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# Mercury concentrations and stable isotope ratios ( $\delta$ 13C and $\delta$ 15N) in pelagic nekton assemblages of the south-western Indian Ocean

Annasawmy Pavanee 1,\*, Point David 1, Romanov Evgeny V. 2, Bodin Nathalie 3,4

- <sup>1</sup> Géosciences Environnement Toulouse (GET), UMR 5563 CNRS, IRD, UPS, CNES, Observatoire Midi Pyrénées (OMP), 31400 Toulouse, France
- <sup>2</sup> Centre technique de recherche et de valorisation des milieux aquatiques (CITEB), 97420 Le Port, Île de la Réunion, France
- <sup>3</sup> Institut de Recherche pour le Développement (IRD), Fishing Port, Victoria, Mahé, Seychelles
- <sup>4</sup> Sustainable Ocean Seychelles, Beau Belle, Mahé, Seychelles
- \* Corresponding author: Pavanee Annasawmy, email address: angelee-pavanee.annasawmy@ird.fr

#### Abstract:

Mercury (Hg) concentrations and stable isotope values ( $\delta 13C$  and  $\delta 15N$ ) were investigated in micronekton collected from La Pérouse and MAD-Ridge seamounts, Reunion Island and the southern Mozambique Channel. Organisms occupying epipelagic habitats showed lower Hg concentrations relative to deeper dwelling benthopelagic ones. Increasing Hg concentrations with increasing body size were recorded in the Mozambique Channel and Reunion Island. Positive relationships were observed between Hg levels and  $\delta 15N$  values in pelagic nekton assemblages collected at MAD-Ridge seamount and the southern Mozambique Channel, suggesting biomagnification of Hg. Concentrations of Hg in organisms across the south-western Indian Ocean were within the same range of values. Total Hg concentrations depend on a range of factors linked to habitat range, body size and trophic position of the individuals. To our knowledge, this is the first study investigating the patterns of Hg concentrations in pelagic nekton assemblages from the south-western Indian Ocean.

#### **Highlights**

▶ Mercury concentrations were relatively homogeneous across the study sites. ▶ Epipelagic organisms showed lower Hg concentrations than deeper dwelling benthic ones. ▶ Mercury concentrations may increase with increasing body size of individuals. ▶ Larger-sized nektonic species have high trophic positions and Hg burdens.

Keywords: Trophic ecology, Mercury, Seamount, Squid, Crustacean, Fish

#### 1. Introduction

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Mercury is a unique trace element, displaying different chemical forms in the environment. 17 Mercury exists in its elemental form (Hg<sup>0</sup>) in the atmosphere and as inorganic Hg in oceanic 18 waters, with a fraction being converted into monomethyl mercury (MMHg) or dimethyl 19 mercury (DMHg) at ocean depths in oxygen minimum zones (Mason and Fitzgerald, 1993; 20 21 Fitzgerald et al., 2007; Choy, 2013). MMHg is known to bioaccumulate and biomagnify 22 along the marine food chain (Monteiro et al., 1996; Lavoie et al., 2013; Chennuri et al., 2020), with predators showing higher concentrations than their main prey items (Bustamante 23 et al., 2006). Biomagnification is the transfer of a chemical from the diet to the consumer, 24 25 generally leading to higher concentrations of the element with increasing trophic level (Gray, 2002) and is thus inferred when a significant positive relationship is detected between the 26 element and  $\delta^{15}N$  values (Cheung and Wang, 2008). The rate at which bioaccumulation and 27 bioconcentration of MMHg occurs in the food web depends on its bioavailability at the base 28 of the food chain, trophic interactions and food web assemblages up to apex marine 29 predators. In many fish, Hg exists in its most stable, but also the most toxic methyl form 30 (Cossa et al., 1990). Almost all Hg (>90%) in top predators is MMHg (Cossa et al., 1990; 31 32 Bloom, 1992; Houssard et al., 2019). MMHg distribution in pelagic fish tends to mimic oceanic MMHg distribution profiles showing higher burdens in fish foraging at depth 33 compared to epipelagic organisms (Choy, 2013; Blum et al., 2013). 34 In marine pelagic food webs, mesopelagic micronekton typically ranges in size from 2 to 20 35 cm and consists of a large and diverse group of organisms which can be divided into the 36 broad categories crustaceans, squids and fishes (Brodeur and Yamamura, 2005; De Forest 37 and Drazen, 2009). This group assemblage represents a substantial biomass in oceanic waters 38 accounting for more than 3.8-11.8 billion tons of mesopelagic fishes reported worldwide 39 (Irigoien et al., 2014; Proud et al., 2018). Available estimates for cephalopods and 40

41 crustaceans suggest global biomass of at least 55 million tons for a single group of Ommastrephid squids (Nigmatullin, 2004) and approximately 380 million tons of Antarctic 42 krill in the Southern ocean (Atkinson et al., 2009). Micronekton exhibits a diverse range of 43 migration strategies including diel vertical migration over several hundreds of meters from 44 deep (below 400 m) to shallower layers (top 200 m) at dusk and inversely at dawn 45 (Lebourges-Dhaussy et al., 2000; Béhagle et al., 2014; Ariza, 2015; Annasawmy et al., 2018, 46 47 2019, 2020a), reverse migration (Alverson, 1961; Gjøsæter, 1977, 1984; Marchal and Lebourges-Dhaussy, 1996), mid-water migration or non-migration (Annasawmy et al., 2018; 48 49 2019). Migratory micronekton plays an essential role in the oceanic biological pump by transporting organic carbon from the euphotic zone to deeper parts of the oceans (Hidaka et 50 al., 2001; Ariza et al., 2015; LeMoigne, 2019). Micronekton is also preyed upon by tunas, 51 52 billfishes, sharks, marine birds and marine mammals (e.g., Guinet et al., 1996; Potier et al., 2007; Lambert et al., 2014; Filmalter et al., 2017; Romanov et al., 2020). 53 While Hg concentrations in pelagic and tropical coastal marine fish were subjected to 54 extensive studies worldwide (e.g., Al-Reasi et al., 2007; Cai et al., 2007; Calatayud et al., 55 2012; Chen et al., 2014; Bodin et al., 2017; Chouvelon et al., 2017; Afandi et al., 2018; 56 57 Briand et al., 2018; Le Croizier et al., 2019; Houssard et al., 2019), micronekton organisms 58 have received little consideration to date with only few studies having determined Hg 59 concentrations in micronekton species (Asante et al., 2008, 2010; Kojadinovic et al., 2011; 60 Brewer et al., 2012; Chai et al., 2012; Queirós et al., 2020). This study therefore documented for the first time Hg levels and distribution in different pelagic nekton assemblages 61 62 displaying contrasted foraging and diel migration strategies from four different study sites 63 located in the south-western Indian Ocean. These sites (La Pérouse and MAD-Ridge seamounts, Reunion Island and the southern Mozambique Channel) exhibit different 64 productivity, mesoscale processes and varied proximity to landmasses (Annasawmy et al., 65

2019; Vianello et al., 2020), hypothesizing that Hg concentrations and local biogeochemistry would possibly differ spatially and vertically in the water column, which could be transferred into the mesopelagic assemblages.

Biomagnification of a chemical along the food web can be investigated using stable isotope analyses (Asante et al., 2008). Stable nitrogen isotopes ( $\delta^{15}$ N) show an enrichment of 2 to 4% at each trophic step and can be used to determine trophic levels and trophic relationships (Vanderklift and Ponsard, 2003; Michener and Kaufman, 2007; Martínez Del Rio et al., 2009). Stable carbon isotopes ( $\delta^{13}$ C) show an enrichment of 0.5 to 1% per trophic step and can be used to indicate sources of primary production, such as aquatic versus terrestrial, inshore versus offshore, or pelagic versus benthic contributions to food intake (Hobson et al., 1994; Rubenstein and Hobson, 2004). Previous studies have shown positive relationships between  $\delta^{13}$ C and  $\delta^{15}$ N values and concentrations of trace elements in micronekton, suggesting biomagnification of these chemicals (Asante et al., 2008, 2010). Stable isotopes of  $^{13}$ C and  $^{15}$ N were further evaluated, whenever possible, to determine the biomagnification of mercury in pelagic nekton assemblages of the south-western Indian Ocean.

The main objectives of this study are to investigate the (1) Hg concentrations in the different pelagic nekton categories (crustaceans, fishes and squids), (2) regional variability in Hg concentrations, (3) Hg concentrations with respect to the habitat ranges and feeding modes of the sampled taxa, (4) influence of body size and  $\delta^{13}$ C and  $\delta^{15}$ N values on Hg concentrations.

### 2. Materials and Methods

- 87 2.1 Study sites
- Pelagic nekton assemblages were sampled during several cruises of the RV *Antea* at the La
- 89 Pérouse and MAD-Ridge seamounts. For comparison with off-seamount locations, pelagic

nekton assemblages were also sampled in proximity to Reunion Island during the IOTA cruise and in the southern Mozambique Channel during the MAD-Ridge cruise. La Pérouse cruise (DOI: 10.17600/16004500) was conducted in September 2016 at the seamount at latitude 19°43′S and longitude 54°10′E. IOTA cruise (DOI: 10.17600/16004600) was conducted in the waters surrounding Reunion Island (within 50 nautical miles) and MAD-Ridge Leg 2 cruise was conducted in December 2016 at the MAD-Ridge seamount (latitude 27°28.38′S and longitude 46°15.67′E; DOI: 10.17600/16004900) (Fig. 1a). During the MAD-Ridge cruise, four additional mesopelagic trawls were conducted in the southern Mozambique Channel.

The four study sites have been chosen with respect to their contrasting oceanographic natures. While La Pérouse seamount is an isolated pinnacle (Marsac et al., 2020) located in a nutrient-poor gyral system (Jena et al., 2013), MAD-Ridge seamount is part of the Madagascar Ridge and in the pathway of mesoscale eddies driving productivity from the Madagascar continental shelf (Vianello et al., 2020; Noyon et al., 2019). Seasonal phytoplankton blooms (between January and March) may occasionally propagate eastwards from South of Madagascar to about 500 km from Reunion Island (Pinet et al., 2012). Reunion Island may thus occasionally experience higher oceanic productivity compared to La Pérouse seamount (Pinet et al., 2012). The southern Mozambique Channel is a site of high oceanic productivity and mesoscale processes due to the prevalence of mesoscale eddies driving productivity from the African continental shelf into the channel (Tew-Kai and Marsac, 2009).

## 2.2 Sampling of pelagic nekton assemblages

Pelagic nekton were sampled with a 40-m long International Young Gadoid Pelagic Trawl, having an 80 mm knotless nylon delta mesh netting at the front tapering, 5 mm at the codend and a mouth opening of ~96 m<sup>2</sup> during all three cruises. The trawl was towed at a vessel

speed of ~2-3 knots at the targeted depths for 60 min at La Pérouse and Reunion Island and 30 min at MAD-Ridge and in the Mozambique Channel. During all cruises, the sampling depth was that of the sound scattering layer at that ship position and time of day, with no rigid plan of sampling preselected depths. The trawl depth was monitored with a Scanmar depth sensor during all cruises. To account for the different trawl durations, the volume of water filtered by the net tows was estimated by multiplying the distance travelled by the area of the trawl mouth opening. Ten epi-mesopelagic tows were conducted at the La Pérouse seamount, six at Reunion Island, seventeen at MAD-Ridge seamount, and four in the southern Mozambique Channel.

The sampled mesopelagic organisms were sorted on board, divided into four broad categories (gelatinous, crustaceans, cephalopods and fishes) and frozen at -20°C. Only the broad categories crustaceans, fishes and squids were analysed during this study and are listed in Table 1. The identified samples were measured (abdomen and carapace length for crustaceans, dorsal mantle length – DML – for squids, and standard length – SL – for fishes).

# 2.3 Mercury analyses

Micronekton samples (muscle tissue taken from abdomen for crustaceans, mantle for squids and dorsal musculature for fishes) were freeze-dried in Christ Alpha 1-4 LSC Freeze Dryers for 48h and ground to a fine homogenous powder using an automatic ball mill RETSCH MM200 at 30 oscillations per second for ~10 minutes. Approximately 10-100 mg of dried samples was measured and total Hg concentrations were determined by combustion, gold trapping and atomic absorption spectrophotometry detection using a Direct Mercury Analyser (DMA-80, Milestone, USA). Two freeze-dried certified biological materials, a lobster hepatopancreas (TORT-3, National Research Council Canada; certified Hg concentration:  $0.29 \pm 0.02 \,\mu g \, g^{-1}$  dry weight) and a mussel tissue (SRM 2976, National Institute of

Standards and Technology; certified Hg concentration:  $61.0 \pm 3.6 \ \mu g \ g^{-1}$  dry weight) reference materials and analyses of blanks were used in each sample batch to establish the analytical quality (i.e. accuracy and reproducibility) of the method. Recovery values for each sample batch were not different from the certified values and their associated uncertainty. Three blanks were analysed at the beginning of each sample batch. The DMA-80 achieves a detection limit of 0.005  $\mu g \ g^{-1}$  dry weight (Le Croizier et al., 2019). Resulting Hg concentrations in pelagic nekton assemblages are given in  $\mu g \ g^{-1}$  dry weight (dw).

2.4 Analysis of stable isotope ratios and trophic level calculations

Since 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 samples using dichloromethane on an accelerated solvent extraction system (ASE®, Dionex; Bodin et al., 2009). Approximately 400-600 µg of dried and ground samples were weighed and placed in tin capsules and were run through continuous flow on a Thermo Scientific Flash 2000 elemental analyser coupled to a Delta V Plus mass spectrometer at the Pôle de Spectrométrie Océan (Plouzané, France). The samples were combusted in the elemental analyser to separate  $CO_2$  and  $N_2$  gases. A reference gas set was used to determine isotopic ratios by comparison. The isotopic ratios were then expressed in the conventional  $\delta$  notations as parts per thousand (‰) deviations from the international standards:

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$$\delta^{13}$$
C or  $\delta^{15}$ N (%*o*) = [(R<sub>sample</sub>/R<sub>standard</sub>) - 1] x 1000

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

Measurement errors for both the nitrogen and carbon isotopes were <0.15%. For each sample, the C: N ratio did not exceed 3.5, confirming that lipids were efficiently removed from the samples (Post et al., 2007).

