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Environmental variability shapes trophic and resource partitioning between epipelagic and mesopelagic biomes in oceanic provinces: Implications in a globally changing ocean

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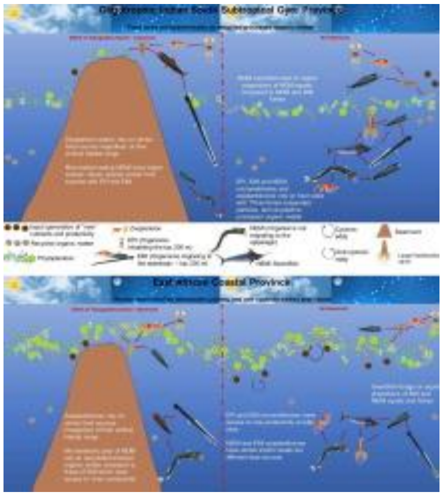
Abstract :

Trophic links between the epipelagic (top 200 m) and mesopelagic layers of the Indian Ocean from 2002 to 2016 were investigated by carbon and nitrogen stable isotope ratios of 2405 samples that encompass the base of trophic webs, and primary, secondary and tertiary consumers. The samples include particulate organic matter, gastropods, gelatinous organisms such as salps and pyrosomes, crustaceans, mesopelagic fishes, micronektonic and nektonic squids, tuna and swordfish. Stable δ13C and δ15N values were used to investigate trophic and resource partitioning between epipelagic vs mesopelagic (migrators and non-migrators), ecological groups (zooplanktivorous vs micronektivorous), and at seamounts and off-seamount locations. We also investigated how contrasting environmental conditions within two biogeographic provinces, the ISSG (Indian South Subtropical Gyre) and EAFR (East African Coastal Province), influenced stable isotope patterns. Our data suggest that broad-scale biogeographic differences and local environmental conditions significantly shape stable isotope values. In oligotrophic systems, epipelagic migrating and non epipelagic-migrating organisms rely on food webs where suspended particles are 15N-enriched and organic matter recycled/re-processed. We show that seamounts form strong isotopic topographic barriers (which we define as "isobiome") that impact the trophic linkages/connections between epipelagic migrants and non-epipelagic migrants, and those with zooplanktivorous feeding strategies. This study reveals that the trophic and resource partitioning in the ocean is more complex than initially thought, when environmental variability, bathymetric gradients, and a wider range of samples are taken into account compared to earlier studies. We also showed that warmer oceans led to a reduction in productivity and potential shifts in food web trophic structure that remain to be investigated further. Finally, we discuss how important it is to unravel this complexity on a global scale given the vulnerability of epipelagic and mesopelagic communities due to anthropogenic pressures in the Anthropocene.

Graphical abstract



Highlights

► Environmental instabilities led to high isotopic niche overlaps. ► Seamounts form distinct “isobiomes” for mesopelagic species. ► Environmental, biogeographic, topographic and ecological variability between species drive trophic specialization of marine organisms. ► A changing ocean will shift the trophic distribution and resource partitioning of epipelagic and mesopelagic organisms.

Keywords : Isotopic niche, Isobiome, Seamounts, Mesoscale eddies, Oligotrophic, Biogeographic provinces

1. Introduction

The ocean is partitioned into several biomes including the epipelagic or euphotic biome that ranges from the sea surface to 200 m depth, the mesopelagic biome that extends from 200 to 1000 m, and the bathypelagic biome that extends below 1000 m (Sutton, 2013). While the euphotic biome supports primary production due to light penetration, the mesopelagic biome receives enough solar illumination for diurnal and nocturnal cycles but not for photosynthesis (Sutton, 2013). Some organisms inhabiting the mesopelagic biome link the epipelagic to deeper depths by their extensive diel vertical migration (DVM) to feed in surface layers at night (e.g., Béhagle et al., 2014; Annasawmy et al., 2018, 2019, 2020a; Eduardo et al., 2023), together with the downward export of organic carbon and potential sequestration at depth (Boyd et al., 2019; Le Moigne, 2019). The mesopelagic migrant biomass contributes to the export of carbon out of the euphotic zone (Ariza et al., 2015; Cotté et al., 2022). They thus provide a privileged unique or model system for investigating trophic connections in the ocean (Bode et al., 2021). For an ecosystem-based fisheries management, it is essential to link exploited commercial species to their prey, and understand the entire food web, including mesopelagic organisms (Gloeckler et al., 2018) which have not been historically considered in fisheries management.

Low-latitude oceanic ecosystems (between 30º and 0º N and S of the equator) are the largest and most ancient ecosystems on Earth that have enabled the evolution of overlapping trophic niches between mesopelagic fishes, crustaceans and squids (Hopkins and Gartner, 1992). The overlapping of niche parameters is linked to the food composition and size, as well as the vertical distribution of organisms. Multiple species co-occur in the epi- and mesopelagic biomes, especially at night when most of the active feeding takes place thus contributing to species "packing" (Hopkins and Gartner, 1992; Hopkins and Sutton, 1998). Nevertheless, some organisms do not migrate to epipelagic layers or feed exclusively at night, or they display specific individual variability in DVM, thus spreading the predation pressure over different spatial and temporal scales (Hopkins and Sutton, 1998; Romero-Romero et al., 2019). Different vertical habitat ranges may influence the trophic (i.e., the division of resources within the food chain or trophic levels of an ecosystem) and resource partitioning (i.e., the division of limited resources within an ecosystem among different species to reduce competition and enable coexistence) (Eduardo et al., 2023). There is a lack of studies investigating the trophic and resource partitioning between organisms inhabiting the epipelagic zone only, those migrating to the epipelagic zone and those that do not migrate, and between organisms displaying zooplanktivorous (i.e., zooplankton-eating) and micronektivorous (i.e., micronekton-eating) feeding strategies, especially in the understudied Indian Ocean.

Stable isotope analyses are common tools for studying marine food webs. Stable nitrogen isotopes ($\delta^{15}N$) provide insights into trophic level and food chain length, and stable carbon isotopes ($\delta^{13}C$) are commonly used to trace food sources (Fry, 2006). Trophic connections between the epi- and mesopelagic biomes have been previously studied on a small subset of samples at regionally localized and environmentally similar sites (Choy et al., 2015, 2016; Gloeckler et al., 2018; Eduardo et al., 2023). In this study, we compiled stable isotope data ($\delta^{13}C$ and $\delta^{15}N$ values) for a wide range of samples through the food web, from particulate organic matter (POM) to the top predator swordfish, *Xiphias gladius*, in the Western Indian Ocean. Our dataset consists of bulk stable isotope data for 2405 samples, opening the possibility to examine the trophic connections between epipelagic and mesopelagic ecosystems at contrasting oceanic provinces and seamounts. This broad-scale approach differs to previous studies that focused on stable isotope patterns within specific, localized regions. General objectives involved investigating (1) the isotopic niche areas and overlaps between broad categories (represented by POM, gastropod, zooplankton, gelatinous, micronekton, nekton, tuna, swordfish, and other pelagic fish), and (2) how environmental gradients between ecosystems and biogeographic provinces and seamounts shape ecological patterns of resource use. More specifically, this study shed light on the trophic and resource partitioning between epipelagic *vs* mesopelagic (migrators and non-migrators), ecological groups (zooplanktivorous *vs* micronektivorous), and at seamounts and off-seamount locations.

2. Materials and Methods

2.1 Study sites

The study sites were located at seamounts and off-seamount locations in the Indian South Subtropical Gyre (ISSG) and East African Coastal (EAFR) biogeochemical provinces (Longhurst, 1998; 2007) of the Western Indian Ocean and (Table 1 and Fig. 1). Longhurst's EAFR province corresponds to Sutton's ecoregion 20 called "Agulhas Current", with enhanced productivity (Sutton et al., 2017). The oligotrophic ISSG province refers to Sutton's Mid-Indian Ocean ecoregion 18, and Southern Indian Ocean ecoregion 19 (Sutton et al., 2017). Data from 15 cruises that occurred from 2002 to 2016 were compiled and analysed. The seamounts considered were La Pérouse, located approximately 160 km to the north-west of Reunion Island, and MAD-Ridge located some 200 km to the south of Madagascar.

2.2 Environmental measurements

For lack of consistent *in situ* observations across sampling sites, satellite observations were used. The mesoscale eddy field was described using level 4 processed daily delayed-time Absolute Dynamic Topography (ADT) at a spatial resolution of 0.25° (https://doi.org/10.48670/moi-00145). The level 4 processed daily mass concentration of chlorophyll *a* in sea water (hereafter referred to as "SSC") at 4-km spatial resolution (https://doi.org/10.48670/moi-00281), and level 4 processed daily sea water potential temperature (hereafter referred to as "SST") at a 0.25° resolution were also downloaded. ADT, SSC and SST data were provided by the E.U. Copernicus Marine Service Information (https://help.marine.copernicus.eu/en/). The elevation which represents the height or depth of the Earth's surface relative to a reference level, typically mean sea level, was obtained from GEBCO's bathymetric grid product version 2023 (GEBCO Compilation Group, 2023).

2.3 Data collection

POM samples were collected from Niskin bottles mounted on Sea-Bird 911 + CTD rosette systems at approximately 5-m depth (hereafter referred to as "POM Surface") and at the depth of the maximum fluorescence (hereafter referred to as "POM Fmax") during cruises conducted in 2009, 2010, and 2016 (Table 1). Between 4 and 8 litres of seawater were filtered on precombusted 25 or 47 mm glassfiber filters of 0.7 µm pore size. The filters were oven-dried at 50°C for 24h and saved at room temperature until further analyses (Section 2.3).

Zooplankton organisms were sampled with a Bongo net of 300 µm mesh towed to a maximum depth of 500 m and 200 µm mesh to a maximum depth of ~200 m during the 2016 cruises. During the Microton cruise conducted in 2010, zooplankton were collected with a 200- and 300-µm mesh size bongo net towed within the top 200 m of the water column (Table 1)and frozen on board at −

20 °C. Only copepods and mysids were selected for further analyses (Annasawmy et al., 2018). At the La Pérouse seamount in the ISSG and MAD-Ridge seamount in the EAFR, all samples were oven-dried at 50°C for 24h and frozen on board at − 20 °C until further analyses (Section 2.3).

Micronekton (crustaceans, fishes, and squids), and gelatinous organisms, of 2 to 20 cm in size, were collected with a MESOPELAGOS trawl net (mesh size of 30 mm in the wings and 4 mm in the codend) during ECOTEM cruises in 2004 and 2008. An International Young Gadoid Pelagic Trawl (IYGPT) net (80-mm mesh in the front reducing to 5 mm at the codend) was used during MESOP 2009, MICROTON, and La Pérouse and MAD-Ridge cruises. An IYGPT net with 10 mm at the codend was used during ECOTEM 5 cruise (Table 1). Samples were sorted into broad taxonomic groups on board and stored at −20ºC. Muscular tissue was analysed for stable isotope composition for fishes (dorsal white muscle), crustaceans (abdomen), squids (mantle), and whole individuals for salps and pyrosomes.

Swordish and tunas were collected with pelagic longlines and their white muscular tissue was sampled and stored at −20°C.

2.4 Stable Isotope Analysis

All samples (except for POM) were freeze-dried in a Christ Alpha 1–4 LSC freeze-dryer for 48 h and ground to a fine homogeneous powder using an automatic ball mill RETSCH MM200. Part of the POM filters and zooplankton samples were delipidated with dichloromethane on an accelerated solvent extraction system (ASE®, Dionex; Bodin et al., 2009) at the Plateau Chimie/Pôle Technique MARBEC (Sète, France) to remove lipids, and decarbonated using 1 N HCl to obtain unbiased δ^{13}C values. Untreated POM and zooplankton subsamples were analysed for δ^{15}N values (similar to Annasawmy et al. 2018). Samples were run through a Thermo Scientific FLASH 2000 elemental analyser coupled to a Delta V Plus mass spectrometer at the Pôle de Spectrométrie Océan (Plouzané, France) for carbon and nitrogen isotope ratios. The δ^{13}C and δ^{15}N values (in ‰) were derived from international standards according to the following equation:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = \left[\left(\frac{\mathrm{R}_{sample}}{\mathrm{R}_{standard}}\right) - 1\right] \times 1000$$

where R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N.

