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 years (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.

Capsule: Myctophids are a key group in the Southern Ocean food web, and have shown a possible decreasing trend in mercury contamination over the decade.

Keywords: Trace element; metal; bioaccumulation; mesopelagic fish; Antarctic

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 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. 1995, 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 planktic crustaceans (Lourenço et al., 2017; Pakhomov et al., 1996; Saunders et al., 2018), and in turn 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; K. L. 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 (G. R. 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

97 globally have investigated Hg bioaccumulation in these fish (Blum et al., 2013;
98 Chouvelon et al., 2012; Gibbs et al., 1974; Lahaye et al., 2006; Martins et al., 2006;
99 Monteiro et al., 1996; Windom et al., 1973), and only two studies have focussed on
100 the Southern Ocean (Bustamante et al., 2003; Cipro et al., 2018b). Due to their central
101 role in the Southern Ocean pelagic food web, evaluating the level of Hg contamination
102 in myctophids is important as a step towards understanding the trophic pathway of this
103 contaminant. Such studies are also essential for establishing robust baselines for
104 future environmental monitoring that will inform potential ecosystem management
105 strategies in the context of the Minamata convention objectives (Gustin et al. 2016).
106 In the present study, Hg concentrations were measured in myctophids collected
107 across the Scotia Sea, one of the most productive regions of the Southern Ocean
108 (Holm-Hansen et al., 2004), and spatial, temporal, inter-specific and ontogenetic
109 patterns were examined. The Scotia Sea is home to globally important populations of
110 higher predator species such as penguins, flying birds, seals and whales (Murphy et
111 al., 2007), and important commercial fisheries (Constable et al., 2000), so
112 understanding Hg pathways is important. Specifically, we assessed the total Hg (T-
113 Hg) concentrations in four tissues (muscle, gills, heart and liver) and organic Hg as a
114 proxy of MeHg (O-Hg) in the muscle of the nine biomass-dominant myctophids
115 (*Electrona antarctica, Electrona carlsbergi, Gymnoscopelus braueri, Gymnoscopelus*
116 *nicholsi, Gymnoscopelus opisthopterus, Gymnoscopelus fraseri*, *Protomyctophum*
117 *bolini*, *Krefftichthys anderssoni* and *Nannobrachium achirus*) from two regionally
118 distinct food webs in the Scotia Sea (South Georgia and South Orkneys Islands) in
119 different years (2007/08, 2015/16 and 2016/17). These regions are characterised by
120 different environmental conditions (South Orkney Islands, an Antarctic island group
121 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.

Material and methods

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 (Figure 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 -20ºC for subsequent laboratory analyses, with each fish species preserved separately in different plastic bags.

Laboratory procedures

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

153 Samples were frozen in sterile containers and lyophilized during two days and
154 ground to a fine powder for further analyses of Hg. T-Hg was determined by atomic
155 absorption spectrometry (AAS) with thermal decomposition and gold amalgamation,
156 using an Advanced Mercury Analyser LECO AMA-254. Quantification of O-Hg was
157 performed through a chemical digestion described in (Válega et al., 2006). Briefly,
158 biological tissues were digested with a mixture of 18% KBr in 5% H_2SO4, followed by
159 extraction of organic mercury into toluene. The aqueous fraction resulting from the
160 addition of a $Na_2S_2O_3$ solution was then analyzed for mercury by thermal
161 decomposition atomic absorption spectrometry with gold amalgamation (all reagents
162 used were Hg-free, p.a. grade). The method does not differentiate different forms of
163 mercury-Hg or other mercury-Hg compounds, such as dimethylHg or ethylHg, and all
164 can be contained in the extract. However, organic forms are only present at very low
165 levels at depth in the world ocean (Hintelmann, 2010) so virtually all the OHg quantified
166 here would be 100% MethylHg. Where there was low individual mass (less than 200
167 mg), samples for O-Hg analyses were obtained by combining multiple individuals of
168 the same species of similar sizes collected from the same location. Analytical precision
169 and accuracy were determined several (>4) times a day for the following certified
170 reference materials: DORM-4 (n = 59, 96 ± 13%) fish protein and ERM-BB422 (n =
171 108, 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).

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. To evaluate differences among years, locations and sexes Wilcoxon rank and Kruskal–Wallis tests were performed.

