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## Foraging depth depicts resource partitioning and contamination level in a pelagic shark assemblage: insights from mercury stable isotopes

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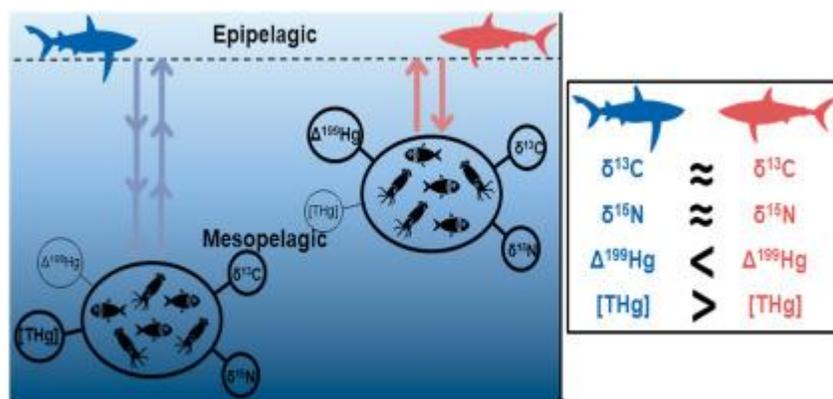
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### Abstract :

The decline of shark populations in the world ocean is affecting ecosystem structure and function in an unpredictable way and new ecological information is today needed to better understand shark roles in their habitats. In particular, the characterization of foraging patterns is crucial to understand and foresee the evolution of dynamics between sharks and their prey. Many shark species use the mesopelagic area as a major foraging ground but the degree to which different pelagic sharks rely on this habitat remains overlooked. In order to depict the vertical dimension of their trophic ecology, we used mercury stable isotopes in the muscle of three pelagic shark species (the blue shark *Prionace glauca*, the shortfin mako shark *Isurus oxyrinchus* and the smooth hammerhead shark *Sphyrna zygaena*) from the northeastern Pacific region. The  $\Delta^{199}\text{Hg}$  values, ranging from 1.40 to 2.13 ‰ in sharks, suggested a diet mostly based on mesopelagic prey in oceanic habitats. We additionally used carbon and nitrogen stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) alone or in combination with  $\Delta^{199}\text{Hg}$  values, to assess resource partitioning between the three shark species. Combining  $\Delta^{199}\text{Hg}$  resulted in a decrease in trophic overlap estimates compared to  $\delta^{13}\text{C}/\delta^{15}\text{N}$  alone, demonstrating that multi-isotope modeling is needed for accurate trophic description of the three species. Mainly, it reveals that they forage at different average depths and that resource partitioning is mostly expressed through the vertical dimension within pelagic shark assemblages. Concomitantly, muscle total mercury concentration (THg) differed between species and increased with feeding depth. Overall, this study highlights the key role of the mesopelagic zone for shark species foraging among important depth gradients and reports new ecological information on trophic competition using mercury isotopes. It also suggests that foraging depth may play a pivotal role in the differences between muscle THg from co-occurring high trophic level shark species.

## Graphical abstract



## Highlights

►  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  were determined in three pelagic shark species. ► Hg isotopes suggested shark species foraged on mesopelagic prey. ►  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  overestimated overlaps between trophic niches. ► Differences in foraging depth better explained resource partitioning. ► Foraging depth influenced mercury contamination level.

**Keywords** : Trophic ecology, Top-predator, Mercury stable isotopes, Resource partitioning, Foraging depth, Mercury accumulation



24 *By analyzing the isotopic ratios of mercury, a major pollutant of marine ecosystems, this study*  
25 *characterized the foraging depth of three shark species. Feeding depth governed resource*  
26 *partitioning between species and explained mercury concentration in shark tissues.*

## 27 **1. INTRODUCTION**

28 Sharks are facing worldwide a large variety of threats such as overfishing, pollution,  
29 ecosystem degradation and others (Dulvy et al., 2014; Hazen et al., 2013; Queiroz et al., 2019). In  
30 recent years, the decline of many shark populations in the global ocean has raised public concern due  
31 to the iconic nature of these top predators and their influence on marine ecosystems over various  
32 temporal and spatial scales (Ferretti et al., 2010; Heithaus et al., 2008). Since the consequences of  
33 their removal are difficult to assess and predict (Baum and Worm, 2009; Ferretti et al., 2010),  
34 ecological information on habitat use and foraging grounds are needed to better assess future  
35 changes in marine ecosystems (Shiffman et al., 2012).

