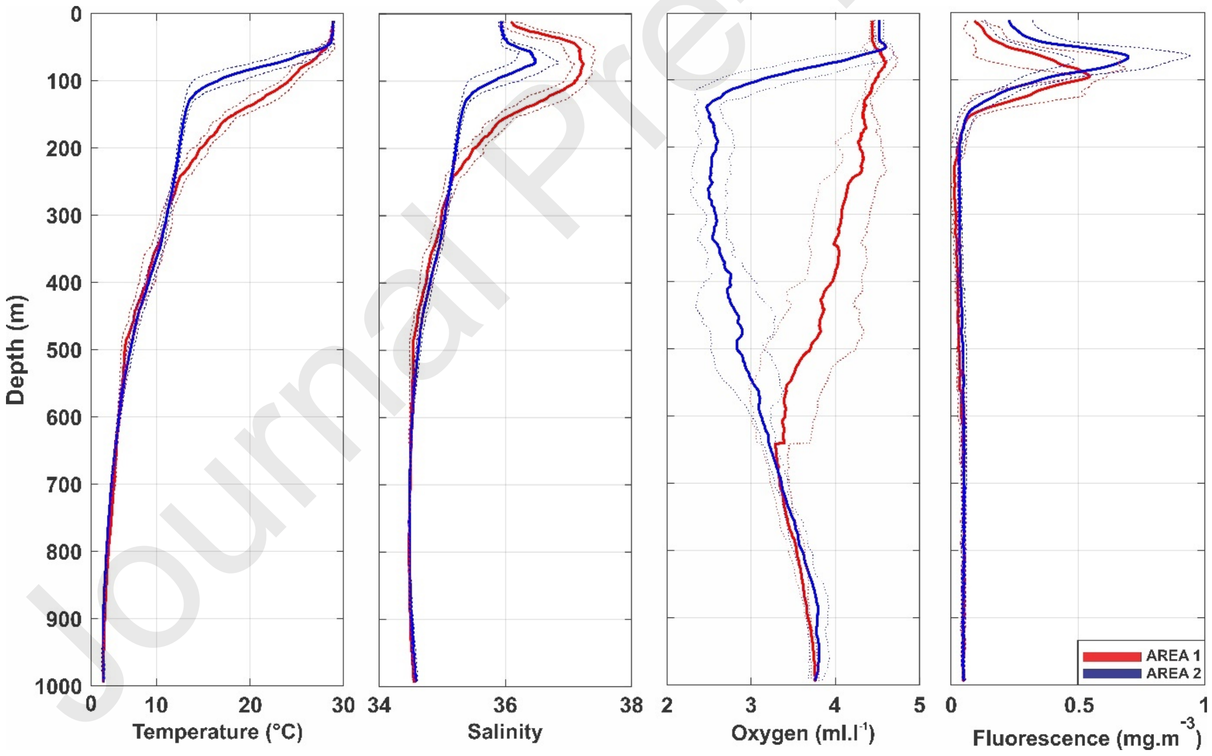

Figure 2. Mean and standard deviation of vertical profiles of temperature, salinity, dissolved oxygen, and fluorescence for the two areas identified along the Fernando de Noronha Ridge, Southwestern Tropical Atlantic, in April–May 2017.

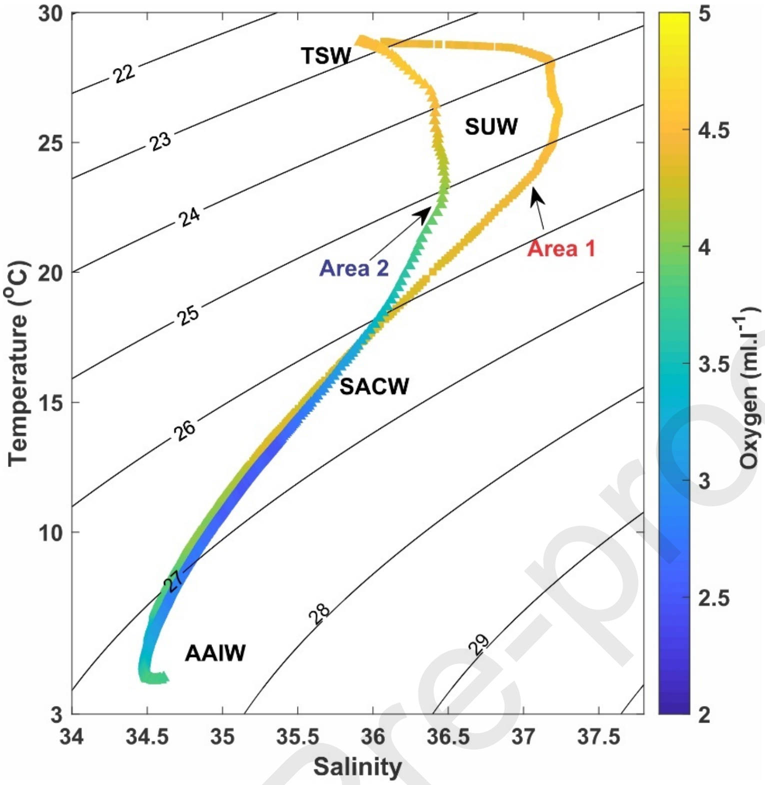

Figure 3. Potential temperature-salinity (TS) diagram showing water-masses diagnosis from the two areas in the SWTA. TSW– Tropical Surface Water; SUW– Subtropical Underwater; SACW– South Atlantic Central Water; AAIW– Antarctic Intermediate Water. The colours of TS-diagram show the oxygen concentration. Isopycnals (kg.m-3) are represented by the transversal black lines along the TS-diagram.

Catch composition and dominance patterns of lanternfishes

The 2,268 individuals collected were distributed across 13 genera and 33 species (Table 3). The genus *Diaphus* had the highest numbers of species and specimens (11 species, 60% of the total number of individuals), followed by *Bolinichthys* (4 species; 14% of the total) and *Lampanyctus* (5 species; 6% of the total). The remaining 20% of the total number of specimens were composed by the genera *Benthosema*, *Ceratoscopelus*, *Dasyscopelus*, *Electrona*, *Hygophum*, *Lampadena*, *Lepidophanes*, *Myctophum*, *Notoscopelus*, and *Taaningichthys*. Considering the relative importance index (RII), the following seven species (66% of the total number of individuals) were classified as highly abundant or frequent: *Bolinichthys distofax, Diaphus brachycephalus, D. perspicillatus, D. splendidus, Electrona risso, Hygophum taaningi*, and *Lampanyctus nobilis* (Table 3). The other species were highly abundant and rare (8 species, 22% of sampled individuals) or scarce and rare (18 species, 12% of sampled individuals). The standard length and wet weight for all species collected are given in Table 3 and Supplementary Material 1. The size of specimens ranged from 0.9 cm (*D. brachycephalus*) to 17.8 cm SL (*Lampanyctus lineatus*).

Vertical migration and distribution

From the 18 species included in vertical migration analyses, 16 are likely performing diel vertical migration. Only *B. distofax* and *E. risso* did not show any clear indication of vertical migration. Overall, all migrant species presented a polymodal vertical distribution, indicating that the species occupy more than one depth stratum and/or possibly only part of the population perform diel vertical migration. Additionally, from the 15 species not included in these analyses (low sample numbers), at least eight were found at epipelagic waters at night, indicating a likely nocturnal vertical ascension. Therefore, at least 73% (24 species) of the collected lanternfishes migrate to epipelagic layers at night. Given the limitations of the gear (see Discussion) and the inherent variability of lanternfish vertical distribution and movements, interpretation of migration patterns was not straightforward. However, since some robust patterns emerged, we pictured four general patterns of species vertical partitioning based on the peaks of abundance during the day and the shallowest distribution at night.

Pattern 1: This pattern was observed for *B. photothorax*, *Ceratoscopelus warmingii*, *Dasyscopelus asper, Diaphus fragilis*, *D. garmani*, *D. lucidus*, *D. perspicillatus*, *D. splendidus*, *H. taaningi*, *Lampadena luminosa*, *L. nobilis*, *L. tenuiformes*, and *Lepidophanes guentheri.* In the day, these species peak and/or were predominant in lower mesopelagic waters (500–1000 m). At night, their distribution expands up to surface waters, with part of the population migrating to the layer 0–100 m (Fig. 4; Table 3). At night, most of the species allocated in this pattern peaked at the upper mesopelagic waters (*C. warmingii*, *D. asper*, *D. fragilis*, *D. garmani*, *D. lucidus*, *D. perspicillatus*, *D. splendidus*, *H. taaningi*, *L. luminosa, L. nobilis,* and *L. guentheri*), while two others at lower mesopelagic waters (*B. photothorax* and *L. tenuiformes*).

Pattern 2: This pattern was observed for *D. brachycephalus*, *D. dumerilii*, and *D. mollis.* In the day, these species peak and/or are predominant in upper mesopelagic waters (200–500 m). At night, their distribution expands up to surface waters, with part of the population migrating to the layer 0–100 m (Fig. 4; Table 3). At night, *D. dumerilii*, and *D. mollis* peaked at the upper mesopelagic waters, while *D. brachycephalus* at lower mesopelagic waters. For both patterns 1 and 2, the thermal and oxygen concentration amplitude ranges were 4–29°C and 2.5–4.4 $ml.l^{-1}$, respectively. All these species can cross the thermocline and migrate at night to depths encompassing the fluorescence maximum.

Pattern 3: This pattern was observed for *B. distofax*. Like the species of pattern 1, the peak of abundance of this species is observed in lower mesopelagic waters during the day (700–800 m). However, no clear pattern of diel vertical ascension is observed (Fig. 4; Table 3). At night, this species also peaked at lower mesopelagic waters, but at 600-700 m. The thermal and oxygen concentration amplitudes ranges were 4.0–7.0°C and 3.5–3.7 ml.l-1, respectively. *Bolinichthys distofax* does not seem to cross the thermocline or migrate to depths close to the fluorescence maximum.

Pattern 4: This pattern was observed for *E. risso*. Like the species of pattern 2, the peak of abundance is in upper mesopelagic waters during the day (300–400 m). However, this species seems to have a bimodal distribution and also present a peak at 700–800 m. No clear pattern of diel vertical ascension is observed (Fig. 4; Table 3). At night, this species also peaked at upper mesopelagic waters, but at 400–500 m. The thermal and oxygen concentration amplitudes ranges were 4.0–9.0°C and 2.8–3.7 ml.l^{-1}, respectively. This species does not seem to cross the thermocline or migrate to depths close to the fluorescence maximum.

