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Pavanee Annasawmy[1,2], Yves Cherel[3], Evgeny V. Romanov[4], François Le Loc'h[5], Frédéric Ménard[6], Jean-François Ternon[1], Francis Marsac[1,2]

[1] *MARBEC, IRD, Univ Montpellier, CNRS, Ifremer, Sète, France*

[2] *Department of Biological Sciences and Marine Research Institute/ICEMASA, University of Cape Town, Cape Town, South Africa*

[3] *Centre d'Etudes Biologiques de Chizé (CEBC), UMR7372 du CNRS- La Rochelle Université, Villiers-en-Bois, France*

[4] *Centre technique d'appui à la pêche réunionnaise (CAP RUN - CITEB), Île de la Réunion, France*

[5] *IRD, Univ Brest, CNRS, Ifremer, LEMAR, IUEM, F-29280 Plouzane, France*

[6] *Aix Marseille Univ, Université de Toulon, CNRS, IRD, MIO, UM110, Marseille, France*

* Corresponding author: angelee-pavanee.annasawmy@ird.fr

ORCID Numbers:

Pavanee Annasawmy: 0000-0001-8803-9687

Yves Cherel: 0000-0001-9469-9489

François Le Loc'h: 0000-0002-3372-6997

Frédéric Ménard: 0000-0003-1162-660X

Jean-François Ternon: 0000-0002-1396-8921

Francis Marsac: 0000-0002-3295-594X

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 $\delta^{15}N$ 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).

Keywords: micronekton, crustaceans, fish, $\delta^{13}C$, $\delta^{15}N$, trophic level

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 & Yamamura, 2005; De Forest & Drazen, 2009; Ménard et al., 2014). They range in size from 2 to 20 cm and represent a substantial biomass in oceanic waters (Brodeur & 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 & 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 & 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 & 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 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 extensively 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 & 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 & Boehlert, 1985; Dower et al., 1992; Mouriño et al., 2001; Mohn & 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses are a valuable tool for foodweb investigations in deep-sea ecosystems (Michener & Kaufman, 2007) and are based on time-integrated assimilated food (Martínez del Rio et al., 2009). Trophodynamic studies commonly employ $\delta^{13}C$ to investigate the source of organic matter and $\delta^{15}N$ to determine trophic level and trophic interactions (Michener & 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 $\delta^{13}C$ 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 & Hobson, 2004). In contrast, $\delta^{15}N$ values increase stepwise by 2-4‰ in a consumer's tissue relative to its diet (Vanderklift & Ponsard, 2003; Michener & 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, $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ values of micronekton, (3) the $\delta^{13}C$ and $\delta^{15}N$ 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, 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

99 a depth of 5000 m from the ocean floor. The pinnacle was sampled on board the RV *Antea*
100 from 15 to 29 September 2016 (DOI: 10.17600/16004500).

101 2.1.2 MAD-Ridge seamount

102 This topographic feature, located ~240 km to the south of Madagascar, along the Madagascar
103 Ridge at latitude 27°29'S and longitude 46°16'E has been named "MAD-Ridge" in this study
104 (Fig. 1a, c). The seamount rises from a depth of 1600 m from the ocean floor to ~240 m
105 below the sea surface. The summit is 33 km long (north to south) and 22 km wide (east to
106 west). MAD-Ridge is surrounded by four smaller pinnacles, reaching depths of 600 m, 900
107 m, 800 m and 1200 m below the sea surface, between latitudes 27°S-28°S and longitudes
108 46°E-46°45'E. The MAD-Ridge pinnacle was sampled on board the RV *Antea* (DOI:
109 10.17600/16004800 and 10.17600/16004900) from 26 November to 14 December 2016.

110 2.2 Satellite observations

111 Sea surface chlorophyll data were downloaded from the MODIS dataset
112 (http://oceancolor.gsfc.nasa.gov) at a daily and 4.5 km resolution. Five-day averages were
113 calculated to obtain a proxy of phytoplankton abundance in the surface layer. To investigate
114 the annual variability in surface chlorophyll *a* concentrations, monthly mean concentrations
115 were averaged from January to December 2016 for the defined regions (La Perouse: 18.5-
116 20°S/53-33°E; MAD-Ridge: 27-28°S/44-48°E) (Fig. 2).

117 2.3 Sampling and sample processing

118 2.3.1 Particulate organic matter (POM)

119 During both cruises, water samples for stable isotope analyses of POM were collected using
120 Niskin bottles mounted on a Sea-Bird 911 + CTD rosette system at approximately 5 m depth
121 (referred to as POM-Surf) and at the depth of maximum fluorescence (referred to as POM-

122 Fmax) between ~60 and 125 m at La Pérouse and ~80 and 150 m at MAD-Ridge. Between 4
123 and 8 l (depending on the load of each sample) of seawater were filtered on precombusted 25
124 or 47 mm glassfibre of 0.7 µm pore size. The filters were oven-dried at 50°C for 24 h and
125 saved at room temperature in aluminium foil until further analyses.

126 2.3.2 Zooplankton sampling

127 Zooplankton samples were collected during daylight only with a Bongo net (300 µm mesh to
128 a maximum depth of 500 m and 200 µm mesh to a maximum depth of ~200 m) towed
129 obliquely at La Pérouse (10 stations). At MAD-Ridge, zooplankton samples were also
130 collected during daylight with a Bongo net (300 µm mesh to a maximum depth of 500 m
131 towed obliquely and 63 µm mesh to the depth of the maximum fluorescence towed vertically)
132 at 19 stations. The nets were fitted with a flowmeter and were towed at a vessel speed of 1.5-
133 2 knots for 15-20 min (0.28 m^2 mouth area). Zooplankton samples from the 200 and 300 µm
134 meshes at La Pérouse and, from the 63 and 300 µm meshes at MAD-Ridge were combined at
135 each station. The combined samples at each station were sieved on a stack of seven sieves of
136 decreasing mesh size and divided into six fractions: >4000 µm, 4000-2000 µm, 2000-1000
137 µm, 1000-500 µm, 500-250 µm, 250-125 µm during La Pérouse and MAD-Ridge and a 7^{th}
138 fraction (125-63 µm) during MAD-Ridge only. Each fraction was oven-dried at 50°C for 24 h
139 and frozen on board at -20°C before being analysed for stable isotope analyses (section 2.4).
140 Zooplankton abundances, biomasses and taxa composition at the seamounts and off-
141 seamount locations are investigated in Noyon et al. (2020).

142 2.3.3 Trawl sampling

143 During both cruises, a 40-m long International Young Gadoid Pelagic Trawl (IYGPT) net
144 (codend with 0.5 cm knotless nylon delta mesh; front tapering end with 8 cm mesh; ~96 m^2
145 mouth opening) was towed at a vessel speed of 2-3 knots for 60 mins during La Pérouse and

146 for 30 min during MAD-Ridge to sample mesopelagic organisms. Trawls were carried out in
147 the shallow (0-200 m), intermediate (200-400 m) and deep (below 400 m) layers during both
148 cruises (Supplementary Material, Table 1). Trawl stations at La Pérouse and MAD-Ridge
149 (Fig. 1b, c) were further classified into the categories summit, flank and vicinity- according to
150 whether they occurred on the summit plateau of the seamounts, along the flanks (seafloor
151 depth of 300-1300 m) or in the immediate vicinity (depth >1300 m) (Supplementary
152 Material, Table 1). Four other mesopelagic trawls (#18-21) were conducted in the southern
153 Mozambique Channel (depth >4000 m) during the MAD-Ridge cruise as reference stations
154 for non-seamount locations within the EAFR province (Fig. 1a).

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

166 2.4 Stable isotope analysis

167 Micronekton and zooplankton samples were freeze-dried using Christ Alpha 1-4 LSC freeze-
168 dryers for 48 h and ground to a fine homogeneous powder using an automatic ball mill
169 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). 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 EA 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:

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

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. 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 in R (version 3.3.1) 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

194 $\delta^{13}C$ and $\delta^{15}N$ values for each foodweb component between La Pérouse and MAD-Ridge. To
195 assess the association between $\delta^{13}C$ and $\delta^{15}N$ values, Spearman rank correlation coefficients
196 were calculated with all foodweb components at each seamount. Wilcoxon rank sum tests
197 investigated the effect of time (day or night) on $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous plankton
198 and micronekton at MAD-Ridge only (because a single daylight trawl was conducted at La
199 Pérouse and too few species were caught). To test for the effect of trawl position with respect
200 to the seamounts on $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish, Wilcoxon Rank
201 sum tests and KW tests were performed on the La Pérouse and MAD-Ridge datasets,
202 respectively.

203 2.5.2 Layman community-wide metrics

204 The Layman community-wide metrics SEA_c and the $\delta^{13}C$ and $\delta^{15}N$ ranges (Layman et al.,
205 2007) were calculated using the SIBER package (version 2.1.4, Jackson et al., 2011). The
206 SEA_c (sample-size-corrected standard ellipse area) describes the overall extent of the isotopic
207 niches. The SEA_c is robust for sample sizes >10 (Daly et al., 2013), which is the case for all
208 the broad categories within this study. The SEA_c of each foodweb component was described
209 in terms of the space occupied by the group on a $\delta^{15}N$-$\delta^{13}C$ plot based on all the individuals
210 sampled within the group. The $\delta^{13}C$ and $\delta^{15}N$ ranges were used to describe and compare the
211 overall extents of the foodwebs at the La Pérouse and MAD-Ridge sites. Increased $\delta^{13}C$ range
212 would be expected in foodwebs with multiple basal sources with varying $\delta^{13}C$ values
213 suggesting niche diversification at the base of the foodweb, whereas the $\delta^{15}N$ range describes
214 the sampled food chain lengths (Portail et al., 2016).

215 2.5.3 Trophic level estimations

216 Different models have been applied across several studies to estimate the trophic level of
217 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 & 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 & 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‰:

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

where, $\delta^{15}N_i$ the nitrogen isotopic composition of any given micronekton taxon i, $\delta^{15}N_{\text{primary consumer}}$ 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 & Kaufman, 2007; Vanderklift & 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 $\delta^{15}N_{\text{primary consumer}}$ 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 $\delta^{15}N_{\text{primary consumer}}$ 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):

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

$$TPC = 2.0 + [(\delta^{15}N_i - \delta^{15}N_{primary\ consumer})/TEF] \quad \text{Eq. 2}$$

2.5.4 Micronekton habitat ranges and feeding mode

Information on habitat ranges of selected micronekton individuals was obtained from the literature (Clarke & Lu, 1975; Pearcy et al., 1977; Smith & Heemstra, 1986; van der Spoel & Bleeker, 1991; Brodeur & 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 & 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 2. 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 & Gulliksen, 2003; Mauchline, 1959; Foxton & 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 & 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 $\delta^{13}C$ and $\delta^{15}N$ values per gelatinous plankton and micronekton species at each seamount and for all sampled stations in PRIMER v6 software according to Clarke & Warwick (2001). Further cluster analyses were performed on log-transformed $\delta^{13}C$ values and normalised $\delta^{13}C$ and $\delta^{15}N$ values of micronekton (excluding the outliers salps, pyrosomes, *Funchalia* sp. and leptocephali) for each seamount.

2.5.5 Effect of size on $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ values of gelatinous and micronekton individuals and to investigate the difference in $\delta^{15}N$ 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 $\delta^{15}N$ 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

290 $\delta^{15}N$ values of these eight taxa according to their body lengths and the seamount factor
291 (whether $\delta^{15}N$ values were significantly different between La Pérouse and MAD-Ridge).To
292 investigate if the seamount has an effect on the size and related diet of fish, $\delta^{15}N$ values of
293 selected omnivorous/ carnivorous fish species collected on the summits, flanks, vicinity of
294 the seamounts and the southern Mozambique Channel, were examined using linear models.

295 **3. Results**

296 3.1 Prevailing environmental conditions at La Pérouse and MAD-Ridge seamounts

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

303 3.2 General foodweb structure

304 The description of the foodweb structure included POM collected at the surface (POM-Surf)
305 and at the depth of maximum fluorescence (POM-Fmax), zooplankton at both seamounts,
306 two taxonomic groups of gelatinous organisms (salps and pyrosomes), and 42 and 49
307 taxonomic groups of micronekton, representing 145 and 180 individuals at La Pérouse and
308 MAD-Ridge respectively. At both La Pérouse and MAD-Ridge, the foodweb components
309 were segregated in their $\delta^{13}C$ (La Pérouse: KW, $H=170.5$, $p < 0.05$; MAD-Ridge: KW,
310 $H=268.1$, $p < 0.05$) and $\delta^{15}N$ values (La Pérouse: KW, $H=153.1$, $p < 0.05$; MAD-Ridge: KW,
311 $H=127.4$, $p < 0.05$) (Fig. 3). POM-Surf and POM-Fmax did not differ significantly in their
312 $\delta^{13}C$ and $\delta^{15}N$ values at both seamounts ($p > 0.05$). At La Pérouse, gelatinous organisms
313 exhibited higher $\delta^{13}C$ values compared with POM-Surf and POM-Fmax ($p < 0.05$), and they

314 exhibited lower $\delta^{13}C$ and $\delta^{15}N$ values than crustaceans, fish and squid at both seamounts ($p < 0.05$). Crustaceans, fish and squid did not differ significantly in their $\delta^{15}N$ values ($p > 0.05$), but they differed in their $\delta^{13}C$ values at La Pérouse ($p < 0.05$). Crustaceans did not differ significantly from squid in their $\delta^{13}C$ values ($p > 0.05$), whereas all other categories differed in their $\delta^{13}C$ values at MAD-Ridge ($p < 0.05$). Squid did not differ significantly from crustaceans and fish in their $\delta^{15}N$ 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 $\delta^{13}C$ range of ~11‰ (-17.2 to -28.0‰), with POM-Fmax and the unidentified caridean crustacean representing the lowest and highest values, respectively. The $\delta^{15}N$ 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 $\delta^{13}C$ 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 $\delta^{15}N$ values of sampled micronekton individuals ranged from 2.3‰ (fish: leptocephali) to 13.5‰ (fish: *Argyropelecus aculeatus*).

329 Standard ellipse corrected areas (SEA_c) refer to the trophic niche widths of the broad 330 categories at La Pérouse and MAD-Ridge. At La Pérouse, POM-Surf and POM-Fmax 331 showed overlapping standard ellipses with the largest SEA_c (3.2 and 3.8‰^{2}, respectively) 332 among all components of the foodweb (Fig. 3). Gelatinous organisms showed the smallest 333 SEA_c of 0.92‰^{2}. Crustaceans, squid and fish had overlapping standard ellipses with SEA_c 334 values of 2.3, 1.2 and 2.9‰^{2}, respectively (Fig. 3). At MAD-Ridge, POM-Surf and POM-335 Fmax also exhibited overlapping standard ellipses (SEAc= 4.8 and 2.0‰^{2}, respectively), but 336 with greater variability in POM-Surf $\delta^{15}N$ values. Crustaceans, squid and fish had 337 overlapping standard ellipses with SEA_c of 3.0, 3.6 and 3.2‰^{2}, respectively.

