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Main drivers of mercury levels in Southern Ocean lantern fish *Myctophidae*☆

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ABSTRACT

Myctophids are the most abundant fish group in the Southern Ocean pelagic ecosystem and are an important link in the Antarctic marine food web. Due to their major ecological role, evaluating the level of mercury (Hg) contamination in myctophids is important as a step towards understanding the trophic pathway of this contaminant. The concentrations of total Hg were determined in muscle, gill, heart and liver tissue of 9 myctophid species to quantify tissue partitioning variability between species. Organic Hg concentration and proportion in muscle was also determined. Hg concentrations were higher in the liver and heart than in muscle and gills, but the proportion of organic Hg was almost 100% in muscle, indicating that the main uptake route for Hg is through the diet. Most of the species analysed have similar vertical and horizontal distributions, and similar feeding modes and prey. Geographical and temporal variability of Hg concentrations was examined using samples from 3 different sampling cruise (2007/08, 2015/16 and 2016/17) and 2 locations (South Georgia and South Orkneys Islands). Our results appear to indicate a decreasing trend in Hg contamination over the last decade, particularly gill tissue, which is in agreement with a previous study on squid from the same region. There was no significant variability in Hg concentration between the different sampling locations. Hg levels were consistent with values reported previously for myctophids around the world, indicating low global-scale geographic variability. A positive relationship between fish size and Hg concentration was found for most species, with the exception of *Electrona antarctica* females, which may be explained through Hg elimination by egg laying. We estimate that myctophids collectively comprise a Southern Ocean mercury 'reserve' of ≈1.82 metric tonnes.

1. Introduction

Mercury (Hg) is one of the most known hazardous elements and it has a global dispersion (Selin, 2009; UNEP, 2013). Hg has a long-range dispersion capacity (Streets et al., 2019) and reaches remote areas such as Antarctica where relatively high Hg concentrations have been reported in seawater (Cossa et al., 2011). Once into the ocean, Hg is methylated by microorganisms enhancing its bioavailability to biota and allowing its bioaccumulation and biomagnification in food webs (Eagles-Smith et al., 2018). Different oceanographic features such as strong upwelling currents in the Southern Ocean, and seasonal sea ice cover at high latitudes, create conditions that favour Hg methylation leading to increased

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methylHg (MeHg) concentrations (Cossa et al., 2011). MeHg detrimental effects include changing biochemical processes, damaging cells and tissues, and reducing reproductive success in fish (Sandheinrich and Wiener, 2011; Scheuhammer et al., 2015). As MeHg biomagnifies along food webs, long-lived apex predatory species are at high toxic risk. As prey from mesopelagic habitats are enriched in MeHg as a result of enhanced methylation rates in deep waters (Monteiro et al., 1996; Chouvelon et al., 2012; Blum et al., 2013), predators feeding on mesopelagic prey are likely to be at higher risk than epipelagic feeders.

Knowledge of deep sea organisms and communities remains fragmentary (Cvitanovic et al., 2015). Mesopelagic fish are a particularly understudied group (Catul et al., 2010), especially lanternfish (Family Myctophidae; hereafter myctophids), which are the most abundant and diverse Family, with ~250 species globally and a biomass of at least 550–660 million tonnes (Bone et al., 1995; Gjøsaeter and Kawaguchi, 1980). As a consequence of their high biomass, myctophids are important components of oceanic ecosystems and global biogeochemical cycles (Irigoien et al., 2014). They are crucial in the transfer of energy and contaminants such as Hg through oceanic food webs, linking primary consumers and macro-zooplankton to higher predators (Saunders et al., 2019). However, major uncertainties still remain regarding the extent of Hg bioaccumulation and Hg speciation in myctophids, particularly in the Southern Ocean (St John et al., 2016).

As elsewhere, myctophids are an important part of the Southern Ocean food web (Murphy et al., 2007). There they consume mainly planktonic crustaceans (Lourenço et al., 2017; Pakhomov et al., 1996; Saunders et al., 2018), and in turn constitutes a major food source for a range of marine predators, including large predatory fish (Fenaughty et al., 2003; Stevens et al., 2012), cephalopods (Cherel and Duhamel, 2003; Olson and Young, 2006; Phillips et al., 2001; Rodhouse et al., 1992), marine mammals (Newland et al., 2011) and seabirds (Xavier et al., 2003). Since most myctophids are opportunistic feeders with a broad dietary range, preying on the most available food resources at their disposal (Cherel et al., 2010; Pakhomov et al., 1996; Saunders et al., 2018; Stowasser et al., 2012), they are considered good bioindicators of contamination levels in the local marine environment.

In mid-trophic level fish such as myctophids, Hg can be accumulated biologically via two main pathways: absorption from the environment through the surfaces involved in respiration (e.g. gills and skin), and absorption through ingestion of contaminated prey. Whilst waterborne uptake can be a significant pathway, particularly under high environmental exposure levels, the majority of Hg is absorbed through food intake (Phillips and Buhler, 1978). Although many studies have examined the general diets and trophodynamics of myctophids across the globe (Hudson et al., 2014; Olivar et al., 2018; Van Noord et al., 2016), only a few studies globally have investigated Hg bioaccumulation in these fish (Blum et al., 2013; Chouvelon et al., 2012; Gibbs et al., 1974; Lahaye et al., 2006; Martins et al., 2006; Monteiro et al., 1996; Windom et al., 1973), and only two studies have focussed on the Southern Ocean (Bustamante et al., 2003; Cipro et al., 2018a). Due to their central role in the Southern Ocean pelagic food web, evaluating the level of Hg contamination in myctophids is important as a step towards understanding the trophic pathway of this contaminant. Such studies are also essential for establishing robust baselines for future environmental monitoring that will inform potential ecosystem management strategies in the context of the Minamata convention objectives (Gustin et al., 2016).

