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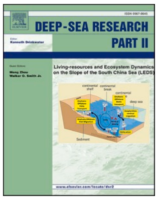

Stable isotope patterns of mesopelagic communities over two shallow seamounts of the south-western Indian Ocean

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ABSTRACT

The stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of soft tissues of micronekton (crustaceans, squid, mesopelagic fish) and zooplankton were measured from organisms collected on the RV *Antea* at two seamounts located in the south-western Indian Ocean: La Pérouse (summit depth ~60 m) and "MAD-Ridge" (thus named in this study; summit depth ~240 m). Surface particulate organic matter (POM-Surf) showed higher $\delta^{13}C$ at the more productive MAD-Ridge than at the oligotrophic La Pérouse seamount. Particulate organic matter and zooplankton were depleted in ^{15}N at La Pérouse pinnacle compared with MAD-Ridge. Gelatinous organisms and crustaceans occupied the lowest and intermediate trophic levels (TL ~2 and 3 respectively) at both seamounts. Mesopelagic fish and smaller-sized squid sampled at both seamounts occupied TL ~3 to 4, whereas the large nektonic squid, *Ommastrephes bartramii,* collected at MAD-Ridge only, exhibited a TL of ~5. The $\delta^{15}N$ values of common open-water mesopelagic taxa were strongly influenced by specimen size and feeding habits at both seamounts, with an increase in $\delta^{15}N$ values with increasing size. Carnivorous fish species sampled exclusively over the seamounts' flanks and summits exhibited TL values of ~4, irrespective of their wide size ranges. The work could not demonstrate any differences in $\delta^{13}C$ values of mesopelagic fish between the seamounts and the surrounding oceanic areas. The study segregated clusters of mesopelagic organisms according to their $\delta^{13}C$ and $\delta^{15}N$ values, with variations in stable isotope values reflecting a complex range of processes possibly linked to productivity as well as biological and ecological traits of the species (size and feeding mode).

1. Introduction

Micronekton are a broad group of organisms mostly dwelling in the mesopelagic zone (<1000 m). They consist of crustaceans (adult euphausiids, hyperiid amphipods, pelagic decapods and mysids), cephalopods (small species and juvenile stages of large oceanic species) and fish (mainly mesopelagic species and juveniles of pelagic fish) (Brodeur and Yamamura, 2005; De Forest and Drazen, 2009; Ménard et al., 2014). They range in size from 2 to 20 cm and represent a substantial biomass in oceanic waters (Brodeur and Yamamura, 2005). Many species exhibit extensive diel vertical migrations (DVM), thus playing an important role in the biological pump by transporting carbon and nutrients from the epipelagic to the mesopelagic zone (Hidaka et al., 2001; Brodeur and Yamamura, 2005; Catul et al., 2011; Bianchi et al., 2013). Micronekton also form a key trophic link between zooplankton and top predators because they are preyed upon by several species of seabird, tuna and billfish (Guinet et al., 1996; Bertrand et al., 2002; Brodeur and Yamamura, 2005; Potier et al., 2007; Karakulak et al., 2009; Cherel et al., 2010; Danckwerts et al., 2014; Jaquemet et al., 2014; Duffy et al., 2017; Watanuki and Thiebot, 2018). Various studies have investigated the trophic interactions of micronekton to better understand their role in foodwebs across numerous ocean basins (Fanelli et al., 2011b; Colaço et al., 2013; Fanelli et al., 2013; Ménard et al., 2014; Valls et al., 2014a, b; Annasawmy et al., 2018). For instance, mesopelagic organisms were

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shown to transfer energy between primary consumers and deeper benthic and benthopelagic animals at Condor seamount in the Atlantic (Colaço et al., 2013).

Tuna, billfish, pelagic armorheads, alfonsinos and orange roughy are common predators fished at seamounts in the Atlantic (Fonteneau, 1991; Morato et al., 2008; Dubroca et al., 2013), Pacific (Rogers, 1994; Koslow, 1997; Holland et al., 1999; Musyl et al., 2003; Paya et al., 2006; Morato et al., 2010) and Indian oceans (Romanov, 2003; Clark et al., 2007; Marsac et al., 2014). Although, La Pérouse does not represent an outstanding fishing spot, tuna (*Thunnus* spp.) and swordfish (*Xiphias gladius*) are present in the vicinity of the seamount throughout the year (Marsac et al., 2020). Albacore (*Thunnus alalunga*), bigeye (*T. obesus*), yellowfin (*T. albacares*) tuna and swordfish commonly occur along the Madagascar Ridge and MAD-Ridge pinnacle (IOTC, www.iotc.org/data-and-statistics). The Madagascar Ridge has also been targeted for orange roughy in 1999/2000 before the catch dropped significantly in subsequent years (Ingole and Koslow, 2005; Lack et al., 2003). Due to the increased pressure on marine organisms, characterizing the overall energy flow within pelagic ecosystems (Young et al., 2015) contributes to making better informed fisheries and ecosystem-based management decisions.

Two seamounts of the southwestern Indian Ocean (SWIO), La Pérouse and an unnamed pinnacle, thereafter named “MAD-Ridge”, were studied in an effort to understand how seamounts may affect diel vertical migrations and aggregations of micronekton (Annasawmy et al., 2019, 2020). While micronekton acoustic densities were not significantly different between the summit and immediate vicinity of the pinnacles, dense aggregations of scatterers, referred to as seamount-associated species, were recorded over the summit of both seamounts during day and night (Annasawmy et al., 2019). La Pérouse is situated in the Indian South Subtropical Gyre (ISSG) province (Longhurst, 2007; Reygondeau et al., 2013) with low mesoscale activities and primary productivity, whereas MAD-Ridge is located within an “eddy corridor” to the south of Madagascar, in a region with high occurrence of cyclonic and anticyclonic eddies and relatively high sea surface chlorophyll concentrations all year round compared to La Pérouse (Halo et al., 2014; Annasawmy et al., 2019; Vianello et al., 2020). The enhanced productivity on the Madagascar shelf and its offshore entrainment by mesoscale eddy interactions (Quartly et al., 2006), were one possible reasons leading to greater micronekton acoustic densities at MAD-Ridge relative to La Pérouse (Annasawmy et al., 2020). Trapped, enclosed circulations known as Taylor columns may also develop over seamounts and contribute to the retention of productivity (Genin and Boehlert, 1985; Dower et al., 1992; Mouriño et al., 2001; Mohn and White, 2007). No Taylor columns were observed at La Pérouse and MAD-Ridge seamounts, however, during the cruises most likely because of the high current speeds observed over the summits and the seamount structure not being favourable for the development and retention of such features (Annasawmy et al., 2020).

Foodwebs are shaped by a complex set of interactions controlled by the availability of organic (C-based nutrients) and inorganic (such as nitrate, nitrite, phosphate and silicate) nutrients, the efficiency of energy transfer to higher trophic levels and the control of species biomass by predators (Pomeroy, 2001). Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analyses are a valuable tool for foodweb investigations in deep-sea ecosystems (Michener and Kaufman, 2007) and are based on time-integrated assimilated food (Martínez del Rio et al., 2009). Trophodynamic studies commonly employ δ^{13}C to investigate the source of organic matter and δ^{15}N to determine trophic level and trophic interactions (Michener and Kaufman, 2007). The heavier isotopes (^{13}C and ^{15}N) are preferentially retained in tissues of consumers relative to their prey, while lighter ^{12}C and ^{14}N isotopes are preferentially excreted (Fry, 2006). Overall, there is a small isotopic enrichment of 0.5–1‰ in the heavier ^{13}C isotope of an organism’s tissue relative to its diet (Fry, 2006). Differences in δ^{13}C values can thus indicate different sources of primary production such as inshore vs offshore, or pelagic vs benthic contributions to food intake (Hobson et al., 1994; Rubenstein and Hobson, 2004). In contrast, δ^{15}N values increase stepwise by 2–4‰ in a consumer’s tissue relative to its diet (Vanderklift and Ponsard, 2003; Michener and Kaufman, 2007; Martínez Del Rio et al., 2009), thus allowing the discrimination of trophic levels.

Identification of the trophic position of various biotic components of the pelagic ecosystem is essential for our understanding of ecosystem functioning and trophic interactions. Food chain length (i.e. number of TLs) is a descriptor of community structure and ecosystem functioning (Post et al., 2000). Measuring the length of a food chain integrates the assimilation of energy flow through all trophic pathways leading to top predators. The understanding of this is essential from an ecosystem-based management perspective, and may provide important insights on ecosystem responses to fisheries pressure and/or climate-induced changes. Knowledge of micronekton trophic interactions at seamount ecosystems of the SWIO are scarce and fragmentary. In order to investigate the trophic pathways at La Pérouse and MAD-Ridge, δ^{13}C and δ^{15}N values of POM, zooplankton and micronekton were measured and trophic levels were estimated using additive isotopic models (as in Post, 2002, and Caut et al., 2009). The main goals of this study were to investigate at La Pérouse and MAD-Ridge seamounts, (1) the trophic interactions of sampled mesopelagic organisms, (2) the influence of trophic groups, specimen size and time of sampling (MAD-Ridge only) on δ^{13}C and δ^{15}N values of micronekton, (3) the δ^{13}C and δ^{15}N values of omnivorous/carnivorous fish collected over the flank relative to the vicinity of La Pérouse; and summit, flanks and vicinity of MAD-Ridge compared with an off-seamount location in the southern Mozambique Channel.

2. Material and methods

2.1. Study sites

2.1.1. La Pérouse seamount

La Pérouse is located on the outskirts of the oligotrophic ISSG province (Longhurst, 1998, 2007; Reygondeau et al., 2013), 160 km northwest of Réunion Island at latitude 19°43′S and longitude 54°10′E (Fig. 1a and b). The seamount summit reaches the euphotic zone, being ~60 m below the sea surface. The summit is 10 km long with narrow and steep flanks and rises from a depth of 5000 m from the ocean floor. The pinnacle was sampled on board the RV *Antea* from 15 to 29 September 2016 (DOI: 10.17600/16004500).

2.1.2. MAD-Ridge seamount

This topographic feature, located ~240 km to the south of Madagascar, along the Madagascar Ridge at latitude 27°29′S and longitude 46°16′E has been named “MAD-Ridge” in this study (Fig. 1a, c). The seamount rises from a depth of 1600 m from the ocean floor to ~240 m below the sea surface. The summit is 33 km long (north to south) and 22 km wide (east to west). MAD-Ridge is surrounded by four smaller pinnacles, reaching depths of 600 m, 900 m, 800 m and 1200 m below the sea surface, between latitudes 27°S-28°S and longitudes 46°E−46°45′E. The MAD-Ridge pinnacle was sampled on board the RV *Antea* (DOI: 10.17600/16004800 and 10.17600/16004900) from 26 November to 14 December 2016.