338 The $\delta^{13}C$ and $\delta^{15}N$ values of the foodweb components POM-Surf, POM-Fmax, zooplankton,
339 gelatinous organisms, crustaceans, squid and fish were significantly different between La
340 Pérouse and MAD-Ridge ($\delta^{13}C$: KW, H=474.4, df=13, $p < 0.05$; $\delta^{15}N$: KW, H=311.3, df=13,
341 $p < 0.05$, Fig. 4). Pairwise comparisons showed $\delta^{13}C$ values of POM-Surf, zooplankton and
342 fish to differ significantly between La Pérouse and MAD-Ridge ($p < 0.05$ each). The median
343 $\delta^{13}C$ and $\delta^{15}N$ values of lower trophic level foodweb components: POM-Surf, POM-Fmax
344 and zooplankton were greater at MAD-Ridge ($\delta^{13}C$: -23.1, -24.1, -20.9‰; $\delta^{15}N$: 6.3, 6.1 and
345 8.9‰, respectively) than at La Pérouse ($\delta^{13}C$: -23.7, -24.1, -22.1‰; $\delta^{15}N$: 5.5, 4.9 and 7.5‰,
346 respectively) (Fig. 4). Gelatinous organisms, crustaceans and fish displayed higher median
347 $\delta^{13}C$ values at La Pérouse (-21.5, -18.4 and -18.7‰, respectively) than at MAD-Ridge (-22.4,
348 -18.6 and -19.1‰, respectively) (Fig. 4). Gelatinous organisms, crustaceans, squid and fish
349 also exhibited higher median $\delta^{15}N$ values at La Pérouse (5.2, 9.8, 10.7 and 10.4‰,
350 respectively) compared to MAD-Ridge (3.7, 8.8, 9.5 and 10.0‰, respectively) (Fig. 4) but
351 differences were not statistically significant ($p > 0.05$ each). The $\delta^{13}C$ values of crustaceans,
352 squid and mesopelagic fish encompassed the same narrow range at La Pérouse and MAD-
353 Ridge (-17.2 to -21.0‰ and -17.1 to -21.1‰, respectively). Gelatinous salps and pyrosomes
354 exhibited $\delta^{13}C$ values of -18.2 to -21.7‰ at La Pérouse and -19.0 to -23.5‰ at MAD-Ridge.

355 3.3 Relationships between $\delta^{13}C$ and $\delta^{15}N$ values

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

361 3.4 Trophic levels at La Pérouse and MAD-Ridge seamounts

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

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

379 3.5 Effect of feeding mode of gelatinous plankton and micronekton on stable isotope values

380 The trophic groups identified by cluster analyses are in general agreement with the postulated
381 feeding habits of the group members at both La Pérouse and MAD-Ridge seamounts,
382 although significant differences exist when individual species are considered. The cluster
383 analyses based on $\delta^{13}C$ and $\delta^{15}N$ values identified two main groups, designated I and II, and
384 two subgroups within group I and group II at La Pérouse and MAD-Ridge (Fig. 6). At La
385 Pérouse, Group I included the filter-feeding pyrosomes (IA) and the detritivorous

386 leptocephali (IB) that showed similar $\delta^{13}C$ values (-21.5 ± 0.2 and -20.4 ± 0.5‰,
387 respectively) and $\delta^{15}N$ values (5.2 ± 0.2 and 4.9 ± 2.1‰, respectively). Group IIa compared a
388 single salp specimen ($\delta^{13}C$: -18.2‰ and $\delta^{15}N$: 5.9‰) and an omnivorous crustacean
389 *Funchalia* sp. with similar $\delta^{13}C$ and $\delta^{15}N$ values (-18.7 ± 0.6 and 7.5 ± 0.5‰, respectively).
390 All other crustaceans having an omnivorous feeding mode displayed greater $\delta^{15}N$ values
391 (10.0 ± 1.1‰) and were thus segregated within subgroup IIB along with carnivorous
392 mesopelagic fish and squid (Fig 6). All values are given in mean ± S.D.

393 At MAD-Ridge, Group I included filter feeding pyrosomes (IA) and salps, and detritivorous
394 leptocephali (IB) which exhibited the most depleted $\delta^{13}C$ and $\delta^{15}N$ values relative to
395 omnivorous and carnivorous micronekton (Fig. 6). Group II was subdivided into Group IIA
396 included the squid *O. bartramii*, the fish *Promethichthys prometheus* and *S. longibarbatus*, all
397 three having carnivorous feeding modes with similar $\delta^{13}C$ values and the highest $\delta^{15}N$ values
398 for the greatest sizes. The single large squid *Histioteuthis* spp. (DML: 367 mm) showed a
399 high $\delta^{15}N$ value of 10.7‰ and a more depleted $\delta^{13}C$ value of -21.0‰ compared with *O.*
400 *bartramii*, *P. prometheus* and *S. longibarbatus*. This squid was hence segregated from
401 subgroup IIA. All other omnivorous and carnivorous organisms exhibited lower $\delta^{15}N$ values
402 (Fig. 6) and were thus included within subgroup IIB. Cluster analyses run on $\delta^{13}C$ and $\delta^{15}N$
403 values of micronekton and excluding the outliers salps, pyrosomes, *Funchalia* sp. and
404 leptocephali, also segregated individuals according to their feeding mode at MAD-Ridge ($p <$
405 0.05).

406 3.6 Effect of size of micronekton on $\delta^{15}N$ values

407 The $\delta^{15}N$ values of individuals were significantly influenced by their sizes at both La Pérouse
408 ($F_{1,113}$=6.70, $p < 0.05$) and MAD-Ridge ($F_{1, 160}$= 23.3, $p < 0.05$), with increasing $\delta^{15}N$ values
409 as the size of the organisms increased (La Pérouse: $\delta^{15}N_{\text{gelatinous and micronekton <100 mm}}$= 8.83 +

410 0.02 x Size; MAD-Ridge: $\delta^{15}N_{\text{gelatinous and micronekton <100 mm}}$= 7.33 + 0.03 x Size). Eight
411 micronekton species were further selected according to sample size, their common
412 occurrence at both seamounts, their wide body length ranges, differing feeding modes and
413 vertical migration patterns. The $\delta^{15}N$ values of the selected species *Sigmops elongatus*
414 (carnivore; diel vertical migrator) and *C. warmingii* (omnivore; diel vertical migrator) were
415 significantly influenced by their lengths (Fig. 7a, b, Table 1), with higher $\delta^{15}N$ values at La
416 Pérouse than at MAD-Ridge. The $\delta^{15}N$ values of the fish *A. aculeatus* (carnivore, mid-water
417 migrant) and of the crustacean *Funchalia* sp. (omnivore, diel vertical migrator) were
418 significantly influenced by their lengths but were not significantly different between La
419 Pérouse and MAD-Ridge (Fig. 7c, d, Table 1). The mesopelagic fish *D. suborbitalis* and the
420 squid *Abraliopsis* sp. (both carnivores and diel vertical migrators) exhibited the same range of
421 $\delta^{15}N$ values irrespective of size at La Pérouse and MAD-Ridge (Fig. 7e, f, Table 1). For the
422 same body length, *Abraliopsis* sp. showed higher $\delta^{15}N$ values at La Pérouse relative to MAD-
423 Ridge (Fig. 7f). Models fitted to *C. sloani* (carnivore, diel vertical migrator) and leptocephali
424 (detritivore, migrant or non-migrant depending on species) were not significant (Fig. 7g, h,
425 Table 1). The detritivorous leptocephali had varied $\delta^{15}N$ values irrespective of size and
426 irrespective of the sampling location.

427 The $\delta^{15}N$ values of omnivorous/ carnivorous fish collected in the vicinity of the La Pérouse
428 and MAD-Ridge seamounts and in the southern Mozambique Channel were significantly
429 influenced by individual body size ($F_{3,171}$ = 10.3, Adjusted R^2=13.8, $p < 0.05$) (Fig. 8a).
430 However, there were no significant influence of body size on the $\delta^{15}N$ values of seamount
431 flank- and summit-associated fish species *D. suborbitalis* (La Pérouse and MAD-Ridge), *B.*
432 *fibulatum*, *D. knappi* and *C. japonicus* ($F_{1,10}$= 0.07, $p > 0.05$) at MAD-Ridge. These seamount
433 flank- and summit-associated fish species (Annasawmy et al., 2019; Cherel et al., 2020)
434 exhibited minimum and maximum $\delta^{15}N$ values of 9.8‰ (*B. fibulatum*) and 11.2‰ (*D.*

435 *suborbitalis*) for individuals ranging in size from 38 mm (*D. suborbitalis*) to 328 mm (*C.*
436 *japonicus*) (Fig. 8b). Despite the differing sizes of these seamount flank- and summit-
437 associated fish species, they exhibited an estimated TL value (TPA model) of ~4 at both La
438 Pérouse and MAD-Ridge pinnacles.

439 3.7 Effect of time of day on $\delta^{13}C$ and $\delta^{15}N$ values at MAD-Ridge seamount

440 Gelatinous and micronekton organisms sampled at MAD-Ridge exhibited similar $\delta^{13}C$ values
441 (-19.6 and -19.4‰ respectively) during day and night ($W= 3055.5$, $p > 0.05$). However,
442 individuals collected during daylight showed higher median $\delta^{15}N$ values (9.22‰) than those
443 collected at night (8.12‰) ($W= 4757.5$, $p < 0.05$).

444 3.8 Seamount effect on $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish

445 The $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous/carnivorous fish had overlapping ranges at La
446 Pérouse flank and vicinity stations as well as overlapping ranges at MAD-Ridge flank,
447 summit and vicinity and Mozambique Channel stations (Fig. 9). There were no significant
448 differences in $\delta^{13}C$ ($W= 1619$, $p > 0.05$) of omnivorous/carnivorous fish collected between
449 flank stations and the vicinity of La Pérouse seamount, whereas a significant difference was
450 observed for $\delta^{15}N$ values between flank (median: 10.1‰) and vicinity (median: 10.8‰)
451 stations ($W= 1876$, $p < 0.05$). There was also no significant difference in $\delta^{13}C$ values (KW,
452 $H= 1.0$, $df= 2$, $p > 0.05$) of omnivorous/carnivorous fish collected in the southern
453 Mozambique Channel, the vicinity, flank and summit of MAD-Ridge. However, there was a
454 significant difference in $\delta^{15}N$ values (KW, $H= 8.5$, $df= 3$, $p > 0.05$) of
455 omnivorous/carnivorous fish collected from the southern Mozambique Channel (median:
456 10.6‰) and in the vicinity of MAD-Ridge (median: 10.0‰).

457

458 **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). There have been concerns in previous studies of the inappropriate use of fixed discrimination factors for trophic position estimations (Caut et al., 2009; Hussey et al., 2014). However, as shown in Olivar et al. (2019) for myctophid species, and in our study for zooplankton and micronekton, the methods for trophic position estimates maintained the essential differences among all species. 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 $\delta^{15}N$

484 and $\delta^{13}C$ values with depth, which have been linked to the increase of $\delta^{15}N$ in POM with
485 depth (Kolasinski et al., 2012; Fanelli et al., 2013). However, as the IYGPT net had no
486 closing device, the effect of sampling depth on $\delta^{13}C$ and $\delta^{15}N$ values of individuals could not
487 be investigated further.

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

500 4.2 Trophic interactions at La Pérouse and MAD-Ridge seamounts

501 Particulate organic matter collected at the surface generally consists of phytoplankton,
502 bacteria, faecal pellets and detritus (Riley, 1971; Saino & Hattori, 1987; Fabiano et al., 1993;
503 Dong et al., 2010; Liénart et al., 2017). The $\delta^{13}C$ values of POM (collected at the surface and
504 at the Fmax depth) were different at the La Pérouse and MAD-Ridge seamounts. $\delta^{13}C$
505 baselines can be affected by various processes such as latitude, nutrient source, depth, ocean
506 mixing and primary productivity (Fry, 2006). Research has found that chlorophyll *a*
507 concentrations explained the variability in POM $\delta^{13}C$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ values relative to surface POM at La Pérouse, which might have consisted of phytoplankton with no terrestrial POM input.

The $\delta^{13}C$-$\delta^{15}N$ 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 $\delta^{13}C$ range. Alternatively, the $\delta^{13}C$-$\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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. Assuming a fixed and additive trophic fractionation of 3.2‰ (for comparison with other SWIO studies), the overall range of $\delta^{15}N$ values implied a two-step (3 trophic levels) and three-step (four 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 ($\delta^{15}N$: 14.0 ± 0.59‰). Specimens collected within the ISSG province had a TL of ~5.2 ($\delta^{15}N$: 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 & 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

558 variations may exist in the $\delta^{13}C$ and $\delta^{15}N$ values of an organism's tissues according to various
559 environmental, behavioural and physiological factors (Ménard et al., 2014; Annasawmy et
560 al., 2018).

561 4.3 Influence of feeding mode and size on $\delta^{13}C$ and $\delta^{15}N$ values

562 The trophic guilds established at La Pérouse and MAD-Ridge seamounts were segregated in
563 terms of $\delta^{13}C$ and $\delta^{15}N$ values, from depleted (detritivores and filter-feeders) to enriched
564 (omnivores and carnivores) isotope values, highlighting the fact that these trophic guilds
565 consist of species that exploit distinct classes of resources (Bulman et al., 2002; Papiol et al.,
566 2013; Choy et al., 2016). The large range of $\delta^{13}C$ values (~17 to -23‰) when gelatinous
567 organisms are considered together with crustaceans, squid and mesopelagic fish suggests that
568 these organisms exploit different sources of production, thus giving rise to different trophic
569 pathways (Ménard et al., 2014). Gelatinous filter feeders such as salps and pyrosomes ingest
570 a variety of suspended particles (Harbou, 2009; Conley, 2017) and leptocephali include a
571 wide range of species feeding on detrital material (Otake et al., 1993) such as larvacean
572 houses and faecal pellets (Lecomte-Finiger et al., 2004; Feunteun et al., 2015) and hence
573 exhibited depleted $\delta^{13}C$ values relative to other micronekton broad categories. Species
574 depleted in ^{13}C reportedly feed near the base of the food chain and are closely associated with
575 plankton relative to fish with higher $\delta^{13}C$ values (Polunin et al., 2001).

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

582 (Ménard et al., 2014; Annasawmy et al., 2018), crustaceans exhibited overlapping isotopic
583 niches with carnivorous mesopelagic fish and squid at both seamounts. The narrow range of
584 $\delta^{13}C$ values and the greater overlap of isotopic niches between crustaceans and carnivorous
585 squid and mesopelagic fish at both seamounts might suggest some degree of similarity in the
586 diet components with low level of resource partitioning and a high level of competition
587 among these broad categories (Fanelli et al., 2009) or alternatively, different diets but with
588 prey items having similar isotopic compositions.

