
Trace elements and $\delta^{15}\text{N}$ values in micronekton of the south-western Indian Ocean

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Abstract :

Trace elements and $\delta^{15}\text{N}$ values were analysed in micronekton (crustaceans, fishes and squids) sampled in the south-western Indian Ocean. Myctophids were associated with high concentrations of arsenic at La Pérouse and MAD-Ridge seamounts, and with lead and manganese at MAD-Ridge and in the Mozambique Channel. The difference in cadmium, copper and zinc concentrations between micronekton broad categories reflected differing metabolic and storage processes. When significant, negative relationships were found between micronekton body size and trace element concentrations, which can possibly be attributed to differing metabolic activity in young and old individuals, dietary shifts and/or dilution effect of growth. No relationships were found between trace element concentrations and $\delta^{15}\text{N}$ values of micronekton (except cobalt which decreased with increasing $\delta^{15}\text{N}$ values), since most trace elements are not biomagnified in food webs due to regulation and excretion processes within organisms. All trace element pairs were positively correlated in fishes suggesting regulation processes.

Highlights

- Elemental concentrations vary among myctophids across the south western Indian Ocean study sites.
- Cu and Zn were higher in crustaceans than fishes.
- Trace element concentrations decreased/showed no change with micronekton body size.
- Only Co decreased with increasing $\delta^{15}\text{N}$ values of fishes.

Keywords : Crustaceans, Fishes, Myctophids, Squids, Body size, Seamounts, Principal Component Analysis

1 Introduction

Micronekton are organisms of 2–20 cm in size, able to swim independently of ocean currents (Brodeur and Yamamura, 2005; De Forest and Drazen, 2009) which differentiate them from phytoplankton (which drift with currents) and micro- to macro- zooplankton (20 μm –2 cm). The crustaceans, small-sized fishes and cephalopods which comprise the micronekton, are the main prey of a wide range of predators including tunas, billfishes, sharks, marine birds and marine mammals (Guinet et al., 1996; Potier et al., 2007; Lambert et al., 2014; Filmlalter et al., 2017; Romanov et al., 2020). Micronekton also play a key role in the biological pump by transporting organic carbon from the euphotic to deeper parts of the ocean (Hidaka et al., 2001; Le Moigne, 2019) through their diel vertical migration patterns (Béhagle et al., 2014; Ariza, 2015; Annasawmy et al., 2018, 2019, 2020a). Within the micronekton, are a widespread group, the myctophids, represented by ~ 250 species in 33 genera, and accounting for 75% of trawled mesopelagic fish biomass and an estimated global biomass of 600 million metric tons (Catul et al., 2011). Myctophid species play an important role in the transfer of contaminants they bioaccumulate to higher trophic levels (Cipro et al., 2018; Figueiredo et al., 2020; Seco et al., 2020). While trace element concentrations in some myctophid and various top predator species such as tunas and swordfish have been previously investigated (Bustamante et al., 2003; Storelli et al., 2005; Chen et al., 2014; Torres et al., 2016; Chouvelon et al., 2017; Cipro et al., 2018; Houssard et al., 2019), the concentrations in crustaceans, fishes and squids have been poorly described in the south-western Indian Ocean.

Trace elements are defined here as those occurring in trace amounts within micronekton (typically < 0.01% of the organism), and excluding the macronutrients calcium, magnesium, potassium and sodium (Marsden and Rainbow, 2004). While trace elements such as iron (Fe), manganese (Mn), selenium (Se) and zinc (Zn) are essential (i.e., micronutrients) to the normal functioning of an organism, cadmium (Cd), lead (Pb) and mercury (Hg) are non-essential elements, with no known biological function (Mason, 2013). Certain metals including copper (Cu) and Zn and the metalloid Se are important in metabolic processes but they can be toxic in high doses (Hastie et al., 2009). Trace elements such as Hg can bioaccumulate to harmful levels when they are stored in the tissues of organisms faster than they can be detoxified and/or excreted (Hastie et al., 2009). Biomagnification of a trace element is its increase at each trophic level (Gray, 2002). Biomagnification is inferred when a significant positive relationship is observed between the element and $\delta^{15}\text{N}$ values (Cheung and Wang, 2008). The rate at which bioaccumulation (concentrations increase along time, so with age/size) and biomagnification

occur, depends on the availability of the trace element and species-specific physiological and ecological characteristics, with the ultimate concentration in an organism's tissue being influenced by the ability of the organism to excrete or store the element (Gray, 2002).

Growing energy demands have led to an increase in industrial production and anthropogenic emissions of trace elements such as Cd, chromium (Cr), Cu, Mn, Pb, Se, and Zn, which enter the atmosphere, aquatic and terrestrial ecosystems (Pacyna and Pacyna, 2001). Natural emissions of trace metals also vary and may arise from deflated soil and sediment, forest fire debris, volcanic, biogenic and oceanic emissions (Nriagu, 1989). This study determined the concentrations of 12 trace elements in pelagic nekton organisms collected from four specific and unique deep-water study sites (La Pérouse and MAD-Ridge seamounts, Reunion Island and the south-western Mozambique Channel) to elucidate their regional differences. Due to the differing oceanic environment at the four sites (shallow and intermediate seamounts vs island vs open ocean), we expected trace element concentrations to vary spatially. These trace elements included arsenic (As), Cd, Cr, cobalt (Co), Cu, Fe, Pb, Mn, nickel (Ni), Se, silver (Ag), and Zn.

The main objectives of this study were to document (1) trace element concentrations in the pelagic nekton assemblages (crustaceans, fishes and squids) in the Indian Ocean, (2) the difference in trace element concentrations between myctophids (most numerous species and individuals sampled) and other specimens, (3) the regional variability in trace element concentrations in myctophids, (4) the influence of body size (bioaccumulation process) and $\delta^{15}\text{N}$ values (biomagnification process) on trace element concentrations, and (5) metal-metal correlations across all four study sites to investigate metabolic or contamination relationships between the elements, and Se-mediated-Hg detoxification processes.

2 Materials and Methods

2.1 Study sites

The mesopelagic organisms were sampled onboard the RV *Antea* in the south-western Indian Ocean at the La Pérouse seamount in September 2016 (La Pérouse cruise, DOI: 10.17600/16004500), at Reunion Island in October 2016 (IOTA cruise, DOI: 10.17600/16004600), and at MAD-Ridge seamount and the Mozambique Channel in December 2016 (MAD-Ridge cruise, DOI: 10.17600/16004900) (Fig. 1).

2.2 Sampling of pelagic nekton

Pelagic nekton assemblages were sampled with an International Young Gadoid Pelagic Trawl net towed at a ship speed of ~2–3 knots for 60 min at La Pérouse (10 tows) and Reunion Island (3 tows) and 30 min at MAD-Ridge seamount (17 tows) and in the Mozambique Channel (4 tows). The trawl had a length of 40 m, an 80 mm knotless nylon delta mesh netting at the front tapering, a 5 mm mesh at the codend and a mouth opening of ~ 96 m². Trawls were conducted in shallow (0–200 m), intermediate (200–400 m) and deep (below 400) layers. La Pérouse trawls were conducted mostly during the night in shallow, intermediate and deep layers (Table 1), except 1 daytime shallow trawl. MAD-Ridge trawls were conducted during the day and night in shallow and deep layers, and during the night in the intermediate layer. Complete summary of these trawl stations is given in Annasawmy et al. (2019). Mozambique Channel trawls were carried out during the night only in shallow and deep layers. Trawls at Reunion Island were completed during the day only within the first 250 m of the water column.

The sampled organisms were sorted on board into gelatinous, crustaceans, fishes and cephalopods, counted and stored at –20°C. Only the micronekton broad categories crustaceans, fishes and squids were analysed during this study and are listed in Table 2. They were identified to the lowest possible taxon, weighed and measured (abdomen and carapace length for crustaceans, dorsal mantle length for squids and standard length for fishes) before further analyses (Sections 2.3–2.4).

A total of 53 taxa, including crustaceans (4 taxa), squids (5) and fishes (44) were sampled for trace element analyses (Table 2). Crustaceans were represented by the families Oplophoridae, Pasiphaeidae, Penaeidae and Sergestidae, and squids, by the families Enoploteuthidae, Histioteuthidae, Ommastrephidae and Pyroteuthidae. Fishes were dominant in the trawl catches (Cherel et al., 2020) and the families analysed for trace elements were Carangidae, Diretmidae, Gonostomatidae, Myctophidae, Neoscopelidae, Sternoptychidae and Stomiidae. Detailed information on the size ranges of the pelagic nekton assemblages can be found in Annasawmy et al. (2022) and Cherel et al. (2020); relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and total Hg concentrations with size, feeding habit and habitat range of pelagic nekton organisms can be found in Annasawmy et al. (2020b, 2022).

2.3 Trace element analyses

Tissue samples from selected specimens (muscular tissues taken from the abdomen for crustaceans, from the dorsal musculature for fishes, and from the mantle for squids) 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 min. The elements As, Ag, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn were analysed by inductively coupled plasma atomic emission spectrometry on a Varian Vista-Pro ICP-OES and by inductively coupled plasma mass spectrometry on a Thermo Fisher Scientific ICP-MS X Series II at the LIENSs laboratory (La Rochelle, France). The certified reference materials, dogfish liver (DOLT–5, National Research Council Canada) and lobster hepatopancreas (TORT–3, NRCC) were used to check the analytical performances for each trace element. Certified and measured trace element concentrations in reference materials TORT–3 and DOLT–5 are given in Supplementary Material 1. The concentrations of all trace elements are given in $\mu\text{g g}^{-1}$ dw (dry weight).

2.4 Stable isotope analyses

Prior to stable isotope analyses, lipids were removed from ground samples using dichloromethane on an accelerated solvent extraction system (ASE[®], Dionex). The lipid-free samples were weighed (~ 400–600 μg) in tin capsules, which were combusted through continuous flow in a Thermo Scientific Flash 2000 elemental analyser coupled to a Delta V Plus mass spectrometer at the Pôle de Spectrométrie Océan (Plouzané, France). The isotopic ratios were expressed in the conventional δ notations as parts per thousand (‰) deviations from international standards:

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

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

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

2.5 Statistical analyses

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) prior to running the statistical tests. Links between concentrations of the trace elements As, Ag, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn, and the micronekton broad categories (crustaceans, fishes and squids) were investigated using Kruskal-Wallis (KW) tests and pairwise Wilcoxon rank sum tests. The latter tests were also used to investigate trace element concentrations in Myctophidae family between the four sampling sites (La Pérouse, MAD-Ridge, Mozambique Channel and Reunion Island). Wilcoxon rank sum tests investigated the trace element concentrations between myctophids and all other specimens. To further investigate the spatial variability of trace element concentrations in myctophids, principal component analysis (PCA) was performed on square-root transformed and normalised data in Primer & Permanova v6 (Clarke and Warwick, 2001). Only the Myctophidae family was investigated between the sampling sites since they were the most numerous and abundant specimens collected across all four sites. Linear regressions were computed to assess the relationships between the above-mentioned trace elements with size of crustaceans, fishes and squids at all four study sites and with $\delta^{15}\text{N}$ values at La Pérouse, MAD-Ridge and the Mozambique Channel. Stable isotope ratios were not available at Reunion Island and hence the link between $\delta^{15}\text{N}$ values and trace element concentrations was not investigated at this site. Linear regressions were also computed to investigate metal-metal correlations in micronekton broad categories at all sites. The Se:Hg molar ratio (noted as Se:Hg) was calculated from the Se and Hg concentrations by dividing concentrations (in $\mu\text{g g}^{-1}$ wet weight) by the molecular weight (78.96 for Se and 200.59 for Hg). The relationships between Se:Hg and body size of crustaceans, fishes and squids were further investigated using linear regressions.

3 Results

3.1 Geographic and vertical distributions of trace elements

The concentrations of the trace elements As, Cu, Fe, Mn, Ni, Pb, Se, and Zn differed significantly across the micronekton broad categories (KW, pairwise comparisons, $p < 0.05$). Fishes and crustaceans showed similar overall median concentrations of Ag, Cd, and Co at all sampling sites (pairwise comparisons, $p > 0.05$). Squids had higher median As, Cd, Co, Cu,

Fe, Mn, Ni, Pb, Se, and Zn concentrations compared to crustaceans and fishes across all sampling sites (KW, pairwise comparisons, $p < 0.05$; Fig. 2). A comparison between families revealed decreasing concentrations of Cd with Enoploteuthids > Onychoteuthids > Histioteuthids > Pyroteuthids.

Co showed different mean concentrations between myctophids collected in the Mozambique Channel and those from Reunion Island and MAD-Ridge seamount (pairwise comparisons, $p < 0.05$; Fig. 3). Fe and Zn were the most predominant elements in myctophids, with values ranging up to $80 \mu\text{g g}^{-1} \text{ dw}$ (Fig. 3), while the elements Ag, Cd, Co, and Pb had the lowest concentrations ($< 1 \mu\text{g g}^{-1} \text{ dw}$). Myctophids showed lower mean As, Cd, Cu, and Zn concentrations compared to the other species ($p < 0.05$; Fig. 4a). The PCA analyses identified PC4 and PC5 that explained 78.6% cumulative variance in the trace metal concentrations in myctophids across the four sites. PC4 was positively associated with Ag and Co in myctophid samples collected from Reunion Island, and with As in myctophids from La Pérouse and MAD-Ridge seamounts (Table 3). PC5 was positively associated with Mn in myctophids from MAD-Ridge seamount and the Mozambique Channel. Similar to the KW tests, the PCA analyses showed that myctophids from Mozambique Channel and Reunion Island had differing trace element concentrations, notably, Co (Fig. 4b).