2.2. Satellite observations

Sea surface chlorophyll data were downloaded from the MODIS dataset (http://oceancolor.gsfc.nasa.gov) at a daily and 4.5 km resolution. Five-day averages were calculated to obtain a proxy of phytoplankton abundance in the surface layer. To investigate the annual variability in surface chlorophyll *a* concentrations, monthly mean concentrations were averaged from January to December 2016 for the defined regions (La Pérouse: 18.5–20°S/53-33°E; MAD-Ridge: 27–28°S/44–48°E) (Fig. 2).

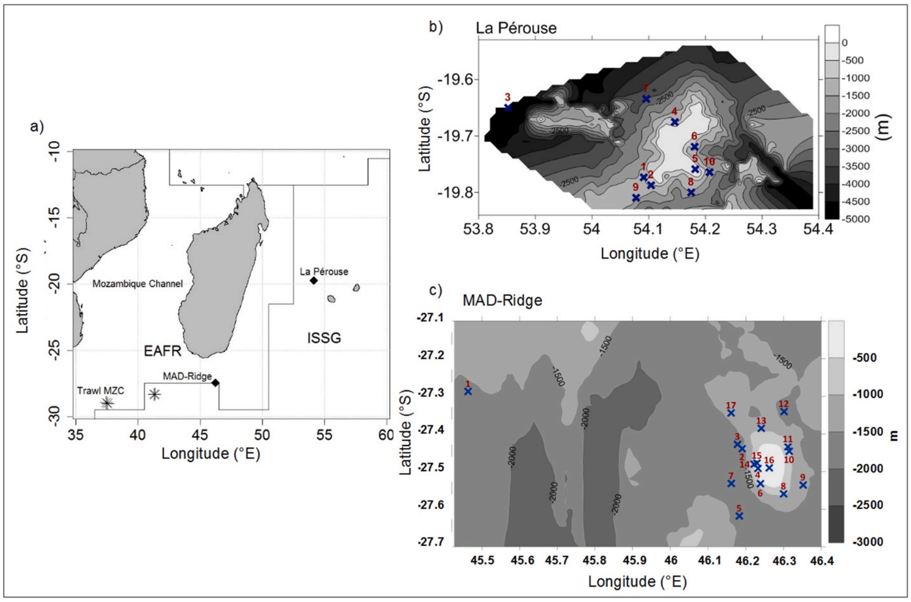

Fig. 1. (a) Location of the MAD-Ridge and La Pérouse seamounts (black diamond symbols) in the East African Coastal (EAFR) and Indian South Subtropical Gyre (ISSG) provinces, respectively. Longhurst's (1998) biogeochemical provinces are delimited by black solid lines. Landmasses are shown in grey. Trawls #18–21 in the southern Mozambique Channel are shown by black stars and labelled "Trawl MZC". Map of (b) La Pérouse trawl stations numbered 1 to 10, (c) MAD-Ridge trawl stations numbered 1 to 17 plotted on the bathymetry (m). The colour bar indicates depth (m) below the sea surface. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

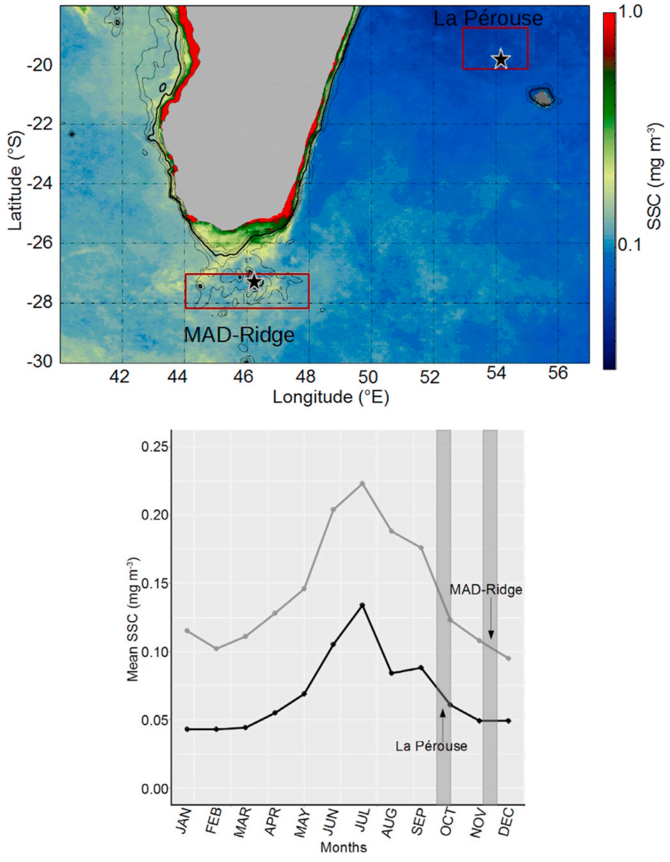

Fig. 2. Averaged satellite image of surface chlorophyll *a* concentrations from 18/09/2016 to 07/12/2016 at La Pérouse and MAD-Ridge (represented by black star symbols). The colour bar indicates the surface mean concentrations in mg m^{-3}. Monthly mean sea surface chlorophyll *a* concentrations (mg m^{-3}) from January to December 2016 for the regions defined by the red squares. The dates of the La Pérouse and MAD-Ridge cruises are marked by grey bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. *Sampling and sample processing*

2.3.1. *Particulate organic matter (POM)*

During both cruises, water samples for stable isotope analyses of POM were collected using Niskin bottles mounted on a Sea-Bird 911 + CTD rosette system at approximately 5 m depth (referred to as POM-Surf) and at the depth of maximum fluorescence (referred to as POM-Fmax) between ~60 and 125 m at La Pérouse and ~80 and 150 m at MAD-Ridge. Between 4 and 8 l (depending on the load of each sample) of seawater were filtered on precombusted 25 or 47 mm glassfibre of 0.7 μm pore size. The filters were oven-dried at 50 °C for 24 h and saved at room temperature in aluminium foil until further analyses.

2.3.2. *Zooplankton sampling*

Zooplankton samples were collected during daylight only with a Bongo net (300 μm mesh to a maximum depth of 500 m and 200 μm mesh to a maximum depth of ~200 m) towed obliquely at La Pérouse (10 stations). At MAD-Ridge, zooplankton samples were also collected during daylight with a Bongo net (300 μm mesh to a maximum depth of 500 m towed obliquely and 63 μm mesh to the depth of the maximum fluorescence towed vertically) at 19 stations. The nets were fitted with a flowmeter and were towed at a vessel speed of 1.5–2 knots for 15–20 min (0.28 m^2 mouth area). Zooplankton samples from the 200 and 300 μm meshes at La Pérouse and, from the 63 and 300 μm meshes at MAD-Ridge were combined at each station. The combined samples at each station were sieved on a stack of seven sieves of decreasing mesh size and divided into six fractions: >4000 μm, 4000-2000 μm, 2000-1000 μm, 1000-500 μm, 500-250 μm, 250-125 μm during La Pérouse and MAD-Ridge and a 7th fraction (125-63 μm) during MAD-Ridge only. Each fraction was oven-dried at 50 °C for 24 h and frozen on board at −20 °C before being analysed for stable isotope analyses (section 2.4). Zooplankton abundances, biomasses and taxa composition at the seamounts and off-seamount locations are investigated in Noyon et al. (2020).

2.3.3. *Trawl sampling*

During both cruises, a 40-m long International Young Gadoid Pelagic Trawl (IYGPT) net (codend with 0.5 cm knotless nylon delta mesh; front tapering end with 8 cm mesh; ~96 m^2 mouth opening) was towed at a vessel speed of 2–3 knots for 60 min during La Pérouse and for 30 min during MAD-Ridge to sample mesopelagic organisms. Trawls were carried out in the shallow (0–200 m), intermediate (200–400 m) and deep (below 400 m) layers during both cruises (Supplementary Material, Table S1). Trawl stations at La Pérouse and MAD-Ridge (Fig. 1b and c) were further classified into the categories summit, flank and vicinity according to whether they occurred on the summit plateau of the seamounts, along the flanks (seafloor depth of 300–1300 m) or in the immediate vicinity (depth >1300 m) (Supplementary Material, Table S1). Four other mesopelagic trawls (#18–21) were conducted in the southern Mozambique Channel (depth >4000 m) during the MAD-Ridge cruise as reference stations for non-seamount locations within the EAFR province (Fig. 1a).

All organisms collected with the trawl were sorted on board, divided into four broad categories (gelatinous, crustaceans, cephalopods and fish), counted and identified to the lowest possible taxon. Individuals from these four broad categories were randomly selected according to their occurrence and abundance and measured (total length for selected gelatinous organisms, abdomen and carapace length for selected crustaceans, dorsal mantle length for cephalopods and standard length for fish). Approximately 2–5 mg of soft tissues of these selected individuals (muscle tissue for leptocephali, muscle abdomen for crustaceans, mantles for squid, dorsal muscle for fish) and whole salps and pyrosomes, were sampled on board in 2 ml Eppendorf tubes and stored at −20 °C, before being processed in the laboratory to determine $\delta^{13}C$ and $\delta^{15}N$ values (section 2.4). A full list of selected gelatinous and micronekton taxa used in stable isotope analyses is given in Supplementary Material, Table S2.