589 Whereas lower trophic level components, POM-Fmax and zooplankton showed significantly
590 different and higher $\delta^{15}N$ values at MAD-Ridge relative to La Pérouse (most likely because
591 of differing productivity and fast turnover rate of these organisms), higher trophic level
592 components such as crustaceans, squid and fish showed no significant differences in their
593 $\delta^{15}N$ values between the two seamounts. There are several hypotheses for similar isotopic
594 signatures of higher trophic levels when baseline levels differ. First, the sampled organisms
595 might not have had time to incorporate the isotopic composition of their most recent diets,
596 especially if transient productivity bouts had impacted the density or composition of their
597 diet. Whereas some studies reported tissue turnover rates of ~0.1-0.2% per day in deep-sea
598 fish (Hesslein et al., 1993), other studies showed a lack of tissue turnover information in more
599 specific mesopelagic families including Myctophidae and Stomiidae (Choy et al., 2012).
600 Second, the difference in the $\delta^{15}N$ values of POM and zooplankton observed at La Pérouse
601 and MAD-Ridge, although significant, may have been too negligible to be reflected in the
602 $\delta^{15}N$ values of higher trophic levels. Third, the number of squid and crustacean specimens
603 analysed for stable isotopes might not be large enough to reflect the full diversity in the
604 isotopic signatures, and hence the apparent lack of variations in $\delta^{15}N$ values for these
605 individuals between the two seamounts. Finally, as a result of movements, zooplankton
606 grazers and subsequent trophic levels might have fed on prey components that are not those

607 sampled in the water column, leading to a mismatch in isotopic signatures between lower and
608 higher trophic levels.

609 In this study, $\delta^{15}N$ values of micronekton were correlated to body size. This phenomenon was
610 observed in various organisms such as phytoplankton, zooplankton, decapods and fish and
611 across numerous studies (Sholto-Douglas et al., 1991; France et al., 1998; Waite et al., 2007;
612 Ventura & Catalan, 2008; Hirch & Christiansen, 2010; Choy et al., 2012, 2015; Papiol et al.,
613 2013) and is probably attributable to size-related predation. As organisms grow in size, they
614 can feed farther up the foodweb on larger prey with greater $\delta^{15}N$ values (Parry, 2008; Ménard
615 et al., 2014). For those species whose $\delta^{15}N$ values (*S. elongatus*, *C. warmingii* and
616 *Abraliopsis* sp.) were significantly influenced by size, their $\delta^{15}N$ values were greater (around
617 1‰ difference) at La Pérouse than at MAD-Ridge for the same body lengths. As suggested in
618 Parry (2008), if the $\delta^{15}N$ values, and hence the TL of an organism, are influenced by size,
619 then the $\delta^{15}N$ signal will also depend on baseline values and the variables that affect an
620 organism's size such as feeding mode, growth rate, body condition and available prey items.
621 As $\delta^{15}N$ values of POM and zooplankton were higher at MAD-Ridge than at La Pérouse, we
622 hypothesize that those intermediate TLs at the oligotrophic La Pérouse seamount had a
623 different trophic functioning, with the diet of those species being based on a larger proportion
624 of higher TL prey than at MAD-Ridge.

625 Body size did not have an effect on $\delta^{15}N$ values of leptocephali which encompass a wide
626 range of species having a detritivorous and opportunistic feeding mode at both seamounts.
627 Such lack of effect was also observed for *C. sloani* individuals ranging in size from 66 to 184
628 mm at La Pérouse and from 77 to 199 mm at MAD-Ridge. These individuals are semi-
629 migrants, caught in deep and intermediate trawls during both day and night. Individuals 45-
630 178 mm long feed on myctophids and other fish species (Utrecht et al., 1987; Butler et al.,
631 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 $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ values of fish species

Omnivorous/carnivorous fish sampled in the southern Mozambique Channel exhibited slightly enriched $\delta^{15}N$ 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 $\delta^{15}N$ values within tissues of micronekton (Tew-Kai & 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 $\delta^{15}N$ 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 $\delta^{13}C$, $\delta^{15}N$ 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; Olivar et al., 2019; Vipin et al., 2018) and chaetognaths (Appelbaum, 1982), organisms present in similar proportions on and away from both seamounts (Noyon et al., 2020).

Although $\delta^{13}C$ and $\delta^{15}N$ values may depend on a range of factors, there were few differences between $\delta^{13}C$ and $\delta^{15}N$ 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* $\delta^{13}C$ and $\delta^{15}N$ values: -18.6 and 9.5‰, *C. sloani*: -18.1 and 9.5‰, and *L. 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 $\delta^{13}C$ and $\delta^{15}N$ 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).

Concluding Remarks

This study has shown that despite the different productivity at the two shallow seamounts and the significant differences in lower trophic level $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{15}N$ values of most individuals, although that also depended on the life strategy and feeding mode of the species considered. The $\delta^{13}C$ and $\delta^{15}N$ 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/resident fish sampled showed similar $\delta^{15}N$ 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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References

Annasawmy, P., Ternon, J.F., Marsac, F., Cherel, Y., Béhagle, N., Roudaut, G., Lebourges-Dhaussy, A., Demarcq, H., Moloney, C.L., Jaquemet, S., Ménard, F., 2018. Micronekton diel migration, community composition and trophic position within two biogeochemical provinces of the South West Indian Ocean: Insight from acoustics and stable isotopes. Deep Sea Research Part I: Oceanographic Research Papers. 138, 85–97. https://doi.org/10.1016/j.dsr.2018.07.002

Annasawmy, P., Ternon, J-F., Cotel, P., Demarcq, H., Cherel, Y, Romanov, E., Roudaut, G., Lebourges-Dhaussy, A., Ménard, F., Marsac, F. 2019. Micronekton distribution and assemblages at two shallow seamounts in the south-western Indian Ocean: Insights from acoustics and mesopelagic trawl data. Progress in Oceanography-accepted.

Annasawmy, P., Ternon, J-F., Lebourges-Dhaussy, A., Roudaut, G., Herbette, S., Ménard, F., Cotel., P., Marsac, F., 2020. Micronekton distribution as influenced by mesoscale eddies, Madagascar shelf and shallow seamounts in the south-western Indian Ocean: An acoustic approach. Deep-Sea Res. II, this issue.

Appelbaum, S., 1982. Studies on food organisms of pelagic fishes as revealed by the 1979 North Atlantic Eel Expedition. Helgoländer Meeresuntersuchungen. 35, 357–367. https://doi.org/10.1007/BF02006143

Arreguín-Sánchez, F., Valero-Pacheco, E., Chávez, E.A., 1993. A Trophic Box Model of the Coastal Fish Communities of the Southwestern Gulf of Mexico. In V. Christensen and D. Pauly (Eds) Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings, 26: 390.

Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci. Mar. 70, 105–122. https://doi.org/10.3989/scimar.2006.70s2105

Bastos, R.F., Corrêa, F., Winemiller, K.O., Garcia, A.M., 2017. Are you what you eat? Effects of trophic discrimination factors on estimates of food assimilation and trophic position with a new estimation method. Ecological Indicators. 75: 234-241. http://dx.doi.org/10.1016/j.ecolind.2016.12.007

Bernal, A., Olivar, M.P., Maynou, F., Fernández de Puelles, M.L., 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. Progr. Oceanogr. 135, 1-17. https://doi.org/10.1016/j.pocean.2015.03.005

Bertrand, A., Bard, F.X. Josse, E., 2002. Tuna food habits related to the micronekton distribution in French Polynesia. Mar Biol. 140: 1023-1037. DOI: 10.1007/s00227-001-0776-3

Bianchi, D., Stock, C., Galbraith, E.D., Sarmiento, J.L., 2013. Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. Global Biogeochem. Cycles. 27: 478-491. DOI: 10.1002/gbc.20031

Birkley, S.-R., Gulliksen, B., Feeding Ecology in Five Shrimp Species (Decapoda, Caridea) from an Arctic Fjord (Isfjorden, Svalbard), with Emphasis on *Sclerocrangon boreas* (Phipps, 1774).

Bodin, N., Budzinski, H., Le Ménach, K., Tapie, N., 2009. ASE extraction method for simultaneous carbon and nitrogen stable isotope analysis in soft tissues of aquatic organisms. Analytica Chimica Acta. 643: 54-60. DOI: 10.1016/j.aca.2009.03.048

Brodeur, R., Yamamura, O., 2005. PICES Scientific Report No. 30 Micronekton of the North Pacific. PICES Scientific Report, Sidney B.C., Canada, pp. 1-115.

Browder, J.A., 1993. A pilot model of the Gulf of Mexico continental shelf. In V. Christensen and D. Pauly (Eds) Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings. 26: 390.

Bulman, C.M., He, X., Koslow, J.A., 2002. Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. Mar. Freshwater Res. 53: 59-72. DOI: 10.1071/MF01057

Butler, M., Bollens, S.M., Burkhalter, B., Madin, L.P., Horgan, E., 2001. Mesopelagic fishes of the Arabian Sea: distribution, abundance and diet of *Chauliodus pammelas*, *Chauliodus sloani*, *Stomias aznis*, and *Stomias nebulosus*. Deep-Sea Res. II. 48: 1369-1383.

Carmo, V., Sutton, T., Menezes, G., Falkenhaug, T., Bergstad, O.A., 2015. Feeding ecology of the Stomiiformes (Pisces) of the northern Mid-Atlantic Ridge. 1. The Sternoptychidae and Phosichthyidae. Prog. Oceanogr. 130: 172-187. https://doi.org/10.1016/j.pocean.2014.11.003

Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review of mesopelagic fishes belonging to family Mcytophidae. Rev. Fish Biol. Fisheries. 21: 339-354. DOI: 10.1007/s11160-010-9176-4

Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology. 46: 443-453. DOI: 10.1111/j.1365-2664.2009.01620.x

Cherel, Y., Fontaine, C., Richard, P., Labat, J.-P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol. Oceanogr. 55, 324–332. https://doi.org/10.4319/lo.2010.55.1.0324

Cherel, Y., Romanov, E.V., Annasawmy, P., Thibault, D., Ménard, F., 2020. Micronektonic fish species over three seamounts in the southwestern Indian Ocean. Deep-Sea Res. II. https://doi.org/10.1016/j.dsr2.2020.104777

Choy, C.A., Davison, P.C., Drazen, J.C., Flynn, A., Gier, E.J., Hoffman, J.C., McClain-Counts, J.P., Miller, T.W., Popp, B.N., Ross, S.W., Sutton, T.T., 2012. Global trophic position comparison of two dominant mesopelagic fish families (Myctophidae, Stomiidae) using amino acid nitrogen isotopic analyses. PLoS One. 7(11): e50133. DOI: 10.1371/journal.pone.0050133

Choy, C.A., Popp, B.N., Hannides, C.C.S., Drazen, J.C., 2015. Trophic structure and food resources of epipelagic and mesopelagic fishes in the North Pacific Subtropical Gyre ecosystem inferred from nitrogen isotopic compositions. Limnol. Oceanogr. 60: 1156-1171.

Choy, C.A., Wabnitz, C.C.C., Weijerman, M., Woodworth-Jefcoats, P.A., Polovina, J.J., 2016. Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. Mar. Ecol. Prog. Ser. 549: 9-25. DOI: 10.3354/meps11680

Christensen, V., Pauly, D., 1993. Flow Characteristics of Aquatic Ecosystems. In V. Christensen and D. Pauly (Eds) Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings. 26: 390.

Clarke, M.R., Lu, C.C., 1975. Vertical distribution of cephalopods at 18°N 25°W in the North Atlantic. J. mar. biol. Ass. 55: 165-182. https://doi.org/10.1017/S0025315400015812

Clarke, T.A., 1982. Feeding habits of stomiatoid fishes from Hawaiian waters. Fishery Bulletin. 80(2): 287-304.

Clarke, K., Warwick, R., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E Ltd: Plymouth, United Kingdom.

Clark, M.R., Vinnichenko, V.I., Gordon, J D M , Beck-Bulat, G..Z., Kukharev, N. N., and. Kakora, A.F., 2007. Large-scale distant-water trawl fisheries on seamounts. In:

Pitcher, T. J., Morato, T., Hart, P. J. B., Clark, M. R., Haggan, N., & Santos, R. S. (Eds.). Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing. 361-399.

Colaço, A., Giacomello, E., Porteiro, F., Menezes, G.M., 2013. Trophodynamic studies on the Condor seamount (Azores, Portugal, North Atlantic). Deep-Sea Res. Part II: Topical Studies in Oceanography. 98: 178–189. https://doi.org/10.1016/j.dsr2.2013.01.010

Conley, K.P., 2017. Mechanics and Selectivity of filtration by tunicates. PhD thesis, University of Oregon, USA.

Cresson, P., Ruitton, S., Fontaine, M-F., Harmelin-Vivien, M., 2012. Marine Pollution Bulletin. 1112-1121. http://dx.doi.org/10.1016/j.marpolbul.2012.04.003

Dalpadado, P., Gjøsæter, J., 1988. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Mar. Biol. 99: 555-567.

Daly, R., Froneman, P.W., Smale, M.J., 2013. Comparative Feeding Ecology of Bull Sharks (*Carcharhinus leucas*) in the Coastal Waters of the Southwest Indian Ocean Inferred from Stable Isotope Analysis. PLoS ONE 8(10): e78229. doi:10.1371/journal.pone.0078229

Danckwerts, D.K., McQuaid, C.D., McGregor, G.K., Dwight, R., Le Corre, M., Jaquemet, S., 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. ICES Journal of Marine Science. 71(9): 2589-2598. DOI: 10.1093/icesjms/fsu093

Davison, P. C., Koslow, J. A., Kloser, R. J., 2015. Acoustic biomass estimation of mesopelagic fish: backscattering from individuals, populations, and communities. ICES Jour. Mar. Sci. 72(5), 1413-1424. https://doi.org/10.1093/icesjms/fsv023

De Forest, L., Drazen, J., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. Deep-Sea Res. I. 56: 232-250. DOI: 10.1016/j.dsr.2008.09.007

Del Giorgio, P.A., Duarte, C.M., 2002. Respiration in the open ocean. Nature. 420: 379-384.

Denda, A., Stefanowitsch, B., Christiansen, B., 2017. From the epipelagic zone to the abyss: Trophic structure at two seamounts in the subtropical and tropical Eastern Atlantic-Part I zooplankton and micronekton. Deep Sea Res. Part I. 130: 63-77.