36 Large sharks, such as most marine predators, influence their ecosystem mainly through trophic  
37 interactions, either by predation on mesopredators, i.e. top-down control (Baum and Worm, 2009;  
38 Ferretti et al., 2010), competition with sympatric (i.e. co-occurring) high trophic level predators  
39 (Matich et al., 2017), or more complex interactions (Heithaus et al., 2008; Jorgensen et al., 2019).  
40 Competition for a shared trophic resource can result in lower food availability, change in  
41 physiological condition, and ultimately, reduced fitness (Jorgensen et al., 2019). Therefore,  
42 evolutionary processes tend to favor resource partitioning in co-occurring top predators (Heithaus et  
43 al., 2013). Tracking studies have highlighted differences in habitat use between shark species  
44 suspected to compete for food (Meyer et al., 2010; Musyl et al., 2011), but this method appears  
45 limited to discriminate the diet of species sharing a same trophic ground. Isotopic trophic tracers,  
46 such as stable carbon and nitrogen isotopes, have been used to assess resource partitioning between  
47 sympatric predators (Heithaus et al., 2013). However, contrary to coastal ecosystems, pelagic trophic  
48 webs are most of the time based on phytoplankton production only resulting in homogeneous

49 isotopic signatures and in overlapping isotopic niches between predators (Kiszka et al., 2015; Klarian  
50 et al., 2018; Rosas-Luis et al., 2017). Rather than competition, overlapping regions of isotopic niches  
51 might therefore be due to some inherent approach limitations. For instance, stable isotopes have a  
52 poor ability to discriminate foraging depth for top-predators likely to feed in deep oceanic habitats  
53 (Choy et al., 2015; Kiszka et al., 2015) and only few studies have investigated the vertical dimension  
54 of resource partitioning in pelagic predator assemblages (Le Croizier et al., 2020b, 2020a).

55 The mesopelagic zone (200-1000 m below the ocean surface) contains one of the most important  
56 animal biomass on earth (Aksnes et al., 2017; Irigoien et al., 2014), principally gathered inside the  
57 “deep scattering layer” community (Costello and Breyer, 2017). It is mainly composed of fishes and  
58 invertebrates that are commonly targeted by marine megafauna (Aksnes et al., 2017; Davison et al.,  
59 2015; Hazen and Johnston, 2010). Among these predators, some pelagic shark species display typical  
60 deep diving patterns suggesting that they rely on this compartment, such as great white (Le Croizier  
61 et al., 2020a), blue (Braun et al., 2019) or scalloped hammerhead sharks (Jorgensen et al., 2009).  
62 Surprisingly, although the combined effect of climate change and fishing pressure is dramatically  
63 changing epipelagic fish biomass and dynamic (Pinsky et al., 2011; Tu et al., 2018), little attention has  
64 been paid to the mesopelagic zone which is also predicted to be affected by climate change (Proud et  
65 al., 2017). In this context, the importance of deeper mesopelagic prey for different oceanic shark  
66 species must be better assessed.

67 Mercury is a globally distributed atmospheric pollutant (Fitzgerald et al., 2007) having deleterious  
68 toxic effects on marine fauna (Eisler, 2006). Entering the ocean in its inorganic form, its bioavailability  
69 increases through methylation by microbial activity (Sunderland et al., 2009). The resulting  
70 methylmercury (MeHg) is incorporated and bioaccumulated, i.e. increase in concentration with  
71 age/length, naturally in marine organisms as well as biomagnified, i.e. increase in concentration with  
72 trophic position (Biton-Porsmoguer et al., 2018; Lavoie et al., 2013; Le Bourg et al., 2019). As long-  
73 lived predators at the top of food webs, sharks naturally exhibit high mercury concentrations

74 (Schartup et al., 2019), predominantly in the MeHg form (Carvalho et al., 2014; Kim et al., 2016;  
75 Storelli et al., 2003). Alongside these processes, mercury accumulation in marine predators appears  
76 to be also driven by other physiological (e.g. metabolism, ontogeny, detoxification mechanisms)  
77 (Bolea-Fernandez et al., 2019; Li et al., 2020), ecological (e.g. habitat, systems productivity, food web  
78 structure, foraging depth) (Ferriss and Essington, 2014; Lavoie et al., 2013; Le Croizier et al., 2019;  
79 Senn et al., 2010) and physical parameters (e.g. oxygen level, sea temperature) (Houssard et al.,  
80 2019; Le Bourg et al., 2019; Schartup et al., 2019). In the ocean, mercury is subject to mass-  
81 independent isotopic fractionation (“MIF”, generally represented through  $\Delta^{199}\text{Hg}$  values) due to its  
82 photochemical transformation in the water column (Bergquist and Blum, 2007). Following light  
83 attenuation with depth,  $\Delta^{199}\text{Hg}$  values decrease from the surface to aphotic waters (Blum et al.,  
84 2013).  $\Delta^{199}\text{Hg}$  values are also not modified during trophic transfer between a prey and its predator  
85 (Kwon et al., 2016; Laffont et al., 2011), making this non-traditional isotope a powerful proxy to  
86 address trophic resources and feeding depth in marine predators (Le Croizier et al., 2020b; Madigan  
87 et al., 2018). Mercury isotopic composition is also affected by mass-dependent fractionation  
88 (“MDF”), studied through  $\delta^{202}\text{Hg}$  values (Bergquist and Blum, 2007; Blum et al., 2013).  $\delta^{202}\text{Hg}$  is  
89 modified during physico-chemical processes such as photoreduction (Bergquist and Blum, 2007) and  
90 volatilization (Zheng et al., 2007), but also during biological processes such as methylation (Janssen et  
91 al., 2016) and demethylation (Perrot et al., 2016). It is therefore a useful tool to study mercury  
92 metabolism in species capable of demethylating MeHg (Bolea-Fernandez et al., 2019; Li et al., 2020).