3.2 Relationships between trace element concentrations with size and $\delta^{15}\text{N}$ values

All significant relationships were negative between the trace element concentrations in crustaceans, fishes and squids, and body size at all sampling sites. Crustaceans showed decreasing Ag, Co, Cu, Fe, Mn, Ni, Pb, and Zn concentrations with increasing size ($p < 0.05$). Concentrations of Co, Cu, Fe, Ni, Se, and Zn decreased with increasing fish size ($p < 0.05$). In squids, Cu was the only trace element which showed a significant relationship with body size ($p < 0.05$) (Fig. 5). All the other trace elements showed no relationship with increasing micronekton size.

Of the trace elements analysed, only Co showed a significant negative relationship with $\delta^{15}\text{N}$ values of fishes ($p < 0.05$). The other trace elements did not show significant relationships with $\delta^{15}\text{N}$ values of crustaceans, fishes and squids at all sampling sites ($p > 0.05$).

3.3 Correlations between trace element concentrations

Correlations between trace element concentrations were investigated to establish whether there were significant links within the pelagic nekton to show possible metabolic or contamination relationships between the elements. All significant pairs showed positive correlations. Cu-Zn was the only trace element pair which was positively correlated in all three micronekton broad categories ($p < 0.05$, Table 4). Zn-Pb and Zn-Fe were positively correlated in squids sampled at all four sampling sites ($p < 0.05$). Cu-Fe, Cd-Ni and Pb-Fe were positively correlated in crustaceans ($p < 0.05$). All trace element pairs analysed (Zn-Fe, Zn-Pb, Zn-Cd, Cu-Pb, Cu-Ni, Cu-Cd, Cd-Fe, Pb-Ni, Pb-Fe, Ni-Cd, Cu-Fe and Ni-Fe) were positively correlated in fishes ($p < 0.05$).

While Se concentrations were positively correlated with Hg in fishes, the relationships between Se and Hg were not significant in crustaceans and squids (Fig. 6). The data showed that there was an excess of Se in relation to Hg (ratio Se:Hg > 1) in all pelagic nekton specimens, except 2 Oplophoridae (crustacean) and 1 *Sigmops elongatus* (fish) at La Pérouse seamount and Reunion Island where Se:Hg < 1 . The ratio Se:Hg exhibited no significant relationships with size of crustaceans, fishes and squids ($p < 0.05$) (Fig. 6). Fishes demonstrated significant positive correlations between Ag-Se, Cd-Se, Cu-Se and Zn-Se ($p < 0.05$) while no correlations were found in crustaceans ($p > 0.05$). The trace element pairs Ag-Se and Cu-Se showed significant positive correlations in squids ($p < 0.05$) (Fig. 7).

4 Discussion

4.1 Variability in trace element concentrations in micronekton broad categories

Trace element accumulation strategies vary between micronekton broad categories and between metals. Concentrations of As were higher in crustaceans relative to fishes, which is in accordance with previous studies (LeBlanc and Jackson, 1973). While crustaceans and fishes showed similar median concentrations of Ag, Cd, and Co, crustaceans showed higher concentrations of Cu and Zn compared to fishes. Higher Cu and Zn concentrations in crustaceans relative to fishes, is in accordance with previous observations (Amiard-Triquet, 1980) since Cu is known to associate with the respiratory pigment haemocyanin, and Zn to be involved in the stabilisation of the quaternary structure of this molecule in crustaceans (White and Rainbow, 1985). Diet is the main pathway of exposure for crustaceans and fish, so direct exposure from waterborne Ag (as for the other elements) is very limited (Mathews and Fisher, 2009; Weeks and Rainbow, 1993). Albeit in small amounts, both Ag and Co may be

accumulated from seawater for eggs, juveniles and adult squids (Bustamante et al., 2004a, 2004b). Furthermore, Ag is mainly stored in the digestive gland of invertebrates and in the liver of vertebrates, making muscles poorly relevant to assess the extent of contamination by this trace element for crustaceans, squids and fishes (Bustamante et al., 2004a, 2004b).

Generally, organisms have mechanisms to regulate body concentrations of essential elements such as Cu and Zn to constant body concentrations over a wide range of ambient trace element availabilities (Rainbow and White, 1989). White and Rainbow (1985) noted that the optimal minimum enzymatic Cu and Zn requirements are ~ 26 and $50 \mu\text{g g}^{-1}$ dw, respectively, in oceanic crustaceans. In our study, 29 crustaceans (all Penaeids and Sergestids) out of 41 (total) showed Cu concentrations less than the minimum metabolic requirement ($2\text{--}18 \mu\text{g g}^{-1}$ dw). Only 11 Penaeid and Sergestid individuals showed Zn concentrations below the minimum metabolic requirement ($41\text{--}49 \mu\text{g g}^{-1}$ dw). All Opolophorid and Pasiphaeid crustaceans showed Zn concentrations above $50 \mu\text{g g}^{-1}$ dw. In oceanic environments, as opposed to coastal ones, ambient trace element concentrations may be limiting and hence species inhabiting these regions may normally function with lower Cu and Zn concentrations. Organisms showing high concentrations of Cu and Zn may be able to metabolically store these elements under conditions of high ambient concentrations (White and Rainbow, 1985).

Squids showed higher concentrations of As, Cd, Co, Cu, Fe, Mn, Ni, Pb, Se, and Zn with respect to fishes and crustaceans at all four sites. Cephalopods are known to bioaccumulate higher concentrations of Cd, Cu, and Zn with respect to fishes (Bocher et al., 2003; Lahaye et al., 2005; Anderson et al., 2010) with the digestive gland of these organisms acting as the main storage organ for non-essential elements such as Ag and Cd, and for essential elements such as Cu, Fe, and Zn (e.g., Bustamante et al., 2006; 2008; Kojadinovic et al., 2011). The higher median Cd concentrations in squids relative to fishes and crustaceans may be related to retention processes that produce very elevated concentrations of this element in the tissues of cephalopods (Koyama et al., 2000; Bustamante et al., 2002). Cephalopods can store essential elements for metabolic processes and Ag, As, Cd, Co, Cr, Ni, and Pb as a result of their detoxification processes (Miramand and Bentley, 1992).

Cephalopod species are known to accumulate different concentrations of trace elements in their tissues, e.g., Histioteuthids and Ommastrephid squids have higher Cd concentrations compared to Loliginids (Lahaye et al., 2005; Pierce et al., 2008). However, the differing Cd concentrations between families observed in the present study may be due to the low number

of individuals per family with decreasing number of individuals Enoploteuthids > Onychoteuthids > Histioteuthids > Pyroteuthids collected at La Pérouse, MAD-Ridge seamounts and Reunion Island, rather than any previously described reasons linked to physical oceanographic processes, migration and foraging strategies of individuals (Lahaye et al., 2005). More investigations on trace elements in mesopelagic squids are needed. Micronekton broad categories therefore show different trace element concentrations possibly due to differential uptake, metabolic processes including assimilation, accumulation and elimination, behaviours and/or habitat use (Boalt et al., 2014).

4.2 Geographical variability in trace element concentrations

Little attention has been given to the concentrations of trace elements in myctophids and mesopelagic fishes in general, compared to the existing literature on several crustacean and squid taxa. The myctophids sampled at the different sites showed similar concentrations of Ag, Cd, Cr, Cu, Fe, Ni, Se, and Zn but higher concentrations of As in myctophids sampled at La Pérouse and MAD-Ridge seamounts compared to Reunion Island and the Mozambique Channel. This can possibly be attributed to the sediment organic matter at the seamounts binding As and anaerobic bacteria making it readily available to the overlying water column and marine organisms (Neff, 1997; LeBlanc and Jackson, 1973) feeding and migrating above the seamounts (Annasawmy et al., 2019; 2020b), as previously demonstrated for fishes at Condor seamount in the Atlantic (Raimundo et al., 2013). Studies showed regional differences in Cd, Cr, and Zn concentrations in tunas from Reunion Island and those in the southern Mozambique Channel (Chouvelon et al., 2017), which were attributed to the main prey of these predators (Kojadinovic et al., 2007). However, as shown in this study, micronekton trace element concentrations poorly reflect the geographic variability of Cd, Cr and Zn, observed previously in top predators. Other unexplained factors (such as differences in foraging behaviour and prey types of individuals, elemental availability, and accumulation, assimilation and regulation mechanisms) may describe the previous regional level differences in tunas.

Overall, Pb concentrations were low in myctophids, in accordance with studies showing a low degree of contamination of the oceanic environment (Morley et al., 1993) and in micronekton predators (skipjack, yellowfin tunas and swordfish) of the western Indian Ocean (Kojadinovic et al., 2007). This also suggests that the volcanic activity in Reunion Island has no measurable effect on Pb input into the surrounding marine ecosystem as observed previously (Torres et al.,

2016), or that the half-life of Pb in water is too short as suggested by Kojadinovic et al. (2007), and/or that Pb bioaccumulates along the food chains. In accordance with studies showing higher Mn concentrations in the liver of Dolphinfish from the Mozambique Channel compared to those from Reunion Island (Kojadinovic et al., 2007), myctophids from the Mozambique Channel and MAD-Ridge seamount were associated with higher Mn concentrations compared to those from Reunion Island. The bottom sediments of the southern African margin are believed to be a source of manganese nodules which can be supplied to the water column by agitation of the seafloor sediments (Summerhayes and Willis, 1975), upwelling within mesoscale activities (as observed for other trace elements in other regions; Bustamante et al., 2003), and/or plankton “recycling” (Summerhayes and Willis, 1975), thereby making Mn available to higher trophic levels.

Myctophids sampled in this study showed a predominance of Fe and Zn, and low concentrations of Ag, Cd, Co, and Pb compared to other nektonic species. Myctophids from the south west coast of India, southwestern Taiwan and the Gulf of California were also found to be enriched in Fe and Zn (Chai et al., 2012; Sankar et al., 2016). Fe is important for many biochemical processes such as the storage and transport of oxygen in fishes (Galbraith et al., 2019). Similar to this study, Co was the least abundant element in myctophids of the Gulf of California (Figueiredo et al., 2020). The prevalence of micronutrients (such as Fe, Se, and Zn) in myctophids, make them attractive candidates for fish meal and dietary supplements to combat mineral deficiencies (Alvheim et al., 2020).

Concentrations of Ag, As, Cd, Co, Cr, Cu, Mn, Pb, Se, and Zn in the mesopelagic fishes *Chauliodus sloani*, *Sigmops elongatus* and *Ceratoscopelus warmingii* were within the same range of values as those recorded for similar specimens of a similar size range from the Sulu, Celebes and Philippine Seas (South China) (Asante et al., 2010). This may be likely due to similar biochemical processes occurring within these organisms irrespective of the location. A significant proportion of the sampled micronekton specimens showed trace metal concentrations slightly above the permitted levels determined by European and worldwide legislations (Cd: 2.0; Cr: 0.65–4.35; Ni: 0.5–0.6; Zn: 50 $\mu\text{g g}^{-1}$ dw) (FAO, 1983; World Health Organization, 1985, 1989). With the worldwide rise in levels of certain pollutants due to anthropogenic activities (Kubier et al., 2020), and the rising interest in the commercial exploitation of micronekton, these organisms will have to be regularly monitored for their trace element concentrations so as not to pose a threat for human consumption.

4.3 Influence of biological processes on trace elements in pelagic nekton assemblages

Generally, concentrations of most trace elements decreased or showed no change with increasing size of micronekton at all sites. This observation is well supported in literature, for example, trace element accumulation is higher in younger fish (Kojadinovic et al., 2007) since metabolic activity would be higher than in older fish (Canli and Atli, 2003), thereby showing the decreasing trace element concentration with size. Decreasing bioaccumulation rate in cephalopod species have been attributed to dietary shifts with increasing body size, with smaller squids feeding on invertebrates with higher trace element burdens and exhibiting longer and more intense feeding activities and faster metabolism than bigger/mature squids feeding mainly on fish (Gerpe et al., 2000; Pierce et al., 2008; Chauvelon et al., 2011) and/or detoxification processes with maturation (Lischka et al., 2018). The negative correlation between trace elements and body size may further be explained by compositional changes in muscle (Díaz et al., 1994) and/or a dilution effect of growth on elemental levels (Kojadinovic et al., 2007, 2011; Pierce et al., 2008). Elements such as Ag are not efficiently bioaccumulated in some marine organisms (except cephalopods) due to detoxification mechanisms and its low bioavailability (Cheung and Wang, 2008). Muscle tissues being analysed may not display high trace element burdens as opposed to the digestive gland, liver and kidneys of organisms since trace element bioaccumulation is also tissue-specific (Bustamante et al., 2003; Bustamante et al., 2006; Murthy et al., 2008; Boalt et al., 2014).

All trace elements, except Co, showed no relationship with $\delta^{15}\text{N}$ values in the micronekton broad categories. Biomagnification of a trace element (i.e., increasing concentrations along the food webs) is trace element-specific (Cheung and Wang, 2008). Most trace elements are not biomagnified in food webs due to regulation and excretion processes within organisms (Gray, 2002), and because of their inefficient trophic transfer (Watras et al., 1998). A lack of biomagnification, as reported in other food chains, may therefore be linked to “trophic dilution” or biodiminution resulting from low bioavailability of the element, low assimilation efficiencies, enhanced excretion rates, and dilution effect by larger organisms (Briand et al., 2018), or by the incomplete inclusion of the entire food web (Cheung and Wang, 2008). The only significant (negative) relationship was observed between Co and $\delta^{15}\text{N}$ values in fishes suggesting a biodiminution of this element along the food chain, which is in accordance with previous observations from the Bay of Biscay in the northeast Atlantic (Chauvelon et al., 2021).