Results

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

197 test, H = 4.859, p = 0.0852, respectively) while significantly lower T-Hg concentrations
198 were observed for *E. antarctica* in 2016/17 than in 2007/08 and 2015/16 (Kruskal-
199 Wallis test, H = 13.81, p = 0.001; Table 1). There were statistically significant
200 differences in gill T-Hg concentration between years in *E. antarctica, G. braueri* and
201 *G. nicholsi* (Kruskal-Wallis test, H = 33.51, p < 0.001; H = 17.84, p < 0.001; H = 14.38,
202 p < 0.001). By contrast, in *Krefftichthys anderssoni* and *Protomyctophum bolini,* which
203 were caught both in 2007/08 and 2016/17, no significant differences in T-Hg muscle
204 concentrations between years was evident (Mann-Whitney test, U = 43, p = 0.426;
205 Mann-Whitney test, U = 66, p = 0.359, respectively).
206 To minimize the effect of temporal variation on the spatial analysis,
207 comparisons were only performed within species between the 2 consecutive sampling
208 years (2015/16 and 2016/17). During these surveys, only 3 species (*E. antarctica, G.*
209 *braueri* and *G. nicholsi*) were caught consistently year on year at both South Georgia
210 (north of the Southern boundary of the Antarctic Circumpolar Current Front; SACCF)
211 and the South Orkneys Islands (south of the SACCF). There was no significant
212 difference in T-Hg muscle concentrations in the two *Gymnoscopelus* species between
213 the two locations (*G. braueri,* Kruskal-Wallis test, H = 5.366, p = 0.068; *G. nicholsi,*
214 Kruskal-Wallis test, H = 4.859, p = 0.085). However, the concentrations of T-Hg in *E.*
215 *antarctica* were significantly lower at the South Orkney Islands (0.126 ± 0.068 μg g^{-1})
216 than at South Georgia (0.216 ± 0.082 μg g^{-1}; Fig. 3).
217
218 *Inter-specific variations in T-Hg concentrations in myctophids*
219 Inter-specific variations in T-Hg concentrations in muscle were apparent for
220 samples pooled by year and location. During 2008/09, the 3 species of Southern
221 Ocean *Gymnoscopelus* (*G. braueri, G. nicholsi* and *G. opisthopterus*) and the two

222 species of *Electrona* (*E. antarctica* and *E. carlsbergi*) had higher T-Hg concentrations
223 than *K. anderssoni* and *P. bolini* (Kruskal-Wallis test, H = 48.66, p < 0.0001). However,
224 the levels of T-Hg in *Nannobrachium achirus* were not significantly different from the
225 other species caught during this time (Fig. 2; Table 1).
226 No statistical differences were observed between T-Hg concentrations in any
227 of the 3 fish species (*E. antarctica, G. braueri* and *G. nicholsi*) caught in 2015/16
228 (Kruskal-Wallis test, H = 4.432, p = 0.109). However, for fish caught in 2016/2017, *E.*
229 *antarctica, G. fraseri, G. nicholsi* each had higher T-Hg concentrations than *K.*
230 *anderssoni,* whilst no significant inter-specific differences were observed for either *G.*
231 *braueri* and *P. bolini* (Kruskal-Wallis test, H = 28.7, p < 0.0001; Fig. 2; Table 1).
232
233 *Gender-specific and ontogenetical variations in T-Hg concentrations*
234 To increase the robustness of our analysis on gender- and size-related effects
235 on T-Hg accumulation in myctophids, only samples with no significant differences
236 across years were pooled for each species. Thus, samples were pooled across all
237 years for every species, except *E. antarctica,* for which only samples from 2007/08
238 and 2015/16 were pooled.
239 No significant gender-related differences in T-Hg muscle concentrations were
240 observed for any species other than *G. nicholsi* and *K. anderssoni* where, in both,
241 males had higher T-Hg concentrations than females (Mann-Whitney test, U = 41, p =
242 0.005 and U = 56, p = 0.017, respectively),
243 Size- (and hence age-) related patterns in T-Hg concentration were evaluated for
244 species where there was a sufficient sample size ($n > 5$) across the full expected size
245 ranges (Fig. 3). Three patterns were noted between the different species/sexes: 1) No
246 influence of size in T-Hg concentrations [in females of *G. braueri,* in males of *G.*

247 *braueri, G. nicholsi, K. anderssoni* and juveniles of *P. bolini*]*;* 2) an increase of
248 concentration of T-Hg with size [in males of *G. nicholsi, K anderssoni* and *P. bolini*, *E.*
249 *antarctica* and *P. bolini* and in juveniles of *G. braueri*]; 3) and a decrease of T-Hg with
250 size, was only found in females of *E. antarctica*.
251
252 *Variations in T-Hg concentrations in the different tissues of Southern Ocean*
253 *myctophids*
254 Four different tissue types, muscle, gills, heart and liver, were analysed for T-Hg
255 levels in each species, except *K. anderssoni* and *P. bolini* that were too small for us to
256 achieve adequate extraction of these tissues (Table 1).
257 Overall, T-Hg concentrations varied between tissues, with different patterns of
258 variation between species and years (Table 1). However, in the majority of the species
259 analysed from 2007/08 (χ^2 = 92.74, p < 0.001) and 2015/16 (χ^2 = 135.8, p < 0.001)
260 samples, the heart and liver had consistently higher T-Hg concentrations than the
261 muscle and gills, which contained the lowest overall concentrations. In 2016/17
262 samples (χ^2 = 70.47, p < 0.001), gills had always lower concentration than muscle.
263 Also, liver from *G. fraseri* was the only tissue to have an average T-Hg concentration
264 greater than 1 μg g^{-1} (1.11 ± 0.644 μg g^{-1}).
265
266 *O-Hg concentrations in Southern Ocean myctophids*
267 Concentrations of O-Hg in muscle of the analysed species ranged between
268 0.051 and 0.493 μg g^{-1}. There were no significant differences in O-Hg concentrations
269 between species (Kruskal-Wallis test, H = 6.428, p = 0.491; Table 2). The overall
270 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.