Table 3. Number of collected specimens (N), frequency of occurrence to overall samples (FO%), standard length (mean and range), total wet weight (mean and range), depth (maximum and minimum depth at which the specimens were captured), vertical migration (VM) pattern (●: migrant; ○: non-migrant; – migration pattern not established due to small sample number), temperature (T), dissolved oxygen (O), and relative importance index (1: highly abundant and frequent; 2: highly abundant and rare; 3: scarce and frequent; 4: scarce and rare). Temperature and oxygen information correspond to the values found in the maximum and minimum depth at which the specimens were captured.

Species	N	FO%	SL (cm)	TW (g)	Depth (m)	VM	T (°C)	O (ml.l^{-1})	Relative importance index		
									Area 1	Area 2	Total
Benthosema suborbitale (Gilbert, 1913)	13	8	2.4 (1.7–3.0)	1.6 (0.6–2.5)	50–440	–	28–8	4.6–3.1	–	4	4
Bolinichthys distofax Johnson, 1975	85	23	6.2 (3.2–9.1)	4.1 (0.3–10.1)	430–1000	○	7–4	3.5–3.7	1	3	1
Bolinichthys photothorax (Parr, 1928)	54	26	5.3 (2.2–6.7)	2.1 (0.1–3.6)	95–1000	●	25–4	4.5–2.5	3	1	2
Bolinichthys supralateralis (Parr, 1928)	4	8	7.5 (5.0–9.2)	6.5 (1.6–11.0)	95–1000	–	25–4	4.5–2.5	4	4	4
Ceratoscopelus warmingii (Lütken, 1892)	33	36	5.2 (1.8–7.4)	2.0 (0.1–6.2)	50–1000	●	28–4	4.6–2.5	3	3	2
Dasyscopelus asper (Richardson, 1845)	50	21	5.9 (1.4–7.5)	3.7 (0.3–5.1)	25–1000	●	29–4	4.4–2.5	4	3	2
Dasyscopelus obtusirostre (Tåning, 1928)	16	15	6.5 (2.5–8.4)	4.8 (1.5–7.8)	50–800	–	28–5	4.6–2.5	–	4	4
Dasyscopelus selenops (Tåning 1928)	2	3	5.4 (5.0–5.9)	2.2 (2.2–2.3)	95–680	–	25–5	4.5–2.5	–	4	4
Diaphus bertelseni Nafpaktitis, 1966	2	6	8.4 (7.4–9.4)	8.0 (6.7–9.3)	90–385	–	25–9	4.5–3.2	–	4	4
Diaphus brachycephalus Tåning, 1928	454	49	3.8 (0.9–5.4)	1.3 (0.1–2.8)	50–1000	●	28–4	4.6–2.5	1	1	1
Diaphus dumerilii (Bleeker, 1856)	52	31	4.5 (2.9–5.9)	1.3 (0.3–9.3)	65–1000	●	26–4	4.3–2.5	3	1	2
Diaphus fragilis Tåning, 1928	131	36	4.7 (1.4–8.6)	1.9 (0.1–11.7)	65–1000	●	26–4	4.3–2.5	3	3	2
Diaphus garmani Gilbert, 1906	111	15	4.0 (2.5–4.9)	0.7 (0.1–1.3)	65–780	●	26–5	4.3–2.5	4	4	4
Diaphus holti Tåning, 1918	1	3	2.0 (2.0–2.0)	0.1 (0.1–0.1)	385–385	–	9–9	3.2–3.2	–	4	4
Diaphus lucidus (Goode & Bean, 1896)	43	18	7.6 (3.1–9.6)	5.2 (0.3–9.7)	25–800	●	29–5	4.4–2.5	4	4	4
Diaphus mollis Tåning, 1928	41	28	4.8 (2.2–5.9)	1.7 (1.0–2.9)	95–1000	●	25–4	4.5–2.5	3	3	2
Diaphus perspicillatus (Ogilby, 1898)	272	36	4.9 (1.8–6.9)	2.0 (1.0–4.6)	65–1000	●	26–4	4.3–2.5	1	1	1
Diaphus problematicus Parr, 1928	3	5	6.8 (5.2–7.7)	4.0 (1.7–5.8)	430–800	–	8–5	3.1–3.5	4	4	4
Diaphus splendidus (Brauer, 1904)	240	36	5.3 (2.0–8.5)	1.9 (1.0–6.6)	90–1000	●	25–4	4.5–2.5	1	3	1
Electrona risso (Cocco, 1829)	72	36	6.6 (5.0–8.1)	7.4 (3.2–12.4)	385–1000	○	9–4	2.8–3.7	1	1	1
Hygophum hygomii (Lütken, 1892)	2	3	5.3 (5.2–5.4)	2.2 (1.9–2.4)	1000–1000	–	4–4	3.7–3.7	4	–	4
Hygophum macrochir (Günther, 1864)	13	15	4.5 (3.4–5.4)	1.4 (0.4–2.3)	50–800	–	28–5	4.6–2.5	4	4	4
Hygophum taaningi Becker, 1965	104	26	5.1 (2.6–6.6)	1.9 (0.2–3.1)	90–1000	●	20–4	3.7–2.5	1	1	1
Lampadena luminosa (Garman, 1899)	30	8	2.8 (1.9–5.1)	0.5 (0.3–1.4)	90–1000	●	20–4	3.7–2.5	–	4	4
Lampanyctus alatus Goode & Bean, 1896	2	3	3.7 (3.7–3.8)	0.3 (0.2–0.3)	430–430	–	8–8	3.1–3.1	–	4	4
Lampanyctus festivus Tåning, 1928	4	3	8.7 (5.6–12.0)	6.8 (1.3–13.7)	95–95	–	25–25	4.5–4.5	–	4	4
Lampanyctus lineatus Tåning, 1928	4	8	16.5(15.2–17.8)	23.6 (17.2–29.4)	430–1000	–	8–4	3.1–3.7	–	4	4
Lampanyctus nobilis (Tåning, 1928)	279	41	5.7 (1.9–12.1)	1.8 (1.0–13.3)	50–1000	●	28–4	4.6–2.5	1	1	1
Lampanyctus tenuiformes (Brauer, 1906)	22	21	11.1 (4.4–13.6)	16.4 (4.0–46.0)	25–1000	●	29–4	4.4–2.5	2	3	2
Lepidophanes guentheri (Goode & Bean, 1896)	109	41	4.7 (2.2–6.2)	0.9 (0.7–1.7)	25–1000	●	29–4	4.4–2.5	3	1	2
Myctophum nitidulum Garman, 1899	8	13	5.5 (3.8–6.5)	2.5 (0.3–4.1)	50–850	–	28–5	4.6–2.5	4	4	4
Notoscopelus resplendens (Richardson, 1845)	2	5	7.5 (6.7–8.4)	3.1 (2.7–3.5)	430–780	–	8–5	3.1–3.5	–	4	4
Taaningichthys bathyphilus (Tåning, 1928)	10	10	6.2 (5.4–7.1)	1.8 (1.1–2.8)	780–1000	–	5–4	3.5–3.7	4	4	4

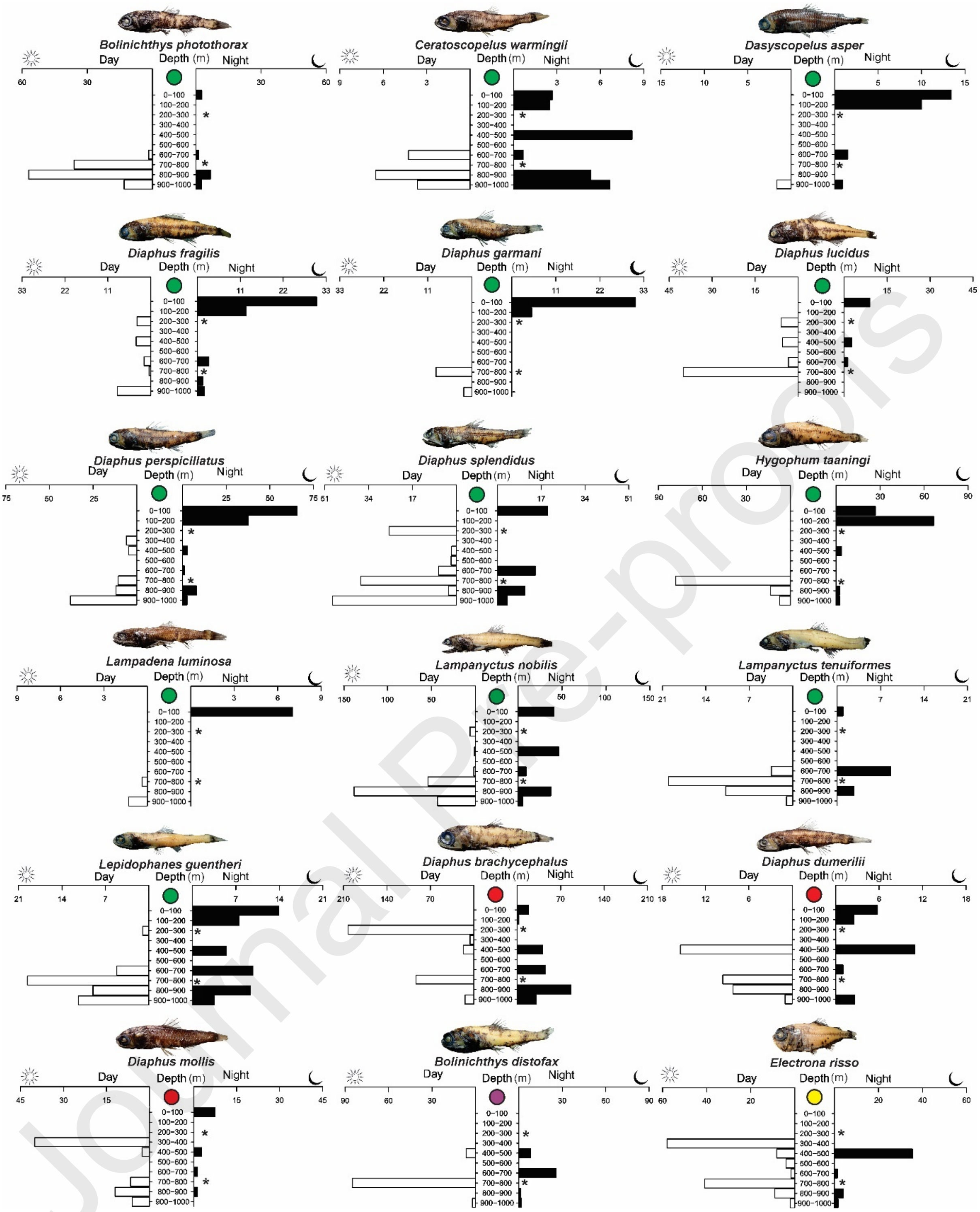

Figure 4. Average of lanternfishes relative abundance (individuals.hour^{-1}) per depth strata and diel period. Circles indicate patterns of diel vertical migration: Pattern 1 (green); Pattern 2 (red); Pattern 3 (purple); Pattern 4 (yellow). *Depth strata not sampled.