The analytical error was <0.15% for the nitrogen and carbon isotope measurements. The international isotopic standards of known δ^{13}C and δ^{15}N values of USGS-61, USGS-62 and USGS-63 Caffeine and IAEA-CH-6 sucrose were used. The home standard (Thermo acetanilide) was analysed every 70 samples for experimental precision and the certified values were reproduced within the confidence limits. Eight blanks were further evaluated at the beginning of each sample batch.

2.5 Data and statistical analyses

Each sample was classified according to a broad category (POM, gastropod, zooplankton, gelatinous, micronekton, nekton, tuna, swordfish, and other pelagic fish), vertical habitat (strictly epipelagic, epipelagic migrant, or non-epipelagic migrant), and trophic guild (detritivore, filter feeder, zooplanktivore, and micronektivore). Strictly epipelagic organisms inhabit only the first 200 m of the water column (referred to as EPI). Mesopelagic species vertically migrating into the upper 200 m of the water column at night are referred to as EMI, while non-epipelagic migrants remaining below 200 m during day and night are labelled as NEMI (Fig. 2; Annasawmy et al., 2020a; Eduardo et al., 2023).. Although swordfish can occupy epipelagic depths, they were shown to mostly forage below 200 m and migrate to the mixed layer mostly at night (Braun et al., 2022; Romanov et al., 2023), and are hence labelled as NEMI. Classifications were based on available information in literature (Supplementary Material 1). Since our datasets were collected across different time periods (Table1), they potentially represent different ecosystem functioning with varied oceanographic conditions. Data were further classified according to their collection in the biogeographic provinces (ISSG and EAFR) and off-seamount and seamount locations (according to Annasawmy et al., 2019 and Marsac et al., 2020).

Assumptions of normality using the Shapiro Wilk's test (Shapiro and Wilk, 1965) and homogeneity of variances using the Bartlett test (Bartlett, 1937), were computed in R (v. 4.2.2), prior to running the following statistical tests. Kruskal-Wallis non-parametric tests robust to the assumption of normality, were conducted to investigate the differences in stable isotope values between strictly epipelagic organisms (EPI), epipelagic migrants (EMI) and non-epipelagic migrating organisms (NEMI). To investigate whether the broad categories previously defined according to literature, are differentiated by their stable isotope values into a similar number of defined groups, a Euclidean similarity matrix based on $\delta^{13}C$ and $\delta^{15}N$ values (using the average method) was computed. The NbClust function in R was used to determine the optimum number of clusters. The isotopic niche widths were estimated using a Bayesian approach (SIBER package) which generated standard ellipse areas (SEA) that contained ~40% of the isotopic data, thereby representing the core isotopic niche of each of the broad categories (POM, gastropod, zooplankton, gelatinous, micronekton, nekton, tuna, swordfish, and other pelagic fish) while correcting for small sample sizes (SEAc). This metric represents a measure of the total amount of the isotopic niche exploited by a group and is thus a proxy for the extent of trophic diversity (Jackson et al., 2011), and of the habitat and resources most commonly used by the species (Damseaux et al., 2021). To investigate the isotopic niche overlap of micronektivores and zooplanktivores with varied habitat ranges at the seamount and off-seamount locations in the ISSG and EAFR provinces, the R package "nicheROVER" (Lysy et al., 2021) was further used at 50 iterations and α level of 0.95. This package uses Bayesian methods to estimate the probability of the size of the isotopic niche area of species A inside that of species B, and is not sensitive to sample size variations (Swanson et al., 2015). Non-epipelagic migrating micronektivores at the ISSG seamount and EAFR off-seamount locations and strictly epipelagic micronektivores at the EAFR seamount locations were selected to encompass representatives from all trophic guilds and migration patterns. The maxLikOverlap function in SIBER estimated the proportion of isotopic niche of micronekton that overlap with each other.

To assess the influence of environmental variables (bathymetry, ADT, SSC, and SST) on $\delta^{13}C$ and $\delta^{15}N$ values, a redundancy analysis (RDA) model was constructed using R's vegan package (v. 2.6.4; Oksanen et al., 2022). Environmental data and stable isotope values were matched temporally (over the cruise sampling period) and spatially (to the nearest°). RDA uses multiple linear combinations to find the best ordination of the multivariate data and are appropriate with compositional data such as stable isotope values. Since draftsman plots showed no major skewness in the datasets, no data transformations were applied prior to running the RDA. To investigate the correlation between environmental variables (SST, SSC and ADT) and stable isotope values, Spearman rank correlation tests were further conducted.

3. Results

3.1 Prevailing oceanographic conditions in the Western Indian Ocean

MAD-Ridge seamount is located along the Madagascar Ridge south of Madagascar Island (Fig. 3a) and rises from a depth of 1600 m from the ocean floor to ~240 m below the sea surface (Annasawmy et al., 2019). La Pérouse seamount rises from the abyssal plain at 5000 m with a summit reaching ~60 m below the sea surface (Marsac et al., 2020). Most of the cruises in the central Mozambique channel in the EAFR province were conducted on the African continental shelf. Sampling occured within mesoscale eddies, which are identified as rotating water masses with higher (anticyclonic) or lower (cyclonic) ADT than the surrounding area (Fig. 3b). To delineate anticyclonic and cyclonic eddies, an arbitrary threshold of 1 m was selected based on surface plots of ADT (Supplementary Material 2). The mesopelagic trawl stations and swordfish sampling were conducted in both anticyclonic and cyclonic eddies in the EAFR province in 2002, 2004, 2008, 2009 and 2010 (Fig. 3b). In the EAFR province in 2003 and 2016, and the ISSG province in 2010 and 2016, sampling was conducted solely in cyclonic eddies. Median values of ADT in the cyclonic eddies were generally lower in the ISSG compared to the EAFR, except in 2016 where an inverse pattern was observed with higher ADT in the ISSG compared to the EAFR. Exceptionally high SSC values were observed in the cyclonic eddies in the ISSG compared to the EAFR in 2016. In 2010, SSC was greater in the EAFR in both cyclonic and anticyclonic eddies compared to the cyclonic eddies in the ISSG (Fig. 3c). Cyclonic eddies were associated with higher SSC than anticyclonic eddies at the EAFR sampling sites in 2008, 2009, and 2010, and with lower SSC in 2002. SST showed a general increase at the sampling sites in the EAFR from 2002 to 2016 (Fig. 3d). SST values showed a sharp decrease by more than 2°C from 2010 to 2016 in the ISSG. The exceptional high SST observed in the EAFR and the ISSG in 2010 could explain the low SSC values. This could also explain the pattern observed in 2002, with lower SSC in the cyclonic eddies which were also characterised by higher SST compared to the anticyclonic eddies.

3.2 General food web structures

A total of 839 and 1566 samples were considered in the ISSG and EAFR provinces, respectively, with mesopelagic fishes constituting about 50% of the total number of organisms analysed (Table 2); Supplementary Material 1). At the off-seamount location in the ISSG province, the $\delta^{13}C$ values of all samples ranged from −25.4 ‰ (POM Fmax) to −16.0 ‰ (swordfish) and $\delta^{15}N$ values, from 2.6 ‰ (zooplankton: copepod) to 16.1 ‰ (swordfish). At La Pérouse seamount in the ISSG, the $\delta^{13}C$ values ranged from −28.0 ‰ (POM Fmax) to −17.2 ‰ (crustacean: Caridea), and $\delta^{15}N$ values, from 2.5 ‰ (leptocephale larvae) to 13.3 ‰ (fishes: *Coccorella atrata*). A $\delta^{15}N$ difference of 2.8 ‰ was measured between the seamounts and off-seamount locations due to the absence of swordfish sampling at the seamounts.

At the off-seamount locations in the EAFR province, $\delta^{13}C$ values ranged from −26.3 ‰ (POM Surface) to −15.4 ‰ (swordfish), and $\delta^{15}N$ values from 2.1 ‰ (POM Fmax) to 16.6 ‰ (fishes: *Decapterus sp.*). At the seamount locations in the EAFR province, $\delta^{13}C$ values ranged from −27.2 ‰ (POM Surface) to −17.1 ‰ (fishes: *Chauliodus sloani*), and $\delta^{15}N$ values ranged from 2.3 ‰ (leptocephale larvae) and 13.5 ‰ (fishes: *Argyropelecus aculeatus*). Similarly, to the ISSG province, a $\delta^{15}N$ difference of 3.1 ‰ was detected between seamount and off-seamount locations due large predatory swordfish not being sampled over seamounts.

3.3 $\delta^{13}C$ and $\delta^{15}N$ values with respect to trophic guilds and habitat preferences

Most of the sampled organisms are EMI (n = 1215) compared to NEMI crustaceans, nektonic squids, mesopelagic fishes,tunas (125), swordfish (418), and EPI (86) (Supplementary Material 1). Some organisms such as *Leptocephalus* sp. and the crustacean Caridea have habitat preferences depending on their life cycle and were hence discarded from further analyses. Mesopelagic fishes also often have different habitat preferences depending on their life stage, with larvae being generally epipelagic (Harris et al., 2020). However, since all mesopelagic fishes sampled were adult specimens, they were not discarded. The vast majority of sampled organisms were micronektivores (920) and zooplanktivores (922).

In the ISSG province, EMI and NEMI (excluding swordfish) did not have significantly different $\delta^{13}C$ and $\delta^{15}N$ values (KW, $p > 0.05$), compared to the EAFR province where values were significantly different (KW, $p < 0.05$). Organisms feeding on micronekton had significantly greater $\delta^{15}N$ values (ISSG: 13.4 ± 3.03 ‰; EAFR: 11.2 ± 2.6 ‰) compared to those feeding on zooplankton, detritus and those having filter feeding strategies (ISSG: 3.3 to 8.8 ‰; EAFR: 5.4 to 10.6 ‰; KW, $p < 0.05$). The magnitudes and patterns of differences in $\delta^{13}C$ and $\delta^{15}N$ values between EPI, EMI and NEMI micronektivores and zooplanktivores, differed between both provinces and between seamount and off-seamount locations in each province. For instance, at the off-seamount locations in the ISSG province, NEMI micronektivorous swordfish had greater $\delta^{13}C$ and $\delta^{15}N$ values than EMI micronekton, nekton, and NEMI micronektivorous nekton (KW, $p < 0.05$; Fig. 4a). No significant differences were detected in $\delta^{15}N$ values (KW, $p > 0.05$), but NEMI zooplanktivorous micronekton and nekton had significantly higher median $\delta^{13}C$ values (KW, $p < 0.05$) compared to EMI micronekton at the off-seamount locations in the ISSG. At the seamount locations in the ISSG province, no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values were found in zooplanktivores (KW, $p > 0.05$, Fig. 4b). Only NEMI feeding on micronekton had significantly higher $\delta^{15}N$ values compared to EMI and EPI ($p < 0.05$), but their $\delta^{13}C$ values were similar ($p > 0.05$)

At the off-seamount locations in the EAFR province, EMI micronektivores with different vertical habitat ranges all had significantly different $\delta^{15}N$ values (KW, $p < 0.05$; Fig. 4c). There were no significant differences in $\delta^{15}N$ values (KW, $p > 0.05$), but significantly higher $\delta^{13}C$ values (KW, $p < 0.05$) in NEMI zooplanktivorous micronekton compared to EMI at the off-seamount locations in the EAFR, similar to the patterns measured at the off-seamount locations in the ISSG. At the seamount locations in the EAFR province, NEMI micronektivores had higher $\delta^{15}N$ and lower $\delta^{13}C$ values compared to EMI micronekton (KW, $p < 0.05$; Fig. 4d). Similar to the seamount locations in the ISSG, all zooplanktivorous organisms irrespective of their vertical habitat ranges displayed similar $\delta^{13}C$ and $\delta^{15}N$ values (KW, $p > 0.05$).