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.

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).

296 The pattern of decline in T-Hg tissue concentrations in both squid and myctophids over
297 this 10-year period suggests a decrease in the bioavailability of Hg around South
298 Georgia in the last decade. However, due to the comparatively shorter life spans of
299 squid than to myctophids (around 1 to 2 years in squid (Arkhipkin, 2004; Boyle and
300 Rodhouse, 2005; Xavier et al., 2018) versus ~ 3 to 8 years in myctophids (Linkowski,
301 1987; 1985; Saunders et al., 2020)), acute changes in environmental pollutants are
302 more likely to be reflected in squid due to a greater turnover in individuals within their
303 populations. In contrast, myctophids are likely to retain and integrate Hg contamination
304 from the environment into their muscle over longer periods of exposure, making it more
305 appropriate to look for patterns of T-Hg decrease in gill tissue as gills will more
306 immediately reflect a difference in bioavailability of Hg in the water. Generally, longer-
307 lived animals take longer to reflect any alteration in habitat contaminant levels
308 (Fränzle, 2006).

309 Habitat use has a major effect on Hg accumulation, since longer exposure in
310 more contaminated areas will result in higher concentrations of this element in tissues
311 (Desta et al., 2008; Le Bourg et al., 2019). In this study, little evidence was found of
312 regional variation in T-Hg concentrations from the 3 species that were caught
313 concurrently at South Georgia and the South Orkneys (*E. antarctica, G. braueri* and
314 *G. nicholsi*), with regional differences only apparent for *E. antarctica. Electrona*
315 *antarctica* specimens from South Georgia had lower concentrations of T-Hg than
316 those from the South Orkneys, but samples from the South Orkneys Islands were, on
317 average, 20 mm smaller, suggesting that the observed spatial pattern could reflect
318 differences due to body size (i.e., bioaccumulation level) rather than differences in
319 environmental factors. Indeed, other studies have shown that body size is typically
320 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 attribute 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,

346 and diet. It seems that myctophids, from a global perspective, have similar T-Hg
347 concentrations, despite their ostensible differences in physiology, biology and ecology.
348 Comparisons among these studies have to be done with caution, however, as
349 methodological differences such as sample preservation, analytical approaches and
350 sample size may invalidate direct comparisons between studies.

351 To the best of our knowledge, there are only two other studies on Hg in
352 Southern Ocean myctophids (Bustamante et al., 2003; Cipro et al., 2018b), both of
353 which are on samples from the sub-Antarctic Kerguelen Islands (Indian Ocean sector).
354 *E. antarctica* from the Kerguelen Islands had T-Hg concentrations between 2 and 4
355 times lower (0.066 ± 0.015 μg g^{-1}; (Cipro et al., 2018b)) than in all of our sampled
356 years/locations, even though there was a high degree of overlap in sizes of fish
357 analysed between studies. In contrast, the *Gymnoscopelus* species that occurred in
358 our and previous studies, G*. fraseri* and *G. nicholsi,* had similar values for equivalent
359 sized individuals (Bustamante et al., 2003; Cipro et al., 2018a). Although there are
360 differences in diet and prey field between the two regions (South Georgia and
361 Kerguelen), *E. antarctica* from Kerguelen Islands appear to feed more frequently on
362 *Thysanoessa macrura* (Clarke et al., 2018), while individuals from South Georgia feed
363 mainly on *Euphausia superba* or *Themisto gaudichaudii* (Saunders et al., 2018). This
364 difference in diet alone seems unlikely to explain the regional differences in T-Hg, as
365 levels of mercury in *T. macrura* from Kerguelen Islands were similar to those in *E.*
366 *superba* from the Scotia Sea (Cipro et al., 2018b; Seco et al., 2019). Furthermore,
367 species-specific estimates of Hg levels across the whole prey field of myctophids from
368 both Kerguelen Islands and the Scotia Sea are unknown, and the role of these taxa in
369 the transfer of Hg to myctophids and upper trophic levels remains unclear. A possible
370 lower fraction of O-Hg in the prey species from the Kerguelen Islands compared to