4.4 Metal-metal correlations

All significant trace element pairs showed positive correlations. Cadmium showed positive correlations with Cu, Fe, Ni and Zn in fishes, and with Ni in crustaceans. In marine invertebrates, trace elements such as Cd may bind to metallothioneins, thereby reducing the amount of free metal ions in the body of the organism (Bustamante et al., 2004a, 2004b). Studies have also noted positive correlations between concentrations of Cd and concentrations of Cu and Zn, suggesting that metallothioneins may act as a sink for toxic Cd and excess Cu and Zn in marine species (Kojadinovic et al., 2007; Mitra et al., 2012; Cipro et al., 2014).

Selenated molecules are metabolized for specific roles in marine organisms such as in the glutathione peroxidase pathway, which offers protection against free radical damage with excess Se being excreted (Keating and Caffrey, 1989; Maher et al., 1992). Selenium may also reduce the availability of methylmercury by sequestering Hg, thus decreasing its toxicity (Sasakura and Suzuki, 1998; Feroci et al., 2005; Ralston and Raymond, 2010). The lack of correlations between Se and Hg in crustaceans and squids may provide an argument for the lack of Se-mediated-Hg detoxification processes in these organisms compared to fishes. The weak positive Se-Hg correlation in fishes is in agreement with previous studies (Kehrig et al., 2013). Se was in molar excess relative to Hg in almost all specimens (Se:Hg > 1). The concentrations of Hg might not be sufficient to lead to a detoxification response by Se. Significant positive relationships were observed between Se and Ag, Cd, Cu, and Zn since Se may likely bind to these trace elements in fishes and to Ag and Cu in squids to form a complex with selenoproteins, thereby decreasing the concentrations of these metal ions in the organisms and protecting against toxicity (Sasakura and Suzuki, 1998; Feroci et al., 2005). Such mechanisms seem to be absent in the crustaceans studied here since none of the metal-Se interactions were significant.

5 Conclusions

Similar patterns of elemental concentrations, and relationships with size and $\delta^{15}\text{N}$ values in crustaceans, fishes and squids were found between the present and previous studies, likely due to similar biochemical processes occurring within these organisms irrespective of the location. However, in myctophids, As showed higher concentrations at La Pérouse seamount, and Mn concentrations were higher at MAD-Ridge seamounts and the Mozambique Channel, which were likely related to the environmental and biophysical parameters at these different sites. The

variable Cd concentrations in different squid families remain to be explained. Se-mediated protection against toxicity was demonstrated for specific trace elements and mostly in fish. Despite some limitations, to our knowledge, this study is the first one to add unprecedented insight on the trace element concentrations in crustaceans, fishes and squids of the south-western Indian Ocean. Since the trace element concentrations were not available for lower trophic levels, future studies will look at element concentrations in the atmosphere, water column, and in zooplankton of the south-western Indian Ocean.

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References

- Alvheim, A.R., Kjellevoll, M., Strand, E., Sanden, M., Wiech, M., 2020. Mesopelagic Species and Their Potential Contribution to Food and Feed Security—A Case Study from Norway. *Foods* 9, 344. <https://doi.org/10.3390/foods9030344>
- Amiard-Triquet, C., 1980. Etude du transfert de Cd, Pb, Cu et Zn dans les chaînes trophiques maritimes et estuariennes—II. Accumulation biologique chez les poissons planctonophages. *Water Res.* 14, 1327–1332. [https://doi.org/10.1016/0043-1354\(80\)90193-1](https://doi.org/10.1016/0043-1354(80)90193-1)
- Anderson, O.R.J., Phillips, R.A., Shore, R.F., McGill, R.A.R., McDonald, R.A., Bearhop, S., 2010. Element patterns in albatrosses and petrels: Influence of trophic position, foraging range, and prey type. *Environ. Pollut.* 158, 98–107. <https://doi.org/10.1016/j.envpol.2009.07.040>
- Annasawmy, P., Point, D., Romanov, E.V., Bodin, N., 2022. Mercury concentrations and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in pelagic nekton assemblages of the south-western Indian Ocean. *Mar. Pollut. Bull.* <https://doi.org/10.1016/j.marpolbul.2021.113151>
- 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 Loc'h, F., Ménard, F., Ternon, J.-F., Marsac, F., 2020b. Stable isotope patterns of mesopelagic communities over two shallow seamounts of the south-western Indian Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 176, 104804. <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. *Prog. Oceanogr.* 178, 102161. <https://doi.org/10.1016/j.pcean.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 Res. Part Oceanogr. Res. Pap.* 138, 85–97. <https://doi.org/10.1016/j.dsr.2018.07.002>
- Ariza, A., 2015. Micronekton diel vertical migration and active flux in the subtropical Northeast Atlantic. Universidad de Las Palmas De Gran Canaria.
- 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 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) 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>
- 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 Res. Part II Top. Stud. Oceanogr.* 100, 164–173. <https://doi.org/10.1016/j.dsr2.2013.10.024>
- 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. *Mar. Pollut. Bull.* 78, 130–136. <https://doi.org/10.1016/j.marpolbul.2013.10.051>
- Bocher, P., Caurant, F., Miramand, P., Cherel, Y., Bustamante, P., 2003. Influence of the diet on the bioaccumulation of heavy metals in zooplankton-eating petrels at Kerguelen archipelago, Southern Indian Ocean. *Polar Biol.* 26, 759–767. <https://doi.org/10.1007/s00300-003-0552-6>
- Briand, M.J., Bustamante, P., Bonnet, X., Churlaud, C., Letourneur, Y., 2018. Tracking trace elements into complex coral reef trophic networks. *Sci. Total Environ.* 612, 1091–1104. <https://doi.org/10.1016/j.scitotenv.2017.08.257>
- Brodeur, R.D., Yamamura, O., 2005. PICES Scientific Report No. 30 Micronekton of the North Pacific. PICES Scientific Report, Sidney, B.C., Canada, pp. 1–115.
- Bustamante, P., González, A.F., Rocha, F., Miramand, P., Guerra, A., 2008. Metal and metalloid concentrations in the giant squid *Architeuthis dux* from Iberian waters. *Mar. Environ. Res.* 66, 278–287. <https://doi.org/10.1016/j.marenvres.2008.04.003>
- Bustamante, P., Bertrand, M., Boucaud-Camou, E., Miramand, P., 2006. Subcellular distribution of Ag, Cd, Co, Cu, Fe, Mn, Pb, and Zn in the digestive gland of the common cuttlefish *Sepia officinalis*. *Journal of Shellfish Research*, 25(3), 987–993.
- Bustamante, P., Morales, C. F., Mikkelsen, B., Dam, M., Caurant, F., 2004. Trace element bioaccumulation in grey seals *Halichoerus grypus* from the Faroe Islands. *Marine Ecology Progress Series*, 267, 291–301.
- Bustamante, P., Teyssié, J-L., Danis, B., Fowler, S., Miramand, P., Cotret, O., Warnau, M., 2004. Uptake, transfer and distribution of silver and cobalt in tissues of the common cuttlefish *Sepia officinalis* at different stages of its life cycle. *Mar. Ecol. Prog. Ser. Inter Research*, 269, 185–195. [10.3354/meps269185](https://doi.org/10.3354/meps269185)
- Bustamante, P., Bocher, P., Chérel, Y., Miramand, P., Caurant, F., 2003. Distribution of trace elements in the tissues of benthic and pelagic fish from the Kerguelen Islands. *Sci. Total Environ.* 313, 25–39. [https://doi.org/10.1016/S0048-9697\(03\)00265-1](https://doi.org/10.1016/S0048-9697(03)00265-1)
- Bustamante, P., Cosson, R. P., Gallien, I., Caurant, F., Miramand, P., 2002. Cadmium detoxification processes in the digestive gland of cephalopods in relation to accumulated cadmium concentrations. *Marine environmental research*, 53(3), 227–241.
- Canli, M., Atli, G., 2003. The relationships between heavy metal (Cd, Cr, Cu, Fe, Pb, Zn) levels and the size of six Mediterranean fish species. *Environ. Pollut.* 121, 129–136. [https://doi.org/10.1016/S0269-7491\(02\)00194-X](https://doi.org/10.1016/S0269-7491(02)00194-X)
- Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21, 339–354. <https://doi.org/10.1007/s11160-010-9176-4>
- 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 Res. Int.* 46, 118–126. <https://doi.org/10.1016/j.foodres.2011.12.008>
- 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*). *Mar. Pollut. Bull.* 85, 606–612. <https://doi.org/10.1016/j.marpolbul.2014.01.039>
- Cherel, Y., Romanov, E.V., Annasawmy, P., Thibault, D., Ménard, F., 2020. Micronektonic fish species over three seamounts in the southwestern Indian Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 176, 104777. <https://doi.org/10.1016/j.dsr2.2020.104777>
- Cheung, M.S., Wang, W.-X., 2008. Analyzing biomagnification of metals in different marine food webs using nitrogen isotopes. *Mar. Pollut. Bull.* 56, 2082–2088. <https://doi.org/10.1016/j.marpolbul.2008.09.004>

- Chouvelon, T., Munsch, C., Bruzac, S., Caurant, F., Churlaud, C., Crochet, S., Guillou, G., Mauffret, A., Méndez-Fernandez, P., Niol, J., Sireau, T., Steinberg, C., Wessel, N., Spitz, J., 2021. High inter-species variability in elemental composition of the twilight zone fauna varies implications for predators and exploitation by humans. *Environ. Res.* 112379. <https://doi.org/10.1016/j.envres.2021.112379>
- Chouvelon, T., Brach-Papa, C., Auger, D., Bodin, N., Bruzac, S., Crochet, S., Degroote, M., Hollanda, S.J., Hubert, C., Knoery, J., Munsch, 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. *Sci. Total Environ.* 596–597, 481–495. <https://doi.org/10.1016/j.scitotenv.2017.04.048>
- Chouvelon, T., Spitz, J., Cherel, Y., Caurant, F., Sirmel, R., Méndez-Fernandez, P., Bustamante, P., 2011. Species and ontogenic-related differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and Hg and Cd concentrations of cephalopods. *Mar. Ecol. Prog. Ser.* 433, 107–120. DOI: 10.3354/meps09159
- Cipro, C.V.Z., Cherel, Y., Bocher, P., Caurant, F., Miramand, P., Bustamante, P., 2018. Trace elements in invertebrates and fish from Kerguelen waters, southern Indian Ocean. *Polar Biol.* 41, 175–191. <https://doi.org/10.1007/s00300-017-2180-6>
- Cipro, C.V.Z., Cherel, Y., Caurant, F., Miramand, P., Méndez-Fernandez, P., Bustamante, P., 2014. Trace elements in tissues of white-chinned petrels (*Procellaria aequinoctialis*) from Kerguelen waters, Southern Indian Ocean. *Polar Biol.* 37, 763–771. <https://doi.org/10.1007/s00300-014-1476-z>
- Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, second ed. PRIMER-E, Plymouth, UK.
- De Forest, L., Drazen, J., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. *Deep Sea Res. Part Oceanogr. Res. Pap.* 56, 232–250. <https://doi.org/10.1016/j.dsr.2008.09.007>
- Díaz, C., Galindo, L., Montelongo, F. G., 1994. Distribution of metals in some fishes from Santa Cruz de Tenerife, Canary Islands. *Bulletin of environmental contamination and toxicology*, 52(3), 374–381.
- FAO, 1983. Compilation of legal limits for hazardous substances in fish and fishery products. *FAO Fish. Circ.* 464, 5–100.
- Feroci, G., Badiello, R., Fini, A., 2005. Interactions between different selenium compounds and zinc, cadmium and mercury. *Journal of Trace Elements in Medicine and Biology*, 18(3), 227–234.
- Figueiredo, C., Baptista, M., Grilo, T., Caetano, M., Markaida, U., Raimundo, J., Rosa, R., 2020. Bioaccumulation of Trace Elements in Myctophids in the Oxygen Minimum Zone Ecosystem of the Gulf of California. *Oceans* 1, 34–46. <https://doi.org/10.3390/oceans1010004>
- 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: feeding of *carcharhinus falciformis* at fads. *J. Fish Biol.* 90, 1321–1337. <https://doi.org/10.1111/jfb.13241>
- Galbraith, E.D., Le Mézo, P., Solanes Hernandez, G., Bianchi, D., Kroodsma, D., 2019. Growth Limitation of Marine Fish by Low Iron Availability in the Open Ocean. *Front. Mar. Sci.* 6, 509. <https://doi.org/10.3389/fmars.2019.00509>
- Gerpe, M. S., De Moreno, J. E. A., Moreno, V. J., Patat, M. L., 2000. Cadmium, zinc and copper accumulation in the squid *Illex argentinus* from the Southwest Atlantic Ocean. *Marine Biology*, 136(6), 1039–1044.