93 In this study, we used a combination of carbon, nitrogen and mercury stable isotope analyses to  
94 address resource partitioning in three sympatric pelagic shark species (blue, shortfin mako and  
95 smooth hammerhead sharks) off the west coast of the Baja California peninsula (Mexico) in the  
96 northeastern Pacific. Based on stomach contents and carbon and nitrogen stable isotopic analyses,  
97 these three species have previously been reported to display highly overlapping trophic niches  
98 (Klarian et al., 2018; Kone et al., 2014). However, because these sharks display different diving  
99 behavior patterns (Logan et al., 2020; Musyl et al., 2011; Santos and Coelho, 2018) leading to

100 different abilities to access potential prey in the mesopelagic layer, we tested the hypothesis that  
101 resource partitioning occurs along the vertical dimension of their habitat. From an ecological  
102 perspective, this would confirm the key importance of the mesopelagic compartment even for  
103 predators spending most of their time in the upper layers (Le Croizier et al., 2020b, 2020a). It would  
104 also highlight the limitations of studying only carbon and nitrogen isotopic composition in pelagic  
105 assemblages to assess the degree of trophic similarities and the importance of the addition of  
106 relevant biomarkers to better address resource partitioning. Finally, as vertical habitat has been  
107 suspected to influence mercury contamination in marine predators (Choy et al., 2009; Le Bourg et al.,  
108 2019), we evaluated if total mercury levels found in all three species could be related to foraging  
109 depth in sharks.

## 110 **2. MATERIALS AND METHODS**

### 111 **2.1. Sampling strategy**

112 From 2014 to 2016, samples were collected in the artisanal fishing camp of Punta Lobos  
113 (southern Baja California Sur, Mexico, northeast Pacific). Sharks were fished using long lines  
114 equipped with hooks. Sex and total length (TL) were recorded for each shark and approximately 1 g  
115 of muscle was extracted from the dorsal muscle between the first dorsal fin and snout. Immediately  
116 after collection, samples were transported to the laboratory on ice packs, preserved at -20 °C and  
117 freeze-dried prior to analysis. In total, 13 blue sharks (*Prionace glauca*), 10 shortfin mako sharks  
118 (*Isurus oxyrinchus*) and 13 smooth hammerhead sharks (*Sphyrna zygaena*) were sampled.

### 119 **2.2. Carbon and nitrogen stable isotopes**

120 Following the methodology proposed by Li et al., 2016b, two extractions were performed  
121 prior to isotopic ratio determination. To avoid  $\delta^{13}\text{C}$  misinterpretation, lipids were extracted by  
122 placing each sample in 6 mL of a 2:1 chloroform:methanol Folch solution (Folch et al., 1957).  
123 Mechanical crushing using a Dounce homogenizer enhanced the extraction. The mixture was then

124 vortexed for 1 minute, left overnight at room temperature and centrifuged for another 10 minutes  
125 before tissue extraction. This process was repeated three times. For  $\delta^{15}\text{N}$  determination, urea was  
126 also removed from the samples. Samples were immersed in 5 mL of distilled water, vortexed for 1  
127 minute and left at room temperature for 24 hours. The aqueous phase was separated from the tissue  
128 after another 5 minutes centrifugation and this process was repeated three consecutive times.  
129 Samples were then re-dried and homogenized prior to analysis.

130 A sample of 0.50 mg of muscle powder was weighted into tin cups using a XPR10 microbalance  
131 (METTLER TOLEDO). Stable carbon and nitrogen isotope measurements were carried out using a  
132 continuous flow on a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus  
133 mass spectrometer (Pole Spectrométrie Océan, IUEM, Plouzané, France). Based on international  
134 standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ ), isotopic ratio ( $\delta$ )  
135 are expressed in per mille (‰) following:  $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$  where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R  
136 is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . We repeatedly measured known international isotopic  
137 standards (i.e. IAEA-600 Caffeine, IAEA-CH-6 Sucrose, IAEA-N-1 and IAEA-N-2 Ammonium Sulphate)  
138 and an in-lab certified standard substance (i.e. Acetanilide) indicating analytical uncertainties of  $\pm$   
139 0.23 ‰ for  $\delta^{13}\text{C}$  and  $\pm$  0.16 ‰ for  $\delta^{15}\text{N}$ . C:N ratios for all samples were ranging from 3.07 to 3.36,  
140 validating good extractions as shown by Li et al., 2016b (i.e. mean C:N ratio after lipid and urea  
141 removal of 3.2 for blue and smooth hammerhead shark and 3.1 for shortfin mako shark).