3.4 Isotopic niches

Biplots of $\delta^{13}C$ and $\delta^{15}N$ values and the cluster analysis identified four major groups at all locations from the Western Indian Ocean (Fig. 5). As expected, POM was generally characterized by low $\delta^{13}C$ and $\delta^{15}N$ values. The isotopic niche space of zooplankton overlapped with gelatinous organisms at the off-seamount locations in the ISSG province, but not at the seamount locations in the ISSG and EAFR provinces. The isotopic niches of gelatinous organisms displayed a large spread along the $\delta^{13}C$ axis at all locations in the two provinces of the Indian Ocean. The proportion of the isotopic niches of crustaceans, mesopelagic fishes, micronektonic and nektonic squids which overlapped, was between 37.9% and 43.5% (Table 3). While the isotopic niche space of swordfish overlapped with micronekton at the off-seamount locations in the EAFR province, it was distinctly separate in the ISSG province.

The isotopic niche area of EMI overlapped that of EPI and NEMI in the Indian Ocean (Fig. 6). NEMI swordfish showed smaller isotopic niche compared to those of EMI micronekton and nekton, with swordfish exhibiting higher $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 6a, c). The isotopic niche areas of EMI, EPI and NEMI differed at the seamount locations in the ISSG and EAFR provinces. EMI and NEMI have similar niche patterns at the seamount in the EAFR. The food sources of EPI differed ($\delta^{13}C$ distribution shifted to the right and multi-modal $\delta^{15}N$ distribution) compared to EMI and NEMI at the EAFR seamount.

Patterns of isotopic niche overlaps differed between micronekton, nekton and swordfish at off-seamount locations in the ISSG (Fig. 7a). Although these organisms are all micronektivores, they have different food sources. The food sources of zooplanktivorous crustaceans and mesopelagic fishes, however, were similar at this location with high niche overlaps (Fig. 7a). Zooplanktivorous migrating crustaceans and mesopelagic fishes have very different isotopic niche patterns, with the latter taking advantage of a wider range range of food sources (spread in $\delta^{13}C$ distribution) at seamount of the ISSG (Fig. 7b). At the off-seamount locations in the EAFR province, zooplanktivorous crustaceans have a wider range of food sources compared to the ISSG province (Fig. 7c). While tuna have similar food sources with mesopelagic fishes (high overlap over their $\delta^{13}C$ distributions), they differed in their $\delta^{15}N$ values (Fig. 7d). Micronektivorous and zooplanktivorous crustaceans and mesopelagic fishes have similar food sources at the EAFR seamount, with EMI taking advantage of a wider range of food sources compared to NEMI (Fig. 7e, f).

3.5 Environmental influence on isotopic values

The environmental variables explained 13.5% of the total variance in isotopic values, suggesting that other factors not included in the model might be influencing the stable isotope values. Stable $\delta^{15}N$ values were strongly influenced by the environmental gradient represented by RDA1, whereas $\delta^{13}C$ values were moderately influenced by RDA2 (Table 4). Bathymetry and SST showed strong positive correlations with the first RDA axis (Table 4; Fig. 8), indicating that the ISSG province with higher elevation and temperature values are driven by $\delta^{15}N$ values. ADT showed a strong negative correlation with the first RDA axis and an equally strong positive correlation with the second axis, and drove stable isotope values in the EAFR province. SSC showed negative correlations with both axes and mostly drive stable isotope values of the EAFR province.

The environmental variables ADT, SSC and SST were significantly correlated with stable δ^{13}C and δ^{15}N isotope values ($p < 0.05$). While ADT and δ^{13}C values showed no clear patterns, high SSC led to an overall increase in δ^{13}C, while high SST led to a decrease (Fig. 9). ADT values showed mixed associates with δ^{15}N, with ADT less than 0.8 m being associated with δ^{15}N values less than 9‰. ADT values between 0.8 to 1 m showed an increasing trend in δ^{15}N to 11‰, while ADT greater than 1 m were associated with a decreasing trend in δ^{15}N. Increasing SSC were associated with increasing δ^{15}N values. Warmer years (for e.g., 2010) showed low δ^{13}C and δ^{15}N values.

4. Discussion

4.1 Limitations and recommendations

While previous studies in the Western Indian Ocean investigated local stable isotope patterns and relationships of a few ecosystem components (Ménard et al., 2014; Annasawmy et al., 2018, 2020b), ours is the first investigating the trophic and resource partitioning of a total of 2405 samples in two contrasting oceanic provinces. Due to the uncertainty in trophic position estimations arising from the determination of baseline species and trophic magnification factors (Wang et al., 2023), we choose to investigate bulk δ^{13}C and δ^{15}N values instead of trophic position.

Although the observed patterns are clear, we acknowledge several limitations in this study. Variability in isotopic baselines and the incorporation of isotopic signals from diets into the tissues of organisms (Martínez Del Rio et al., 2009) could influence the results. Oceanographic conditions varied between the broad time scale and across seasons (Fig. 3; Supplementary Material 2), and may have influenced the results. Since individuals were not consistently sampled at the same depths or under the same oceanographic conditions across years and regions, we could not compare stable isotope values of similarly sized species across identical depths and conditions. Although efforts were made to analyse samples from similar time periods—e.g., seamounts in 2016, off-seamount locations in the ISSG in 2010, and in the EAFR from 2002 to 2010—ideally, sampling and analyses should have been conducted over comparable time scales. Additionally, sampling was to conducted to a maximum depth of 500 m, thereby restricting the analysis to organisms inhabiting the epipelagic and upper mesopelagic zones. The lack of isotopic studies at greater depths means it is uncertain whether fewer diel vertical migrators exist at these depths or if their migration and feeding behaviors differ (as observed by Eduardo et al., 2020), and how this might affect resource and trophic partitioning. Furthermore, only two *Cyclothone* fish specimens were collected due to the 30 mm mesh size, despite these species being highly abundant at depths greater than 200 m (Peña et al., 2023). As a result, our study may have overlooked a significant proportion of similarly non-epipelagic migrants.

Our meta-analysis is in line with previous findings that marine pelagic ecosystems have less than five trophic groups even when microbial pathways are taken into account, possibly due to the efficient transfer of energy and biomass caused by only a small number of trophic links (Valls et al., 2014; Bode et al., 2021). However, as this study demonstrated, small variabilities in trophic indices are detected within trophic groups when migration and feeding strategies are considered. Future studies would benefit from consistent sampling of all trophic groups at similar depths, oceanographic conditions (for e.g., similar seasons), and regions across several years with additional compound-specific stable isotope analysis of amino acids.

4.2 Broad-scale environmental patterns influence stable isotope values

Broad-scale biogeographic differences and local environmental conditions significantly shape the observed patterns in stable isotope values. The ISSG and EAFR provinces are primarily separated by differences in bathymetry and temperature, and within each province, local variations in the mesoscale eddy field and productivity play a significant role on isotope values. The small proportion (13.47%) of the total variance in the stable isotope values explained by the environmental variables could be attributed to the use of satellite observations of the surface ocean (for lack of better measurements), while stable isotope values were recorded at depths. Nonetheless, the observed influence of surface conditions on deeper isotope values suggests that surface oceanic conditions partially extend into the deeper oceanic layers.

Trophic differences between migrants (EMI) and non-epipelagic migrants (NEMI) were detected at the off-seamount sites in the EAFR province, dominated by intense mesoscale eddies occurring frequently in this region (Supplementary Material 2; Vianello et al., 2020a). At these locations, EPI and EMI micronektivores had higher δ^{15}N values than NEMI staying at greater depths, while δ^{13}C values were not significantly different (excluding swordfish). Oceanic regions dominated by mesoscale eddies such as the EAFR province (Sabarros et al., 2009; Tew-Kai and Marsac, 2009), exhibit active generation of productivity, enhanced vertical mixing and transport of dissolved and suspended POM extending deep into the water column (Burd et al., 2010; Boyd et al., 2019; Vianello et al., 2020b). The mesoscale eddy dynamics potentially drive a stronger connection between epipelagic and mesopelagic layers compared to regions less dominated by these turbulent water masses. EPI and EMI may have access to food-rich sources at highly productive eddy sites within the euphotic zone.

Furthermore, oligotrophic gyres have low food availability within the euphotic zone (Annasawmy et al., 2018) and lower carbon transport than productive areas (Gloeckler et al., 2018). The input of “new” nutrients being sporadic in oligotrophic systems, food webs in these areas may rely mostly on recycled and re-processed organic matter (Bode et al., 2021) or ^{15}N-enriched suspended particles (Hannides et al., 2013). The δ^{15}N values of zooplankton collected in subtropical gyres also increased with depth (Hannides et al., 2013; Romero-Romero et al., 2019), subsequently potentially artificially increasing the trophic positions of the micronekton feeding and residing at depth. Organisms relying on nitrogen from a suspended particle-based food web generally have greater δ^{15}N with depth (Altabet, 1988; Hannides et al., 2013; Gloeckler et al., 2018; Romero-Romero et al., 2019) similar to results of this study. While NEMI and EMI zooplanktivores at off-seamount locations in the ISSG and EAFR have similar δ^{15}N values, they differed in their δ^{13}C values, suggesting feeding patterns at the same trophic position but from different carbon sources, similarly to Valls et al. (2017). Micronekton exploit trophic webs fueled by a variety of sources such as surface-dwelling productivity and bacteria, sinking and suspended particles (Gloeckler et al., 2018), which influence their trophic values.

4.3 Trophic and resource partitioning between ecological groups and vertical habitat ranges

Although our study includes highly mobile species such as tuna and swordfish, we demonstrate that these predators have a small isotopic niche space and exhibit isotopic specialization in the Indian Ocean. Flaherty and Ben-David (2010) also demonstrated that the isotopic signatures of wide-ranging organisms do not necessarily vary more than those of "sedentary" ones. We hypothesize that the isotopic niches of predators are not a function of their wide oceanic habitat ranges but rather a function of their diet. Ongoing studies (Romanov et al., in prep) of stomach contents showed higher importance of squids (55.6% in mean reconstituted weight) than fish (36.5%) in the ISSG province compared to the EAFR, where their contributions were similar (squids 47.3%; fish 41.4%). Crustaceans were a minor component in the diet of swordfish (Romanov et al., in prep.).

In the ISSG, NEMI (excluding swordfish) and EMI showed similar food sources since organisms possibly rely on the microbial food pathway through the remineralization of suspended particles. Similar to previous work, the isotopic niche of migrating micronekton overlap those of NEMI because both groups may take advantage of similar food sources available at each depth (Bode et al., 2021). Considerable overlap at niche boundaries was also measured among crustaceans, fishes and squids of small and large sizes, similar to previous studies (Hopkins and Gartner, 1992). The high niche overlaps raise the question of resource competition between epipelagic migrating and non- epipelagic migrating organisms in oligotrophic areas. To reduce competition in a species-dense environment, organisms were suggested to partition resources in terms of predation at different depths, time periods with asynchronous migration patterns, prey sizes and life-history stages (Hopkins and Gartner, 1992). Other variables not available in our study may explain the underlying observations. Future studies may consider additional oceanographic variables (for e.g., nutrient availability, upwelling intensity, and oxygen concentrations from the surface to the deeper ocean), prey availability and distribution, life-history traits of sampled individuals, and consistent vertical, spatial and temporal sampling of zooplankton and micronekton across seasons, years and regions, and using compound-specific stable isotope analysis of amino acids.

4.4 Seamounts form distinct "isobiomes" in the ocean

Micronektivores have different niche patterns at the La Pérouse seamount of the ISSG province, possibly reflecting different food preferences. The non-epipelagic migrating micronektivores represented by *Chauliodus sloani*, *Neoscopelus macrolepidotus*, *N. microchir* and *Histioteuthis* spp., may be physically constrained to forage on micronekton at greater depths at this seamount and hence exhibited specific trophic specializations which differed from migrating organisms. The latter are represented by several crustacean species and the fishes *Eustomias* sp., *Stomias longibarbatus*, *Echiostoma barbatum*, and *Melanostomias* sp., which have access to both epipelagic and mesopelagic resources. At the seamount of the ISSG, zooplanktivorous crustaceans and fishes also have different trophic specializations with the latter exploiting a wider range of food sources. Crustaceans have a narrow $\delta^{13}C$ distribution at the seamount of the ISSG compared to the EAFR, suggesting exploitation of a narrow range of food sources at the oligotrophic seamount of the ISSG. The underlying causes of these observations cannot be further investigated with the present dataset.