- Gray, J.S., 2002. Biomagnification in marine systems: the perspective of an ecologist. *Mar. Pollut. Bull.* 45, 46–52. [https://doi.org/10.1016/S0025-326X\(01\)00323-X](https://doi.org/10.1016/S0025-326X(01)00323-X)
- 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. *Antarct. Sci.* 8. <https://doi.org/10.1017/S0954102096000053>
- 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 80.
- 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.
- 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 from the Western and Central Pacific Ocean: Influence of Physiology, Ecology and Environmental Factors. *Environ. Sci. Technol.* 53, 1422–1431. <https://doi.org/10.1021/acs.est.8b06058>
- Keating, K.I., Caffrey, P.B., 1989. Selenium deficiency induced by zinc deprivation in a crustacean. *Proc. Natl. Acad. Sci.* 86, 6436–6440. <https://doi.org/10.1073/pnas.86.16.6436>
- Kehrig, H.A., Seixas, T.G., Di Benedetto, A.P.M., Malm, O., 2013. Selenium and mercury in widely consumed seafood from South Atlantic Ocean. *Ecotoxicol. Environ. Saf.* 93, 156–162. <https://doi.org/10.1016/j.ecoenv.2013.03.034>
- Kojadinovic, J., Jackson, C.H., Cherel, Y., Jackson, G.D., Bustamante, P., 2011. Multi-elemental concentrations in the tissues of the oceanic squid *Todarodes filippovae* from Tasmania and the southern Indian Ocean. *Ecotoxicol. Environ. Saf.* 74, 1238–1249. <https://doi.org/10.1016/j.ecoenv.2011.03.015>
- Kojadinovic, J., Potier, M., Le Corre, M., Cosson, R. P., Bustamante, P., 2007. Bioaccumulation of trace elements in pelagic fish from the Western Indian Ocean. *Environmental pollution*, 146(2), 548–566.
- Koyama, J., Nanamori, N., Segawa, S., 2000. Bioaccumulation of waterborne and dietary cadmium by oval squid, *Sepioteuthis lessoniana*, and its distribution among organs. *Marine Pollution Bulletin*, 40(11), 961–967.
- Kubier, A., Wilkin, R.T., Pichler, T., 2020. Cadmium in soils and groundwater: A review. *Appl. Geochem.* 108: 1–16. doi: 10.1016/j.apgeochem.2019.104388
- Lahaye, V., Bustamante, P., Spitz, J., Dabin, W., Das, K., Pierce, G., Caurant, F., 2005. Long-term dietary segregation of common dolphins *Delphinus delphis* in the Bay of Biscay, determined using cadmium as an ecological tracer. *Mar. Ecol. Prog. Ser.* 305, 275–285. <https://doi.org/10.3354/meps305275>
- 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 Tropical Regions. *PLoS ONE* 9, e105958. <https://doi.org/10.1371/journal.pone.0105958>
- Le Moigne, F.A.C., 2019. Pathways of Organic Carbon Downward Transport by the Oceanic Biological Carbon Pump. *Front. Mar. Sci.* 6, 634. <https://doi.org/10.3389/fmars.2019.00634>
- LeBlanc, P. J., Jackson, A. L. 1973. Arsenic in marine fish and invertebrates. *Marine Pollution Bulletin*, 4(6), 88–90.
- Lischka, A., Lacoue-Labarthe, T., Hoving, H.J.T., JavidPour, J., Pannell, J.L., Merten, V., Churlaud, C., Bustamante, P., 2018. High cadmium and mercury concentrations in the tissues of the orange-back flying squid, *Sthenoteuthis pteropus*, from the tropical

- Eastern Atlantic. *Ecotoxicol. Environ. Saf.* 163, 323–330.
<https://doi.org/10.1016/j.ecoenv.2018.07.087>
- Longhurst, A., 1998. In: *Ecological Geography of the Sea*. Academic Press, San Diego, p. 398.
- Maher, W., Baldwin, S., Deaker, M., Lrving, M., 1992. Characteristics of selenium in australian marine biota. *Appl. Organomet. Chem.* 6, 103–112.
<https://doi.org/10.1002/aoc.590060203>
- Marsden, I.D., Rainbow, P.S., 2004. Does the accumulation of trace metals in crustaceans affect their ecology - the amphipod example? *J. Exp. Mar. Biol. Ecol.* 300, 373–408.
[doi:10.1016/j.jembe.2003.12.009](https://doi.org/10.1016/j.jembe.2003.12.009)
- Mason, R.P., 2013. *Trace Metals in Aquatic Systems*. Blackwell Publishing Ltd (431 pp).
- Mathews, T., Fisher, N.S., 2009. Dominance of dietary intake of metals in marine elasmobranch and teleost fish. *Sci. Total Environ.* 407, 5156–5161.
[doi:10.1016/j.scitotenv.2009.06.003](https://doi.org/10.1016/j.scitotenv.2009.06.003)
- Miramand, P., Bentley, D., 1992. Concentration and distribution of heavy metals in tissues of two cephalopods, *Eledone cirrhosa* and *Sepia officinalis*, from the French coast of the English Channel. *Mar. Biol.* 114, 407–414. <https://doi.org/10.1007/BF00350031>
- Mitra, A., Barua, P., Zaman, S., Banerjee, K., 2012. Analysis of Trace Metals in Commercially Important Crustaceans Collected from UNESCO Protected World Heritage Site of Indian Sundarbans 15.
- Morley, N.H., Statham, P.J., Burton, J.D., 1993. Dissolved trace metals in the southwestern Indian Ocean. *Deep Sea Res. Part Oceanogr. Res. Pap.* 40, 1043–1062.
[https://doi.org/10.1016/0967-0637\(93\)90089-L](https://doi.org/10.1016/0967-0637(93)90089-L)
- Murthy, L. N., Panda, S. K., Madhu, V. R., Ashokan, P. K., Ghosh, S., Das, S., Badonia, R., 2008. Cadmium in the purple back flying squid *Sthenoteuthis oualanieensis* (Lesson 1830) along north west coast of India. *J. Mar. Biol. Ass. India.* 50(2), 191–195.
- Neff, J. M., 1997. Ecotoxicology of arsenic in the marine environment. *Environmental Toxicology and Chemistry: An International Journal*, 16(5), 917–927.
- Nriagu, J.O., 1989. A global assessment of natural sources of atmospheric trace metals. *Letters to Nature*, 338(2): 47–49.
- Pacyna, J.M., Pacyna, E.G., 2001. An assessment of global and regional emissions of trace metals to the atmosphere from anthropogenic sources worldwide. *Environmental Reviews*, 9(4): 269–298. <https://www.jstor.org/stable/10.2307/envirevi.9.4.269>
- Pierce, G.J., Stowasser, G., Hastie, L.C., Bustamante, P., 2008. Geographic, seasonal and ontogenetic variation in cadmium and mercury concentrations in squid (*Cephalopoda: Teuthoidea*) from UK waters. *Ecotoxicol. Environ. Saf.* 70, 422–432.
<https://doi.org/10.1016/j.ecoenv.2007.07.007>
- 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. *Fish. Res.* 83, 60–72.
<https://doi.org/10.1016/j.fishres.2006.08.020>
- Raimundo, J., Vale, C., Caetano, M., Giacomello, E., Anes, B., Menezes, G.M., 2013. Natural trace element enrichment in fishes from a volcanic and tectonically active region (Azores archipelago). *Deep-Sea Res. II*, 98, 137–147.
- Rainbow, P.S., White, S.L., 1989. Comparative strategies of heavy metal accumulation by crustaceans: zinc, copper and cadmium in a decapod, an amphipod and a barnacle. *Hydrobiologia* 174, 245–262. <https://doi.org/10.1007/BF00008164>
- Ralston, N.V.C., Raymond, L.J., 2010. Dietary selenium's protective effects against methylmercury toxicity. *Toxicology* 278, 112–123.
<https://doi.org/10.1016/j.tox.2010.06.004>

- 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. *Mar. Freshw. Res.* 71, 1517. <https://doi.org/10.1071/MF19332>
- Sankar, T.V., Baby, L., Anandan, R., 2016. Organochlorine Pesticides, Polychlorinated Biphenyls and Heavy Metals Residues in Myctophids off South West Coast of India. *Fishery Technology.* 53, 250-256.
- Sasakura, C., Suzuki, K. T., 1998. Biological interaction between transition metals (Ag, Cd and Hg), selenide/sulfide and selenoprotein P. *Journal of inorganic biochemistry*, 71(3-4), 159-162.
- Seco, J., Xavier, J.C., Bustamante, P., Coelho, J.P., Saunders, R.A., Ferreira, N., Fielding, S., Pardal, M.A., Stowasser, G., Viana, T., Tarling, G.A., Pereira, E., Brierley, A.S., 2020. Main drivers of mercury levels in Southern Ocean lantern fish Myctophidae. *Environ. Pollut.* 264, 114711. <https://doi.org/10.1016/j.envpol.2020.114711>
- 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>.
- Storelli, M.M., Giacomini-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. *Mar. Pollut. Bull.* 50, 1004–1007. <https://doi.org/10.1016/j.marpolbul.2005.06.041>
- Summerhayes, C.P., Willis, J.P., 1975. Geochemistry of manganese deposits in relation to environment on the sea floor around southern Africa. *Mar. Geol.* 18, 159–173. [https://doi.org/10.1016/0025-3227\(75\)90094-8](https://doi.org/10.1016/0025-3227(75)90094-8)
- Torres, P., Rodrigues, A., Soares, L., Garcia, P., 2016. Metal Concentrations in Two Commercial Tuna Species from an Active Volcanic Region in the Mid-Atlantic Ocean. *Arch. Environ. Contam. Toxicol.* 70, 341–347. <https://doi.org/10.1007/s00244-015-0249-1>
- Watras, C.J., Back, R.C., Halvorsen, S., Hudson, R.J.M., Morrison, K.A., Wentz, S.P., 1998. Bioaccumulation of mercury in pelagic freshwater food webs. *Sci. Total Environ.* 219, 183–208. [https://doi.org/10.1016/S0048-9697\(98\)00228-9](https://doi.org/10.1016/S0048-9697(98)00228-9)
- Weeks, J.M., Rainbow, P.S., 1993. The relative importance of food and seawater as sources of copper and zinc to Talitrid Amphipods (Crustacea: Amphipoda; Talitridae). *J. Appl. Ecol.* 30(4), 722-735.
- White, S.L., Rainbow, P.S., 1985. On the metabolic requirements for copper and zinc in molluscs and crustaceans. *Mar. Environ. Res.* 16, 215–229. [https://doi.org/10.1016/0141-1136\(85\)90139-4](https://doi.org/10.1016/0141-1136(85)90139-4)
- World Health Organization, 1985. Guidelines for drinking water quality (ii): Health criteria and supporting information. Geneva: p. 130.
- World Health Organization, 1989. Evaluation of certain food additives and the contaminants mercury, lead and cadmium. WHO Technical report Series No. 505.

Table 1. Summary of trawl stations at La Pérouse, MAD-Ridge seamounts, Mozambique Channel and Reunion Island.

Region	Trawl No.	Depth Category	Time of day
La Pérouse	1	Deep	Night
	2	Deep	Night
	3	Shallow	Night
	4	Shallow	Night
	5	Shallow	Day
	6	Shallow	Night
	7	Deep	Night
	8	Deep	Night
	9	Intermediate	Night
	10	Intermediate	Night
MAD-Ridge	1	Deep	Day
	2	Deep	Night
	3	Shallow	Night
	4	Shallow	Day
	5	Intermediate	Night
	6	Shallow	Night
	7	Deep	Day
	8	Shallow	Night
	9	Shallow	Night
	10	Deep	Day
	11	Shallow	Night
	12	Deep	Night
	13	Deep	Day
	14	Intermediate	Night
	15	Shallow	Night
	16	Intermediate	Night
	17	Deep	Day
Mozambique Channel	18	Deep	Night
	19	Shallow	Night
	20	Deep	Night
	21	Shallow	Night
Reunion Island	1	Intermediate	Day
	3	Intermediate	Day
	5	Intermediate	Day

Table 2. Concentrations ($\mu\text{g g}^{-1}$ dw) of trace elements, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in pelagic nekton assemblages at La Pérouse and MAD-Ridge seamounts, the south-western Mozambique Channel (MZC) and Reunion Island. Values are given in mean \pm standard deviation.