### 142 **2.3. Total mercury concentration**

143 As total mercury concentration (THg) is known to be almost exclusively in the MeHg form in  
144 shark muscle, including for the species analyzed here, e.g. 95 to 98% in blue sharks (Carvalho et al.,  
145 2014; Kim et al., 2016; Storelli et al., 2003), THg was used as a proxy for MeHg. THg is expressed on a  
146 dry weight basis with an analytical detection limit of  $0.005 \mu\text{g}\cdot\text{g}^{-1}$  dw. A 20 mg aliquot section of dry  
147 muscle was analyzed using a DMA80 analyzer (Milestone, USA) after combustion, gold trapping and  
148 atomic absorption spectrophotometry detection. The analysis accuracy and reproducibility was

149 assessed from repeated measurements of two reference materials, a lobster hepatopancreas (TORT  
150 3, NRCC,  $0.292 \pm 0.022 \mu\text{g}\cdot\text{g}^{-1}$  dw) and a homogenate of tuna flesh (IAEA 436, INMM,  
151  $4.19 \pm 0.36 \mu\text{g}\cdot\text{g}^{-1}$  dw). Both reference materials were reproduced within the confidence limits (i.e.  
152  $0.286 \pm 0.024 \mu\text{g}\cdot\text{g}^{-1}$  dw for TORT 3,  $n = 10$ , and  $4.20 \pm 0.09 \mu\text{g}\cdot\text{g}^{-1}$  dw for IAEA 436,  $n = 10$ ).

## 153 2.4. Mercury isotopes

154 A segment of 20 mg of dry muscle was immersed into 3 mL of pure bi-distilled nitric acid  
155 ( $\text{HNO}_3$ ) and left at room temperature overnight. Samples were then digested at  $85^\circ\text{C}$  for 6 hours in  
156 pyrolyzed glass vessels closed by Teflon caps on a hotplate. After the addition of 1 mL of hydrogen  
157 peroxide ( $\text{H}_2\text{O}_2$ ), digestion continued for another 6 hours and 100  $\mu\text{L}$  of  $\text{BrCl}$  were added to complete  
158 the extraction. Finally, the solution was diluted in an inverse aqua regia (3:1  $\text{HNO}_3$ : $\text{HCl}$  with 20 vol.%  
159 MilliQ water) to reach a total mercury concentration of  $1 \text{ ng}\cdot\text{mL}^{-1}$ .

160 Mercury isotopic compositions were measured at the Observatoire Midi-Pyrénées (Toulouse, France)  
161 using inductively coupled plasma mass spectrometry (MC-ICP-MS, Thermo Finnigan Neptune) with  
162 continuous-flow cold vapor (CV) generation using  $\text{Sn(II)}$  reduction (CETAC HGX-200), according to a  
163 previously published method (e.g. Le Croizier et al., 2020b). Mercury isotopic composition is  
164 expressed in  $\delta$  notation, reported in per mil (‰) deviation from the NIST SRM 3133 standard and  
165 determined by sample-standard bracketing according to the following equation:  $\delta^{\text{XXX}}\text{Hg}$  (‰) =  
166  $\left( \left[ \frac{({}^{\text{XXX}}\text{Hg}/{}^{198}\text{Hg})_{\text{sample}}}{({}^{\text{XXX}}\text{Hg}/{}^{198}\text{Hg})_{\text{standard}}} \right] - 1 \right) \times 1000$  where XXX represents mercury isotope different  
167 masses.  $\delta^{202}\text{Hg}$  represents Hg MDF, and  $\Delta$  notation is used to express Hg MIF by the following  
168 equation:  $\Delta^{\text{XXX}}\text{Hg}$  (‰) =  $\delta^{\text{XXX}}\text{Hg} - (\delta^{202}\text{Hg} \times a)$  (Bergquist and Blum, 2007), where  $a = 0.252, 0.502,$   
169  $0.752$  and  $1.493$  for isotopes 199, 200, 201 and 204, respectively.

170 Blanks as well as certified materials (i.e. NRC TORT-3 and ERM-BCR-464) were analyzed with the  
171 same procedure. Total mercury concentration in the diluted digest mixtures was monitored by the  
172  $^{202}\text{Hg}$  signals provided by MC-ICP-MS. A recovery rate of  $96 \pm 7\%$  ( $n = 37$ ) for shark samples and  $95 \pm$   
173  $6\%$  ( $n = 7$ ) for certified reference materials was obtained. Reproducibility of mercury isotope

174 measurements was assessed by analyzing UM-Almadén (n = 4), ETH-Fluka (n = 4) and the biological  
175 tissue procedural standards NRC TORT-3 (n = 3) and ERM-BCR-464 (n = 4). Only one analysis was  
176 performed per sample, but measured isotope signatures as well as analytical reproducibility of  
177 standards agreed with previously published values (Table S1).

