

From the light blue sky to the dark deep sea: Trophic and resource partitioning between epipelagic and mesopelagic layers in a tropical oceanic ecosystem

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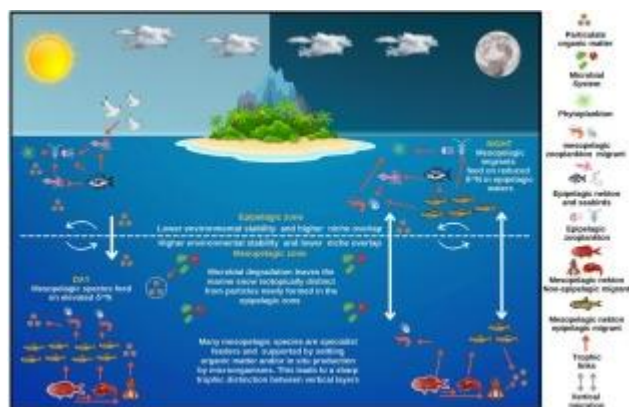
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Abstract :

The connection between epipelagic and deep-sea mesopelagic realms controls a variety of ecosystem processes including oceanic carbon storage and the provision of harvestable fish stocks. So far, these two layers have been mostly addressed in isolation and the ways they connect remain poorly understood. Furthermore, both systems are affected by climate change, exploitation of resources, and increasing pervasion of pollutants. Here we use bulk isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of 60 ecosystem components to evaluate the trophic linkage between epipelagic and mesopelagic ecosystems in warm oligotrophic waters. Additionally, we determined and compare isotopic-niche sizes and overlaps for multiple species to evaluate how environmental gradients between epipelagic and mesopelagic ecosystems shape ecological patterns of resource use and competition between species. Our database comprises siphonophores, crustaceans, cephalopods, salpas, fishes, and seabirds. It also includes five zooplankton size classes, two groups of fish larvae, and particulate organic matter collected at different depths. Through this wide taxonomic and trophic variety of epipelagic and mesopelagic species, we show that

pelagic species access resources originating from different food sources, mostly autotrophic-based (epipelagics) and microbial heterotrophic-based (mesopelagics). This leads to a sharp trophic dissimilarity between vertical layers. Additionally, we show that trophic specialization increases in deep-sea species and argue that food availability and environmental stability are among the main drivers of this pattern. Finally, we discuss how the ecological traits of pelagic species highlighted in this study can respond to human impacts and increase their vulnerability in the Anthropocene.

Graphical abstract



Highlights

► Pelagic trophic dissimilarity seems to be prominent in warm oligotrophic waters. ► Mesopelagic species rely mostly on microbial heterotrophic-based food sources. ► Epipelagic species rely mostly on autotrophic-based food sources. ► Food availability and environmental stability lead to a high trophic specialization and high niche partitioning in mesopelagic species. ► High trophic specialization increases the vulnerability of deep-sea species.

Keywords : Stable Isotopes, Biological Carbon Pump, Environmental stability, Oceanic Islands, Microbial Trophic Pathways, Fernando de Noronha Archipelago

1. Introduction

Pelagic waters host a remarkable diversity of animals ranging from millimetric planktonic organisms to large top predators. The biophysical heterogeneity of this habitat is structured by depth, latitude, longitude, distance from shore, and time (Barnes, 1995). Sun's energy is absorbed in the uppermost meters of the water column and sufficient light for photosynthesis does not go deeper than 100–150 m (Ryther, 1956). Pelagic communities, therefore, are mainly bounded by differences in light, temperature, salinity, oxygen, and nutrient quantities (Bertrand et al., 2010, 2014). While in shallow-water, organisms benefit from enlightened warm waters and the vicinity of energy and oxygen production, there is a continuum of change with depth in which species are exposed to distinct trophic sources and diminishing amounts of light, heat, and oxygen.

To cope with these environmental gradients, pelagic animals evolved a series of adaptations to optimize energy gains in relation to costs (Stephens and Krebs, 1986; Abrams, 1992; Priede, 2017). These adaptations include multidimensional niche partitioning, complex bioluminescence systems, and the most massive daily migration of animals on earth (Hays, 2003; Johnsen, 2014; Eduardo et al., 2021). Together, these traits are the foundation of key ecosystem processes, such as oceanic carbon storage, nutrient recycling, and connection between shallow and deep-sea waters (Sutton, 2013). In fact, from a trophic perspective, shallow and deep-sea ecosystems are strongly linked through key species groups, such as migrating zooplankton and micronekton and, more generally, through particulate organic matter (POM) exported out of surface waters and/or remineralized by microbial food-webs (Choy et al., 2015, 2016; Drazen and Sutton, 2017; Gloeckler et al., 2018). These interactions comprise the basis of deep-sea food webs and shape the functioning of pelagic ecosystems.

Although trophic connections between shallow and mesopelagic ecosystems are known for decades, these two systems have traditionally been addressed as two isolated layers, and only a few works were carried out integrating the processes vertically (Choy et al., 2015, 2016; Gloeckler et al., 2018). Consequently, there is a large uncertainty regarding the level of vertical connectivity and a poor representation of key trophic pathways in the current carbon and

ecosystem models. For instance, vertical migration is a crucial mechanism that connects photosynthetic carbon to the deep-sea biota, which eventually contributes to carbon storage in the oceans (Boyd et al., 2019). However, our understanding of this process is limited by the lack of even basic biological information for many of the species involved. Additionally, the respiratory demand for carbon by the mesopelagic community exceeds the carbon supply through the particulate sinking flux by up to three orders of magnitude (Boyd et al., 2019; Burd et al., 2010), implying that deep-sea communities rely on additional carbon sources that are still poorly understood (Gloeckler et al., 2018). The lack of information on the trophic connection between shallow and deep-sea waters also hampers the understanding of broader ecological patterns, such as the complex interactions between pelagic species and competition for food resources. This information is therefore essential for evaluating the mechanisms of coexistence and for predicting the consequences of changes in ecosystems and communities (Chase and Leibold, 2003)

Examining the trophic ecology of shallow and deep-sea ecosystems in a unified framework is difficult since it is expensive, time-consuming, and methodologically challenging. As an example, deep-sea animals are difficult to catch and diet studies are unable to capture all the complexity of the food web because of the challenges in identifying all prey items (Eduardo et al., 2020a). However, Stable Isotopic Analyses (SIA) have been proven particularly useful for illuminating trophic dynamics in remote environments like the deep-sea, since it provides time-integrated information on all the material assimilated by organisms. For instance, nitrogen isotopes undergo larger levels of trophic fractionation and can be used to estimate trophic position and food chain length, while carbon isotopes undergo small fractionation levels during trophic transfer and can be used to define energy sources (Fry, 2006). SIA can also provide valuable information on the role of the POM and microbial pathways in the structuring and functioning of pelagic food webs. For instance, microbial reworking leaves the residual material isotopically distinct (Mintenbeck et al., 2007). Therefore, trophic pathways based on newly formed sources of energy in epipelagic waters have isotopic compositions different than those based on remineralized POM in deep waters.

In the past few years (2015–2019), stable isotope data (bulk carbon and nitrogen) have been obtained for a wide trophic variety of epipelagic and deep-sea species (60 ecosystem components) in the vicinity of the Fernando de Noronha Archipelago (Brazil), an insular tropical ecosystem in the western South Atlantic. This opened the possibility to study the trophic connections and ecological patterns of vertical pelagic layers as never before. In this context, here we take advantage of this dataset to determine the trophic sources and connection between epipelagic and mesopelagic ecosystems in a tropical oligotrophic region. Additionally, we established and compared isotopic-niche sizes and overlaps for multiple species to evaluate how environmental gradients between epipelagic and mesopelagic ecosystems shape ecological patterns of resource use and competition between species. Finally, we discuss how the ecological traits of pelagic species highlighted in this study can respond to human impacts and increase their vulnerability in the Anthropocene.

2. Methodology

2.1 Study area

The study area encompassed the Fernando de Noronha Archipelago (FNA) and associated seamounts, off northeast Brazil (3°50'S, 32°25'W; Fig. 1). The main oceanographic physicochemical features of the region were described by Assunção et al. (2020), Dossa et al. (2021) and Costa da Silva et al. (2021). Overall, the Southwestern Tropical Atlantic is considered oligotrophic (Farias et al., 2022). However, locally the banks and islands act as topographic obstacles to currents, driving subsurface enriched waters to the surface. This process increases primary production and enhances the mass and energy fluxes throughout the food web (Travassos et al., 1999; Tchamabi et al., 2017; Salvetat et al., 2022). Consequently, this biogeographic unit holds remarkable biodiversity (Eduardo et al., 2022) and has been classified as EBSA (Ecologically or Biologically Significant Area – 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).