Seamounts are topographic obstacles in the ocean which greatly influence the trophic dynamics and resource partitioning between the epipelagic and mesopelagic layers, distinct from off-seamount oceanic regions. At these topographic features, organisms may benefit from similar zooplanktivorous food sources irrespective of their migration patterns. Mesopelagic fishes may benefit from a wide range of zooplankton food sources, which accumulate due to various local processes at seamounts: (1) topographic blockage of zooplankton after daily vertical migration, (2) organisms maintaining their depths against upwelling, (3) organisms swimming against downwelling, (4) enhanced fluxes of suspended food (Annasawmy, 2019). This accumulation of zooplankton may support strictly epipelagic, migrating and non-migrating zooplanktivores. At the seamount of the ISSG, while micronektivores have similar food sources, they feed at different trophic levels depending on their vertical habitat ranges. Seamounts create "isotopic topographic barriers" that strongly influence resource utilization patterns between migrating and non-epipelagic migrating organisms and those feeding on zooplankton, hence forming distinct "isobiomes" in the ocean.4.5 Conclusion

Spatial differences in δ^{15}N values may be a consequence of trophic plasticity whereby individuals adapt to environmental heterogeneity and site-specific variability in the prey availability (Valls et al., 2014). While some studies have suggested that environmental stability are the drivers of trophic specialization in deep-sea species (Eduardo et al., 2023), we argue that the ocean is hardly stable and it is in fact the environmental, biogeographic (through the mesoscale dynamics and productivity), topographic (through seamounts) and ecological variability between species that drive trophic specialization of marine organisms. The niche widths and patterns evolve in response to the magnitude of environmental variations (Kassen, 2002). Habitat-derived differences, habitat use and foraging behaviour are important for the estimation of the ecological niche of organisms (Flaherty and Ben-David, 2010).

Given that ocean warming and subsequent decline in chlorophyll are expected to impact mesoscale eddy dynamics (Beech et al., 2022), decrease biomass and deepen micronekton in the tropics (Ariza et al., 2022a), we anticipate a shift in the trophic distribution and resource partitioning of epipelagic and mesopelagic organisms. As shown in this study, increasing temperature impacts productivity and stable isotope values of organisms. We therefore expect climate change to impact the structure of food webs and destabilize communities, which remains to be investigated in the context of future global-scale stable isotope comparisons. While existing literature has contributed valuable insights into stable isotope patterns at localized study sites, a more extensive global-scale comparison is necessary to investigate the epipelagic and mesopelagic stable isotope partitioning across diverse oceanic settings and at seamounts, employing similar statistical approaches as described in this study..

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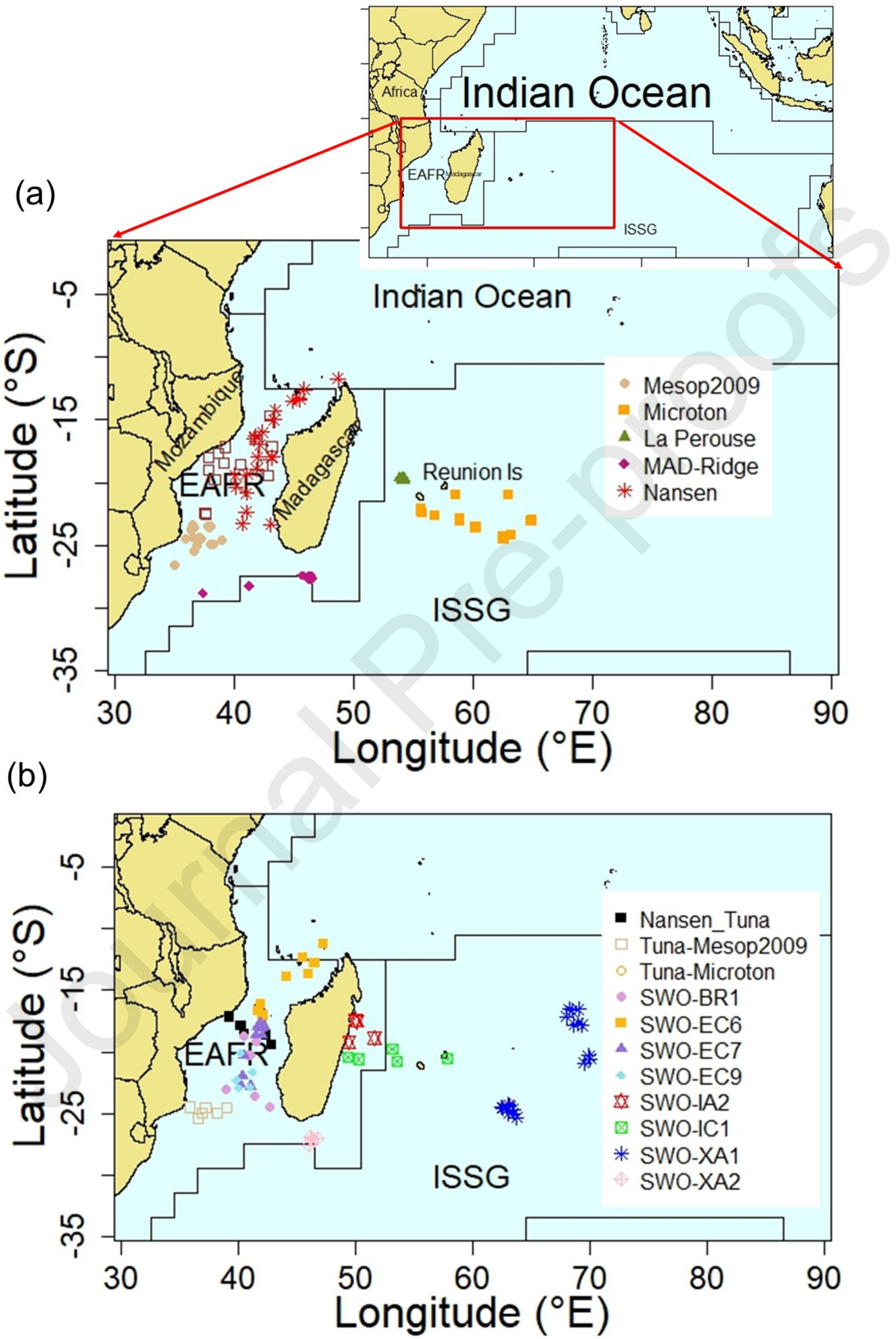
Fig. 7 NicheROVER plots of $\delta^{13}C$ and $\delta^{15}N$ values for (a) epipelagic migrating micronekton, nekton and mesopelagic migrating swordfish at the off-seamount locations in the ISSG, (b) epipelagic migrating crustaceans and mesopelagic fishes at the seamount location in the ISSG, (c) epipelagic migrating crustaceans, fishes, squids, mesopelagic migrating swordfish and other organisms at the off-seamount locations in the EAFR, grouped by trophic guilds (zooplanktivores and micronektivores), (d) non-epipelagic migrating micronekton-feeding crustaceans and fishes at the off-seamount location in the EAFR, (e) epipelagic migrating crustaceans and mesopelagic fishes feeding on micronekton and zooplankton, (f) epipelagic non-epipelagic migrating micronekton-feeding fishes and squids at the seamount in the EAFR. Panel I: Density distributions of $\delta^{15}N$ values; Panel II: random two-dimensional elliptical projections of a specified niche area of 95% for each group and pair of isotopic ratios; Panel III: two-dimensional scatterplots for each species and pair of isotopic ratios; Panel IV: Density distributions of $\delta^{13}C$ values.

Fig. 8 Redundancy analysis (RDA) using $\delta^{13}C$ and $\delta^{15}N$ values as response variables and elevation (m), mean absolute dynamic topography (ADT, m), sea surface chlorophyll (SSC, mg m^{-3}), and sea surface temperature (SSC °C) as predictor variables across the (Indian South Subtropical Gyre) province and EAFR (East African Coastal Province). The direction and length of the arrows mark the direction and rate of steepest increase of the given environmental variable.Fig. 9 Relationships between stable $\delta^{13}C$ and $\delta^{15}N$ values with the absolute dynamic topography (ADT, m), sea surface chlorophyll *a* (SSC, mg m^{-3}), and sea surface temperature (SST, °C). Straight lines represent the estimated smoothing (loess) curves. Broad categories and year of sampling are plotted as red labels.

Supplementary Material

Supplementary Material 1. List of samples, taxonomic classification, trophic guilds, migration patterns and habitat ranges, and stable isotope values of all species included in the analyses.

Supplementary Material 2. The following plots show the elevation (m) across the Western Indian Ocean. The Absolute Dynamic Topography (m), sea surface chlorophyll (SSC, mg m-3), and sea surface temperature (SST, °C) of the Western Indian Ocean are also shown. Cruise sampling sites of Ecotem 5, 9, 6, 7, Nansen, Mesop 2009, Microton, La Pérouse and MAD-Ridge are shown by the black rectanges. La Pérouse and MAD-Ridge seamounts are further shown by the black squares.


Indian Ocean
Africa
EAFR
Madagascar
ISSG
(a)
Latitude (°S)
-5
-15
-25
-35
Longitude (°E)
30
40
50
60
70
80
90
Indian Ocean
Mozambique
EAFR
Madagascar
Reunion Is
ISSG
Mesop2009
Microton
La Perouse
MAD-Ridge
Nansen
(b)
Latitude (°S)
-5
-15
-25
-35
Longitude (°E)
30
40
50
60
70
80
90
EAFR
ISSG
Nansen_Tuna
Tuna-Mesop2009
Tuna-Microton
SWO-BR1
SWO-EC6
SWO-EC7
SWO-EC9
SWO-IA2
SWO-IC1
SWO-XA1
SWO-XA2

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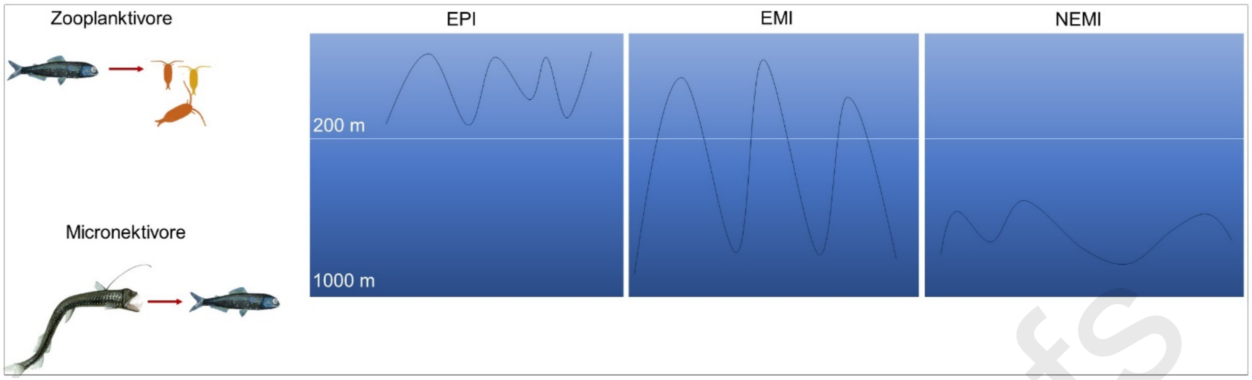