## 178 2.5. Data analysis

179 For comparison between shark species, data was first checked for normality using Shapiro–  
180 Wilk test and for equality of variances using Bartlett’s test. When both conditions were met, one-way  
181 ANOVA were performed followed by a post-hoc Tukey’s HSD test. Otherwise, we used its non-  
182 parametric analogue, the Kruskal-Wallis test, followed by Dunn’s post hoc test with Bonferroni's  
183 adjustment in the presence of several groups. Between sexes comparisons (Student t test or its non-  
184 parametric analogue Wilcoxon test) are described in Table S2.

185 We used 2D ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) standard ellipse areas encompassing 95% of the data ( $\text{SEA}_B$ ) calculated  
186 using the SIBER package (Jackson et al., 2011) from R programming language (R Core Team, 2019). 3D  
187 ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\Delta^{199}\text{Hg}$ ) standard ellipsoid volumes encompassing 95% of the data ( $\text{SEV}_B$ ) were  
188 calculated using the SIBER-derived model described by Skinner et al., 2019, for three-dimensional  
189 coordinate systems. To allow for comparison between the two model outputs, we expressed isotopic  
190 overlap as a proportion of the non-overlapping area of the two 2D ellipses ( $\text{SEA}_B$ ) or 3D ellipsoids  
191 ( $\text{SEV}_B$ ).

192 Pearson correlation test was used to describe the linear correlation between THg and  $\Delta^{199}\text{Hg}$ .  
193 Generalized linear models (GLMs) were used to evaluate the influence of species, total length, C, N  
194 and Hg isotope signatures on muscle mercury levels. GLMs were built with the LME4 package (Bates  
195 et al., 2015) using THg as the response variable. Based on diagnostic plots of the residuals, a Gaussian  
196 distribution and identity link function were used in the GLMs. Predictor variables were species, age,  
197  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$ . Age was estimated for each individual using growth parameters  
198 established for blue (Blanco-Parra et al., 2008), shortfin mako (Ribot-Carballal et al., 2005) and

199 smooth hammerhead sharks (Morán Villatoro et al., 2018) in the studied region. Models were built  
200 using backward stepwise selection which consists in building a model containing all predictor  
201 variables and removing gradually each predictor variable until no variable is left in the model (i.e.  
202 null model). Akaike's Information Criterion (AIC) was used to define the order of deletion as the  
203 model with the lowest AIC is retained for the next step. All models were ranked based on Akaike's  
204 Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w) using the R  
205 package WIQID (Meredith, 2020). Marginal  $R^2$  were applied to assess each model predictive power  
206 using the R package R2GLMM (Jaeger, 2017).

### 207 **3. RESULTS AND DISCUSSION**

#### 208 **3.1. Carbon and nitrogen isotopic composition**

209 A summary of the results is presented in Table 1. For all variables (TL,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\Delta^{199}\text{Hg}$ ,  
210  $\delta^{202}\text{Hg}$  and THg), no significant difference between sexes within species was detected (Table S2). In  
211 marine ecosystems,  $\delta^{13}\text{C}$  is known to vary between habitats (e.g. coastal versus oceanic), according  
212 to primary producers supporting the food webs (e.g. benthic producers versus phytoplankton) (Fry  
213 and Sherr, 1984). Here, no significant difference in  $\delta^{13}\text{C}$  was detected between the three species  
214 ( $\chi^2_{35,2} = 6.1$ ,  $p > 0.05$ ). These similarities in  $\delta^{13}\text{C}$  profiles (Table 1) between the three species suggest  
215 that they forage on equivalent pelagic food webs derived from phytoplankton production, in  
216 accordance with reported data on shortfin mako and blue sharks in the study area (Hernández-  
217 Aguilar et al., 2016; Tamburin et al., 2019).