161 The trophic level of each selected taxa was calculated using the following equation, based on

162 Minagawa and Wada (1984) and Post (2002):

$$163 \qquad 2.0 + \frac{\delta^{15}N_i - \delta^{15}N_{primary consumer}}{3.2}$$

where,  $\delta^{15}N_i$  is the nitrogen isotopic value of any given taxon i,  $\delta^{15}N_{primary\,consumer}$  is the nitrogen isotopic value of the baseline at trophic level of 2, and 3.2‰ is the estimated trophic enrichment factor between consumers and their primary prey (Michener and Kaufman, 2007; Vanderklift and Ponsard, 2003). In this study,  $\delta^{15}N_{primary\,consumer}$  was estimated from the mean  $\delta^{15}N$  values (5.31 ± 0.31‰) of six pyrosomes and one salp at La Pérouse seamount and from six salps with mean  $\delta^{15}N$  values of 4.22 ± 1.01‰ at MAD-Ridge (Annasawmy et al., 2020b).

## 2.5 Ecological data of selected species

The pelagic nekton organisms were classified into different habitat ranges according to literature (Clarke and Lu, 1975; Pearcy et al., 1977; Smith and Heemstra, 1986; van der Spoel and Bleeker, 1991; Brodeur and Yamamura, 2005; Hastie et al., 2009; 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 and ~100 m from the seafloor) and benthopelagic (living near the bottom but performing excursions into the pelagic realm) according to definitions of the vertical zonation of the pelagic ocean from Del Giorgio and Duarte (2002) and Sutton (2013). The different taxa were thus classified into the groups Epipelagic-Mesopelagic < Mesopelagic < Mesopelagic-Bathypelagic < Mesopelagic, according to their known habitats described in literature.

Organisms were further classified as carnivores (all squids, most mesopelagic fishes except Warming's lanternfish *Ceratoscopelus warmingii*) and omnivores (all crustaceans). Most

mesopelagic fishes were classified as carnivores since they were reported to feed on copepods, amphipods, euphausiids and ostracods (Dalpadado and Gjøsæter, 1988; Pakhomov et al., 1996; Tanaka et al., 2007; Hudson et al., 2014; Bernal et al., 2015; Carmo et al., 2015; Young et al., 2015), with no herbivorous feeding strategy except *C. warmingii* which has developed an adaptive response to competition in low-productive environment (Robison, 1984). Crustaceans were classified as omnivores since they were reported to prey on zooplankton, euphausiids, and copepods and are known for occasional herbivory (Hopkins et al., 1994; Birkley and Gulliksen, 2003; Mauchline, 1959; Foxton and Roe, 1974). For species with unknown diets, the feeding mode was determined based on the feeding habits identified from species within the same genus.

## 2.6 Satellite data acquisition

Sea surface chlorophyll (SSC) data at a daily and 4.5 km resolution were downloaded from MODIS (http://oceancolor.gsfc.nasa.gov) and were used to calculate 5-day averages to obtain a proxy of surface oceanic primary production for the period from 18/09/2016 to 07/12/2016. Delayed-time mean sea level anomalies (MSLAs) at a daily and 1/4° resolution were produced and distributed by the Copernicus Marine Environment Monitoring Service project (CMEMS) and available at http://marine.copernicus.eu/. MSLAs were used to describe the mesoscale eddy field at the time of MAD-Ridge cruise.

### 2.7 Statistical analyses

Prior to running statistical tests, assumptions of normality using the Shapiro Wilk's test (Shapiro and Wilk, 1965) and homogeneity of variances using the Bartlett test (Bartlett, 1937), were computed in R (v. 3.6.1). To investigate variation in Hg concentrations between broad categories, non-parametric Kruskal-Wallis tests were performed followed by pairwise Wilcoxon rank sum tests. Differences in Hg concentrations of the most common taxa

(Sergestidae, Penaeidae, Stomiidae, Gonostomatidae and Myctophidae) across the four sampling sites - La Pérouse, MAD-Ridge, Mozambique Channel and Reunion Island - were investigated using Kruskal-Wallis tests. The latter tests were also conducted to assess the variation in Hg concentrations according to the habitat ranges of the sampled micronekton species. Non-parametric Wilcoxon rank sum tests were carried out to investigate the influence of feeding mode (carnivorous or omnivorous) on Hg concentrations at each of the four sampling sites. Linear regressions were computed to assess the relationships between Hg concentration and micronekton body size. Links between  $\delta^{13}$ C and  $\delta^{15}$ N values of all selected micronekton at the sampling sites La Pérouse, MAD-Ridge and Mozambique Channel were investigated using Kruskal-Wallis tests and pairwise Wilcoxon rank sum tests. Statistical models were further applied to test for the influence of  $\delta^{13}$ C and  $\delta^{15}$ N values on Hg concentrations of the broad categories crustaceans, fishes and squids at La Pérouse, MAD-Ridge and in the Mozambique Channel. Links between stable isotope values and Hg concentrations were not investigated at Reunion Island because stable isotope ratios were not available at this site.

#### 3. Results

- 3.1 Prevailing bathymetry and oceanographic processes at the study sites
- La Pérouse seamount is located within the Indian South Subtropical Gyre (ISSG) province and MAD-Ridge seamount is located ~1300 km southwards from the Madagascar landmass within the East African Coastal province (EAFR) (Fig. 1a). The La Pérouse seamount summit is 10 km long and reaches ~60 m below the sea surface rising from a seabed at ~5000 m (Fig. 1b). MAD-Ridge seamount is 33 km long (North to South) and 22 km wide (East to West).

231 The seamount rises from 1600 m from the ocean floor to a summit depth of ~240 m below the sea surface (Fig. 1c). 232 233 Mean sea surface chlorophyll concentrations were higher at the MAD-Ridge seamount and the southern Mozambique Channel compared to the La Pérouse seamount and Reunion Island 234 (Fig. 2a). During MAD-Ridge cruise in November 2016, a strong anticyclonic eddy was 235 236 stationed at MAD-Ridge. A weak anticyclonic eddy was stationed at La Pérouse seamount, whereas Reunion Island was under the influence of a weak cyclonic eddy in November 2016 237 (Fig. 2b). During the La Pérouse cruise in September 2016, a weak cyclonic eddy was 238 stationed at the seamount (Annasawmy et al., 2019). 239 3.2 Pelagic nekton species composition, size variability by sampled area and ecological group 240 241 A total of 60 pelagic nekton taxa were sampled during this study, including 4 crustaceans, 10 squids, and 46 fishes (Table 1). Crustaceans were represented by pelagic caridean, penaeid, 242 and sergestid shrimps. Cephalopods consisted of five families of squids (Enoploteuthidae, 243 Histioteuthidae, Ommastrephidae, Onychoteuthidae, and Pyroteuthidae). Fishes were 244 represented by 11 common pelagic families Carangidae, Diretmidae, Gempylidae, 245 246 Gonostomatidae, Myctophidae, Neoscopelidae, Scombrolabracidae, Phosichthyidae, Sternoptychidae, Stomiidae, and benthopelagic Priacanthidae. In terms of diversity and 247 biomass, sampling was dominated by Myctophidae (22 species) and Stomiidae (12 species) 248 249 (Table 1). A total of 256 taxa represented small animals of less than a maximum length of 200 mm. 250 Larger organisms were also collected in the trawl including two large individuals of neon 251 flying squids, Ommastrephes bartramii (DML = 364.8 and 489.8 mm) and fishes: Roudi 252 escolar, Promethichthys prometheus (n = 2, SL = 235.4 and 365.0 mm) and longfinned 253

bullseye, Cookeolus japonicus (n = 2, SL range 207.9-328.0 mm). These six specimens

represent outliers from the micronektonic community in terms of sizes (neon flying squid and Roudi escolar) and habitat (Roudi escolar and longfinned bullseye) and were hence analysed separately. All calculations of means and medians by broad categories, regions, habitats, feeding modes, sizes and stable isotope values, are presented without taking these species into consideration. The size ranges of fishes were SL 30.8-244.8 mm (mean of 84.9 mm) at La Pérouse, 30.3-289.9 mm (mean of 74.7 mm) at MAD-Ridge seamount, 33.6-371.0 mm (mean of 99.6 mm) in the Mozambique Channel and 18.9-184.9 mm (mean of 121.4 mm) at Reunion Island. Crustaceans showed size ranges of 39.1-84.9 mm (mean of 59.9 mm) at La Pérouse, 33.2-78.5 mm (mean of 56.1 mm) at MAD-Ridge, 55.5-79.2 mm (mean of 69.3 mm) in the Mozambique Channel and 29.5-78.6 mm (mean of 54.2 mm) at Reunion Island. The size ranges of squids were DML 18.3-36.4 mm (mean of 28.3 mm) at La Pérouse, 22.2-163.3 mm (mean of 59.7 mm) at MAD-Ridge and 18.9-81.9 mm (mean of 31.8 mm) at Reunion Island. 3.3 Variability in micronekton Hg concentrations Mercury concentrations of all sampled taxa are given in Table 1. No significant differences were observed in Hg concentrations of Gonostomatidae, Myctophidae, Sergestidae, Penaeidae, and Stomiidae between La Pérouse, MAD-Ridge seamounts, the southern Mozambique Channel and Reunion Island (Fig. 3a; Kruskal-Wallis, p > 0.05). All micronekton species sampled at Reunion Island showed lower mean Hg concentrations than at La Pérouse and MAD-Ridge seamounts (Kruskal-Wallis, H= 21.9, p < 0.05) (Fig 3b). Squids exhibited lower median Hg concentrations compared to crustaceans and fishes at La Pérouse, MAD-Ridge and Reunion Island (Kruskal-Wallis, H= 65.2, p < 0.05; Fig 3c). The

two large nektonic neon flying squids collected in the Mozambique Channel and at MAD-

Ridge seamount showed high Hg concentrations of 0.92 µg g<sup>-1</sup> dw and 0.82 µg g<sup>-1</sup> dw

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compared to the other sampled squids (Table 2). At La Pérouse and Reunion Island, Oplophoridae sp. exhibited higher Hg concentrations (1.69 and 1.57 µg g<sup>-1</sup> dw, respectively) than other sampled taxa. The Funchalia sp. (Penaeidae) showed lower Hg concentrations  $(0.05\text{-}0.06~\mu g~g^{\text{-}1}~dw)$  than the other crustaceans at MAD-Ridge, the southern Mozambique Channel and Reunion Island. Fishes exhibited higher median Hg concentrations at MAD-Ridge than the other broad categories (with hatchetfish Argyropelecus aculeatus showing highest concentrations of 1.12 µg g<sup>-1</sup> dw). The mackerel scad *Decapterus macarellus* showed lower Hg concentrations of 0.03 µg g<sup>-1</sup> dw among all other sampled fishes at MAD-Ridge seamount, in the southern Mozambique Channel and at Reunion Island (Table 2). Hg concentrations in the sampled micronekton increased from organisms collected near the surface (Epipelagic-Mesopelagic) to deeper parts (Mesopelagic-Benthopelagic) (Kruskal-Wallis, H=23.8, p < 0.05) (Fig. 3d). Feeding mode (omnivore vs carnivore) of sampled micronekton did not significantly influence Hg concentrations (MAD-Ridge: W= 685, p > 0.05; Mozambique Channel: W= 59, p > 0.05; Reunion Island: W= 339, p > 0.05), except at La Pérouse seamount (W= 229, p < 0.05) (Fig. 3e) where omnivorous organisms (representing crustaceans and C. warmingii individuals) recorded higher Hg concentrations compared to carnivorous ones. Body size of organisms had a significant positive influence on Hg concentrations in the southern Mozambique Channel ( $F_{1, 28} = 18.6$ , p < 0.05) and at Reunion Island ( $F_{1,74} = 5.14$ , p < 0.05) with Hg concentrations increasing with micronekton's body size [Mozambique Channel:  $Hg(\mu g g^{-1} dw) = 0.04 + 0.001 \times Size (mm)$ ; Reunion Island:  $Hg(\mu g g^{-1} dw) = 0.07 + 0.001 \times Size (mm)$ ]. No relation was found between Hg concentrations and body size of all micronekton species at the La Pérouse ( $F_{1,58} = 0.006$ , p > 0.05) and MAD-Ridge seamounts  $(F_{1, 93} = 0.30, p > 0.05)$  (Fig 4).

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3.3 Relationships between Hg concentrations and stable isotope ( $\delta^{13}$ C and  $\delta^{15}$ N) values

Stable isotope values of  $\delta^{13}$ C and  $\delta^{15}$ N were significantly different between La Pérouse and MAD-Ridge seamounts ( $\delta^{13}$ C: Kruskal-Wallis, H= 16.4, p < 0.05;  $\delta^{15}$ N: Kruskal-Wallis, H= 15.8, p < 0.05), with micronekton showing higher  $\delta^{13}$ C and  $\delta^{15}$ N values at La Pérouse compared to MAD-Ridge (Fig. 5). Micronekton assemblages also exhibited higher  $\delta^{13}$ C values at La Pérouse compared to the Mozambique Channel (pairwise comparisons, p < 0.05). Hg concentrations in the micronekton broad categories were significantly influenced by  $\delta^{15}$ N values at MAD-Ridge (F<sub>1</sub>, 95 = 18.0, p < 0.05) and in the Mozambique Channel (F<sub>1</sub>, 28 = 10.2, p < 0.05), with an increase in Hg concentrations with increasing  $\delta^{15}$ N values. No significant increase in Hg concentrations with increasing  $\delta^{15}$ N values were observed at La Pérouse (F<sub>1</sub>, 28 = 1.64, p > 0.05). No clear relationships were found between Hg concentrations and  $\delta^{13}$ C values at the La Pérouse (F<sub>1</sub>, 28 = 2.37, p > 0.05), MAD-Ridge seamounts (F<sub>1</sub>, 95=0.56, p > 0.05) and the Mozambique Channel (F<sub>1</sub>, 28 = 1.21, p > 0.05) (Fig. 6).