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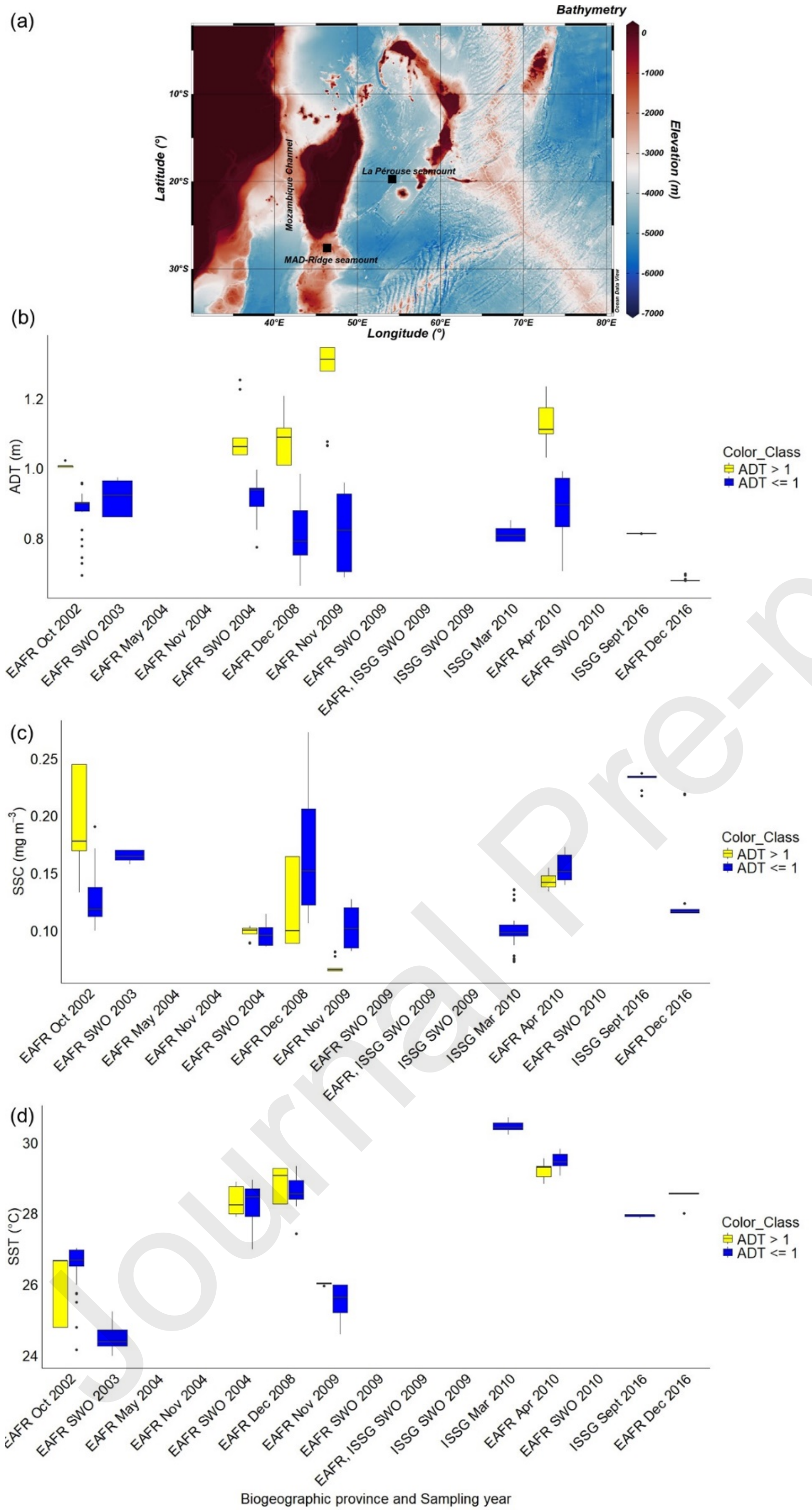

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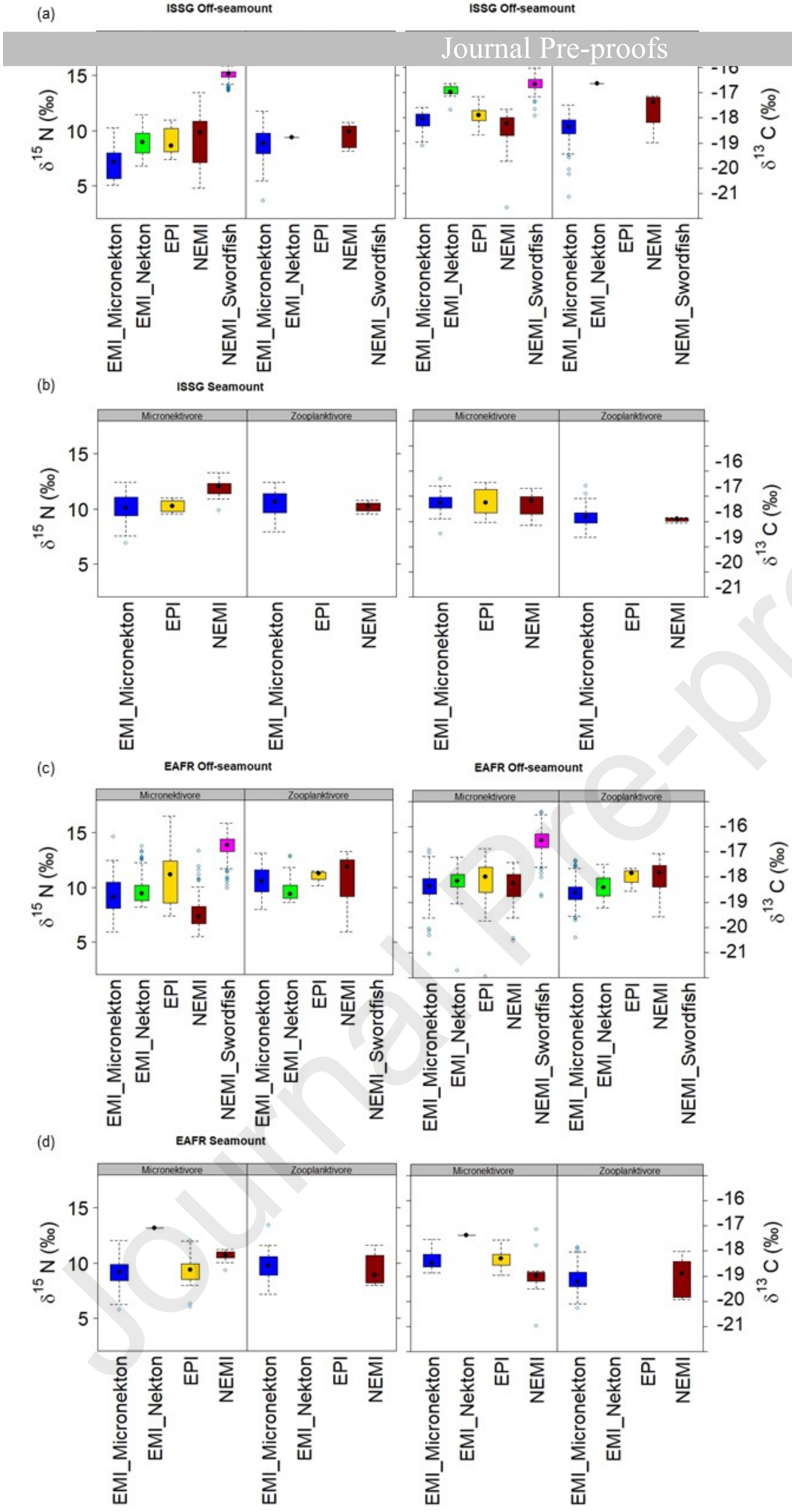

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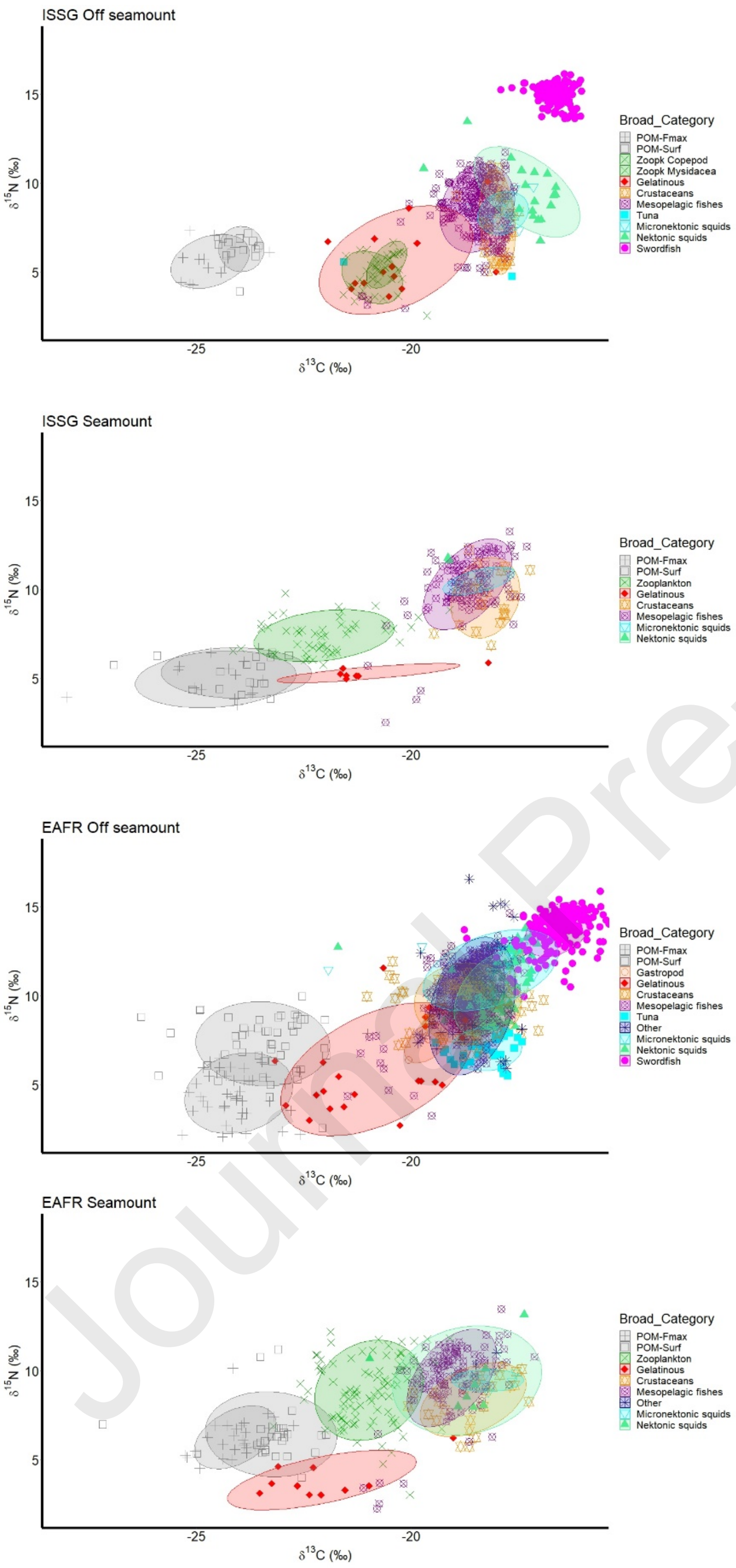
migrants) at seamounts and off-seamount locations in the ISSG and EAFR provinces. The mean

lines) are shown.