371 their counterparts in the Scotia Sea (Seco et al., 2019) could lead to a lower rate of
372 Hg accumulation in myctophids in this region, given the shorter turnover of MeHg in
373 fish tissue (~400 days (Downs et al., 1998)), and the more limited trophic transfer
374 potential of inorganic Hg compare to O-Hg. These diverse results reinforce the
375 importance of species-specific analyses of Hg levels, when trying to understand
376 spatial patterns in myctophid Hg accumulation patterns through regional predator-prey
377 interactions.
378
379 *Gender-based and ontogenetic patterns in T-Hg concentration in Southern Ocean*
380 *myctophids*
381 Physiological and biological factors, such as sex and size, are known to
382 influence Hg concentration in fish (Bastos et al., 2016; Dang and Wang, 2012; Gewurtz
383 et al., 2011; Le Bourg et al., 2019). When assessing the effect of body size in T-Hg
384 concentration in the muscle of Southern Ocean myctophids, we observed a general
385 positive trend of increasing T-Hg with increasing size, except for *E. antarctica* females,
386 for which this relationship was negative. In other species, such as *E. carlsbergi, G.*
387 *fraseri,* and *G. opisthopterus*, the correlations were not significant (see Fig. 3). The
388 positive relationship between T-Hg and size in fish is well established (Dang and
389 Wang, 2012; Gewurtz et al., 2011; Somers and Jackson, 1993), with a tendency for
390 increased Hg bioaccumulation with age, mainly in muscle tissue. Also, larger fish tend
391 to feed on larger prey that usually bioaccumulates greater Hg concentrations
392 (Chouvelon et al., 2014) which, coupled with the tendency for lower Hg excretion rates
393 in larger fish, (Trudel and Rasmussen, 1997) results in higher concentrations in larger
394 (older) individuals. This is also true for our results, where T-Hg increases with size in
395 males, however, females generally show a trend for lower T-Hg accumulation rates

396 with size than males. Thus, females in some myctophid species may have a Hg
397 excretion system that does not occur in males. Egg laying is a well-known Hg
398 elimination mechanism for most oviparous animals [e.g., arthropods (Bakker et al.,
399 2017; Saxton et al., 2013), crustaceans (Seco et al., 2019), amphibians (Bergeron et
400 al., 2010), fish (Khadra et al., 2019; Sackett et al., 2013) and in seabirds (Brasso et
401 al., 2012; Pedro et al., 2015)], and this mechanism might explain the different
402 bioaccumulation patterns between sexes.
403
404 *Inter-specific variations in T-Hg concentrations in muscle of Southern Ocean*
405 *myctophids*
406 Species-specific traits like feeding ecology, vertical and horizontal distribution,
407 metabolism or physiology play an important role in Hg accumulation. In the present
408 study, however, size and sex seemed to more important drivers for Hg accumulation
409 in myctophids, as the smallest species had the lowest Hg concentrations in muscle (*K.*
410 *anderssoni* and *P. bolini*), whilst concentrations were broadly congruent within the
411 larger species. The lack of an inter-specific signal may be due to overlap in the
412 distribution and diet patterns in the studied community. Most of the analysed species
413 feed upon the same zooplankton prey species, such as the copepods *Metridia* spp.,
414 *Rhincalanus gigas, Pleuromamma robusta* and *Calanoides acutus* and the euphausiid
415 *Thysanoessa* spp. (Lourenço et al., 2017; Saunders et al., 2018), with the exception
416 of *E. antarctica* that feeds mostly on *E. superba* and on the hyperiid amphipod *T.*
417 *gaudichaudii* (Saunders et al., 2018). Most species were found across the Scotia Sea,
418 with all species co-occurring in the northern Scotia Sea region (see Fig. 1). The vertical
419 distribution patterns were also broadly similar among most species with the greatest
420 concentrations of fish occurring above 400 m, particular at night (Collins et al., 2012;

Saunders et al., 2019; 2018). 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.

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 levels 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

446 bald rockcod *Pagothenia borchgrevinki,* which also showed Hg concentrations in the
447 liver to be twice that in muscle (Honda et al., 2014).
448 The main uptake route of T-Hg in fish is through the diet, with only low
449 percentages (~10%) of the whole body burden T-Hg originating from waterborne Hg
450 absorbed by the gills (G. R. Phillips and Buhler, 1978). Nevertheless, muscle
451 comprises the majority of individual biomass and therefore is the tissue with the
452 highest ecological relevance, as it will be the carrier for most Hg to the next trophic
453 level. Myctophids are an important prey to several Southern Ocean predators
454 (Sabourenkov, 1991) and are also the most abundant mesopelagic fish family in the
455 Southern Ocean (70-200 Mt) (Catul et al., 2010). Assuming the conservative lowest
456 muscle concentration found in the present study, for all species, and the lowest
457 biomass estimation, this would mean that ≈ 1.82t of Hg are potentially bioavailable to
458 Southern Ocean predators, in this family of mesopelagic fish alone. It is therefore likely
459 that myctophids may be viewed as “Hg light bulbs” in the Southern Ocean, given their
460 significant role in Hg bioaccumulation and trophic transfer processes in this remote
461 environment.
462
463 **Conclusions**
464 Our study indicates a decreasing trend in Hg levels in myctophids over the last
465 decade, especially in the gills, suggesting a decreasing bioavailability of this element
466 in the water over this period. Further monitoring is required to confirm this pattern.
467 There was little evidence of any regional variability in Hg contamination in the Southern
468 Ocean, and indeed myctophid species appeared to have the same Hg range globally.
469 Hg concentration generally increased with fish body size, which is a proxy for age, with
470 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 species size, gender and developmental stage, as well as temporal variation in Hg availability in the environment.