#### 4. Discussion

- To our knowledge, this study is the first to investigate Hg concentrations in pelagic nekton assemblages in the south-western Indian Ocean, including two yet undocumented shallow seamounts. While Hg concentrations were relatively homogeneous in micronekton sampled at the seamounts, the open ocean and the Mascarene shelf, other factors such as vertical distribution, body size and trophic position may influence Hg levels.
- 4.1 Spatial variability in Hg concentrations in the south-western Indian Ocean
- Average Hg concentrations in organisms collected at Reunion Island were lower compared to those from the southern Mozambique Channel and at La Pérouse and MAD-Ridge seamounts. However, no significant differences were found in Hg concentrations of the most

common and similar taxa between the four sampling sites. Although higher levels of methyl mercury (MeHg) have been recorded in areas of higher productivity due to relatively active microbial activity (Topping and Davies, 1981; Ferriss and Essington, 2014; Laurier et al., 2004; Zhang et al., 2020), levels of Hg in micronekton sampled at the more productive MAD-Ridge seamount and the southern Mozambique Channel were not significantly different from those collected at the oligotrophic La Pérouse seamount. The lack of difference in Hg between the study sites is possibly due to horizontal migratory behaviour of micronekton. MeHg concentrations in micronekton may also be likely influenced by its concentrations in zooplanktonic prey, with concentrations of MeHg in zooplankton being influenced by the concentrations found in various phytoplankton species (Zhang et al., 2020). Future work is necessary to determine Hg speciation in zooplankton so as to investigate the trophic transfer of Hg between zooplankton and micronekton. The Hg concentrations in mesopelagic fishes from the four study sites in the Indian Ocean were higher (0.08-1.4  $\mu g$  g<sup>-1</sup> dw) than concentrations recorded for similar specimens with similar or higher size ranges (Cyclothone sp., C. warmingii, Chauliodus sloani, Sigmops elongatus, and Idiacanthus fasciola) collected from the Sulu, Celebes and Philippine Seas (0.05 µg g<sup>-1</sup> dw) (Asante et al., 2010). The crustaceans Oplophoridae and Sergestidae also showed higher Hg concentrations of 0.00-1.69 and 0.06-0.38 µg g<sup>-1</sup> dw, respectively, relative to smaller individuals collected off Niolam Island within the Papua New Guinea Province where values ranged from ~0.1-0.2 µg g<sup>-1</sup> dw for Oplophoridae and less than 0.1 µg g<sup>-1</sup> dw for Sergestidae (Brewer et al., 2012). These spatial differences operating at large ocean scale could potentially reflect variations in the local net production and bioavailability of MeHg at the base of the foodweb (Chakraborty et al., 2016) and/or differences in the vertical niche occupied by these organisms that may also vary among ocean regions. Further research is

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needed to provide precise MeHg depth water profiles to further address the questions behind these spatial differences.

#### 4.2 Vertical distribution of Hg concentrations

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Hg concentrations in the sampled micronekton increased from organisms collected near the surface (Epipelagic-Mesopelagic) to deeper parts (Mesobenthopelagic). MeHg has long been thought to originate from marine sediments leading to the bioaccumulation of Hg in soft tissues of organisms (Fitzgerald et al., 2007; Chakraborty and Babu, 2015; Chakraborty et al., 2016; Chakraborty et al., 2019; Padalkar et al., 2019; Chennuri et al., 2020) from lower to higher trophic compartments. Recent mass balance estimates suggest that the stock of marine MeHg cannot be solely supplied by shelf/margin or deep sediment source (Mason et al., 2012). MeHg depth profiles in the open ocean consistently show MeHg production and accumulation in the subthermocline oxygen minimum zone (Cossa et al., 2009; Heimbürger et al., 2010). Sulfate-reducing bacteria (Compeau and Bartha, 1985; Benoit et al., 2001; Ranchou-Peyruse et al., 2009), and other anaerobic microorganisms involved in the remineralization of organic matter and hosting specific methylation genes have been identified as possible methylators at ocean depth (Gilmour et al., 2013; Parks et al. 2013). The nine *Onychoteuthis* sp. squid specimens showing epipelagic-mesopelagic habitat ranges were collected within the first 250 m of the water column from Reunion Island, and showed Hg concentrations in the range of 0.02-0.08 µg g<sup>-1</sup> dw. All other organisms from Reunion Island were also collected in the first 250 m but they showed mesopelagic and bathypelagic habitat ranges unlike Onychoteuthis sp., i.e. they migrate vertically and reside deeper in the water column during the day, potentially having access to a wider range of prey from different habitat ranges and having higher Hg burdens.

The five organisms classified as benthopelagic were all fishes collected from MAD-Ridge seamount (two flank-associated *N. macrolepidotus*, one flank-associated *Neoscopelus microchir* and two summit-associated *Cookeolus japonicus*) which showed concentrations of 0.20-0.64 µg g<sup>-1</sup> dw. These species showed high trophic levels of 4 and were all seamount-associated, hence being close to the MAD-Ridge seamount sediments, thus possibly accounting for their higher Hg concentrations compared to epipelagic species. Enhanced Hg bioaccumulation was found in mesopelagic prey species compared to epipelagic ones in several ecosystems (Monteiro et al., 1996; Choy et al., 2009; Choy, 2013; Chouvelon et al., 2012). Authors have reported a four-fold increase in Hg concentrations from epipelagic to mesopelagic species (Monteiro et al., 1996), with seabirds feeding on mesopelagic prey also exhibiting a four-fold increase in Hg levels in breast feathers compared to those feeding on epipelagic prey (Monteiro et al., 1998). The data collected during this study suggest approximately a three-fold increase in mean Hg concentrations from epipelagic to mesopelagic species.

## 4.3 Factors influencing Hg concentrations in micronekton

Body size of organisms in the Mozambique Channel and at Reunion Island and trophic position at MAD-Ridge seamount and the Mozambique Channel were shown to significantly influence Hg concentrations in micronekton. Different marine organisms absorb Hg *via* different pathways, either through adsorption on to the cell membrane and diffusion into cells, or through suspended particles and sediments, through the gills, or from their prey (Bryan et al., 1979). The individuals sampled at the different study sites may show differences in Hg accumulation possibly due to differential uptake and elimination, different trophic relationships, behaviours and habitat uses. Mercury concentrations typically show a positive relationship with fish age and increasing size (Cai et al., 2007; Choy et al., 2009; Hanchet et al., 2012; Boalt et al., 2014; Chen et al., 2014) as a result of longer exposure time

to the trace element (Pellegrini and Barghigiani, 1989), intake rates exceeding excretion rates (Cai et al., 2007; Houssard et al., 2019) and/or a shift in diet (Mason et al., 2000), with larger fishes attaining higher body sizes and feeding at higher trophic levels (Cai et al., 2007). Larger zooplankton types have higher MeHg concentrations than smaller species (Zhang et al., 2020). Micronekton species feeding on larger zooplankton, would thus possibly show higher MeHg concentrations relative to those feeding on smaller zooplankton.

Compared to studies which showed Hg concentrations lower than the detection limit (<0.05).

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μg g<sup>-1</sup> dw) in small-sized mesopelagic fishes sampled in the Sulu and Celebes Seas in the south-western area of the Philippines, only nine among 174 fishes sampled at the four study sites in the Indian Ocean showed Hg concentrations <0.05  $\mu$ g g<sup>-1</sup> dw and  $\delta$ <sup>15</sup>N and TL values from 6.0 to 10.2% and 2.6 to 3.9, respectively. In fact, seven carnivorous fishes (five from MAD-Ridge, one from the Mozambique Channel and one from Reunion Island) showed Hg concentrations >0.5 µg g<sup>-1</sup> dw. These fish include two mesopelagic A. aculeatus (54.4 and 77.3 mm), one bathypelagic Neoscopelus macrolepidotus (46 mm), one seamount-associated Diaphus suborbitalis (81.2 mm), one mesopelagic Astronesthes (122.3 mm), one bathypelagic Stomias longibarbatus (371 mm) and one mesopelagic Sigmops elongatus (173.8 mm). The  $\delta^{15}$ N of these fishes ranged from 9.2 to 11.8%, i.e. from TL 3.6 to 4.4. All other fishes showed Hg concentrations <0.5 µg g<sup>-1</sup> dw, despite some of them being bathypelagic, having high body sizes and  $\delta^{15}N$  values. In addition to habitat range, size and trophic level, some other factors may hence influence Hg concentration in mesopelagic fishes. Small fish such as A. aculeatus previously reported as residents of deep-water layers in the Pacific (Receveur et al., 2020) and sampled in greater proportions below 400 m during both day and night at MAD-Ridge seamount (Annasawmy et al., 2019) may show high Hg concentrations because of their deep habitat range and absence of diel vertical migration. Differences in trace element concentrations were also found between migrant and nonmigrant deep-water mesopelagic fish in the south-western Philippines (Asante et al., 2010). The skin of *A. aculeatus*, which is difficult to dissociate from the tissue during the sampling process, may also be an important site for metal uptake due to their high surface area to body

ratio as shown for other fish species (Afandi et al., 2018), thus contributing to higher overall

428 Hg concentrations.

The two *O. bartramii* specimens sampled at MAD-Ridge and the southern Mozambique Channel were the only squids showing Hg concentrations greater than 0.5 µg g<sup>-1</sup> dw. Squids also showed higher Hg concentrations relative to the fish species Acanthuridae, Monacanthidae and *Stolephorus* sp. off Niolam Island within the Papua New Guinea Province (Brewer et al., 2012). The *O. bartramii* had higher TL of 4.8 and 5.0 than the other sampled micronekton taxa and are known to feed on mesopelagic fish and other cephalopods (Hastie et al., 2009; Coll et al., 2013; Navarro et al., 2013), thus bioaccumulating Hg concentrations from their micronektonic prey. Size and hence age might be a factor influencing Hg concentrations in the *O. bartramii* specimens which had DML of 365 and 490 mm relative to the other smaller sampled squids which ranged in size from 18 mm (*Abraliopsis* sp.) to 163 mm (*Ornithoteuthis volatilis*). Shorter life span of some species may further reduce their exposure to Hg (Pellegrini and Barghigiani, 1989) relative to species having longer life spans and hence potentially showing higher Hg concentrations due to persistent exposure over time.

4.4 Biomagnification of Hg in pelagic nekton assemblages

Biomagnification of Hg along marine food webs has been previously investigated using stable isotope analyses (Asante et al., 2008). Previous studies have shown positive relationships between  $\delta^{13}$ C and  $\delta^{15}$ N values and concentrations of trace elements in micronekton, suggesting biomagnification of these chemicals (Asante et al., 2008, 2010). The

lack of clear relationship between Hg concentrations and  $\delta^{13}$ C values may be attributed to micronekton across the four sites having offshore/pelagic habitats with inshore/coastal/demersal inputs (Goutte et al., 2015; Le Croizier et al., 2019). The positive relationships between Hg levels and stable nitrogen isotope values in micronekton collected at MAD-Ridge seamount and the southern Mozambique Channel, suggests biomagnification of Hg through the food webs that characterise these ecosystems. This might imply that higher trophic mesopelagic organisms retained higher Hg concentrations than lower trophic ones (Asante et al., 2008). Increases in Hg concentrations with trophic position were observed across zooplankton, micronekton and large predators in the North Pacific subtropical gyre (Choy, 2013). Significant positive relationships between Hg concentration and trophic position were also observed in pelagic marine top predators (Storelli et al., 2005; Cai et al., 2007; Bodin et al., 2017) due to organisms feeding at higher trophic positions consuming larger prey with higher body burdens than smaller prey (Watras et al., 1998; Bowles et al., 2001; Cai et al., 2007). The lack of relationship between Hg and  $\delta^{15}$ N values at La Pérouse may be attributed to the complex food webs in oligotrophic tropical ecosystems with variable Hg concentrations as observed in previous tropical ecosystems (Al-Reasi et al., 2007). The length of the studied food chains at La Pérouse, MAD-Ridge and the Mozambique Channel may also explain the difference in Hg biomagnification observed in micronekton between sites. While a two-step (3 trophic levels) pelagic food chain has been observed at La Pérouse, a three-step (4 trophic levels) food chain has been observed at MAD-Ridge and in the Mozambique Channel due to the sampling of micronekton feeding O. bartramii specimens at the two later sites (Annasawmy et al., 2020b). Higher trophic level organisms such as large squids which potentially have high Hg concentrations and possibly account for Hg biomagnification were not sampled during La Pérouse cruise possibly due to their net avoidance abilities and smaller number of trawls conducted relative to MAD-Ridge cruise.

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Previous studies have found differences in the degree of trace metal biomagnification between Clearwater Bay and Butterfly Bay from Hong Kong because of the length of the food webs at these two sites (Cheung and Wang, 2008). Similar to our results, other studies on albacore, yellowfin and bigeye tunas in the western and central Pacific have found that trophic effects on Hg concentrations are of lower importance relative to foraging depth and feeding ecology (Houssard et al., 2019).

## **Limits and perspectives**

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Since research was conducted during a declining phase of productivity in the region (Annasawmy et al., 2019) the full variability in stable isotope and Hg concentrations may not have been captured. This work is the first to investigate Hg concentrations in pelagic nekton organisms at only four sites in the Indian Ocean (two shallow seamounts, the Mascarene shelf and the open ocean). Further studies will be conducted to investigate trace mineral concentrations in pelagic nekton at other sites influenced by riverine input such as the African shelf in the Mozambique Channel and open areas in the north-western and southern Indian Ocean. Additional insights could have been gained with the investigation of Hg concentrations in the water column and the relationship between sedimentary organic matter and Hg of the south-western Indian Ocean. Organisms may also incorporate the isotopic signal and Hg concentrations of their diets at varying rates and within varying tissues in their body (Martínez del Rio et al., 2009; Afandi et al., 2018). The incomplete inclusion of the entire food web at La Pérouse may result in the absence of biomagnification of Hg observed at the seamount. The full variability in Hg concentrations within pelagic nekton assemblages could not be further described due to limited information on Hg concentrations within lower trophic compartments. Future work will investigate the Hg concentrations within various tissues in similar organisms and in lower trophic compartments.