Family/ Species	Region	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Hg	Ag	As	Cd	Co	Cr	Cu	Fe	Mn	Ni	Pb	Se	Zn
Crustaceans																	
Oplophoridae	La Pérouse	5	11.4	-18.1	0.78	0.22	28.7	0.15	0.10	0.39	51.3	29.9	0.79	0.47	0.04	2.10	64.6
			\pm 0.16	\pm 0.45	\pm 0.57	\pm 0.18	\pm 15.2	\pm 0.08	\pm 0.03	\pm 0.18	\pm 26.2	\pm 14.6	\pm 0.15	\pm 0.32	\pm 0.02	\pm 0.36	\pm 0.36
	MAD-Ridge	4	9.63	-18.3	0.40	0.35	24.1	0.07	0.11	1.10	54.3	26.2	0.89	0.42	0.08	2.41	71.5
			\pm 0.56	\pm 0.35	\pm 0.16	\pm 0.08	\pm 0.75	\pm 0.04	\pm 0.07	\pm 0.24	\pm 26.0	\pm 4.57	\pm 0.29	\pm 0.07	\pm 0.02	\pm 0.86	\pm 0.86
	Reunion Is	3			0.64	0.39	46.5	0.41	0.14	0.43	53.5	23.3	0.86	0.39	0.05	2.22	85.2
					\pm 0.81	\pm 0.09	\pm 24.5	\pm 0.20	\pm 0.02	\pm 0.17	\pm 25.4	\pm 3.85	\pm 0.12	\pm 0.16	\pm 0.02	\pm 0.25	\pm 0.25
Pasiphaeidae																	
<i>Pasiphaea</i> spp.	La Pérouse	2	9.82	-18.0	0.18	0.07	99.1	0.09	0.07	0.53	13.5	21.0	0.44	0.47	0.06	4.09	61.1
Penaeidae																	
<i>Funchalia</i> sp.	La Pérouse	2	7.77	-19.2	0.07	0.05	44.0	0.19	0.10	0.41	5.88	16.4	0.25	0.29	0.05	2.04	50.4
	MAD-Ridge	5	7.28	-18.5	0.11	0.02	48.6	0.14	0.03	2.22	5.38	18.6	0.51	0.24	0.03	2.02	51.8
			\pm 0.68	\pm 0.18	\pm 0.04	\pm 0.00	\pm 12.7	\pm 0.05	\pm 0.01	\pm 1.66	\pm 2.76	\pm 11.7	\pm 0.14	\pm 0.16	\pm 0.01	\pm 0.39	\pm 0.39

	MZC	2	7.15	-19.1 ± 0.44	0.09 ± 0.04	0.02	23.1	0.09	0.04	0.54	7.62	8.19	0.36	0.33	0.02	1.43	60.1
	Reunion Is	4			0.08 ± 0.02	0.01 ± 0.00	42.0 ± 18.1	0.08 ± 0.07	0.04 ± 0.01	0.14 ± 0.05	9.67 ± 2.16	6.88 ± 2.84	0.31 ± 0.05	0.11 ± 0.01	0.02 ± 0.01	2.25 ± 0.29	50.9 ± 4.55
Sergestidae	La Pérouse	4	11.2 ± 1.50	-18.7 ± 0.01	0.32 ± 0.05	0.03 ± 0.01	24.9 ± 5.37	0.11 ± 0.03	0.04 ± 0.01	0.43 ± 0.19	4.53 ± 1.83	27.2 ± 11.7	0.57 ± 0.19	0.22 ± 0.04	0.04 ± 0.01	2.21 ± 0.08	57.2 ± 6.89
	MAD- Ridge	1	9.01	-18.8	0.18	0.02	7.16	0.77	0.02	0.60	6.06	7.80	0.47	0.34	0.03	2.24	40.6
	MZC	4	9.79 ± 0.54	-19.2 ± 0.22	0.20 ± 0.08	0.03 ± 0.01	24.1 ± 15.1	0.75 ± 0.72	0.04 ± 0.02	1.19 ± 1.12	9.98 ± 4.49	11.5 ± 7.19	0.53 ± 0.11	0.78 ± 0.78	0.03 ± 0.02	3.08 ± 1.47	57.1 ± 18.0
	Reunion Is	5			0.17 ± 0.13	0.05 ± 0.04	36.2 ± 12.2	0.57 ± 0.47	0.05 ± 0.03	0.31 ± 0.29	10.0 ± 1.91	7.79 ± 2.62	0.60 ± 0.25	0.51 ± 0.27	0.09 ± 0.08	3.53 ± 1.05	60.9 ± 27.5
Squids																	
Enoploteuthidae	MAD- Ridge	2	8.04	-18.6	0.05 ± 0.01	0.02	80.6	2.08	0.07	2.82	14.4	48.2	1.45	1.87	0.07	5.13	67.7
	Reunion Is	7			0.09 ± 0.05	0.20 ± 0.12	57.0 ± 15.2	18.4 ± 8.26	0.21 ± 0.10	0.50 ± 0.21	39.0 ± 14.2	34.5 ± 9.62	2.85 ± 2.11	1.06 ± 0.43	0.20 ± 0.04	7.32 ± 2.03	97.7 ± 14.6

<i>Abraliopsis</i> sp.	La Pérouse	11	10.5 ± 0.45	-18.4 ± 0.48	0.07 ± 0.02	0.07 ± 0.10	81.0 ± 30.7	0.77 ± 1.03	0.12 ± 0.09	1.33 ± 1.30	27.3 ± 16.7	233.5 ± 218.8	1.79 ± 1.03	0.96 ± 0.54	0.22 ± 0.21	6.38 ± 2.53	145.6 ± 84.1
	MAD-Ridge	6	9.50 ± 0.48	-18.3 ± 0.59	0.10 ± 0.02	0.07 ± 0.07	26.9 ± 15.4	4.60 ± 5.41	0.17 ± 0.15	3.09 ± 1.85	19.0 ± 4.37	41.6 ± 17.3	2.88 ± 1.30	0.45 ± 0.15	0.28 ± 0.26	5.23 ± 2.41	85.5 ± 22.5
	Reunion Is	4			0.06 ± 0.01	0.23 ± 0.27	50.1 ± 6.67	12.4 ± 7.29	0.29 ± 0.22	0.25 ± 0.03	33.6 ± 19.0	28.3 ± 11.1	4.97 ± 2.53	0.80 ± 0.04	0.14 ± 0.08	10.8 ± 9.33	68.3 ± 9.95
Histioteuthidae																	
<i>Histioteuthis</i> spp.	La Pérouse	2	11.7	-19.1 ± 0.01	0.06 ± 0.002	0.05	91.0	2.35	0.13	1.33	19.1	123.7	3.71	1.13	0.62	5.88	117.3
	MAD-Ridge	1				0.02	51.5	0.07	0.03	1.71	26.9	33.8	2.30	0.56	0.13	2.29	78.6
	Reunion Is	3			0.07 ± 0.01	0.14 ± 0.04	71.5 ± 16.7	6.66 ± 5.70	0.13 ± 0.04	1.70 ± 1.38	26.2 ± 10.6	125.4 ± 84.4	2.98 ± 1.55	2.03 ± 1.55	0.42 ± 0.23	6.35 ± 3.13	153.9 ± 49.5
Onychoteuthidae																	
<i>Onychoteuthis</i> sp.	Reunion Is	9			0.05 ± 0.02	0.14 ± 0.08	63.4 ± 30.2	34.9 ± 30.2	0.16 ± 0.05	0.26 ± 0.07	25.9 ± 11.8	33.7 ± 28.1	3.61 ± 3.37	0.91 ± 0.32	0.11 ± 0.03	6.63 ± 0.90	86.9 ± 16.2
Pyroteuthidae																	

<i>Pyroteuthis</i> sp.	Reunion Is	2			0.14	0.52	43.6	8.19	0.18	1.37	48.0	48.4	4.47	3.45	0.19	14.1	97.6
Fishes																	
Diretmidae																	
<i>Diretmus argenteus</i>	MAD-Ridge	1	8.82	-19.9	0.31	0.02	34.9	0.03	0.04	0.53	1.62	14.2	2.04	0.73	0.04	4.19	27.6
Neoscopelidae																	
<i>Neoscopelus macrolepidotus</i>	MAD-Ridge	2	10.8	-19.2	0.42	0.03	7.58	0.03	0.04	1.79	2.70	18.7	0.86	1.00	0.07	2.74	27.5
<i>Neoscopelus microchir</i>	MAD-Ridge	2	11.0	-19.1	0.46	0.05	44.2	0.05	0.05	0.51	2.80	19.1	0.50	0.26	0.06	3.11	30.7
Myctophidae																	
<i>Benthoosema fibulatum</i>	MAD-Ridge	2	9.75	-18.7	0.32	0.02	17.0	0.08	0.06	0.63	4.01	36.2	0.70	0.42	0.02	4.67	25.0
<i>Benthoosema suborbitale</i>	MAD-Ridge	1				0.09	4.39	0.48	0.10	1.99		68.7		1.32	0.51	3.70	
<i>Bolinichthys photothorax</i>	La Pérouse	2	10.9	-18.7		0.09	23.3	0.10	0.09	0.84	4.44	33.3	0.93	0.55	0.09	5.56	38.1
<i>Ceratoscopelus warmingii</i>	La Pérouse	1			0.09	0.02		0.37	0.15	0.46	2.57	40.5	1.75	0.66	0.04	4.79	25.6

	MAD-Ridge	6	8.00 ± 0.73	-18.8 ± 0.45	0.11 ± 0.04	0.05 ± 0.02	4.62 ± 0.66	0.20 ± 0.09	0.12 ± 0.02	0.44 ± 0.20	5.62 ± 1.19	40.6 ± 6.73	3.26 ± 1.81	0.82 ± 0.35	0.17 ± 0.12	3.63 ± 0.84	50.4 ± 14.0
Myctophidae sp.	Reunion Is	3			0.09 ± 0.05	0.08 ± 0.08	8.36 ± 1.69	0.23 ± 0.14	0.19 ± 0.08	0.87 ± 0.72	5.29 ± 2.79	43.6 ± 22.0	0.84 ± 0.52	0.69 ± 0.28	0.09 ± 0.07	4.56 ± 1.95	42.5 ± 37.5
<i>Diaphus brachycephalus</i>	MAD-Ridge	2	10.8	-19.2	0.17	0.04	11.1	0.12	0.07	0.45	4.41	23.0	1.65	0.67	0.06	5.9	54.4
<i>Diaphus diadematus</i>	MAD-Ridge	4	9.52 ± 0.27	-19.9 ± 0.19	0.12 ± 0.14	0.06 ± 0.01	8.23 ± 3.24	0.37 ± 0.20	0.08 ± 0.01	1.62 ± 0.99	5.69 ± 0.80	55.6 ± 20.8	2.34 ± 0.64	0.83 ± 0.34	0.19 ± 0.04	5.90 ± 2.31	90.9 ± 26.9
<i>Diaphus effulgens</i>	MAD-Ridge	2	10.3	-19.1 ± 0.21	0.32 ± 0.16	0.02	4.04	0.06	0.03	0.57	2.42	17.9	0.66	0.31	0.02	2.91	21.8
<i>Diaphus knappi</i>	MAD-Ridge	2	10.2	-19.4	0.12	0.02	9.62	0.03	0.06	1.25	5.37	18.4	1.53	0.85	0.25	3.62	28.3
<i>Diaphus lucidus</i>	La Pérouse	3			0.34 ± 0.03	0.02 ± 0.00	6.48 ± 0.17	0.06 ± 0.08	0.05 ± 0.01	0.24 ± 0.10	3.08 ± 0.69	24.8 ± 1.82	0.80 ± 0.35	0.42 ± 0.24	0.03 ± 0.01	2.98 ± 0.36	17.0 ± 4.58
	MZC	2	11.3	-19.2	0.23	0.03	4.01	0.10	0.04	0.41	4.78	39.2	0.74	0.33	0.07	3.40	36.6
<i>Diaphus metoclampus</i>	MZC	2	12.1	-19.6	0.36	0.02	5.90	0.09	0.03	0.74	3.20	20.7	0.63	0.81	0.02	4.13	24.6

<i>Diaphus mollis</i>	MAD-Ridge	4	10.6 ± 1.01	-19.3 ± 0.02	0.22 ± 0.11	0.03 ± 0.01	15.7 ± 1.61	0.34 ± 0.38	0.09 ± 0.06	1.23 ± 0.49	3.18 ± 0.51	32.2 ± 16.7	1.44 ± 0.50	0.83 ± 0.42	0.04 ± 0.02	5.44 ± 2.06	35.5 ± 16.0
<i>Diaphus perspicillatus</i>	La Pérouse	1	11.1	-19.2	0.39	0.04	4.30	0.28	0.11	0.38	5.12	41.0	0.60	0.25	0.04	6.04	35.0
	MAD-Ridge	8	10.2 ± 0.55	-19.0 ± 0.20	0.37 ± 0.11	0.02 ± 0.01	5.30 ± 1.09	0.31 ± 0.22	0.10 ± 0.04	1.18 ± 0.97	4.93 ± 24.1	51.7 ± 9.17	1.60 ± 0.73	0.69 ± 0.17	0.05 ± 0.03	6.60 ± 1.14	31.4 ± 9.55
	MZC	2	10.9	-19.1	0.16	0.02	3.52	0.05	0.06	0.43	6.73	51.4	1.24	0.39	0.04	4.78	38.1
<i>Diaphus richardsoni</i>	MAD-Ridge	2	9.44	-19.5	0.09	0.04	9.59	0.16	0.09	0.77	7.03	80.2	1.52	1.00	0.08	4.91	59.6
	MZC	2	10.9	-19.3	0.11	0.02	7.06	0.18	0.08	0.50	5.75	33.5	1.86	0.74	0.02	3.27	49.9
<i>Diaphus suborbitalis</i>	MAD-Ridge	6	11.2 ± 0.25	-18.8 ± 0.49	0.31 ± 0.22	0.02 ± 0.00	5.13 ± 0.72	0.09 ± 0.06	0.04 ± 0.01	2.20 ± 2.25	2.96 ± 0.57	37.0 ± 29.1	0.94 ± 0.23	1.50 ± 0.98	0.03 ± 0.01	3.72 ± 0.88	29.1 ± 14.5
<i>Hygophum hygomii</i>	MAD-Ridge	12	9.95 ± 0.95	-19.2 ± 0.65	0.19 ± 0.06	0.02 ± 0.01	3.89 ± 1.21	0.09 ± 0.09	0.07 ± 0.02	0.55 ± 0.37	3.83 ± 1.93	28.4 ± 15.1	2.07 ± 1.47	0.41 ± 0.17	0.05 ± 0.05	3.59 ± 1.13	29.1 ± 10.4
	MZC	2	9.63	-19.5	0.09	0.03	3.48	0.04	0.05	1.01	4.95	15.6	1.33	0.48	0.03	2.13	49.4
<i>Lampanyctus sp.</i>	La Pérouse	2	10.2	-18.5	0.10	0.13	6.03	0.50	0.13	1.47	5.15	49.1	1.07	0.63	0.13	4.91	49.1