De Ruijter, W.P.M., Aken, H.M. van, Beier, E.J., Lutjeharms, J.R.E., Matano, R.P., Schouten, M.W., 2004. Eddies and dipoles around South Madagascar: formation, pathways and large-scale impact. Deep Sea Res. Part Oceanogr. Res. Pap. 51: 383–400. https://doi.org/10.1016/j.dsr.2003.10.011

Dong, H-P., Wang, D-Z., Dai, M., Hong, H-S., 2010. Characterization of particulate organic matters in the water column of the South China Sea using a shotgun proteomic approach. Limnol. Oceanogr. 55(4): 1565-1578. DOI: 10.4319/lo.2010.55.4.1565

Dower, J., Freeland, H., Juniper, K., 1992. A strong biological response to oceanic flow past Cobb Seamount. Deep Sea Res. Part Oceanogr. Res. Pap. 39: 1139–1145. https://doi.org/10.1016/0198-0149(92)90061-W

Dubroca, L., Chassot, E., Floch, L., Demarcq, H., Assan, C., Delgado de Molina, A., 2013. Seamounts and tuna fisheries: Tuna hotspots or fishermen habits? Collect. Vol. Sci. Pap. ICCAT. 69(5): 2087-2102.

Duffy, L.M., Kuhnert, P.M., Pethybridge, H.R., Young, J.W., Olson, R.J., Logan, J.M., Goñi, N., Romanov, E., Allain, V., Staudinger, M.D., Abecassis, M., Choy, C.A., Hobday, A.J., Simier, M., Galván-Magaña, F., Potier, M., Ménard, F., 2017. Global trophic ecology of yellowfin, bigeye, and albacore tunas: Understanding predation on micronekton communities at ocean-basin scales. Deep-Sea Res. II. 40: 55-73.

http://dx.doi.org/10.1016/j.dsr2.2017.03.003
Fabiano, M., Povero, P., Danovaro, R., 1993. Distribution and composition of particulate organic matter in the Ross Sea (Antarctica). Polar Biol. 13: 525-533.
Fanelli, E., Cartes, J.E., Rumolo, P., Sprovieri, M., 2009. Food-web structure and trophodynamics of mesopelagic-suprabenthic bathyal macrofauna of the Algerian Basin based on stable isotopes of carbon and nitrogen. Deep-Sea Res. I. 56: 1504-1520.
DOI: 10.1016/j.dsr.2009.04.004
Fanelli, E., Papiol, V., Cartes, J.E., Rumolo, P., Brunet, C., Sprovieri, M., 2011a. Food web structure of the epibenthic and infaunal invertebrates on the Catalan slope (NW Mediterranean): Evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Deep-Sea Res. I: Oceanographic Research Papers. 58: 98–109. https://doi.org/10.1016/j.dsr.2010.12.005
Fanelli, E., Cartes, J.E., Papiol, V., 2011b. Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: Insight from stable isotopes. Journal of Marine Systems. 87: 79-89. DOI: 10.1016/j.jmarsys.2011.03.003
Fanelli, E., Papiol, V., Cartes, J.E., Rumolo, P., López-Pérez, C., 2013. Trophic webs of deep-sea megafauna on mainland and insular slopes of the NW Mediterranean: a comparison by stable isotope analysis. Mar. Ecol. Prog. Ser. 490: 199-221.
DOI: 10.3354/meps10430
Feunteun, E., Miller, M.J., Carpentier, A., Aoyama, J., Dupuy, C., Kuroki, M., Pagano, M., Réveillac, E., Sellos, D., Watanabe, S., Tsukamoto, K., Otake, T., 2015. Stable isotopic composition of anguiliform leptocephali and other food web components from west of the Mascarene Plateau. Prog. Oceanogr. 137: 69-83.
http://dx.doi.org/10.1016/j.pocean.2015.05.024
Fonteneau, A., 1991. Monts sous-marins et thons dans l'Atlantique tropical est. Aquat. Living. Resour. 4: 13-25.
Foxton, P., Roe, H.S.J., 1974. Observations on the Nocturnal Feeding of some Mesopelagic Decapod Crustacea. Mar. Biol. 28: 37-49.
France, R., Chandler, M., Peters, R., 1998. Mapping trophic continua of benthic foodwebs: body size-δ15N relationships. Mar. Ecol. Prog. Ser. 174: 301-306.
Fry, B., 1996. $^{13}C/^{12}C$ fractionation by marine diatoms. Mar. Ecol. Prog. Ser. 134: 283-294.
Fry, B., 2006. Stable Isotope Ecology. Springer, New York. 308pp.
Genin, A., Boehlert, G.W., 1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. J. Mar. Res. 43: 907–924. https://doi.org/10.1357/002224085788453868
Go, Y.B., 1986. Diet and feeding chronology of mesopelagic micronektonic fish, *Diaphus suborbitalis*, in Suruga Bay, Japan. In: 1. Asian Fisheries Forum, Manila (Philippines), 26-31 May 1986.
Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962-85. Antarctic Science. 8(1): 23-30
Halo, I., Backeberg, B., Penven, P., Ansorge, I., Reason, C., Ullgren, J.E., 2014. Eddy properties in the Mozambique Channel: A comparison between observations and two numerical ocean circulation models. Deep Sea Res. Part II Top. Stud. Oceanogr. 100: 38-53. http://dx.doi.org/10.1016/j.dsr2.2013.10.015
Harbou, L.V., 2009. Trophodynamics of salps in the Atlantic Southern Ocean. PhD thesis, Universität Bremen, Germany.

Heffernan, J.T., Hopkins, T.L., 1981. Vertical Distribution and Feeding of the Shrimp Genera *Gennadas* and *Bentheogennema* (Decapoda: Penaeida) in the Eastern Gulf of Mexico. Journal of Crustacean Biology. 1(4): 461-473.

Hesslein, R.H., Hallard, K.A., Ramlal, P., 1993. Replacement of Sulfur, Carbon, and Nitrogen in Tissue of Growing Broad Whitefish (Coregonus nasus) in Response to a Change in Diet Traced by δ34S, δ13C, and δ15N. Can. J. Fish. Aquat. Sci. 50: 2071-2076.

Hidaka, K., Kawaguchi, K., Murakami, M., Takahashi, M., 2001. Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific: its quantitative and qualitative importance. Deep-Sea Res. I. 48: 1923-1939

Hirch, S., Christiansen, B., 2010. The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. Marine Ecology. 31: 107–120. https://doi.org/10.1111/j.1439-0485.2010.00366.x

Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology. 63: 786-798.

Holland, K.N., Kleiber, P., Kajiura, S.M., 1999. Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. Fish. Bull. 97: 392–395.

Hopkins, T.L., Flock, M.E., Gartner, J.V. Jr., Torres, J.J., 1994. Structure and trophic ecology of a low latitude midwater decapod and mysid assemblage. Mar. Ecol. Prog. Ser. 109: 143-156.

Hudson, J.M., Steinberg, D.K., Sutton, T.T., Graves, J.E., Latour, R.J., 2014. Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. Deep-Sea Res. I. 93:104-116. https://doi.org/10.1016/j.dsr.2014.07.002

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F.J., Cliff, G., Wintner, S.P., Fennessy, S.T., Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs. Ecology Letters, 17: 239-250. DOI: 10.1111/ele.12226

Ingole, B., Koslow, J.A., 2005. Deep-sea ecosystems of the Indian Ocean. Indian Journal of Marine Sciences. 34(1): 27-34.

IOTC Catch and Effort database. 2018. Available at https://www.iotc.org/data/datasets?__cf_chl_jschl_tk__=ebffbdbd808fe0fa2e0ce342d88a0e0fa97fc63c-1578403316-0-AbYRwW88C8MO-1LnSVqSvpMqY3x_PGoxouNKuvgZy2X8De9NCy6mFx07f7GFtJjokedKCvEkJ5b7BwcYQtIX-A4KidGt1a6J9aAY9H8Y2ormKM543ixwdYh8d0HrniHi9P31fM1U8qyHBGexlhPFKYzXUxMKbV509-vD1mrSjYwW77ozbytXjlWcy3O2h_1C12C2-RJGWCsaxE2gxxw4xIWzXEFZ4tCh-YqOZRzXUpqxNgWBVaOxSTgNMboZj9PAKa1dIsFRs93SwtgNflbIgQg

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology. 80: 595-602. DOI: 10.1111/j.1365-2656.2011.01806.x

Jaquemet, S., Ternon, J.F., Kaehler, S., Thiebot, J.B., Dyer, B., Bemanaja, E., Marteau, C., Le Corre, M., 2014. Contrasted structuring effects of mesoscale features on the seabird community in the Mozambique Channel. Deep-Sea Res. II. 100: 200-211. http://dx.doi.org/10.1016/j.dsr2.2013.10.027

Kolasinski, J., Rogers, K., Frouin, P., 2008. Effects of acidification on carbon and nitrogen stable isotopes of benthic macrofauna from a tropical coral reef. Rapid Commun Mass Spectrom. 22: 2955–2960. DOI: 10.1002/rcm.3694

Kolasinski, J., Kaehler, S., Jaquemet, S., 2012. Distribution and sources of particulate organic matter in a mesoscale eddy dipole in the Mozambique Channel (south-western Indian

Ocean): Insight from C and N stable isotopes. J. Mar. Syst. 96-97: 122-131. https://doi.org/10.1016/j.jmarsys.2012.02.015

Karakulak, F.S., Salman, A., Oray, I.K., 2009. Diet composition of bluefin tuna (*Thunnus thynnus* L. 1758) in the Eastern Mediterranean Sea, Turkey. J. Appl. Ichthyol. 25: 757-761. DOI: 10.1111/j.1439-0426.2009.01298.x

Koslow, J.A., 1997. Seamounts and the Ecology of Deep-Sea Fisheries: The firm-bodied fishes that feed around seamounts are biologically distinct from their deepwater neighbors-and may be especially vulnerable to overfishing. American Scientist. 85(2): 168-176.

Lack, M., Short, K., Willock, A., 2003. Managing risk and uncertainty in deep-sea fisheries: lessons from Orange Roughy. TRAFFIC Oceania and WWF Endangered Seas Programme.

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology. 88: 42–48.

Lecomte-Finiger, R., Maunier, C., Khafif, M., 2004. Leptocephali, these unappreciated larvae. Cybium. 28(2): 83-95.

Liénart, C., Savoye, N., Bozec, Y., Breton, E., Conan, P., David, V., Feunteun, E., Grangeré, K., Kerhervé, P., Lebreton, B., Lefebvre, S., L'Helguen, S., Mousseau, L., Raimbault, P., Richard, P., Riera, P., Sauriau, P.-G., Schaal, G., Aubert, F., Aubin, S., Bichon, S., Boinet, C., Bourasseau, L., Bréret, M., Caparros, J., Cariou, T., Charlier, K., Claquin, P., Cornille, V., Corre, A.-M., Costes, L., Crispi, O., Crouvoisier, M., Czamanski, M., Del Amo, Y., Derriennic, H., Dindinaud, F., Durozier, M., Hanquiez, V., Nowaczyk, A., Devesa, J., Ferreira, S., Fornier, M., Garcia, F., Garcia, N., Geslin, S., Grossteffan, E., Gueux, A., Guillaudeau, J., Guillou, G., Joly, O., Lachaussée, N., Lafont, M., Lamoureux, J., Lecuyer, E., Lehodey, J.-P., Lemeille, D., Leroux, C., Macé, E., Maria, E., Pineau, P., Petit, F., Pujo-Pay, M., Rimelin-Maury, P., Sultan, E., 2017. Dynamics of particulate organic matter composition in coastal systems: A spatio-temporal study at multi-systems scale. Progress in Oceanography 156: 221–239. https://doi.org/10.1016/j.pocean.2017.03.001

Longhurst, A., 1998. Ecological Geography of the Sea. Academic Press, San Diego. 398p.

Longhurst, A., 2007. The Indian Ocean-Indian South Subtropical Gyre Province (ISSG). In: Academic Press (Ed.), Ecological Geography of the Sea, 2nd ed. Elsevier, USA, pp 285.

Lorrain, A., Graham, B.S., Popp, B.N., Allain, V., Olson, R.J., Hunt, B.P.V., Potier, M., Fry, B., Galván-Magaña, F., Menkes, C.E.R., Kaehler, S., Ménard, F., 2015. Nitrogen isotopic baselines and implications for estimating foraging habitat and trophic position of yellowfin tuna in the Indian and Pacific Oceans. Deep-Sea Res. II. 113: 188-198. https://doi.org/10.1016/j.dsr2.2014.02.003

Marsac, F., Fonteneau, A., Michaud, P., 2014. Le « Coco de Mer », une montagne sous la mer. In: L'or bleu des Seychelles: Histoire de la pêche industrielle au thon dans l'océan Indien. IRD Editions. 151-163.

Marsac, F., Annasawmy, P., Noyon, M., Demarcq, H., Soria, M., Rabearisoa, N., Bach, P., Cherel, Y., Grelet, J., Romanov, E., 2020. Seamount effect on circulation and distribution of ocean taxa at and near La Pérouse, a shallow seamount in the southwestern Indian Ocean. Deep-Sea II.

Martínez del Rio, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. 84: 91-111. DOI: 10.1111/j.1469-185X.2008.00064.x

Mauchline, J., The Biology of the Euphausiid Crustacean, *Meganyctiphanes norvegica* (M. Sars). Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences. 67(2): 141-179

Ménard, F., Benivary, H.D., Bodin, N., Coffineau, N., Le Loc'h, F., Mison, T., Richard, P., Potier, M., 2014. Stable isotope patterns in micronekton from the Mozambique Channel. Deep-Sea Research Part II: Topical Studies in Oceanography 100, 153–163. https://doi.org/10.1016/j.dsr2.2013.10.023

Michener, R.H., Kaufman, L., 2007. Stable isotope ratios as tracers in marine food webs: an update. R.H. Michener, K. Lajtha (Eds.), Stable Isotopes in Ecology and Environmental Science (2nd ed.), Blackwell, Malden, MA (2007). pp. 238-282.

Mill, A.C., Sweeting, C.J., Barnes, C., Al-Habsi, S.H., MacNeil, M.A., 2008. Mass-spectrometer bias in stable isotope ecology. Limnol. Oceanogr: Methods. 6(1): 34-39.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta. 48: 1135-1140.