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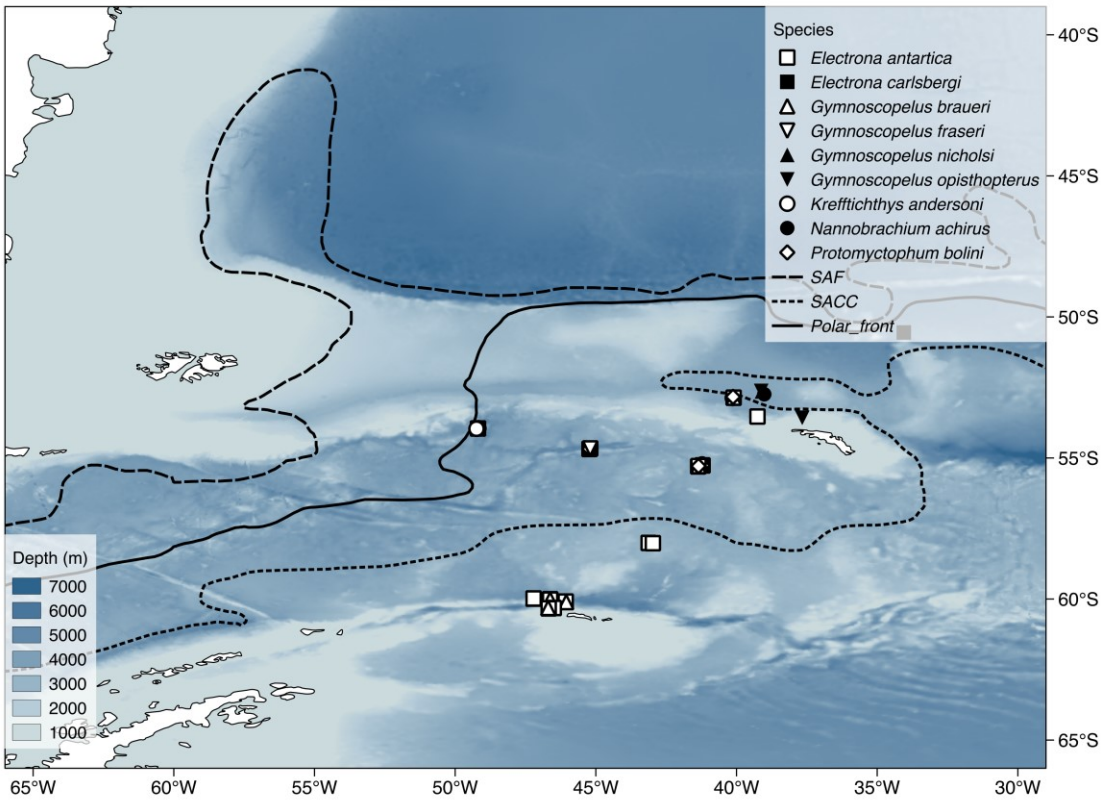

Figure 1. Sampling sites and distributions of species captured around the Scotia Sea across all sampling years. SAF – Sub Antarctic Front; SACCF - Southern boundary of the Antarctic Circumpolar Current Front.