In the present study, Hg concentrations were measured in myctophids collected across the Scotia Sea, one of the most productive regions of the Southern Ocean (Holm-Hansen et al., 2004), and spatial, temporal, inter-specific and ontogenetic patterns were examined. The Scotia Sea is home to globally important populations of higher predator species such as penguins, flying birds, seals and whales (Murphy et al., 2007), and important commercial fisheries (Constable et al., 2000), so understanding Hg pathways is important. Specifically, we assessed the total Hg (T-Hg) concentrations in four tissues (muscle, gills, heart and liver) and organic Hg as a proxy of MeHg (O-Hg) in the muscle of the nine biomass-dominant myctophids (*Electrona antarctica, Electrona carlsbergi, Gymnoscopelus braueri, Gymnoscopelus nicholsi, Gymnoscopelus opisthopterus, Gymnoscopelus fraseri*, *Protomyctophum bolini*, *Krefftichthys anderssoni* and *Nannobrachium achirus*) from two regionally distinct food webs in the Scotia Sea (South Georgia and South Orkneys Islands) in different austral summers (2007/08, 2015/16 and 2016/17). These regions are characterised by different environmental conditions (South Orkney Islands, an Antarctic island group which experiences winter sea ice (Murphy et al., 1995); South Georgia, a sub-Antarctic island free of sea ice (Rogers et al., 2015)), zooplankton population dynamics and myctophid community composition/structure, as well as different higher predator-prey dynamics (Murphy et al., 2013), so together facilitate an interesting comparison into how Hg may affect different components of the overall Southern Ocean ecosystem. This study therefore provides important insights on T-Hg and O-Hg accumulation in Southern Ocean myctophids that are essential for monitoring the health of the Southern Ocean food web in a resource management context.

2. Material and methods

2.1. Sampling

Myctophids were caught on three multidisciplinary research cruises aboard the RRS *James Clark Ross* around South Georgia (north of the Southern boundary of the Antarctic Circumpolar Current Front [SACC]) and the South Orkney Islands (south of the SACC) during austral summer between 2007/08 and 2016/17 (Fig. 1). The surveys around South Georgia were undertaken between December 2007 and February 2008 and December 2016 and January 2017, whilst the survey around the South Orkneys islands was undertaken between December 2015 and January 2016.

All samples were caught during at night, between 0 and 1000 m, using either 8 m^2 or 25 m^2 mouth-opening Rectangular Midwater Trawl nets (RMT8 or RMT25; (Piatkowski et al., 1994; Roe and Shale, 1979). Myctophids were identified onboard to species level and standard length (SL) measured to the nearest mm. Individuals were then frozen at −20 °C for subsequent laboratory analyses, with each fish species preserved separately in different plastic bags.

2.2. Laboratory procedures

In the laboratory, all 200 specimens were re-measured and weighed to the nearest 0.01g before dissection. Sex and maturity of post-juveniles was determined (Hulley, 1990). For most specimens, the gills, heart and liver were extracted, as well as a sample of muscle (without the skin). For the 2 smallest species, *Krefftichthys anderssoni* and *Protomyctophum bolini*, organ dissection was not possible and only muscle was collected.

Samples were frozen in sterile containers and lyophilized during two days and ground to a fine powder for further analyses of Hg. T-Hg was determined by atomic absorption spectrometry (AAS) with thermal decomposition and gold amalgamation, using an Advanced Mercury Analyser LECO AMA-254. Quantification of O-Hg was performed through a chemical digestion described in Válega et al., (2006). Briefly, biological tissues were digested with a mixture of 18% KBr in 5% H_2SO4, followed by extraction of organic mercury into toluene. The aqueous fraction resulting from the addition of a

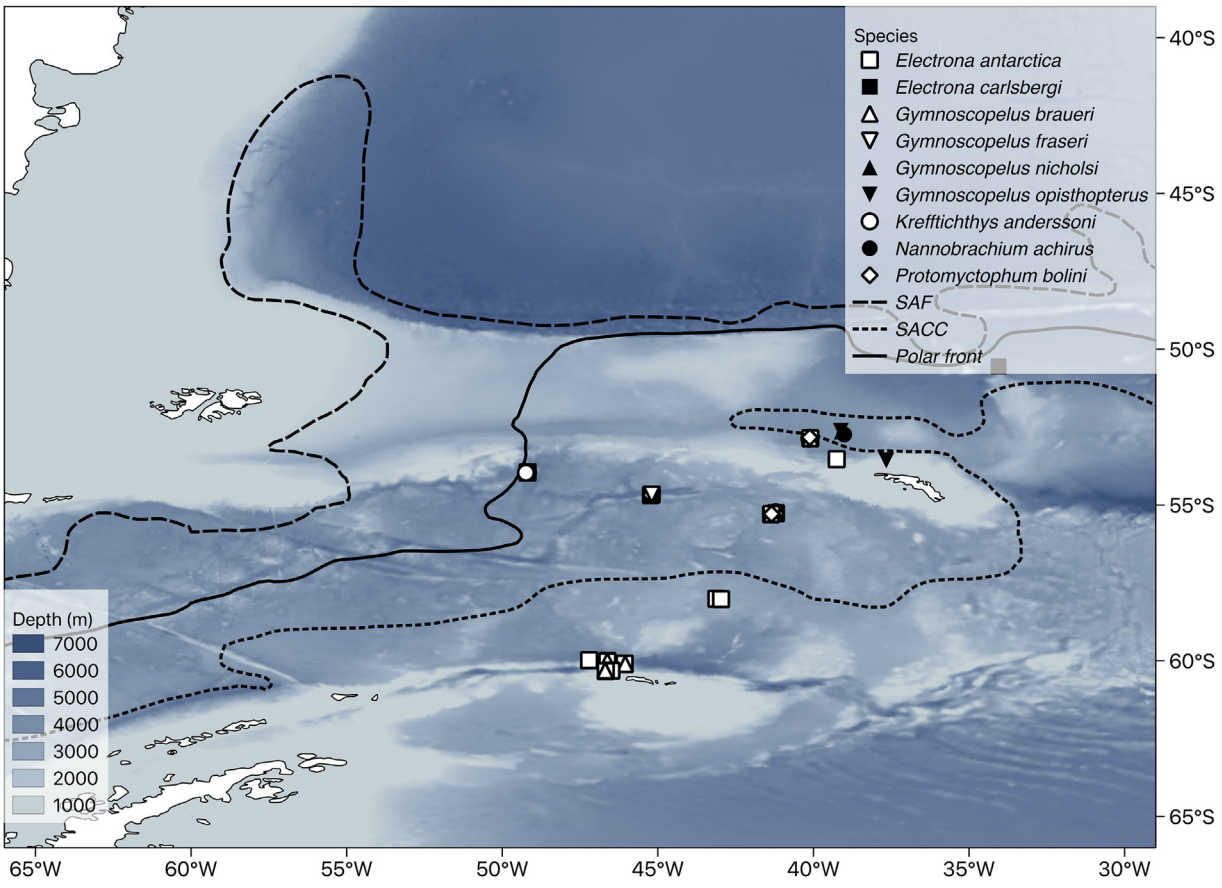

Fig. 1. Sampling sites and distributions of species captured around the Scotia Sea across all sampling years. SAF – Sub Antarctic Front; SACCF - Southern boundary of the Antarctic Circumpolar Current Front.