2.2 Data collection

Data from the following projects were merged: ABRACOS 2 (Bertrand, 2017), PROTUNA (Martins et al., 2021), MAFALDA, and TABASCO. The main collection procedures are summarized as follows:

ABRACOS 2: Specimens of mesopelagic fishes, crustaceans, cephalopods, and gelatinous organisms (siphonophores and salpas) were collected aboard the French RV *Antea* around the Fernando de Noronha Archipelago (FNA), in April and May 2017 (Bertrand, 2017). Sampling was conducted day and night at 22 stations using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm, estimated opening area: 120 m²) from 10 to 115 m depth (Fig. 1; Eduardo et al., 2020a, 2020b, 2021). 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 33, 70, 120, and 200 kHz. Zooplankton samples were collected using bongo nets (four nets simultaneously deployed with mesh sizes of 64, 120, 300, and 500 µm) that were towed from 200 m depth up to the surface at 12 stations (Fig. 1). After collection, these samples were pooled, sieved, and divided into six size fractions (64–100; 100–200; 200–500; 500–1000; 1000–2000; >2000 µm). Captured organisms were sorted, identified, and frozen (-20°C). Finally, Particulate Organic Matter (POM) was sampled at the same stations of micronekton trawls by filtering seawater collected at the surface and the maximum fluorescence depth through pre-combusted GF/F filters (47 mm). Samples collection methods were approved and conducted following relevant guidelines and regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 47270–5). See Eduardo et al. (2020a, 2020b, 2021) and Figueiredo et al. (2020) for more information on field procedures.

PROTUNA: Epipelagic fishes were sampled on board a recreational fishing vessel using a rod and reel off the FNA. Sampling was conducted during 8–10 days expeditions in 2018 (second semester) and 2019 (first semester). Occasionally, samples from artisanal fishing boats were obtained during fish landings at the local port. All biological material was collected during fish evisceration at the end of each fishing cruise and the samples were frozen (-20°C) until laboratory analyses. Sampling methods were approved and conducted following relevant guidelines and

regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 62915-6). See Martins et al. (2021) for further information on field procedures.

MAFALDA and TABASCO: Adult seabirds were captured by hand or using pole and line at their breeding sites in FNA, April and September from 2015 to 2019. Blood samples (~1 ml) were obtained by puncturing the tarsal vein with sterile syringes and needles and stored in microtubes containing ethanol 70%. Individuals were banded to avoid resampling and released into the nests after handling. Flying fish were collected from material spontaneously regurgitated by seabirds during handling. Regurgitates were identified at species level, measured, and muscle samples (1 cm³) from each individual were collected and stored in ethanol 70%. Sampling methods were approved and conducted following relevant guidelines and regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 52583-5).

Stable isotopes analyses

To obtain unbiased values of $\delta^{13}\text{C}$, zooplankton and POM samples were acidified to remove the carbonates. POM filters were exposed to hydrochloric acid (HCl) vapor, while whole zooplankton samples were clustered into six-size classes and mixed with approximately 2 ml of 0.5 mol.l⁻¹ HCl (Cresson et al., 2012). Both samples went through the acidification process for four hours and then dried at 40°C for 36h. The untreated sub-samples of POM and zooplankton were used to measure $\delta^{15}\text{N}$.

For each fish and crustacean, white muscular tissue was extracted and cleaned with distilled water to remove exogenous material such as carapace, scales, and bones. For fish larvae, the headless body was used, while for gelatinous organisms the whole specimens were used. For seabirds, blood samples were used. Each sample of fish, crustaceans, gelatinous, and seabirds was dried in an oven at 60°C for 48h and grounded into a fine powder with a mortar and pestle.

Each dried 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were derived from the relation of the isotopic value from the sample and a known standard according to:

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

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

As differing lipid contents can bias the interpretation of $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$. A few samples consistent with high lipid content (C:N > 3.5) were normalized using the equation for aquatic animals provided in Hoffman and Sutton (2010; for fish) and Post et al. (2007; for other taxa).

2.3 Data analyses

Species were classified according to their taxonomic groups (siphonophores, crustaceans, cephalopods, salpas, fishes, and seabirds), vertical habitat (epipelagic or mesopelagic), and trophic guild (zooplanktivores and planktonivores; Drazen and Sutton, 2017). Additionally, mesopelagic species were further categorized according to migration patterns (epipelagic migrant; non-epipelagic migrant). Mesopelagic species were considered as those having daytime depth distributions ranging between 200 and 1000 m as adults. All classifications were made based on the information available in our database and literature (see Table 1).

To evaluate the isotopic differences and similarities between each species, we computed an Euclidean similarity matrix based on the mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which was then used to perform a Hierarchical Clustering (Average method; Borcard et al., 2011). The NbClust method proposed by Charrad et al. (2014) was used to determine the optimal number of clusters. This method provides 30 indexes to evaluate the relevant number of clusters, where the number of groups indicated by the highest number of indices is chosen. In addition, the trophic groups identified with the clustering were tested for significant differences ($p < 0.05$) using a non-parametric multivariate permutational analysis of variance (PERMANOVA). Differences in $\delta^{13}\text{C}$

and $\delta^{15}\text{N}$ between species groups of different habitat, migration pattern, and trophic guild were evaluated through the non-parametric Kruskal-Wallis test ($p < 0.05$).

Trophic niches and their overlapping were estimated based on the probabilistic method of Swanson et al. (2015). This method is not sensitive to variations in sample size and is available as the R package 'nicheROVER'. It uses Bayesian methods to calculate probability distributions of the overlaps between the isotopic niche space of species *A* versus species *B*, and *vice versa* (Swanson et al., 2015). Within 'nicheROVER', overlap estimates were run for 10,000 iterations and incorporated 95% of the data to represent overlap in total trophic niche space. Selecting the proportion of data included in niche calculations does not affect relative comparisons of niche width between species; however, it can heavily influence estimates of relative niche overlap. Therefore, we used the total trophic niche (i.e., ellipses incorporating 95% of data) to calculate relative niche overlap to balance type I (false-positive overlap) and type II (false-negative overlap) errors and account for individual variability across the sampled population (Shipley et al., 2019). Species were grouped according to habitat and migration patterns to assess the overlap between ecological groups (epipelagic migrant, mesopelagic migrant, and mesopelagic non-migrant). Additionally, 24 taxa were selected to analyse niche space at the species level to assess overlap within ecological groups. These species were selected to encompass representatives from all trophic guilds, habitats, and migration patterns.

3. Results

Fifty-one species were considered in our analyses. From those, two were siphonophores, eight crustaceans, five cephalopods, two salpas, thirty-one fishes, and three seabirds. Additionally, we included five size classes of zooplankton and two groups of fish larvae and POM (Table 1). This data encompassed species from different habitats (17 epipelagic vs. 32 mesopelagic), feeding guilds (30 zooplanktivores vs. 17 micronektonivores.), and migration patterns (17 epipelagic migrant vs. 15 non-epipelagic migrant). Our data also encompassed a broad size spectrum, ranging from zooplankton (64–100 μm) to large predators such as seabirds and epipelagic fishes

(> 120 cm standard length). Overall, mean stable carbon isotope values ranged from -20.3‰ to -16.6‰, and stable nitrogen isotope values ranged from 1.9‰ to 12.6‰ (Table 1, Fig. 3).

Cluster analysis based on mean stable isotope ratio values identified five major groups (Fig. 2), revealing significant differences between habitats (epipelagic and mesopelagic; $p < 0.01$). The largest group, named “Mesopelagic” (group I), comprised migrant and non-migrant mesopelagic species. Within this group, mean isotopic values ranged from -19.2‰ (*Diaphus mollis*) to -17.8‰ (*Argyropelecus aculeatus*) for $\delta^{13}\text{C}$, and from 8.2‰ (*Argyropelecus aculeatus*) to 12.8‰ (*Ectreposebastes imus*) for $\delta^{15}\text{N}$. The second largest group, named “Epipelagic” (II), was composed of epipelagic species, including seabirds. Mean isotopic values for this group ranged from -17.7‰ (*Enoploteuthis leptura*) to -15.9‰ (*Schizothorax barracuda*), and from 7.7‰ (*Oxyporhamphus micropterus*) to 11.3‰ (*Sula dactylatra*) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. A third group, named “Zooplankton” (III), encompassing gelatinous zooplankton (Thaliacea) and all zooplankton size fractions, with isotopic values ranging from -20.3‰ (ZOO E) to -19.1‰ (ZOO D) and from 1.9‰ (ZOO B) to 4.9‰ (ZOO C) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The fourth group, named “Others” (IV), included zooplankton species (fish larvae and euphausiids) that were caught with the micronekton net and are larger than the size classes analysed for zooplankton bongo samples. These species likely represent an intermediary stage between zooplankton size fractions and the “Mesopelagic” and “Epipelagic” groups. Mean isotopic values for this group ranged from -19.6‰ (Teleostei larvae 5–10 mm) to -18.5‰ (Teleostei larvae 15–20 mm) and from 5.9‰ (Teleostei larvae 5–10 mm) to 7.3‰ (Euphausiidae sp. 2) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Finally, the last group encompassed POM only (V). POM samples of the maximum fluorescence depth presented higher values of $\delta^{15}\text{N}$ (3.1‰ vs. 2.5‰; $p < 0.01$) and were more depleted in $\delta^{13}\text{C}$ (-20.3‰ vs. -19.6‰; $p < 0.01$) than samples from surface waters.