218 We found significant  $\delta^{15}\text{N}$  differences among species ( $F_{35,2} = 17.2$ ,  $p < 0.001$ ). The smooth  
219 hammerhead shark presented significantly higher  $\delta^{15}\text{N}$  than both the shortfin mako (Tukey's HSD  
220 test,  $p < 0.05$ ) and the blue shark (Tukey's HSD test,  $p < 0.001$ ). In contrast, the blue shark was  $^{15}\text{N}$   
221 depleted compared to the shortfin mako shark (Tukey's HSD test,  $p < 0.05$ ). In the case of mobile top-  
222 predator species evolving in the pelagic habitat, these differences in  $\delta^{15}\text{N}$  can reflect either  
223 differences in relative trophic position (Cabana and Rasmussen, 1994) or foraging in different regions

224 with contrasted  $\delta^{15}\text{N}$  baselines (Lorrain et al., 2015). In the northeastern Pacific region, no  
225 information is available on smooth hammerhead shark movement, while both blue and shortfin  
226 mako are known to perform limited horizontal movement without a clear seasonal pattern that could  
227 suggest foraging on broad different  $\delta^{15}\text{N}$  ecosystem baselines (Musyl et al., 2011; Queiroz et al.,  
228 2019; Sepulveda et al., 2004). Therefore, their isotopic signatures likely represent an integrated  
229 signal of these shared habitat baselines. The significant differences observed in  $\delta^{15}\text{N}$  signature  
230 between the three species might overall be due to differences in trophic levels, with blue sharks  
231 occupying the lowest trophic level and smooth hammerhead sharks the highest. In the study region,  
232 all three species are known to principally rely on different cephalopod species as observed in  
233 previous stomach content analyses. Shortfin mako sharks feed on *Dosidicus gigas* (Velasco Tarelo  
234 and Galván-Magaña, 2005), blue sharks on *Onychoteuthis banksii*, *Gonatus californiensis* and *D. gigas*  
235 and smooth hammerhead sharks on *D. gigas*, *Ancistrocheirus lesueurii* and *O. banksii* (Galván-Magaña  
236 et al., 2013). The apparent differences between the trophic levels of the three shark species could be  
237 the result of broad differences in cephalopods trophic levels. Indeed, the observed mean difference  
238 in  $\delta^{15}\text{N}$  values between blue and smooth hammerhead sharks (2.15 ‰) matches the important  
239 variation in  $\delta^{15}\text{N}$  signatures previously observed for cephalopod species sampled in the region  
240 (Madigan et al., 2012).

### 241 **3.2. Inter-specific differences in foraging depth**

242 Both  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  signals vary vertically throughout the water column due to  
243 photochemical transformation of Hg following solar radiation decrease from surface to deep water  
244 layers (Bergquist and Blum, 2007; Blum et al., 2013). As they are transferred from prey to predator,  
245 they therefore can be used as trophic biomarkers to assess foraging depth. However, while  $\Delta^{199}\text{Hg}$  is  
246 only affected through photochemical reactions and is conserved from prey to predator,  $\delta^{202}\text{Hg}$  is also  
247 modified by physiological processes like methylation or demethylation of mercury (Bolea-Fernandez  
248 et al., 2019; Janssen et al., 2016; Li et al., 2020; Perrot et al., 2016) and undergoes inconstant trophic

249 discrimination factors from prey to predator (Kwon et al., 2016; Laffont et al., 2011), especially in  
250 shark species (Le Croizier et al., 2020b). Moreover, for blue, shortfin mako and smooth hammerhead  
251 sharks, metabolic MeHg detoxification pathways seems to occur. Indeed, the  $\Delta^{199}\text{Hg}/\delta^{202}\text{Hg}$  slope is  
252 traditionally used to assess the influence of photodegradation *versus* microbial transformation on the  
253 isotopic signature of mercury before its incorporation into the food web (Blum et al., 2013; Madigan  
254 et al., 2018). Here, no significant linear regression could be obtained between  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  for  
255 all shark species at the inter- or intraspecific level (Figure S1). This lack of correlation between  $\Delta^{199}\text{Hg}$   
256 and  $\delta^{202}\text{Hg}$  is observed in species showing *in vivo* demethylation modifying the  $\delta^{202}\text{Hg}$  values (Li et al.,  
257 2020) and suggests possible MeHg detoxification processes in the shark species studied here (Le  
258 Croizier et al., 2020b). Therefore, as  $\delta^{202}\text{Hg}$  in all three shark species appeared to depend on both  
259 trophic and physiological features, this isotopic ratio was not taken into account to assess differences  
260 in species trophic ecology and subsequently to study the possible food competition between them.

261 In nearshore ecosystems,  $\Delta^{199}\text{Hg}$  can vary seasonally and spatially due to coastal phenomena  
262 affecting water turbidity (Senn et al., 2010). In this study, the fact that all three shark species were  
263 pelagic species using oceanic habitats (as inferred by  $\delta^{13}\text{C}$  values) confirms that reported  $\Delta^{199}\text{Hg}$  may  
264 vary primarily over a vertical gradient depending on photochemical process affected by depth (Blum  
265 et al., 2013). Therefore, the range of individual  $\Delta^{199}\text{Hg}$  values (1.40 to 2.13 ‰) observed in this study  
266 highlights the importance of mesopelagic prey in the diet of all three oceanic species. In the north  
267 Pacific oceanic region, similar  $\Delta^{199}\text{Hg}$  signatures in fish muscles have been observed for species  
268 foraging in the twilight zone near Hawaii, i.e. 1.00 to 2.56 ‰ (Blum et al., 2013), and off the coast of  
269 California, i.e. 0.95 to 2.31 ‰ (Madigan et al., 2018), including for the great white shark,  
270 *Carcharodon carcharias*, i.e. 1.25 to 1.95 ‰ (Le Croizier et al., 2020a). This conclusion is supported by  
271 the consistent presence of mesopelagic species in stomach contents of blue (Hernández-Aguilar et  
272 al., 2016; Markaida and Sosa-Nishizaki, 2010), shortfin mako (Lopez et al., 2009; Preti et al., 2012)  
273 and smooth hammerhead sharks (Estupiñán-Montaño et al., 2019; Galván-Magaña et al., 2013)  
274 sampled off the west coast of Baja California and across the Pacific Ocean. As mercury has a similar