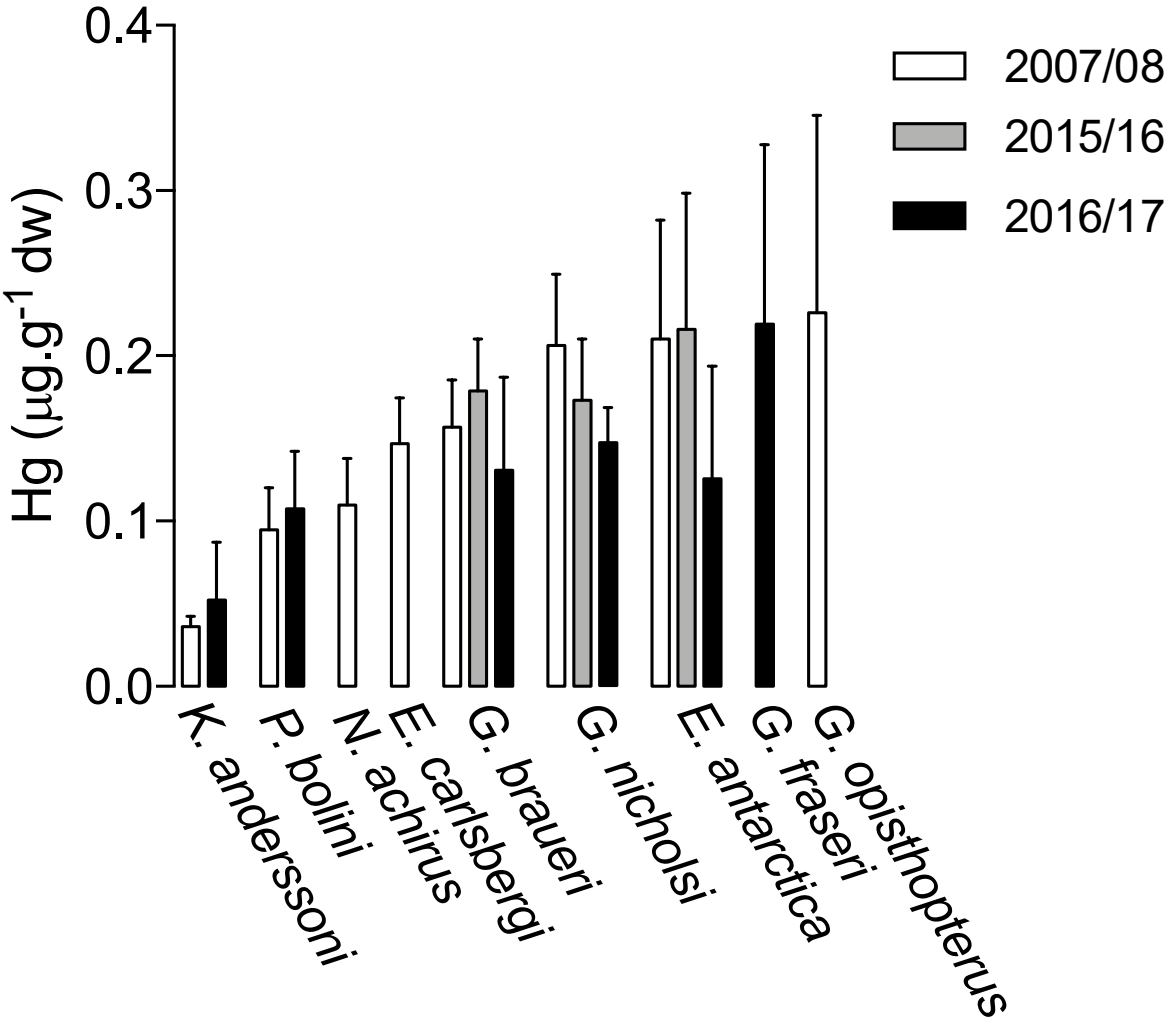

Figure 2 - Total mercury concentrations (Mean ± 1SD, µg g^{-1} dw) in the muscles of Southern Ocean myctophids, collected in the Scotia Sea in the austral summers of 2007/08, 2015/16 and 2016/17.