Significant differences in the isotopic composition were also found when epipelagic and mesopelagic species were grouped by habitat, trophic guilds, and migration patterns ($p < 0.01$) (Fig. 3). In general, the deeper the distribution, the higher the $\delta^{15}\text{N}$ and the lower the $\delta^{13}\text{C}$. For instance, mesopelagic non-migrating zooplanktivorous species had mean isotopic values of 11.2‰ $\delta^{15}\text{N}$ and -18.8‰ $\delta^{13}\text{C}$, while the same trophic group exhibited mean values of 9.2‰ $\delta^{15}\text{N}$

and -17.1‰ $\delta^{13}\text{C}$ in epipelagic waters. Mesopelagic migrant species displayed intermediate values (10.3‰ $\delta^{15}\text{N}$ and -18.4‰ $\delta^{13}\text{C}$), likely revealing trophic connections with both mesopelagic and epipelagic energy sources (Fig. 3).

A similar trend was observed when analysing probabilistic niche areas (95% level of inclusion). The probability of mesopelagic migrants overlapping the niche of epipelagic species was 20% (inferred from probability distributions mean; Fig. 4), while for overlap non-migrant mesopelagic species was 85%. Interesting patterns of niche overlap were also observed within ecological groups. For instance, the niche overlapping was higher within epipelagic groups than within the mesopelagic groups (Figs. 5 and 6; Supp. Files S1-S9), illustrating differences in resource partitioning. Additionally, except for seabirds, epipelagic species exhibited a wider isotopic niche (Figs. 5 and 6).

4. Discussion

Here we use bulk isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on a wide taxonomic and trophic variety of ecosystem components to evaluate the trophic coupling between epipelagic and mesopelagic ecosystems in warm oligotrophic waters. Additionally, we determined and compared isotopic-niche sizes and overlaps for multiple species to evaluate how environmental gradients between epipelagic and mesopelagic ecosystems shape ecological patterns of resource use and competition between species. Among others, we show a trophic dissimilarity between vertical layers that seems to be stronger in warm oligotrophic waters. Additionally, we demonstrate how trophic specialization varies with depth and explain the main factors that are likely driving the observed patterns. Finally, we discuss how the ecological traits of pelagic species highlighted in this study can respond to human impacts and increase their vulnerability in the Anthropocene.

4.1 Methodological constraints

SIA provides important clues to assess ecological interactions. However, some limitations could blur the interpretation of our results. First, although most of the data come from the white muscle of frozen specimens collected during the same period, we also used samples (seabirds and epipelagic fishes) from different years and based on different preservation modes and tissues (see

Methodology). Second, diet and timing of isotopic integration change according to organism sizes (e.g., Jennings et al. 2008, Vander Zanden et al. 2015). The inclusion of groups of very different size classes (e.g., zooplankton and large predators) can indeed make it difficult to interpret ecological models. Third, our analyses include highly migratory species (e.g., *Thunnus albacares* and *T. obesus*) where variability in the isotopic composition may represent not only trophic aspects but also oceanographic features affecting other localities (e.g., nutrient sources). Therefore, we acknowledge that isotopic incorporation into animal tissues is variable and baselines may vary locally and intra-annually, which may increase the variance of isotopic data and hampers the definition of statistically significant groups. However, based on our results, that was not the case, since robust and coherent isotopic groups could be clearly defined. Additionally, all direct niche overlap calculations were made between species caught in the same period and subjected to similar isotope extraction methodology. For highly migratory species, the coherence of isotopic niche patterns was also checked through gut content studies. Finally, given the nature of this work, it was not possible to incorporate all the size classes encompassed by the species analysed, which may lead to a loss of information in temporal and ontogenetic trophic variation. Therefore, here we do not address ontogenetic variability, focusing instead on broad ecological patterns among vertical pelagic layers.

4.2 Diverse trophic sources and microbial pathways in pelagic tropical ecosystems

Cluster analysis identified five major isotopic groups (I–Mesopelagic; II–Epipelagic; III–Zooplankton; IV–Others; and V–POM). Groups III, IV, and V were expected since they represent different size classes, trophic guilds, and ecosystem compartments. However, the fact that epipelagic and mesopelagic species present significantly different isotopic signatures is more intriguing since they both include organisms with similar sizes and trophic guilds.

The isotopic dissimilarity between the epipelagic and mesopelagic groups is related to the isotopic enrichment in $\delta^{15}\text{N}$ and depletion in $\delta^{13}\text{C}$ along depth gradient. This pattern was also reported in other pelagic ecosystems, as in the central North Pacific (Romero-Romero et al., 2019), eastern tropical North Atlantic (Czudaj et al., 2020), and Gulf of Mexico (Richards et al.,

2018). The most likely explanation for the enrichment in $\delta^{15}\text{N}$ is the microbial reworking, which preferentially breaks bonds containing ^{14}N and leaves the residual material isotopically heavier from newly formed particles in the epipelagic zone (Mintenbeck et al., 2007; Hannides et al., 2013). Additionally, biological reworking and disturbance of zooplankton also cause fractionation of $\delta^{13}\text{C}$ towards lighter isotopic values, since these activities enhance physical degradation and boost the formation of isotopically distinct suspended particles (Jeffrey et al., 1983; Altabet, 1988;).

The isotopic segregation with depth and migration pattern thus reveals that pelagic species access resources originating from different food sources mostly autotrophic-based (epipelagics) and microbial heterotrophic-based (mesopelagics). This result is in line with increasing evidence of an active deep-sea pelagic food web supported by microbial pathways *via* remineralized organic particles (Gloeckler et al., 2018; Bode et al., 2021). Additionally, by considering a broad taxonomic and trophic variety of species, we observed a trophic dissimilarity between epipelagic and mesopelagic communities stronger than previously reported elsewhere. Indeed, additionally to the clear isotopic segregation through cluster analyses, the mean probability of niche overlap between epipelagic and mesopelagic species was relatively low even for vertical migrants (ranging from 21 to 44%). Contrarily, in Hawaiian waters mesopelagic migrant species presented isotopic values similar to epipelagic species, suggesting a trophic activity mostly based on surface-derived material (Gloeckler et al., 2018). Likewise, in the Gulf of Mexico, deep-living fish predators receive most of their carbon source (>73%) from epipelagic food resources (Richards et al., 2018).

The higher trophic distinction between vertical layers in the SWTA may be due to the predominance of heterotrophy at the base of the food-web, as suggested by recent studies (Farias et al., 2022; *under review*). Despite being a typical oligotrophic system with strong nitrogen limitation all year round, the SWTA has a lower nitrogen:phosphorus ratio (3:1; Farias et al., 2021) than other oligotrophic systems like the Tropical Pacific (7-10:1; Yasunaka et al., 2019) and the Mediterranean Sea (5:1; Mena et al., 2019). This difference leads to significant structural changes in phytoplankton communities that could further enhance the relevance of heterotrophy

(Farias et al., 2022, under review). Likewise, studies comparing regions with contrasting productivity levels have observed higher $\delta^{15}\text{N}$ values in mesopelagic species from warmer and less productive waters, indicating a stronger link with heterotrophic activity and the dominance of an alternative microbial food web (heterotrophic nanoflagellates–ciliated protozoa–meso–zooplankton–fish; Czudaj et al., 2020). Another factor that could be relevant is the high abundance of gelatinous organisms in the SWTA (Tosseto et al., 2021). These gelatinous micro-filter feeders play a significant role in grazing on heterotrophic bacteria and nanoflagellates and providing energy to mesopelagic communities (Eduardo et al., 2020a, 2021), potentially promoting a shortcut in the microbial food web and increasing trophic dissimilarities.

In addition to the increased heterotrophic activity, warm oligotrophic waters are likely to have a more restricted direct connection between epipelagic and mesopelagic layers, due to intense temperature gradients, strong thermohaline stratification, higher luminosity, and low density of prey (Eduardo et al., 2020b; Hernández-León et al., 2020). As an example, in the equatorial upwelling more large phytoplankton cells are produced than in oligotrophic areas (Le Bouteiller et al., 1992; Bertrand et al., 1999). As a result, the zooplankton diet consists of a greater proportion of phytoplankton in the former case, leading to a closer relationship between zooplankton and surface food production. The inverse situation is observed in the oligotrophic areas, where the system generates a smaller proportion of larger phytoplankton cells and zooplankton likely rely more on alternative sources of energy in deep waters, such as those heterotrophic based (Le Bouteiller et al., 1992; Bertrand et al., 1999). Furthermore, the trophodynamics, migratory behaviour, and functional roles of some mesopelagic fishes are expected to be modulated by the latitudinal change in thermohaline structure. For instance, in most tropical regions, the viperfish (*Chauliodus sloani*) remains in deep layers to feed, while in temperate regions it comes up to shallow waters and interacts with epipelagic prey and predators (Eduardo et al., 2020b).

The high energetic costs and predation risks of migration from deep layers must be also balanced by the access to the abundant prey in the epipelagic layer (Robison, 2004). However, this requirement may not always be met in warm oligotrophic ocean areas where the density of

zooplankton is relatively low (Robison, 2004; Hernández-León et al., 2020). For instance, the deeper distribution of mesopelagic fishes in oligotrophic waters has also been correlated with the lower abundance of zooplankton and lower shading, which is translated into a higher luminosity and a less advantageous “anti-predation window” (Prihartato et al., 2016). Hence, in tropical oligotrophic waters, suspended particles remineralized by microbial pathways are likely to have greater nutritional importance for mesopelagic communities, as reflected in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, although mesopelagic migrants show a stronger association with a heterotrophic-based food web, the isotopic composition of some migrant species (e.g., *Argyropelecus aculeatus*, *Diaphus brachycephalus* and *Lepidophanes guenteri*) reveals the use of energy produced by autotrophic processes. Thus, even in warm oligotrophic waters, vertical migrants directly benefit from epipelagic resources and contribute to the carbon storage and provisioning of food for deep-sea biota.