Trophic ecology

Mean $\delta^{13}C$ for lanternfishes ranged from -19.20 ± 0.21‰ to -18.19 ± 0.23‰, with a difference of 1‰ separating the most depleted (*D. mollis*) from the most enriched (*H. taaningi*) (Fig 5; Supp. Material 2). When considering mean $\delta^{15}N$ values, 2.4‰ separated the most enriched (*E. risso*: 11.41 ± 0.13‰) and depleted (*D. dumerilii*: 8.99 ± 1.15‰) species (Fig. 5; Supp. Material 2).

Likewise, within lanternfish prey groups, $\delta^{13}C$ values mostly ranged between -19‰ and -20‰, while a broader isotopic range was found for $\delta^{15}N$ values. Amongst lanternfishes prey, gelatinous organisms presented the highest range of $\delta^{15}N$, varying from 2.99 ± 0.68‰ (*Pyrosoma atlanticum*) to 9.10 ± 0.25‰ (Siphonophorae sp.). Crustaceans ranged from 5.9 ± 0.28‰ (*Phronima* sp.) to 7.31 ± 0.50‰ (*Euphausia* sp.). Lastly, $\delta^{15}N$ values of zooplankton ranged from 1.87 ± 0.76‰ (10–20 µm) to 4.94 ± 0.40‰ (>200 µm) (Supp. Material 2). Within predators, the similarities in $\delta^{13}C$ and differences in $\delta^{15}N$ values between the deep-sea species (mean $\delta^{13}C$: -18.7‰; $\delta^{15}N$: 11.85‰) and lanternfishes ($\delta^{13}C$: -18.5‰; $\delta^{15}N$:10.1‰) may indicates a tight trophic linkage between them. The difference in $\delta^{13}C$ and similarity of $\delta^{15}N$ values between the epipelagic predators ($\delta^{13}C$: -16.25; $\delta^{15}N$:10.5‰) and lanternfishes, however, probably indicates a weaker trophic linkage (Fig. 5).

Overall, given the set of prey included in our mixing model, fish larvae (Teleostei larvae 5–10 m and Teleostei larvae 15–20 mm), euphausiids (*E. gibboides*), and gelatinous organisms (*A. tetragona*, *Salpa* sp., and *S. zonaria*) seem to have the highest contribution for lanternfishes. Additionally, based on mixing models, it appears that lanternfishes have different patterns of prey composition. For instance, three patterns could be observed (Fig. 6). The first Trophic Pattern clusters *D. dumerilii*, *D. mollis*, *E. risso*, *H. taaningi*, and *L. nobilis*, and is characterised by a high contribution of Teleostei larvae 15–20 mm (19–23%), *A. tetragona* (18–21%), and *E. gibboides* (14–17%). The second Trophic Pattern clusters *D. fragilis* and *L. guentheri* and is characterised by a high contribution of Teleostei larvae 5–10 mm (20–22%), *S. zonaria* (14–15%), *Salpa* sp. (12%), and *E. gibboides* (12–13%; Fig. 6). Finally, the third Trophic Pattern clusters *D. brachycephalus* and *D. perspicillatus* and is characterised by a high contribution of Teleostei larvae 5–10 mm (19–24%), Teleostei larvae 15–20 mm (15–18%), and *E. gibboides* (13–16%).

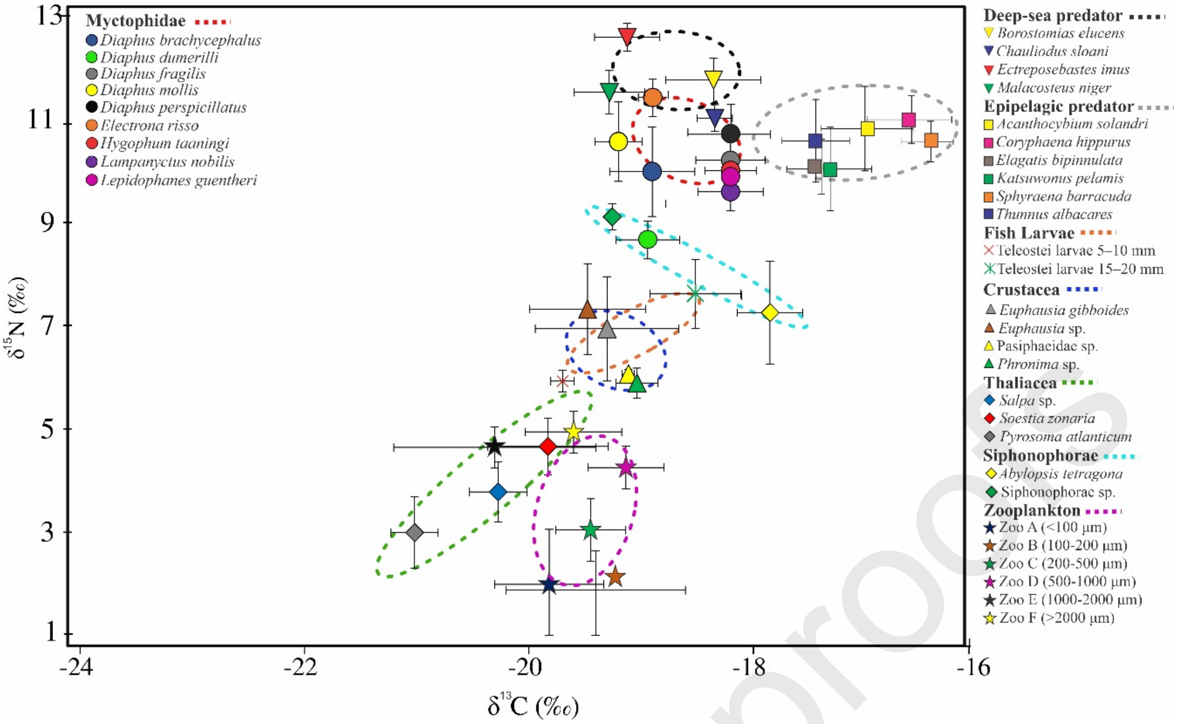

Figure 5. Stable carbon and nitrogen isotope mean values of lanternfishes and their potential prey and predator from Fernando de Noronha Ridge, Southwestern Tropical Atlantic. Dashed lines represent the corrected standard ellipses area (SEAc) for each group. Black lines indicate the standard deviation of the $\delta^{13}C$ (horizontal) and ($\delta^{15}N$ vertical) ratios.

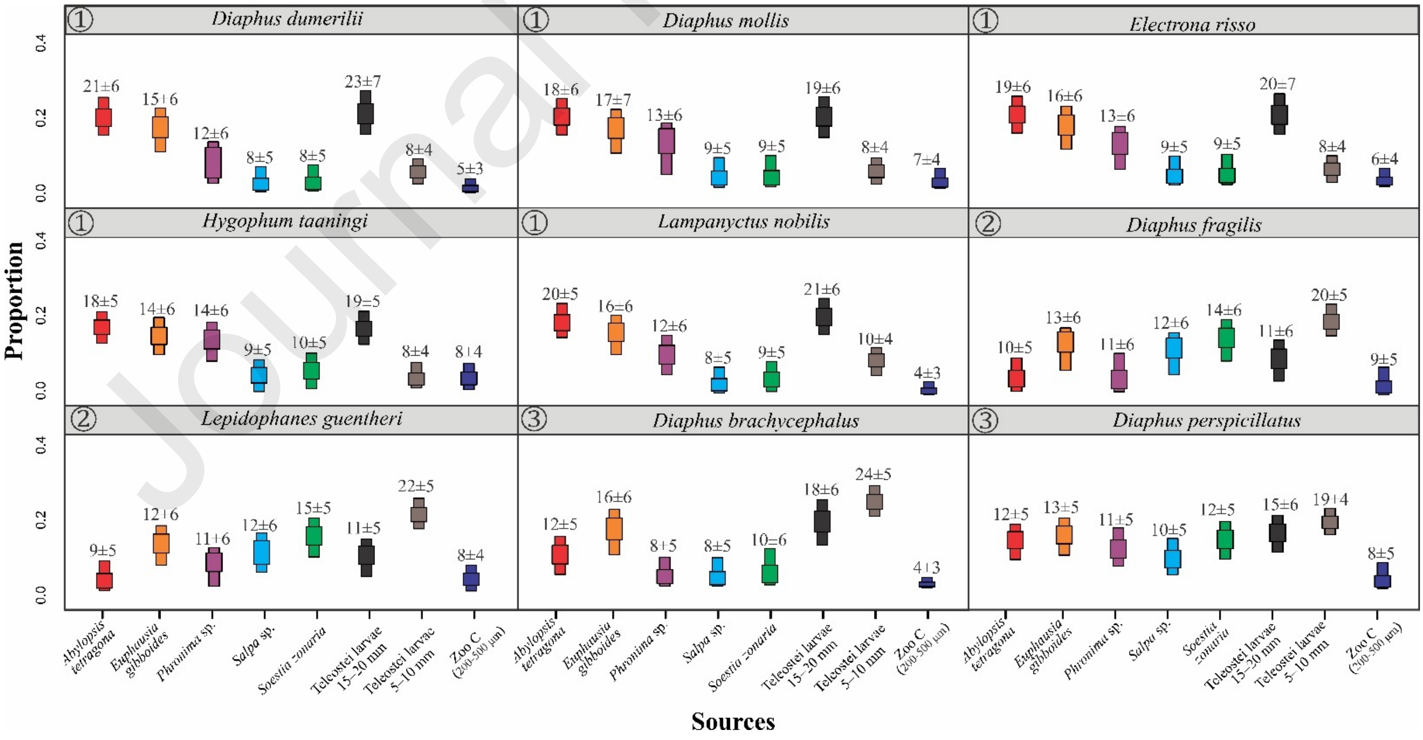

Figure 6. Estimated contribution in % (proportion; mean ± SD) based on stable isotope mixing model of potential prey to the diet of lanternfishes from Fernando de Noronha Ridge, Southwestern Tropical Atlantic. Coloured boxes represent 25% and 50% quantiles. Numbers in the circles indicate trophic patterns. The trophic patterns do not reflect a fine-scale description of the diet of lanternfishes but rather demonstrate the likely trophic segregation among species and the expected most important prey groups given the organism included in the mixing model (see Discussion).