<i>Lampanyctus alatus</i>	MAD-Ridge	5	8.52 ± 0.28	-18.6 ± 0.33	0.19 ± 0.06	0.04 ± 0.02	5.86 ± 1.25	0.55 ± 0.14	0.06 ± 0.01	1.23 ± 0.47	5.86 ± 2.00	41.1 ± 14.3	1.51 ± 0.15	0.68 ± 0.09	0.21 ± 0.14	4.57 ± 0.80	55.3 ± 19.5
<i>Lobianchia dofleini</i>	MZC	2	12.6	-18.6	0.22	0.03	3.23	0.37	0.06	0.82	6.05	40.1	1.31	0.78	0.06	5.43	40.1
<i>Lobianchia gemellarii</i>	La Pérouse	1			0.48	0.06	5.60	0.36	0.08	0.59	5.97	57.9	1.14	0.66	0.09	6.65	29.5
	MAD-Ridge	4	10.3	-19.1	0.24	0.04 ± 0.01	4.82 ± 1.87	0.22 ± 0.12	0.06 ± 0.10	1.21 ± 0.35	10.4 ± 2.55	56.1 ± 9.67	1.54 ± 0.28	1.03 ± 0.46	0.15 ± 0.15	5.51 ± 1.00	57.4 ± 13.3
<i>Myctophum fissunovi</i>	MAD-Ridge	3	9.84 ± 0.17	-19.2 ± 0.25	0.10 ± 0.01	0.02 ± 0.01	4.51 ± 1.29	0.09 ± 0.06	0.07 ± 0.02	1.02 ± 0.55	2.87 ± 0.33	32.7 ± 1.1	0.93 ± 0.07	0.52 ± 0.41	0.03 ± 0.01	1.96 ± 0.42	24.8 ± 4.34
<i>Myctophum nitidulum</i>	MAD-Ridge	2	9.46	-19.3	0.20	0.02	10.2	0.02	0.14	1.67	2.82	36.5	0.79	0.54	0.25	2.19	17.5
<i>Notoscopelus resplendens</i>	MAD-Ridge	2	8.08	-18.4	0.10	0.06	4.01	0.29	0.13	1.01	8.32	66.7	6.58	0.92	0.41	4.15	81.6
	MZC	2	10.4	-19.5	0.12	0.02	5.05	0.10	0.07	1.12	5.38	30.3	1.86	0.65	0.04	2.29	36.5
<i>Scopelopsis multipunctatus</i>	MAD-Ridge	2	10.0	-20.3	0.08	0.07 ± 0.02	10.3 ± 3.56	0.30 ± 0.14	0.13 ± 0.00	0.97 ± 0.20	9.99 ± 3.28	39.7 ± 0.88	2.77 ± 0.18	0.86 ± 0.06	0.12 ± 0.01	3.08 ± 0.08	53.3 ± 0.09
	MZC	2	10.2	-19.6	0.04	0.03	6.33	0.12	0.06	1.24	4.20	38.2	1.68	0.8	0.09	1.98	60.8
Carangidae																	

<i>Decapterus macarellus</i>	MAD-Ridge	2	6.16	-18.4	0.03	0.02	5.22	0.02	0.05	0.46	2.81	26.8	0.65	0.14	0.03	2.15	28.4
	MZC	2	7.46	-18.7	0.04	0.02	3.82	0.02	0.04	0.70	4.23	19.0	0.59	0.26	0.02	1.69	29.4
	Reunion Is	3			0.04 ± 0.01	0.01 ± 0.01	7.01 ± 0.76	0.43 ± 0.30	0.03 ± 0.01	0.14 ± 0.08	5.00 ± 0.64	30.0 ± 8.59	0.38 ± 0.07	0.08 ± 0.02	0.01 ± 0.01	4.07 ± 0.54	34.6 ± 3.43
Gonostomatidae																	
<i>Diplophos rebaini</i>	MAD-Ridge	2				0.06	26.2	0.57	0.06	0.91	9.51	66.6	2.65	0.56	0.11	3.60	52.7
<i>Diplophos taenia</i>	MAD-Ridge	1	9.86	-18.9	0.21	0.01	15.8	0.14	0.02	0.66	1.85	15.5	3.83	0.30	0.03	2.11	22.7
	MZC	2	8.77	-19.4	0.08	0.02	11.9	0.26	0.04	1.45	5.88	23.9	2.00	0.46	0.05	2.20	32.8
<i>Margrethia obtusirostra</i>	MAD-Ridge	2				0.11	9.60	0.20	0.11	2.04	9.80	54.3	0.87		0.12	4.12	63.3
<i>Sigmops elongatus</i>	La Pérouse	1			0.08	0.02	12.7	0.05	0.03	0.56	0.92	10.2	1.37	0.33	0.02	3.76	20.4
	MAD-Ridge	8	10.7 ± 0.42			0.06 ± 0.03	17.2 ± 3.44	0.24 ± 0.18	0.07 ± 0.03	3.27 ± 1.62	7.51 ± 3.99	37.9 ± 11.8	2.44 ± 0.75	1.33 ± 0.58	0.08 ± 0.04	3.23 ± 0.75	54.1 ± 20.2
	MZC	2	12.0	-18.3	0.26	0.02	10.9	0.06	0.03	0.62	3.29	15.7	1.17	0.41	0.02	3.18	29.2
	Reunion Is	24			0.23 ± 0.25	0.03 ± 0.03	15.0 ± 3.14	0.18 ± 0.17	0.04 ± 0.03	0.50 ± 0.43	2.64 ± 1.44	20.1 ± 11.4	0.59 ± 0.37	0.31 ± 0.17	0.05 ± 0.03	3.99 ± 0.62	28.3 ± 12.6

Sternoptychidae																	
<i>Argyropelecus aculeatus</i>	La Pérouse	1			0.15	0.05		0.77	0.63	0.65	3.07	50.7	3.68	1.22	0.06	5.39	36.2
	MAD-Ridge	11	10.8 ± 1.04	-18.4 ± 0.42	0.55 ± 0.42	0.06 ± 0.07	60.9 ± 31.0	0.18 ± 0.18	0.18 0.23	1.58 ± 1.34	5.59 ± 4.58	47.7 ± 29.3	3.28 ± 2.94	0.85 ± 0.52	0.10 ± 0.07	4.03 ± 2.57	53.9 ± 28.7
	Reunion Is	1			0.08	0.12		1.08	0.27								
<i>Argyropelecus hemigymnus</i>	MAD-Ridge	1				0.07	25.3	0.21	0.09		5.11	87.6	3.06	2.48	0.26	3.25	
Stomiidae																	
<i>Astronesthes</i> sp.	La Pérouse	1	9.39	-18.0	0.11	0.08	6.09	0.39	0.08	0.75	8.88	30.2	1.68	0.56	0.08	3.86	54.6
	MAD-Ridge	1	10.1	-18.0	0.76	0.02	5.78	0.11	0.04	0.38	2.24	12.3	2.04	0.32	0.02	3.37	24.3
<i>Chauliodus sloani</i>	La Pérouse	1			0.11	0.03	17.9	0.23	0.05	0.28	1.66	11.2	1.23	0.55	0.03	3.53	26.1
	MAD-Ridge	6	10.9 ± 0.47	-18.9 ± 0.13	0.11 ± 0.01	0.04 ± 0.02	12.0 ± 6.21	0.09 ± 0.07	0.05 0.04	0.82 ± 0.57	3.10 ± 1.23	20.5 ± 14.3	1.93 ± 0.84	0.47 ± 0.25	0.13 ± 0.14	2.73 ± 0.82	43.8 ± 18.2
	MZC	2	10.8	-19.1	0.11	0.03	5.69	0.08	0.03	1.02	2.42	19.7	1.24	0.51	0.06	2.37	27.2

	Reunion Is	1			0.10	0.03	12.3	0.20	0.03	0.26	1.74	10.9	0.77	0.40	0.07	3.20	18.8
<i>Echiostoma barbatum</i>	MAD-Ridge	6	9.48 ± 1.11	-18.5 ± 0.30	0.15 ± 0.06	0.04 ± 0.01	8.29 ± 1.42	0.69 ± 0.47	0.10 ± 0.02	1.78 ± 0.69	4.50 ± 1.38	41.2 ± 19.3	5.44 ± 2.03	1.36 ± 0.29	0.09 ± 0.05	3.20 ± 0.45	76.8 ± 20.9
	MZC	1	10.5	-18.5	0.12	0.03	6.74	0.77	0.08	1.47	4.79	72.5	3.46	0.70	0.06	2.97	61.8
<i>Eustomias</i> sp.	MAD-Ridge	3				0.04 ± 0.02	10.9 ± 0.33	0.81 ± 0.28	0.09 ± 0.03	1.08	7.47 ± 2.25	56.4 ± 28.8	3.65	0.69	0.14 ± 0.07	3.30 ± 0.67	57.6 ± 14.9
	MZC	1	9.65	-18.5	0.06	0.02	17.9	0.31	0.06	1.00	4.06	17.2	3.43	0.49	0.07	4.43	51.2
<i>Melanostomias</i> sp.	MAD-Ridge	3	9.81 ± 0.81	-18.1 ± 0.53	0.20 ± 0.07	0.04 ± 0.02	12.3 ± 4.74	0.41 ± 0.20	0.10 ± 0.05	0.31	5.23 ± 1.61	12.6	5.10 ± 2.60	1.15 ± 0.82	0.13 ± 0.08	2.93 ± 0.40	61.7 ± 5.43
	MZC	1	11.1	-18.3	0.26	0.01	6.81	0.38	0.05	1.41	3.33	26.4	5.42	0.61	0.06	2.72	50.3
<i>Leptostomias</i> sp.	Reunion Is	1			0.26	0.14	4.47	0.29	0.14	1.37	6.07	54.8		0.86	0.17	5.48	69.0
<i>Photonectes</i> sp.	La Pérouse	2	11.8	-18.1	0.22	0.03	7.75	0.28	0.05	0.21	2.51	8.47	1.72	0.38	0.04	2.96	27.7
<i>Photostomias</i> sp.	La Pérouse	1	11.1	-18.4	0.14	0.04	12.3		0.11	0.41	3.18	16.2	7.49	1.05	0.07	3.43	44.5
<i>Stomias boa</i>	La Pérouse	1	10.8	-18.4	0.13	0.01	9.61	0.34	0.04	0.24	1.97	5.98	1.38	0.33	0.03	3.18	27.2

<i>Stomias longibarbus</i>	MAD-Ridge	1	12.0	-18.3	0.38	0.01	5.93	0.93	0.04	0.56	2.65			0.44	0.21	2.80	52.7
	MZC	1	11.8	-18.6	0.90	0.02	3.15	0.15	0.05		1.99	61.2	6.03	0.89	0.04	3.26	41.3

Table 3. The relative importance of the principal component axes, PC4 and PC5, in trace element loadings in myctophid samples collected from La Pérouse and MAD-Ridge seamounts, Reunion Island and the southern Mozambique Channel.

Variable	PC4	PC5
Hg	-0.051	0.239
Ag	0.404	-0.201
As	0.700	0.497
Cd	-0.041	-0.210
Co	0.298	-0.383
Cr	0.027	-0.044
Cu	-0.146	-0.002
Fe	-0.148	0.057
Mn	-0.422	0.314
Ni	0.056	-0.175
Pb	-0.028	0.549
Se	0.083	0.168
Zn	-0.146	-0.023

Table 4. Metal-metal correlations (Cu-Zn, Cu-Cd, Cu-Pb, Cu-Ni, Cu-Fe, Zn-Cd, Zn-Pb, Zn-Ni, Zn-Fe, Cd-Ni, Cd-Fe, Pb-Ni, Pb-Fe, and Ni-Fe) in $\mu\text{g g}^{-1}$ dw in crustaceans, fishes and squids at all four study sites. The Pearson correlation coefficients R are given and significant values at $\alpha < 0.05$ are asterisk marked.

Broad category	Trace element	Cu	Zn	Cd	Pb	Ni
Crustaceans						
	Zn	0.43*				
	Cd	-0.17	-0.06			
	Pb	0.11	0.19			
	Ni	0.07	0.09	0.70*	0.27	
	Fe	0.40*	0.28	-0.18	0.33*	0.22
Fishes						
	Zn	0.62*				
	Cd	0.25*	0.41*			
	Pb	0.43*	0.57*			
	Ni	0.32*	0.44*	0.23*	0.33*	
	Fe	0.55*	0.46*	0.30*	0.42*	0.47*
Squids						
	Zn	0.36*				
	Cd	0.18	-0.19			
	Pb	0.10	0.45*			
	Ni	0.24	0.26	-0.02	0.22	
	Fe	0.04	0.50*	-0.27	0.26	0.10