It is important to note that due to variations in isotopic baseline with depth, using bulk $\delta^{15}\text{N}$ values is not adequate to calculate trophic levels within mesopelagic communities, as well as to differentiate the trophic importance of organic particles from different sizes. For that, amino acid compound-specific isotope analysis (AA-CSIA) would be more appropriate. This technique allows the estimation of the contribution of heterotrophic protists to the trophic position of metazoan consumers (Glockler et al., 2018; Bode et al., 2021). However, based on our results, we conclude that, when including a broad taxonomic and trophic variety of species, bulk isotopes can be a valuable tool for tracing the vertical nutrient export pathways, as the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are modified by heterotrophic microbial activities in physical processes at depth. This is particularly important considering that AA-CSIA is an expensive tool still not available for most research groups worldwide, especially in developing countries.

4.3 Niche overlap and resource partitioning in tropical pelagic ecosystems

We also compared epipelagic and deep-sea ecosystems to determine how environmental gradients shape ecological patterns of resource use and competition between pelagic species. Most species showed a relatively wide niche breadth and large overlaps in the epipelagic realm, consistent with

generalist habits. Indeed, about 20 prey categories were found for epipelagic micronektonivores through gut content analyses along our study area, supporting evidence of a generalist feeding habit (Albuquerque et al., 2019; Martins et al., 2021). Contrarily, in the mesopelagic realm species displayed smaller niche breadth and overlap, consistent with specialist habits. This finding is also supported by gut content analyses (Eduardo et al., 2020a, 2020b). Although earlier studies argued that the decreasing food abundance in deep-sea waters would lead to generalist habits, there are only a few examples corroborating the “eat anything you see in a food-poor environment” hypothesis (Drazen and Sutton, 2017). For instance, many deep-sea taxa are predictable in their primary prey, showing specialization through multidimensional niches and several mechanisms to avoid competitive exclusion (Hopkins and Gartner Jr., 1997; Hopkins and Sutton, 1998; Eduardo et al., 2020a; Eduardo et al., 2021). Additionally, many of the unique adaptations in mesopelagic species, such as bioluminescence, large expandable mouths, and long teeth, are more likely to ensure a higher capture-per-encounter rate than a greater diversity of prey (Drazen and Sutton, 2017; Priede, 2017).

The pattern of trophic specialization in deep-sea species fits the classical competition theory, which envisages that during food scarcity species will specialize and reduce interspecific dietary overlap (Schoener, 1974; Abrams, 1983). However, in shallow demersal habitats, substrates with fewer food resources included specimens with larger isotopic niches, suggesting that a resource-limited context led to generalist diets (Pelage et al., 2022). Similarly, two herbivorous characids in a floodplain lake had broadly overlapping diets during the dry season and lower dietary overlap during the wet season when food resources are more available (Esteves and Galetti Jr., 1995). This evidence indicates that in addition to food availability other major factors may drive the trophic specialization of species. For instance, specialization has been proposed as an evolutionary response to an environment that is stable over space and time (Kassen, 2002). Environmental heterogeneity generates diversifying selection, so if there are no constraints on the ecological niche evolution, the breadth of adaptation evolves to match the amount of environmental variation (Via and Lande, 1985). Therefore, ecological specialists evolve in environments that are relatively homogeneous in space and time whereas ecological

generalists evolve in environments that are heterogeneous in either dimension (Kassen, 2002). In summary, in addition to the decreasing food availability, the high stability of deep-sea waters may also explain the high trophic specialization of mesopelagic species.

4.4 Main findings and implications in the Anthropocene

Here we show that pelagic species access resources originating from different sources, mostly autotrophic-based (epipelagics) and microbial heterotrophic-based (mesopelagics). This leads to a trophic dissimilarity between vertical layers, which seems to be prominent in warm oligotrophic waters. Additionally, we show that trophic specialization increases in deep-sea species and argue that food availability and environmental stability are among the main drivers of this pattern. Together, both the feeding on suspended particles and specialization have allowed mesopelagic species to adapt and thrive throughout the evolutionary course. However, in the context of strong anthropic impacts and rapid ecological changes, these traits can also increase the vulnerability of mesopelagic communities.

Mesopelagic ecosystems are stable environments, which favour species specialization. However, in the past decades, the adverse impacts of climate change (Levin et al., 2019; Ariza et al., 2022), plastic pollution (Justin et al., 2022; Ferreira et al., 2022, 2023), and exploitation of deep-sea resources are rapidly growing (Hidalgo and Browman, 2019; Drazen et al., 2020). Changes in the mesopelagic domain will probably reduce specialists fitness and affect species local persistence (Clavel et al., 2011). In many cases, global change may have the same effects (positive or negative) on specialists and generalists, but not to the same degree. Competition induced by these differential responses will determine the relative success of generalists over specialist species (Clavel et al., 2011). Specialist species can also be more vulnerable to contaminants. For example, morphological traits and niche partitioning were primary predictors of the microplastic intake rates in abundant mesopelagic species (Ferreira et al., 2023)

The high nutritional dependence on remineralized suspended particles can also make mesopelagic species vulnerable since changes in the size of dominant plankton cells and the occurrence of gelatinous blooms predicted in climatic change scenarios can profoundly influence

the export of fresh organic matter to great depths (Smith et al., 2013; Levin et al., 2019). Additionally, the expected increase in thermal stratification can reduce the depth of the surface mixed layer, favouring remineralization in surface layers, which hinders the export of particles and nutrients to deeper water (Smith et al., 2013; Levin et al., 2019). Contaminants may also be present in suspended particles. For example, high microplastic contamination rates in mesopelagic vampire squid have been associated with its feeding strategy of ingesting marine snow (Ferreira et al., 2022). Finally, pelagic faunas of low and mid-latitudes are predicted to lose up to 22% of their biomass by the end of the 21st century (Ariza et al., 2022). This decrease will also act synergistically with all other sources of impact and threat to marine communities along with many of their essential ecosystem processes.

Acknowledgement

We acknowledge the officers and crew of the FV *Antea* for their contribution to the success of the operations. Thanks also to the BIOIMPACT (UFRPE) and LEMAR (UFRPE) students for their support. For running stable isotopes, we thank Jean-Marie Munaron. We thank the CNPq (Brazilian National Council for Scientific and Technological Development) for providing research grants to Flávia Lucena-Frédou, Thierry Frédou, and Michael Mincarone (grants 308554/2019-1, 307422/2020-8, and 314644/2020-2, respectively).

Funding

This study is a contribution to the LMI TAPIOCA, program CAPES/COFECUB (88881.142689/2017-01), EU H2020 TRIATLAS project (grant agreement 817578), Boticario foundation project MAFALDA and JEAÍ TABASCO. Surveys of ABRACOS were funded by the French oceanographic fleet.

Figures Caption

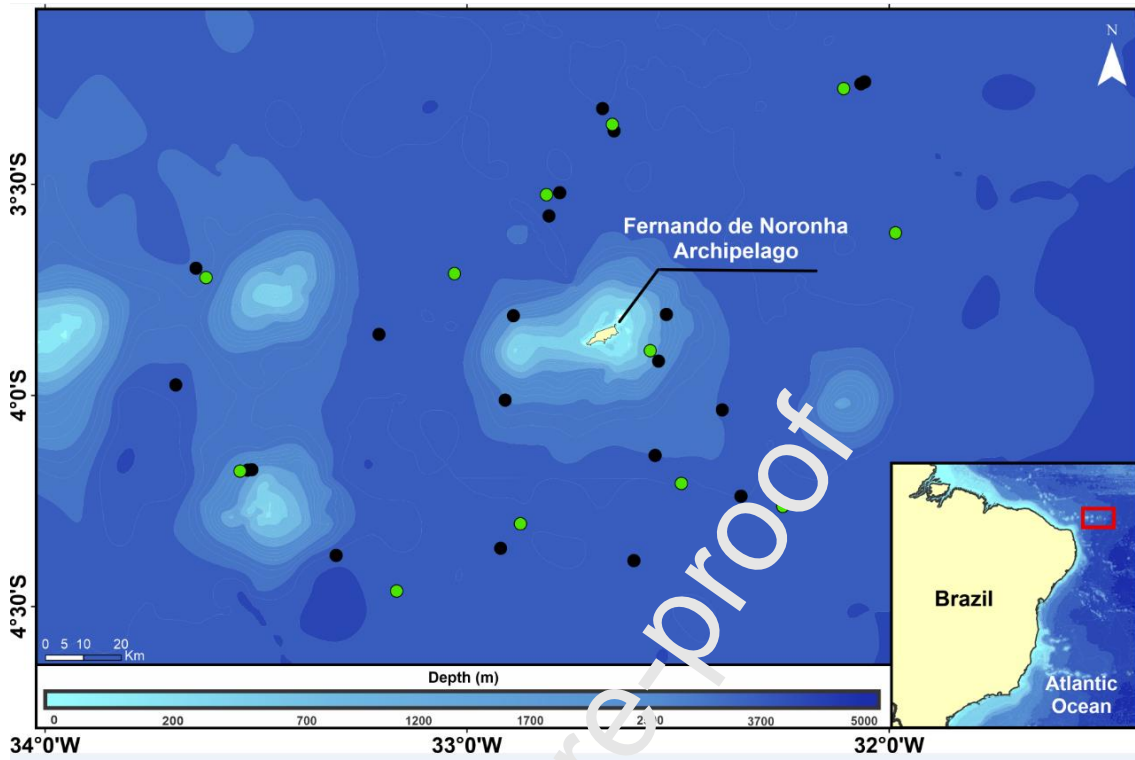


Figure 1. Fernando de Noronha Archipelago, off northeast Brazil. Dots indicate the position of the pelagic (black) and bongo (green) trawls of the survey ABRACOS 2.