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#### References

Afandi, I., Talba, S., Benhra, A., Benbrahim, S., Chfiri, R., Labonne, M., Masski, H., Laë, R., 523 524 Tito De Morais, L., Bekkali, M., Bouthir, F.Z., 2018. Trace metal distribution in pelagic fish species from the north-west African coast (Morocco). International 525 Aguatic Research 10, 191–205. https://doi.org/10.1007/s40071-018-0192-7 526 Al-Reasi, H.A., Ababneh, F.A., Lean, D.R., 2007. Evaluating mercury biomagnification in 527 fish from a tropical marine environment using stable isotopes ( $\delta^{13}$ C and  $\delta^{15}$ N). 528 529 Environmental Toxicology and Chemistry 26, 1572. https://doi.org/10.1897/06-359R.1 530

Alverson, F.G., 1961. Daylight Surface Occurrence of Myctophid Fishes off the coast of Central America. Pacific Science, 15(3), 35-43.

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- Annasawmy, P., Ternon, J-F., Lebourges-Dhaussy, A., Roudaut, G., Herbette, S., Ménard, F., Cotel., P., Marsac, F., 2020a. 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. https://doi.org/10.1016/j.dsr2.2020.104812
  - Annasawmy, P., Cherel, Y., Romanov, E.V., Le Loch, F., Ménard, F., Ternon, J-F., Marsac, F., 2020b. Stable isotope patterns of micronekton at two shallow seamounts of the south-western Indian Ocean. Deep-Sea Res. II. https://doi.org/10.1016/j.dsr2.2020.104804
- Annasawmy, P., Ternon, J.-F., Cotel, P., Cherel, Y., Romanov, E.V., Roudaut, G.,
  Lebourges-Dhaussy, A., Ménard, F., Marsac, F., 2019. Micronekton distributions and
  assemblages at two shallow seamounts of the south-western Indian Ocean: Insights
  from acoustics and mesopelagic trawl data. Progress in Oceanography 178, 102161.
  https://doi.org/10.1016/j.pocean.2019.102161
- 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
  - Ariza, V. A., 2015. Micronekton diel vertical migration and active flux in the subtropical Northeast Atlantic. Universidad de Las Palmas de Gran Canaria. Doctoral Thesis.
    - Ariza, A., Garijo, J.C., Landeira, J.M., Bordes, F., Hernández-León, S., 2015. Migrant biomass and respiratory carbon flux by zooplankton and micronekton in the subtropical northeast Atlantic Ocean (Canary Islands). Progress in Oceanography 134, 330–342. https://doi.org/10.1016/j.pocean.2015.03.003
    - Asante, K.A., Agusa, T., Kubota, R., Mochizuki, H., Ramu, K., Nishida, S., Ohta, S., Yeh, H., Subramanian, A., Tanabe, S., 2010. Trace elements and stable isotope ratios ( $\delta^{13}$ C and  $\delta^{15}$ N) in fish from deep-waters of the Sulu Sea and the Celebes Sea. Marine Pollution Bulletin 60, 1560–1570. https://doi.org/10.1016/j.marpolbul.2010.04.011
    - Asante, K.A., Agusa, T., Mochizuki, H., Ramu, K., Inoue, S., Kubodera, T., Takahashi, S., Subramanian, A., Tanabe, S., 2008. Trace elements and stable isotopes ( $\delta^{13}$ C and  $\delta^{15}$ N) in shallow and deep-water organisms from the East China Sea. Environmental Pollution 156, 862–873. https://doi.org/10.1016/j.envpol.2008.05.020
- Atkinson, A., Siegel, V., Pakhomov, E.A., Jessopp, M.J., Loeb, V., 2009. A re-appraisal of
   the total biomass and annual production of Antarctic krill. Deep Sea Research Part I:
   Oceanographic Research Papers 56, 727–740.
   https://doi.org/10.1016/j.dsr.2008.12.007
- Bartlett, M.S., 1937. Properties of sufficiency and statistical tests. Proc. R. Soc. Lond. A 160, 268–282. https://doi.org/10.1098/rspa.1937.0109.
- Béhagle, N., du Buisson, L., Josse, E., Lebourges-Dhaussy, A., Roudaut, G., Ménard, F.,
   2014. Mesoscale features and micronekton in the Mozambique Channel: An acoustic
   approach. Deep Sea Research Part II: Topical Studies in Oceanography 100, 164–173.
   https://doi.org/10.1016/j.dsr2.2013.10.024
- Benoit, J.M., Gilmour, C.C., Mason, R.P., 2001. Aspects of bioavailability of mercury for
   methylation cultures of *Desulfobulbus propionicus* (1pr3). Applied and Enviromental
   Microbiology 67(1): 51-58. 10.1128/AEM.67.1.51–58.2001

- Bernal, A., Olivar, M.P., Maynou, F., Fernández de Puelles, M.L., 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. Progress in Oceanography 135, 1–17. https://doi.org/10.1016/j.pocean.2015.03.005
- Birkley, S.-R., Gulliksen, B., 2003. Feeding Ecology in Five Shrimp Species (Decapoda,
   Caridea) from an Arctic Fjord (Isfjorden, Svalbard), with Emphasis on Sclerocrangon
   boreas. Phipps.
- Bloom, N.S., 1992. On the Chemical Form of Mercury in Edible Fish and Marine
   Invertebrate Tissue. Canadian Journal of Fisheries and Aquatic Sciences 49, 1010–
   1017. https://doi.org/10.1139/f92-113
- Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nature Geoscience 6, 879–884. https://doi.org/10.1038/ngeo1918
- Boalt, E., Miller, A., Dahlgren, H., 2014. Distribution of cadmium, mercury, and lead in
   different body parts of Baltic herring (*Clupea harengus*) and perch (*Perca fluviatilis*):
   Implications for environmental status assessments. Marine Pollution Bulletin 78, 130–
   136. https://doi.org/10.1016/j.marpolbul.2013.10.051
- Bodin, N., Lesperance, D., Albert, R., Hollanda, S., Michaud, P., Degroote, M., Churlaud, C.,
   Bustamante, P., 2017. Trace elements in oceanic pelagic communities in the western
   Indian Ocean. Chemosphere 174, 354–362.
   https://doi.org/10.1016/j.chemosphere.2017.01.099
- 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.
   https://doi.org/10.1016/j.aca.2009.03.048
- Bowles, K. C., Apte, S. C., Maher, W. A., Kawei, M., Smith, R., 2001. Bioaccumulation and biomagnification of mercury in lake Murray, Papua New Guinea. Canadian Journal of Fisheries and Aquatic Sciences, 58(5), 888-897.
- Brewer, D.T., Morello, E.B., Griffiths, S., Fry, G., Heales, D., Apte, S.C., Venables, W.N.,
   Rothlisberg, P.C., Moeseneder, C., Lansdell, M., Pendrey, R., Coman, F., Strzelecki,
   J., Jarolimek, C.V., Jung, R.F., Richardson, A.J., 2012. Impacts of gold mine waste
   disposal on a tropical pelagic ecosystem. Marine Pollution Bulletin 64, 2790–2806.
   https://doi.org/10.1016/j.marpolbul.2012.09.009
  - Briand, M.J., Bustamante, P., Bonnet, X., Churlaud, C., Letourneur, Y., 2018. Tracking trace elements into complex coral reef trophic networks. Science of The Total Environment 612, 1091–1104. https://doi.org/10.1016/j.scitotenv.2017.08.257
- 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.
- Bryan, G. W., Waldichuk, M., Pentreath, R.J., Darracott, A., 1979. Bioaccumulation of
   marine pollutants. Philosophical Transactions of the Royal Society of London. B,
   Biological Sciences, 286(1015), 483-505.

612

- Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C., Caurant, F., 2006. Total and organic Hg concentrations in cephalopods from the North Eastern Atlantic waters: Influence of geographical origin and feeding ecology. Science of The Total Environment 368, 585–596. https://doi.org/10.1016/j.scitotenv.2006.01.038
- Cai, Y., Rooker, J.R., Gill, G.A., Turner, J.P., 2007. Bioaccumulation of mercury in pelagic
   fishes from the northern Gulf of Mexico. Canadian Journal of Fisheries and Aquatic
   Sciences 64, 458–469. https://doi.org/10.1139/f07-017
- Calatayud, M., Devesa, V., Virseda, J.R., Barberá, R., Montoro, R., Vélez, D., 2012. Mercury and selenium in fish and shellfish: Occurrence, bioaccessibility and uptake by Caco-2

```
    cells. Food and Chemical Toxicology 50, 2696–2702.
    https://doi.org/10.1016/j.fct.2012.05.028
```

- 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. Progress in Oceanography 130, 172–187.
   https://doi.org/10.1016/j.pocean.2014.11.003
- Chai, H.-J., Chan, Y.-L., Li, T.-L., Chen, Y.-C., Wu, C.-H., Shiau, C.-Y., Wu, C.-J., 2012.
   Composition characterization of Myctophids (*Benthosema pterotum*): Antioxidation
   and safety evaluations for Myctophids protein hydrolysates. Food Research
   International 46, 118–126. https://doi.org/10.1016/j.foodres.2011.12.008
  - Chakraborty, P., Babu, P.V.R., 2015. Environmental controls on the speciation and distribution of mercury in surface sediments of a tropical estuary, India. Marine Pollution Bulletin 95, 350-357. http://dx.doi.org/10.1016/j.marpolbul.2015.02.035
- Chakraborty, P., Mason, R.P., Jayachandran, S., Vudamala, K., Armoury, K., Sarkar, A.,
   Chakraborty, S., Bardhan, P., Naik, R., 2016. Effects of bottom water oxygen
   concentrations on mercury distribution and speciation in sediments below the oxygen
   minimum zone of the Arabian Sea. Marine Chemistry 186, 24-32.
   http://dx.doi.org/10.1016/j.marchem.2016.07.005
  - Chakraborty, P., Jayachandran, S., Lekshmy, J., Padalkar, P., Sitlhou, L., Chennuri, K., Shetye, S., Sardar, A., Khandeparker, R., 2019. Seawater intrusion and resuspension of surface sediment control mercury (Hg) distribution and its bioavailability in water column of a monsoonal estuarine system. Science of the Total Environment 660, 1441-1448. https://doi.org/10.1016/j.scitotenv.2018.12.477
    - Chen, C.-Y., Lai, C.-C., Chen, K.-S., Hsu, C.-C., Hung, C.-C., Chen, M.-H., 2014. Total and organic mercury concentrations in the muscles of Pacific albacore (*Thunnus alalunga*) and bigeye tuna (*Thunnus obesus*). Marine Pollution Bulletin 85, 606–612. https://doi.org/10.1016/j.marpolbul.2014.01.039
  - Chennuri, K., Chakraborty, P., Jayachandran, S., Mohakud, S.K., Ishita, I., Ramteke, D., Padalkar, P.P., Babu, P.C., Babu, K.R., 2020. Operationally defined mercury (Hg) species can delineate Hg bioaccumulation in mangrove sediment systems: A case study. Science of the Total Environment 701, 134842. https://doi.org/10.1016/j.scitotenv.2019.134842
    - Cheung, M.S., Wang, W.-X., 2008. Analyzing biomagnification of metals in different marine food webs using nitrogen isotopes. Marine Pollution Bulletin 56, 2082–2088. https://doi.org/10.1016/j.marpolbul.2008.09.004
- Chouvelon, T., Brach-Papa, C., Auger, D., Bodin, N., Bruzac, S., Crochet, S., Degroote, M.,
   Hollanda, S.J., Hubert, C., Knoery, J., Munschy, C., Puech, A., Rozuel, E., Thomas,
   B., West, W., Bourjea, J., Nikolic, N., 2017. Chemical contaminants (trace metals,
   persistent organic pollutants) in albacore tuna from western Indian and south-eastern
   Atlantic Oceans: Trophic influence and potential as tracers of populations. Science of
   The Total Environment 596–597, 481–495.
   https://doi.org/10.1016/j.scitotenv.2017.04.048
- Chouvelon, T., Spitz, J., Caurant, F., Mèndez-Fernandez, P., Autier, J., Lassus-Débat, A.,
   Chappuis, A., Bustamante, P., 2012. Enhanced bioaccumulation of mercury in deep sea fauna from the Bay of Biscay (north-east Atlantic) in relation to trophic positions
   identified by analysis of carbon and nitrogen stable isotopes. Deep Sea Research Part
   I: Oceanographic Research Papers, 65, 113-124.
- Choy, C., 2013. Pelagic food web connectivity in the North Pacific Subtropical Gyre: a
   combined perspective from multiple biochemical tracers and diet. University of
   Hawaii, Manoa. Doctoral Thesis.