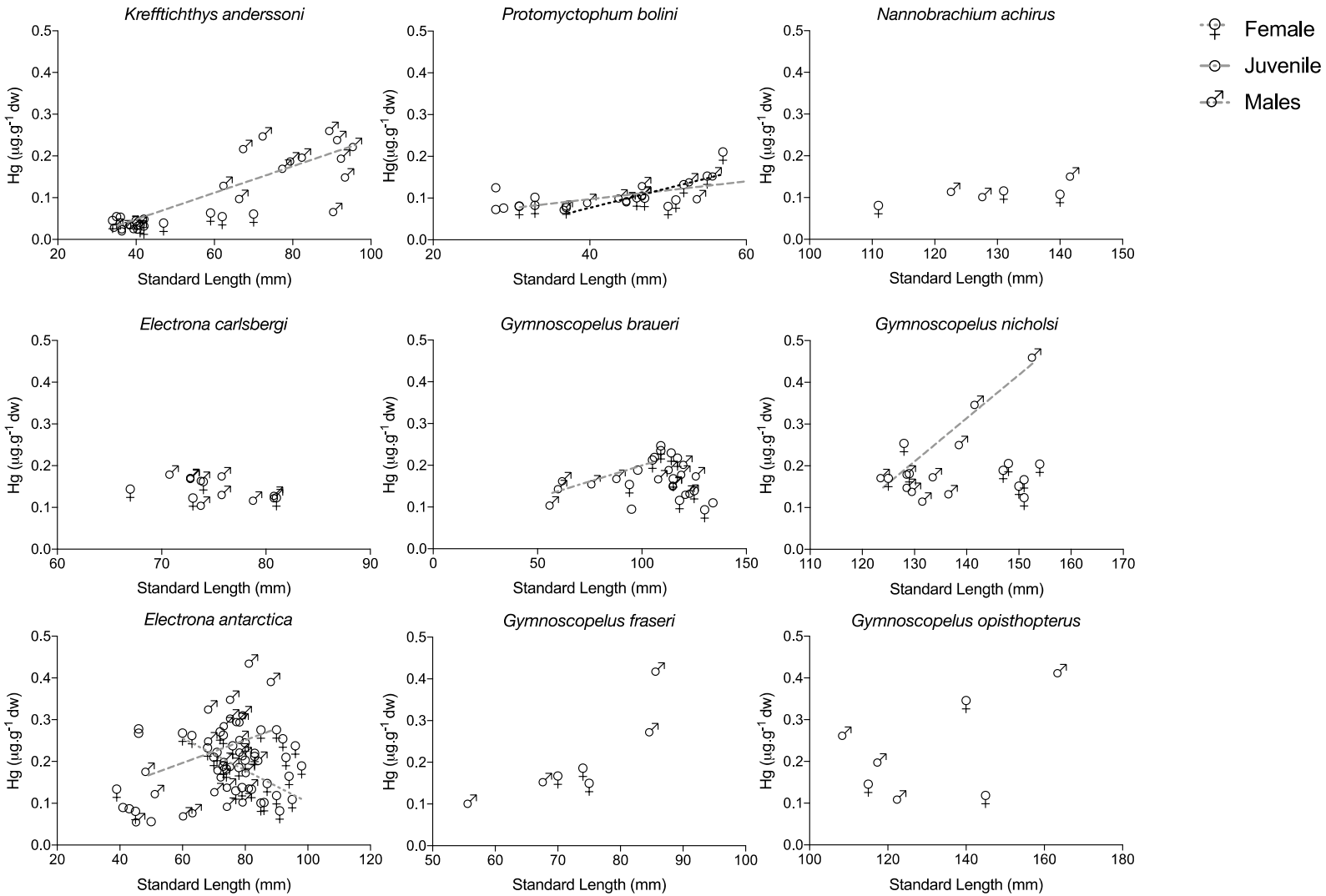

Figure 3 - Total mercury concentrations (Mean ± 1SD, µg g^{-1} dw) versus standard length (mm) in the muscles of Southern Ocean myctophids and significant regression lines, collected in the Scotia Sea in the austral summers of 2007/08, 2015/16 and 2016/17. Regression equations given in supplementary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