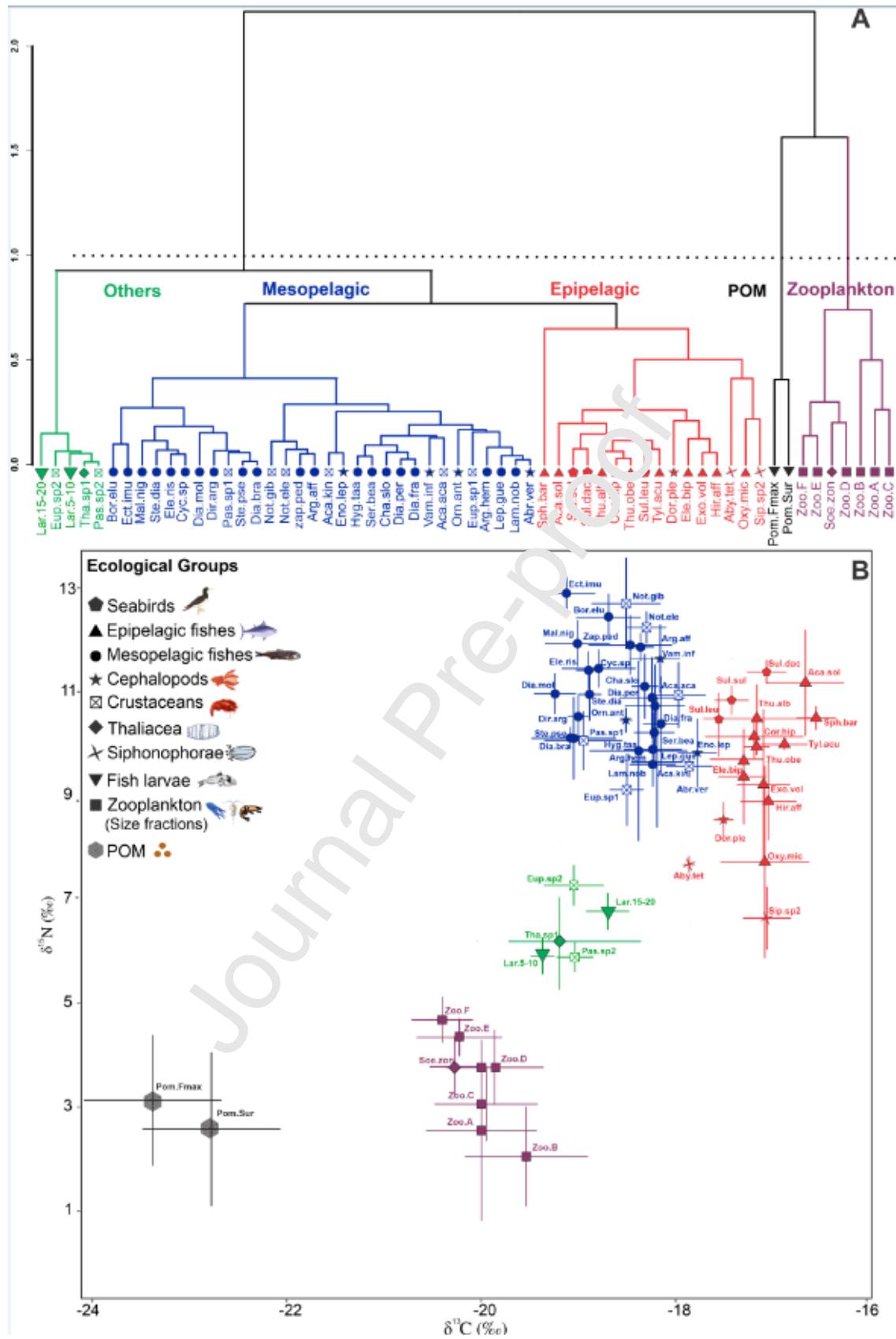


Figure 2. Dendrogram from cluster analyses (A) and biplot based on stable isotopes of bulk carbon and nitrogen of pelagic species and groups collected off the Fernando de Noronha Archipelago (B). Colours indicate different groups identified by the cluster analysis.

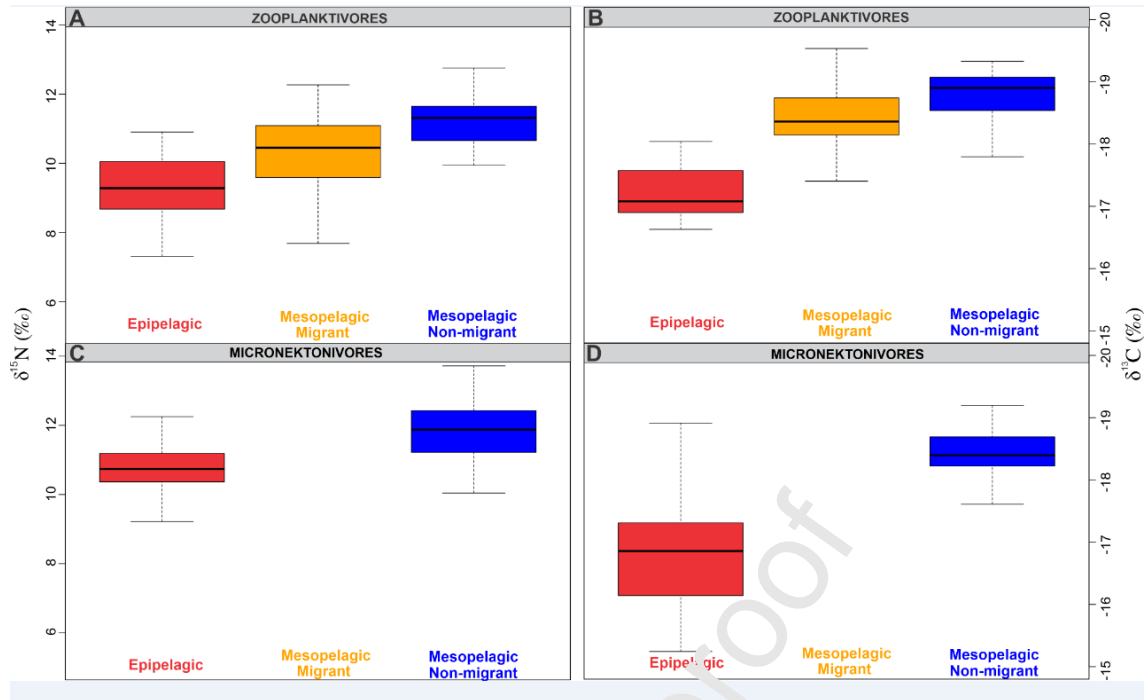


Figure 3. Boxplot of bulk stable isotopes of nitrogen (A, C) or carbon (B, D) for zooplanktivores (A, B) and micronektonivores (C, D) pelagic species collected off the Fernando de Noronha Archipelago. Species were grouped considering their habitat, migratory behaviour, and trophic guild. Black horizontal lines and boxes represent median values and interquartile ranges, respectively. Dashed lines represent the data range limits. There are no species to represent the mesopelagic migrant micronektonivores.