Horizontal distribution and assemblage structure

Most of the species (22; 67% of the total) were found in Area 1 and 2 (Figs. 7 and 8). Nevertheless, ten species (30%) were only captured in Area 2 (*Benthosema suborbitale*, *D. obtusirostre*, *Dasyscopelus selenops*, *Diaphus bertelseni*, *D. holti*, *Lampadena luminosa*, *Lampanyctus alatus*, *L. festivus*, *L. lineatus*, and *Notoscopelus resplendens*), and one species (3%) was only captured in Area 1 (*Hygophum hygomii*; Fig. 8). Absence of species from one of the areas, however, was probably associated with the sample size, as all these species were also classified as scarce and rare.

Cluster analysis based on the log-transformed dataset revealed five major assemblages at the resemblance level of 25% (Fig. 9), showing a rather weak but significant difference in the species composition among zones (Areas 1 and 2; ANOSIM $R = 0.28$; $p < 0.01$) and depth categories (Epipelagic 0–200 m, Upper mesopelagic 200−500 m, and Lower mesopelagic 500–1000 m; $R = 0.15$; $p < 0.01$). No significant differences in horizontal distribution were found between diel periods (Day and Night; $R < 0.01$; $p > 0.01$). **Assemblage A** (Area 2, 0–200 m) included only samples collected in epipelagic waters of Area 2 (Fig. 9). **Assemblage B** (Area 1, 200–1000 m) encompassed samples collected in mesopelagic waters (upper and lower) of Area 1 (Fig. 9). **Assemblage C** (Areas 1 and 2, 0–200m) encompassed samples collected in both Areas but in epipelagic waters only (Fig. 9). Samples from **Assemblage D** (Area 2, 300–500 m) were restricted to upper mesopelagic waters of Area 2 (Fig. 9). All samples from **Assemblage E** (Area 2, 600–1000 m) were collected in lower mesopelagic waters of Area 2 (Fig. 9). Overall, all assemblages were composed by many species (see the full list at Supp. Material 3) and characterized through differences on abundance plus presence/absence of lanternfishes included in the analyses. Additionally, many species occupied more than one assemblage (Supp. Material 3).

SIMPER analysis showed high dissimilarity levels between assemblages, ranging from 62% to 92% (Supp. Material 3). The following species were considered as consolidating species (cumulatively contributing over 70% to the dissimilarity between assemblages): *B. distofax*, *B. photothorax*, *D. asper, D. brachycephalus*, *D. dumerilii*, *D. mollis*, *D. perspicillatus*, *D. splendidus*, *E. risso*, *H. taaningi*, *L. nobilis*, and *L. guentheri*. Dissimilarities between assemblages were primarily driven by differences in the average abundance of species rather than presence/absence. As an example, the high abundances of *D. brachycephalus* in Assemblage A and *L. nobilis* in

Assemblage D contributed to as much as 53% of the total dissimilarities between assemblages (e.g., A–D). However, the absence of *D. perspicillatus* from Assemblages A and B was important for dissimilarities of the interactions B–C (30% contribution) and A–C (24%) (Supp. Material 3)

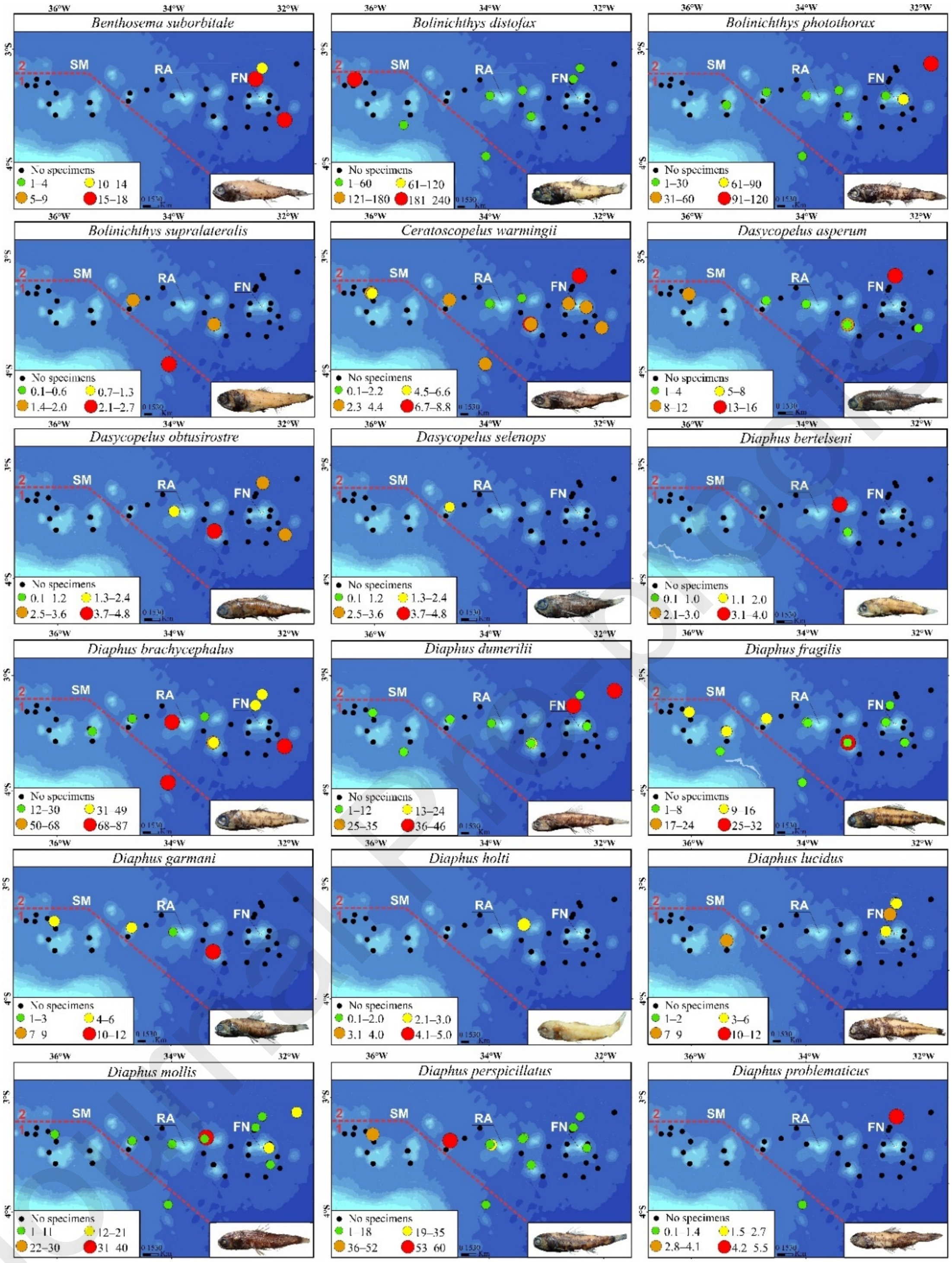

Figure 7. Catch per unit of effort (CPUE; individuals/hour) of lanternfishes from islands and seamounts of the Fernando de Noronha Ridge, Southwestern Tropical Atlantic – Part I. Dashed red line shows the limit between Area 1 and Area 2 (adapted from Assunção et al., 2020). SM – Seamounts; RA –Rocas Atoll; FN – Fernando de Noronha Archipelago. Numbers outside the maps indicate the latitude (x axes) and longitude (y axes). The colors of the circles indicate the variation in CPUE values, changing from lowest to highest in the following order: green, yellow, orange, and red.

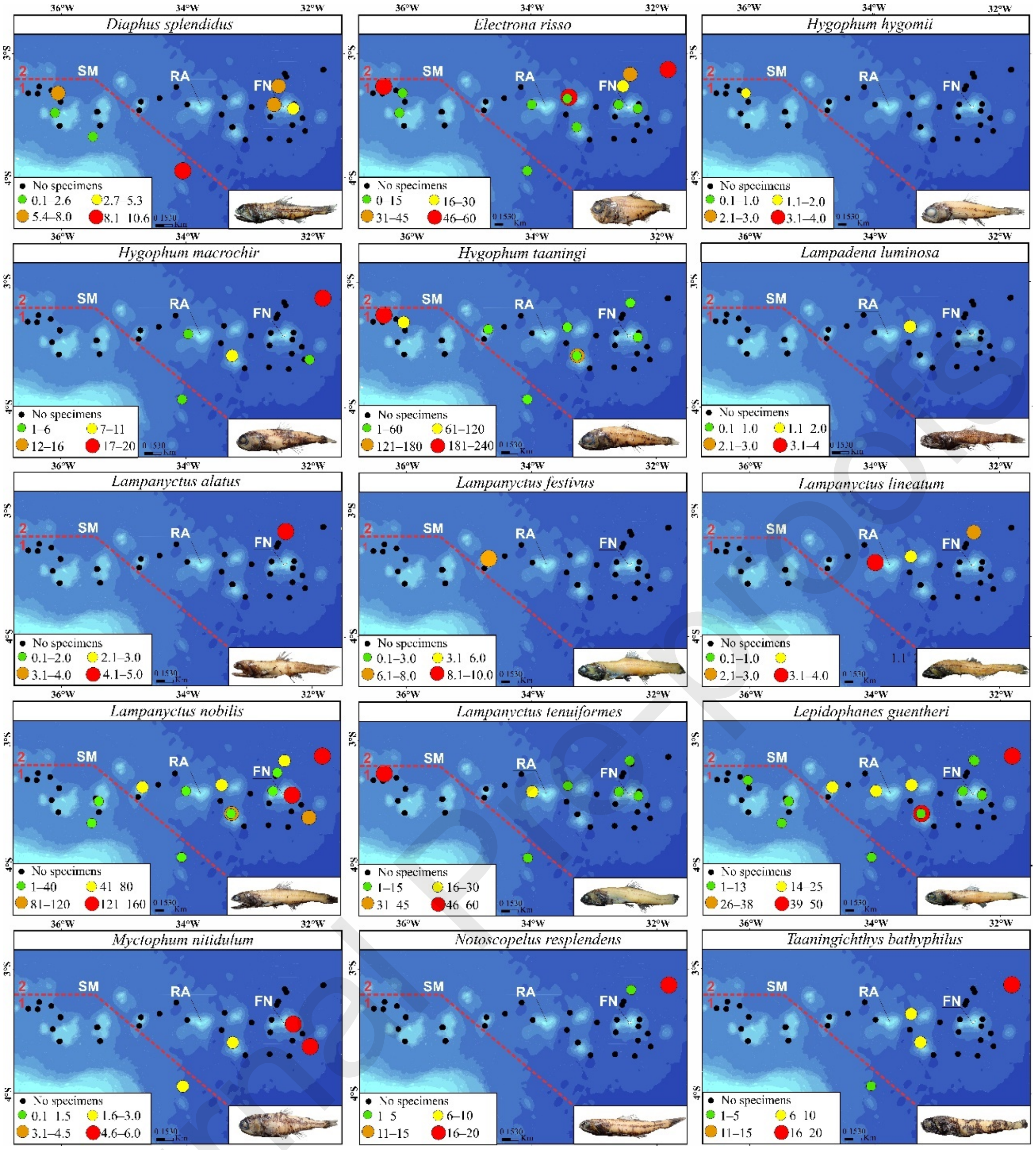

Figure 8. Catch per unit of effort (CPUE; individuals/hour) of lanternfishes from oceanic islands and seamounts of the Fernando de Noronha Ridge, Southwestern Tropical Atlantic – Part II. Dashed red line shows the limit between Area 1 and Area 2 (adapted from Assunção et al., 2020). SM – Seamounts; RA –Rocas Atoll; FN – Fernando de Noronha Archipelago. Numbers outside the maps indicate the latitude (x axes) and longitude (y axes). The colors of the points indicate the variation in CPUE values, changing from lowest to highest in the following order: green, yellow, orange, and red.