ISSG Off seamount
15
10
5
-25
-20
δ15N (‰)
δ13C (‰)
Broad_Category
POM-Fmax
POM-Surf
Zoopk Copepod
Zoopk Mysidacea
Gelatinous
Crustaceans
Mesopelagic fishes
Tuna
Micronektonic squids
Nektonic squids
Swordfish
ISSG Seamount
15
10
5
-25
-20
δ15N (‰)
δ13C (‰)
Broad_Category
POM-Fmax
POM-Surf
Zooplankton
Gelatinous
Crustaceans
Mesopelagic fishes
Micronektonic squids
Nektonic squids
EAFR Off seamount
15
10
5
-25
-20
δ15N (‰)
δ13C (‰)
Broad_Category
POM-Fmax
POM-Surf
Gastropod
Gelatinous
Crustaceans
Mesopelagic fishes
Tuna
Other
Micronektonic squids
Nektonic squids
Swordfish
EAFR Seamount
15
10
5
-25
-20
δ15N (‰)
δ13C (‰)
Broad_Category
POM-Fmax
POM-Surf
Zooplankton
Gelatinous
Crustaceans
Mesopelagic fishes
Other
Micronektonic squids
Nektonic squids

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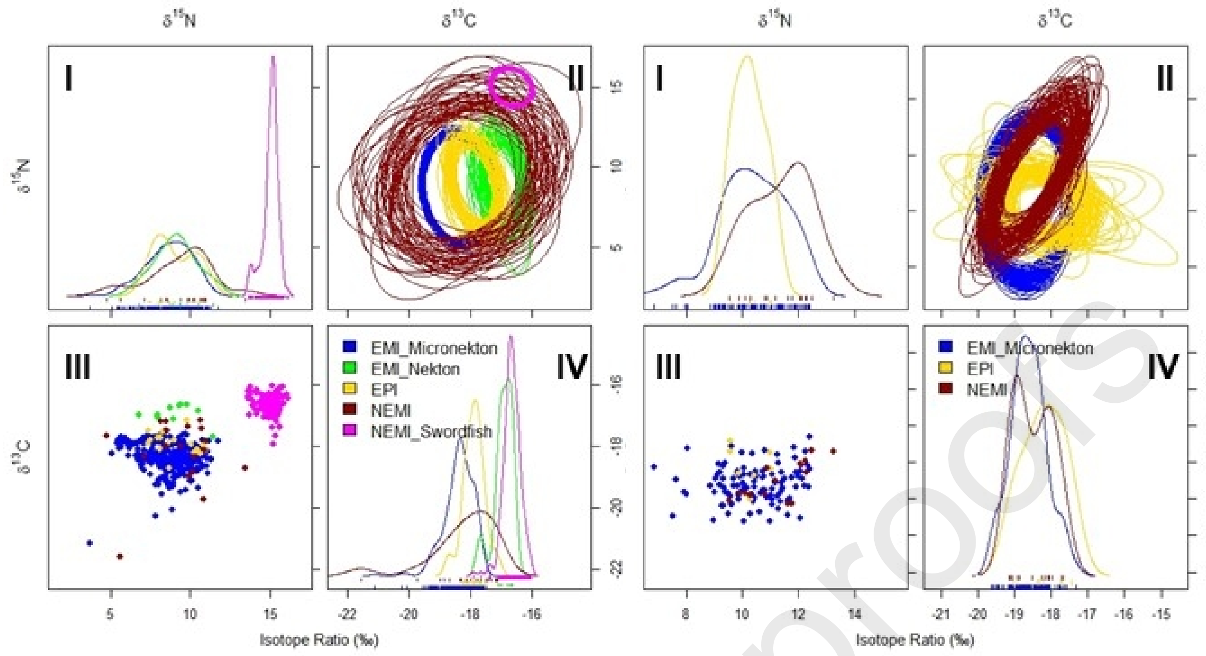
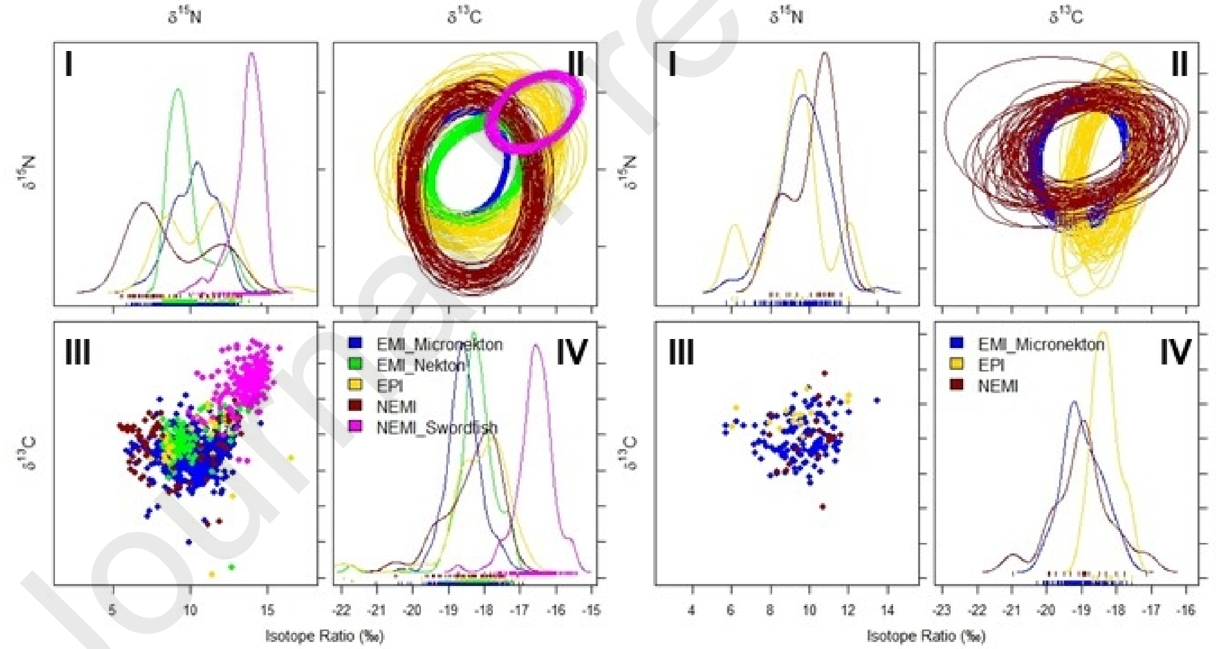
(a) ISSG Off seamount

(b) ISSG Seamount



(c) EAFR Off seamount

(d) EAFR Seamount



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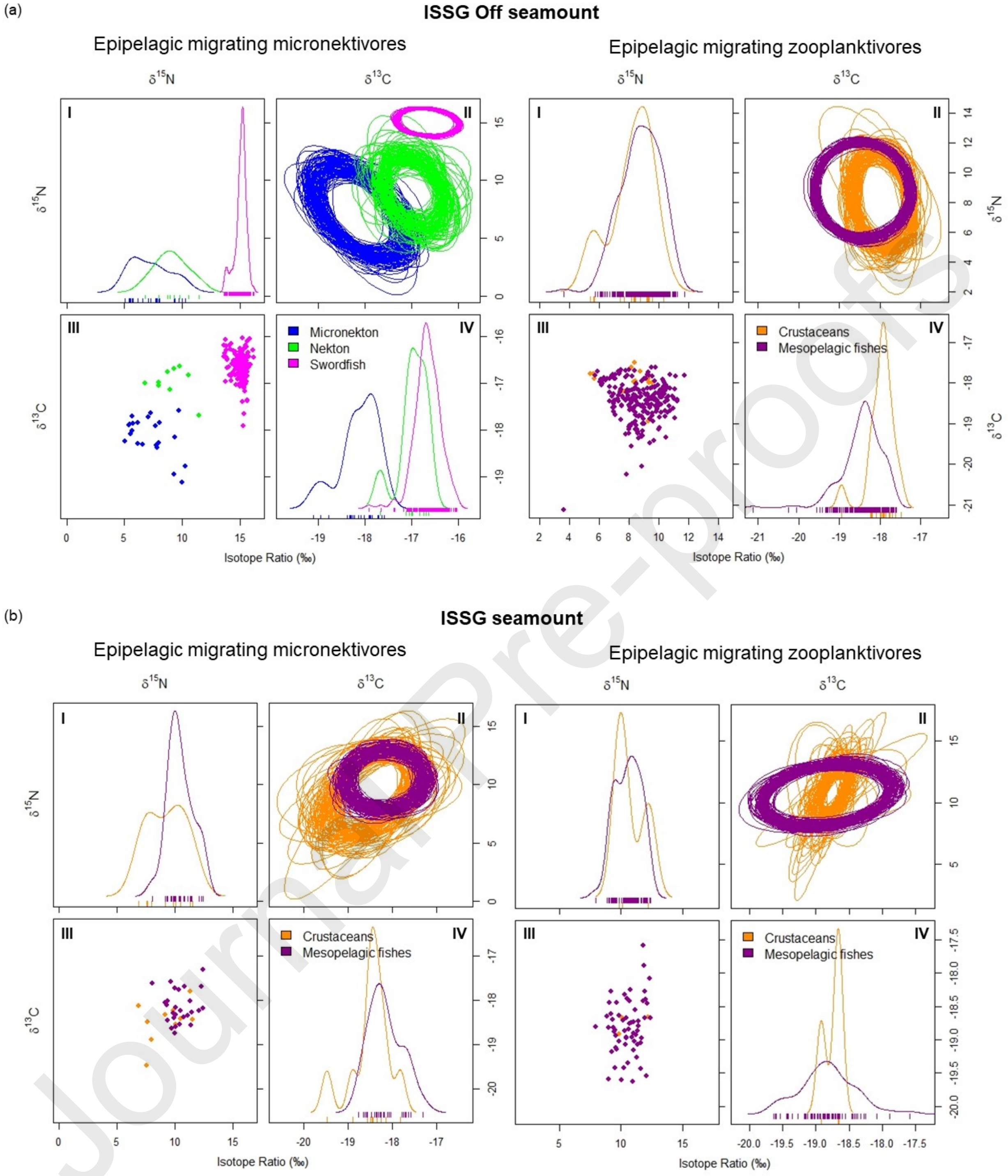
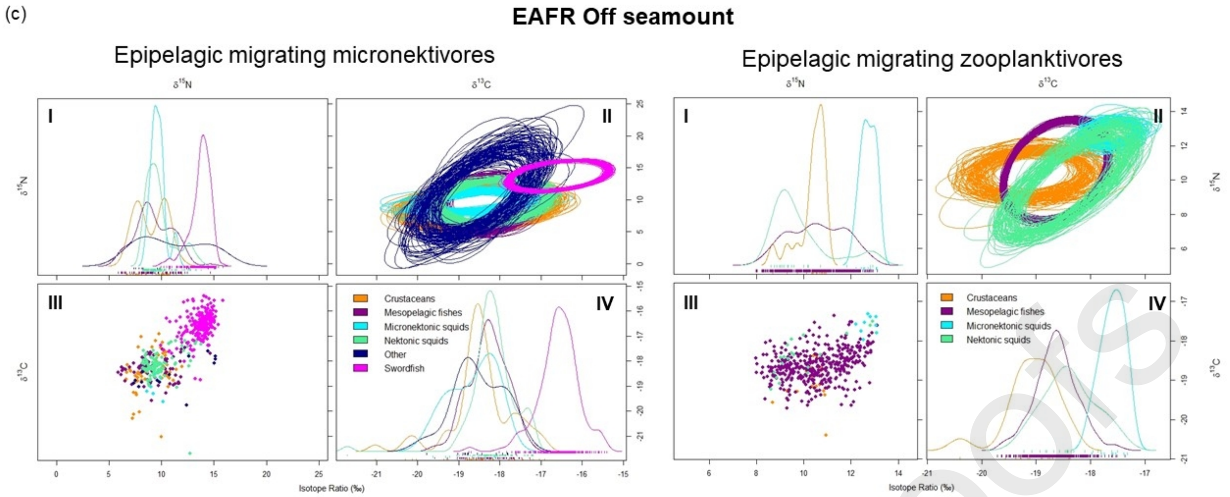

(a)
ISSG Off seamount
Epipelagic migrating micronektivores
Epipelagic migrating zooplanktivores
δ15N
δ13C
I
II
III
IV
Micronekton
Nekton
Swordfish
Crustaceans
Mesopelagic fishes
Isotope Ratio (‰)
(b)
ISSG seamount
Epipelagic migrating micronektivores
Epipelagic migrating zooplanktivores
Crustaceans
Mesopelagic fishes
Isotope Ratio (‰)

Fig. 7(a), (b)


(c)
EAFR Off seamount
Epipelagic migrating micronektivores
δ15N
δ13C
I
II
III
IV
Crustaceans
Mesopelagic fishes
Micronektonic squids
Nektonic squids
Other
Swordfish
0
5
10
15
20
25
-21
-20
-19
-18
-17
-16
-15
Isotope Ratio (‰)
Epipelagic migrating zooplanktivores
Crustaceans
Mesopelagic fishes
Micronektonic squids
Nektonic squids
6
8
10
12
14
-21
-20
-19
-18
-17
Isotope Ratio (‰)