2.4. Stable isotope analysis

Micronekton and zooplankton samples were freeze-dried using Christ Alpha 1–4 LSC freeze-dryers for 48 h and ground to a fine homogeneous powder using an automatic ball mill RETSCH MM200. As variations in lipid composition may influence $\delta^{13}C$ and $\delta^{15}N$ values (Bodin et al., 2009; Ryan et al., 2012), lipids were removed from zooplankton and micronekton samples with dichloromethane on an accelerated solvent extraction system (ASE®, Dionex; Bodin et al., 2009) at the Plateau Chimie/Pôle Technique MARBEC (Sète, France). Prior to $\delta^{13}C$ analyses, POM filters and zooplankton samples were reacted with 1 N HCl to remove carbonates (Cresson et al., 2012). Untreated subsamples of POM and zooplankton were used to measure $\delta^{15}N$ because acid treatment may lead to the loss of nitrogenous compounds (Kolasinski et al., 2008). POM filters were cut, folded and put into tin capsules. Approximately 400–600 μg of each zooplankton and micronekton sample were weighed and placed in tin capsules. These samples were run through continuous flow on a Thermo Scientific FLASH 2000 elemental analyser coupled to a Delta V Plus mass spectrometer at the Pôle de Spectrométrie Océan (Plouzané, France). The samples were combusted in the elemental analyser to separate CO_2 and N_2. A reference gas set was used to determine isotopic ratios by comparison. The isotopic ratios are expressed in the conventional δ notations as parts per thousand (‰) deviations from the international standards:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.5. Data analyses

2.5.1. Overall $\delta^{13}C$ and $\delta^{15}N$ signatures

Shapiro-Wilk and Bartlett tests were computed to test for assumptions of normality and homogeneity of variances in R (version 3.3.1). Links between $\delta^{13}C$ and $\delta^{15}N$ values and the foodweb components (POM-Surf, POM-Fmax, zooplankton, gelatinous organisms, crustaceans, squid and fish), were investigated using Kruskal-Wallis (KW) tests and pairwise comparisons because the data did not follow normal distributions. Kruskal-Wallis tests and pairwise comparisons were also computed to investigate whether there was a significant difference in $\delta^{13}C$ and $\delta^{15}N$ values for each foodweb component between La Pérouse and MAD-Ridge. To assess the association between $\delta^{13}C$ and $\delta^{15}N$ values, Spearman rank correlation coefficients were calculated with all foodweb components at each seamount. Wilcoxon rank sum tests investigated the effect of time (day or night) on $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous plankton and micronekton at MAD-Ridge only (because a single daylight trawl was conducted at La Pérouse and too few species were caught). To test for the effect of trawl position with respect to the seamounts on $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish, Wilcoxon Rank sum tests and KW tests were performed on the La Pérouse and MAD-Ridge datasets, respectively.

2.5.2. Layman community-wide metrics

The Layman community-wide metrics SEA_c and the $\delta^{13}C$ and $\delta^{15}N$ ranges (Layman et al., 2007) were calculated using the SIBER package (version 2.1.4, Jackson et al., 2011). The SEA_c (sample-size-corrected standard ellipse area) describes the overall extent of the isotopic niches. The SEA_c is robust for sample sizes >10 (Daly et al., 2013), which is the case for all the broad categories within this study. The SEA_c of each foodweb component was described in terms of the space occupied by the group on a $\delta^{15}N$-$\delta^{13}C$ plot based on all the individuals sampled within the group. The $\delta^{13}C$ and $\delta^{15}N$ ranges were used to describe and compare the overall extents of the foodwebs at the La Pérouse and MAD-Ridge sites. Increased $\delta^{13}C$ range would be expected in foodwebs with multiple basal sources with varying $\delta^{13}C$ values suggesting niche diversification at the base of the foodweb, whereas the $\delta^{15}N$ range describes the sampled food chain lengths (Portail et al., 2016).

2.5.3. Trophic level estimations

Different models have been applied across several studies to estimate the trophic level of organisms: additive model with a fixed enrichment factor, additive enrichment model with a variable isotopic enrichment or scaled model with decreasing isotopic enrichment factors (Minagawa and Wada, 1984; Post, 2002; Caut et al., 2009; Hussey et al., 2014). Ménard et al. (2014) and Annasawmy et al. (2018) used a fixed enrichment factor of 3.2‰ to estimate trophic levels of foodweb components POM, zooplankton, gelatinous plankton and micronekton collected in the SWIO. In this study, two alternative trophic enrichment assumptions were compared to estimate the trophic level of all the measured individuals within the groups (zooplankton, gelatinous organisms, crustaceans, squid and fish) at La Pérouse and MAD-Ridge.

The TPA model (additive model with constant isotopic enrichment) was proposed by Minagawa and Wada (1984) and Post (2002) with the reference level set at a trophic level of 2 for the primary consumer and a fixed and additive enrichment factor of 3.2‰:

$$\text{Trophic level, TPA} = 2.0 + \frac{\delta^{15}N_i - \delta^{15}N_{primary\ consumer}}{3.2} \quad \text{Eq. 1}$$

where, $\delta^{15}N_i$ the nitrogen isotopic composition of any given micronekton taxon i, $\delta^{15}N_{primary\ consumer}$ the $\delta^{15}N$ reference baseline value at trophic level 2, and 3.2‰ is an estimate of the trophic enrichment factor between consumers and their primary prey (Michener and Kaufman, 2007; Vanderklift and Ponsard, 2003). The $\delta^{15}N$ values of POM, primary consumers and zooplankton have been used in trophic level calculations as isotopic baseline (e.g. Lorrain et al., 2015). Primary consumers are generally used as baseline to reduce errors in estimations (Martínez Del Rio et al., 2009). Salps are known filter feeders which have been used as baseline in previous studies in the region (Ménard et al., 2014). At La Pérouse, the mean $\delta^{15}N$ values of six pyrosomes and one salp specimen was estimated at 5.31 ± 0.31‰ and was used as $\delta^{15}N_{primary\ consumer}$ to estimate the trophic position of all upper trophic level individuals that were collected. At MAD-Ridge, the mean $\delta^{15}N$ values of six salps was 4.22 ± 1.01‰ and was used as $\delta^{15}N_{primary\ consumer}$ to estimate the trophic position of all individuals sampled.

The second model, TPC, is an additive trophic enrichment model with variable isotopic enrichment, estimated from a meta-analysis study on fish muscle (Caut et al., 2009):

$\text{TEF} = -0.281\ \delta^{15}\text{N}_{\text{primary consumer}} + 5.879$, where TEF is the trophic enrichment factor

$$\text{TPC} = 2.0 + [(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{primary consumer}})/\text{TEF}] \qquad \text{Eq. 2}$$

2.5.4. Micronekton habitat ranges and feeding mode

Information on habitat ranges of selected micronekton individuals was obtained from the literature (Clarke and Lu, 1975; Pearcy et al., 1977; Smith and Heemstra, 1986; van der Spoel and Bleeker, 1991; Brodeur and Yamamura, 2005; Davison et al., 2015; Romero-Romero et al., 2019). Organisms were classified as being epipelagic (<200 m), mesopelagic (from 200 to 1000 m), bathypelagic (below 1000 m to ~100 m from the seafloor) and benthopelagic (living near the bottom) according to definitions of the vertical zonation of the pelagic ocean from Del Giorgio and Duarte (2002) and Sutton (2013). The feeding modes of gelatinous plankton and selected micronekton were obtained from the literature and are summarised in Supplementary Material, Table S2. Organisms were classified into the four trophic groups filter-feeders (salps and pyrosomes), detritivores (leptocephali), omnivores (mainly crustaceans and the fish species *Ceratoscopelus warmingii*) and carnivores (most mesopelagic fish and squid). Crustaceans were classified as omnivores because they prey on zooplankton, such as euphausiids and copepods and are also known for occasional herbivory (Hopkins et al., 1994; Birkley and Gulliksen, 2003; Mauchline, 1959; Foxton and Roe, 1974). Most mesopelagic fish were classified as carnivores because they were reported to be zooplankton feeders, preying on copepods, amphipods, euphausiids and ostracods (Dalpadado and Gjøsæter, 1988; Pakhomov et al., 1996; Tanaka et al., 2007; Hudson et al., 2014; Bernal et al., 2015; Carmo et al., 2015; Young et al., 2015), with no herbivorous feeding strategy except *C. warmingii*, which has developed an adaptive response to competition in low-productive environments (Robison, 1984). For species with unknown diets, the feeding mode was determined based on the feeding habit identified from species within the same genus.

In order to give an overview of the foodwebs at the La Pérouse and MAD-Ridge seamounts, hierarchical cluster analyses (average grouping methods) were carried out on resemblance matrices (calculated using Euclidean distances) of normalised δ^{13}C and δ^{15}N values per gelatinous plankton and micronekton species at each seamount and for all sampled stations in PRIMER v6 software according to Clarke and Warwick (2001). Further cluster analyses were performed on log-transformed δ^{13}C values and normalised δ^{13}C and δ^{15}N values of micronekton (excluding the outliers salps, pyrosomes, *Funchalia* sp. and leptocephali) for each seamount.

2.5.5. Effect of size on δ^{15}N values of micronekton

The size distributions of all gelatinous and micronekton organisms captured during the La Pérouse and MAD-Ridge cruises were heavily right-skewed with most organisms being <100 mm in length due to net catchability and selectivity. To test for the effect of size on δ^{15}N values, gelatinous and micronekton organisms <100 mm were considered and linear regressions were computed. Linear models were developed to investigate the effect of body lengths on δ^{13}C and δ^{15}N values of gelatinous and micronekton individuals and to investigate the difference in δ^{15}N values with respect to size between La Pérouse and MAD-Ridge. Additionally, eight micronekton specimens were selected according to their common occurrence at both seamounts, relatively large sample sizes and wide body length ranges, and their δ^{15}N values were compared between the two seamounts. Information on the migration patterns of these eight taxa was obtained from the literature (Utrecht et al., 1987; Butler et al., 2001; Feunteun et al., 2015; Romero-Romero et al., 2019). Linear regressions were fitted to δ^{15}N values of these eight taxa according to their body lengths and the seamount factor (whether δ^{15}N values were significantly different between La Pérouse and MAD-Ridge). To investigate if the seamount has an effect on the size and related diet of fish, δ^{15}N values of selected omnivorous/carnivorous fish species collected on the summits, flanks, vicinity of the seamounts and the southern Mozambique Channel, were examined using linear models.

3. Results

3.1. Prevailing environmental conditions at the La Pérouse and MAD-Ridge seamounts

Sea surface chlorophyll concentrations followed the same seasonal pattern in both regions of the La Pérouse and MAD-Ridge seamounts, although concentrations were twice as high at MAD-Ridge (0.10–0.22 mg m^{-3}) than at La Pérouse (0.04–0.13 mg m^{-3}) all year round (Fig. 2). A peak in productivity was observed in July in both the ISSG and EAFR provinces because of intense mixing caused by austral trade winds. Both the La Pérouse and MAD-Ridge cruises took place during a declining phase of oceanic productivity in the region.