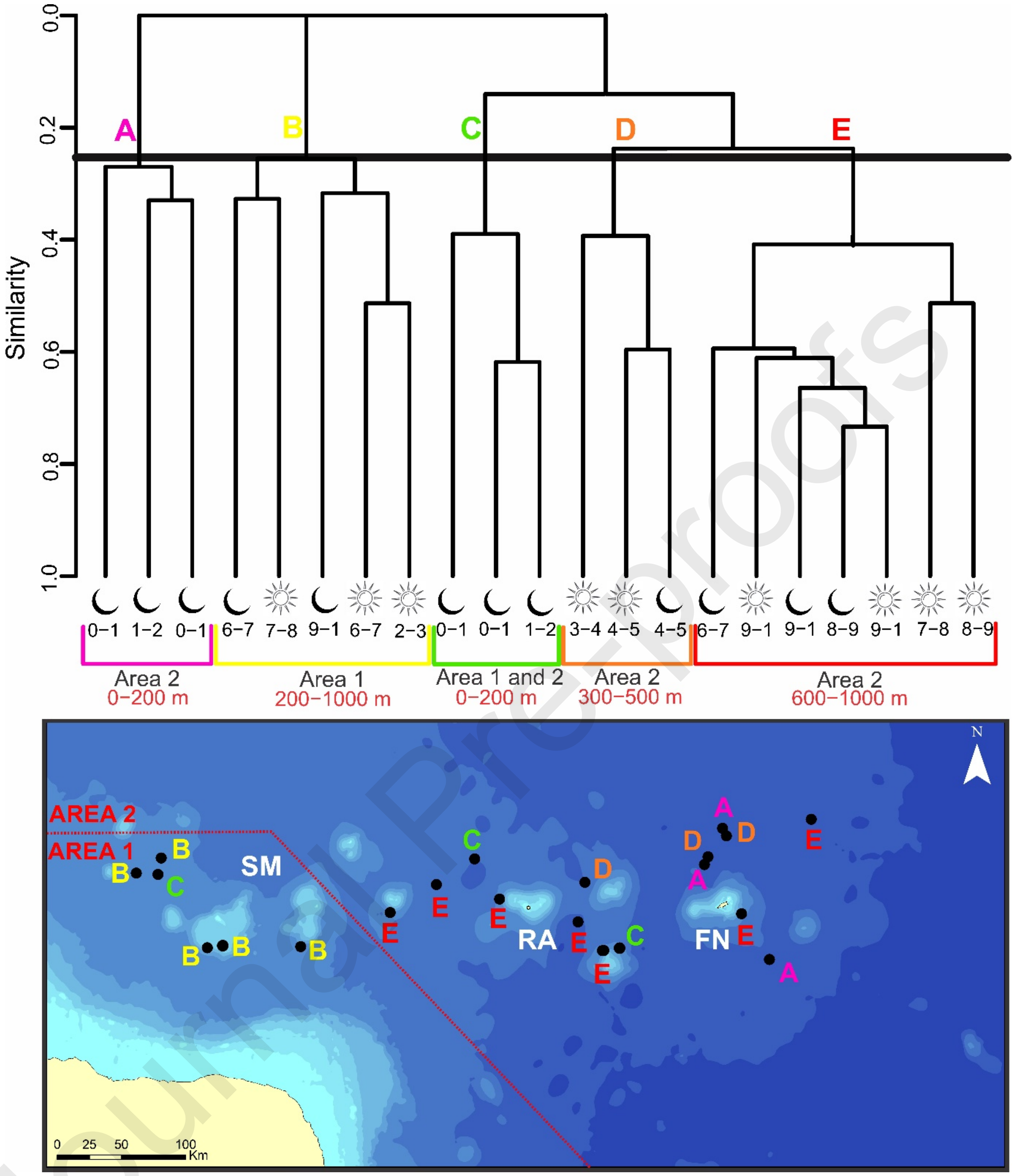

Figure 9. Dendrogram showing assemblages obtained after cluster analysis applied on the Bray Curtis similarities calculated among hauls (abundance data) for lanternfishes from oceanic islands and seamounts of the Fernando de Noronha Ridge, Southwestern Tropical Atlantic. The variables day period (sun pictogram: Day; moon pictogram: Night), Zone (Area 1; Area 2), and depth (0–1 = 0–100 m; 1–2 = 100–200 m;9–1 = 900–1000m; etc.) are shown. Limits of Area 1 and Area 2 (dashed red line) adapted from Assunção et al. (2020). SM: Seamounts; RA: Rocas Atoll; FN: Fernando de Noronha Archipelago.

Straight black line cutting through the dendrogram shows the resemble level of 25%, utilized to define five assemblages (A, B, C, D, and E).

DISCUSSION

We investigated the vertical migration and trophic ecology of lanternfishes in the Southwestern Tropical Atlantic, as well as the influence of physicochemical factors on their horizontal structuring, by combining information on their species composition, distribution, stable isotopic composition, and habitat. We found multiple patterns of vertical and trophic behaviour, revealing multidimensional niches, underestimated trophic links, and several underlying mechanisms to avoid competitive exclusion. Moreover, we show that lanternfish assemblage structuring are not strongly influencied by environmental conditions analysed here, leading to weak horizontal assemblage segregation.

Sample and analyses limitations

Different limitations could blur the interpretation of our results. First, any mesopelagic fish sampling is subject to technical hitches, as it includes complex interactions between the features of the gear (e.g., mesh size and mouth-area of the net) and the different body morphologies (e.g., fusiform, eel-like, or compressiform) and behaviours (Kaartvedt et al., 2012; Kwong et al., 2018). For example, some mesopelagic species show net avoidance behaviour, escaping from the trawls in the same way they do from predators (Kaartvedt et al., 2012). Additionally, many pelagic organisms have a strong light-escape response in the presence of artificial light from a vessel and may, therefore, be repulsed at night (Ludvigsen et al., 2018; Peña et al., 2019).

Pelagic trawl characteristics also impact the diversity and size of collected specimens. For instance, comparisons between gears reveal that the taxonomic composition and contribution of the main size groups to the total catch of pelagic trawls varies between different types (Kwong et al., 2018). Overall, the gear utilised here enabled the capture of a wide number of fish species (206), ranging from 0.3 to 180 cm in length (ABRACOS, unpubl. data). Nonetheless, the lanternfish composition and size structure we observed may reflect not only the *in situ* biogeographic patterns of this group but also the selectivity of gear used. Furthermore, although we took precautions to minimize the collection of specimens during the lowering or hoisting (see Material and Methods), our gear did not have an opening-closing mechanism, so the collection of a few specimens may have occurred during these stages. Therefore, we focused only on vertical migration patterns, avoiding fine-scale analyses and precise delimitations of vertical distribution. Further sampling using different gears (e.g., opening-closing Tucker trawls or MOCNESS nets) may reveal more precise patterns.

A second limitation of our approach concerns diet determination from isotopic mixing models closely related to the trophic discrimination factor (TDF) and the sources used to run the analysis (Fry, 2006). Additionally, isotopic incorporation (turnover) into animal tissues is highly variable and can blur the interpretation of isotopic measurements (Fry, 2006). As an example, depending on tissue-specific isotopic turnover, stable isotope measurements may reflect average dietary records that range from days to years (Fry, 2006). In this study, mixing models were applied with the overall goal of assessing variability in the trophic ecology of lanternfishes. However, the three patterns of prey importance (see Results) defined for lanternfishes were based solely on organisms included in the model. Hence, despite our careful selection of TDF values and prey, the inclusion of other prey, gut content analyses, and turnover rates could provide further insights into the trophic ecology of myctophids (Fry, 2006; Olivar et al., 2018).

Third, to increase the robustness of our analysis, all tests were conducted by coupling different size classes, which may have led to a loss of information on both vertical and trophic patterns of ontogenetic variation (Catul et al., 2011; Olivar et al., 2015). Therefore, our findings cannot exhaustively describe the ecological aspects of myctophids. Nevertheless, they further the understanding of a central and insufficiently studied deep-sea group, as well as providing new information on important aspects of its ecology.

Species richness and dominance patterns

Based on the material collected in our trawls, the number of species and individuals of lanternfishes make the Myctophidae one of the most important mesopelagic fish families of the SWTA in terms of abundance, biomass, and richness (40% of the collected specimens in our samples; ABRACOS, unpubl. data). Among this group, seven species were dominant (*B. distofax, D. brachycephalus, D. perspicillatus, D. splendidus, E. risso, H. taaningi*, and *L. nobilis*), accounting for 66% of the total number of individuals. Similar species composition was found in the eastern Tropical Atlantic (Olivar et al., 2017) and eastern coast of Brazil (11°−22° S; Braga et al., 2014). In these areas, the predominance of a few lanternfish species was also observed but with clear differences in the dominant species. For instance, on the eastern coast of Brazil (from Bahia to Rio de Janeiro), *D. garmani* accounted for 84% of all myctophids (Braga et al., 2014), while in our study area, this species was classified as scarce and rare (5% of all specimens). Likewise, in the eastern Tropical Atlantic, *B. suborbitale*, *C. warmingii*, and *H. macrochir* were dominant (Olivar et al., 2017), although these species accounted for less than 4% of the total abundance here. These differences in species dominance are likely related to intrinsic biogeographic features (e.g., productivity, water masses, and hydrographic fronts), which have been described as significant factors driving the structure and composition of myctophid assemblages (Hulley and Krefft, 1985; Hulley, 1992; Olivar et al., 2017). Moreover, fishing gear, sampling strategy, and effort were different among the studies, which may have affected the overall picture they give of biodiversity.