275 turnover rate as carbon and nitrogen in fish muscle, i.e. 1 year or more (Kwon et al., 2016), deep  
276 foraging appears as a constant strategy through time. The three shark species remain most of the  
277 time inside the boundaries of the surface mixed layer but exhibit differences in their diving behaviors  
278 in the study length range. Indeed, while blue sharks perform frequent deep dives (Campana et al.,  
279 2011; Queiroz et al., 2010), shortfin mako sharks seem to exploit deep water more sporadically  
280 undergoing less frequent dives in the mesopelagic zone (Abascal et al., 2011; Musyl et al., 2011).  
281 Finally, although no study reported depth habitat use in smooth hammerhead sharks in the Pacific  
282 region, data from the Atlantic Ocean demonstrated limited diving frequency associated with  
283 shallower dives than both shortfin mako and blue sharks (Logan et al., 2020; Santos and Coelho,  
284 2018). Here,  $\Delta^{199}\text{Hg}$  corroborates the deep diving behavior observed for blue and shortfin mako  
285 sharks and proves that they are associated with foraging in the mesopelagic layer. It also suggests  
286 that smooth hammerhead sharks might feed at depth and that populations from the northeastern  
287 Pacific region might differ from the Atlantic ones by using deeper water layers (Logan et al., 2020;  
288 Santos and Coelho, 2018).

289 We observed significant inter-specific differences in  $\Delta^{199}\text{Hg}$  ratio ( $X^2_{35,2} = 17.8$ ,  $p < 0.001$ ) revealing  
290 differences in mean foraging depth. Blue sharks presented  $\Delta^{199}\text{Hg}$  value significantly lower than  
291 shortfin mako sharks (Dunn's test,  $p < 0.001$ ) and smooth hammerhead sharks (Dunn's test,  $p < 0.01$ ).  
292 This could not be explained by different isotope fractionation between prey and predator, as  $\Delta^{199}\text{Hg}$   
293 values are conserved during trophic transfers (Kwon et al., 2016; Laffont et al., 2011). Thus, the  
294 significant gap in  $\Delta^{199}\text{Hg}$  between species suggests systematic differences in foraging depths (Le  
295 Croizier et al., 2020b). The lower  $\Delta^{199}\text{Hg}$  of the blue shark suggests constant foraging in deeper water  
296 than the two other species. This conclusion is supported by stomach content analyses, which  
297 revealed that this species was the only one with bathypelagic prey in its gut (Galván-Magaña et al.,  
298 2013). On the other hand, epipelagic prey were also commonly reported in the stomach of the three  
299 shark species (Galván-Magaña et al., 2013; Hernández-Aguilar et al., 2016; Wood et al., 2009).  $\Delta^{199}\text{Hg}$   
300 signatures observed in this study may thus be the result of the consumption of both epi- and

301 mesopelagic prey as reported for the Pacific bluefin tuna *Thunnus orientalis* (Madigan et al., 2018).  
302 Differences in the relative importance of prey from these two compartments could therefore result  
303 in the observed  $\Delta^{199}\text{Hg}$  differences between shark species. Compared to deeper species, epipelagic  
304 prey may form dense aggregations with higher nutritive and energetic value (Madigan et al., 2018;  
305 Spitz et al., 2010). However, they are more scattered across time and space resulting in shark feeding  
306 opportunistically on them depending on the season, geographic position and maturity stage  
307 (Hernández-Aguilar et al., 2016; Maia et al., 2006; Rosas-Luis et al., 2017). This behavior is frequently  
308 observed in shortfin mako sharks, which favor a diet dominated by shallower teleost when seasonally  
309 and locally available (Harford, 2013; Maia et al., 2006). Compared to the shortfin mako, blue sharks  
310 display a more consistent diet targeting less nutritive but more reliable mesopelagic prey (Preti et al.,  
311 2012; Vollenweider et al., 2011). The mesopelagic food web indeed appears more stable through  
312 time and supports high prey biomasses in the northeast Pacific (Davison et al., 2015; Hazen and  
313 Johnston, 2010). Therefore, foraging on these deeper prey might represent a more reliable feeding  
314 strategy and involve less metabolic costs associated to foraging on more scattered epipelagic prey.  
315 Overall, the highest  $\Delta^{199}\text{Hg}$  of blue sharks compared to shortfin mako sharks might be the result of  
316 different foraging strategies, with the blue shark occupying a deeper ecological niche and the  
317 shortfin mako shark favoring opportunistic foraging on epipelagic prey. Smooth hammerhead shark  
318  $\Delta^{199}\text{Hg}$  was not significantly different from the shortfin mako shark (Dunn's test,  $p>0.05$ ), hence,  
319 suggesting feeding at shallower depths than blue sharks and/or at equivalent rates on deeper  
320 organisms than shortfin mako sharks.