- Choy, C.A., Popp, B.N., Kaneko, J.J., Drazen, J.C., 2009. The influence of depth on mercury
   levels in pelagic fishes and their prey. Proceedings of the National Academy of
   Sciences 106, 13865–13869. https://doi.org/10.1073/pnas.0900711106
- Clarke, M.R., Lu, C.C., 1975. Vertical distribution of cephalopods at 18°N 25°W in the North Atlantic. Journal of the Marine Biological Association of the United Kingdom 55, 165. https://doi.org/10.1017/S0025315400015812
- Coll, M., Navarro, J., Olson, R.J., Christensen, V., 2013. Assessing the trophic position and
   ecological role of squids in marine ecosystems by means of food-web models. Deep
   Sea Research Part II: Topical Studies in Oceanography 95, 21–36.
   https://doi.org/10.1016/j.dsr2.2012.08.020
- 688 Compeau, G.C., Bartha, R., 1985. Sulfate-Reducing Bacteria: Principal Methylators of 689 Mercury in Anoxic Estuarine Sediment. Applied and Environmental Microbiology 690 50(2), 498-502.
- Cossa, D., Thibaud, Y., Roméo, M., Gnassia-Barelli, M., 1990. Le mercure en milieu marin.
   Biogéochime et Ecotoxicologie. Rapports scientifiques et techniques de l'IFREMER,
   Nº 19.
- Cossa, D., Averty, B., Pirrone, N., 2009. The origin of methylmercury in open Mediterranean
   waters. Limnology and Oceanography 54, 837–844.
   https://doi.org/10.4319/lo.2009.54.3.0837
- Dalpadado, P., Gjøsæter, J., 1988. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Mar. Biol. 99, 555–567.
- 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 Research Part I: Oceanographic Research Papers 56, 232–
   250. https://doi.org/10.1016/j.dsr.2008.09.007
- Del Giorgio, P.A., Duarte, C.M., 2002. Respiration in the open ocean. Nature 420, 379–384.
- Ferriss, B. E., Essington, T. E., 2014. Does trophic structure dictate mercury concentrations
   in top predators? A comparative analysis of pelagic food webs in the Pacific Ocean.
   Ecological modelling, 278, 18-28.
- Filmalter, J. D., Cowley, P. D., Potier, M., Ménard, F., Smale, M. J., Cherel, Y., Dagorn, L.,
   2017. Feeding ecology of silky sharks *Carcharhinus falciformis* associated with
   floating objects in the western Indian Ocean. Journal of Fish Biology, 90, 1321–1337.
   https://doi.org/10.1111/jfb.13241
- Fitzgerald, W. F., Lamborg, C. H., Hammerschmidt, C. R., 2007. Marine biogeochemical cycling of mercury. Chemical Reviews, 107(2), 641–662. https://doi.org/10.1021/cr050353m
- Foxton, P., Roe, H.S.J., 1974. Observations on the nocturnal feeding of some mesopelagic decapod Crustacea. Mar. Biol. 28, 37–49.
- Gilmour, C.C., Podar, M., Bullock, A.L., Graham, A.M., Brown, S.D., Somenahally, A.C.,
   Johs, A., Hurt, Jr., R.A., Bailey, K.L., Elias, D.A., 2013. Mercury Methylation by
   Novel Microorganisms from New Environments. Environmental Science &
   Technology 47, 11810-11820.
- Goutte, A., Cherel, Y., Churlaud, C., Ponthus, J-P., Massé, G., Bustamante, P., 2015. Trace elements in Antarctic fish species and the influence of foraging habitats and dietary habits on mercury levels. Science of the Total Environment 538, 743-749. http://dx.doi.org/10.1016/j.scitotenv.2015.08.103
- Gray, J.S., 2002. Biomagnification in marine systems: the perspective of an ecologist. Marine Pollution Bulletin 45, 46–52. https://doi.org/10.1016/S0025-326X(01)00323-X

- Gjøsæter, J. 1984. Mesopelagic fish, a large potential resource in the Arabian Sea. Deep Sea Research Part A. Oceanographic Research Papers, 31(6-8), 1019-1035.
- Gjøsæter, J. 1977. Aspects of the distribution and ecology of the Myctophidae from the
   western and northern Arabian Sea. Department of Fisheries Biology, University of
   Bergen.
- 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. https://doi.org/10.1017/S0954102096000053
- Hanchet, S.M., Tracey, D., Dunn, A., Horn, P., Smith, N., 2012. Mercury concentrations of
   two toothfish and three of its prey species from the Pacific sector of the Antarctic.
   Antarctic Science 24, 34–42. https://doi.org/10.1017/S0954102011000654
- Hastie, L. C., Pierce, G. J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., Robin, J. P.,
   2009. Cephalopods in the north-eastern Atlantic: species, biogeography, ecology,
   exploitation and conservation. Oceanography and marine biology, 47(80), 111-190.
- Heimbürger, L-E., Cossa, D., Marty, J-C., Migon, C., Averty, B., Dufour, A., Ras, J., 2010.
   Methyl mercury distributions in relation to the presence of nano- and
   picophytoplankton in an oceanic water column (Ligurian Sea, North-western
   Mediterranean). Geochimica et Cosmochimica Acta 74(19): 5549-5559.
   http://dx.doi.org/10.1016/j.gca.2010.06.036
- 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.

751

760

761

- Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63, 786–798.
- Hopkins, T.L., Flock, M.E., Gartner Jr., J.V., Torres, J.J., 1994. Structure and trophic ecology of a low latitude midwater decapod and mysid assemblage. Mar. Ecol. Prog. Ser. 109, 143–156.
- Houssard, P., Point, D., Tremblay-Boyer, L., Allain, V., Pethybridge, H., Masbou, J., Ferriss,
   B. E., Baya, P. A., Lagane, C., Menkes, C. E., Letourneur, Y., Lorrain, A., 2019. A
   model of mercury distribution in tuna form the Western and Central Pacific Ocean:
   Influence of Physiology, Ecology and Environmental factors. Environ. Sci. Technol.
   53: 1422-1431. DOI: 10.1021/acs.est.8b06058
  - 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 Research Part I: Oceanographic Research Papers 93, 104–116. https://doi.org/10.1016/j.dsr.2014.07.002
- Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A.,
   Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L.,
   Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic
   efficiency in the open ocean. Nature Communications 5.
   https://doi.org/10.1038/ncomms4271
- Jena, B., Sahu, S., Avinash, K., Swain, D., 2013. Observation of oligotrophic gyre variability
   in the south Indian Ocean: Environmental forcing and biological response. Deep Sea
   Research Part I: Oceanographic Research Papers 80, 1–10.
   https://doi.org/10.1016/j.dsr.2013.06.002
- Kojadinovic, J., Jackson, C. H., Cherel, Y., Jackson, G. D., Bustamante, P., 2011. Multielemental concentrations in the tissues of the oceanic squid *Todarodes filippovae* from Tasmania and the southern Indian Ocean. Ecotoxicology and Environmental Safety, 74(5), 1238–1249. https://doi.org/10.1016/j.ecoenv.2011.03.015

- 777 Lambert, C., Mannocci, L., Lehodey, P., Ridoux, V., 2014. Predicting Cetacean Habitats from Their Energetic Needs and the Distribution of Their Prey in Two Contrasted 778 779 Tropical Regions. PLoS ONE. 9: e105958. https://doi.org/10.1371/journal.pone.0105958 780
- Laurier, F. J. G., Mason, R. P., Gill, G. A., Whalin, L., 2004. Mercury distributions in the 781 North Pacific Ocean—20 years of observations. Marine Chemistry, 90(1-4), 3-19. 782
- 783 Lavoie, R., Jardine, T. D., Chumchall, M. M., Kidd, K. A., Campbell, L. M., 2013. Biomagnification rate of mercury in aquatic food webs: a world-wide meta-analysis. 784 Environmental Science & Technology, 47(23), 13385–13394. 785
- 786 Le Croizier, G., Schaal, G., Point, D., Le Loc'h, F., Machu, E., Fall, M., Munaron, J.-M., Boyé, A., Walter, P., Laë, R., Tito De Morais, L., 2019. Stable isotope analyses 787 revealed the influence of foraging habitat on mercury accumulation in tropical coastal 788 marine fish. Science of The Total Environment 650, 2129–2140. 789 https://doi.org/10.1016/j.scitotenv.2018.09.330 790
- Lebourges-Dhaussy, A., Marchal, É., Menkès, C., Champalbert, G., Biessy, B., 2000. 791 Vinciguerria nimbaria (micronekton), environment and tuna: their relationships in the 792 793 Eastern Tropical Atlantic. Oceanologica Acta 23, 515–528. https://doi.org/10.1016/S0399-1784(00)00137-7 794
- LeMoigne, F. A. C. 2019., Pathways of organic carbon downward transport by the oceanic 795 796 biological carbon pump. Front. Mar. Sci. 6(634): 1-8. doi: 10.3389/fmars.2019.00634 797

800

801 802

803

804

805

806

807

- Longhurst, A., 1998. Ecological Geography of the Sea. Academic Press, San Diego, p. 398.
- Marchal, E., Lebourges, A., 1996. Acoustic evidence for unusual diel behaviour of a mesopelagic fish (Vinciguerria nimbaria) exploited by tuna. ICES Journal of Marine Science, 53(2), 443-447.
  - 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 in the vicinity of La Pérouse, a shallow seamount in the southwestern Indian Ocean. Deep Sea Research Part II: Topical Studies in Oceanography, 176, 104806. https://doi.org/10.1016/j.dsr2.2020.104806
  - 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. https:// doi.org/10.1111/j.1469-185X.2008.00064.x.
- Mason, R.P., Laporte, J.-M., Andres, S., 2000. Factors Controlling the Bioaccumulation of 809 Mercury, Methylmercury, Arsenic, Selenium, and Cadmium by Freshwater 810 Invertebrates and Fish. Archives of Environmental Contamination and Toxicology 38, 811 812 283–297. https://doi.org/10.1007/s002449910038
- Mason, R.P., Choi, A.L., Fitzgerald, W.F., Hammerschmidt, C.R., Lamborg, C.H., 813 Soerensen, A. L., Sunderland, E.M., 2012 Mercury biogeochemical cycling in the 814 815 ocean and policy implications. Environmental Research 119, 101-117. http://dx.doi.org/10.1016/j.envres.2012.03.013 816
- Mason, R.P., Fitzgerald, W.F., 1993. The distribution and biogeochemical cycling of mercury 817 in the equatorial Pacific Ocean. Deep Sea Research Part I: Oceanographic Research 818 Papers 40, 1897–1924. https://doi.org/10.1016/0967-0637(93)90037-4 819
- 820 Mauchline, J., 1959. The biology of the euphausiid Crustacean, Meganyctiphanes norvegica (M. Sars). Proc. Roy. Soc. Edinb. B Biol. Sci. 67 (2), 141–179. 821
- Michener, R.H., Kaufman, L., 2007. Stable isotope ratios as tracers in marine food webs: an 822 update. In: Michener, R.H., Lajtha, K. (Eds.), Stable Isotopes in Ecology and 823 824 Environmental Science, second ed. Blackwell, Malden, MA, pp. 238–282. 2007.
- Minagawa, M., Wada, E., 1984. Stepwise enrichment of <sup>15</sup>N along food chains: further 825 evidence and the relation between  $\delta^{15}N$  and animal age. Geochem. Cosmochim. Acta 826

827 48, 1135–1140.

850

851 852

- Monteiro, L., Granadeiro, J., Furness, R., 1998. Relationship between mercury levels and diet in Azores seabirds. Marine Ecology Progress Series 166, 259–265.

  https://doi.org/10.3354/meps166259
- Monteiro, L., Costa, V., Furness, R., Santos, R., 1996. Mercury concentrations in prey fish indicate enhanced bioaccumulation in mesopelagic environments. Marine Ecology Progress Series 141, 21–25. https://doi.org/10.3354/meps141021
- Navarro, J., Coll, M., Somes, C.J., Olson, R.J., 2013. Trophic niche of squids: Insights from isotopic data in marine systems worldwide. Deep Sea Research Part II: Topical Studies in Oceanography 95, 93–102. https://doi.org/10.1016/j.dsr2.2013.01.031
- Nigmatullin, Ch. M, 2004. Estimation of biomass, production and fishery potential of *Ommastrephid* squids in the World Ocean and problems of their fishery forecasting.

  ICES CM 2004 / CC: 06-14 p.
- Noyon, M., Morris, T., Walker, D., Huggett, J., 2019. Plankton distribution within a young cyclonic eddy off south-western Madagascar. Deep Sea Res. II. 166, 141-150. https://doi.org/10.1016/j.dsr2.2018.11.001.
- Padalkar, P.P., Chakraborty, P., Chennuri, K., Jayachandran, S., Sitlhou, L., Nanajkar, M.,
  Tilvi, S., Singh, K., 2019. Molecular characteristics of sedimentary organic matter in
  controlling mercury (Hg) and elemental mercury (Hg<sup>0</sup>) distribution in tropical
  estuarine sediments. Science of the Total Environment 668, 592-601.
  https://doi.org/10.1016/j.scitotenv.2019.02.353
- 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.
  - Parks, J.M., Johs, A., Podar, M., Bridou, R., Hurt Jr., R.A., Smith, S.D., Tomanicek, S.J., Qian, Y., Brown, S.D., Brandt, C.C., Palumbo, A.V., Smith, J.C., Wall, J.D., Elias, D.A., Liang, L., 2013. The Genetic Basis for Bacterial Mercury Methylation. Science 339, 1332-1335.
- Pearcy, W.G., Krygier, E.E., Mesecar, R., Ramsey, F., 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep Sea Research 24, 223–245. https://doi.org/10.1016/S0146-6291(77)80002-7
- Pellegrini, D., Barghigiani, C., 1989. Feeding behaviour and mercury content in two flat fish in the northern Tyrrhenian sea. Marine Pollution Bulletin 20, 443–447. https://doi.org/10.1016/0025-326X(89)90064-7
- Pinet, P., Jaquemet, S., Phillips, R. A., Le Corre, M., 2012. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel.