Horizontal distribution and potential influence of physicochemical features

Assunção et al. (2020) divided our study area into two significantly different areas (Area 1 and Area 2) based on the thermohaline structure and current systems (NBUC/NBC *vs.* cSEC/SEUC). Additionally, our results revealed differences in the oxygen and fluorescence profiles of these areas. Together, all these oceanographic features resulted in significant variations in zooplankton biomass (Figueiredo et al., 2020) and planktonic cnidarian composition (Tosetto et al., 2021). Based on our analyses, it may also partially explain the assemblage structuring of lanternfishes. For instance, Assemblage B included only samples from mesopelagic waters of Area 1, being dissimilar from other assemblages by the higher abundance of *B. distofax* and low occurrence of *D. brachycephalus* and *D. splendidus*. Indeed, the variability of *B. distofax* distribution has been closely related to oceanographic processes in both the Pacific and Atlantic Oceans (Hulley and Duhamel, 2009). Additionally, assemblages A, E, and D were found only in Area 2, being characterized, among others, by the higher abundance of *D. brachycephalus* and *L. nobilis* and low occurrence of *B. distofax*. However, the Assemblage C encompassed the two areas and a weak explanatory response was found when considering the pre-established areas as a factor. Therefore, although the formation of some assemblages may be driven by oceanographic characteristics of these areas (e.g., current systems, thermohaline structures, and oxygen availability), neither of these sets of features alone fully explains the lanternfish structuring observed here.

One possible explanation for the weak horizontal structuring of myctophids is that, despite the thermohaline structure and stratification at shallow layers (0–300 m) being significantly different between Areas 1 and 2, the thermal gradients between surface and deeper layers were alike. Additionally, water masses below 400 m depth were similar. At the scale of this study, another likely explanation is the high dispersion potential of myctophids, as vertically migrating species can be transported for relatively large horizontal distances depending on the oceanographic conditions through which they travel (Milligan and Sutton, 2020). Moreover, their ability to actively choose a depth stratum that provides favourable environmental conditions may also be an important factor. Similar patterns were observed in the Atlantic, Indian, and Pacific oceans, where environmental characteristics explain only a small portion of the myctophid composition (Flynn and Marshall, 2013; Olivar et al., 2015; Milligan and Sutton, 2020).

Vertical migration, trophic ecology, and niche partitioning

Of the 33 lanternfish species collected here, 73% (24 species) were found in epipelagic layers at night, indicating a likely pattern of vertical migration. Based on literature, 90% (30 species) of the lanternfishes collected here seem to perform vertical migration elsewhere (Supp. Material 4). Indeed, most myctophids undertake substantial daily vertical migrations, whether to feed, reproduce, or seek refuge (Watanabe et al., 1999; Catul et al., 2011; Sutton, 2013).

All 18 lanternfish species selected to investigate vertical distribution patterns can withstand a wide range of environmental conditions (e.g., daily temperature ranges up to 25°C) and show a likely pattern of asynchronous migrations (e.g., the entire population might not respond synchronously to diel variation in light intensity), as has been observed before (Catul et al., 2011; Sutton, 2013). Moreover, we observed high variability of space occupation during both day and night. For instance, while species from Pattern 1 peak at the lower mesopelagic layers (200–500 m) and partially migrate to the epipelagic layer at night, species from Patterns 3 and 4 seem to remain in lower and upper mesopelagic waters during both day and night (Fig. 4). This agrees with information previously available for these species elsewhere (Supp. Material 4). Interestingly, a similar pattern was found for hatchetfishes (Sternoptychidae), the second most abundant mesopelagic fish group in the SWTA (Eduardo et al., 2020a). Therefore, the two most abundant fish groups of the SWTA (70% of all sampled specimens) seem to be distributed throughout the vertical layers, thereby diminishing competition for resources (Eduardo et al., 2020a; Sutton, 2013).

Our findings on trophic ecology also support this pattern. Despite all the nine species investigated being zooplanktivores (i.e., foraging on fish larvae, gelatinous organisms, and euphausiids), the isotopic mixing models revealed at least three possible patterns of prey importance. For instance, the most important prey for Trophic pattern 1 seem to be fish larvae of 15–20 mm, *A. tetragona* and *E. gibboides*, whereas the most important prey of Trophic pattern 2 are fish larvae of 5–10 mm, *S. zonaria*, and *Salpa* sp. Additionally, lanternfishes do not seem to present the same trophic pattern and vertical space occupation. For example, *D. dumerilii*, *H. taaningi*, and *L. nobilis* were allocated to Trophic Pattern 1, but none of them peaked at the same depth strata at day (Fig. 10). *Diaphus mollis* and *E. risso*, nevertheless, are both from Trophic Pattern 1 and peaked at the same depth (300–400 m). However, while *D. mollis* migrates to epipelagic waters at night, *E. risso* seems to stay at mesopelagic waters at day and night. Similar findings were noted in the Southern Ocean and Gulf of Mexico, where most of the lanternfishes presented distinct isotopic niches differing by at least one of the two niche axes. Hence, coupling the information from the present study with previous work, it seems that, when living in the same depth layer, the segregation of lanternfishes operates through different feeding habits (e.g., habitat and trophic level; Hopkins et al., 1996; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Cherel et al., 2010).

Three other patterns were demonstrated in myctophid trophodynamics. First, Euphausiids (*E. gibboides*) seems to be important prey for all the nine lanternfish species included in the trophic analyses, which agrees with previous studies on mesopelagic zooplanktivores (e.g., Hopkins and Gartner, 1992; Eduardo et al., 2020a). Second, gelatinous organisms (Siphonophorae and Thaliacea) also appeared to be an important prey (e.g., amongst the most import prey of Trophic Pattern 1 and 2). This pattern diverges from most studies based solely on stomach content analyses and/or not including stable isotopic on gelatinous species (Shreeve et al., 2009; Noord, 2013; Battaglia et al., 2016). Although some of these studies indicate the presence of gelatinous organisms, this type of prey does not usually stand out as an important component in the diet of lanternfishes since quickly digested gelatinous organisms are often unidentifiable in stomachs, especially after chemical preservation (Robison, 2009). A high importance of gelatinous prey has also been noticed in recent studies applying stable isotope analyses to mesopelagic species (e.g., McClain-Counts et al., 2017; Eduardo et al., 2020a). For instance, in the SWTA, gelatinous organisms were among the main prey of hatchetfishes (Eduardo et al., 2020a). Therefore, it is likely that key trophic relationships between lanternfishes and gelatinous organisms have been globally underestimated due to methodological limitations. This trophic link may also play an important role in the use of resources and niche differentiation. Finally, we also found a high trophic contribution of fish larvae, which is a divergence from previous studies (e.g., Bernal et al., 2015). This pattern is likely driven by the local food availability, as the study area includes several coral reefs, islands, and seamounts that could enhance the larval abundance of several species (CBD, 2014). Indeed, a recent study addressing zooplankton communities in the same location highlights a high biovolume of fish larvae in sample size fractions larger than 2000 µm (Figueiredo et al., 2020).

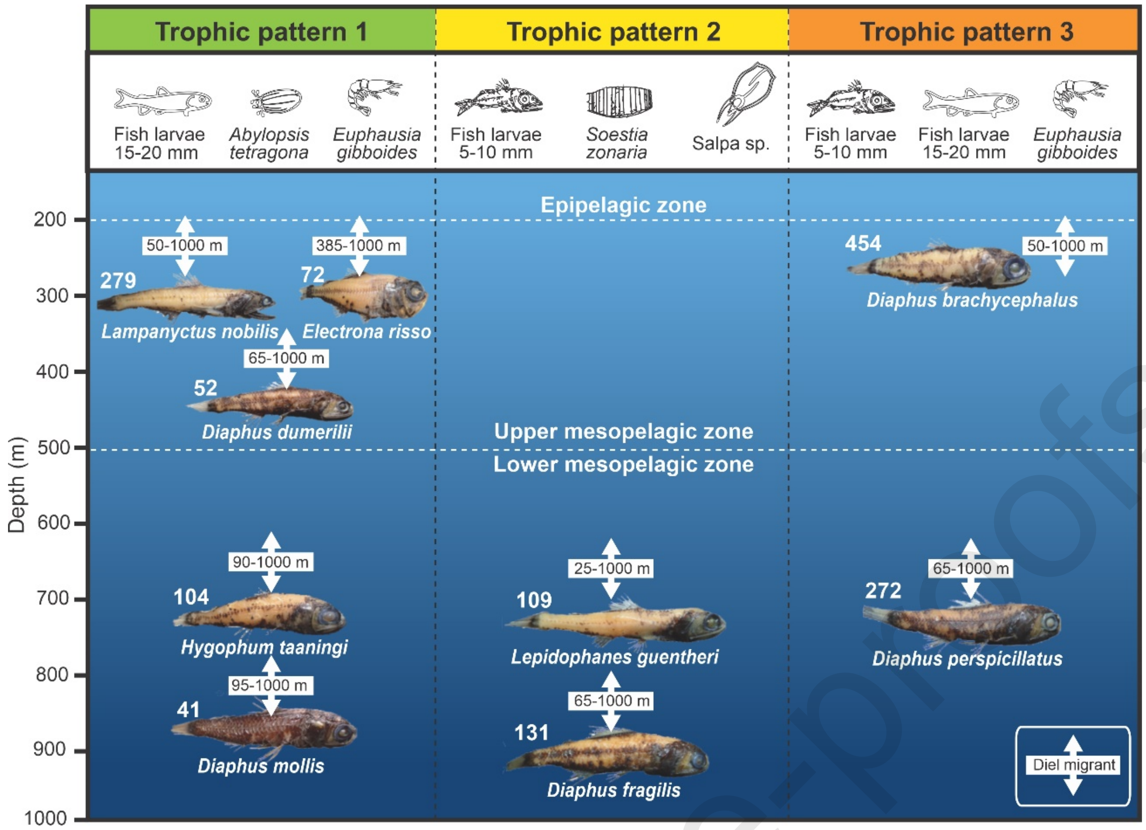

Figure 10. Conceptual model exhibiting vertical niche partitioning of lanternfishes at day. Numbers inside the white boxes indicate the depth range of each species, while numbers outside the boxes indicate the number of specimens sampled. Depth where species are placed indicate the peak of abundance of each species at day. It does not necessarily mean that the species are fully partitioned, but rather that their distribution centres are different. Given the limitations of our methodology (see sample and analysis drawbacks), this model does not intend to provide a precise vision of vertical niche partitioning but rather exemplify how niche differentiation of these species may occur.