$Na_2S_2O_3$ solution was then analysed for mercury by thermal decomposition atomic absorption spectrometry with gold amalgamation (all reagents used were Hg-free, p.a. grade). The method does not differentiate different forms of Hg or other organic-Hg compounds, such as dimethylHg or ethylHg, and all can be contained in the extract. However, these organic forms are only present at very low levels at depth in the world ocean (Hintelmann, 2010) so virtually all the O-Hg quantified here would be 100% MeHg. Where there was low individual mass (less than 200 mg), samples for O-Hg analyses were obtained by combining multiple individuals of the same species of similar sizes collected from the same location. Analytical precision and accuracy were determined several (>4) times a day for the following certified reference materials: DORM-4 (n = 59, 96 ± 13%) fish protein and ERM-BB422 (n = 108, 100 ± 4%). DORM-4 was used to certify O-Hg analyses, with an efficiency of 99 ± 8% (n = 24). All analyses were repeated 2–3 times until a relative standard deviation < 10% was achieved. Detection limits for thermal decomposition atomic absorption spectrometry is 0.01 ng of T-Hg and 0.004 μg g^{-1} for O-Hg. Hg concentrations are given as μg g^{-1} dry weight (dw).

2.3. Statistical analysis

Relationships between Hg concentration and myctophid standard length were examined by correlation. Shappiro-Wilk and Bartlett's test were used to test the normality and homogeneity of the data respectively. For the comparison of Hg in tissues (muscle, gills, heart and liver), Friedman tests were performed. To evaluate differences among years, locations and sexes Wilcoxon rank and Kruskal–Wallis tests were performed.

3. Results

3.1. Spatial and temporal variation in T-Hg concentrations in myctophids

T-Hg concentrations in the muscle of the 8 analysed myctophid species sampled during 2007/08 varied between 0.026 μg g^{-1} (in *K. anderssoni*) and 0.418 μg g^{-1} (in *G. opisthopterus*; Fig. 2; Table 1). In 2015/16, only 3 species were caught and T-Hg concentrations in the muscle ranged from 0.072 to 0.441 μg g^{-1}, with the highest and lowest values observed in *E. antarctica* (Fig. 2; Table 1). During 2016/17, T-Hg concentrations varied across the 6 species from 0.022 μg g^{-1} (*K. anderssoni)* to 0.424 μg g^{-1} (*Gymnoscopelus fraseri*; Fig. 2; Table 1). Of the sampled myctophids, only 3 species (*E. antarctica, G. braueri* and *G. nicholsi*) were caught repeatedly each year. There were no significant differences in muscle T-Hg concentrations between years for *G. braueri* or *G. nicholsi* (Kruskal-Wallis test, H = 5.366, p = 0.068; Kruskal-Wallis test, H = 4.859, p = 0.0852, respectively) while significantly lower T-Hg concentrations were observed for *E. antarctica* in 2016/17 than in 2007/08 and 2015/16 (Kruskal-Wallis test, H = 13.81, p = 0.001; Table 1). There were statistically significant differences in gill T-Hg concentrations between years in *E. antarctica, G. braueri* and *G. nicholsi* (Kruskal-Wallis test, H = 33.51, p < 0.001; H = 17.84, p < 0.001; H = 14.38, p < 0.001). By contrast, in *Krefftichthys anderssoni* and *Protomyctophum bolini,* which were caught both in 2007/08 and 2016/17, no significant differences in T-Hg muscle concentrations

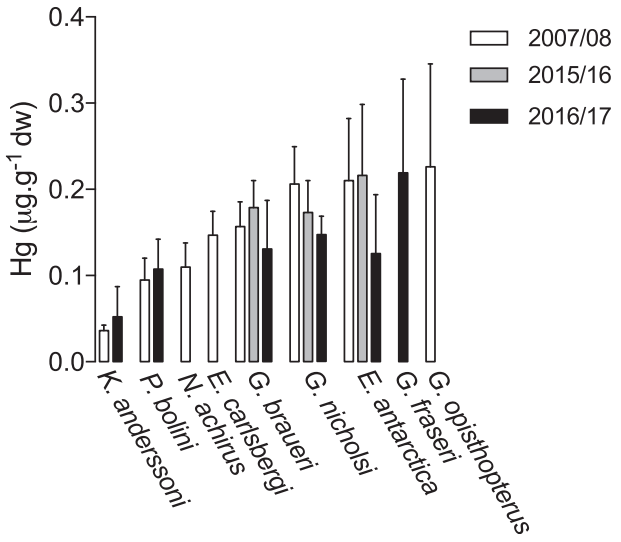

Fig. 2. Total mercury concentrations (Mean ± 1SD, μg g^{-1} dw) in the muscles of Southern Ocean myctophids, collected in the Scotia Sea in the austral summers of 2007/08, 2015/16 and 2016/17.

between years was evident (Mann-Whitney test, U = 43, p = 0.426; Mann-Whitney test, U = 66, p = 0.359, respectively).

To minimize the effect of temporal variation on the spatial analysis, comparisons were only performed within species between the 2 consecutive sampling years (2015/16 and 2016/17). During these surveys, only 3 species (*E. antarctica, G. braueri* and *G. nicholsi*) were caught consistently year on year at both South Georgia (north of the Southern boundary of the Antarctic Circumpolar Current Front; SACCF) and the South Orkneys Islands (south of the SACCF). There was no significant difference in T-Hg muscle concentrations in the two *Gymnoscopelus* species between the two locations (*G. braueri,* Kruskal-Wallis test, H = 5.366, p = 0.068; *G. nicholsi,* Kruskal-Wallis test, H = 4.859, p = 0.085). However, the concentrations of T-Hg in *E. antarctica* were significantly lower at the South Orkney Islands (0.126 ± 0.068 μg g^{-1}) than at South Georgia (0.216 ± 0.082 μg g^{-1}; Fig. 3).

3.2. Inter-specific variations in T-Hg concentrations in myctophids

Inter-specific variations in T-Hg concentrations in muscle were apparent for samples pooled by year and location. During 2008/09, the 3 species of Southern Ocean *Gymnoscopelus* (*G. braueri, G. nicholsi* and *G. opisthopterus*) and the two species of *Electrona* (*E. antarctica* and *E. carlsbergi*) had higher T-Hg concentrations than *K. anderssoni* and *P. bolini* (Kruskal-Wallis test, H = 48.66, p < 0.0001). However, the levels of T-Hg in *Nannobrachium achirus*

Table 1
Number of analysed individuals, standard length (mm), weight (g) and total mercury concentrations (Mean ± 1SD, min - max, μg g^{-1} dw) in different tissues of Southern Ocean myctophids collected in the Scotia sea in the austral summer of 2007/08, 2015/16 and 2016/17. n.a.: not analysed.