Mohn, C., White, M., 2007. Remote sensing and modelling of bio-physical distribution patterns at Porcupine and Rockall Bank, Northeast Atlantic. Cont. Shelf Res. 27: 1875-1892. DOI:10.1016/j.csr.2007.03.006

Morato, T., Varkey, D.A., Damaso, C., Machete, M., Santos, M., Prieto, R., Santos, R.S., Pitcher, T.J., 2008. Evidence of a seamount effect on aggregating visitors. Mar. Ecol. Prog. Ser. 357: 23-32. DOI: 10.3354/meps07269

Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Tuna longline fishing around West and Central Pacific seamounts. PLoS ONE. 5(12): e14453. DOI: 10.1371/journal.pone.0014453

Mouriño, B., Fernández, E., Serret, P., Harbour, D., Sinha, B., Pingree, R., 2001. Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). Oceanol. Acta 24: 167–185. https://doi.org/10.1016/S0399-1784(00)01138-5

Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., Seki, M.P., 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. Fish. Oceanogr. 12: 152–169. https://doi.org/10.1046/j.1365-2419.2003.00229.x

Noyon, M., Morris, T., Walker, D., Huggett, J., 2018. Plankton distribution within a young cyclonic eddy off south-western Madagascar. Deep Sea Res. Part II Top. Stud. Oceanogr. In Press. https://doi.org/10.1016/j.dsr2.2018.11.001

Noyon, M., Rasoloarijao, Z.T., Huggett, J., Roberts, M., Ternon, J-F., 2020. Comparison of mesozooplankton communities at three shallow seamounts in the South Western Indian Ocean using size spectrum analysis. Deep-Sea Res. II.

Olivar, M.P., Bode, A., López-Pérez, C., Hulley, P.A., Hernández-León, S., 2019. Trophic position of lanternfishes (Pisces: Myctophidae) of the tropical and equatorial Atlantic estimated using stable isotopes. ICES Journal of Marine Science. DOI: 10.1093/icesjms/fsx243.

Otake, T., Nogami, K., Maruyama, K., 1993. Dissolved and particulate organic matter as possible food sources for eel leptocephali. Mar. Ecol. Prog. Ser. 92: 27-34.

Pakhomov, E. A., Perissinotto, R., & McQuaid, C. D., 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. Mar. Ecol. Prog. Ser. 134, 1-14.

Pakhomov, E.A., Henschke, N., Hunt, B.P.V., Stowasser, G., Cherel, Y., 2019. Utility of salps as a baseline proxy for food web studies. J. Plankton Res. 1-9.

DOI: 10.1093/plankt/fby051
Papiol, V., Cartes, J.E., Fanelli, E., Rumolo, P., 2013. Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: Relationship with available food sources. Journal of Sea Research, 77: 53-69. http://dx.doi.org/10.1016/j.seares.2012.10.002
Parry, M., 2008. Trophic variation with length in two ommastrephid squids, *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis*. Mar. Biol. 153: 249-256. DOI: 10.1007/s00227-007-0800-3
Paya, I., Montecinos, M., Ojeda, V., Cid, L., 2006. An overview of the orange roughy (*Hoplostethus* sp.) fishery off Chile. In: Shotton, R. (Ed.) Deep Sea 2003: Conference on the Governance and Management of Deep-sea fisheries. Part 2: Conference poster papers and workshop papers. Queenstown, New Zealand, 1-5 December 2003 and Dunedin, New Zealand 27-29 November 2003. FAO Fisheries Proceedings No. 3/2, Rome, FAO. 487 pp.
Pearcy, W.G., Krygier, E.E., Mesecar, R., Ramsey, F., 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24: 223-245.
Polunin, N.V.C., Morales-Nin, B., Pawsey, W.E., Cartes, J.E., Pinnegar, J.K., Moranta, J., 2001. Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. Mar. Ecol. Prog. Ser. 220: 13-23.
Pomeroy, L.R., 2001. Caught in the food web: complexity made simple? Sci. Mar. 65 (Suppl. 2): 31-40.
Portail, M., Olu, K., Dubois, S.F., Escobar-Briones, E., Gelinas, Y., Menot, L, Sarrazin, J., 2016. Food-Web Complexity in Guaymas Basin Hydrothermal Vents and Cold Seeps. PLoS ONE. 11(9): e0162263. DOI: 10.1371/journal.pone.0162263
Post, D.M., Pace, M.L., Hairston, N.G.J., 2000. Ecosystem size determines food chain length in lakes. Nature. 405: 1047-1049.
Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology. 83(3): 703-718.
Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. Fisheries Res. 83: 60-72. DOI: 10.1016/j.fishres.2006.08.020
Preciado, I., Cartes, J.E., Punzón, A., Frutos, I., López-López, L., Serrano, A., 2017. Food web functioning of the benthopelagic community in a deep-sea seamount based on diet and stable isotope analyses. Deep-Sea Res. II: 137: 56–68. https://doi.org/10.1016/j.dsr2.2016.07.013
Quartly, G.D., Buck, J.J.H., Srokosz, M.A., Coward, A.C., 2006. Eddies around Madagascar-The retroflection re-considered. J. Mar. Sci. 63: 115-129. DOI:10.1016/j.jmarsys.2006.06.001
Ramanantsoa, J. D., Krug, M., Penven, P., Rouault, M., Gula, J., 2018. Coastal upwelling south of Madagascar: Temporal and spatial variability. Journal of Marine Systems, 178: 29–37. https://doi.org/10.1016/j.jmarsys.2017.10.005
Reygondeau, G., Longhurst, A., Martinez, E., Beaugrand, G., Antoine, D., and Maury, O., 2013. Dynamic biogeochemical provinces in the global ocean. Global Biogeochemical Cycles, 27(4): 1046-1058. http://doi.org/10.1002/gbc.20089
Riley, G.A., 1971. Particulate organic matter in sea water. Advances in Marine Biology. 8: 1-118. https://doi.org/10.1016/S0065-2881(08)60491-5
Robison, B.H., 1984. Herbivory by the myctophid fish *Ceratoscopelus warmingii*. Mar. Biol. 84: 119-123.

Rogers, A.D., 1994. The biology of seamounts. In Advances in marine biology. Academic Press. 30: 305-350.

Romanov, E.V., 2003. Summary and review of Soviet and Ukrainian scientific and commercial fishing operations on the deep-water ridges of the southern Indian Ocean. (E. V Romanov, Ed.), FAO Fisheries Circular C991. Rome: FAO. http://www.fao.org/DOCREP/006/Y4884E/Y4884E00.HTM

Romero-Romero, S., Choy, C.A., Hannides, C.C.S., Popp, B.N., Drazen, J.C., 2019. Differences in the trophic ecology of micronekton driven by diel vertical migration. Limnol. Oceanogr. 1-11. DOI: 10.1002/lno.11128

Rubenstein, D.R., Hobson, K.A., 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology and Evolution. 19(5): 256-263.

Ryan, C., McHugh, B., Trueman, C.N., Harrod, C., Berrow, S., O'Connor, I., 2012. Accounting for the effects of lipids in stable isotope ($\delta^{13}C$ and $\delta^{15}N$ values) analysis of skin and blubber of balaenopterid whales. Rapid Commun. Mass Spectrom. 26: 2745-2754. DOI: 10.1002/rcm.6394

Saino, T., Hattori, A., 1987. Geographical variation of the water column distribution of suspended particulate organic nitrogen and its ^{15}N natural abundance in the Pacific and its marginal seas. Deep-Sea Res. 34(5/6): 807-827.

Savoye, N., Aminot, A., Tréguer, P., Fontugne, M., Naulet, N., Kérouel, R., 2003. Dynamics of particulate organic matter $\delta^{15}N$ and $\delta^{13}C$ during spring phytoplankton blooms in a macrotidal ecosystem (Bay of Seine, France). Mar. Ecol. Prog. Ser. 255: 27-41.

Sholto-Douglas, A.D., Field, J.G., James, A.G., van der Merwe, N.J., 1991. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios in the Southern Benguela Ecosystem: indicators of food web relationships among different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. Mar. Ecol. Prog. Ser. 78: 23-31.

Smith, M.M., Heemstra, P.C., 1986. Smith's Sea Fishes. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. 1047 p.

Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. J. Fish. Biol. 83: 1508-1527. DOI: 10.1111/jfb.12263

Tanaka, H., Ohshimo, S., Sassa, C., & Aoki, I., 2007. Feeding habits of mesopelagic fishes off the coast of western Kyushu, Japan. PICES 16th: Bio, p-4200. 1st November.

Tew-Kai, E., Marsac, F., 2009. Patterns of variability of sea surface chlorophyll in the Mozambique Channel: a quantitative approach. J. Mar. Syst. 77 (1-2): 77-88. DOI: 10.1016/j.jmarsys.2008.11.007

Utrecht, W.L., van Utrecht-Cock, C.N., De Graaf, A.M.J., 1987. Growth and seasonal variations in distribution of *Chauliodus sloani* and *C. danae* (pisces) from the mid north atlantic. Bijdragen tot de Dierkunde. 57(2): 164-182.

Valls, M., Sweeting, C.J., Olivar, M.P., Fernández de Puelles, M.L., Pasqual, C., Polunin, N.V.C., Quetglas, A., 2014a. Structure and dynamics of food webs in the water column on shelf and slope grounds of the western Mediterranean. Journal of Marine Systems. 138: 171: 181. http://dx.doi.org/10.1016/j.jmarsys.2014.04.002

Valls, M., Olivar, M.P., Fernández de Puelles, M.L., Molí, B., Bernal, A., Sweeting, C.J., 2014b. Trophic structure of mesopelagic fishes in the western Mediterranean based on stable isotopes of carbon and nitrogen. Journal of Marine Systems. 138: 160-170. http://dx.doi.org/10.1016/j.jmarsys.2014.04.007

van der Spoel, S., Bleeker, J., 1991. Distribution of Myctophidae (Pisces, Myctophiformes) during the four seasons in the mid North Atlantic. Contributions to Zoology. 61(2): 89-106.

Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia. 136(2): 169-182.

Ventura, M., Catalan, J., 2008. Incorporating life histories and diet quality in stable isotope interpretations of crustacean zooplankton. Freshwater Biology. 53: 1453-1469. DOI: 10.1111/j.1365-2427.2008.01976.x

Vianello, P., Ternon, J-F., Herbette, S., Demarcq, H., Roberts, M.J., 2020. Circulation and hydrography in the vicinity of a shallow seamount on the northern Madagascar Ridge. Deep-Sea Res. II.

Vipin, P.M., Harikrishnan, M., Renju, R., Boopendranath, M.R., Remesan, M.P., 2018. Population Dynamics of Spinycheek Lanternfish *Benthosema fibulatum* (Gilbert and Cramer 1897), Caught off the South- west Coast of India. Asian Fisheries Science. 31: 161-171.

Waite, A.M., Muhling, B.A., Holl, C.M., Beckley, L.E., Montoya, J.P., Strzelecki, J., Thompson, P.A., Pesant, S., 2007. Food web structure in two counter-rotating eddies based on $\delta^{15}N$ and $\delta^{13}C$ isotopic analyses. Deep-Sea Res. II. 54: 1055-1075. DOI: 10.1016/j.dsr2.2006.12.010

Watanuki, Y., Thiebot, J-B., 2018. Factors affecting the importance of myctophids in the diet of the world's seabirds. Mar. Biol. 165: 79. https://doi.org/10.1007/s00227-018-3334-y

Young, J.W., Hunt, B.P.V., Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccareli, D., Lorrain, A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloser, R.J., Arrizabalaga, H., Choy, C.A., 2015. The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. Deep Sea-Res. II. 113: 170-187. http://dx.doi.org/10.1016/j.dsr2.2014.05.015

List of tables and figures:

Figure 7. $\delta^{15}N$ 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 $\delta^{15}N$ values versus size are plotted for (a)-(d).

Figure 8(a) $\delta^{15}N$ 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 $\delta^{15}N$ and $\delta^{13}C$ 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.

Figure 9. Boxplots of $\delta^{13}C$ and $\delta^{15}N$ 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.