Local differences in food availability also seem to reflect the trophodynamics between myctophids and their potential predators. While lanternfishes may be the most important prey for epipelagic predators in some locations (Karakulak et al., 2009; Battaglia et al., 2013), the stable isotopes results did not show a well-defined trophic relationship between these species. Indeed, studies involving gut content analyses of epipelagic predators over the SWTA show myctophids as a secondary prey, usually after species of Exocoetidae and cephalopods (Vaske Júnior et al., 2011; Albuquerque et al., 2019; Silva et al., 2019). In fact, the epipelagic predators included here (e.g., tunas) are mostly opportunistic feeders; therefore, their diet is expected to vary both spatially and temporally (Bertrand et al., 2002; Albuquerque et al., 2019). However, the isotopic compositions of myctophids and deep-sea predators are well-matched. This is also supported by previous studies in the SWTA (Eduardo et al., 2020b) and elsewhere (Sutton and Hopkins, 1996; Butler et al., 2001; Battaglia et al., 2018), where myctophids are the primary prey items of several deep-sea species. For instance, in the study area, lanternfishes constitute up to 85% of the viperfish diet, which is the most abundant mesopelagic micronektivore (Eduardo et al., 2020c). In summary, in the SWTA, myctophids act as a relevant food source for both epipelagic and deep-sea predators. However, the trophic contribution for epipelagic predators is probably smaller, as these species feed on several additional epipelagic prey.

Conclusion

Lanternfishes are a highly diverse and abundant fish family of the Southwestern Tropical Atlantic, comprising at least 33 species and 40% of all mesopelagic specimens collected in our samples. This species composition is comparable to those found in the tropical and subtropical Atlantic, but with clear differences in dominance patterns. Species evaluated here showed weak horizontal structuring, suggesting that well-defined assemblages of lanternfishes are not maintained. Although the discrepancies between the two areas considered here (i.e., differences in current systems, thermohaline structures, and oxygen availability) seem to play a role in the structuring of some assemblages, these sets of features alone do not fully explain the lanternfish structuring observed. Therefore, the dispersion of species and their ability to actively select vertical layers and favourable environmental conditions may be overriding the oceanographic features analysed here.

Lanternfishes show variability on prey composition and vertical migration and distribution. Indeed, three possible patterns of prey composition and four patterns of vertical distribution were observed, showing a likely multidimensional resource partitioning. For instance, based on this study and previous ones, it seems that, when living in the same habitat, the segregation of lanternfishes operates through differences in feeding habits, which diminish competitive exclusion. Moreover, these species likely feed on gelatinous organisms (Thaliacea and Siphonophorae), a trophic relationship that has generally been underestimated because gelatinous organisms were probably poorly accounted in previous studies based solely on stomach contents. This trophic link may play an important role in the use of resources and thus niche differentiation. Additionally, at least 73% of lanternfishes observed here migrate vertically to the surface to feed at night and actively transport the carbon ingested to deep waters during day, a pathway enhancing the oceanic carbon transport (Cavan et al., 2019). Finally, in the SWTA, myctophids act as a secondary prey for epipelagic predators and a central food source for deep-sea species. These processes are relevant for the connection between shallow and deep-sea ecosystems.

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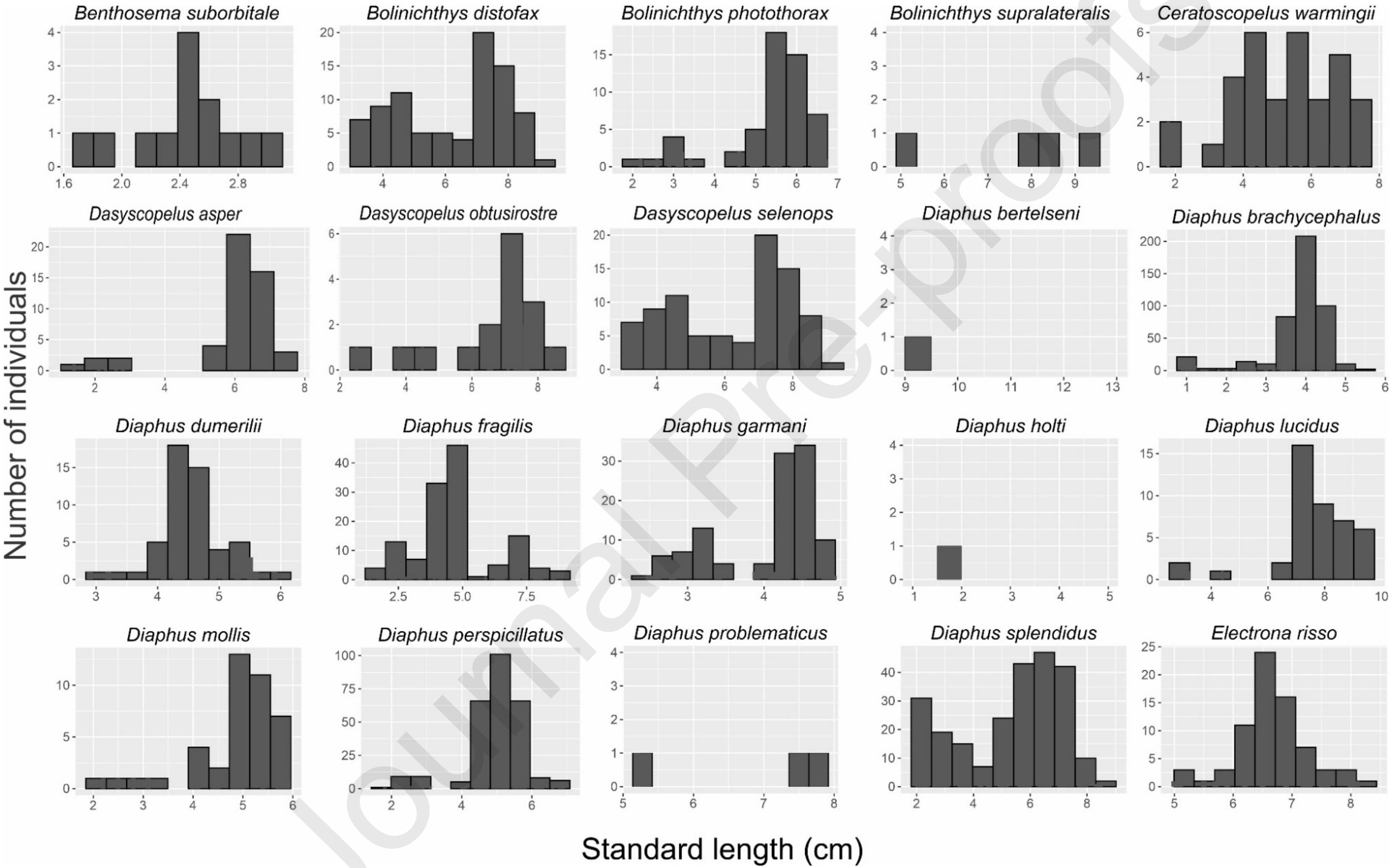
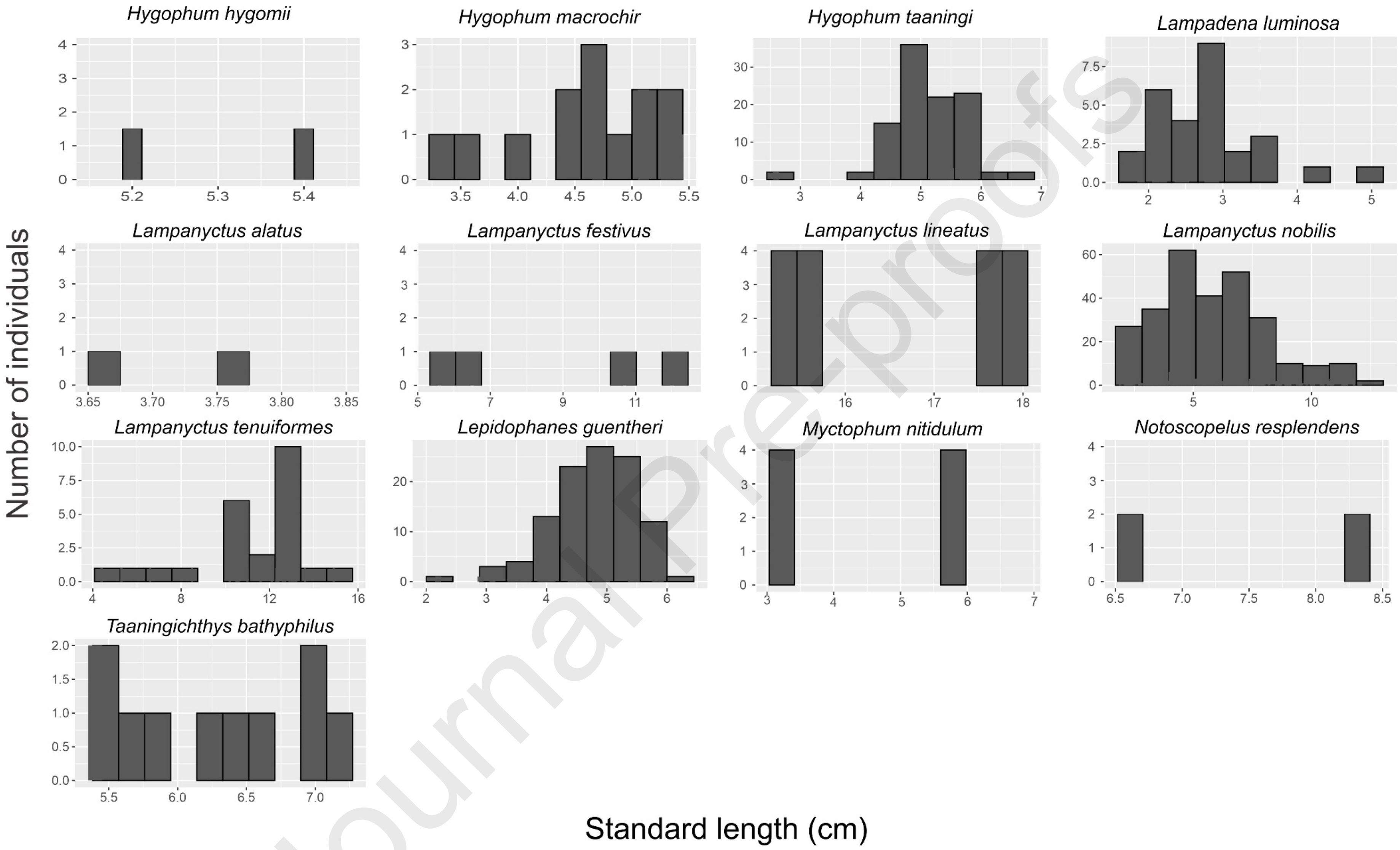
Supplementary Material



Supplementary material 1– Histogram (Standard length, cm) of lanternfishes from oceanic islands and seamounts of the western Tropical Atlantic. Part I.