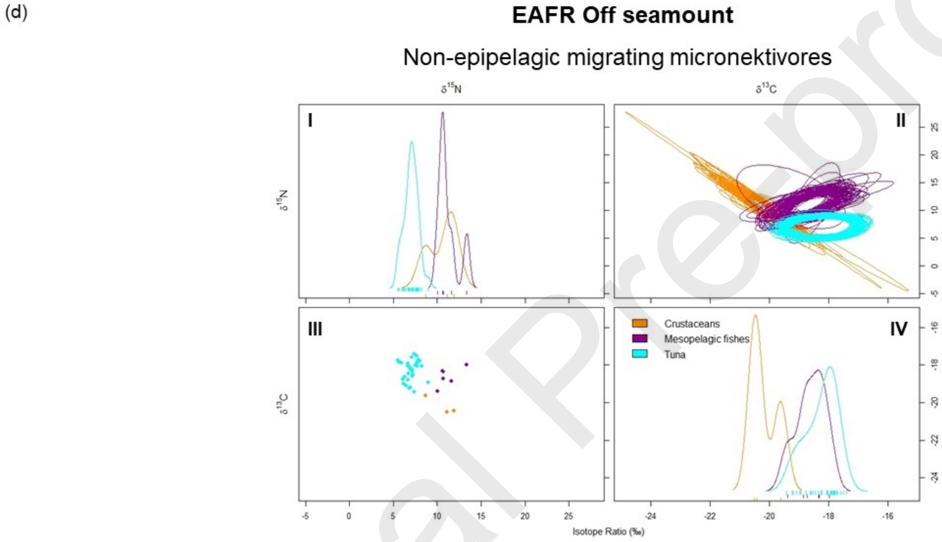

(d)
EAFR Off seamount
Non-epipelagic migrating micronektivores
δ15N
δ13C
I
II
III
IV
Crustaceans
Mesopelagic fishes
Tuna
-5
0
5
10
15
20
25
-24
-22
-20
-18
-16
Isotope Ratio (‰)

Fig. 7(c), (d)

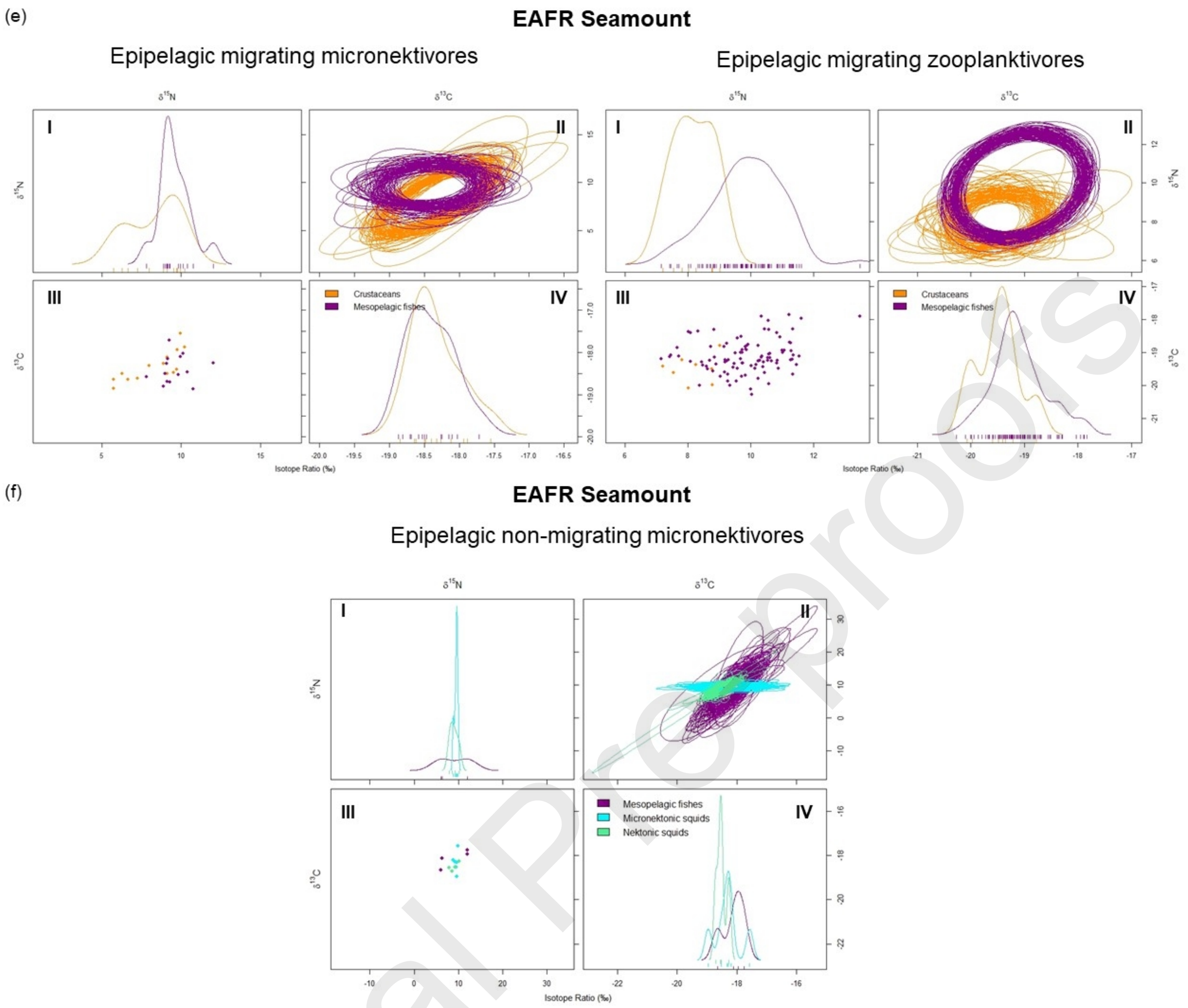
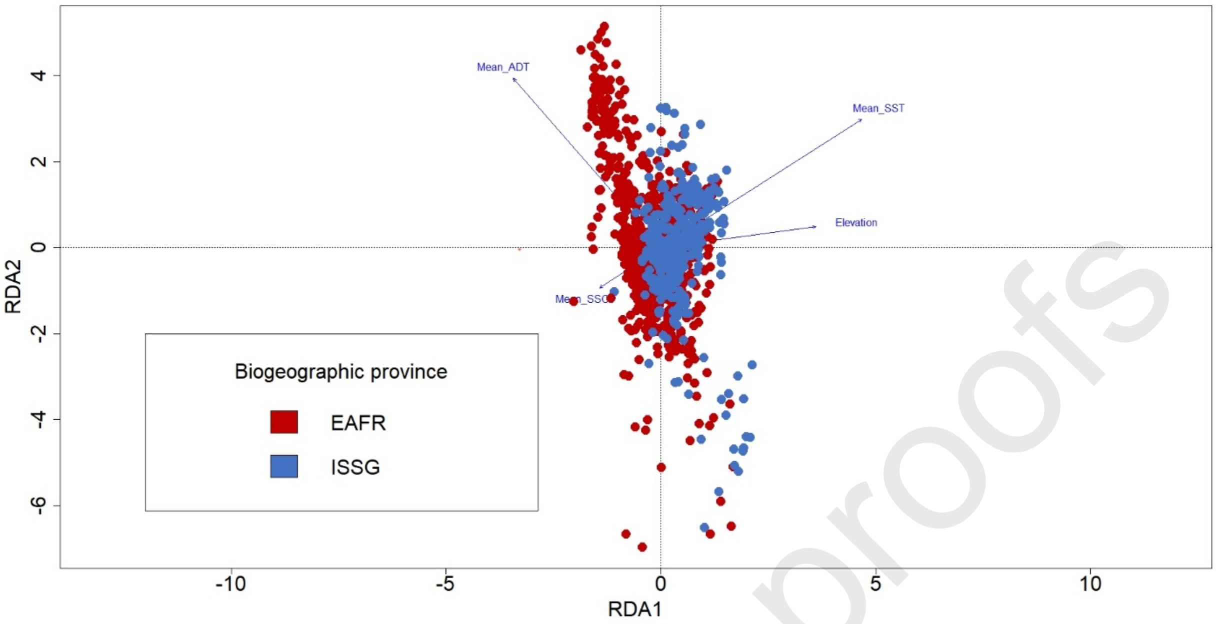


Fig. 7(e), (f) NicheROVER plots of δ^{13}C and δ^{15}N values for (a) epipelagic migrating micronekton, nekton and mesopelagic migrating swordfish at the off-seamount locations in the ISSG, (b) epipelagic migrating crustaceans and mesopelagic fishes at the seamount location in the ISSG, (c) epipelagic migrating crustaceans, fishes, squids, mesopelagic migrating swordfish and other organisms at the off-seamount locations in the EAFR, grouped by trophic guilds (zooplanktivores and micronektivores), (d) non-epipelagic migrating micronekton-feeding crustaceans and fishes at the off-seamount location in the EAFR, (e) epipelagic migrating crustaceans and mesopelagic fishes feeding on micronekton and zooplankton, (f) epipelagic non-epipelagic migrating micronekton-feeding fishes and squids at the seamount in the EAFR. Panel I: Density distributions of δ^{15}N values; Panel II: random two-dimensional elliptical projections of a specified niche area of 95% for each group and pair of isotopic ratios; Panel III: two-dimensional scatterplots for each species and pair of isotopic ratios; Panel IV: Density distributions of δ^{13}C values.



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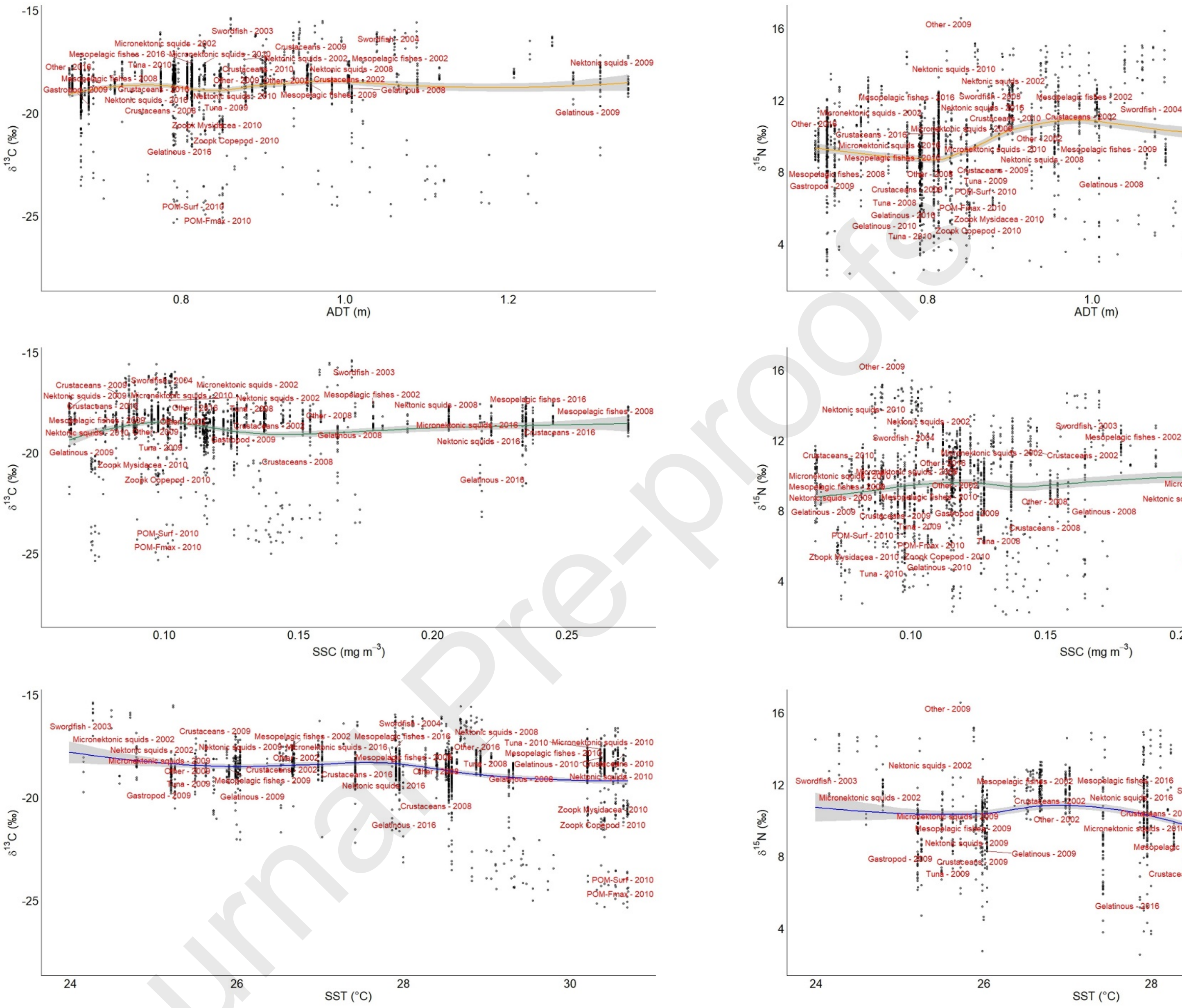


Fig. 9 Relationships between stable δ13C and δ15N values with the absolute dynamic topography (ADT, m), sea surface chlorophyll *a* (SSC, mg m-3), and sea surface temperature (SST, °C). Straight lines represent the estimated smoothing (loess) curves. Broad categories and year of sampling are plotted as red labels.