3.2. General foodweb structure

The description of the foodweb structure included POM collected at the surface (POM-Surf) and at the depth of maximum fluorescence (POM-Fmax), zooplankton at both seamounts, two taxonomic groups of gelatinous organisms (salps and pyrosomes), and 42 and 49 taxonomic groups of micronekton, representing 145 and 180 individuals at La Pérouse and MAD-Ridge, respectively. At both La Pérouse and MAD-Ridge, the foodweb components were segregated in their δ^{13}C (La Pérouse: KW, H = 170.5, $p < 0.05$; MAD-Ridge: KW, H = 268.1, $p < 0.05$) and δ^{15}N values (La Pérouse: KW, H = 153.1, $p < 0.05$; MAD-Ridge: KW, H = 127.4, $p < 0.05$) (Fig. 3). POM-Surf and POM-Fmax did not differ significantly in their δ^{13}C and δ^{15}N values at both seamounts ($p > 0.05$). At La Pérouse, gelatinous organisms exhibited higher δ^{13}C values compared with POM-Surf and POM-Fmax ($p < 0.05$), and they exhibited lower δ^{13}C and δ^{15}N values than crustaceans, fish and squid at both seamounts ($p < 0.05$). Crustaceans, fish and squid did not differ significantly in their δ^{15}N values ($p > 0.05$), but they differed in their δ^{13}C values at La Pérouse ($p < 0.05$). Crustaceans did not differ significantly from squid in their δ^{13}C values ($p > 0.05$), whereas all other categories differed in their δ^{13}C values at MAD-Ridge ($p < 0.05$). Squid did not differ significantly from crustaceans and fish in their δ^{15}N values ($p > 0.05$), but ^{15}N was more depleted in crustaceans relative to fish at MAD-Ridge ($p < 0.05$). At La Pérouse (all depths combined), POM, zooplankton and micronekton covered a large δ^{13}C range of ~11‰ (−17.2 to −28.0‰), with POM-Fmax and the unidentified caridean crustacean representing the lowest and highest values, respectively. The δ^{15}N values of all micronekton individuals ranged from 2.5‰ (fish: leptocephali) to 13.3‰ (fish: *Coccorella atrata*). At MAD-Ridge (all depths combined), POM, zooplankton and micronekton also covered a large δ^{13}C range of ~10‰ (−17.1 to −27.2‰), with POM-Surf and the fish species *Chauliodus sloani* representing the lowest and highest values, respectively. The δ^{15}N values of sampled micronekton individuals ranged from 2.3‰ (fish: leptocephali) to 13.5‰ (fish: *Argyropelecus aculeatus*).

Standard ellipse corrected areas (SEA$_c$) refer to the trophic niche widths of the broad categories at La Pérouse and MAD-Ridge. At La Pérouse, POM-Surf and POM-Fmax showed overlapping standard ellipses with the largest SEA$_c$ (3.2 and 3.8‰^{2}, respectively) among all components of the foodweb (Fig. 3). Gelatinous organisms showed the smallest SEA$_c$ of 0.92‰^{2}. Crustaceans, squid and fish had overlapping standard ellipses with SEA$_c$ values of 2.3, 1.2 and 2.9‰^{2}, respectively (Fig. 3). At MAD-Ridge, POM-Surf and POM-Fmax also exhibited overlapping standard ellipses (SEA$_c$ = 4.8 and 2.0‰^{2}, respectively), but with greater variability in POM-Surf δ^{15}N values. Crustaceans, squid and fish

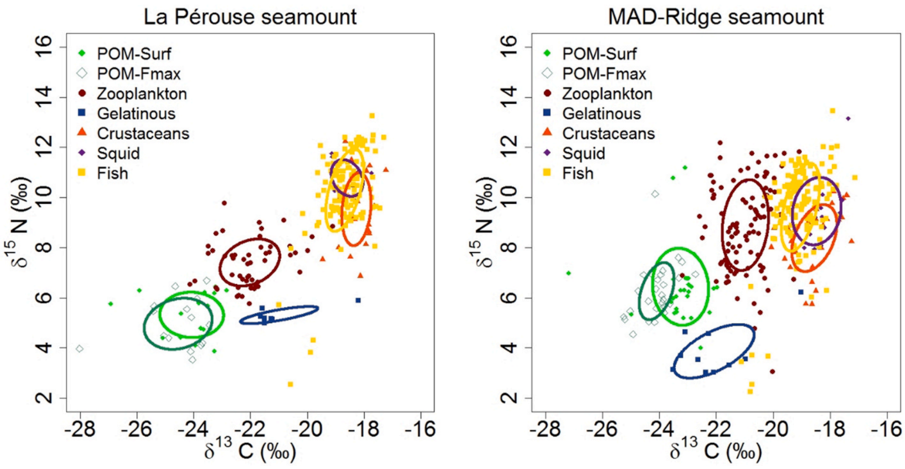

Fig. 3. Bivariate plots of δ^{15}N and δ^{13}C values (‰) for particulate organic matter at the surface (POM-Surf) and the maximum fluorescence (POM-Fmax), zooplankton, gelatinous organisms, crustaceans, squid and mesopelagic fish sampled at La Pérouse and MAD-Ridge seamounts. Standard ellipse areas (coloured solid lines), calculated using SIBER, provide estimates of the size of the isotopic niche for each of these categories. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

had overlapping standard ellipses with SEA$_c$ of 3.0, 3.6 and 3.2‰^{2}, respectively.

The δ^{13}C and δ^{15}N values of the foodweb components POM-Surf, POM-Fmax, zooplankton, gelatinous organisms, crustaceans, squid and fish were significantly different between La Pérouse and MAD-Ridge (δ^{13}C: KW, H = 474.4, df = 13, $p < 0.05$; δ^{15}N: KW, H = 311.3, df = 13, $p < 0.05$, Fig. 4). Pairwise comparisons showed δ^{13}C values of POM-Surf, zooplankton and fish to differ significantly between La Pérouse and MAD-Ridge ($p < 0.05$ each). The median δ^{13}C and δ^{15}N values of lower trophic level foodweb components: POM-Surf, POM-Fmax and zooplankton were greater at MAD-Ridge (δ^{13}C: −23.1, −24.1, −20.9‰; δ^{15}N: 6.3, 6.1 and 8.9‰, respectively) than at La Pérouse (δ^{13}C: −23.7, −24.1, −22.1‰; δ^{15}N: 5.5, 4.9 and 7.5‰, respectively) (Fig. 4).

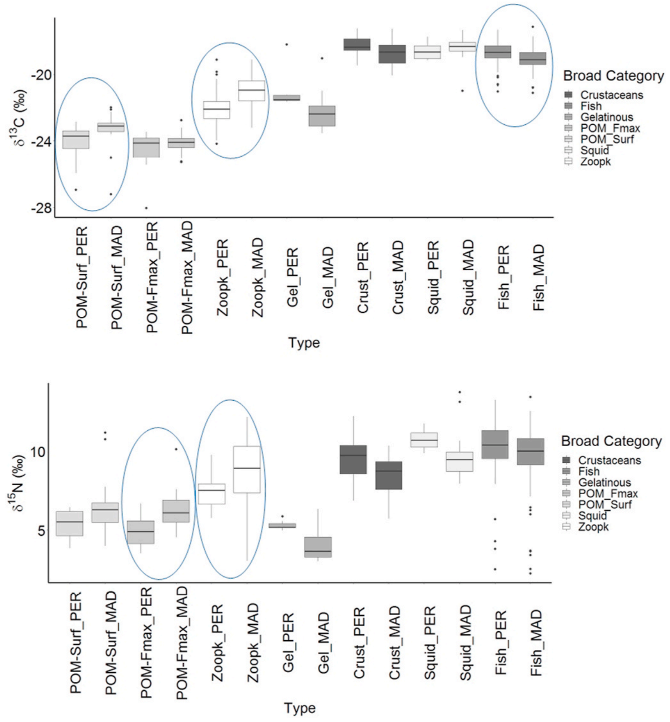

Fig. 4. Boxplots of δ^{13}C and δ^{15}N values (‰) of the foodweb components POM-Surf, POM-Fmax, zooplankton (Zoopk), gelatinous organisms (Gel), crustaceans (Crust), squid and mesopelagic fish at La Pérouse (PER) and MAD-Ridge (MAD). Groups having significantly different δ^{13}C and δ^{15}N values (‰) are shown by solid blue lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Gelatinous organisms, crustaceans and fish displayed higher median δ^{13}C values at La Pérouse (−21.5, −18.4 and −18.7‰, respectively) than at MAD-Ridge (−22.4, −18.6 and −19.1‰, respectively) (Fig. 4). Gelatinous organisms, crustaceans, squid and fish also exhibited higher median δ^{15}N values at La Pérouse (5.2, 9.8, 10.7 and 10.4‰, respectively) than at MAD-Ridge (3.7, 8.8, 9.5 and 10.0‰, respectively) (Fig. 4), but differences were not statistically significant ($p > 0.05$ each). The δ^{13}C values of crustaceans, squid and mesopelagic fish encompassed the same narrow range at La Pérouse and MAD-Ridge (−17.2 to −21.0‰ and −17.1 to −21.1‰, respectively). Gelatinous salps and pyrosomes exhibited δ^{13}C values of −18.2 to −21.7‰ at La Pérouse and −19.0 to −23.5‰ at MAD-Ridge.

3.3. Relationships between δ^{13}C and δ^{15}N values

Ascending the foodweb, from POM-Surf to mesopelagic fish at La Pérouse and MAD-Ridge seamounts, there was a general increase in δ^{13}C and δ^{15}N values (Figs. 3 and 4). There was a significantly positive correlation between δ^{13}C and δ^{15}N values of all sampled components of the foodweb at La Pérouse and MAD-Ridge seamount stations ($p < 0.05$), with Spearman correlation coefficients of $r = 0.74$ and $r = 0.51$, respectively.

3.4. Trophic levels at La Pérouse and MAD-Ridge seamounts

Albeit small differences in trophic positions between the TPA and TPC methods, they both identified the same organisms at the lowest (leptocephali and gelatinous organisms) and highest (mesopelagic fish excluding leptocephali, and squid) trophic positions. For comparison with other studies published in the region (Ménard et al., 2014; Annasawmy et al., 2018), the additive trophic enrichment model with fixed enrichment factor, TPA, (Eq. (1)), is explored in further details.

Leptocephali showed estimated TL values (from Eq. (1)) of 1.9 and 1.8 at both La Pérouse and MAD-Ridge, respectively (Fig. 5). TL values of crustaceans fell between 2.7 (La Pérouse and MAD-Ridge: *Funchalia* sp.) and 3.7 (La Pérouse: Sergestidae; MAD-Ridge: Oplophoridae). Squid had TL values of 3.6 (*Abraliopsis* sp.) and 4.0 (*Histioteuthis* spp.) at La Pérouse. At MAD-Ridge seamount, smaller-sized nektonic squid (26–111 mm dorsal mantle length, DML) displayed TL values of 3.2 (Enoploteuthidae) and 3.6 (*Abraliopsis* sp.), and larger-sized nektonic squid (365–367 mm DML) had TL values of 4.0 (*Histioteuthis* spp.) and 4.8 (*O. bartramii*). TL values of fish (excluding leptocephali) fell between 3.2 (*C. warmingii*) and 4.5 (*C. atrata*) at La Pérouse and between 2.6 (*Decapterus macarellus*) and 4.4 (*Stomias longibarbatus*) at MAD-Ridge (Fig. 5). Overall, the TL values of the micronekton broad categories displayed the same range of TL values at both seamounts.