Species	n	Standard Length	Weight	*Tissues*	Gills	Heart	Liver	*Friedman test*	
				Muscle				X2	p
2007/08									
Electrona antarctica	16	73 ± 16	5.5 ± 3.4	0.210 ± 0.072	0.283 ± 0.050	0.590 ± 0.163	0.357 ± 0.160	30.5	<0.001
		46–98	1.1–12.7	0.091–0.331	0.189–0.369	0.347–0.999	0.175–0.799		
Electrona carlsbergi	15	75 ± 4	6.0 ± 0.9	0.147 ± 0.028	0.311 ± 0.06	0.570 ± 0.125	0.290 ± 0.118	25.6	<0.001
		67–81	4.7–7.7	0.110–0.185	0.264–0.434	0.417–0.802	0.189–0.562		
Gymnoscopelus braueri	5	102 ± 40	14 ± 16	0.157 ± 0.029	0.39 ± 0.123	0.766 ± 0.283	0.514 ± 0.125	14.0	<0.001
		63–164	2.0–38.8	0.106–0.175	0.236–0.563	0.610–1.289	0.374–0.615		
Gymnoscopelus nicholsi	5	137 ± 11	28 ± 6.3	0.287 ± 0.122	0.248 ± 0.042	0.500 ± 0.084	0.594 ± 0.087	14.0	<0.001
		124–153	21–36	0.177–0.466	0.184–0.293	0.419–0.624	0.521–0.726		
Gymnoscopelus opisthopterus	7	131 ± 20	24 ± 10	0.226 ± 0.119	0.142 ± 0.052	0.523 ± 0.083	0.422 ± 0.192	16.0	<0.001
		109–164	13–39	0.108–0.336	0.078–0.233	0.412–0.623	0.202–0.692		
Nannobrachium achirus	6	129 ± 11	18 ± 5.4	0.110 ± 0.028	0.149 ± 0.041	0.236 ± 0.049	0.650 ± 0.227	17.0	<0.001
		111–142	11–25	0.071–0.156	0.096–0.201	0.188–0.318	0.340–0.940		
Krefftichthys anderssoni	10	38 ± 4	1.0 ± 1.8	0.0436 ± 0.006	n.a.	n.a.	n.a.		
		34–47	0.3–6.0	0.026–0.045					
Protomyctophum bolini	10	42 ± 8	1.2 ± 0.7	0.094 ± 0.026	n.a.	n.a.	n.a.		
		31–56	0.5–2.6	0.070–0.158					
2015/16									
Electrona antarctica	36	80 ± 8	6.9 ± 2.6	0.216 ± 0.082	0.216 ± 0.067	0.487 ± 0.167	0.363 ± 0.145	79.6	<0.001
		63–96	3.1–14	0.072–0.441	0.112–0.373	0.274–0.912	0.091–0.792		
Gymnoscopelus braueri	18	114 ± 9	12 ± 3.3	0.179 ± 0.031	0.170 ± 0.074	0.568 ± 0.106	0.580 ± 0.165 0.240–0.943	19.5	<0.001
		94–127	5.7–16	0.130–0.225	0.091–0.410	0.431–0.816			
Gymnoscopelus nicholsi	9	142 ± 11	30 ± 5.8	0.173 ± 0.037	0.160 ± 0.016	0.313 ± 0.035	0.327 ± 0.054	41.7	<0.001
		125–154	20–39	0.114–0.244	0.138–0.190	0.269–0.360	0.257–0.378		
2016/17									
Electrona antarctica	15	61 ± 16	3.3 ± 2.5	0.126 ± 0.068	0.067 ± 0.036	0.189 ± 0.133	0.150 ± 0.089	22.9	<0.001
		39–83	0.7–7.7	0.056–0.300	0.035–0.148	0.067–0.478	0.053–0.328		
Gymnoscopelus braueri	7	92 ± 34	9.0 ± 9.2	0.123 ± 0.056	0.083 ± 0.029	0.406 ± 0.432	0.505 ± 0.305	17.0	<0.001
		57–134	1.1–25	0.076–0.237	0.047–0.137	0.147–1.275	0.199–0.987		
Gymnoscopelus fraseri	8	75 ± 10	4.1 ± 1.7	0.219 ± 0.109	0.147 ± 0.062	0.392 ± 0.357	1.111 ± 0.644	22.9	<0.001
		56–86	1.5–6.5	0.107–0.424	0.101–0.258	0.116–1.031	0.254–2.115		
Gymnoscopelus nicholsi	5	132 ± 3	21 ± 1.4	0.147 ± 0.022	0.101 ± 0.011	0.286 ± 0.072	0.391 ± 0.120	14.0	<0.001
		129–137	20–23	0.121–0.179	0.089–0.114	0.199–0.382	0.195–0.484		
Krefftichthys anderssoni	11	52 ± 12	1.87 ± 1.35	0.052 ± 0.036	n.a.	n.a.	n.a.		
		40–70	0.7–3.9	0.022–0.135					
Protomyctophum bolini	17	43 ± 10	1.24 ± 0.76	0.108 ± 0.034	n.a.	n.a.	n.a.		
		28–57	0.2–2.6	0.071–0.201					