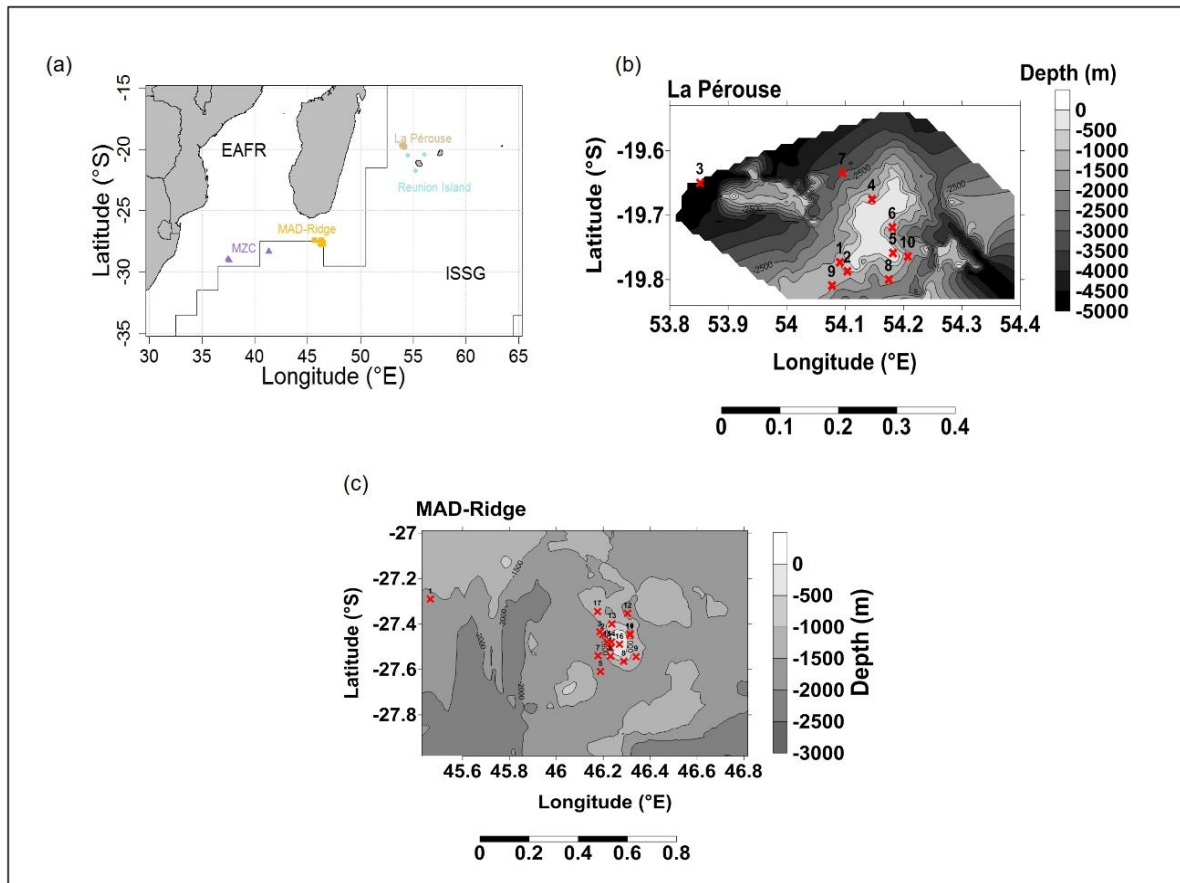


Figure 1(a). Map of the south-western Indian Ocean showing trawl locations at La Pérouse seamount, Reunion Island, MAD-Ridge seamount and the south-western Mozambique Channel (MZC). Longhurst's (1998) biogeochemical provinces are delimited by black solid lines and are labelled as EAFR (East African Coastal Province) and ISSG (Indian South Subtropical Gyre). The western African, Madagascar and Mascarene landmasses are shown in grey. (b) La Pérouse and (c) MAD-Ridge trawl stations (red crosses) are further plotted on the bathymetry with the color bar representing the depth (m) below the sea surface.

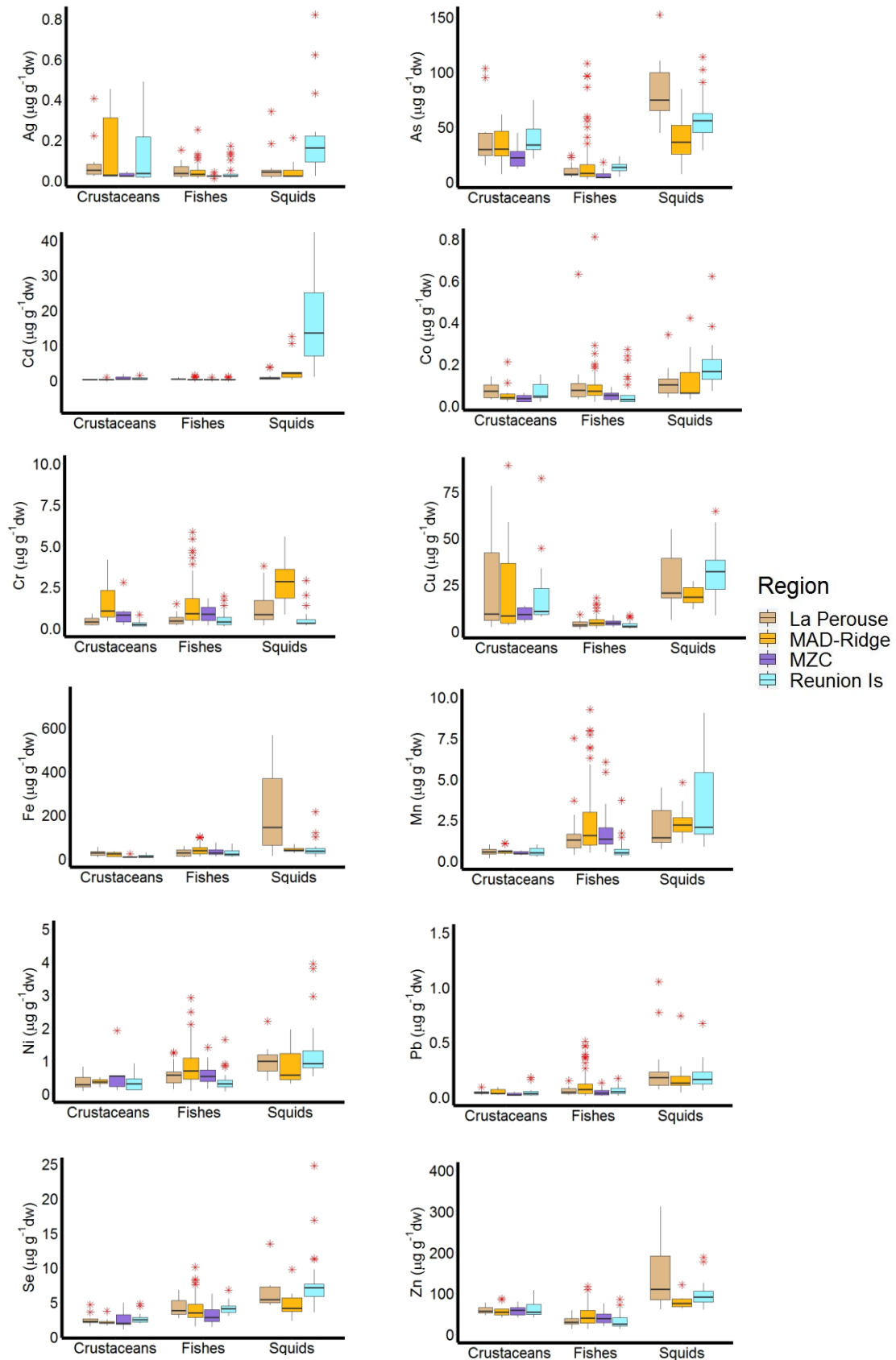


Figure 2 Boxplots of the trace element concentrations Ag, As, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn ($\mu\text{g g}^{-1}\text{dw}$) in crustaceans, fishes and squids from the study sites (La Pérouse, MAD-Ridge, Mozambique Channel-MZC and Reunion Island). The median (thick black line in box plots), interquartile range (the lower and upper boundaries), the spread (thin lines extending from box plots) and outliers (red stars) are shown.

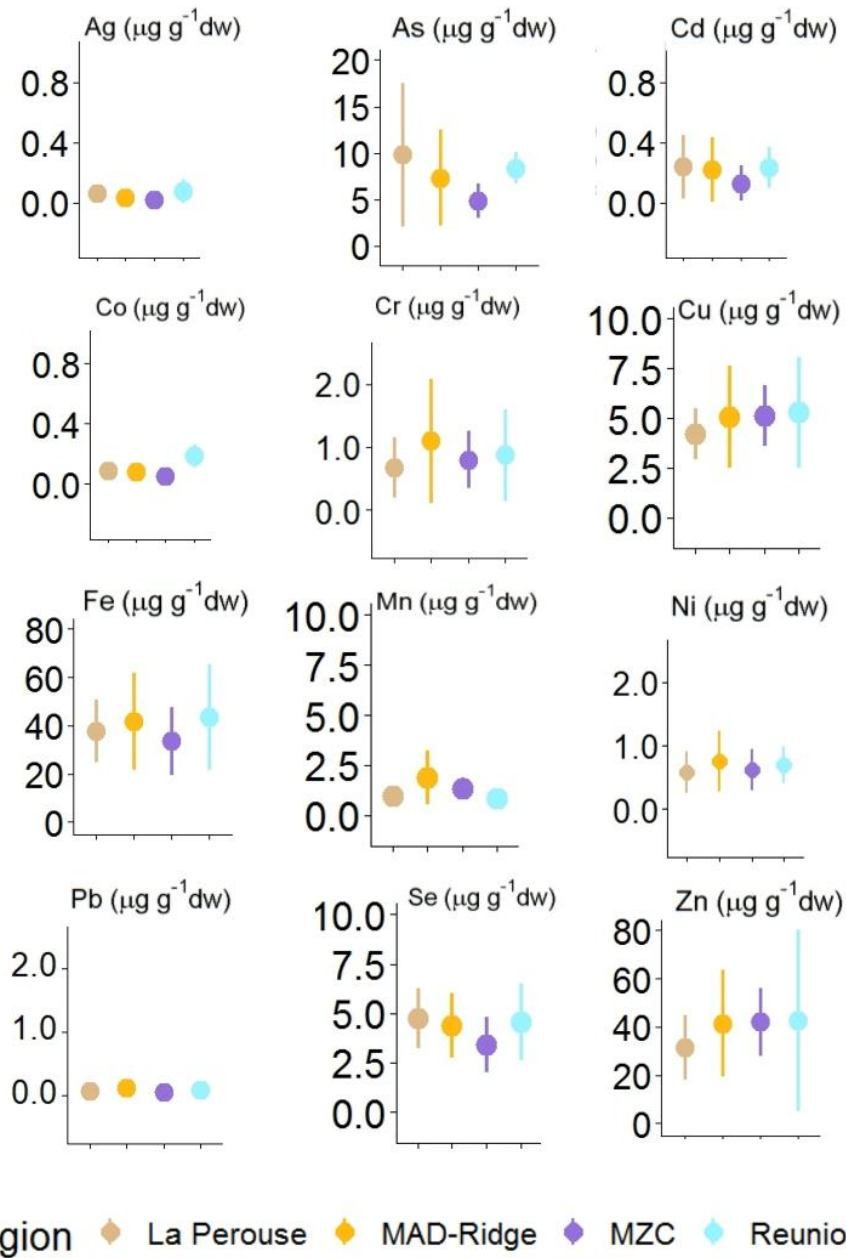


Figure 3. Mean and standard deviation of the trace elements Ag, As, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn ($\mu\text{g g}^{-1}\text{dw}$) in myctophids collected from the study sites (La Pérouse, MAD-Ridge, Mozambique Channel-MZC and Reunion Island).

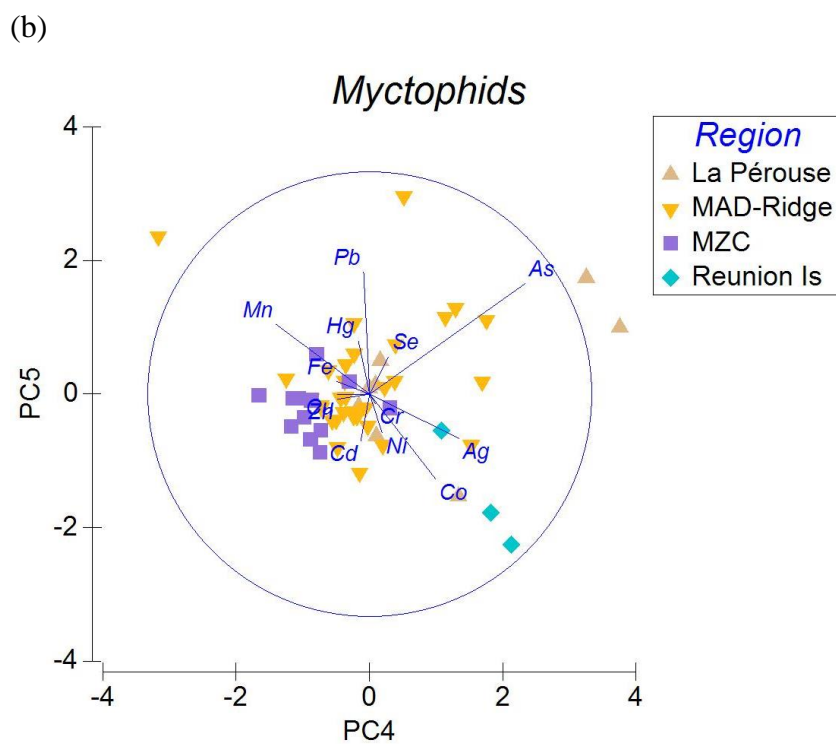
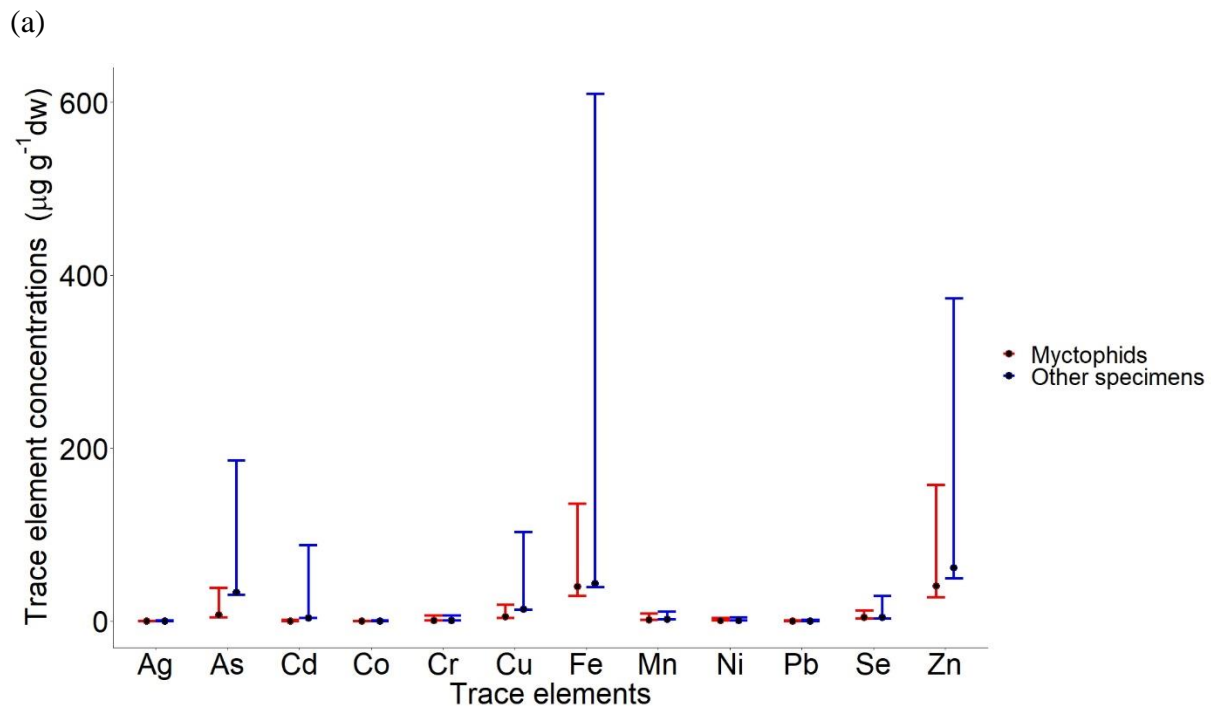