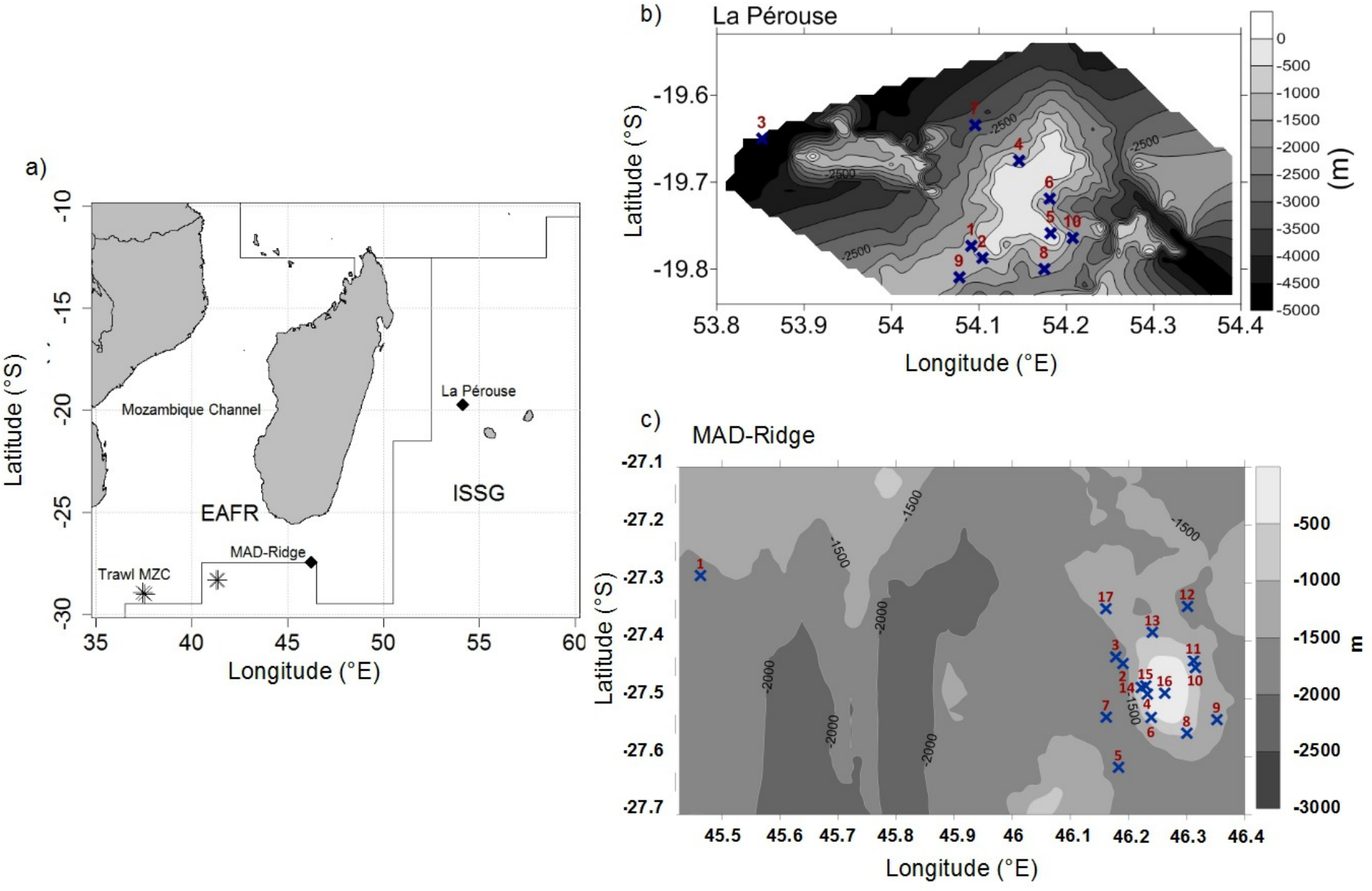
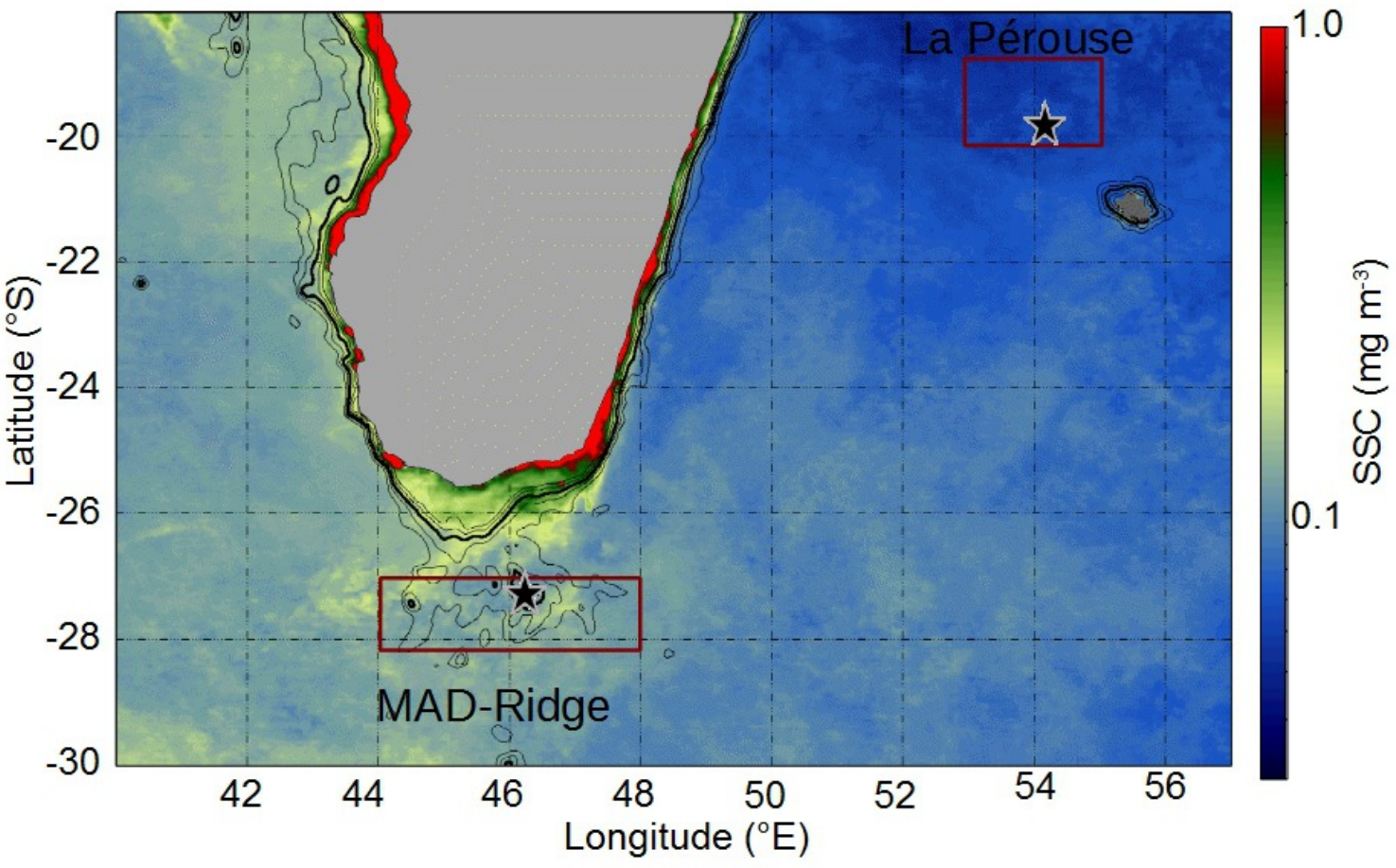

a)
Latitude (°S)
Longitude (°E)
Mozambique Channel
La Pérouse
ISSG
EAFR
MAD-Ridge
Trawl MZC
b)
La Pérouse
Latitude (°S)
Longitude (°E)
(m)
c)
MAD-Ridge
Latitude (°S)
Longitude (°E)
m

Figure 1


La Pérouse
MAD-Ridge
Latitude (°S)
-20
-22
-24
-26
-28
-30
42
44
46
48
50
52
54
56
Longitude (°E)
1.0
0.1
SSC (mg m-3)

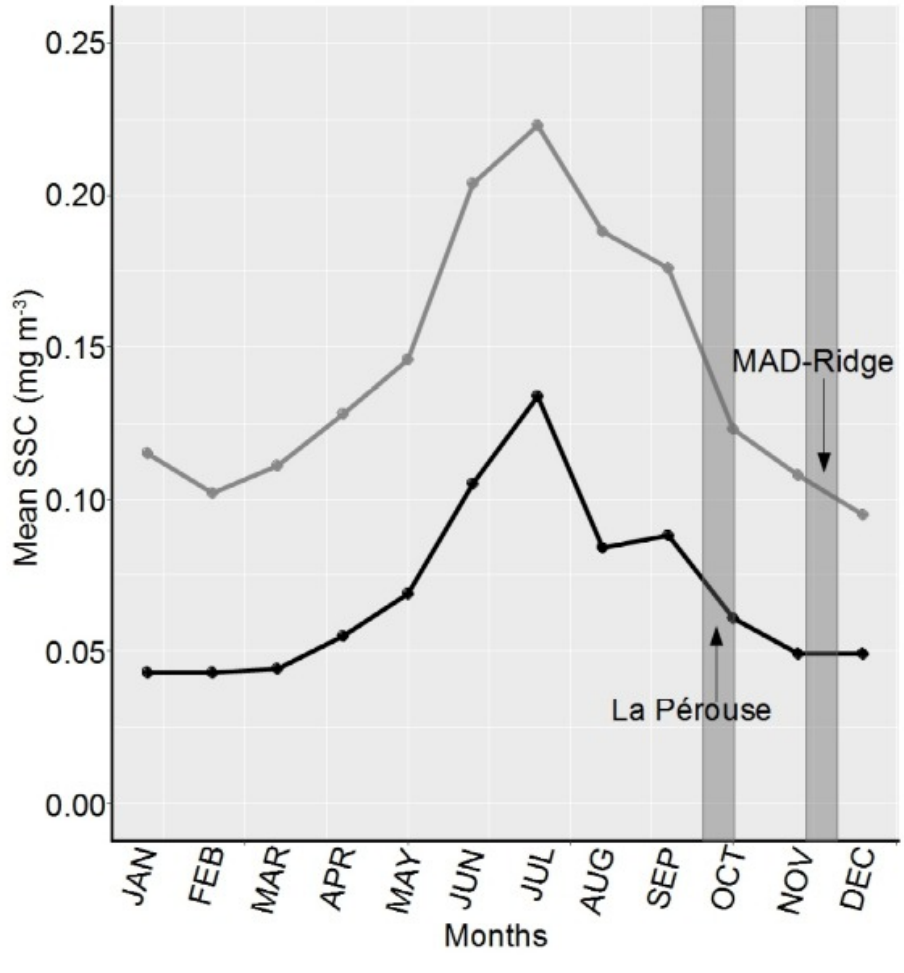

Mean SSC (mg m-3)
0.25
0.20
0.15
0.10
0.05
0.00
MAD-Ridge
La Pérouse
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Months

Figure 2

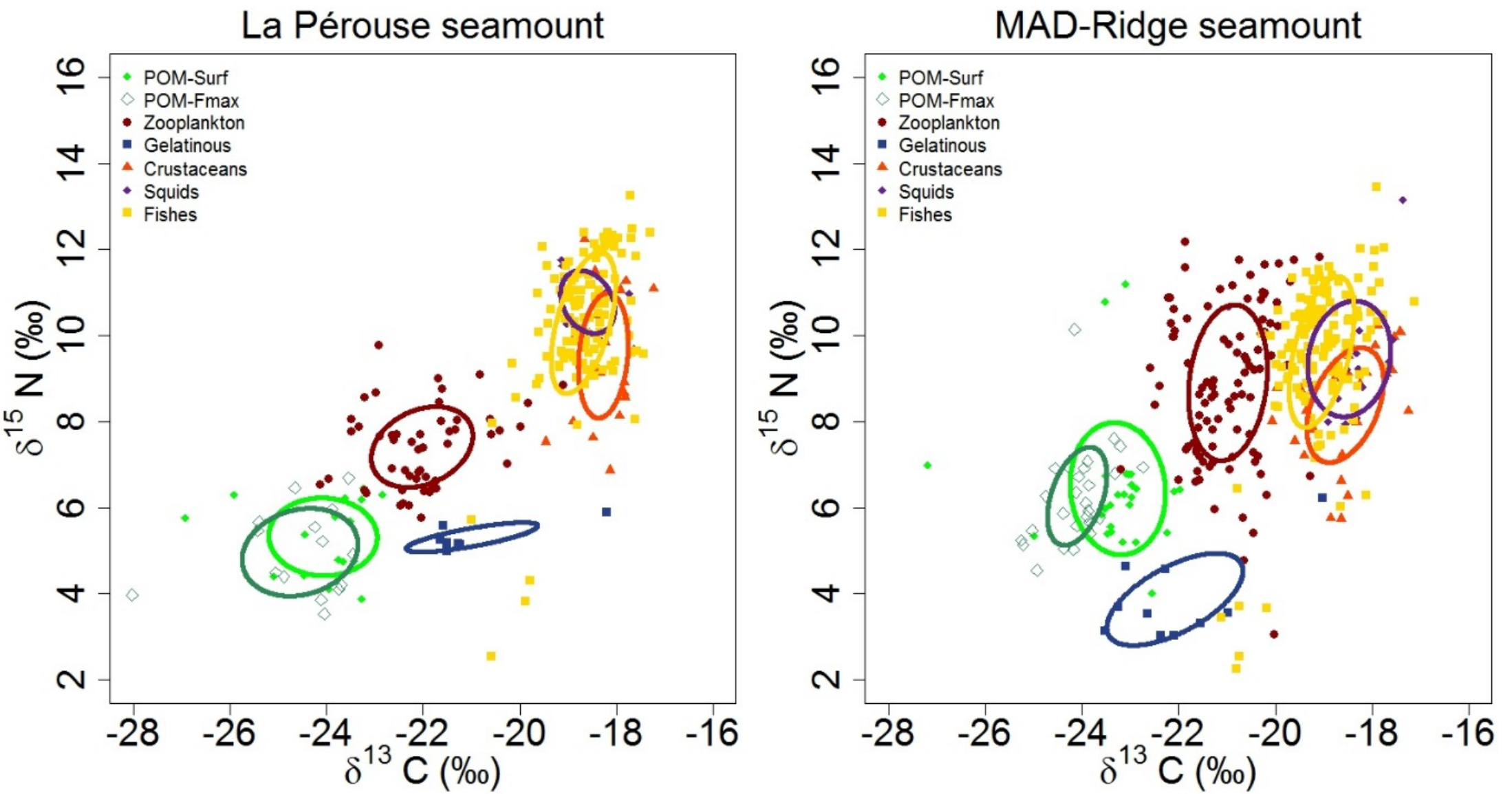

La Pérouse seamount
MAD-Ridge seamount
POM-Surf
POM-Fmax
Zooplankton
Gelatinous
Crustaceans
Squids
Fishes
δ15 N (‰)
δ13 C (‰)
2
4
6
8
10
12
14
16
-28
-26
-24
-22
-20
-18
-16

Figure 3

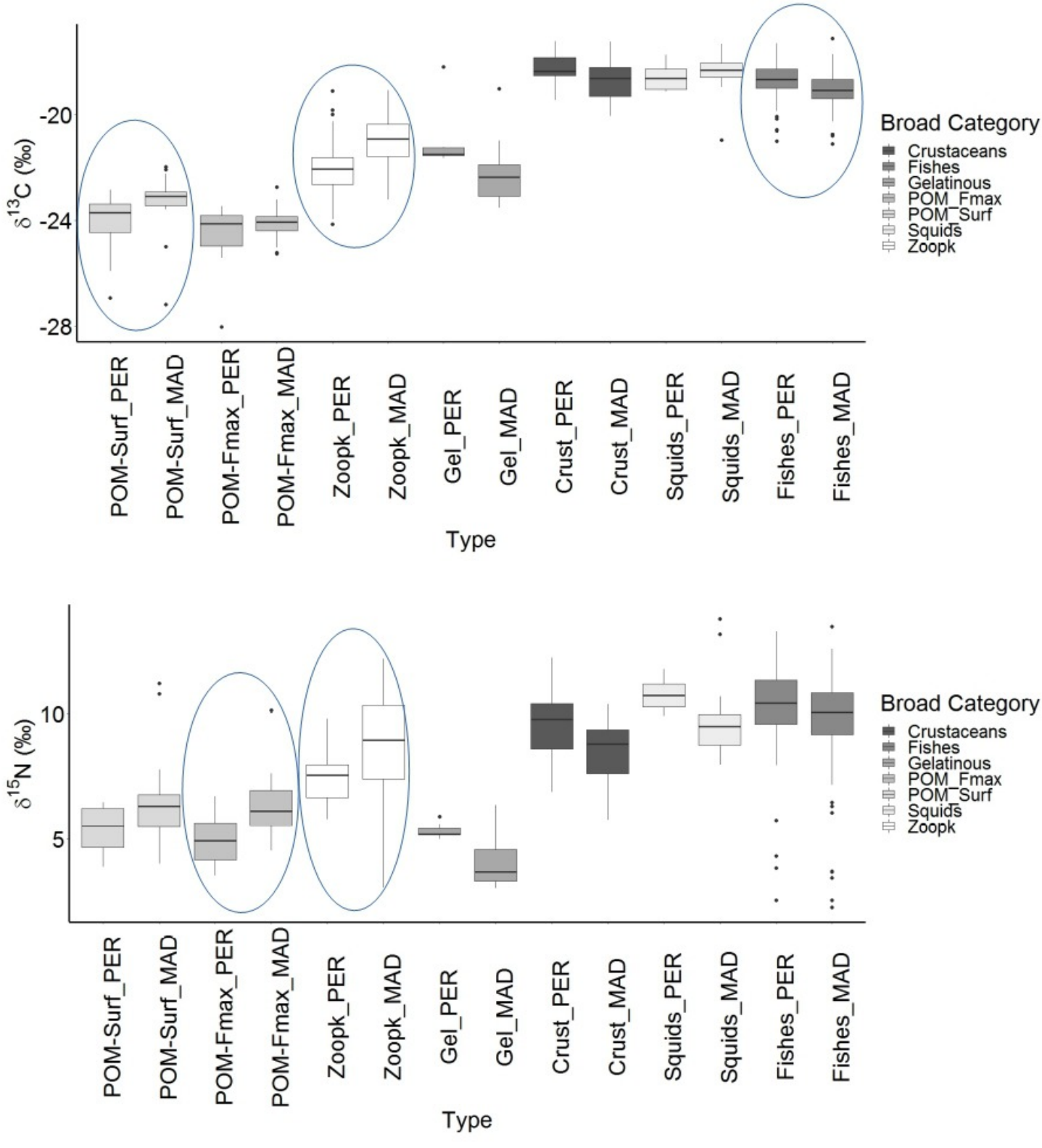

δ13C (‰)
-20
-24
-28
POM-Surf_PER
POM-Surf_MAD
POM-Fmax_PER
POM-Fmax_MAD
Zoopk_PER
Zoopk_MAD
Gel_PER
Gel_MAD
Crust_PER
Crust_MAD
Squids_PER
Squids_MAD
Fishes_PER
Fishes_MAD
Type
Broad Category
Crustaceans
Fishes
Gelatinous
POM_Fmax
POM_Surf
Squids
Zoopk
δ15N (‰)
10
5
POM-Surf_PER
POM-Surf_MAD
POM-Fmax_PER
POM-Fmax_MAD
Zoopk_PER
Zoopk_MAD
Gel_PER
Gel_MAD
Crust_PER
Crust_MAD
Squids_PER
Squids_MAD
Fishes_PER
Fishes_MAD
Type
Broad Category
Crustaceans
Fishes
Gelatinous
POM_Fmax
POM_Surf
Squids
Zoopk