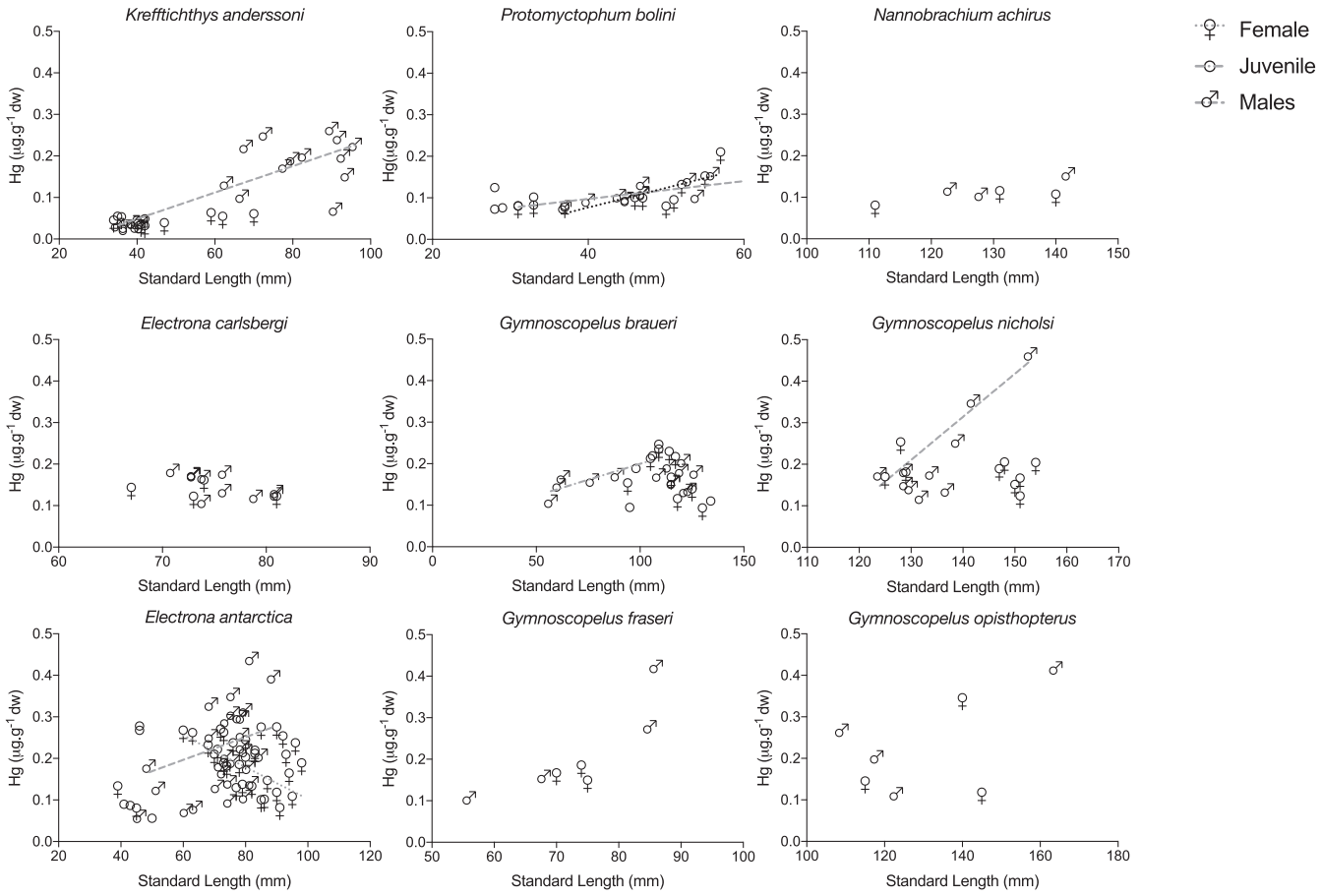

Fig. 3. Total mercury concentrations (Mean ± 1SD, µg g^{-1} dw) versus standard length (mm) in the muscles of Southern Ocean myctophids and significant regression lines, collected in the Scotia Sea in the austral summers of 2007/08, 2015/16 and 2016/17. Regression equations given in supplementary material.

were not significantly different from the other species caught during this time (Fig. 2; Table 1).

No statistical differences were observed between T-Hg concentrations in any of the 3 fish species (*E. antarctica, G. braueri* and *G. nicholsi*) caught in 2015/16 (Kruskal-Wallis test, H = 4.432, p = 0.109). However, for fish caught in 2016/2017, *E. antarctica, G. fraseri, G. nicholsi* each had higher T-Hg concentrations than *K. anderssoni,* whilst no significant inter-specific differences were observed for either *G. braueri* and *P. bolini* (Kruskal-Wallis test, H = 28.7, p < 0.0001; Fig. 2; Table 1).

3.3. Gender-specific and ontogenetical variations in T-Hg concentrations

To increase the robustness of our analysis on gender- and size-related effects on T-Hg accumulation in myctophids, only samples with no significant differences across years were pooled for each species. Thus, samples were pooled across all years for every species, except *E. antarctica,* for which only samples from 2007/08 and 2015/16 were pooled.

No significant gender-related differences in T-Hg muscle concentrations were observed for any species other than *G. nicholsi* and *K. anderssoni* where, in both, males had higher T-Hg concentrations than females (Mann-Whitney test, U = 41, p = 0.005 and U = 56, p = 0.017, respectively), Size- (and hence age-) related patterns in T-Hg concentration were evaluated for species where there was a sufficient sample size ($n > 5$) across the full expected size ranges (Fig. 3). Three patterns were noted between the different species/sexes: 1) No influence of size in T-Hg concentrations [in females of *G. braueri,* in males of *G. braueri, G. nicholsi, K. anderssoni* and juveniles of *P. bolini*]; 2) an increase of concentration of T-Hg with size [in males of *G. nicholsi, K anderssoni* and *P. bolini*, *E. antarctica* and *P. bolini* and in juveniles of *G. braueri*]; 3) and a decrease of T-Hg with size, was only found in females of *E. antarctica.*

3.4. Variations in T-Hg concentrations in the different tissues of Southern Ocean myctophids

Four different tissue types, muscle, gills, heart and liver, were analysed for T-Hg levels in each species, except *K. anderssoni* and *P. bolini* that were too small for us to achieve adequate extraction of these tissues (Table 1).

Overall, T-Hg concentrations varied between tissues, with different patterns of variation between species and years (Table 1). However, in the majority of the species analysed from 2007/08 ($\chi^2 = 92.74$, $p < 0.001$) and 2015/16 ($\chi^2 = 135.8$, $p < 0.001$) samples, the heart and liver had consistently higher T-Hg concentrations than the muscle and gills, which contained the lowest overall concentrations. In 2016/17 samples ($\chi^2 = 70.47$, $p < 0.001$), gills had always lower concentration than muscle. Also, liver from *G. fraseri* was the only tissue to have an average T-Hg concentration greater than 1 µg g^{-1} (1.11 ± 0.644 µg g^{-1}).

3.5. O-Hg concentrations in Southern Ocean myctophids

Concentrations of O-Hg in muscle of the analysed species ranged between 0.051 and 0.493 μg g^{-1}. There were no significant differences in O-Hg concentrations between species (Kruskal-Wallis test, H = 6.428, p = 0.491; Table 2). The overall percentage of muscle O-Hg relative to muscle T-Hg was consistently greater than 75%, and close to 100% in most species (Table 2), indicating that the T-Hg found in myctophid muscle is predominantly the organic form.

4. Discussion

Prior to this study, knowledge of Hg in Southern Ocean myctophids was quite limited, despite their major role in the Southern Ocean food webs. In this study, we identified the main intrinsic (e.g., sex, size) and extrinsic (e.g., year, sampling location) drivers that influence Hg levels in myctophids. Furthermore, our results showed that myctophids represent an important reservoir of bioavailable Hg across the Southern Ocean.

4.1. Spatial and temporal trends in muscle T-Hg concentration

In this study we examined, for the first time, short-term changes in T-Hg concentrations in the biomass-dominant myctophid community at South Georgia and the South Orkney Islands.