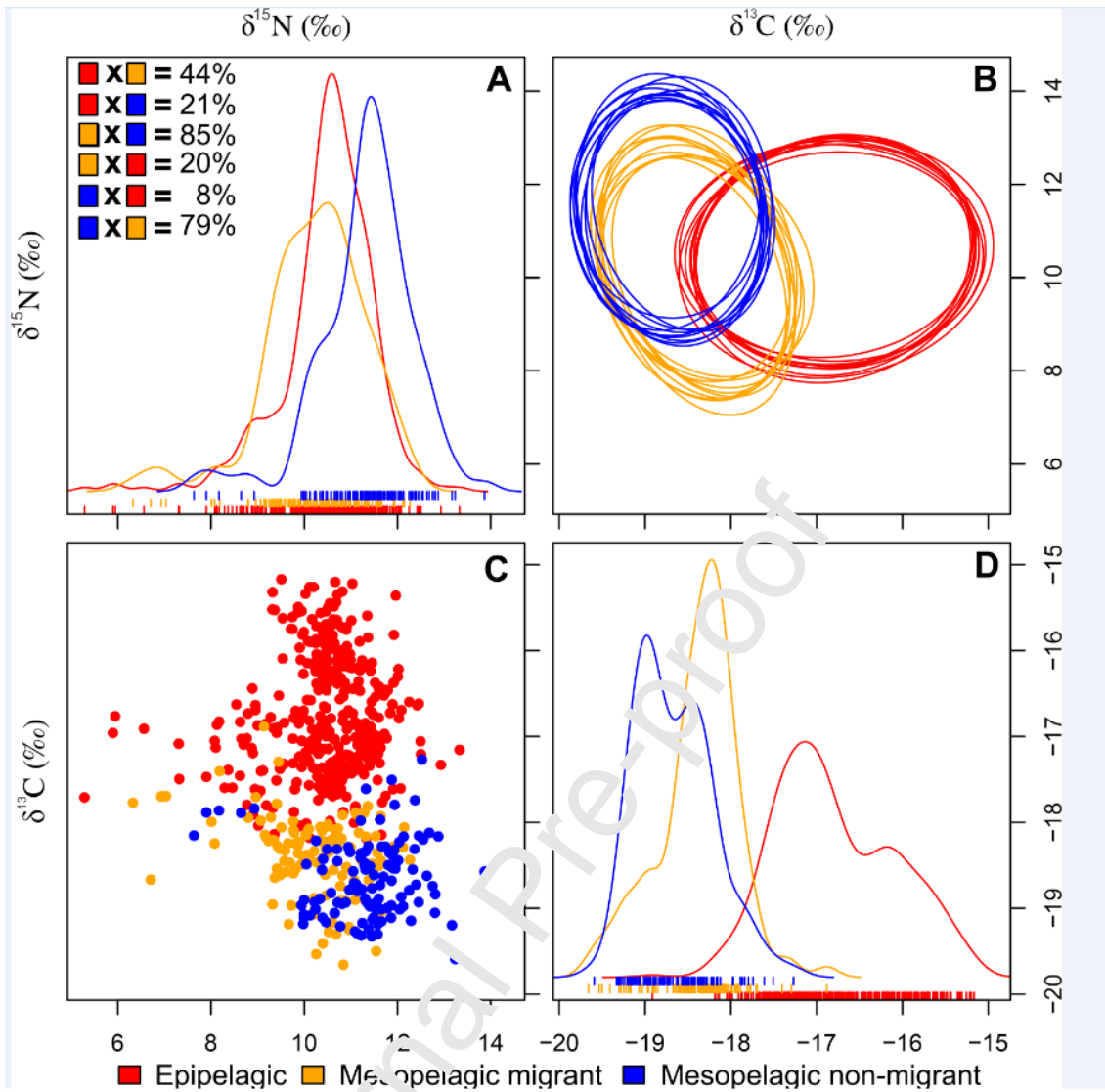


Figure 4. NicheROVER plots for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the species grouped by habitat and migration pattern. Panel A: one-dimensional density distributions for $\delta^{15}\text{N}$; Panel B: random two-dimensional elliptical projections of a specified niche area of 95% for each group and pair of isotopic ratios; Panel C: two-dimensional scatterplots of raw data for each species and pair of isotopic ratios; Panel D: one-dimensional density distributions for $\delta^{13}\text{C}$. Numbers in Panel A represent the mean value of the probability distributions from the overlap metric (probability of species group displayed on the left side overlapping onto those displayed on the right side considering a specified niche area of 95%).

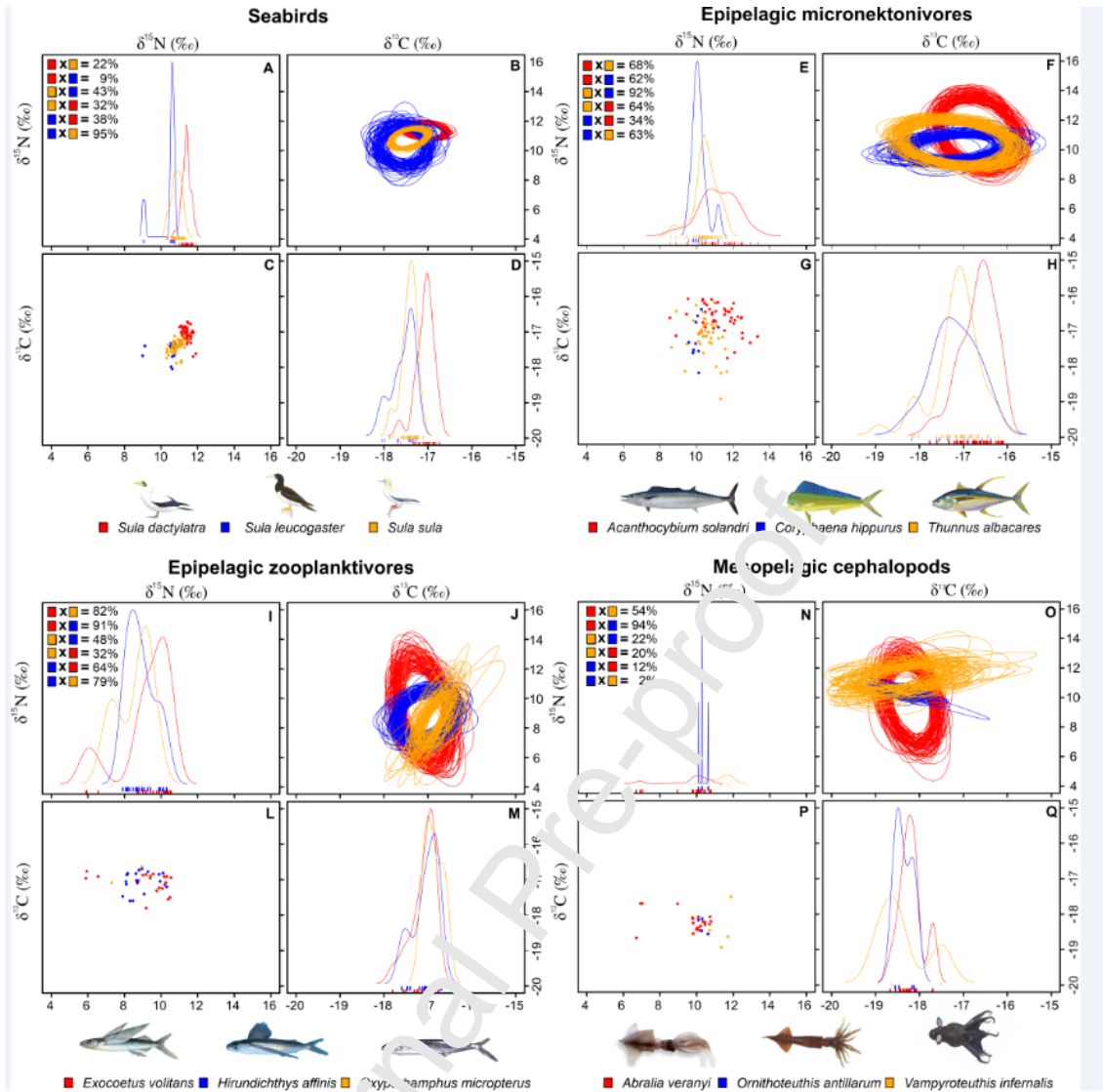


Figure 5. NicheROVER plots for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for within groups organized by taxonomic group, habitat (epipelagic or mesopelagic), and trophic guild (zooplanktivores and micronektonivores). Panels A, E, I, and N: one-dimensional density distributions for $\delta^{15}\text{N}$; Panels B, F, J, and O: random two-dimensional elliptical projections of a specified niche area of 95% for each group and pair of isotopic ratios; Panels C, G, L, and P: two-dimensional scatterplots of raw data for each species and pair of isotopic ratios; Panels D, H, M, and Q: one-dimensional density distributions for $\delta^{13}\text{C}$. Numbers in Panel A, E, I, and N represent the mean value of the probability distributions from the overlap metric (probability of species group displayed on the left side overlapping onto those displayed on the right side considering a specified niche area of 95%).