Supplementary material 1– Histogram (Standard length, cm) of lanternfishes from oceanic islands and seamounts of the western Tropical Atlantic. Part II.

Supplementary material 2. Number of samples, standard length (cm) and stable isotope values of lanternfishes, potential predator (DP - deep-sea; EP - epipelagic), potential prey, and POM. *Lipid corrected species.

Group	Species	Category	N	SL (cm) Mean ± SD	δ^{13}C (‰) Mean ± SD	δ^{15}N (‰) Mean ± SD	C:N Mean ± SD
Myctophidae	*Diaphus brachycephalus*	–	10	5.0±2.1	-18.9±0.4	10.0±0.9	3.4±0.1
	Diaphus dumerilii	–	6	16.2±9.5	-19.0±0.5	9.0±1.1	3.5±0.2
	Diaphus fragilis	–	11	7.3±0.5	-18.2±0.3	10.2±0.5	3.4±0.1
	Diaphus mollis	–	5	5.2±0.3	-19.2±0.2	10.6±0.8	3.4±0.1
	Diaphus perspicillatus	–	8	3.2±0.3	-18.2±0.2	10.9±0.7	3.4±0.1
	Electrona risso	–	9	5.6±0.1	-18.9±0.1	11.4±0.1	3.2±0.1
	Hygophum taaningi	–	9	5.5±0.2	-18.2±0.2	10.0±0.6	3.3±0.1
	Lampanyctus nobilis	–	7	7.4±1.5	-18.2±0.3	9.6±0.4	3.3±0.2
	Lepidophanes guentheri	–	13	5.7±0.6	-18.2±0.2	9.8±0.7	3.3±0.1
Stomiidae	*Borostomias elucens*	DP	9	16.2±1.9	-18.3±0.4	11.9±0.5	3.3±0.1
	Chauliodus sloani	DP	10	18.1±1.3	-18.3±0.2	11.1±0.7	3.3±0.0
	Malacosteus niger	DP	5	10.7±2.0	-19.2±0.3	11.7±0.5	3.4±0.1
Scorpaenidae	*Ectreposebastes imus**	DP	5	19.1±1.8	-19.1±0.3	12.9±0.3	4.3±0.2
Sphyraenidae	*Sphyraena barracuda*	EP	7	151.2±30.0	-16.2±0.5	10.7±0.5	3.2±0.1
Coryphaenidae	*Coryphaena hippurus*	EP	6	85.2±12.0	-16.5±0.4	11.3±0.6	3.2±0.1
Carangidae	*Elagatis bipinnulata*	EP	6	53.3±10.4	-19.3±0.2	9.4±0.5	3.4±0.2
Scombridae	*Acanthocybium solandri*	EP	8	100.0±35.0	-16.9±0.4	11.0±1.0	3.2±0.1
	Katsuwonus pelamis	EP	3	44.6±4.1	-17.2±0.4	10.2±1.0	3.2±0.1
	Thunnus albacares	EP	12	65.0±20.0	-17.4±0.2	10.8±1.1	3.1±0.1
Fish larvae	Teleostei larvae 5–10 mm	Prey	10	–	-19.7±0.1	5.9±0.2	3.2±0.1
	Teleostei larvae 15–20 mm	Prey	6	–	-18.5±0.4	7.2±0.7	3.2±0.1
Crustacea	*Euphausia gibboides*	Prey	6	1.5±0.1	-19.3±1.0	6.9±0.1	3.2±0.1
	Euphausia sp.	Prey	3	1.4±0.1	-19.5± 0.5	7.3±0.9	3.2±0.1
	Pasiphaeidae sp.	Prey	3	–	-19.1±0.1	6.1±0.1	3.1±0.1
	Phronima sp.	Prey	3	–	-19.0±0.2	5.9±0.3	3.6±0.2
Siphonophorae	*Abylopsis tetragona*	Prey	3	–	-17.8±0.3	7.2±1.0	3.3±0.1
	Siphonophorae sp.	Prey	3	–	-19.2±0.1	9.1±0.2	3.4±0.1
Thaliacea	*Pyrosoma atlanticum**	Prey	11	–	-21.5±0.2	3.0±0.7	5.3±0.2
	Salpa sp.*	Prey	6	–	-19.8±0.5	5.5±0.5	4.5±0.7
	Soestia zonaria	Prey	6	–	-20.3±0.2	3.8±0.6	3.3±0.1
Zooplankton	Zoo A (<10 μm)*	Prey	19	–	-19.8±0.5	2.0±1.1	4.7±0.2
	Zoo B (100–200 μm)*	Prey	19	–	-19.4±0.5	1.9±0.8	4.6±0.7
	Zoo C (200–500 μm)*	Prey	19	–	-19.4±0.3	3.0±0.6	5.6±1.2
	Zoo D (5000–1000 μm)*	Prey	18	–	-19.1±0.3	4.2±0.4	4.2±0.4
	Zoo E (1000–2000 μm)*	Prey	18	–	-20.3±0.9	4.6±0.4	4.8±0.6
	Zoo F (>2000 μm)*	Prey	13	–	-19.6±0.4	4.9±0.4	4.5±0.3
POM			17	–	-22.4±0.7	2.8±1.2	–

Species	**Record of epipelagic**	**References**

	vertical Migration	
Benthosema suborbitale (Gilbert, 1913)	Yes	Clarke, (1973); Santos and Figueiredo, (2008)
Bolinichthys distofax Johnson, 1975*	No	Clarke, (1973); Hulley, (1990); Hulley and Duhamel, (2009)
Bolinichthys photothorax (Parr, 1928)	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Bolinichthys supralateralis (Parr, 1928)	Yes	Santos and Figueiredo, (2008); Hulley and Duhamel, (2009)
Ceratoscopelus warmingii (Lütken, 1892)	Yes	Clarke, (1973); Gartner Jr et al., (1987); Santos and Figueiredo, (2008); Watanabe et al., (1999)
Dasyscopelus asper Richardson 1845	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Dasyscopelus obtusirostre Tåning, 1928	Yes	Clarke, (1973); Hulley, (1990)
Dasyscopelus selenops (Tåning, 1928)	Yes	Clarke, (1973); Hopkins et al., (1981); Hulley, (1990)
Diaphus bertelseni Nafpaktitis, 1966	Yes	Clarke, (1973); Hulley, (1990); Mundy, (2005)
Diaphus brachycephalus Tåning, 1928	Yes	Clarke, (1973); Santos and Figueiredo, (2008)
Diaphus dumerilii (Bleeker, 1856)	Yes	Gartner Jr et al., (1987); Kinzer and Schulz, (1985)
Diaphus fragilis Tåning, 1928	Yes	Clarke, (1973); Hulley, (1990)
Diaphus garmani Gilbert 1906	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Diaphus holti Tåning, 1918	Yes	Hulley, (1990); Olivar et al., (2017)
Diaphus lucidus (Goode & Bean, 1896)	Yes	Hulley, (1986); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Diaphus mollis Tåning, 1928	Yes	Hulley, (1990); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Diaphus perspicillatus (Ogilby, 1898)	Yes	Hulley, (1990); Mundy, (2005)
Diaphus problematicus Parr, 1928	Yes	Figueiredo et al., (2002); Hopkins et al., (1981)
Diaphus splendidus (Brauer, 1904)	Yes	Hopkins et al., (1981); Hulley, (1990)
Electrona risso (Cocco, 1829)*	No	Battaglia et al., (2016); Moser and Ahlstrom, (1996)
Hygophum hygomii (Lütken, 1892)	Yes	Hulley, (1990)
Hygophum macrochir (Günther, 1864)	Yes	Hulley, (1990); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Hygophum taaningi Becker, 1965	Yes	Hopkins et al., (1981); Hulley, (1990); Santos and Figueiredo, (2008)
Lampadena luminosa (Garman, 1899)	Yes	Clarke, (1973); Hopkins et al., (1981)
Lampanyctus alatus Goode & Bean, 1896	Yes	Hopkins et al., (1981); Hulley, (1990); Kinzer and Schulz, (1985)
Lampanyctus lineatus (Tåning, 1928)	Yes	Hulley, (1990); Zahuranec, (2000)
Lampanyctus festivus Tåning, 1928	Yes	Hulley, (1990)
Lampanyctus nobilis (Tåning, 1928)	Yes	Clarke, (1973); Hulley, (1986)
Lampanyctus tenuiformes (Brauer, 1906)	Yes	Clarke, (1973); Kinzer and Schulz, (1985)
Lepidophanes guentheri Goode & Bean 1896	Yes	(Hulley, 1990; Kinzer and Schulz, 1985)
Myctophum nitidulum Garman 1899	Yes	Hulley, (1990); Kinzer and Schulz, (1985)
Notoscopelus resplendens (Richardson, 1845)	Yes	Hulley, (1990); Kinzer and Schulz, (1985); van der Spoel and Bleeker, (1991)
Taaningichthys bathyphilus (Tåning, 1928)	No	Douglas and Partridge, (1997); Gartner Jr et al., (1987); Hulley, (1990)

Supplementary material 4 – Literature review on the vertical migration of lanternfishes species found in this study. *small specimens have been reported in the upper 100-200 m at night.

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Highlights

- Lanternfishes are a highly diverse and abundant fish family of the Southwestern Tropical Atlantic.
- Lanternfishes presented a high variability of prey composition and migratory behaviour.
- At least 73% of lanternfishes observed here vertically migrate to the surface to feed at night.
- Lanternfishes act as a secondary prey for epipelagic predators and a central food source for deep-sea species.
- Lanternfish assemblages are not strongly affected by the thermohaline structure and current systems of the region

Conflict of interest:

None.