We found no differences in T-Hg concentrations in muscle between sampling years for most species, although the high standard deviation may have masked the decreasing trend shown in those species that were caught in all sampling years. The high SD arose possibly due to the low sample size in some species that was in part due to logistical constraints for sampling in remote environments like the Southern Ocean. However, *Electrona antarctica* had statistically lower concentrations in 2016/17 than in the other years (see Fig. 2). Furthermore, the significantly lower T-Hg concentrations in gills in 2016/17 than in 2007/08 indicates a possible decreasing trend of Hg bioavailability in the water. Such a decreasing pattern over time has been observed for squid from the same region at the same time scale (Seco et al., 2020). The pattern of decline in T-Hg tissue concentrations in both squid and myctophids over this 10-year period suggests a decrease in the bioavailability of Hg around South Georgia in the last decade. However, due to the comparatively shorter life spans of squid than to myctophids (around 1–2 years in squid (Arkhipkin, 2004; Boyle and Rodhouse, 2005; Xavier et al., 2018) versus ~ 3–8 years in myctophids (Linkowski, 1987, 1985; Saunders et al., 2020)), acute changes in environmental pollutants are more likely to be reflected in squid due to a greater turnover in individuals within their populations. In contrast, myctophids are likely to retain and integrate Hg contamination from the environment into their muscle over longer periods of exposure, making it more appropriate to look for patterns of T-Hg decrease in gill tissue as gills will more immediately reflect a difference in bioavailability of Hg in the water. Generally, longer-lived animals take longer to reflect any alteration in habitat contaminant levels (Fränzle, 2006).

Habitat use has a major effect on Hg accumulation, since longer exposure in more contaminated areas will result in higher concentrations of this element in tissues (Desta et al., 2008; Le Bourg et al., 2019). In this study, little evidence was found of regional variation in T-Hg concentrations from the 3 species that were caught concurrently at South Georgia and the South Orkneys (*E. antarctica, G. braueri* and *G. nicholsi*), with regional differences only apparent for *E. antarctica. Electrona antarctica* specimens from South Georgia had lower concentrations of T-Hg than those from the South Orkneys, but samples from the South Orkneys Islands were, on average, 20 mm smaller, suggesting that the observed spatial pattern could reflect differences due to body size (i.e., bioaccumulation level) rather than differences in environmental factors. Indeed, other studies have shown that body size is typically positively correlated with T-Hg concentration in fish (Barghigiani et al., 2000; Bosch et al., 2016; Somers and Jackson, 1993); present study). However, *G. braueri* and *G. nicholsi* had similar T-Hg concentrations in both locations, regardless of body size, whilst an opposite trend was apparent for the pelagic euphausiid Antarctic krill (*Euphausia superba*), collected in the same surveys (Seco et al., 2019). In this last study, Antarctic krill collected around the South Orkney Islands had higher T-Hg concentrations than those caught at South Georgia, a pattern that was attributed to the presence of sea ice around the South Orkney Islands, as ice formation may act as a trap for contaminants precipitating from the atmosphere. Both *G. braueri* and *G. nicholsi* feed on Antarctic krill at South Georgia and the South Orkneys (*G. braueri* 10% and *G. nicholsi* 25% of Index of relative importance (Saunders et al., 2018)), which suggests that the regional differences in Hg levels of this prey species should also be reflected in these myctophids if Hg accumulation by ingestion was the predominant pathway in the Scotia Sea [e.g. (Anderson et al., 2009; Paiva et al., 2008)]. However, the intake of T-Hg from other shorter-lived prey, such as copepods, small euphausiids and amphipods, and the long-term incorporation of Hg in the myctophid tissues might mask this krill-myctophid interaction on small spatial and temporal scales, such as those in the study of Seco et al. (2019). Myctophids migrate across the Scotia Sea (Saunders et al., 2018) and variability in time across this spatially extensive habitat may also mask any regional difference in Hg bioavailability. Such a question deserves further investigation to clarify the importance of spatial variation of Hg in myctophids and the role of their different prey in Hg bioaccumulation.

At a global scale, the concentrations of T-Hg found in the literature for myctophids studied globally were consistent with those reported here (Table 3). The approximately uniform concentrations are unexpected given the large range of habitats and species sampled, each with different ecology, depth distribution, growth, and diet. It seems that myctophids, from a global perspective, have similar T-Hg concentrations, despite their ostensible differences in physiology, biology and ecology. Comparisons among these studies have to be done with caution, however, as methodological differences such as sample preservation, analytical approaches and sample size may invalidate direct comparisons between studies.

To the best of our knowledge, there are only two other studies on Hg in Southern Ocean myctophids (Bustamante et al., 2003; Cipro et al., 2018b), both of which are on samples from the sub-Antarctic Kerguelen Islands (Indian Ocean sector). *E. antarctica* from the Kerguelen Islands had T-Hg concentrations between 2 and 4 times lower (0.066 ± 0.015 μg g^{-1} (Cipro et al., 2018b)) than in all of our sampled years/locations, even though there was a high

Table 2
Total mercury (T-Hg, ± 1SD) and organic mercury (O-Hg, ± 1SD) concentrations (μg g^{-1} dw) and percentage (±1SD) of O-Hg in in the muscles of Southern Ocean myctophid, collected in the Scotia Sea in the austral summers of 2007/08, 2015/16 and 2016/17.

Species	T-Hg	O-Hg	%O-Hg
Electrona antarctica	0.172 ± 0.071	0.141 ± 0.068	79 ± 9
Electrona carlsbergi	0.121 ± 0.011	0.107 ± 0.019	88 ± 8
Gymnoscopelus braueri	0.167 ± 0.058	0.114 ± 0.029	80 ± 11
Gymnoscopelus nicholsi	0.332 ± 0.144	0.331 ± 0.181	95 ± 17
Gymnoscopelus opisthopterus	0.125 ± 0.015	0.099 ± 0.017	79 ± 4
Gymnoscopelus fraseri	0.161 ± 0.004	0.157 ± 0.034	97 ± 18
Krefftichthys anderssoni	0.103 ± 0.045	0.096 ± 0.063	88 ± 13
Protomyctophum bolini	0.127 ± 0.022	0.123 ± 0.024	96 ± 2

Table 3
Standard length (SL; average or range; in mm), total mercury (T-Hg) average and/or range concentrations (μg g^{-1} dw), sampling location and year and preservation method of global myctophids from published data.