Table 1 – Number of analyzed 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				*Tissues*				*Friedman test*	
2007/08	n	Standard Length	Weight	Muscle	Gills	Heart	Liver	X2	p
Electrona antarctica	16	73 ± 16 46 – 98	5.5 ± 3.4 1.1 - 12.7	0.21 ± 0.07 0.09 - 0.33	0.28 ± 0.05 0.19 - 0.37	0.59 ± 0.16 0.35 - 0.99	0.36 ± 0.16 0.18 - 0.80	30.5	<0.001
Electrona carlsbergi	15	75 ± 4 67 – 81	6.0 ± 0.9 4.7 - 7.7	0.15 ± 0.03 0.11 - 0.18	0.31 ± 0.06 0.26 - 0.43	0.57 ± 0.12 0.42 - 0.80	0.29 ± 0.12 0.19 - 0.56	25.6	<0.001
Gymnoscopelus braueri	5	102 ± 40 63 – 164	14 ± 16 2.0 - 38.8	0.16 ± 0.03 0.11 - 0.18	0.40 ± 0.12 0.24 - 0.56	0.77 ± 0.28 0.61 - 1.29	0.51 ± 0.12 0.37 - 0.62	14.0	<0.001
Gymnoscopelus nicholsi	5	137 ± 11 124 - 153	28 ± 6.3 21 - 36	0.29 ± 0.12 0.18 - 0.47	0.25 ± 0.04 0.18 - 0.29	0.50 ± 0.08 0.42 - 0.62	0.59 ± 0.09 0.52 - 0.73	14.0	<0.001
Gymnoscopelus opisthopterus	7	131 ± 20 109 - 164	24 ± 10 13 - 39	0.23 ± 0.12 0.11 - 0.34	0.14 ± 0.05 0.08 - 0.23	0.52 ± 0.08 0.41 - 0.62	0.42 ± 0.19 0.20 - 0.69	16.0	<0.001
Nannobrachium achirus	6	129 ± 11 111 - 142	18 ± 5.4 11 - 25	0.11 ± 0.03 0.07 - 0.16	0.15 ± 0.041 0.10 - 0.20	0.24 ± 0.05 0.19 - 0.32	0.65 ± 0.23 0.34 - 0.94	17.0	<0.001
Krefftichthys anderssoni	10	38 ± 4 34 – 47	1.0 ± 1.8 0.3 – 6.0	0.04 ± 0.01 0.03 - 0.04	n.a.	n.a.	n.a.		
Protomyctophum bolini	10	42 ± 8 31 – 56	1.2 ± 0.7 0.5 - 2.6	0.09 ± 0.03 0.07 - 0.16	n.a.	n.a.	n.a.		
2015/16									
Electrona antarctica	36	80 ± 8 63 – 96	6.9 ± 2.6 3.1 - 14	0.22 ± 0.08 0.07 - 0.44	0.22 ± 0.06 0.11 - 0.37	0.49 ± 0.17 0.27 - 0.91	0.36 ± 0.14 0.09 - 0.79	79.6	<0.001
Gymnoscopelus braueri	18	114 ± 9 94 – 127	12 ± 3.3 5.7 - 16	0.18 ± 0.03 0.13 - 0.22	0.17 ± 0.07 0.09 - 0.41	0.57 ± 0.11 0.43 - 0.82	0.58 ± 0.16 0 .24 - 0.94	19.5	<0.001
Gymnoscopelus nicholsi	9	142 ± 11 125 - 154	30 ± 5.8 20 – 39	0.17 ± 0.04 0.11 - 0.24	0.16 ± 0.02 0.14 - 0.19	0.31 ± 0.04 0.27 - 0.36	0.33 ± 0.05 0.26 - 0.38	41.7	<0.001
2016/17									
Electrona antarctica	15	61 ± 16 39 - 83	3.3 ± 2.5 0.7 - 7.7	0.13 ± 0.07 0.06 - 0.30	0.07 ± 0.04 0.03 - 0.15	0.19 ± 0.13 0.07 - 0.48	0.15 ± 0.09 0.05 - 0.33	22.9	<0.001
Gymnoscopelus braueri	7	92 ± 34 57 - 134	9.0 ± 9.2 1.1 - 25	0.12 ± 0.06 0.08 - 0.24	0.08 ± 0.03 0.05 - 0.14	0.41 ± 0.43 0.15 - 1.28	0.50 ± 0.30 0.20 - 0.99	17.0	<0.001
Gymnoscopelus fraseri	8	75 ± 10 56 - 86	4.1 ± 1.7 1.5 - 6.5	0.22 ± 0.11 0.12 - 0.42	0.15 ± 0.06 0.10 - 0.26	0.39 ± 0.36 0.12 - 1.03	1.11 ± 0.64 0.25 - 2.11	22.9	<0.001
Gymnoscopelus nicholsi	5	132 ± 3 129 - 137	21 ± 1.4 20 - 23	0.15 ± 0.02 0.12 - 0.18	0.10 ± 0.01 0.09 - 0.11	0.29 ± 0.07 0.20 - 0.38	0.39 ± 0.12 0.19 - 0.48	14.0	<0.001
Krefftichthys anderssoni	11	52 ± 12 40 - 70	1.87 ± 1.35 0.7 - 3.9	0.05 ± 0.04 0.02 - 0.14	n.a.	n.a.	n.a.		
Protomyctophum bolini	17	43 ± 10 28 - 57	1.24 ± 0.76 0.2 - 2.6	0.11 ± 0.03 0.07 - 0.20	n.a.	n.a.	n.a.		

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 antartica	0.17 ± 0.07	0.141 ± 0.07	79 ± 9
Electrona carlsbergi	0.12 ± 0.01	0.107 ± 0.02	88 ± 8
Gymnoscopelus braueri	0.17 ± 0.06	0.114 ± 0.03	80 ± 11
Gymnoscopelus nicholsi	0.33 ± 0.14	0.331 ± 0.18	95 ± 17
Gymnoscopelus opisthopterus	0.12 ± 0.02	0.099 ± 0.02	79 ± 4
Gymnoscopelus fraseri	0.16 ± 0.004	0.157 ± 0.03	97 ± 18
Krefftichthys anderssoni	0.10 ± 0.04	0.096 ± 0.06	88 ± 13
Protomyctophum bolini	0.13 ± 0.02	0.123 ± 0.02	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 Island	1997-99	Frozen	Cipro et al. 2018
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 Island	1997-99	Frozen	Cipro et al. 2018
Gymnoscopelus nicholsi	129 - 164	0.137 ± 0.047	0.096– 0.200	Kerguelen Island	1997-99	Frozen	Cipro et al. 2018
Gymnoscopelus nicholsi	144 ± 15	0.205 ± 0.126	0.157- 0.297	Kerguelen Island	1998	Frozen	Bustamante et al. 2003
Gymnoscopelus piabilis	114 - 162	0.179 ± 0.078	0.067– 0.333	Kerguelen Island	1997-99	Frozen	Cipro et al. 2018
Gymnoscopelus piabilis	151 ± 11	0.310 ± 0.126	0.177- 0.475	Kerguelen Island	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 Island	1997-99	Frozen	Cipro et al. 2018

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