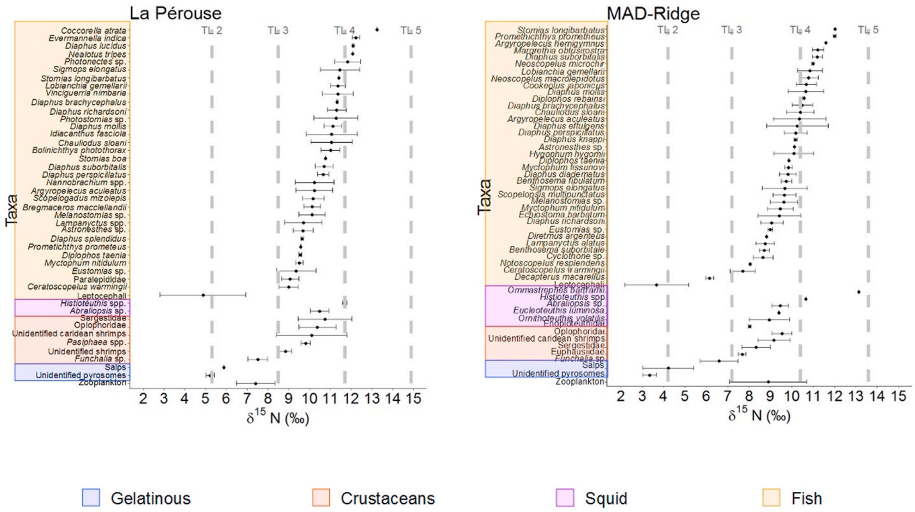

Fig. 5. δ^{15}N (mean ± S.D.) values (‰) and estimated trophic level (TL estimated from the TPA method) of zooplankton, gelatinous and sampled micronekton species at the La Pérouse and MAD-Ridge seamounts. Taxa are placed in broad categories and δ^{15}N compositions are sorted in ascending order of their values.

3.5. *Effect of feeding mode of gelatinous plankton and micronekton on stable isotope values*

The trophic groups identified by cluster analyses are in general agreement with the postulated feeding habits of the group members at both La Pérouse and MAD-Ridge seamounts, although significant differences exist when individual species are considered. The cluster analyses based on δ^{13}C and δ^{15}N values identified two main groups, designated I and II, and two subgroups within group I and group II at La Pérouse and MAD-Ridge (Fig. 6). At La Pérouse, Group I included the filter-feeding pyrosomes (IA) and the detritivorous leptocephali (IB) that showed similar δ^{13}C values (-21.5 ± 0.2 and -20.4 ± 0.5‰, respectively) and δ^{15}N values (5.2 ± 0.2 and 4.9 ± 2.1‰, respectively). Group IIa compared a single salp specimen (δ^{13}C: -18.2‰ and δ^{15}N: 5.9‰) and an omnivorous crustacean *Funchalia* sp. with similar δ^{13}C and δ^{15}N values (-18.7 ± 0.6 and 7.5 ± 0.5‰, respectively). All other crustaceans having an omnivorous feeding mode displayed greater δ^{15}N values (10.0 ± 1.1‰) and were thus segregated within subgroup IIB along with carnivorous mesopelagic fish and squid (Fig. 6). All values are given in mean ± S.D.

At MAD-Ridge, Group I included filter-feeding pyrosomes (IA) and salps, and detritivorous leptocephali (IB) which exhibited the most depleted δ^{13}C and δ^{15}N values relative to omnivorous and carnivorous micronekton (Fig. 6). Group II was subdivided into Group IIA and included the squid *O. bartramii*, the fish *Promethichthys prometheus* and *S. longibarbatus*, all three having carnivorous feeding modes with similar δ^{13}C values and the highest δ^{15}N values for the greatest sizes. The single large squid *Histioteuthis* spp. (DML: 367 mm) showed a high δ^{15}N value of 10.7‰ and a more depleted δ^{13}C value of -21.0‰ compared with *O. bartramii*, *P. prometheus* and *S. longibarbatus*. This squid was hence segregated from subgroup IIA. All other omnivorous and carnivorous organisms exhibited lower δ^{15}N values (Fig. 6) and were thus included within subgroup IIB. Cluster analyses run on δ^{13}C and δ^{15}N values of micronekton and excluding the outliers salps, pyrosomes, *Funchalia* sp. and leptocephali, also segregated individuals according to their feeding mode at MAD-Ridge ($p < 0.05$).

3.6. *Effect of size of micronekton on δ^{15}N values*

The δ^{15}N values of individuals were significantly influenced by their sizes at both La Pérouse ($F_{1,\ 113} = 6.70$, $p < 0.05$) and MAD-Ridge ($F_{1,\ 160} = 23.3$, $p < 0.05$), with increasing δ^{15}N values as the size of the organisms increased (La Pérouse: $\delta^{15}N_{\text{gelatinous and micronekton} <100\text{ mm}} = 8.83 + 0.02 \times \text{Size}$; MAD-Ridge: $\delta^{15}N_{\text{gelatinous and micronekton} <100\text{ mm}} = 7.33 + 0.03 \times \text{Size}$). Eight micronekton species were further selected according to sample size, their common occurrence at both seamounts, their wide body length ranges, differing feeding modes and vertical migration patterns. The δ^{15}N values of the selected species *Sigmops elongatus* (carnivore; diel vertical migrator) and *C. warmingii* (omnivore; diel vertical migrator) were significantly influenced by their lengths (Fig. 7a and b, Table 1), with higher δ^{15}N values at La Pérouse than at MAD-Ridge. The δ^{15}N values of the fish *A. aculeatus* (carnivore, mid-water migrant) and of the crustacean *Funchalia* sp. (omnivore, diel vertical migrator) were significantly influenced by their lengths but were not significantly different between La Pérouse and MAD-Ridge (Fig. 7c and d, Table 1). The mesopelagic fish *Diaphus suborbitalis* and the squid *Abraliopsis* sp. (both carnivores and diel vertical migrators) exhibited the same range of δ^{15}N values irrespective of size at La Pérouse and MAD-Ridge (Fig. 7e and f, Table 1). For the same body length, *Abraliopsis* sp. showed higher δ^{15}N values at La Pérouse relative to MAD-Ridge (Fig. 7f). Models fitted to *C. sloani* (carnivore, diel vertical migrator) and leptocephali (detritivore, migrant or non-migrant depending on species) were not significant (Fig. 7g and h, Table 1). The detritivorous leptocephali had varied δ^{15}N values irrespective of size and irrespective of the sampling location.

The δ^{15}N values of omnivorous/carnivorous fish collected in the vicinity of the La Pérouse and MAD-Ridge seamounts and in the southern Mozambique Channel were significantly influenced by individual body size ($F_{3,\ 171} = 10.3$, Adjusted $R^2 = 13.8$, $p < 0.05$) (Fig. 8a). However, there were no significant influence of body size on the δ^{15}N values of seamount flank- and summit-associated fish species *D. suborbitalis* (La Pérouse and MAD-Ridge), *Benthosema fibulatum*, *Diaphus knappi* and *Cookeolus japonicus* ($F_{1,\ 10} = 0.07$, $p > 0.05$) at MAD-Ridge. These seamount flank- and summit-associated fish species (Annasawmy et al., 2019; Cherel et al., 2020) exhibited minimum and maximum δ^{15}N values of 9.8‰ (*B. fibulatum*) and 11.2‰ (*D. suborbitalis*) for individuals ranging in size from 38 mm (*D. suborbitalis*) to 328 mm (*C. japonicus*) (Fig. 8b). Despite the differing sizes of these seamount flank- and summit-associated fish species, they exhibited an estimated TL value (TPA model) of ~4 at both La Pérouse and MAD-Ridge pinnacles.

3.7. *Effect of time of day on δ^{13}C and δ^{15}N values at MAD-Ridge seamount*

Gelatinous and micronekton organisms sampled at MAD-Ridge

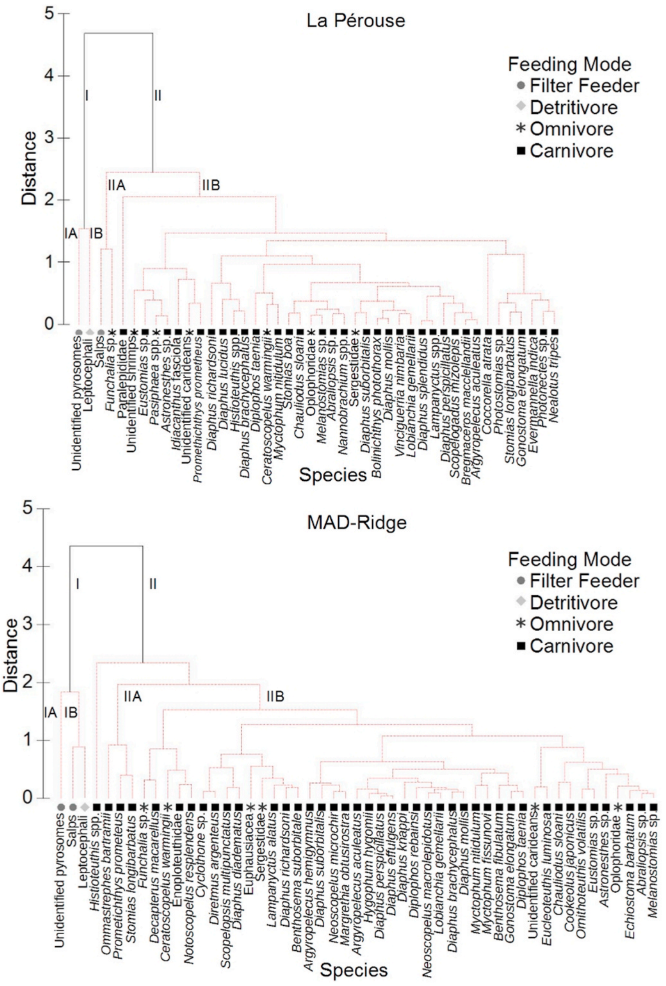

Fig. 6. Hierarchical clustering (Euclidean distance of normalised data subjected to averaged grouping) of $\delta^{13}C$ and $\delta^{15}N$ values (‰) of sampled gelatinous organisms, crustaceans, squid and mesopelagic fish at La Pérouse and MAD-Ridge. Roman numerals at the tree branches identify groups of species belonging to the different trophic guilds: group I – filter-feeders and detritivores; group II- omnivores and carnivores; subgroup IA: filter-feeders at La Pérouse and MAD-Ridge; subgroup IB: detritivores at both seamounts; subgroup IIA: filter-feeders and omnivorous crustaceans at La Pérouse, and squid highest trophic level mesopelagic fish at MAD-Ridge; subgroups IIB: omnivorous and carnivorous micronekton at La Pérouse and MAD-Ridge.

exhibited similar $\delta^{13}C$ values (−19.6 and −19.4‰ respectively) during day and night ($W = 3055.5$, $p > 0.05$). However, individuals collected during daylight showed higher median $\delta^{15}N$ values (9.22‰) than those collected at night (8.12‰) ($W = 4757.5$, $p < 0.05$).