Species	SL	T-Hg	Range	Location	Year	Preservation method	Reference
Benthosema glaciale	39–53	0.11	–	Gulf Stream	1993	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.14	–	Gulf Stream	1952	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.15	–	Gulf Stream	1971	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.17	–	Gulf Stream	1976	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.2	–	Gulf Stream	1936	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.22	–	Gulf Stream	1963	Formaldehyde/Ethanol	Martins et al. (2006)
Benthosema glaciale	39–53	0.45	–	Gulf Stream	1942	Formaldehyde/Ethanol	Martins et al. (2006)
Bolinichthys distofax	8.7–8.8		0.174–0.218	North Pacific Ocean	2007	Frozen	Blum et al. (2013)
Bolinichthys distofax	4.9–7.8		0.037–0.040	North Pacific Ocean	2011	Frozen	Blum et al. (2013)
Bolinichthys indicus	30–35	0.16	–	Bermuda	1974	Frozen	Gibbs et al. (1974)
Bolinichthys indicus	–	0.2	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Bolinichthys longipes	3.9–4.2		0.015–0.042	North Pacific Ocean	2007	Frozen	Blum et al. (2013)
Bolinichthys longipes	4.5		0.017	North Pacific Ocean	2011	Frozen	Blum et al. (2013)
Ceratoscopelus rnaderensls	65–75	0.377 ± 0.009	0.318–0.423	Azores	1978	Ethanol	Monteiro et al. (1996)
Ceratoscopelus warmingi	45–60	–	0.21–0.26	Bermuda	1974	Frozen	Gibbs et al. (1974)
Ceratoscopelus warmingii	–	0.2	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Diaphus mollis	–	0.1	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Diaphus mollis	25–30	0.11	–	Bermuda	1974	Frozen	Gibbs et al. (1974)
Electrona antarctica	48–78	0.066 ± 0.015	0.046–0.100	Kerguelen Islands	1997–99	Frozen	Cipro et al. (2018b)
Electrona rissoni	68–90	0.323 ± 0.045	0.145–0.533	Azores	1995	Ethanol	Monteiro et al. (1996)
Gymnoscopelus fraseri	65–82	0.197 ± 0.101	0.094–0.424	Kerguelen Islands	1997–99	Frozen	Cipro et al. (2018b)
Gymnoscopelus nicholsi	129–164	0.137 ± 0.047	0.096–0.200	Kerguelen Islands	1997–99	Frozen	Cipro et al. (2018b)
Gymnoscopelus nicholsi	144 ± 15	0.205 ± 0.126	0.157–0.297	Kerguelen Islands	1998	Frozen	Bustamante et al. (2003)
Gymnoscopelus piabilis	114–162	0.179 ± 0.078	0.067–0.333	Kerguelen Islands	1997–99	Frozen	Cipro et al. (2018b)
Gymnoscopelus piabilis	151 ± 11	0.310 ± 0.126	0.177–0.475	Kerguelen Islands	1998	Frozen	Bustamante et al. (2003)
Hygophum hygomii	–	0.3	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Hygophum hygomii	45–55	–	0.18–0.31	Bermuda	1974	Frozen	Gibbs et al. (1974)
Lampanyctus photonotus	45–60	–	0.16–.21	Bermuda	1974	Frozen	Gibbs et al. (1974)
Lampanyctus pusillus	–	0.3	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Lampanyctus pusillus	25–30	0.34	–	Bermuda	1974	Frozen	Gibbs et al. (1974)
Lobianchia dofleini	–	0.2	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Lobianchia dofleini	20–25	–	0.2–0.27	Bermuda	1974	Frozen	Gibbs et al. (1974)
Myctophum punctatum	70–83	0.320 ± 0.035	0.15–0.367	Azores	1994	Ethanol	Monteiro et al. (1996)
Myctophum punctatum	71 ± 76	0.078 ± 0.024	0.063–0.121	Bay of Biscay	2001–10	Frozen	Chouvelon et al. (2012)
Notoscopelus caudispinosus	60–75	0.24	–	Bermuda	1974	Frozen	Gibbs et al. (1974)
Notoscopelus caudispinous	–	0.2	–	Sargasso Sea	1973	Frozen	Windom et al. (1973)
Notoscopelus kroeyeri	93 ± 23	0.105 ± 0.080	0.029–0.210	Bay of Biscay	2001–03	Frozen	Lahaye et al. (2006)
Protomyctophum bolini	49–58	0.086 ± 0.022	0.059–0.135	Kerguelen Islands	1997–99	Frozen	Cipro et al. (2018b)

degree of overlap in sizes of fish analysed between studies. In contrast, the *Gymnoscopelus* species that occurred in our and previous studies, G. *fraseri* and *G. nicholsi* had similar values for equivalent sized individuals (Bustamante et al., 2003; Cipro et al., 2018a). Although there are differences in diet and prey field between the two regions (South Georgia and Kerguelen), *E. antarctica* from Kerguelen Islands appear to feed more frequently on *Thysanoessa macrura* (Clarke et al., 2018), while individuals from South Georgia feed mainly on *Euphausia superba* or *Themisto gaudichaudii* (Saunders et al., 2018). This difference in diet alone seems unlikely to explain the regional differences in T-Hg, as levels of mercury in *T. macrura* from Kerguelen Islands were similar to those in *E. superba* from the Scotia Sea (Cipro et al., 2018b; Seco et al., 2019). Furthermore, species-specific estimates of Hg levels across the whole prey field of myctophids from both Kerguelen Islands and the Scotia Sea are unknown, and the role of these taxa in the transfer of Hg to myctophids and upper trophic levels remains unclear. A possible lower fraction of O-Hg in the prey species from the Kerguelen Islands compared to their counterparts in the Scotia Sea (Seco et al., 2019) could lead to a lower rate of Hg accumulation in myctophids in this region, given the turnover of MeHg in fish tissue (~400 days (Downs et al., 1998)), and the more limited trophic transfer potential of inorganic Hg compare to O-Hg. These diverse results reinforce the importance of species-specific analyses of Hg levels, when trying to understand spatial trends in myctophid Hg accumulation patterns through regional predator-prey interactions.