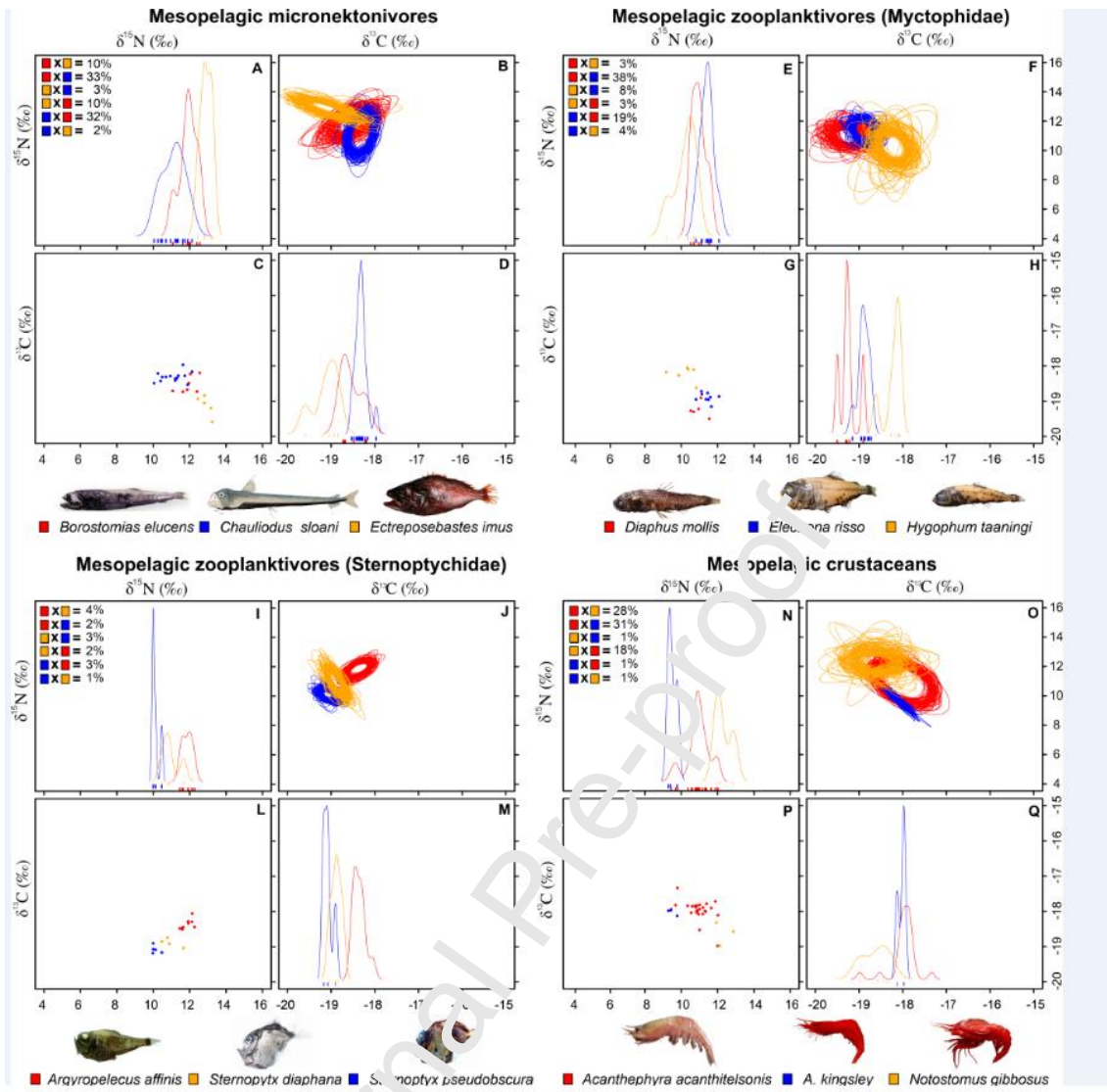


Figure 6. NicheROVER plots for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for within groups organized by taxonomic group, habitat (epipelagic or mesopelagic), and trophic guild (zooplanktivores and micronektonivores). Panels A, E, I, and N: one-dimensional density distributions for $\delta^{15}\text{N}$; Panels B, F, J, and O: random two-dimensional elliptical projections of a specified niche area of 95% for each group and pair of isotopic ratios; Panels C, G, L, and P: two-dimensional scatterplots of raw data for each species and pair of isotopic ratios; Panels D, H, M, and Q: one-dimensional density distributions for $\delta^{13}\text{C}$. Numbers in Panel A, E, I, and N represent the mean value of the probability distributions from the overlap metric (probability of species group displayed on the left side overlapping onto those displayed on the right side considering a specified niche area of 95%).

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Table 1. Taxonomic classification, trophic guild (Zoo–Zooplanktivore; Micro–Micronektonivore.; UND–Undetermined; NA–Not Applicable), migration pattern (EM–Epipelagic Migrant; NEMI–Non-Epipelagic Migrant; UND–Undetermined; NA–Not Applicable), size (Seabirds–wing span; Fish–standard length; Crustaceans and Cephalopods–total length), and stable isotopes values of all species included in the analyses. All specimens were collected off the Fernando de Noronha Archipelago and associated seamounts. C:N ratio corresponds to the values before the lipid correction.

Ecological groups / Species	Species Code	Trophic Guild	Migration Pattern	<i>n</i>	Size (cm), mean ± SD	$\delta^{15}\text{N}$ (‰) mean ± SD	$\delta^{13}\text{C}$ (‰) mean ± SD	C:N mean ± SD
SEABIRDS								
<i>Sula dactylatra</i>	Sul.dac	Micro ¹	NEMI	44	42.2±1.3	11.3±0.2	-17.0±0.2	3.41±0.1
<i>Sula leucogaster</i>	Sul.leu	Micro ²	NEMI	12	-	10.3±0.6	-17.5±0.2	3.35±0.1
<i>Sula sula</i>	Sul.sul	Micro ¹	NEMI	48	39.4±1.1	10.8±0.3	-17.4±0.2	3.37±0.1
EPIPELAGIC FISHES								
<i>Acanthocybium solandri</i>	Aca.sol	Micro	NEMI	46	112.9±18.4	11.1±1.0	-16.6±0.4	3.21±0.1
<i>Coryphaena hippurus</i>	Cor.hip	Micro ³	NEMI	12	104.4±16.4	10.1±0.4	-17.1±0.5	3.41±0.2
<i>Elagatis bipinnulata</i>	Ela.bip	Micro ⁴	NEMI	3	67.3±9.2	9.4±0.9	-17.2±0.4	3.44±0.3
<i>Exocoetus volitans</i>	Exo.vo	Zoo ⁵	NEMI	20	16.1±2.0	9.2±1.4	-17.0±0.3	3.16±0.0
<i>Hirundichthys affinis</i>	Hir.aff	Zoo ⁶	NEMI	19	19.4±1.7	8.9±0.7	-17.0±0.3	3.16±0.0
<i>Oxyporhamphus micropterus</i>	Oxy.mic	Zoo ⁵	NEMI	4	13.2±3.7	7.7±1.8	-17.0±0.4	3.14±0.0
<i>Thunnus albacares</i>	Thu.alb	Micro ³	NEMI	39	77.1±19.7	10.4±0.7	-17.1±0.5	3.24±0.2
<i>Thunnus obesus</i>	Thu.obe	Micro ⁷	NEMI	3	56.3±8.5	9.9±0.1	-17.1±0.1	3.21±0.1
<i>Tylosurus acus</i>	Tyl.acu	Micro ⁸	NEMI	3	89.6±2.3	10.0±0.1	-16.8±0.2	3.27±0.1

MESOPELAGIC FISHES

<i>Argyropelecus aculeatus</i>	Arg.acu	Zoo ⁹	EMI ⁹	3	5.2±1.3	8.2±1.6	-17.8±0.1	3.30±0.0
<i>Argyropelecus affinis</i>	Arg.aff	Zoo ⁹	EMI ⁹	10	5.2±0.8	11.8±0.3	-18.3±0.1	3.31±0.0
<i>Argyropelecus hemigymnus</i>	Arg.hem	Zoo ⁹	NEMI ⁹	10	2.4±0.4	9.9±1.7	-18.3±0.5	3.39±0.0
<i>Borostomias elucens</i>	Bor.elu	Micro ¹¹	NEMI ¹⁰	9	16.2±1.2	11.9±0.5	-18.3±0.4	3.34±0.2
<i>Chauliodus sloani</i>	Cha.slo	Micro ¹²	NEMI ¹²	15	18.1±1.1	11.1±0.6	-18.3±0.1	3.26±0.0
<i>Cyclothone</i> sp.	Cyc.sp	Zoo ¹⁵	NEMI ¹⁰	24	3.3±1.1	11.4±0.4	-18.7±0.4	3.45±0.0
<i>Diaphus brachycephalus</i>	Dia.bra	Zoo ¹³	EMI ¹³	13	5.0±2.1	10.1±0.8	-19.0±0.4	3.48±0.1
<i>Diaphus fragilis</i>	Dia.fra	Zoo ¹³	EMI ¹³	11	7.3±0.4	10.7±0.8	-18.2±0.3	3.47±0.2
<i>Diaphus mollis</i>	Dia.mol	Zoo ¹³	EMI ¹³	5	5.2±0.3	10.9±0.4	-19.2±0.2	3.46±0.1
<i>Diaphus perspicillatus</i>	Dia.per	Zoo ¹³	EMI ¹³	8	3.2±0.3	10.8±0.8	-18.2±0.3	3.50±0.1
<i>Dirtemus argenteus</i>	Dir.arg	Zoo ¹¹	NEMI ¹⁴	13	5.3±1.5	10.5±0.4	-19.0±0.1	3.24±0.0
<i>Ectreposebastes imus</i> *	Ect.imu	Micro ¹¹	NEMI ¹⁴	5	19.1±1.7	11.9±0.3	-19.1±0.3	4.30±0.2
<i>Electrona risso</i>	Ele.ris	Zoo ¹³	NEMI ¹³	9	5.6±0.1	11.4±0.4	-18.8±0.1	3.24±0.0
<i>Hygophum taaningi</i>	Hyg.ta	Zoo ¹³	EMI ¹³	6	5.5±0.2	10.2±0.6	-18.2±0.2	3.32±0.1
<i>Lampanyctus nobilis</i>	Lam.nob	Zoo ¹³	EMI ¹³	7	7.4±1.5	9.6±0.4	-18.2±0.2	3.31±0.0
<i>Lepidophanes guenterii</i>	Lep.gue	Zoo ¹³	EMI ¹³	13	5.7±0.6	9.9±0.7	-18.2±0.3	3.34±0.0
<i>Malacosteus niger</i>	Mal.nig	Zoo ¹⁶	NEMI ¹⁰	4	10.7±2.0	11.9±0.4	-19.0±0.3	3.35±0.0
<i>Serrivomer beanii</i>	Ser.bea	Zoo ¹¹	EMI ¹⁴	4	42.2±6.0	10.3±0.9	-18.1±0.2	3.31±0.0
<i>Sternoptyx pseudobscura</i>	Ste.pse	Zoo ⁹	NEMI ⁹	5	3.5±1.1	10.1±0.2	-19.0±0.1	3.50±0.0