3.8. *Seamount effect on $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish*

The $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish had overlapping ranges at La Pérouse flank and vicinity stations as well as overlapping ranges at MAD-Ridge flank, summit and vicinity and Mozambique Channel stations (Fig. 9). There were no significant differences in $\delta^{13}C$ ($W = 1619$, $p > 0.05$) of omnivorous/carnivorous fish collected between flank stations and the vicinity of La Pérouse seamount, whereas a significant difference was observed for $\delta^{15}N$ values between flank (median: 10.1‰) and vicinity (median: 10.8‰) stations ($W = 1876$, $p < 0.05$). There was also no significant difference in $\delta^{13}C$ values (KW, $H = 1.0$, $df = 2$, $p > 0.05$) of omnivorous/carnivorous fish collected in the southern Mozambique Channel, the vicinity, flank and summit of MAD-Ridge. However, there was a significant difference in $\delta^{15}N$ values (KW, $H = 8.5$, $df = 3$, $p > 0.05$) of omnivorous/carnivorous fish collected from the southern Mozambique Channel (median: 10.6‰) and in the vicinity of MAD-Ridge (median: 10.0‰).

4. Discussion

To our knowledge, this study is the first to investigate trophic interactions of mesopelagic communities at La Pérouse and MAD-Ridge seamounts using $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. The foodweb components POM-Surf, POM-Fmax, zooplankton, gelatinous organisms and 42 and 49 taxonomic groups of micronekton were identified at La Pérouse and MAD-Ridge, respectively. Despite the low sample sizes for some species, our datasets provide a first overview of the trophic relationships of micronekton at both seamounts.

4.1. *Sampling bias and constraints*

The full suite of foodweb components could not be sampled at both seamounts because of trawl gear catchability, selectivity and net avoidance of some species of squid and larger fish. Stable isotopes also have numerous limitations in the extent to which they can be used to elucidate complex foodweb dynamics. Isotopic baselines vary seasonally and spatially (Ménard et al., 2014), and organisms or tissues within a single individual may incorporate the isotopic signal of their diets at varying rates, thereby influencing the stable isotope values of individuals (Martínez Del Rio et al., 2009). The use of pelagic tunicates as isotopic baseline in TL calculations can also be problematic because pelagic tunicates may be members of an alternate microbial foodweb (Pakhomov et al., 2019). Furthermore, the $\delta^{15}N$ values of gelatinous plankton and micronekton were significantly different between day and night samples at MAD-Ridge. This was probably due to the sampling depth, because night-time samples were collected in the shallow, intermediate and deep layers, whereas daylight samples were collected mostly in the deep layer (apart from two leptocephali collected in the shallow depth category). Previous studies found higher $\delta^{15}N$ and $\delta^{13}C$ values with depth, which have been linked to the increase of $\delta^{15}N$ in POM with depth (Kolasinski et al., 2012; Fanelli et al., 2013). However, as the IYGPT net had no closing device, the effect of sampling depth on $\delta^{13}C$ and $\delta^{15}N$ values of individuals could not be investigated further.

Recent studies have cautioned against the use of a fixed additive nitrogen enrichment factor of ~3.2–3.4‰ that is commonly used to estimate the trophic position of an organism relative to its diet. Caut et al. (2009) showed that the consumer taxonomic group and consumer tissue significantly affect the discrimination factor used in trophic level calculations, and Hussey et al. (2014) stressed that the enrichment between consumers and their primary prey items becomes narrower in the upper parts of a food chain. Bastos et al. (2017) developed a novel method using food-specific trophic discrimination factors to estimate trophic positions of omnivorous fish given that plant-based and animal-based materials in diets are not assimilated in the same manner. Olivar et al. (2019) observed small variations in trophic level calculations of mesopelagic fish when using alternative models to estimate trophic positions. However, those authors also concluded that the important differences among species are retained by all trophic models, similarly to the findings of this study.

4.2. *Trophic interactions at La Pérouse and MAD-Ridge seamounts*

Particulate organic matter collected at the surface generally consists of phytoplankton, bacteria, faecal pellets and detritus (Riley, 1971; Saino and Hattori, 1987; Fabiano et al., 1993; Dong et al., 2010; Liénart et al., 2017). The $\delta^{13}C$ values of POM (collected at the surface) were different at the La Pérouse and MAD-Ridge seamounts. $\delta^{13}C$ baselines can be affected by various processes such as latitude, nutrient source, depth, ocean mixing and primary productivity (Fry, 2006). Research has

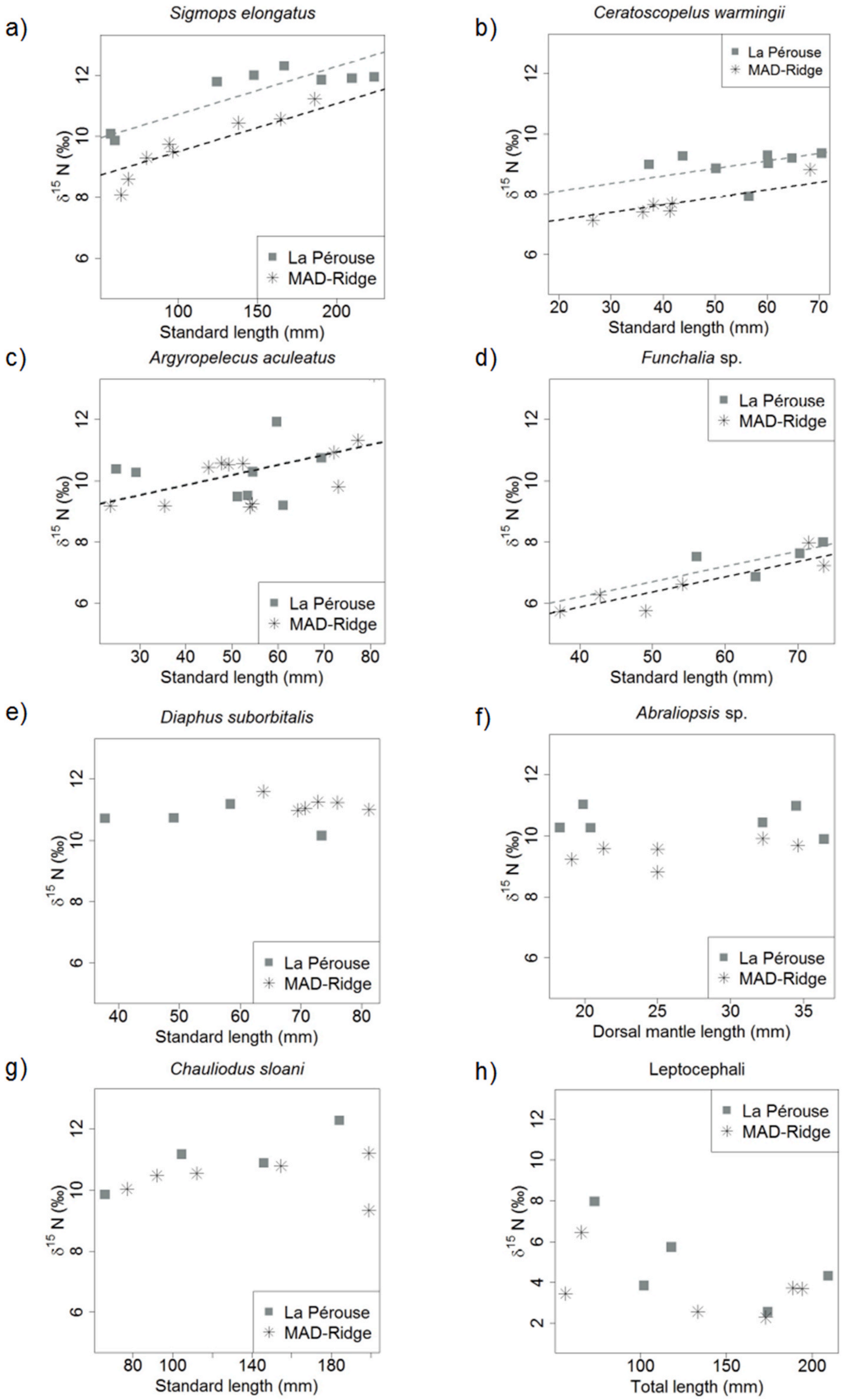

Fig. 7. δ^{15}N values (‰) of (a) fish: *Sigmops elongatus*, (b) fish: *Ceratoscopelus warmingii*, (c) fish: *Argyropelecus aculeatus*, (d) crustacean: *Funchalia* sp., (e) fish: *Diaphus suborbitalis*, (f) squid: *Abraliopsis* sp., (g) fish: *Chauliodus sloani*, (h) fish: leptocephali, plotted against size in mm [standard length for (a)–(c), (e), (g)–(h); abdomen and carapace length for (d); dorsal mantle length for (f)] at La Pérouse (squares) and MAD-Ridge (stars). Simple linear regressions for δ^{15}N values versus size are plotted for (a)–(d).

found that chlorophyll *a* concentrations explained the variability in POM δ^{13}C values within the EAFR province but not in the ISSG (Annasawmy et al., 2018). Surface chlorophyll *a* concentrations at MAD-Ridge (within the EAFR province) was greater than at La Pérouse (within the ISSG) all year round (Annasawmy et al., 2019), likely a result of terrestrial input of nutrients from the Madagascar landmass, upwelling events on the shelf to the south of Madagascar (Ramanantsoa et al., 2018), offshore advection of this shelf productivity through cross-shelf transport (Noyon et al., 2018) and vertical mixing in the mesoscale eddy system over MAD-Ridge (De Ruijter et al., 2004; Vianello et al., 2020). High levels of photosynthetic rate (currently occurring at the south Madagascar upwelling and being transported south), would induce higher δ^{13}C POM values at MAD-Ridge compared with the oligotrophic La Pérouse (Fry, 1996; Savoye et al., 2003). Surface POM at MAD-Ridge might have possibly been both of marine and terrestrial origin, yielding higher δ^{13}C values relative to surface POM at La Pérouse, which might have consisted of phytoplankton with no terrestrial POM input.