4.2. Gender-based and ontogenetic patterns in T-Hg concentration in Southern Ocean myctophids

Physiological and biological factors, such as sex and size, are known to influence Hg concentration in fish (Bastos et al., 2016; Dang and Wang, 2012; Gewurtz et al., 2011; Le Bourg et al., 2019). When assessing the effect of body size in T-Hg concentration in the muscle of Southern Ocean myctophids, we observed a general positive trend of increasing T-Hg with increasing size, except for *E. antarctica* females, for which this relationship was negative. In other species, such as *E. carlsbergi, G. fraseri,* and *G. opisthopterus*, the correlations were not significant (see Fig. 3). The positive relationship between T-Hg and size in fish is well established (Dang and Wang, 2012; Gewurtz et al., 2011; Somers and Jackson, 1993), with a tendency for increased Hg bioaccumulation with age, mainly in muscle tissue. Also, larger fish tend to feed on larger prey that usually bioaccumulates greater Hg concentrations (Chouvelon et al., 2014) which, coupled with the tendency for lower Hg excretion rates in larger fish (Trudel and Rasmussen, 1997), results in higher concentrations in larger (older) individuals. This is also true for our results, where T-Hg increases with size in males, however, females generally show a trend for lower T-Hg accumulation rates with size than males. Thus, females in some myctophid species may have a Hg excretion system that does not occur in males. Egg laying is a well-known Hg elimination mechanism for most oviparous animals e.g., arthropods (Bakker et al., 2017; Saxton et al., 2013), crustaceans (Seco et al., 2019), amphibians (Bergeron

et al., 2010), fish (Khadra et al., 2019; Sackett et al., 2013) and in seabirds (Brasso et al., 2012; Pedro et al., 2015), and this mechanism might explain the different bioaccumulation patterns between sexes.

4.3. Inter-specific variations in T-Hg concentrations in muscle of Southern Ocean myctophids

Species-specific traits like feeding ecology, vertical and horizontal distribution, metabolism or physiology play an important role in Hg accumulation. In the present study, however, size and sex seemed to more important drivers for Hg accumulation in myctophids, as the smallest species had the lowest Hg concentrations in muscle (*K. anderssoni* and *P. bolini*), whilst concentrations were broadly congruent within the larger species. The lack of an inter-specific signal may be due to overlap in the distribution and diet patterns in the studied community. Most of the analysed species feed upon the same zooplankton prey species, such as the copepods *Metridia* spp., *Rhincalanus gigas, Pleuromamma robusta* and *Calanoides acutus* and the euphausiid *Thysanoessa* spp. (Lourenço et al., 2017; Saunders et al., 2018), with the exception of *E. antarctica* that feeds mostly on *E. superba* and on the hyperiid amphipod *T. gaudichaudii* (Saunders et al., 2018). Most species were found across the Scotia Sea, with all species co-occurring in the northern Scotia Sea region (see Fig. 1). The vertical distribution patterns were also broadly similar among most species with the greatest concentrations of fish occurring above 400 m, particular at night (Collins et al., 2012; Sauderns et al., 2018, 2019). Specific details of metabolic and physiological characteristics of myctophids are still unknown but, due to the phylogenetic proximity of the analysed species, one would assume that there should not be significant differences on Hg accumulation or excretion mechanisms among these species.

4.4. Tissue allocation of Hg in the Southern Ocean myctophids

Significant differences in T-Hg levels were observed in muscle, heart, liver and gill tissues in all species examined. Heart and liver tissues consistently showed higher concentrations than muscle and gill tissues. Large variations in Hg concentrations in heart tissue was consistently observed between individuals, probably due to differences in blood volume inside the heart chambers. The presence of blood fluid in the heart would decrease the overall Hg content in this organ, as Hg in fish blood was between 3 and 15 times lower than muscle in different fish species (Eilser, 2010; Hamada et al., 1977; Shultz and Crear, 1976).

The liver, as an organ responsible for detoxification and transformation of toxins (Maršálek et al., 2007; Yamashita et al., 2005), was expected to have high concentrations of T-Hg. Indeed, higher T-Hg concentrations occur in the liver of fish than in muscle tissue (liver/muscle index), such that a high liver: muscle contamination ratio is regarded to be an appropriate bioindicator for highly contaminated habitats (Evans and Dodoo, 1993; Gonzalez et al., 2005; Havelková et al., 2008). Although the Southern Ocean is thought of as a fairly pristine environment, it is already known that, due to the Hg atmospheric cycle and special conditions for Hg methylation processes, greater than expected O-Hg concentrations occur in the region (Cossa et al., 2011). It is likely that this bioavailability of O-Hg can be reflected on the high liver/muscle index. Present results are in agreement with a previous study in the Southern Ocean on the bald rockcod *Pagothenia borchgrevinki*, which also showed Hg concentrations in the liver to be twice that in muscle (Honda et al., 2014).

The main uptake route of T-Hg in fish is through the diet, with only low percentages (~10%) of the whole body burden T-Hg originating from waterborne Hg absorbed by the gills (Phillips and Buhler, 1978). Nevertheless, muscle comprises the majority of individual biomass and therefore is the tissue with the highest ecological relevance, as it will be the carrier for most Hg to the next trophic level. Myctophids are an important prey to several Southern Ocean predators (Sabourenkov, 1991) and are also the most abundant mesopelagic fish family in the Southern Ocean (70–200 Mt) (Catul et al., 2010). Assuming the conservative lowest muscle concentration found in the present study, for all species, and the lowest biomass estimation, this would mean that ≈1.82t of Hg are potentially bioavailable to Southern Ocean predators, in this family of mesopelagic fish alone. It is therefore likely that myctophids may be viewed as “Hg light bulbs” in the Southern Ocean, given their conspicuous use of bioluminescence and the significant role in Hg bioaccumulation and trophic transfer processes in this remote environment.

5. Conclusions

Our study indicates a decreasing trend in Hg levels in myctophids over the last decade, especially in the gills, suggesting a decreasing bioavailability of this element in the water over this period. Further monitoring is required to confirm this pattern. There was little evidence of any regional variability in Hg contamination in the Southern Ocean, and indeed myctophid species appeared to have the same Hg range globally. Hg concentration generally increased with fish body size, which is a proxy for age, with the exception of *E. antarctica* females, that had a decreasing pattern, most likely a result of Hg elimination through egg laying. Higher concentrations of Hg were found in the liver and heart followed by muscle and gills. At a species level, Hg accumulation is mainly driven by size, gender and developmental stage, as well as temporal variation in Hg availability in the environment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

José Seco: Writing - original draft. **José C. Xavier:** Resources, Writing - review & editing, Supervision, Project administration. **Paco Bustamante:** Writing - review & editing, Supervision. **João P. Coelho:** Writing - review & editing. **Ryan A. Saunders:** Writing - review & editing. **Nicole Ferreira:** Writing - review & editing. **Sophie Fielding:** Resources, Supervision. **Miguel A. Pardal:** Writing - review & editing. **Gabriele Stowasser:** Writing - review & editing. **Thainara Viana:** Writing - review & editing. **Geraint A. Tarling:** Resources, Supervision, Project administration. **Eduarda Pereira:** Resources. **Andrew S. Brierley:** Writing - review & editing.

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Appendix A. Supplementary data

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