<i>Sternopytx diaphana</i>	Ste.dia	Zoo ⁹	EMI ⁹	4	2.2±0.4	10.9±0.5	-18.8±0.1	3.41±0.1
<i>Zaphotias pedaliotus</i>	Zap.ped	Zoo ¹⁵	NEMI ¹⁰	12	5.7±1.0	11.8±0.6	-18.5±0.4	3.45±0.1
EPIPELAGIC								
CEPHALOPODS								
<i>Doryteuthis plei</i>	Dor.ple	Zoo ¹⁷	NEMI	4	5.5±2.1	8.5±0.9	-17.5±0.1	3.34±0.0
<i>Enoploteuthis leptura</i>	Eno.lep	Zoo ¹¹	NEMI	12	4.1±1.5	9.8±0.7	-17.7±0.2	3.51±0.1
MESOPELAGIC								
CEPHALOPODS								
<i>Abralia veranyi</i>	Abr.ver	Zoo ¹⁸	EMI ¹⁸	20	4.1±2.5	9.6±1.2	-18.1±0.3	3.48±0.1
<i>Ornithoteuthis antillarum</i>	Orn.ant	Zoo ¹⁹	EMI ¹⁹	2	4.5±2.1	10.4±0.2	-18.5±0.1	3.48±0.0
<i>Vampyroteuthis infernalis</i>	Vam.inf	Micro ²⁰	NEMI ²⁰	5	3.7±1.3	11.6±0.6	-18.1±0.7	3.53±0.2
CRUSTACEANS								
<i>Acanthephyra acanthitelsonis</i>	Aca.aca	Zoo ²¹	NEMI ²¹	26	2.2±0.4	10.9±0.6	-17.9±0.3	3.27±0.2
<i>Acanthephyra kingsley</i>	Aca.kin	Zoo ²¹	NEMI ²¹	5	1.8±0.2	9.6±0.5	-17.8±0.2	3.25±0.1
Euphasiidae sp. 1	Eup.sp.1	Zoo ¹¹	EMI ¹¹	4	1.5±0.1	9.1±0.7	-18.5±0.2	3.21±0.1
Euphasiidae sp. 2	Eup.sp2	Zoo ¹¹	EMI ¹¹	3	1.4±0.1	7.3±0.4	-19.0±0.3	3.28±0.1
<i>Notostomus elegans</i>	Not.ele	Micro ²²	NEMI ¹¹	2	2.5±1.1	12.2±0.3	-18.2±0.2	3.39±0.1
<i>Notostomus gibbosus</i>	Not.gib	Micro ²²	NEMI ¹¹	4	4.1±0.6	12.6±0.9	-18.5±0.3	3.42±0.1
Pasiphaeidae sp. 1	Pas.sp1	Zoo ¹¹	UND	11	4.1±0.8	10.0±0.6	-18.9±0.4	3.18±0.1
Pasiphaeidae sp. 2	Pas.sp2	UND	UND	8	2.2±0.6	6.11±0.1	-19.0±0.1	3.92±0.1

THALIACEA

<i>Soestia zonaria</i>	Soe.zon*	UND	EMI ¹¹	2	-	3.8±0.6	-20.2±0.2	5.35±0.2
Thaliacea sp.	Tha.sp*	UND	UND	6	-	6.18±1.9	-19.1±0.8	4.86±0.8

SIPHONONOPHORAE

<i>Abylopsis tetragona</i>	Aby.tet	Zoo ¹¹	EMI ¹¹	3	-	7.8±0.2	-17.8±0.1	3.31±0.0
Siphonophorae sp.	Sip.sp	UND	UND	3	-	6.7±0.6	-17.0±0.2	3.48±0.1

FISH LARVAE

Teleostei larvae 15–20 mm	Lar.15-20	UND	NEMI ¹¹	5	-	7.1±0.6	-18.5±0.4	3.2±0.1
Teleostei larvae 5–10 mm	Lar.5-10	UND	NEMI ¹¹	10	-	5.9±0.4	-19.6±0.1	3.2±0.1

ZOOPLANKTON (size fractions)

Zoo A (<64-100 µm)	Zoo.A*	UND	UND	19	-	2.0±1.	-19.8±0.5	4.7±0.2
Zoo B (100–200 µm)	Zoo.B*	UND	UND	19	-	1.9±0.8	-19.4±0.5	4.6±0.7
Zoo C (200–500 µm)	Zoo.C*	UND	UND	19	-	3.0±0.6	-19.4±0.3	5.6±1.2
Zoo D (500–1000 µm)	Zoo.L*	UND	UND	18	-	4.2±0.4	-19.1±0.3	4.2±0.4
Zoo E (1000–2000 µm)	Zoo.E*	UND	UND	17	-	4.6±0.4	-20.3±0.9	4.8±0.6
Zoo F (>2000 µm)	Zoo.F*	UND	UND	13	-	4.9±0.4	-19.6±0.4	4.5±0.3

POM

POM Max fluorescence	Pom.Fmax	NA	NA	26	-	3.1±1.2	-20.3±0.9	4.5±0.9
POM Surface	Pom.Sur	NA	NA	30	-	2.5±1.4	-19.6±0.4	4.6±1.1

¹Schreiber and Hensley (1976); ²Mancini and Bugoni (2014); ³Martins et al. (2021); ⁴Albuquerque et al. (2019); ⁵Van Noord et al. (2013); ⁶Lewis and Brundritt (1962); ⁷Silva et al. (2019); ⁸Châari et al. (2016); ⁹Eduardo et al. (2020a); ¹⁰Villarins et al. (2022); ¹¹Our dataset; ¹²Eduardo et al. (2020b); ¹³Eduardo et al., (2021); ¹⁴Eduardo et al. (2022); ¹⁵Hopkins et al. (1996); ¹⁶Sutton (2005); ¹⁷Gasalla et al. (2010); ¹⁸Guerra-Marrero et al. (2020); ¹⁹Arkhipkin et al. (1998); ²⁰Golikov et al. (2019); ²¹Hopkins et al. (1994); ²² Podeswa and Pakhomov (2015). * Lipid corrected species.

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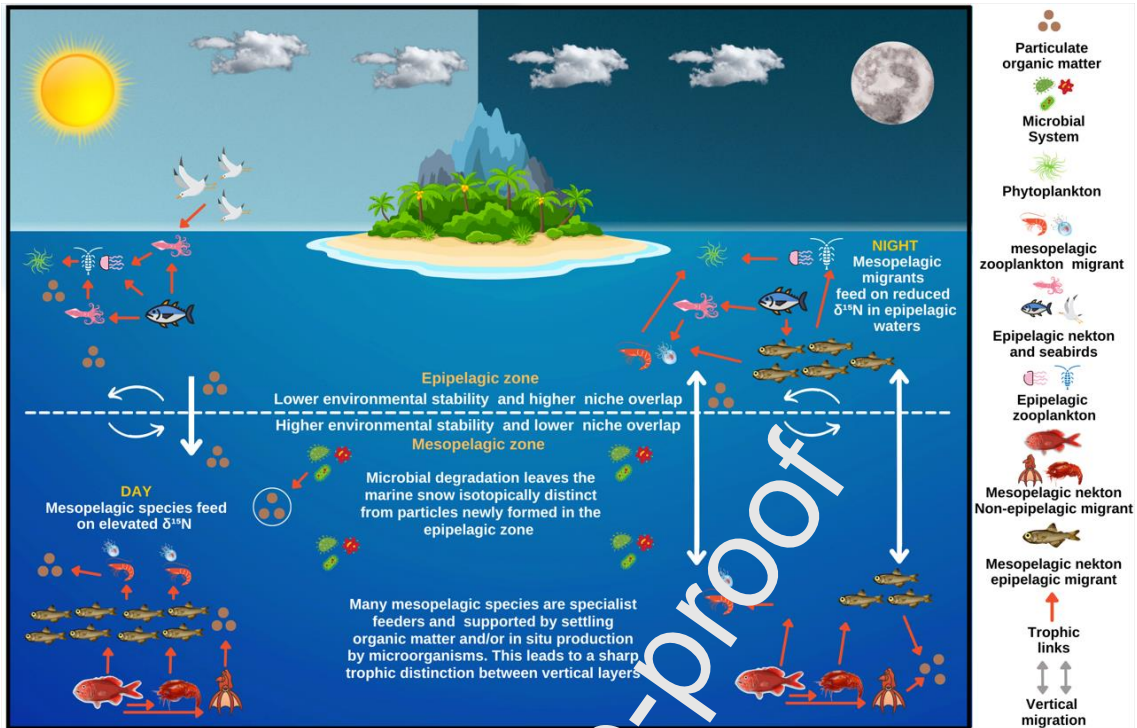
Declaration of interests

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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Graphical abstract



Highlights:

- Pelagic trophic dissimilarity seems to be prominent in warm oligotrophic waters.
- Mesopelagic species rely mostly on microbial heterotrophic-based food sources.
- Epipelagic species rely mostly on autotrophic-based food sources.
- Food availability and environmental stability lead to a high trophic specialization and high niche partitioning in mesopelagic species.
- High trophic specialization increases the vulnerability of deep-sea species.

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