Figure 4(a). Mean (black dots) and minimum and maximum values of the trace elements Ag, As, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn ($\mu\text{g g}^{-1}\text{ dw}$) in myctophids (red bars) and all other fishes, crustaceans and squid specimens (blue bars) at the four study sites La Pérouse, MAD-Ridge, Mozambique Channel-MZC and Reunion Island. (b) Principal component analysis biplots of the trace element concentrations in myctophids, with the 2 major axes (PC4 and PC5). The direction and length of the blue lines mark the direction and rate of steepest increase of the given trace element.

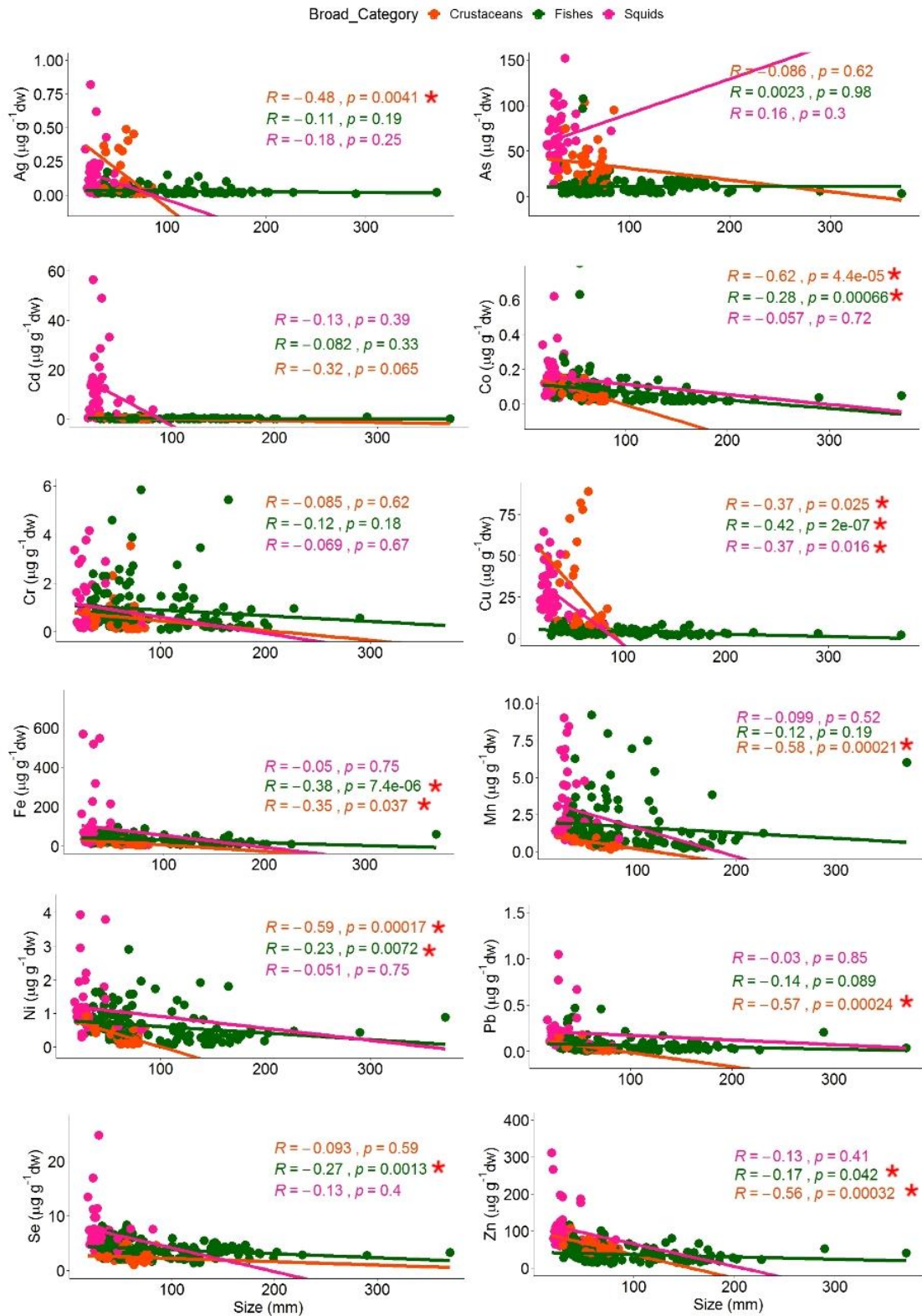


Figure 5. Trace element (Ag, As, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, Se, and Zn) concentrations ($\mu\text{g g}^{-1} \text{dw}$) in crustaceans, fishes and squids vs. body size (abdomen and carapace length for crustaceans, standard length for fishes and dorsal mantle length for squids) in mm, from all four study sites. The Pearson correlation coefficients R and p-values are shown. Significant relationships between trace element and body size are shown by the red stars.

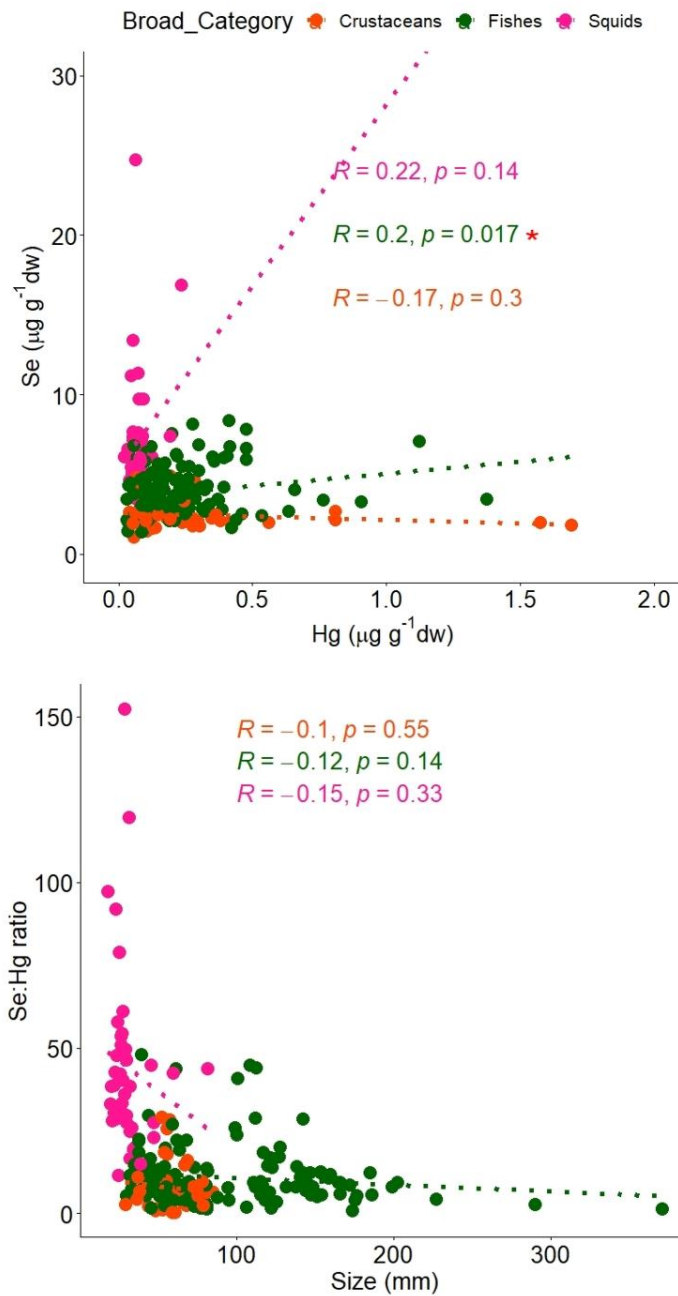


Figure 6. The relationships between Se and Hg ($\mu\text{g g}^{-1}\text{ dw}$) and the link between the ratio Se:Hg and body size (mm) in crustaceans, fishes and squids from all four study sites. The Pearson correlation coefficients R and p-values are shown. The significant correlation is shown by the red star.

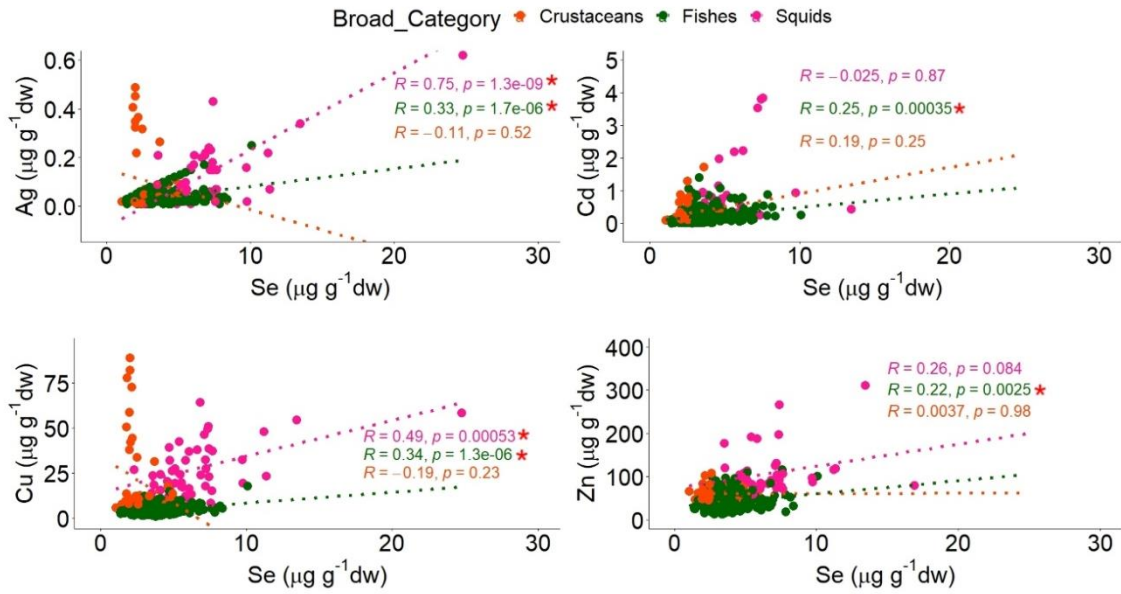


Figure 7. The relationships between the trace elements Ag, Cd, Cu and Zn with Se ($\mu\text{g g}^{-1}\text{dw}$) in crustaceans, fishes and squids from all four study sites. The Pearson correlation coefficients R and p-values are shown. Significant correlations are shown by the red stars.

Supplementary Material

Table S1. Mean \pm Standard deviation of certified and measured trace element concentrations ($\mu\text{g g}^{-1}$ dry weight) in reference materials TORT-3 and DOLT-5.

Element	TORT-3		DOLT-5	
	Certified values	Measured values	Certified values	Measured values
Cd	42.3 ± 1.8	0.99 ± 0.004	14.5 ± 0.6	0.94 ± 0.004
Pb	0.225 ± 0.018	0.74 ± 0.002	0.16 ± 0.03	0.88 ± 0.007
As	59.5 ± 3.8	1.04 ± 0.003	34.6 ± 2.4	0.96 ± 0.003
Co	1.06	0.97 ± 0.004	0.27 ± 0.03	0.99 ± 0.16
Ni	5.30 ± 0.24	0.88 ± 0.003	1.71 ± 0.56	
Se	10.9 ± 1.0	1.11 ± 0.006	8.3 ± 1.8	1.02 ± 0.04
Zn	136 ± 6	0.99 ± 0.004	105.3 ± 5.4	1.03 ± 0.005
Ag			2.05 ± 0.08	0.67 ± 0.001
Cr	1.95 ± 0.24	0.90 ± 0.008	2.35 ± 0.58	
Cu	497 ± 22	0.90 ± 0.005	35.0 ± 2.4	0.99 ± 0.004
Fe	179 ± 8	0.92 ± 0.007	1070 ± 80	0.95 ± 0.004
Mn	15.6 ± 1.0	0.93 ± 0.005	8.91 ± 0.70	