Table 1
Linear regression models fitted to δ^{15}N values (‰) with respect to body length in mm (SL, standard length for fish; Tl, total length for leptocephali larvae; ACL, abdomen and carapace length for the crustacean; DML, dorsal mantle length for the squid specimen) and the seamount variable (whether values were significantly different between La Pérouse and MAD-Ridge) of 8 micronekton taxa- *Sigmops elongatus* (fish), *Ceratoscopelus warmingii* (fish), *Argyropelecus aculeatus* (fish), *Funchalia* sp. (crustacean), *Diaphus suborbitalis* (fish), *Abraliopsis* sp. (squid), *Chauliodus sloani* (fish), and leptocephali (fish).

Taxon	Regression equation	Adjusted r^2 (%)	F-statistic	Degrees of freedom	P-value
Sigmops elongatus	$\delta^{15}N = 9.15 + 0.0157$ x SL – 1.2210 x seamount La Pérouse: $\delta^{15}N = 9.15 + 0.0157$ x SL MAD-Ridge: $\delta^{15}N = 7.93 + 0.0157$ x SL	85.2	46.0	13	< 0.05 for size and seamount
Ceratoscopelus warmingii	$\delta^{15}N = 7.61 + 0.0249$ x SL - 0.9521 x seamount La Pérouse: $\delta^{15}N = 7.61 + 0.0249$ x SL MAD-Ridge: $\delta^{15}N = 6.66 + 0.0249$ x SL	72.4	18.0	11	< 0.05 for size and seamount
Argyropelecus aculeatus	$\delta^{15}N = 8.57 + 0.0331$ x SL - 0.0272 x seamount	16.5	2.87	17	< 0.05 for size; > 0.05 for seamount
Funchalia sp.	$\delta^{15}N = 4.23 + 0.0496$ x ACL - 0.3460 x seamount	72.7	13.0	7	< 0.05 for size; > 0.05 for seamount
Diaphus suborbitalis	$\delta^{15}N = 11.5–0.0151$ x SL + 0.7594 x seamount	43.8	4.51	7	> 0.05 for size; < 0.05 for seamount
Abraliopsis sp.	$\delta^{15}N = 10.3 + 0.0069$ x DML - 1.006 x seamount	56.2	8.06	9	> 0.05 for size; < 0.05 for seamount
Chauliodus sloani	$\delta^{15}N = 10.2–0.0065$ x SL + 0.7431 x seamount	12.5	1.64	7	> 0.05 for size and seamount
Leptocephali larvae	$\delta^{15}N = 7.18–0.0170$ x Tl – 1.1971 x seamount	25.3	2.69	8	> 0.05 for size and seamount

The δ^{13}C-δ^{15}N correlations of all foodweb components were not relatively strong at the La Pérouse and MAD-Ridge seamounts ($r = 0.74$ and 0.51 respectively) at the times of the cruises. A strong correlation during periods of high productivity would have supported the hypothesis of a unique and isotopically homogeneous pelagic food source (Fanelli et al., 2013; Papiol et al., 2013; Preciado et al., 2017), i.e. a single source of carbon for plankton (Fanelli et al., 2009). The relatively weaker correlation observed in our study suggests a wide array of sources of production sustaining the different assemblages once the main input from surface production has decreased (Fanelli et al., 2011a, b; Papiol et al., 2013), or exploitation of organic matter at different stages of degradation from fresh phytodetritus to highly recycled (Fanelli et al., 2009), or refractory materials such as chitin from copepod exoskeleton becoming abundant in sinking marine snow or inorganic carbonates (Polunin et al., 2001). This would be the case in low productive environments such as the ISSG, where production at La Pérouse would be reduced in September (Annasawmy et al., 2019) and thus zooplankton would have to expand their food spectrum, as demonstrated by the larger span of their niche widths over the δ^{13}C range. Alternatively, the δ^{13}C-δ^{15}N correlations could reflect temporal variations in the baseline isotope values coupled with varying rates of isotopic incorporation (Fanelli et al., 2009, 2011b, 2013). Higher trophic level organisms such as large crustaceans and fish reportedly do not show seasonal patterns in their isotope values owing to their much slower tissue turnover rates (Polunin et al., 2001). Additional seasonal studies are required to investigate POM and resulting zooplankton δ^{13}C and δ^{15}N signatures in July when surface oceanic phytoplankton production is enhanced within the ISSG and EAFR provinces (Annasawmy et al., 2018, 2019).

Among the mesopelagic organisms sampled, gelatinous plankton exhibited the lowest trophic level (~2), crustaceans showed an intermediate trophic level (~3), and smaller squid and mesopelagic fish exhibited TL values between 3 and 4, as estimated from the TPA method. The large nektonic squid, *O. bartramii*, exhibited a TL of ~5 at MAD-Ridge. Assuming a fixed and additive trophic fractionation of 3.2‰ (for comparison with other SWIO studies), the overall range of δ^{15}N values implied a two-step (3 trophic levels) and three-step (4 trophic levels) pelagic food chain at La Pérouse and MAD-Ridge seamounts, respectively. Unfortunately, no top predators were sampled during these cruises to provide information on higher trophic level organisms. Earlier studies within the EAFR province, showed swordfish *Xiphias gladius* collected off the coast of Madagascar to have a TL of ~4.7 (δ^{15}N: 14.0 ± 0.59‰). Specimens collected within the ISSG province had a TL of ~5.2 (δ^{15}N: 15.1 ± 0.36‰) (Annasawmy et al., 2018). Several authors described the number of trophic levels averaging between four and six in marine ecosystems, from primary consumers to top predators, and appearing higher in coastal environments, reefs and shelves and lower in oceanic upwelling systems (Arreguín-Sánchez et al., 1993; Browder, 1993; Christensen and Pauly, 1993; Bulman et al., 2002). Similar to those studies, it seems that both La Pérouse and MAD-Ridge seamounts exhibit trophic levels typical of oceanic systems, although small variations may exist in the δ^{13}C and δ^{15}N values of an organism's tissues according to various environmental, behavioural and physiological factors (Ménard et al., 2014; Annasawmy et al., 2018).

4.3. *Influence of feeding mode and size on δ^{13}C and δ^{15}N values*

The trophic guilds established at La Pérouse and MAD-Ridge seamounts were segregated in terms of δ^{13}C and δ^{15}N values, from depleted (detritivores and filter-feeders) to enriched (omnivores and carnivores) isotope values, highlighting the fact that these trophic guilds consist of species that exploit distinct classes of resources (Bulman et al., 2002; Papiol et al., 2013; Choy et al., 2016). The large range of δ^{13}C values (~−17 to −23‰) when gelatinous organisms are considered together with crustaceans, squid and mesopelagic fish suggests that these organisms exploit different sources of production, thus giving rise to different trophic pathways (Ménard et al., 2014). Gelatinous filter feeders such as salps and pyrosomes ingest a variety of suspended particles (Harbou, 2009; Conley, 2017) and leptocephali include a wide range of species feeding on detrital material (Otake et al., 1993) such as larvacean houses and faecal pellets (Lecomte-Finiger et al., 2004; Feunteun et al., 2015) and hence exhibited depleted δ^{13}C values relative to other micronekton broad categories. Species depleted in ^{13}C reportedly feed near the base of the food chain and are closely associated with plankton relative to fish with higher δ^{13}C values (Polunin et al., 2001).

Crustacean taxa were at intermediate trophic levels at both seamounts, below that of strict carnivores and above that of detritivores or filter-feeding organisms. Some species of crustaceans would prey on chaetognaths (Heffernan and Hopkins, 1981), molluscs, olive-green debris containing phytoplankton and protists (Hopkins et al., 1994), and they would share common food sources with mesopelagic fish by foraging on copepods, decapods and euphausiids (Fanelli et al., 2009). Similar to previous studies conducted in the SWIO (Ménard et al., 2014; Annasawmy et al., 2018), crustaceans exhibited overlapping isotopic

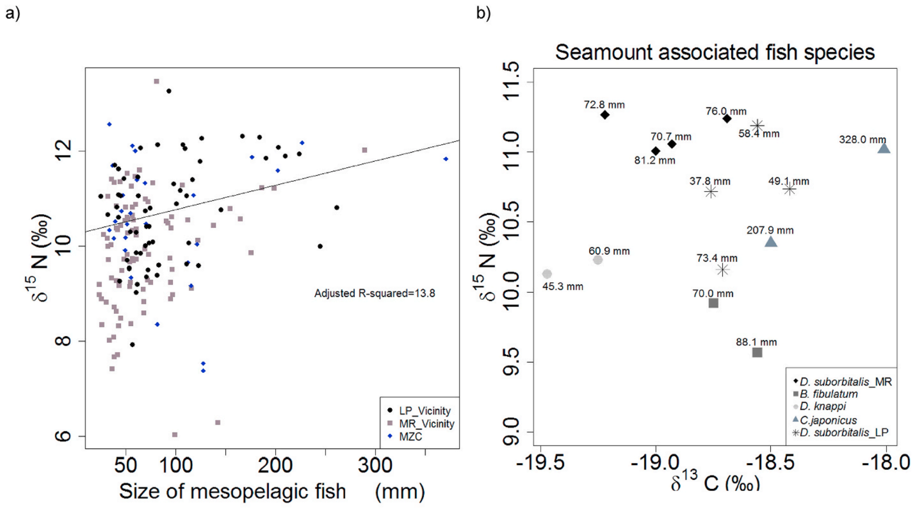

Fig. 8. (a) δ^{15}N values (‰) of mesopelagic fish from La Pérouse and MAD-Ridge seamount vicinities (LP_Vicinity and MR_Vicinity respectively) and from the Mozambique Channel, plotted against their standard lengths (mm). Simple linear regressions are plotted. (b) Bivariate plots of δ^{15}N and δ^{13}C values (‰) for selected seamount flank- and summit-associated fish species *D. suborbitalis* at La Pérouse (LP) and *B. fibulatum*, *D. knappi*, *C. japonicus* and *D. suborbitalis* at MAD-Ridge (MR) seamounts. Standard lengths are given in mm.