  Animal Behaviour, 83(4), 979-989. https://doi.org/10.1016/j.anbehav.2012.01.019
- Post, D.M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., Montana, C. G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, 152(1), 179-189.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: Models, Methods, and Assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
- 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 Research 83, 60–72. https://doi.org/10.1016/j.fishres.2006.08.020
- Proud, R., Handegard, N. O., Kloser, R. J., Cox, M. J., Brierley, A. S., 2018. From
   siphonophores to deep scattering layers: uncertainty ranges for the estimation of
   global mesopelagic fish biomass. ICES Journal of Marine Science. 76(3): 718-733.
   https://doi.org/10.1093/icesjms/fsy037

- Queirós, J. P., Bustamante, P., Cherel, Y., Coelho, J. P., Seco, J., Roberts, J., Pereira, E.,
  Xavier, J. C., 2020. Cephalopod beak sections used to trace mercury levels throughout
  the life of cephalopods: The giant warty squid *Moroteuthopsis longimana* as a case
  study. Marine Environmental Research, 161.
  https://doi.org/10.1016/j.marenvres.2020.105049
- Ranchou-Peyruse, M., Monperrus, M., Bridou, R., Duran, R., Amouroux, D., Salvado, J.C.,
   Guyoneaud, R., 2009. Overview of Mercury Methylation Capacities among
   Anaerobic Bacteria Including Representatives of the Sulphate-Reducers: Implications
   for Environmental Studies. Geomicrobiology Journal 26(1): 1-8. DOI:
   10.1080/01490450802599227
- Receveur, A., Vourey, E., Lebourges-Dhaussy, A., Menkes, C., Ménard, F., Allain, V., 2020.
   Biogeography of micronekton assemblages in the Natural Park of the Coral Sea.
   Frontiers in Marine Science, 7(449), 1–20. https://doi.org/10.3389/fmars.2020.00449
  - Robison, B.H., 1984. Herbivory by the myctophid fish *Ceratoscopelus warmingii*. Marine Biology 84, 119–123. https://doi.org/10.1007/BF00392995

891

892

893

894

895 896

897

898 899

900

901

902

903

904 905

906

907

908

909

914

- Romanov, E. V, Nikolic, N., Dhurmeea, Z., Bodin, N., Puech, A., Norman, S., Hollanda, S., Bourjea, J., West, W., Potier, M., 2020. Trophic ecology of albacore tuna (*Thunnus alalunga*) in the western tropical Indian Ocean and adjacent waters. Marine and Freshwater Research, 71(11), 1517–1542. https://doi.org/10.1071/MF19332
- 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. https://doi.org/10.1002/lno.11128.
- Rubenstein, D.R., Hobson, K.A., 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol. Evol. 19 (5), 256–263.
- Ryan, C., McHugh, B., Trueman, C.N., Harrod, C., Berrow, S.D., O'Connor, I., 2012. Accounting for the effects of lipids in stable isotope (δ<sup>13</sup>C and δ<sup>15</sup>N values) analysis of skin and blubber of balaenopterid whales: Lipid extraction in stable isotope analysis of whale skin and blubber. Rapid Communications in Mass Spectrometry 26, 2745–2754. https://doi.org/10.1002/rcm.6394
- Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611. https://doi.org/10.2307/2333709.
- Smith, M.M., Heemstra, P.C., 1986. Smith's Sea Fishes. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, p. 1047.
- Storelli, M.M., Giacominelli-Stuffler, R., Storelli, A., Marcotrigiano, G.O., 2005.
   Accumulation of mercury, cadmium, lead and arsenic in swordfish and bluefin tuna
   from the Mediterranean Sea: A comparative study. Marine Pollution Bulletin 50,
   1004–1007. https://doi.org/10.1016/j.marpolbul.2005.06.041
  - Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. J. Fish. Biol. 83, 1508–1527. https://doi.org/10.1111/jfb.12263.
- Tanaka, H., Ohshimo, S., Sassa, C., Aoki, I., 2007. Feeding Habits of Mesopelagic Fishes off the Coast of Western Kyushu. PICES 16th: Bio, Japan, p. 4200, 1st November.
- 918 Tew-Kai, E., Marsac, F., 2009. Patterns of variability of sea surface chlorophyll in the 919 Mozambique Channel: a quantitative approach. J. Mar. Syst. 77 (1–2), 77–88. 920 https://doi.org/10.1016/j.jmarsys.2008.11.007.
- Topping, G., Davies, I.M., 1981. Methylmercury production in the marine water column.
  Nature 290, 243–244. https://doi.org/10.1038/290243a0
- van der Spoel, S., Bleeker, J., 1991. Distribution of Myctophidae (pisces, myctophiformes) during the four seasons in the mid north atlantic. Contrib. Zool. 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.

Vianello, P., Ternon, J-F., Demarcq, H., Herbette, S., Roberts, M.J., 2020. Ocean currents
 and gradients of surface layer properties in the vicinity of the Madagascar Ridge
 (including seamounts) in the South West Indian Ocean. Deep Sea Res II, 176, 104816.
 https://doi.org/10.1016/j.dsr2.2020.104816

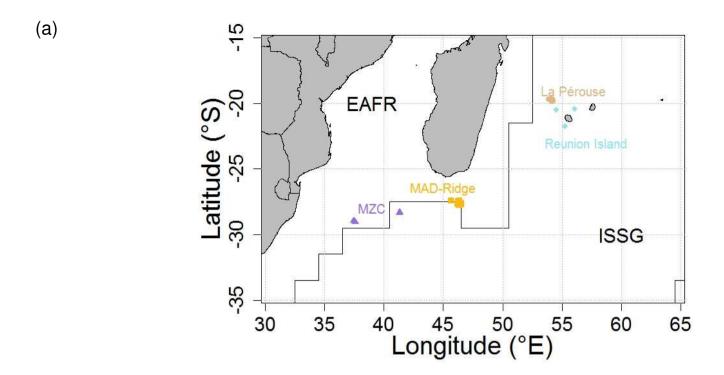
Watras, C.J., Back, R.C., Halvorsen, S., Hudson, R.J.M., Morrison, K.A., Wente, S.P., 1998.
 Bioaccumulation of mercury in pelagic freshwater food webs. Science of The Total
 Environment 219, 183–208. https://doi.org/10.1016/S0048-9697(98)00228-9

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

Zhang, Y., Soerensen, A. L., Schartup, A. T., Sunderland, E. M., 2020. A global model for methylmercury formation and uptake at the base of marine food webs. Global Biogeochemical Cycles, 34(2), e2019GB006348.

## List of figures

- Fig. 1(a) Map of the south-western Indian Ocean showing the trawl stations conducted at two
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- 948 delimited by black solid lines and are labelled as EAFR (East African Coastal Province) and
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- 950 landmasses are shown in grey. A 3D-bathymetry of (b) La Pérouse and (c) MAD-Ridge
- 951 seamounts. Colour bar represents the depth (m) below the sea surface.
- 952 Fig. 2(a) Averaged satellite image of sea surface chlorophyll a concentrations from
- 953 18/09/2016 to 07/12/2016 at the La Pérouse and MAD-Ridge seamounts (represented by
- black star symbols) in the south-western Indian Ocean. Colour bar indicates the surface mean
- 955 concentrations in mg m<sup>-3</sup>. (b) Averaged mean sea level anomaly (MSLA) map, with La
- 956 Pérouse and MAD-Ridge seamounts shown as black star symbols, and dated 14-23
- November 2016. Colour bar indicates the SLA in cm, with positive SLA (red) and negative
- 958 SLA (blue).
- 959 Fig. 3 Boxplots of mercury (Hg) concentrations ( $\mu g \ g^{-1} \ dw$ ) in (a) the most common
- 960 crustacean and fish families from the study sites (La Pérouse, n= 32; MAD-Ridge, n= 72;
- 961 Mozambique Channel-MZC, n= 28; Reunion Island, n= 40), (b) micronekton from all study
- sites, (c) the broad categories (Crustaceans, Fishes and Squids), (d) selected taxa according to
- the minimum and maximum habitat ranges of the identified species (Epipelagic-Mesopelagic,
- n= 9; Mesopelagic, n= 178; Mesopelagic-Bathypelagic, n= 79; Mesopelagic-Benthopelagic,
- 965 n= 3), (e) selected taxa according to feeding mode (carnivorous and omnivorous) from the
- 966 four study sites. The median (thick black line in box plots), interquartile range (the lower and
- 967 upper boundaries), the spread (thin lines extending from box plots) and outliers (black stars)
- 968 are shown.
- 969 Fig. 4 Mercury (Hg) concentrations (µg g<sup>-1</sup> dw) in selected taxa vs body size (abdomen and
- 970 carapace length for crustaceans, standard length for fishes and dorsal mantle length for
- 971 squids) in mm, from the different study sites (La Pérouse, MAD-Ridge, Mozambique
- 972 Channel, and Reunion Island). The data from Mozambique Channel and Reunion Island fit a
- 973 linear curve (regression equations are given) but no relationship were found between Hg
- 974 concentrations and nekton body size at La Pérouse and MAD-Ridge seamounts.
- 975 Fig. 5 Boxplots of  $\delta^{15}$ N and  $\delta^{13}$ C stable isotope values in selected taxa from the study sites
- 976 (La Pérouse, n= 30; MAD-Ridge, n= 97; Mozambique Channel-MZC, n= 30). The median
- 977 (thick black line in box plots), mean (diamond symbols), interquartile range (the lower and
- 978 upper boundaries), the spread (thin lines extending from box plots) and outliers (red stars) are
- 979 shown.
- 980 Fig. 6 Mercury (Hg) concentrations ( $\mu g \, g^{-1} \, dw$ ) in selected taxa  $vs \, \delta^{13}C$  and  $\delta^{15}N$  stable
- 981 isotope values (%0) from the study sites (La Pérouse, MAD-Ridge and Mozambique
- 982 Channel). The data ( $\delta^{15}N$  values) from MAD-Ridge and the Mozambique Channel fit
- 983 exponential curves. No significant relationships were found between Hg concentrations and
- 984  $\delta^{13}$ C values at La Pérouse, MAD-Ridge seamounts and the Mozambique Channel, and
- 985 between Hg and  $\delta^{15}$ N values at La Pérouse.