Figure 4

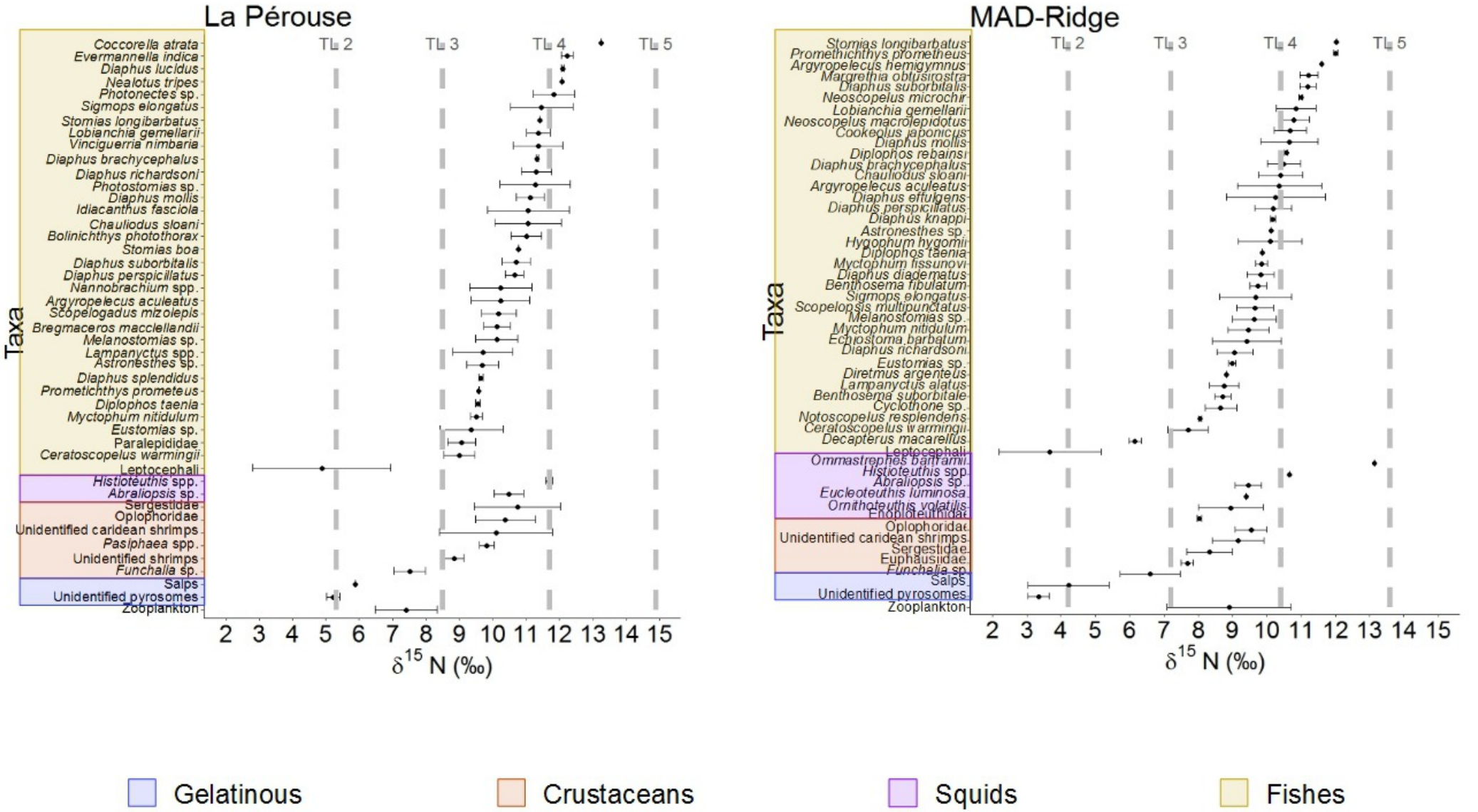

La Pérouse
MAD-Ridge
Taxa
TL 2
TL 3
TL 4
TL 5
Coccorella atrata
Evermannella indica
Diaphus lucidus
Nealotus tripes
Photonectes sp.
Sigmops elongatus
Stomias longibarbatus
Lobianchia gemellarii
Vinciguerria nimbaria
Diaphus brachycephalus
Diaphus richardsoni
Photostomias sp.
Diaphus mollis
Idiacanthus fasciola
Chauliodus sloani
Bolinichthys photothorax
Stomias boa
Diaphus suborbitalis
Diaphus perspicillatus
Nannobrachium spp.
Argyropelecus aculeatus
Scopelogadus mizolepis
Bregmaceros macclellandii
Melanostomias sp.
Lampanyctus spp.
Astronesthes sp.
Diaphus splendidus
Prometichthys prometeus
Diplophos taenia
Myctophum nitidulum
Eustomias sp.
Paralepididae
Ceratoscopelus warmingii
Leptocephali
Histioteuthis spp.
Abraliopsis sp.
Sergestidae
Oplophoridae
Unidentified caridean shrimps
Pasiphaea spp.
Unidentified shrimps
Funchalia sp.
Salps
Unidentified pyrosomes
Zooplankton
Stomias longibarbatus
Promethichthys prometheus
Argyropelecus hemigymnus
Margrethia obtusirostra
Diaphus suborbitalis
Neoscopelus microchir
Lobianchia gemellarii
Neoscopelus macrolepidotus
Cookeolus japonicus
Diaphus mollis
Diplophos rebainsi
Diaphus brachycephalus
Chauliodus sloani
Argyropelecus aculeatus
Diaphus effulgens
Diaphus perspicillatus
Diaphus knappi
Astronesthes sp.
Hygophum hygomii
Diplophos taenia
Myctophum fissunovi
Diaphus diadematus
Benthosema fibulatum
Sigmops elongatus
Scopelopsis multipunctatus
Melanostomias sp.
Myctophum nitidulum
Echiostoma barbatum
Diaphus richardsoni
Eustomias sp.
Diretmus argenteus
Lampanyctus alatus
Benthosema suborbitale
Cyclothone sp.
Notoscopelus resplendens
Ceratoscopelus warmingii
Decapterus macarellus
Leptocephali
Ommastrephes bartramii
Histioteuthis spp.
Abraliopsis sp.
Eucleoteuthis luminosa
Ornithoteuthis volatilis
Enoploteuthidae
Oplophoridae
Unidentified caridean shrimps
Sergestidae
Euphausiidae
Funchalia sp.
Salps
Unidentified pyrosomes
Zooplankton
2 3 4 5 6 7 8 9 10 11 12 13 14 15
δ15 N (‰)
Gelatinous
Crustaceans
Squids
Fishes

Figure 5

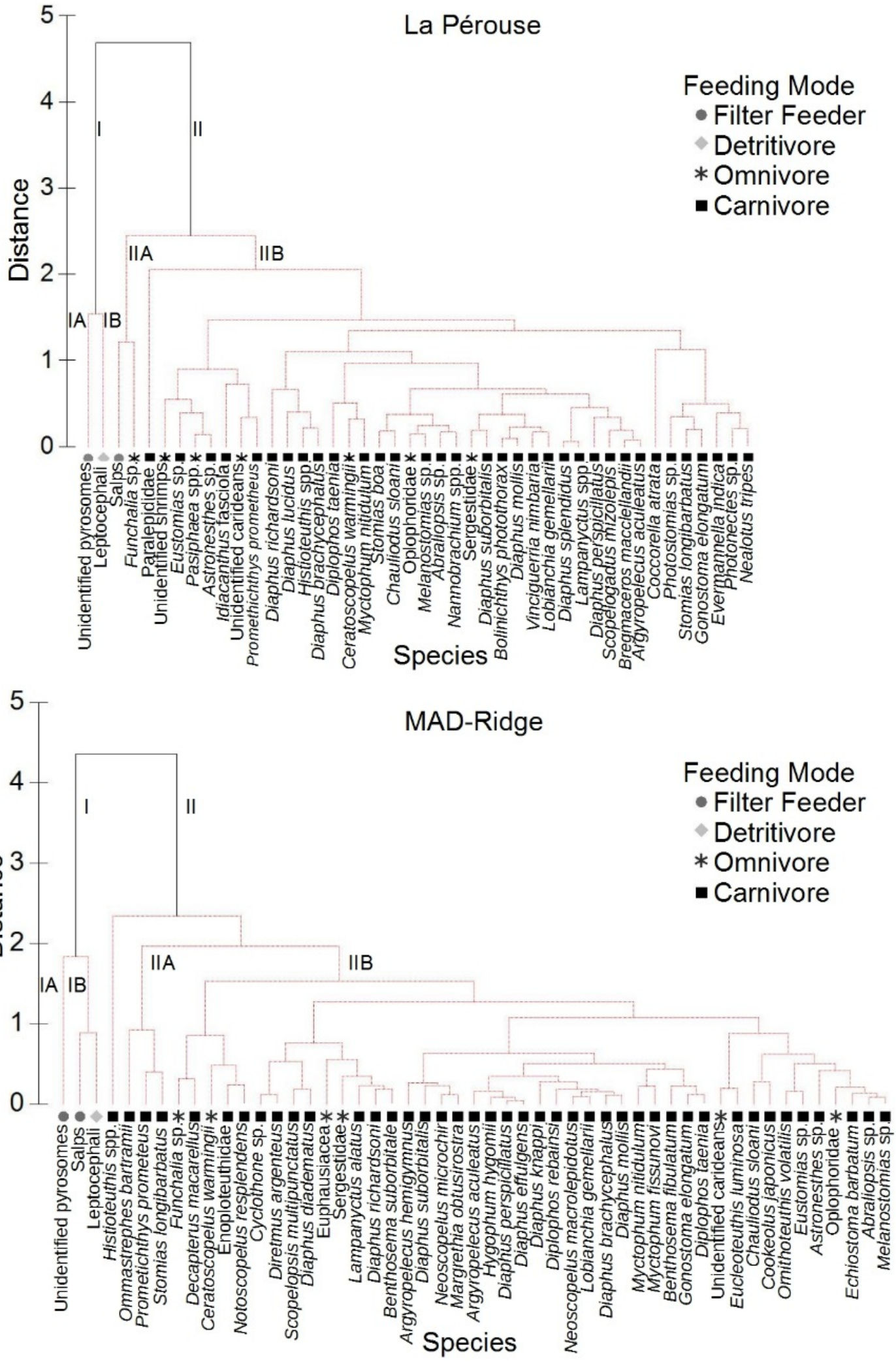

La Pérouse
Feeding Mode
Filter Feeder
Detritivore
Omnivore
Carnivore
Distance
Species
I
II
IA
IB
IIA
IIB
Unidentified pyrosomes
Leptocephali
Salps
Funchalia sp.
Paralepididae
Unidentified Shrimps
Eustomias sp.
Pasiphaea spp.
Astronesthes sp.
Idiacanthus fasciola
Unidentified carideans
Promethichthys prometheus
Diaphus richardsoni
Diaphus lucidus
Histioteuthis spp.
Diaphus brachycephalus
Diplophos taenia
Ceratoscopelus warmingii
Myctophum nitidulum
Stomias boa
Chauliodus sloani
Oplophoridae
Melanostomias sp.
Abraliopsis sp.
Nannobrachium spp.
Sergestidae
Diaphus suborbitalis
Bolinichthys photothorax
Diaphus mollis
Vinciguerria nimbaria
Lobianchia gemellarii
Diaphus splendidus
Lampanyctus spp.
Diaphus perspicillatus
Scopelogadus mizolepis
Bregmaceros macclellandii
Argyropelecus aculeatus
Coccorella atrata
Photostomias sp.
Stomias longibarbatus
Gonostoma elongatum
Evermannella indica
Photonectes sp.
Nealotus tripes
MAD-Ridge
Feeding Mode
Filter Feeder
Detritivore
Omnivore
Carnivore
Distance
Species
I
II
IA
IB
IIA
IIB
Unidentified pyrosomes
Salps
Leptocephali
Histioteuthis spp.
Ommastrephes bartramii
Prometichthys prometeus
Stomias longibarbatus
Funchalia sp.
Decapterus macarellus
Ceratoscopelus warmingii
Enoploteuthidae
Notoscopelus resplendens
Cyclothone sp.
Diretmus argenteus
Scopelopsis multipunctatus
Diaphus dademates
Euphausiacea
Sergestidae
Lampanyctus alatus
Diaphus richardsoni
Benthosema suborbitale
Argyropelecus hemigymnus
Diaphus suborbitalis
Neoscopelus microchir
Margrethia obtusirostra
Argyropelecus aculeatus
Hygophum hygomii
Diaphus perspicillatus
Diaphus effulgens
Diaphus knappi
Diplophos rebainsi
Neoscopelus macrolepidotus
Lobianchia gemellarii
Diaphus brachycephalus
Diaphus mollis
Myctophum nitidulum
Myctophum fissunovi
Benthosema fibulatum
Gonostoma elongatum
Diplophos taenia
Unidentified carideans
Eucleoteuthis luminosa
Chauliodus sloani
Cookeolus japonicus
Omithoteuthis volatilis
Eustomias sp.
Astronesthes sp.
Oplophoridae
Echiostoma barbatum
Abraliopsis sp.
Melanostomias sp