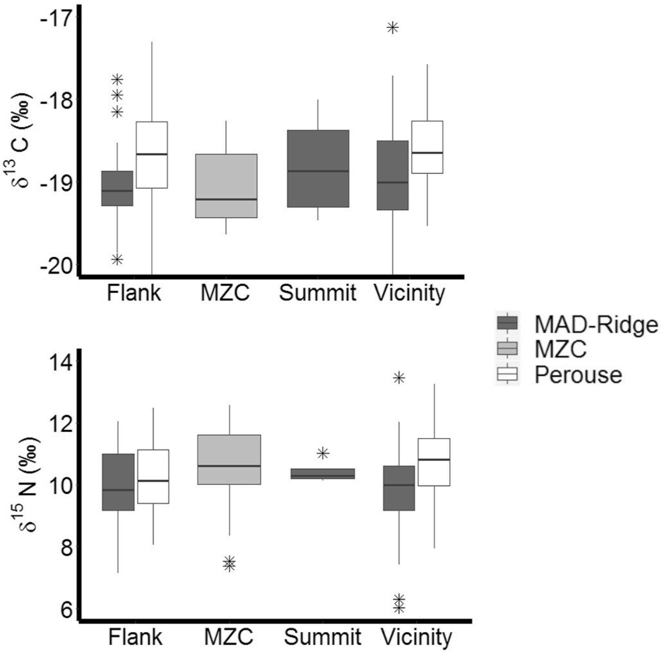

Fig. 9. Boxplots of δ^{13}C and δ^{15}N values (‰) of omnivorous/carnivorous mesopelagic fish at La Pérouse flank (n = 50 samples) and vicinity (n = 60 samples) stations and, MAD-Ridge vicinity (n = 91 samples), flank (n = 38 samples) and summit (n = 4 samples) stations, and stations from the southern Mozambique Channel (n = 28 samples). Outliers are shown as star symbols.

niches with carnivorous mesopelagic fish and squid at both seamounts. The narrow range of δ^{13}C values and the greater overlap of isotopic niches between crustaceans and carnivorous squid and mesopelagic fish at both seamounts might suggest some degree of similarity in the diet components with low level of resource partitioning and a high level of competition among these broad categories (Fanelli et al., 2009) or alternatively, different diets but with prey items having similar isotopic compositions.

Whereas lower trophic level components, POM-Fmax and zooplankton showed significantly different and higher δ^{15}N values at MAD-Ridge relative to La Pérouse (most likely because of differing productivity and fast turnover rate of these organisms), higher trophic level components such as crustaceans, squid and fish showed no significant differences in their δ^{15}N values between the two seamounts. There are several hypotheses for similar isotopic signatures of higher trophic levels when baseline levels differ. First, the sampled organisms might not have had time to incorporate the isotopic composition of their most recent diets, especially if transient productivity bouts had impacted the density or composition of their diet. Whereas some studies reported tissue turnover rates of ~0.1–0.2% per day in deep-sea fish (Hesslein et al., 1993), other studies showed a lack of tissue turnover information in more specific mesopelagic families including Myctophidae and Stomiidae (Choy et al., 2012). Second, the difference in the δ^{15}N values of POM and zooplankton observed at La Pérouse and MAD-Ridge, although significant, may have been too negligible to be reflected in the δ^{15}N values of higher trophic levels. Third, the number of squid and crustacean specimens analysed for stable isotopes might not be large enough to reflect the full diversity in the isotopic signatures, and hence the apparent lack of variations in δ^{15}N values for these individuals between the two seamounts. Finally, as a result of movements, zooplankton grazers and subsequent trophic levels might have fed on prey components that are not those sampled in the water column, leading to a mismatch in isotopic signatures between lower and higher trophic levels.

In this study, δ^{15}N values of micronekton were correlated to body size. This phenomenon was observed in various organisms such as phytoplankton, zooplankton, decapods and fish and across numerous studies (Sholto-Douglas et al., 1991; France et al., 1998; Waite et al., 2007; Ventura and Catalan, 2008; Hirch and Christiansen, 2010; Choy et al., 2012, 2015; Papiol et al., 2013) and is probably attributable to size-related predation. As organisms grow in size, they can feed farther up the foodweb on larger prey with greater δ^{15}N values (Parry, 2008; Ménard et al., 2014). For those species whose δ^{15}N values (*S. elongatus*, *C. warmingii* and *Abraliopsis* sp.) were significantly influenced by size, their δ^{15}N values were greater (around 1‰ difference) at La Pérouse than at MAD-Ridge for the same body lengths. As suggested in Parry (2008), if the δ^{15}N values, and hence the TL of an organism, are influenced by size, then the δ^{15}N signal will also depend on baseline values and the variables that affect an organism's size such as feeding mode, growth rate, body condition and available prey items. As δ^{15}N values of POM and zooplankton were higher at MAD-Ridge than at La Pérouse, we hypothesize that those intermediate TLs at the oligotrophic La Pérouse seamount had a different trophic functioning, with the diet of those species being based on a larger proportion of higher TL prey than at MAD-Ridge.

Body size did not have an effect on δ^{15}N values of leptocephali which encompass a wide range of species having a detritivorous and opportunistic feeding mode at both seamounts. Such lack of effect was also observed for *C. sloani* individuals ranging in size from 66 to 184 mm at

La Pérouse and from 77 to 199 mm at MAD-Ridge. These individuals are semi-migrants, caught in deep and intermediate trawls during both day and night. Individuals 45–178 mm long feed on myctophids and other fish species (Utrecht et al., 1987; Butler et al., 2001) with prey items being more than 63% of their own length (Clarke, 1982). Smaller individuals were reported to feed on euphausiids (Butler et al., 2001). Our trawls failed to capture smaller *C. sloani* individuals which may have had a different diet and possibly different δ^{15}N values relative to larger individuals. There might also be a trophic plateau whereby subsequent increases in trophic position with size are not possible due to physical constraints on the organism or lack of appropriate prey of higher trophic levels, as was observed with *O. bartramii* specimens from the Central North Pacific (Parry, 2008).

4.4. Seamount effect on δ^{13}C and δ^{15}N values of fish species

Omnivorous/carnivorous fish sampled in the southern Mozambique Channel exhibited slightly enriched δ^{15}N values relative to those sampled in the vicinity of the MAD-Ridge seamount. Productivity in the southern Mozambique Channel may be both entrained from the African landmass and locally generated within mesoscale eddies, hence leading to enhanced chlorophyll *a* concentration, micronekton abundances and enriched δ^{15}N values within tissues of micronekton (Tew-Kai and Marsac, 2009; Annasawmy et al., 2018). For an increase in phytoplankton biomass to take place at the seamounts, physical processes leading to retention (e.g. Taylor columns trapping a body of water), enrichment (e.g. localised upwelling and uplift of nutrients) and concentration of productivity must co-occur (Bakun, 2006). However, as seen at La Pérouse and MAD-Ridge seamounts, the current speeds were too strong during the cruise, and the seamount structures unfavourable for Taylor column formation and for significant retention and assimilation of productivity (Annasawmy et al., 2020). This would have inhibited any subsequent energy transfer to higher trophic levels, potentially explaining the lack of differences in δ^{15}N values between the seamount and the area not influenced by the seamount.

Seamount-associated fish species *D. suborbitalis*, *B. fibulatum* and *C. japonicus* (Annasawmy et al., 2019; Cherel et al., 2020), sampled at the summit and on the flanks of MAD-Ridge showed similar δ^{13}C, δ^{15}N and TL values irrespective of their size, similarly to *D. suborbitalis* sampled at La Pérouse. This most likely reflects similar food sources at the summit and flanks of both pinnacles or ingestion of different prey items having similar isotopic composition. These fish may associate with the La Pérouse and MAD-Ridge summits and flanks owing to enhanced availability of prey and/or the quiescent shelters offered by the topography (Annasawmy et al., 2019). All seamount-associated fish individuals collected on the summit and flanks of La Pérouse and MAD-Ridge with the IYGPT net were adults, previously reported to prey on copepods (Go, 1986; Vipin et al., 2018; Olivar et al., 2019) and chaetognaths (Appelbaum, 1982), organisms present in similar proportions on and away from both seamounts (Noyon et al., 2020).

Although δ^{13}C and δ^{15}N values may depend on a range of factors, there were few differences between δ^{13}C and δ^{15}N values of mesopelagic fish sampled at La Pérouse and MAD-Ridge and those collected in the Indian Ocean, within the oligotrophic ISSG province (*A. aculeatus* δ^{13}C and δ^{15}N values: −18.6 and 9.5‰, *C. sloani*: −18.1 and 9.5‰, and *Lobianchia gemellarii*: −18.5 and 9.9‰; Annasawmy et al., 2018) and the western Mozambique Channel (*A. aculeatus*: −18.4 and 10.0‰ and *L. gemellarii*: −18.4 and 11.1‰; Annasawmy et al., 2018). Even though mesopelagic fish exhibit small variations in their δ^{13}C and δ^{15}N values across different studies in various oceanic environments, they generally occupy trophic positions between 2 and 4, irrespective of the approach used to estimate trophic positions (Fanelli et al., 2011b; Choy et al., 2012, 2015, 2016; Colaço et al., 2013; Ménard et al., 2014; Valls et al., 2014a,b; Denda et al., 2017; Annasawmy et al., 2018; Olivar et al., 2019). Despite the possible bias induced by the different time-scales in sampling (Mill et al., 2008), within a stable isotope approach, the trophic positions of mesopelagic fish across numerous studies confirmed similar dietary patterns and food sources with similar isotopic compositions. Hence, these mesopelagic fish species by their opportunistic feeding mode may play a similar trophic role across different environments (Olivar et al., 2019).

5. Concluding remarks

This study has shown that despite the different productivity at the two shallow seamounts and the significant differences in lower trophic level δ^{13}C and δ^{15}N values, crustaceans, smaller-sized squid and mesopelagic fish, because of their varied feeding modes, occupy trophic positions between 3 and 4. Specimen size had an influence on the δ^{15}N values of most individuals, although that also depended on the life strategy and feeding mode of the species considered. The δ^{13}C and δ^{15}N values of mesopelagic organisms sampled during both cruises reflected those of typical oceanic systems and the seamounts did not seem to have any impact on the overall isotopic signatures of the mesopelagic taxa sampled. However, the few seamount-associated fish sampled showed similar δ^{15}N values and trophic levels irrespective of their size at the summits and flanks of the pinnacles. La Pérouse and MAD-Ridge seamounts may hence be important foraging grounds for the few taxa that preferentially associate with their slopes and summits, and thus benefit from the varied habitat types that the seamounts offer compared to the open ocean environment.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2020.104804.

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