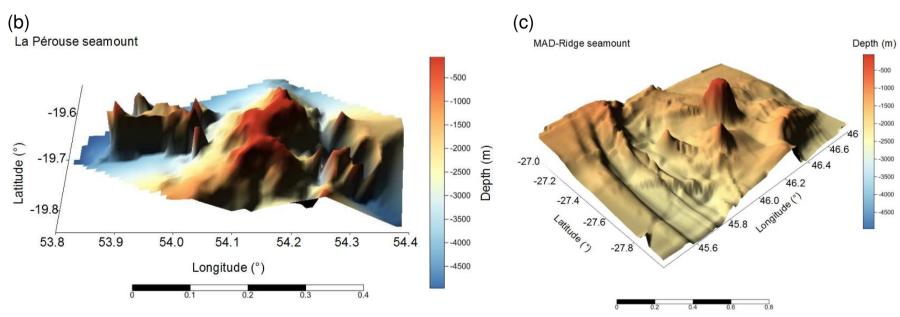


Figure 1

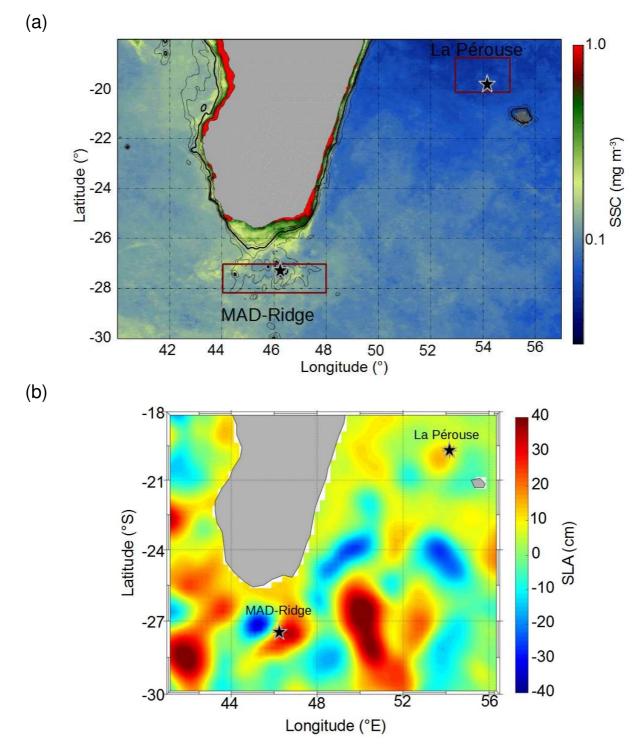


Figure 2

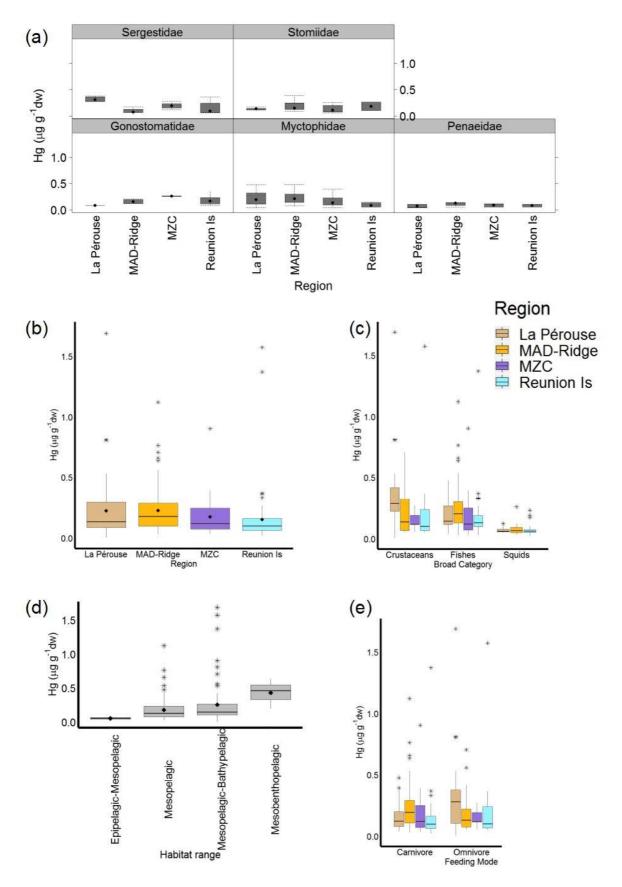


Figure 3

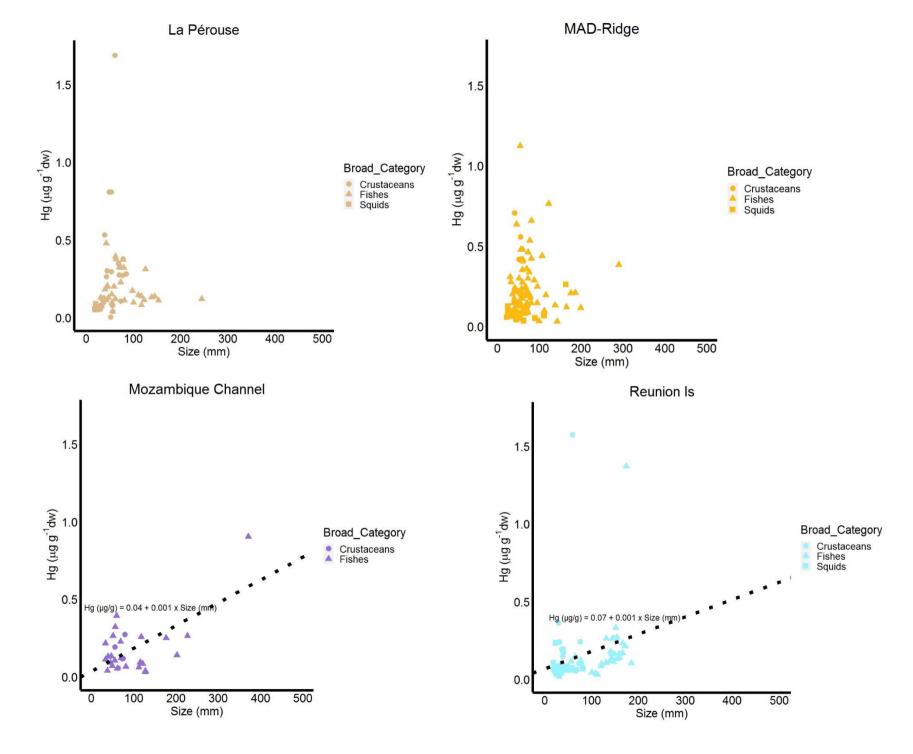


Figure 4

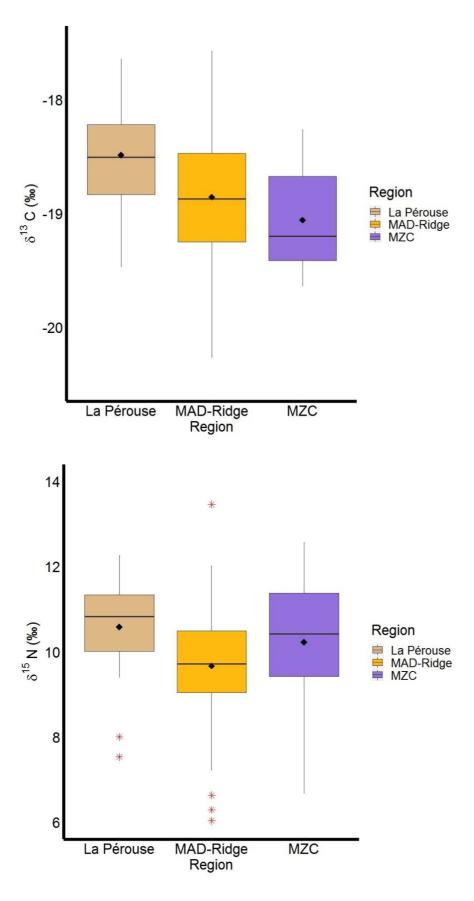


Figure 5

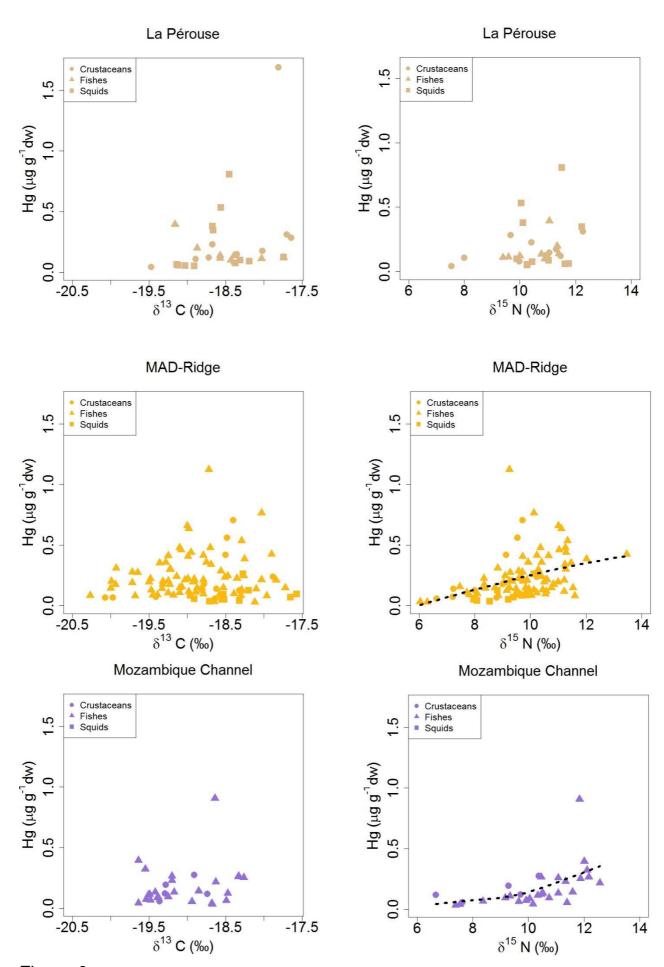


Figure 6

Table 1. Mean body length (mm) of crustaceans (abdomen and carapace length); squids (dorsal mantle length); fishes (standard length), total number of specimens (n), habitat range and feeding mode obtained from literature,  $\delta^{15}N$  and  $\delta^{13}C$  (%o), mean mercury (Hg) concentrations (µg g<sup>-1</sup> dw) and mean estimated trophic level (Mean TL) for the species or taxa on which stable isotope analyses were performed at La Pérouse (ISSG) and MAD-Ridge (EAFR) seamounts, the south-western Mozambique Channel (MZC) and Reunion Island. Values are mean  $\pm$  standard deviation.

Order, Suborder, Infraorder, Superfamily	Family / Species	Habitat	Feeding Mode	Region	Trawl No.	n	Size range (mm)	Mean Size (mm)	Mean δ <sup>15</sup> N (‰)	Mean δ <sup>13</sup> C (‰)	Mean Hg (μg g <sup>-1</sup> dw)	Mean TL
Crustaceans												
Decapoda												
Pleocyemata	Oplophoridae	Mesopelagic	Omnivore	La Pérouse	1, 7	8	39-61	$49.3 \pm 7.03$	$10.9 \pm 0.79$	-18.3 ± 0.41	$0.59 \pm 0.53$	$3.8 \pm 0.25$
Caridea		- Bathypelagic										
				MAD-Ridge	1, 2, 5	4	41-67	$53.6 \pm 10.7$	$9.7 \pm 0.46$	$-18.3 \pm 0.29$	$0.48 \pm 0.20$	$3.7 \pm 0.14$
				Reunion Is	1	4	31-59	$41.4 \pm 12.3$			$0.54 \pm 0.69$	
	Pasiphaeidae											
	Pasiphaea spp.	Mesopelagic	Omnivore	La Pérouse	9	2	56-85	$70.4 \pm 20.5$	$9.8 \pm 0.23$	$-18.0 \pm 0.53$	$0.18 \pm 0.14$	$3.4 \pm 0.07$
		- Bathypelagic										
Dendrobranchiata Penaeoidea	Penaeidae											
	Funchalia sp.	Mesopelagic	Omnivore	La Pérouse	8	2	56-74	$64.8 \pm 12.3$	$7.8 \pm 0.33$	$-19.2 \pm 0.41$	$0.07\pm0.05$	$2.8 \pm 0.10$
		- Bathypelagic										
				MAD-Ridge	5, 6	3	54-74	$66.4 \pm 10.7$	$7.3 \pm 0.68$	$-18.5 \pm 0.18$	$0.11 \pm 0.04$	$3.0 \pm 0.21$
				MZC	21	2	63-74	$68.6 \pm 7.42$	$7.2 \pm 0.68$	-19.1 ± 0.44	$0.09 \pm 0.04$	$2.9 \pm 0.21$
				Reunion Is	1	4	67-79	$71.7 \pm 5.16$			$0.08 \pm 0.02$	
Sergestoidea	Sergestidae	Mesopelagic	Omnivore	La Pérouse	2	4	68-78	73.5 ± 5.21	11.2 ± 1.50	-18.7 ± 0.01	$0.32 \pm 0.05$	$3.8 \pm 0.47$

MAD-Ridge	2	4	33-79	$50.8 \pm 19.4$	$8.3 \pm 0.82$	$-19.6 \pm 0.59$	$0.09 \pm 0.06$	$3.3 \pm 0.26$
MZC	18	3	56-79	$69.9 \pm 12.6$	$9.8 \pm 0.54$	$-19.2 \pm 0.22$	$0.20\pm0.08$	$3.7 \pm 0.17$
Reunion Is	1	5	30-76	$50.5 \pm 18.1$			$0.17 \pm 0.13$	

Order	Family / Species	Habitat	Feeding Mode	Region	Trawl No.	n	Size range (mm)	Mean Size (mm)	Mean δ <sup>15</sup> N (‰)	Mean δ <sup>13</sup> C (%)	Mean Hg (µg g <sup>-1</sup> dw)	Mean TL (TPA model)
Squids												
Oegopsida	Enoploteuthidae	Mesopelagic-	Carnivore	MAD-Ridge	11	2	22-46	34.1 ± 16.8	$8.0 \pm 0.06$	-18.6 ± 0.42	$0.05 \pm 0.01$	$3.2 \pm 0.02$
		Bathypelagic		Reunion Is	1, 3	7	21-39	$27.2 \pm 6.51$			$0.09 \pm 0.05$	
	Abralia sp.	Mesopelagic	Carnivore	Reunion Is	3, 5	4	20-30	$26.4 \pm 4.6$			$0.06 \pm 0.01$	
	Abraliopsis sp.	Mesopelagic- Bathypelagic	Carnivore	La Pérouse	3, 4, 6	11	18-36	28.1 ± 6.19	$10.5 \pm 0.45$	-18.4 ± 0.48	$0.07 \pm 0.02$	3.6 ± 0.14
				MAD-Ridge	2, 9, 10	4	25-35	$29.2 \pm 4.95$	$9.5 \pm 0.48$	$-18.3 \pm 0.59$	$0.10\pm0.02$	$3.6 \pm 0.15$
				Reunion Is	1	1	29.2	29.2			0.06	
	Histioteuthidae											
	Histioteuthis spp.	Mesopelagic	Carnivore	La Pérouse	9	2	28.9-29.4	$29.2 \pm 0.35$	$11.7 \pm 0.10$	$-19.1 \pm 0.01$	$0.06 \pm 0.002$	$4.0 \pm 0.03$
				Reunion Is	1, 3	4	19-47	$35.0 \pm 14.6$			$0.08 \pm 0.02$	
	Ommastrephidae											
	Ornithoteuthis volatilis	Mesopelagic	Carnivore	MAD-Ridge	12, 14, 16	4	45-163	$90.1 \pm 52.2$	$9.0 \pm 0.93$	$-18.5 \pm 0.18$	$0.10 \pm 0.11$	$3.5 \pm 0.29$
	Sthenoteuthis oualaniensis	Mesopelagic	Carnivore	Reunion Is	1	3	33-40	$36.5 \pm 3.5$			$0.09 \pm 0.08$	
	Ommastrephes bartramii	Mesopelagic	Carnivore	MAD-Ridge	1	1		364.8	13.2	-17.4	0.82	4.8
				MZC	20	1		489.8	13.8	-17.3	0.92	5.0
	Eucleoteuthis luminosa	Mesopelagic	Carnivore	MAD-Ridge	2	1	111.3	111.3	9.4	-17.7	0.07	3.6
	Onychoteuthidae											
	Onychoteuthis sp.	Epipelagic- Mesopelagic	Carnivore	Reunion Is	1,3,5	9	24-82	$37.0 \pm 20.1$			$0.05 \pm 0.02$	
	Pyroteuthidae											

Pyroteuthis sp. Mesopelagic Carnivore Reunion Is 1 2 23  $23.4 \pm 0.0$   $0.14 \pm 0.13$ 

Order/ Suborder/Infraorder	Family/ Species	Habitat Range	Feeding Mode	Region	Trawl No.	n	Size range (mm)	Mean Size (mm)	Mean δ <sup>15</sup> N (‰)	Mean δ <sup>13</sup> C (‰)	Mean Hg (μg g <sup>-1</sup> dw)	Mean TL
shes												
ryciformes	Diretmidae	Managara	Ci	MAD Did	7	1	30.3	30.3	8.82	-19.9	0.31	3.4
ctophiformes	Diretmus argenteus	Mesopelagic	Carnivore	MAD-Ridge	/	1	30.3	30.3	8.82	-19.9	0.31	3.4
yctophilorines	Neoscopelidae Neoscopelus macrolepidotus	Mesopelagic- Benthopelagic over slope regions	Carnivore	MAD-Ridge	10	2	46-116	$80.9 \pm 49.3$	$10.8 \pm 0.44$	$-19.2 \pm 0.37$	$0.42 \pm 0.31$	$4.1 \pm 0.14$
	Neoscopelus microchir	Mesopelagic- Benthopelagic over slope regions	Carnivore	MAD-Ridge	10	1	73.4	73.4	11.0	-19.1	0.46	4.1
	Myctophidae											
	Benthosema fibulatum	Mesopelagic	Carnivore	MAD-Ridge	14	2	70-88	$79.1 \pm 12.8$	$9.75 \pm 0.25$	$-18.7 \pm 0.13$	$0.32 \pm 0.05$	$3.7 \pm 0.08$
	Bolinichthys photothorax	Mesopelagic	Carnivore	La Pérouse	10	2	62-73	$67.5 \pm 7.78$	$10.9 \pm 0.74$	-18.7 ± 0.04	$0.17 \pm 0.08$	$3.8 \pm 0.23$
	Ceratoscopelus warmingii	Mesopelagic	Omnivore	La Pérouse	8	1	54.8	54.8			0.09	
	· ·			MAD-Ridge	2, 3, 6	3	41-68	$50.4 \pm 15.5$	$8.0 \pm 0.73$	$-18.8 \pm 0.45$	$0.12 \pm 0.04$	$3.2 \pm 0.23$
	Myctophidae sp.	Mesopelagic		Reunion Is	1	4	40-65	55.1 ± 10.7			$0.09 \pm 0.05$	
	Diaphus brachycephalus	Mesopelagic	Carnivore	MAD-Ridge	5	1	40.4	40.4	10.8	-19.2	0.17	4.1
	Diaphus diadematus	Mesopelagic	Carnivore	MAD-Ridge	5	2	33-36	$34.2 \pm 2.40$	$9.52 \pm 0.27$	-19.9 ± 0.19	$0.24 \pm 0.05$	$3.7 \pm 0.08$
	Diaphus effulgens	Mesopelagic	Carnivore	MAD-Ridge	5	2	75-107	90.7 ± 22.5	$10.3 \pm 1.44$	-19.1 ± 0.21	$0.32 \pm 0.16$	$3.9 \pm 0.45$
	Diaphus knappi	Mesopelagic	Carnivore	MAD-Ridge	16	2	45-61	53.1 ± 11.0	$10.2 \pm 0.07$	-19.4 ± 0.16	$0.12 \pm 0.02$	$3.9 \pm 0.02$
	Diaphus lucidus	Mesopelagic	Carnivore	La Pérouse	10	3	74-80	$77.2 \pm 2.87$		· · · · · · · · · · · · · · · · · · ·	$0.34 \pm 0.03$	
	- ······			MZC	20	1	69.2	69.2	11.3	-19.2	0.23	4.2
	Diaphus metoclampus	Mesopelagic	Carnivore	MZC	20	2	57-60	58.1 ± 2.12	12.1 ± 0.07	$-19.6 \pm 0.06$	$0.36 \pm 0.05$	$4.4 \pm 0.02$
	Diaphus mollis	Mesopelagic	Carnivore	La Pérouse	10	2	40-47	$43.5 \pm 5.23$			$0.15 \pm 0.04$	
	Diapinis monis	Mesopeingie	Curinvoic	MAD-Ridge	5, 7	3	46-59	$53.9 \pm 6.97$	$10.6 \pm 1.01$	$-19.3 \pm 0.02$	$0.13 \pm 0.04$ $0.22 \pm 0.11$	$4.0 \pm 0.32$
	Diaphus perspicillatus	Mesopelagic	Carnivore	La Pérouse	10	3	42-62	$53.5 \pm 10.1$	11.1	-19.2	$0.18 \pm 0.19$	3.8
	pe. spienums			MAD-Ridge	2, 5, 7, 9, 12	10	48-61	$56.0 \pm 4.59$	$10.2 \pm 0.53$	$-19.1 \pm 0.24$	$0.35 \pm 0.10$	$3.9 \pm 0.17$
				MZC	21	2	51-61	$56.2 \pm 7.21$	$10.9 \pm 0.66$	$-19.1 \pm 0.18$	$0.16 \pm 0.15$	$4.1 \pm 0.21$
	Diaphus richardsoni	Mesopelagic	Carnivore	MAD-Ridge	15	1	44.0	44.0	9.44	-19.5	0.09	3.6
		F0		MZC	21	2	46-47	$46.2 \pm 0.92$	$10.9 \pm 0.23$	$-19.3 \pm 0.15$	$0.11 \pm 0.03$	$4.1 \pm 0.07$
	Diaphus suborbitalis	Mesopelagic-over slope regions	Carnivore	La Pérouse	2	2	59-71	$64.7 \pm 8.20$			$0.26 \pm 0.09$	
	22 3			MAD-Ridge	10. 14, 17	5	64-81	$72.7 \pm 6.57$	$11.2 \pm 0.25$	$-18.8 \pm 0.49$	$0.31 \pm 0.22$	$4.2 \pm 0.08$
	Hygophum hygomii	Mesopelagic	Carnivore	MAD-Ridge	2, 6, 12, 17	8	51-60	$55.1 \pm 3.50$	9.95 ± 0.95	-19.2 ± 0.65	$0.19 \pm 0.06$	$3.8 \pm 0.30$
				MZC	21	2	49-55	$52.4 \pm 4.17$	$9.6 \pm 0.41$	$-19.5 \pm 0.02$	$0.09 \pm 0.02$	$3.7 \pm 0.13$

	Lampanyctus sp.	Mesopelagic	Carnivore	La Pérouse	10	2	101-123	$111.5 \pm 15.6$	$10.2 \pm 0.92$	$-18.5 \pm 0.10$	$0.10 \pm 0.01$	$3.5 \pm 0.29$
	Lampanyctus alatus	Mesopelagic	Carnivore	MAD-Ridge	3	2	38-43	$40.5 \pm 3.25$	$8.52 \pm 0.28$	$-18.6 \pm 0.33$	$0.19 \pm 0.06$	$3.3 \pm 0.09$
	Lobianchia dofleini	Mesopelagic	Carnivore	MZC	20	1	33.6	33.6 42.3	12.6	-18.6	0.22	4.6
	Lobianchia gemellarii	Mesopelagic	Carnivore	La Pérouse	10	1	42.3	42.3			0.48	
	O .			MAD-Ridge	5	1	41.5	41.5	10.3	-19.1	0.24	3.9
	Myctophum fissunovi	Mesopelagic	Carnivore	MAD-Ridge	6, 14	3	61-66	$62.7 \pm 2.70$	9.84 ± 0.17	-19.2 ± 0.25	$0.10 \pm 0.01$	$3.8 \pm 0.05$
	Myctophum nitidulum	Mesopelagic	Carnivore	MAD-Ridge	6, 14	2	64-71	$67.4 \pm 4.88$	9.5 ± 0.59	-19.3 ± 0.66	$0.20 \pm 0.02$	$3.6 \pm 0.19$
	Notoscopelus resplendens	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	3	1	37.7	37.7	8.08	-18.4	0.10	3.2
	<b>.</b>			MZC	21	2	34-39	$36.5 \pm 4.10$	$10.4 \pm 0.13$	$-19.5 \pm 0.05$	$0.12 \pm 0.01$	$3.9 \pm 0.04$
	Scopelopsis multipunctatus	Mesopelagic	Carnivore	MAD-Ridge	5	1	35.3	35.3	10.0	-20.3	0.08	3.8
	*			MZC	21	1	38.0	38.0	10.2	-19.6	0.04	3.9
Perciformes	Carangidae Decapterus macarellus	Mesopelagic	Carnivore	MAD-Ridge	7	2	99-143	121 ± 30.5	$6.16 \pm 0.18$	-18.4 ± 0.37	$0.03 \pm 0.002$	$2.6 \pm 0.06$
	тасатениѕ			MZC Reunion Is	21 5	2 3	128 101-113	$127.6 \pm 0.07$ $107.3 \pm 6.11$	$7.5 \pm 0.11$	$-18.7 \pm 0.01$	$0.04 \pm 0.004$ $0.04 \pm 0.01$	$3.0\pm0.03$
	Gempylidae			Reulion 13			101-113	107.3 ± 0.11			0.04 ± 0.01	
	Promethichthys prometheus	Mesopelagic- Benthopelagic	Carnivore	MAD-Ridge	14	2	235.4-365	$300 \pm 91.5$	$12.0 \pm 0.06$	$-17.9 \pm 0.13$	$0.14 \pm 0.02$	$4.4 \pm 0.02$
	Priacanthidae	Benurepenagre										
	Cookeolus japonicus	Mesopelagic- Benthopelagic	Carnivore	MAD-Ridge	16	2	207.9-328	$268 \pm 84.9$	$10.7 \pm 0.47$	$-18.3 \pm 0.35$	$0.25 \pm 0.01$	$4.0 \pm 0.15$
	Scombrolabracidae Scombrolabrax heterolepis			Reunion Is	1	2	77.1	77.1			$0.14 \pm 0.03$	
Stomiiformes	Gonostomatidae											
	Cyclothone sp.	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	7	1	59.9	59.9	8.34	-19.9	0.17	3.6
	Sigmops elongatus	Mesopelagic-Bathypelagic	Carnivore	La Pérouse	8	1	117.2	117.2			0.08	
				MAD-Ridge	2, 12	3	138-186	$163.0 \pm 24.2$	$10.7 \pm 0.42$	$-18.1 \pm 0.26$	$0.15 \pm 0.05$	$4.0 \pm 0.13$
				MZC	20	2	177-227	$201.8 \pm 35.6$	$12.0 \pm 0.21$	$-18.3 \pm 0.05$	$0.26 \pm 0.01$	$4.4 \pm 0.07$
				Reunion Is	1, 3, 5	25	120-174	$148.9 \pm 14.9$			$0.22 \pm 0.25$	
	<b>Phosichthyidae</b> Vinciguerria nimbaria	Mesopelagic	Carnivore	La Pérouse	8	3	31-45	$39.7 \pm 7.73$	11.3	-18.9	$0.18 \pm 0.04$	3.9
	Sternoptychidae											
	Argyropelecus aculeatus	Mesopelagic	Carnivore	La Pérouse	7	2	54-63	$58.9 \pm 6.29$			$0.26 \pm 0.16$	
				MAD-Ridge	1, 2, 5, 12	4	54-81	$66.6 \pm 14.5$	$10.8 \pm 2.0$	$-18.4 \pm 0.42$	$0.55 \pm 0.42$	$4.1 \pm 0.64$
				Reunion Is	1	3	19-38	$30.6 \pm 10.3$			$0.09 \pm 0.01$	
	<b>Stomiidae</b> Astronesthes sp.	Mesopelagic	Carnivore	La Pérouse	10	1	81.2	81.2	9.4	-18.0	0.11	3.3
				MAD-Ridge	5	1	122.3	122.3	10.1	-18.0	0.76	3.8

Chauliodus sloani	Mesopelagic-Bathypelagic	Carnivore	La Pérouse	8, 9	2	139-153	146.1 ± 10.4			$0.12 \pm 0.01$	
	71		MAD-Ridge	1	2	112-199	$155.5 \pm 61.4$	$10.9 \pm 0.47$	$-18.9 \pm 0.13$	$0.11 \pm 0.01$	$4.1 \pm 0.15$
			MZC	20	2	121-202	$161.8 \pm 57.3$	$10.8 \pm 1.1$	$-19.1 \pm 0.38$	$0.11 \pm 0.04$	$4.1 \pm 0.34$
			Reunion Is	3	1	184.9	184.9			0.10	
Diplophos taenia	Mesopelagic	Carnivore	MAD-Ridge	5	1	175.5	175.5	9.9	-18.9	0.21	3.8
			MZC	21	2	82-115	$98.5 \pm 23.9$	$8.8 \pm 0.57$	$-19.4 \pm 0.16$	$0.08 \pm 0.02$	$3.4 \pm 0.18$
Echiostoma barbatum	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	9, 10, 11	5	68-81	$72.3 \pm 5.21$	9.48 ± 1.11	$-18.5 \pm 0.30$	$0.15 \pm 0.06$	$3.6 \pm 0.35$
			MZC	19	1	70.2	70.2	10.5	-18.5	0.12	4.0
Eustomias sp.	Mesopelagic-Bathypelagic	Carnivore	MZC	18	1	112.2	112.2	9.7	-18.5	0.06	3.7
Idiacanthus fasciola	Mesopelagic-Bathypelagic	Carnivore	La Pérouse	10	1	244.8	244.8	10.0	-17.7	0.12	3.5
Melanostomias sp.	Mesopelagic	Carnivore	La Pérouse	9	1	97.9	97.9	11.3	-18.0	0.17	3.9
			MAD-Ridge	5, 9	2	95	$95.1 \pm 0.29$	$9.81 \pm 0.81$	$-18.1 \pm 0.53$	$0.20 \pm 0.07$	$3.7 \pm 0.25$
			MZC	20	1	118.0	118.0	11.1	-18.3	0.26	4.1
Leptostomias sp.			Reunion Is	3	1	131.4	131.4			0.26	
Photonectes sp.	Mesopelagic	Carnivore	La Pérouse	9, 10	2	117-126	121.1 ± 6.43	$11.8 \pm 0.62$	-18.1 ± 0.62	$0.22 \pm 0.12$	$4.0 \pm 0.19$
Photostomias sp.	Mesopelagic	Carnivore	La Pérouse	9	1	110.8	110.8	11.1	-18.4	0.14	3.8
Stomias boa	Mesopelagic	Carnivore	La Pérouse	10	1	145.0	145.0	10.8	-18.4	0.13	3.7
Stomias Iongibarbatus	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	2	1	290	290	12.0	-18.3	0.38	4.4
-			MZC	20	1	371	371.0	11.8	-18.6	0.90	4.4

Table 2. Minimum (Min), Maximum (Max) and mean  $\pm$  standard deviations of Hg concentrations ( $\mu$ g g<sup>-1</sup> dw) of the broad categories (crustaceans, fishes and squids) at La Pérouse, MAD-Ridge seamounts, the southern Mozambique Channel and Reunion Island.

			Bro	ad Ca	tegory		
Region	Statistics	Cı	rustaceans		Fishes		Squids
La	Min	0.003	Oplophoridae	0.04	D. perspicillatus	0.05	Abraliopsis
Pérouse	Max	1.69	Oplophoridae	0.48	L. gemellarii	0.08	Abraliopsis
	Mean ±		$0.40 \pm 0.41$		$0.19 \pm 0.11$		$0.06 \pm 0.01$
	S.D.						
MAD-	Min	0.05	Funchalia	0.03	D. macarellus	0.04	O. volatilis
Ridge	Max	0.71	Oplophoridae	1.12	A. aculeatus	0.26	O. volatilis
	Mean ±		$0.24 \pm 0.22$		$0.24 \pm 0.18$		$0.15 \pm 0.22$
	S.D.						
MZC	Min	0.06	Funchalia	0.03	D. macarellus		
	Max	0.27	Sergestidae	0.90	S. longibarbatus		
	Mean ±		$0.15 \pm 0.08$	•	$0.18 \pm 0.18$		
	S.D.						
Reunion	Min	0.05	Funchalia	0.03	D. macarellus	0.02	Onychoteuthis
Island	Max	1.57	Oplophoridae	1.37	S. elongatus	0.19	Abralia
	Mean ±		$0.25 \pm 0.41$		$0.18 \pm 0.21$		$0.07 \pm 0.04$
	S.D.						