Figure 6

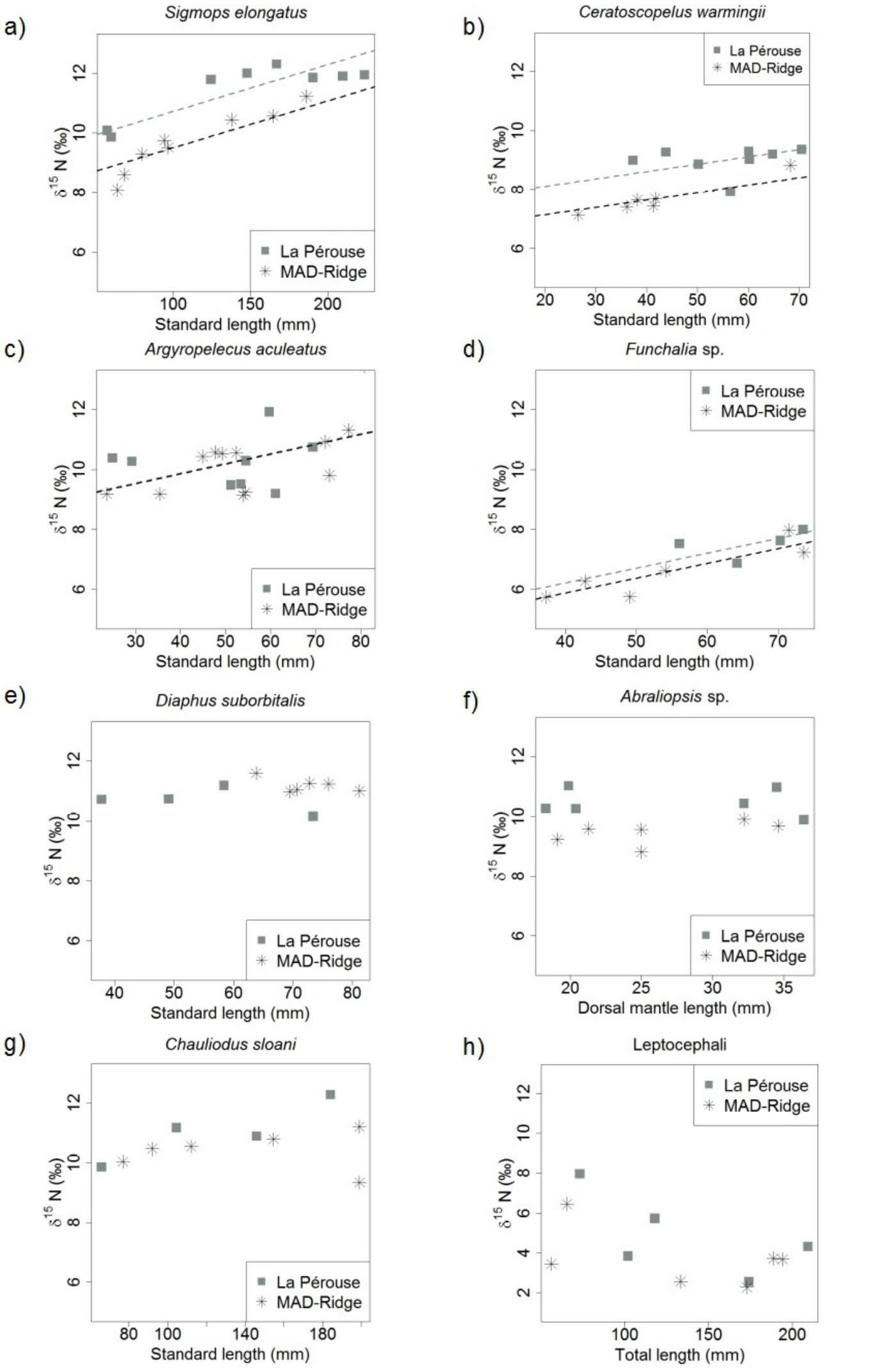

a)
Sigmops elongatus
δ15 N (‰)
Standard length (mm)
La Pérouse
MAD-Ridge
b)
Ceratoscopelus warmingii
c)
Argyropelecus aculeatus
d)
Funchalia sp.
e)
Diaphus suborbitalis
f)
Abraliopsis sp.
Dorsal mantle length (mm)
g)
Chauliodus sloani
h)
Leptocephali
Total length (mm)

Figure 7

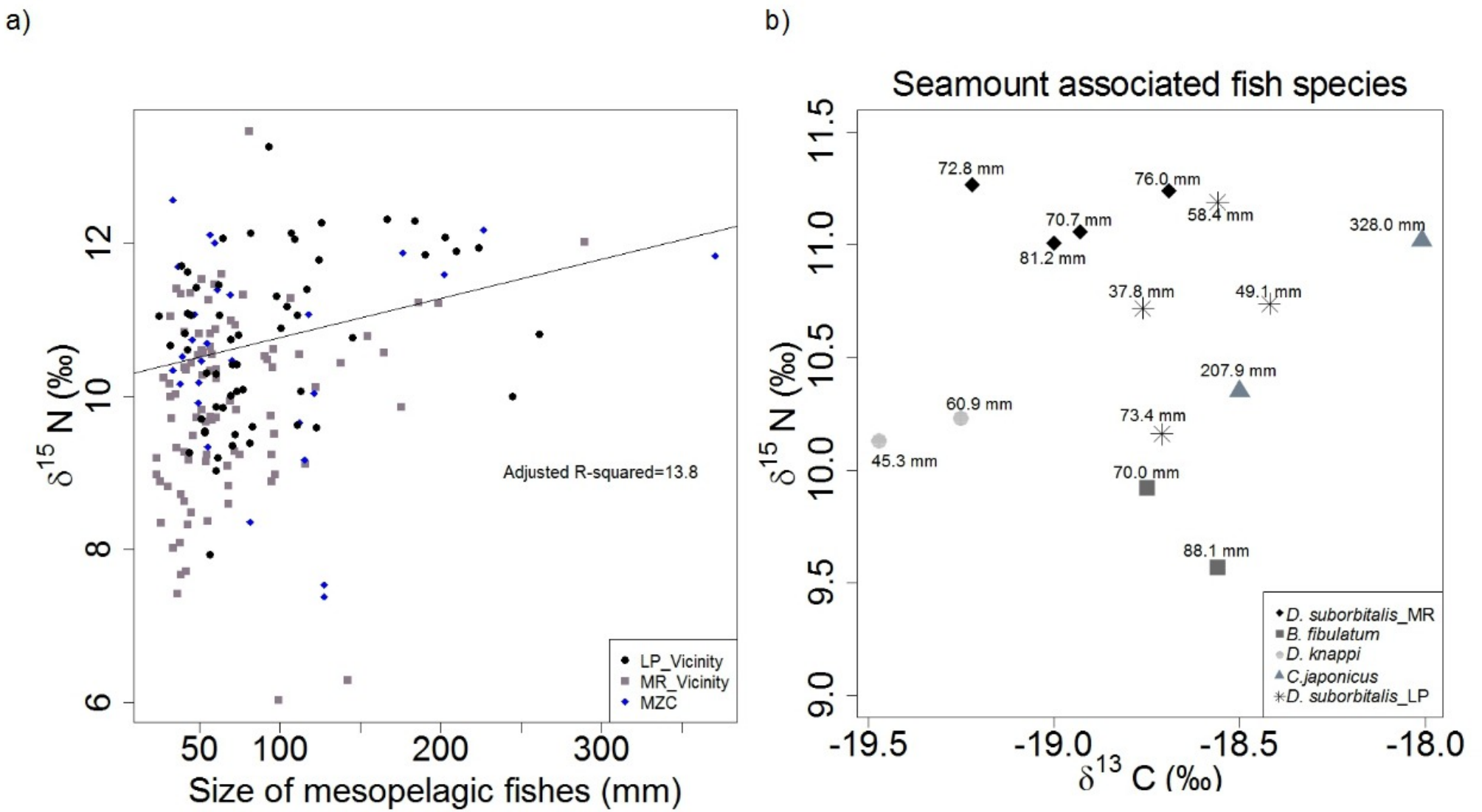

a)
b)
Seamount associated fish species
Adjusted R-squared=13.8
LP_Vicinity
MR_Vicinity
MZC
Size of mesopelagic fishes (mm)
δ15 N (‰)
δ13 C (‰)
72.8 mm
76.0 mm
58.4 mm
70.7 mm
81.2 mm
328.0 mm
37.8 mm
49.1 mm
207.9 mm
60.9 mm
73.4 mm
45.3 mm
70.0 mm
88.1 mm
D. suborbitalis_MR
B. fibulatum
D. knappi
C.japonicus
D. suborbitalis_LP

Figure 8

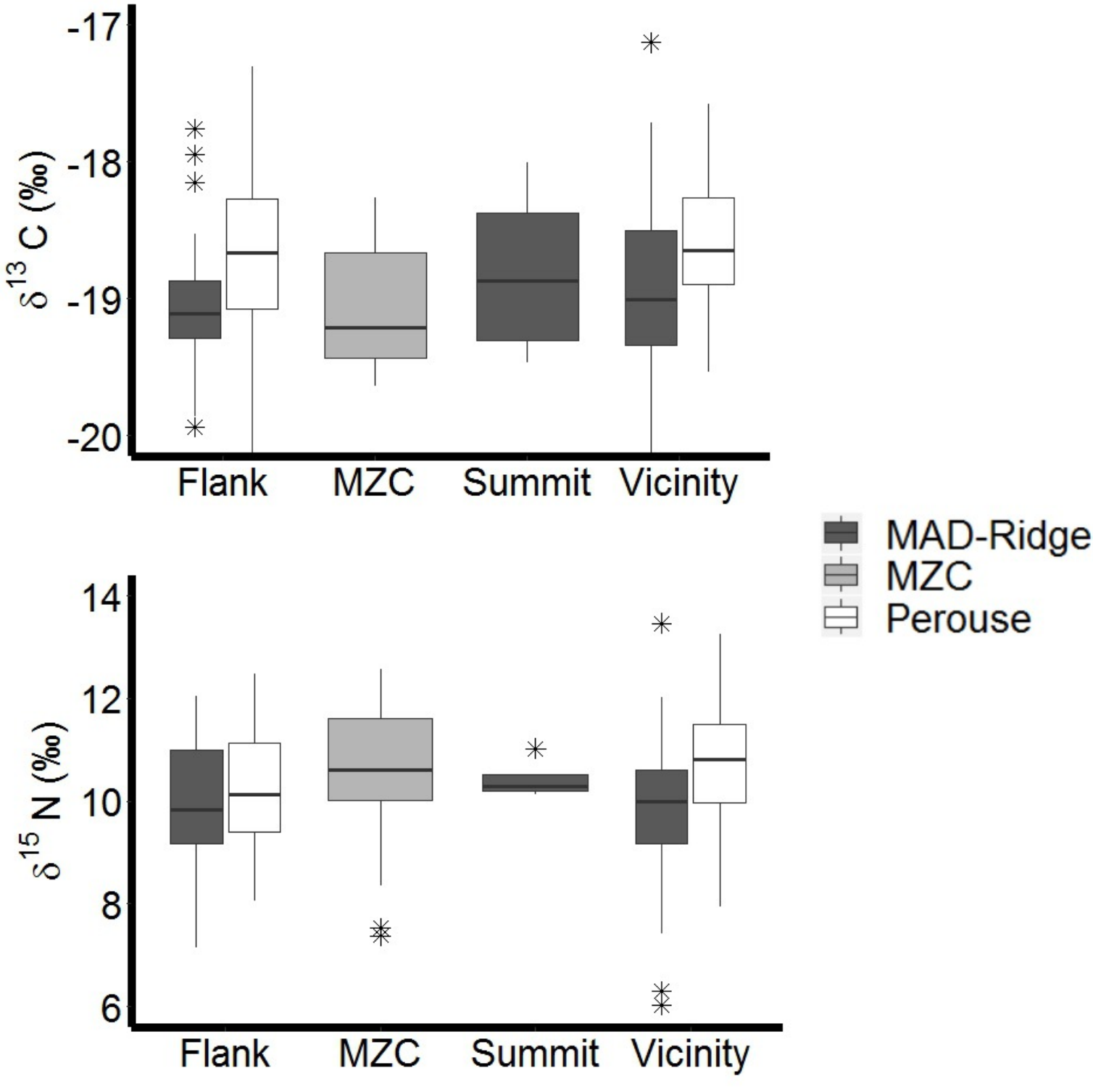

-17
-18
-19
-20
δ13 C (‰)
Flank
MZC
Summit
Vicinity
14
12
10
8
6
δ15 N (‰)
Flank
MZC
Summit
Vicinity
MAD-Ridge
MZC
Perouse

Figure 9

Table 1 Linear regression models fitted to $\delta^{15}N$ values (‰) with respect to body length in mm (SL, standard length for fishes; 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	$\delta^{15}N = 9.15 + 0.0157 \times SL - 1.2210 \times seamount$ La Pérouse: $\delta^{15}N = 9.15 + 0.0157 \times SL$ MAD-Ridge: $\delta^{15}N = 7.93 + 0.0157 \times SL$	85.2	46.0	13	< 0.05 for size and seamount
Ceratoscopelus warmingii	$\delta^{15}N = 7.61 + 0.0249 \times SL - 0.9521 \times seamount$ La Pérouse: $\delta^{15}N = 7.61 + 0.0249 \times SL$ MAD-Ridge: $\delta^{15}N = 6.66 + 0.0249 \times SL$	72.4	18.0	11	< 0.05 for size and seamount
Argyropelecus aculeatus	$\delta^{15}N = 8.57 + 0.0331 \times SL - 0.0272 \times seamount$	16.5	2.87	17	< 0.05 for size; > 0.05 for seamount
Funchalia sp.	$\delta^{15}N = 4.23 + 0.0496 \times ACL - 0.3460 \times seamount$	72.7	13.0	7	< 0.05 for size; > 0.05 for seamount
Diaphus suborbitalis	$\delta^{15}N = 11.5 - 0.0151 \times SL + 0.7594 \times seamount$	43.8	4.51	7	> 0.05 for size; < 0.05 for seamount
Abraliopsis sp.	$\delta^{15}N = 10.3 + 0.0069 \times DML - 1.006 \times seamount$	56.2	8.06	9	> 0.05 for size; < 0.05 for seamount
Chauliodus sloani	$\delta^{15}N = 10.2 - 0.0065 \times SL + 0.7431 \times seamount$	12.5	1.64	7	> 0.05 for size and seamount
Leptocephali larvae	$\delta^{15}N = 7.18 - 0.0170 \times TL - 1.1971 \times seamount$	25.3	2.69	8	> 0.05 for size and seamount