Table 1 Code, vessel names (*RV*: research vessel; *FV*: fishing vessel), sampling period and number of samples collected (n), at the seamount or off-seamount locations in the ISSG and EAFR provinces.

Code	Vessel	Cruise name	Sampling period	Sample collection	n	Biogeographic province	On or Off seamount
EC5	*RV* La Curieuse	Ecotem 5 *DOI: 10.18142/94*	17 Sept to 4 Oct 2002	micronekton, nekton and other pelagic fishes	235	EAFR	Off seamount
EC9	*FV* Cap Morgane	Ecotem 9 *DOI: 10.18142/94*	2 to 25 Sept 2003	swordfish	16	EAFR	Off seamount
EC6	*FV* Cap Morgane	Ecotem 6 *DOI: 10.18142/94*	2 to 20 May 2004	micronekton, swordfish and other pelagic fishes	51	EAFR	Off seamount
EC7	*FV* Cap Morgane	Ecotem 7 *DOI: 10.18142/94*	10 to 30 Nov 2004	micronekton, nekton, swordfish, flying fish	39	EAFR	Off seamount
MC08	*RV* Fridtjof Nansen	Nansen	28 Nov to 17 Dec 2008	micronekton, nekton, tuna, other pelagic fishes	322	EAFR	Off seamount
IA2	*FV* Laksmi	IOSSS	2009	swordfish	33	EAFR	Off seamount

IC1	*FV* Laksmi	IOSSS	2009	swordfish	30	EAFR	Off seamount
XA1	*FV* Brahma	IOSSS	2009	swordfish	170	ISSG	Off seamount
XA2	*FV* Brahma	IOSSS	2009	swordfish	50	EAFR	Off seamount
MC09	*RV* Antea	Mesop 2009 *DOI: 10.176000/9110050*	4 to 18 Nov 2009	gastropod, POM, gelatinous, micronekton, nekton, tuna, other pelagic fishes	350	EAFR	Off seamount
MC10	*RV* Antea	Mesop 2010 *DOI: 10.176000/10110020* *&* *10.176000/10110030*	12 Apr to 6 May 2010	POM	38	EAFR	Off seamount
BR1	*FV* Brahma	IOSSS	2010	swordfish	38	EAFR	Off seamount
Microton	*RV* Antea	Microton *DOI: 10.17600/10110010*	19 Mar to 5 Apr 2010	POM, zooplankton, gelatinous, micronekto	418	ISSG	Off seamount

				n, nekton, tuna			
La Pérouse	*RV* Antea	La Pérouse *DOI: 10.17600/16004500*	15 to 29 Sept 2016	POM, zooplankton, gelatinous, micronekton, nekton, other pelagic fishes	234	ISSG	Seamount
MAD-Ridge	*RV* Antea	MAD-Ridge *DOI: 10.176000/16004800* & *10.176000/16004900*	26 Nov to 14 Dec 2016	POM, zooplankton, gelatinous, micronekton, nekton, other pelagic fishes	381	EAFR	Seamount

Table 2. Summary statistics of broad categories of organisms collected in the ISSG and EAFR provinces. n is the total number of samples and the mean ± standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values and corrected standard ellipse areas (SEAc) are given. Blanks represent non-available data.

Broad categories	ISSG off seamount				ISSG seamount				EAFR off seamount				EAFR seamount			
	n	$\delta^{13}C$	$\delta^{15}N$	SEAc	n	$\delta^{13}C$	$\delta^{15}N$	SEAc	n	$\delta^{13}C$	$\delta^{15}N$	SEAc	n	$\delta^{13}C$	$\delta^{15}N$	SEAc
POM-Surf	14	−24.0 ± 0.3	6.3 ± 0.8	0.86	16	−24.1 ± 1.1	5.3 ± 0.9	3.19	48	−23.5 ± 1.0	7.3 ± 1.5	4.80	27	−23.3 ± 1.0	6.4 ± 1.5	4.75
POM-Fmax	14	−24.7 ± 0.6	5.6 ± 0.9	1.72	15	−24.6 ± 1.2	5.0 ± 1.0	3.78	45	−24.0 ± 0.8	4.5 ± 1.4	3.66	27	−24.1 ± 0.6	6.3 ± 1.1	1.99
Gastropod									5	−19.7 ± 0.3	7.4 ± 0.6	0.65				
Zooplankton	44	−20.7 ± 0.4	5.1 ± 0.9	0.99	51	−22.0 ± 1.0	7.4 ± 0.9	2.98					99	−21.0 ± 0.8	8.9 ± 1.8	4.58
Gelatinous	14	−20.4 ± 1.1	5.7 ± 1.9	6.39	7	−21.0 ± 1.2	5.3 ± 0.3	0.92	21	−20.8 ± 1.4	5.9 ± 2.3	9.55	10	−22.1 ± 1.3	3.9 ± 1.0	3.74

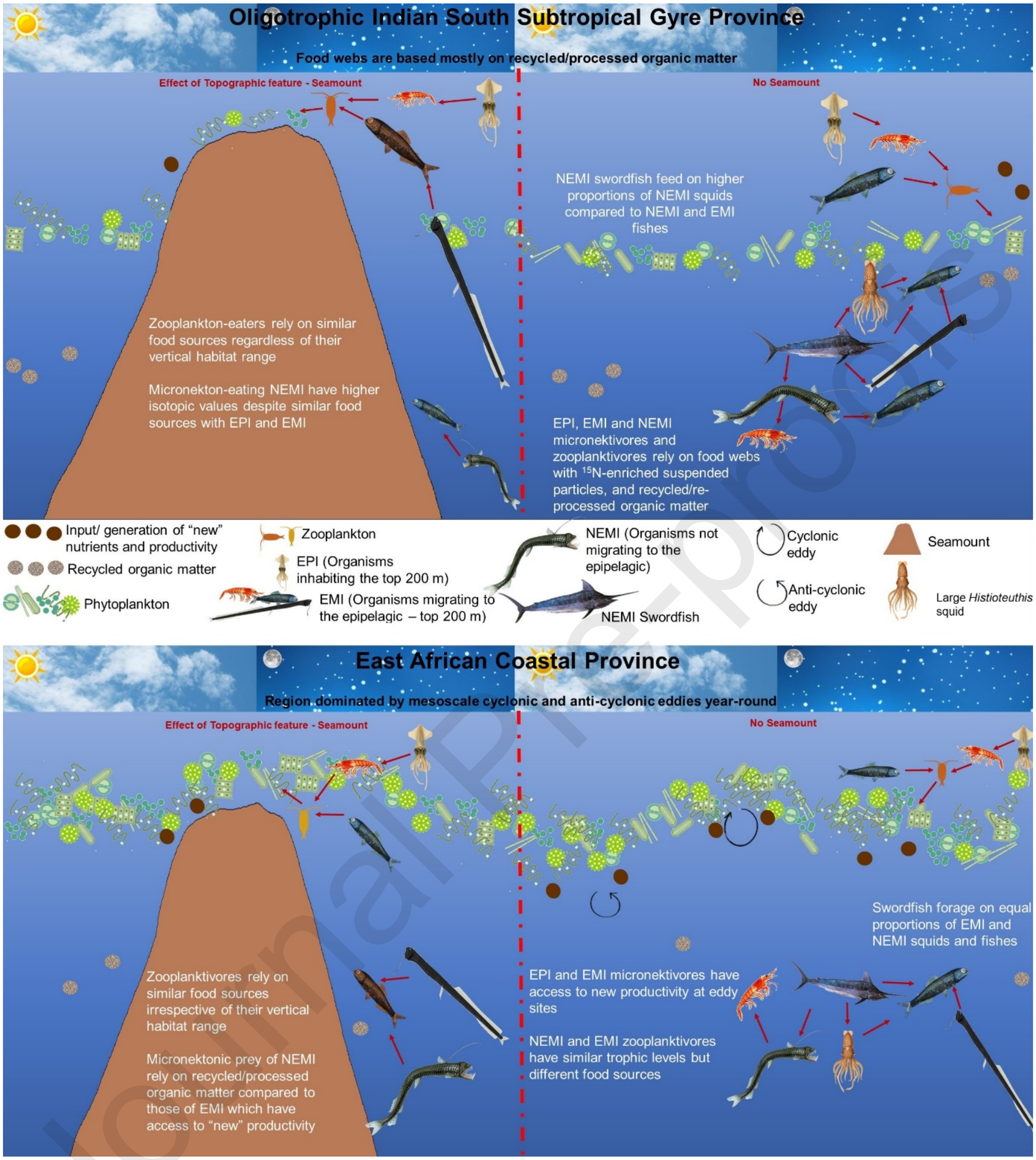
Crustaceans	38	−18.0 ± 0.3	7.8 ± 1.9	1.56	22	−18.3 ± 0.5	9.5 ± 1.4	2.31	95	−18.7 ± 0.8	9.6 ± 1.5	3.72	26	−18.6 ± 0.8	8.4 ± 1.3	3.02
Mesopelagic fishes	257	−18.5 ± 0.6	8.6 ± 1.6	2.74	115	−18.7 ± 0.7	10.3 ± 1.6	2.92	524	−18.6 ± 0.5	10.3 ± 1.5	2.32	137	−19.1 ± 0.7	9.6 ± 1.8	3.25
Micronektonic squids	17	−17.9 ± 0.4	8.3 ± 0.8	0.91	6	−18.4 ± 0.5	10.5 ± 0.4	0.67	32	−18.1 ± 1.0	11.4 ± 1.4	4.20	7	−18.2 ± 0.5	9.5 ± 0.4	0.65
Nektonic squids	18	−17.3 ± 0.8	9.5 ± 1.6	3.39	2	−19.1 ± 0.01	11.7 ± 0.1		128	−18.1 ± 0.6	10.2 ± 1.5	2.44	8	−18.7 ± 1.0	9.5 ± 1.8	6.70
Tuna	2	−19.6 ± 2.8	5.2 ± 0.6						35	−18.3 ± 0.5	7.0 ± 0.8	1.33				
Swordfish	187	−16.7 ± 0.3	15.0 ± 0.5	0.42					231	−16.6 ± 0.5	13.7 ± 1.0	1.44				
Other pelagic fishes									59	−18.6 ± 0.6	9.4 ± 2.5	4.84	2	−18.3 ± 0.3	10.7 ± 0.5	

Table 3. Proportion of isotopic niche of micronekton that overlap with each other.

	Crustaceans	Mesopelagic fishes	Micronektonic squids
Mesopelagic fishes	0.41		
Micronektonic squids	0.39	0.38	
Nektonic squids	0.38	0.38	0.44

Table 4 Scores resulting from the redundancy analysis showing the first and second axes (RDA1 and RDA2). ADT refers to the absolute dynamic topography (m), SSC to the sea surface chlorophyll a (mg m^{-3}), and SST to the sea surface temperature (°C).

	RDA1	RDA2
$\delta^{13}C$	−3.29	−0.03
$\delta^{15}N$	−0.17	0.53
Bathymetry	0.63	0.08
ADT	−0.60	0.69
SSC	−0.25	−0.16
SST	0.81	0.52



Highlights

- Environmental instabilities led to high isotopic niche overlaps.
- Seamounts form distinct "isobiomes" for mesopelagic species.
- Environmental, biogeographic, topographic and ecological variability between species drive trophic specialization of marine organisms.
- A changing ocean will shift the trophic distribution and resource partitioning of epipelagic and mesopelagic organisms.

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: