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

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Abstract

Mercury (Hg) concentrations and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) 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 $\delta^{15}N$ values in pelagic nekton assemblages collected at MAD-Ridge seamount and the southern Mozambique Channel, suggesting biomagnification of Hg. Concentrations of Hg in organisms of 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.

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

1. Introduction

Mercury is a unique trace element, displaying different chemical forms in the environment. Mercury exists in its elemental form (Hg^0) in the atmosphere and as inorganic Hg in oceanic waters, with a fraction being converted into monomethyl mercury (MMHg) or dimethyl mercury (DMHg) at ocean depths in oxygen minimum zones (Mason and Fitzgerald, 1993; Fitzgerald et al., 2007; Choy, 2013). MMHg is known to bioaccumulate and biomagnify 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 et al., 2006). Biomagnification is the transfer of a chemical from the diet to the consumer, 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 element and $\delta^{15}N$ values (Cheung and Wang, 2008). The rate at which bioaccumulation and bioconcentration of MMHg occurs in the food web depends on its bioavailability at the base of the food chain, trophic interactions and food web assemblages up to apex marine predators. In many fish, Hg exists in its most stable, but also the most toxic methyl form (Cossa et al., 1990). Almost all Hg (>90%) in top predators is MMHg (Cossa et al., 1990; 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 compared to epipelagic organisms (Choy, 2013; Blum et al., 2013).

In marine pelagic food webs, mesopelagic micronekton typically ranges in size from 2 to 20 cm and consists of a large and diverse group of organisms which can be divided into the broad categories crustaceans, squids and fishes (Brodeur and Yamamura, 2005; De Forest and Drazen, 2009). This group assemblage represents a substantial biomass in oceanic waters accounting for more than 3.8-11.8 billion tons of mesopelagic fishes reported worldwide (Irigoien et al., 2014; Proud et al., 2018). Available estimates for cephalopods and

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 krill in the Southern ocean (Atkinson et al., 2009). Micronekton exhibits a diverse range of migration strategies including diel vertical migration over several hundreds of meters from deep (below 400 m) to shallower layers (top 200 m) at dusk and inversely at dawn (Lebourges-Dhaussy et al., 2000; Béhagle et al., 2014; Ariza, 2015; Annasawmy et al., 2018, 2019, 2020a), reverse migration (Alverson, 1961; Gjøsæter, 1977, 1984; Marchal and Lebourges-Dhaussy, 1996), mid-water migration or non-migration (Annasawmy et al., 2018; 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 al., 2001; Ariza et al., 2015; LeMoigne, 2019). Micronekton is also preyed upon by tunas, 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).

While Hg concentrations in pelagic and tropical coastal marine fish were subjected to extensive studies worldwide (e.g., Al-Reasi et al., 2007; Cai et al., 2007; Calatayud et al., 2012; Chen et al., 2014; Bodin et al., 2017; Chouvelon et al., 2017; Afandi et al., 2018; Briand et al., 2018; Le Croizier et al., 2019; Houssard et al., 2019), micronekton organisms have received little consideration to date with only few studies having determined Hg concentrations in micronekton species (Asante et al., 2008, 2010; Kojadinovic et al., 2011; 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 displaying contrasted foraging and diel migration strategies from four different study sites located in the south-western Indian Ocean. These sites (La Pérouse and MAD-Ridge seamounts, Reunion Island and the southern Mozambique Channel) exhibit different productivity, mesoscale processes and varied proximity to landmasses (Annasawmy et al.,

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

2.1 Study sites

Pelagic nekton assemblages were sampled during several cruises of the RV *Antea* at the La 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^2 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 ± 0.02 µg g^{-1} dry weight) and a mussel tissue (SRM 2976, National Institute of

Standards and Technology; certified Hg concentration: 61.0 ± 3.6 µg 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 µg g^{-1} dry weight (Le Croizier et al., 2019). Resulting Hg concentrations in pelagic nekton assemblages are given in µg 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 δ notations as parts per thousand (‰) deviations from the international standards:

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

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

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).

The trophic level of each selected taxa was calculated using the following equation, based on Minagawa and Wada (1984) and Post (2002):

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

where, $\delta^{15}N_i$ is the nitrogen isotopic value of any given taxon i, $\delta^{15}N_{\text{primary consumer}}$ 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, $\delta^{15}N_{\text{primary consumer}}$ 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 < Mesobenthopelagic, 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

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

223

224 **3. Results**

225 3.1 Prevailing bathymetry and oceanographic processes at the study sites

226 La Pérouse seamount is located within the Indian South Subtropical Gyre (ISSG) province
227 and MAD-Ridge seamount is located ~1300 km southwards from the Madagascar landmass
228 within the East African Coastal province (EAFR) (Fig. 1a). The La Pérouse seamount summit
229 is 10 km long and reaches ~60 m below the sea surface rising from a seabed at ~5000 m (Fig.
230 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
232 the sea surface (Fig. 1c).

233 Mean sea surface chlorophyll concentrations were higher at the MAD-Ridge seamount and
234 the southern Mozambique Channel compared to the La Pérouse seamount and Reunion Island
235 (Fig. 2a). During MAD-Ridge cruise in November 2016, a strong anticyclonic eddy was
236 stationed at MAD-Ridge. A weak anticyclonic eddy was stationed at La Pérouse seamount,
237 whereas Reunion Island was under the influence of a weak cyclonic eddy in November 2016
238 (Fig. 2b). During the La Pérouse cruise in September 2016, a weak cyclonic eddy was
239 stationed at the seamount (Annasawmy et al., 2019).

240 3.2 Pelagic nekton species composition, size variability by sampled area and ecological group

241 A total of 60 pelagic nekton taxa were sampled during this study, including 4 crustaceans, 10
242 squids, and 46 fishes (Table 1). Crustaceans were represented by pelagic caridean, penaeid,
243 and sergestid shrimps. Cephalopods consisted of five families of squids (Enoploteuthidae,
244 Histioteuthidae, Ommastrephidae, Onychoteuthidae, and Pyroteuthidae). Fishes were
245 represented by 11 common pelagic families Carangidae, Diretmidae, Gempylidae,
246 Gonostomatidae, Myctophidae, Neoscopelidae, Scombrolabracidae, Phosichthyidae,
247 Sternoptychidae, Stomiidae, and benthopelagic Priacanthidae. In terms of diversity and
248 biomass, sampling was dominated by Myctophidae (22 species) and Stomiidae (12 species)
249 (Table 1).

250 A total of 256 taxa represented small animals of less than a maximum length of 200 mm.
251 Larger organisms were also collected in the trawl including two large individuals of neon
252 flying squids, *Ommastrephes bartramii* (DML = 364.8 and 489.8 mm) and fishes: Roudi
253 escolar, *Promethichthys prometheus* (n = 2, SL = 235.4 and 365.0 mm) and longfinned
254 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^{-1} dw and 0.82 µg g^{-1} dw

279 compared to the other sampled squids (Table 2). At La Pérouse and Reunion Island,
280 Oplophoridae sp. exhibited higher Hg concentrations (1.69 and 1.57 µg g^{-1} dw, respectively)
281 than other sampled taxa. The *Funchalia* sp. (Penaeidae) showed lower Hg concentrations
282 (0.05-0.06 µg g^{-1} dw) than the other crustaceans at MAD-Ridge, the southern Mozambique
283 Channel and Reunion Island. Fishes exhibited higher median Hg concentrations at MAD-
284 Ridge than the other broad categories (with hatchetfish *Argyropelecus aculeatus* showing
285 highest concentrations of 1.12 µg g^{-1} dw). The mackerel scad *Decapterus macarellus* showed
286 lower Hg concentrations of 0.03 µg g^{-1} dw among all other sampled fishes at MAD-Ridge
287 seamount, in the southern Mozambique Channel and at Reunion Island (Table 2).

288 Hg concentrations in the sampled micronekton increased from organisms collected near the
289 surface (Epipelagic-Mesopelagic) to deeper parts (Mesopelagic-Benthopelagic) (Kruskal-
290 Wallis, H=23.8, $p < 0.05$) (Fig. 3d). Feeding mode (omnivore *vs* carnivore) of sampled
291 micronekton did not significantly influence Hg concentrations (MAD-Ridge: W= 685, $p >$
292 0.05; Mozambique Channel: W= 59, $p > 0.05$; Reunion Island: W= 339, $p > 0.05$), except at
293 La Pérouse seamount (W= 229, $p < 0.05$) (Fig. 3e) where omnivorous organisms
294 (representing crustaceans and *C. warmingii* individuals) recorded higher Hg concentrations
295 compared to carnivorous ones. Body size of organisms had a significant positive influence on
296 Hg concentrations in the southern Mozambique Channel ($F_{1, 28} = 18.6$, $p < 0.05$) and at
297 Reunion Island ($F_{1, 74} = 5.14$, $p < 0.05$) with Hg concentrations increasing with micronekton's
298 body size [Mozambique Channel: $Hg(\mu g\ g^{-1}\ dw) = 0.04 + 0.001 \times Size\ (mm)$; Reunion
299 Island: $Hg(\mu g\ g^{-1}\ dw) = 0.07 + 0.001 \times Size\ (mm)$]. No relation was found between Hg
300 concentrations and body size of all micronekton species at the La Pérouse ($F_{1, 58} = 0.006$, $p >$
301 0.05) and MAD-Ridge seamounts ($F_{1, 93} = 0.30$, $p > 0.05$) (Fig 4).

302 3.3 Relationships between Hg concentrations and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values

303 Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ were significantly different between La Pérouse and
304 MAD-Ridge seamounts ($\delta^{13}C$: Kruskal-Wallis, H= 16.4, $p < 0.05$; $\delta^{15}N$: Kruskal-Wallis, H=
305 15.8, $p < 0.05$), with micronekton showing higher $\delta^{13}C$ and $\delta^{15}N$ values at La Pérouse
306 compared to MAD-Ridge (Fig. 5). Micronekton assemblages also exhibited higher $\delta^{13}C$
307 values at La Pérouse compared to the Mozambique Channel (pairwise comparisons, $p <$
308 0.05). Hg concentrations in the micronekton broad categories were significantly influenced
309 by $\delta^{15}N$ values at MAD-Ridge ($F_{1, 95} = 18.0$, $p < 0.05$) and in the Mozambique Channel ($F_{1, 28}$
310 $= 10.2$, $p < 0.05$), with an increase in Hg concentrations with increasing $\delta^{15}N$ values. No
311 significant increase in Hg concentrations with increasing $\delta^{15}N$ values were observed at La
312 Pérouse ($F_{1, 28} = 1.64$, $p > 0.05$). No clear relationships were found between Hg
313 concentrations and $\delta^{13}C$ values at the La Pérouse ($F_{1, 28} = 2.37$, $p > 0.05$), MAD-Ridge
314 seamounts ($F_{1, 95}= 0.56$, $p > 0.05$) and the Mozambique Channel ($F_{1, 28} = 1.21$, $p > 0.05$) (Fig.
315 6).

316

317 **4. Discussion**

318 To our knowledge, this study is the first to investigate Hg concentrations in pelagic nekton
319 assemblages in the south-western Indian Ocean, including two yet undocumented shallow
320 seamounts. While Hg concentrations were relatively homogeneous in micronekton sampled
321 at the seamounts, the open ocean and the Mascarene shelf, other factors such as vertical
322 distribution, body size and trophic position may influence Hg levels.

323 4.1 Spatial variability in Hg concentrations in the south-western Indian Ocean

324 Average Hg concentrations in organisms collected at Reunion Island were lower compared to
325 those from the southern Mozambique Channel and at La Pérouse and MAD-Ridge
326 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 μg g^{-1} 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^{-1} 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^{-1} 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^{-1} dw for Oplophoridae and less than 0.1 μg g^{-1} 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

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

4.2 Vertical distribution of Hg concentrations

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^{-1} 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.

374 The five organisms classified as benthopelagic were all fishes collected from MAD-Ridge
375 seamount (two flank-associated *N. macrolepidotus*, one flank-associated *Neoscopelus*
376 *microchir* and two summit-associated *Cookeolus japonicus*) which showed concentrations of
377 0.20-0.64 µg g^{-1} dw. These species showed high trophic levels of 4 and were all seamount-
378 associated, hence being close to the MAD-Ridge seamount sediments, thus possibly
379 accounting for their higher Hg concentrations compared to epipelagic species. Enhanced Hg
380 bioaccumulation was found in mesopelagic prey species compared to epipelagic ones in
381 several ecosystems (Monteiro et al., 1996; Choy et al., 2009; Choy, 2013; Chouvelon et al.,
382 2012). Authors have reported a four-fold increase in Hg concentrations from epipelagic to
383 mesopelagic species (Monteiro et al., 1996), with seabirds feeding on mesopelagic prey also
384 exhibiting a four-fold increase in Hg levels in breast feathers compared to those feeding on
385 epipelagic prey (Monteiro et al., 1998). The data collected during this study suggest
386 approximately a three-fold increase in mean Hg concentrations from epipelagic to
387 mesopelagic species.

388 4.3 Factors influencing Hg concentrations in micronekton

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

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

405 Compared to studies which showed Hg concentrations lower than the detection limit (<0.05
406 µg g^{-1} dw) in small-sized mesopelagic fishes sampled in the Sulu and Celebes Seas in the
407 south-western area of the Philippines, only nine among 174 fishes sampled at the four study
408 sites in the Indian Ocean showed Hg concentrations <0.05 µg g^{-1} dw and $\delta^{15}N$ and TL values
409 from 6.0 to 10.2‰ and 2.6 to 3.9, respectively. In fact, seven carnivorous fishes (five from
410 MAD-Ridge, one from the Mozambique Channel and one from Reunion Island) showed Hg
411 concentrations >0.5 µg g^{-1} dw. These fish include two mesopelagic *A. aculeatus* (54.4 and
412 77.3 mm), one bathypelagic *Neoscopelus macrolepidotus* (46 mm), one seamount-associated
413 *Diaphus suborbitalis* (81.2 mm), one mesopelagic *Astronesthes* (122.3 mm), one
414 bathypelagic *Stomias longibarbatus* (371 mm) and one mesopelagic *Sigmops elongatus*
415 (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
416 other fishes showed Hg concentrations <0.5 µg g^{-1} dw, despite some of them being
417 bathypelagic, having high body sizes and $\delta^{15}N$ values. In addition to habitat range, size and
418 trophic level, some other factors may hence influence Hg concentration in mesopelagic
419 fishes. Small fish such as *A. aculeatus* previously reported as residents of deep-water layers
420 in the Pacific (Receveur et al., 2020) and sampled in greater proportions below 400 m during
421 both day and night at MAD-Ridge seamount (Annasawmy et al., 2019) may show high Hg
422 concentrations because of their deep habitat range and absence of diel vertical migration.
423 Differences in trace element concentrations were also found between migrant and non-

migrant 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 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^{-1} 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

448 lack of clear relationship between Hg concentrations and $\delta^{13}C$ values may be attributed to
449 micronekton across the four sites having offshore/pelagic habitats with no
450 inshore/coastal/demersal inputs (Goutte et al., 2015; Le Croizier et al., 2019). The positive
451 relationships between Hg levels and stable nitrogen isotope values in micronekton collected
452 at MAD-Ridge seamount and the southern Mozambique Channel, suggests biomagnification
453 of Hg through the food webs that characterise these ecosystems. This might imply that higher
454 trophic mesopelagic organisms retained higher Hg concentrations than lower trophic ones
455 (Asante et al., 2008). Increases in Hg concentrations with trophic position were observed
456 across zooplankton, micronekton and large predators in the North Pacific subtropical gyre
457 (Choy, 2013). Significant positive relationships between Hg concentration and trophic
458 position were also observed in pelagic marine top predators (Storelli et al., 2005; Cai et al.,
459 2007; Bodin et al., 2017) due to organisms feeding at higher trophic positions consuming
460 larger prey with higher body burdens than smaller prey (Watras et al., 1998; Bowles et al.,
461 2001; Cai et al., 2007). The lack of relationship between Hg and $\delta^{15}N$ values at La Pérouse
462 may be attributed to the complex food webs in oligotrophic tropical ecosystems with variable
463 Hg concentrations as observed in previous tropical ecosystems (Al-Reasi et al., 2007).

464 The length of the studied food chains at La Pérouse, MAD-Ridge and the Mozambique
465 Channel may also explain the difference in Hg biomagnification observed in micronekton
466 between sites. While a two-step (3 trophic levels) pelagic food chain has been observed at La
467 Pérouse, a three-step (4 trophic levels) food chain has been observed at MAD-Ridge and in
468 the Mozambique Channel due to the sampling of micronekton feeding *O. bartramii*
469 specimens at the two later sites (Annasawmy et al., 2020b). Higher trophic level organisms
470 such as large squids which potentially have high Hg concentrations and possibly account for
471 Hg biomagnification were not sampled during La Pérouse cruise possibly due to their net
472 avoidance abilities and smaller number of trawls conducted relative to MAD-Ridge cruise.

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

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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943

List of figures

Fig. 1(a) Map of the south-western Indian Ocean showing the trawl stations conducted at two seamounts (La Pérouse and MAD-Ridge) and the open ocean investigation at Reunion Island and Mozambique Channel (MZC). Longhurst's (1998) biogeochemical provinces are delimited by black solid lines and are labelled as EAFR (East African Coastal Province) and ISSG (Indian South Subtropical Gyre). The western African, Madagascar and Mascarene landmasses are shown in grey. A 3D-bathymetry of (b) La Pérouse and (c) MAD-Ridge seamounts. Colour bar represents the depth (m) below the sea surface.

Fig. 2(a) Averaged satellite image of sea surface chlorophyll *a* concentrations from 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 concentrations in mg m^{-3}. (b) Averaged mean sea level anomaly (MSLA) map, with La 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 SLA (blue).

Fig. 3 Boxplots of mercury (Hg) concentrations (µg g^{-1} dw) in (a) the most common crustacean and fish families from the study sites (La Pérouse, n= 32; MAD-Ridge, n= 72; 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, n= 3), (e) selected taxa according to feeding mode (carnivorous and omnivorous) from the four study sites. The median (thick black line in box plots), interquartile range (the lower and upper boundaries), the spread (thin lines extending from box plots) and outliers (black stars) are shown.

Fig. 4 Mercury (Hg) concentrations (µg g^{-1} dw) in selected taxa *vs* body size (abdomen and carapace length for crustaceans, standard length for fishes and dorsal mantle length for squids) in mm, from the different study sites (La Pérouse, MAD-Ridge, Mozambique Channel, and Reunion Island). The data from Mozambique Channel and Reunion Island fit a linear curve (regression equations are given) but no relationship were found between Hg concentrations and nekton body size at La Pérouse and MAD-Ridge seamounts.

Fig. 5 Boxplots of $\delta^{15}N$ and $\delta^{13}C$ stable isotope values in selected taxa from the study sites (La Pérouse, n= 30; MAD-Ridge, n= 97; Mozambique Channel-MZC, n= 30). The median (thick black line in box plots), mean (diamond symbols), interquartile range (the lower and upper boundaries), the spread (thin lines extending from box plots) and outliers (red stars) are shown.

Fig. 6 Mercury (Hg) concentrations (µg g^{-1} dw) in selected taxa *vs* $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (‰) from the study sites (La Pérouse, MAD-Ridge and Mozambique Channel). The data ($\delta^{15}N$ values) from MAD-Ridge and the Mozambique Channel fit exponential curves. No significant relationships were found between Hg concentrations and $\delta^{13}C$ values at La Pérouse, MAD-Ridge seamounts and the Mozambique Channel, and between Hg and $\delta^{15}N$ values at La Pérouse.

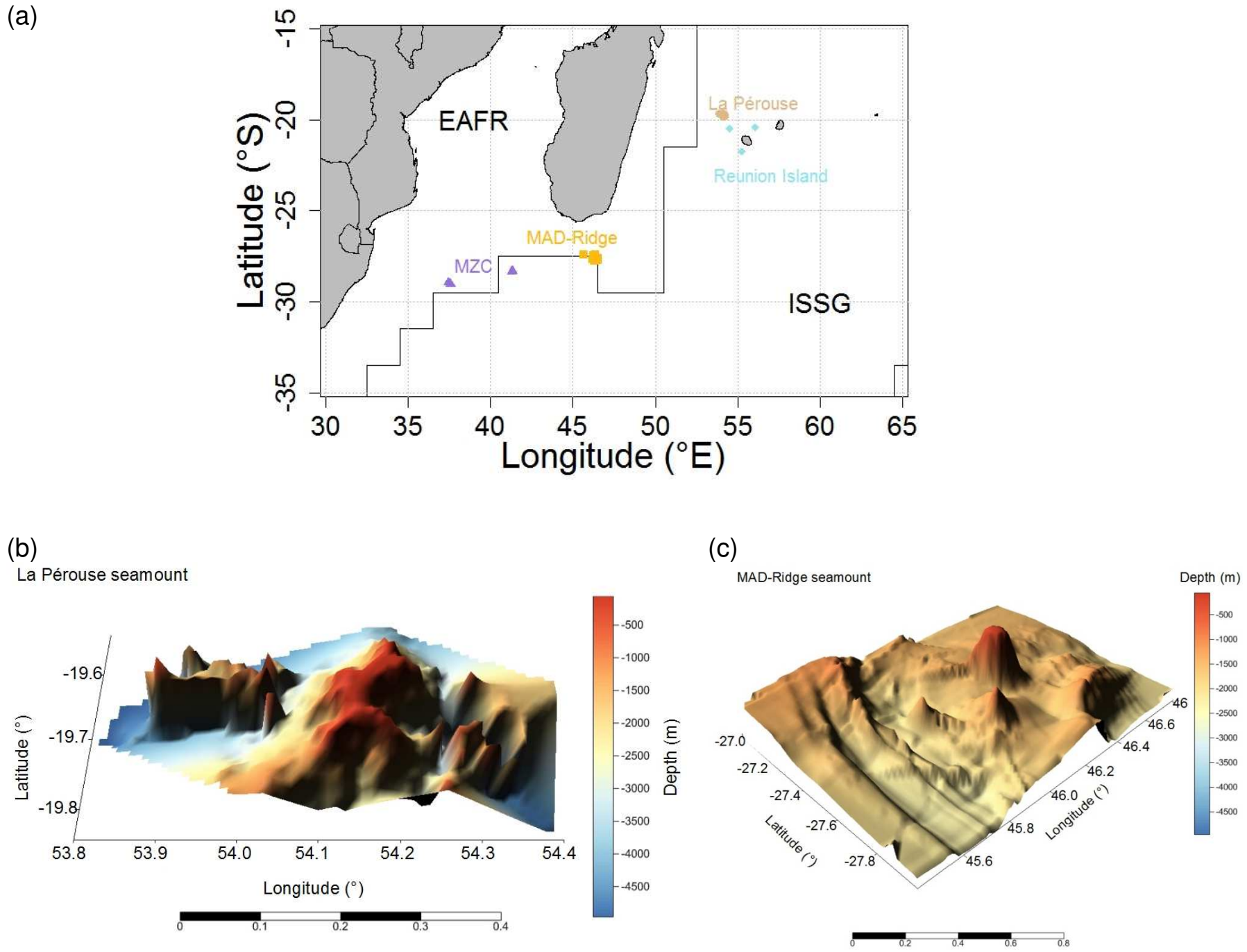
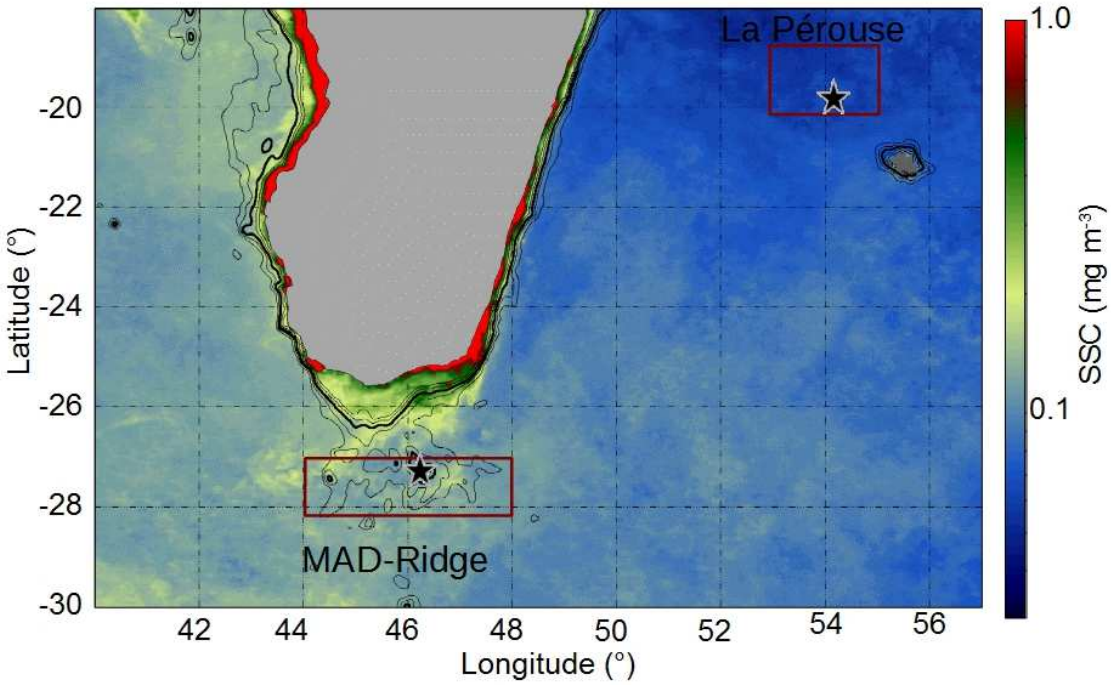

(a)
EAFR
La Pérouse
Reunion Island
MAD-Ridge
MZC
ISSG
Latitude (°S)
Longitude (°E)
(b)
La Pérouse seamount
Latitude (°)
Longitude (°)
Depth (m)
(c)
MAD-Ridge seamount
Depth (m)
Latitude (°)
Longitude (°)

Figure 1

(a)


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

(b)

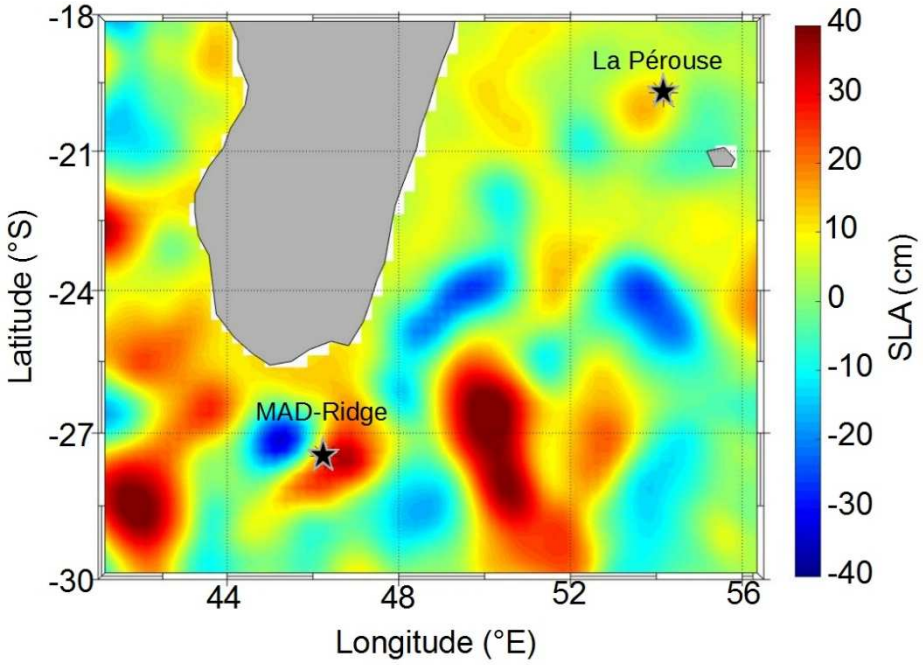

La Pérouse
MAD-Ridge
Latitude (°S)
Longitude (°E)
SLA (cm)
-18
-21
-24
-27
-30
44
48
52
56
40
30
20
10
0
-10
-20
-30
-40

Figure 2

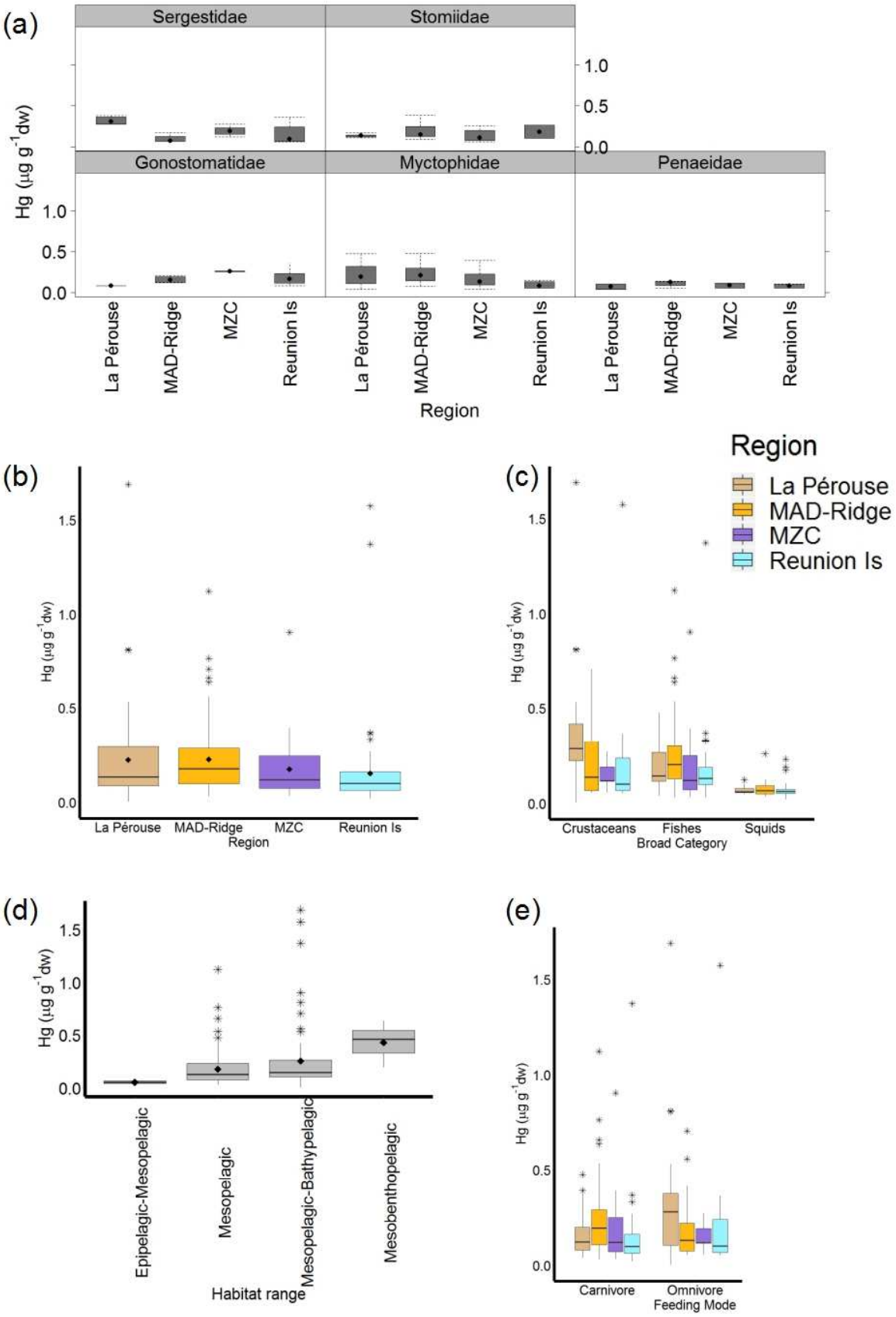

(a)
Sergestidae
Stomiidae
Gonostomatidae
Myctophidae
Penaeidae
Hg (µg g-1dw)
La Pérouse
MAD-Ridge
MZC
Reunion Is
Region
(b)
Region
(c)
Region
La Pérouse
MAD-Ridge
MZC
Reunion Is
Crustaceans
Fishes
Squids
Broad Category
(d)
Epipelagic-Mesopelagic
Mesopelagic
Mesopelagic-Bathypelagic
Mesobenthopelagic
Habitat range
(e)
Carnivore
Omnivore
Feeding Mode

Figure 3

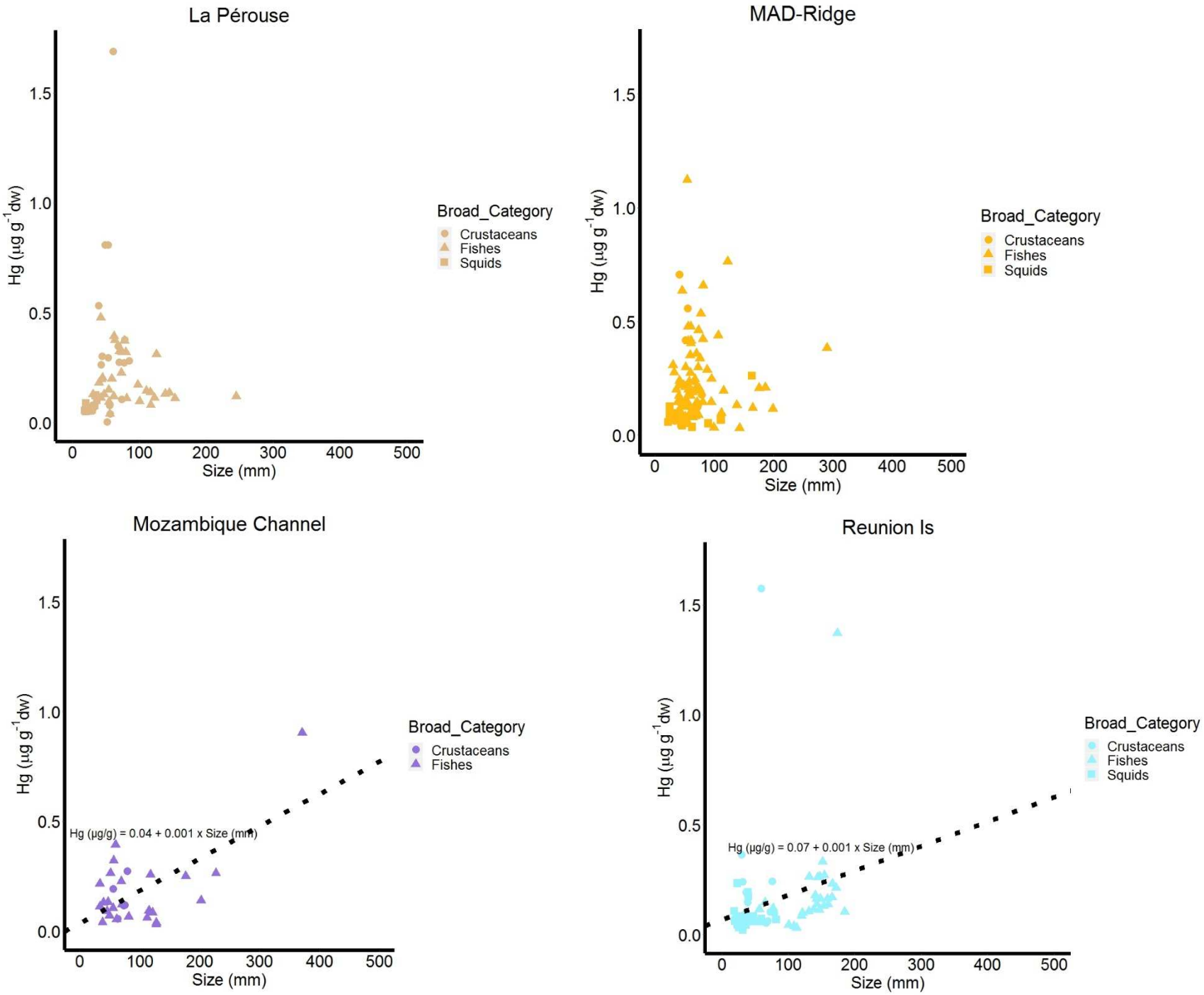

La Pérouse
MAD-Ridge
Mozambique Channel
Reunion Is
Hg (µg g-1dw)
Size (mm)
Broad_Category
Crustaceans
Fishes
Squids
Hg (µg/g) = 0.04 + 0.001 x Size (mm)
Hg (µg/g) = 0.07 + 0.001 x Size (mm)

Figure 4

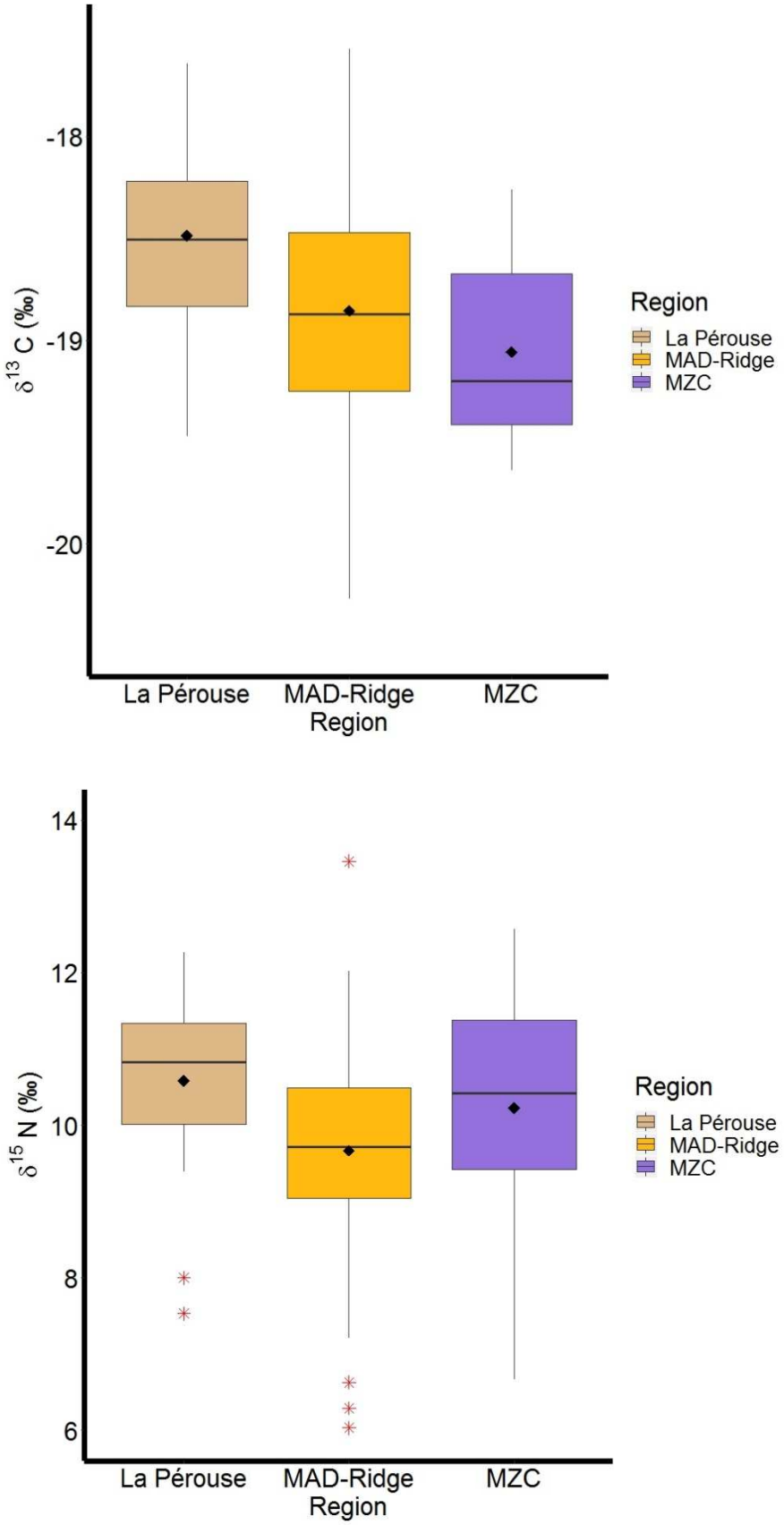

-18
-19
-20
δ13 C (‰)
La Pérouse
MAD-Ridge
MZC
Region
Region
La Pérouse
MAD-Ridge
MZC
14
12
10
8
6
δ15 N (‰)
La Pérouse
MAD-Ridge
MZC
Region
Region
La Pérouse
MAD-Ridge
MZC

Figure 5

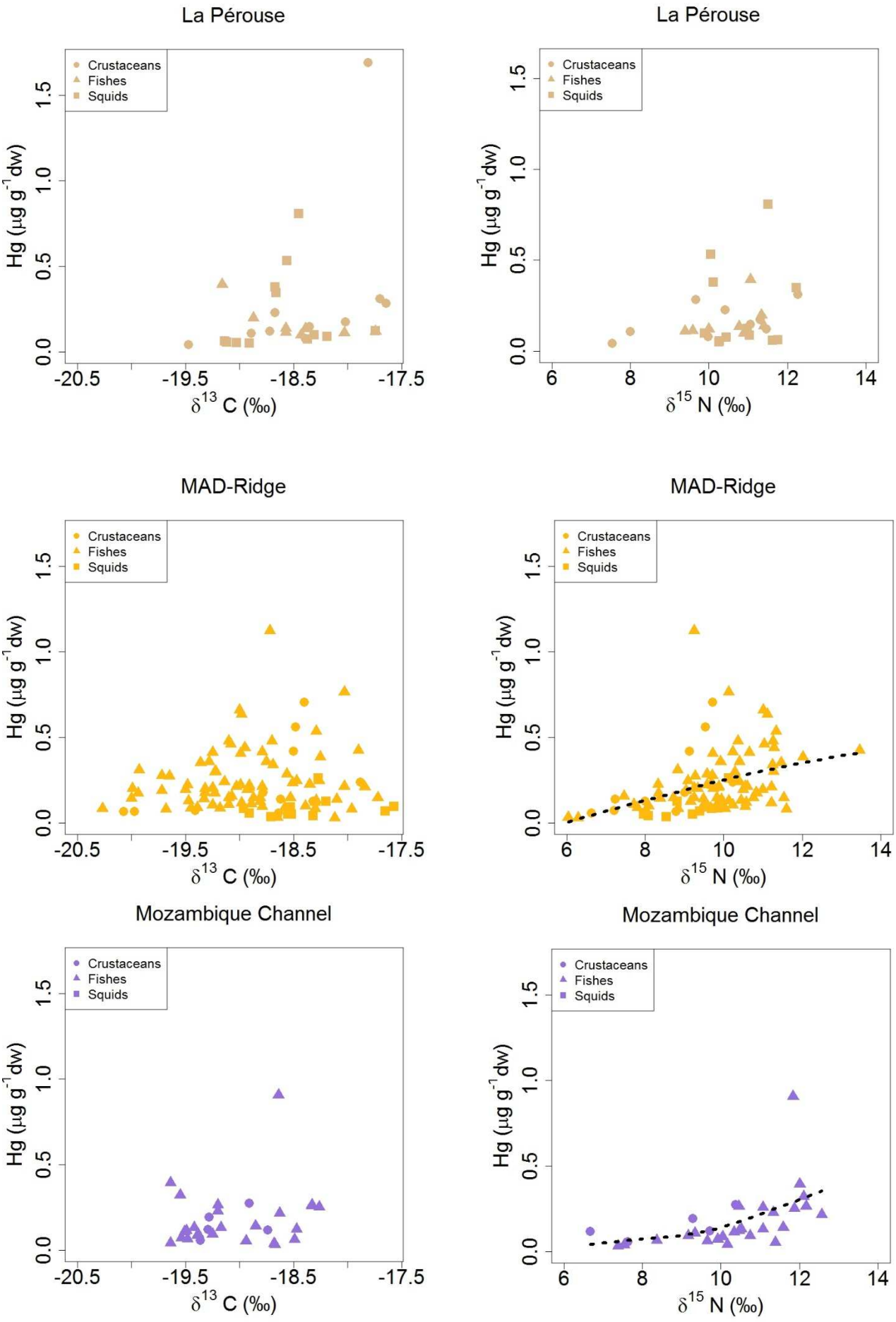

La Pérouse
Crustaceans
Fishes
Squids
Hg (µg g-1 dw)
δ13 C (‰)
δ15 N (‰)
MAD-Ridge
Mozambique Channel

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 $\delta^{13}C$ (‰), mean mercury (Hg) concentrations (µg g^{-1} 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 ± standard deviation.

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

MAD-Ridge	2	4	33-79	50.8 ± 19.4	8.3 ± 0.82	-19.6 ± 0.59	0.09 ± 0.06	3.3 ± 0.26
MZC	18	3	56-79	69.9 ± 12.6	9.8 ± 0.54	-19.2 ± 0.22	0.20 ± 0.08	3.7 ± 0.17
Reunion Is	1	5	30-76	50.5 ± 18.1			0.17 ± 0.13	

Order	Family / Species	Habitat	Feeding Mode	Region	Trawl No.	n	Size range (mm)	Mean Size (mm)	Mean $\delta^{15}N$ (‰)	Mean $\delta^{13}C$ (‰)	Mean Hg (µg g^{-1} dw)	Mean TL (TPA model)
Squids												
Oegopsida	**Enoploteuthidae**	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	11	2	22-46	34.1 ± 16.8	8.0 ± 0.06	-18.6 ± 0.42	0.05 ± 0.01	3.2 ± 0.02
				Reunion Is	1, 3	7	21-39	27.2 ± 6.51			0.09 ± 0.05	
	Abralia sp.	Mesopelagic	Carnivore	Reunion Is	3, 5	4	20-30	26.4 ± 4.6			0.06 ± 0.01	
	Abraliopsis sp.	Mesopelagic-Bathypelagic	Carnivore	La Pérouse	3, 4, 6	11	18-36	28.1 ± 6.19	10.5 ± 0.45	-18.4 ± 0.48	0.07 ± 0.02	3.6 ± 0.14
				MAD-Ridge	2, 9, 10	4	25-35	29.2 ± 4.95	9.5 ± 0.48	-18.3 ± 0.59	0.10 ± 0.02	3.6 ± 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 ± 0.35	11.7 ± 0.10	-19.1 ± 0.01	0.06 ± 0.002	4.0 ± 0.03
				Reunion Is	1, 3	4	19-47	35.0 ± 14.6			0.08 ± 0.02	
	Ommastrephidae											
	Ornithoteuthis volatilis	Mesopelagic	Carnivore	MAD-Ridge	12, 14, 16	4	45-163	90.1 ± 52.2	9.0 ± 0.93	-18.5 ± 0.18	0.10 ± 0.11	3.5 ± 0.29
	Sthenoteuthis oualaniensis	Mesopelagic	Carnivore	Reunion Is	1	3	33-40	36.5 ± 3.5			0.09 ± 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 ± 20.1			0.05 ± 0.02	
	Pyroteuthidae											

Pyroteuthis sp.	Mesopelagic	Carnivore	Reunion Is	1	2	23	23.4 ± 0.0			0.14 ± 0.13

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

	Lampanyctus sp.	Mesopelagic	Carnivore	La Pérouse	10	2	101-123	111.5 ± 15.6	10.2 ± 0.92	-18.5 ± 0.10	0.10 ± 0.01	3.5 ± 0.29
	Lampanyctus alatus	Mesopelagic	Carnivore	MAD-Ridge	3	2	38-43	40.5 ± 3.25	8.52 ± 0.28	-18.6 ± 0.33	0.19 ± 0.06	3.3 ± 0.09
	Lobianchia dofleini	Mesopelagic	Carnivore	MZC	20	1	33.6	33.6	12.6	-18.6	0.22	4.6
	Lobianchia gemellarii	Mesopelagic	Carnivore	La Pérouse	10	1	42.3	42.3			0.48	
				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 ± 2.70	9.84 ± 0.17	-19.2 ± 0.25	0.10 ± 0.01	3.8 ± 0.05
	Myctophum nitidulum	Mesopelagic	Carnivore	MAD-Ridge	6, 14	2	64-71	67.4 ± 4.88	9.5 ± 0.59	-19.3 ± 0.66	0.20 ± 0.02	3.6 ± 0.19
	Notoscopelus resplendens	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	3	1	37.7	37.7	8.08	-18.4	0.10	3.2
				MZC	21	2	34-39	36.5 ± 4.10	10.4 ± 0.13	-19.5 ± 0.05	0.12 ± 0.01	3.9 ± 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 ± 0.18	-18.4 ± 0.37	0.03 ± 0.002	2.6 ± 0.06
				MZC	21	2	128	127.6 ± 0.07	7.5 ± 0.11	-18.7 ± 0.01	0.04 ± 0.004	3.0 ± 0.03
				Reunion Is	5	3	101-113	107.3 ± 6.11			0.04 ± 0.01	
	Gempylidae											
	Promethichthys prometheus	Mesopelagic-Benthopelagic	Carnivore	MAD-Ridge	14	2	235.4-365	300 ± 91.5	12.0 ± 0.06	-17.9 ± 0.13	0.14 ± 0.02	4.4 ± 0.02
	Priacanthidae											
	Cookeolus japonicus	Mesopelagic-Benthopelagic	Carnivore	MAD-Ridge	16	2	207.9-328	268 ± 84.9	10.7 ± 0.47	-18.3 ± 0.35	0.25 ± 0.01	4.0 ± 0.15
	Scombrolabracidae											
	Scombrolabrax heterolepis			Reunion Is	1	2	77.1	77.1			0.14 ± 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 ± 24.2	10.7 ± 0.42	-18.1 ± 0.26	0.15 ± 0.05	4.0 ± 0.13
				MZC	20	2	177-227	201.8 ± 35.6	12.0 ± 0.21	-18.3 ± 0.05	0.26 ± 0.01	4.4 ± 0.07
				Reunion Is	1, 3, 5	25	120-174	148.9 ± 14.9			0.22 ± 0.25	
	Phosichthyidae											
	Vinciguerria nimbaria	Mesopelagic	Carnivore	La Pérouse	8	3	31-45	39.7 ± 7.73	11.3	-18.9	0.18 ± 0.04	3.9
	Sternoptychidae											
	Argyropelecus aculeatus	Mesopelagic	Carnivore	La Pérouse	7	2	54-63	58.9 ± 6.29			0.26 ± 0.16	
				MAD-Ridge	1, 2, 5, 12	4	54-81	66.6 ± 14.5	10.8 ± 2.0	-18.4 ± 0.42	0.55 ± 0.42	4.1 ± 0.64
				Reunion Is	1	3	19-38	30.6 ± 10.3			0.09 ± 0.01	
	Stomiidae											
	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 ± 0.01	
			MAD-Ridge	1	2	112-199	155.5 ± 61.4	10.9 ± 0.47	-18.9 ± 0.13	0.11 ± 0.01	4.1 ± 0.15
			MZC	20	2	121-202	161.8 ± 57.3	10.8 ± 1.1	-19.1 ± 0.38	0.11 ± 0.04	4.1 ± 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 ± 23.9	8.8 ± 0.57	-19.4 ± 0.16	0.08 ± 0.02	3.4 ± 0.18
Echiostoma barbatum	Mesopelagic-Bathypelagic	Carnivore	MAD-Ridge	9, 10, 11	5	68-81	72.3 ± 5.21	9.48 ± 1.11	-18.5 ± 0.30	0.15 ± 0.06	3.6 ± 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 ± 0.29	9.81 ± 0.81	-18.1 ± 0.53	0.20 ± 0.07	3.7 ± 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 ± 0.62	-18.1 ± 0.62	0.22 ± 0.12	4.0 ± 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 longibarbatus	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 ± standard deviations of Hg concentrations (µg g^{-1} dw) of the broad categories (crustaceans, fishes and squids) at La Pérouse, MAD-Ridge seamounts, the southern Mozambique Channel and Reunion Island.

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