### 3.3. Resource partitioning between co-occurring predators

322 The overlaps between the three species  $\text{SEA}_B$  (i.e.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , Figure 1) and  $\text{SEV}_B$  (i.e.  $\delta^{13}\text{C}$ ,  
323  $\delta^{15}\text{N}$  and  $\Delta^{199}\text{Hg}$ , Figure 2) are presented in Table 2. The limited differences between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
324 isotopic compositions resulted in significant isotopic overlaps between species except between blue  
325 and smooth hammerhead sharks (16.8%). The overlap decreased by adding  $\Delta^{199}\text{Hg}$  for all pairs of

326 species. This decrease was the strongest for shortfin mako and blue sharks (from 42.0% to 23.0%). A  
327 smaller overlap decrease was observed between shortfin mako and smooth hammerhead sharks,  
328 which presented no significant difference in  $\Delta^{199}\text{Hg}$ , and between blue and smooth hammerhead  
329 sharks, already well separated by  $\delta^{15}\text{N}$  and to a less extent by  $\delta^{13}\text{C}$  (i.e. 5.9% and 3.9% decrease  
330 respectively). In the latter case, even if significant differences occurred in  $\Delta^{199}\text{Hg}$ ,  $\text{SEA}_B$  and  $\text{SEV}_B$   
331 overlapping areas appeared equivalent suggesting that carbon and nitrogen isotopic ratios can be  
332 sufficient to depict resource partitioning in the case of co-existing shark species feeding on different  
333 habitats or prey (Curnick et al., 2019), although always overlooking the vertical dimension.

334 Resource partitioning within pelagic shark assemblages has been extensively studied using  $\delta^{13}\text{C}$  and  
335  $\delta^{15}\text{N}$ , yielding frequent records of important overlapping areas (Kiszka et al., 2015; Li et al., 2016a)  
336 suggesting similar foraging niches. In the eastern Pacific, similar overlaps were recorded between  
337 shortfin mako and blue shark (Klarian et al., 2018; Rosas-Luis et al., 2017). From a methodological  
338 perspective, these similarities could however be expected in the case of these pelagic species.  
339 Indeed, by foraging in the same region and on similar phytoplankton derived food web, sympatric  
340 pelagic sharks would exhibit similar  $\delta^{13}\text{C}$  signatures (Bird et al., 2018), and possibly similar  $\delta^{15}\text{N}$   
341 depending on prey trophic position, even when feeding on different prey. The observed similarities in  
342 carbon and nitrogen isotopic niches between blue and shortfin mako sharks (overlapping at 42.0%) in  
343 this study may therefore be due to these processes, rather than to a clear similarity in dietary habits.  
344 Moreover, important overlaps in isotopic signatures are not in accordance with previous stomach  
345 content analysis of both species in the northeastern Pacific region (Prete et al., 2012; Rosas-Luis et al.,  
346 2017). Hence, the differences in mean foraging depth between the two species increased resource  
347 partitioning estimation between the blue shark and the shortfin mako shark (19.0% decrease in  
348 overlapping area).

349 Our results therefore demonstrate that carbon and nitrogen isotopic signatures overestimate  
350 overlapping areas by not reflecting the importance of foraging depth, which was estimated here by

351  $\Delta^{199}\text{Hg}$ . In the case of pelagic sharks migrating vertically, carbon and nitrogen stable isotopes analysis  
352 has shown some limitations in its capacity to address foraging depth issues. Indeed, even if vertical  
353 patterns in nitrogen isotopic baselines have been reported in zooplankton (Hannides et al., 2013),  
354 such patterns are rarely observed for top predators (Choy et al., 2015). However, the vertical  
355 foraging component has been suspected of critical importance in the ecology of marine predators.  
356 For example, computational models based on prey distribution systematically resulted in the  
357 emergence of vertical movements in tropical oceanic predatory fishes (Dagorn et al., 2000).  
358 Furthermore, in pelagic systems, differences in vertical movement patterns in sympatric top-  
359 predator species, including sharks, have already been demonstrated (Choy et al., 2015; Musyl et al.,  
360 2011). In our study, the systematic decreases in overlapping area for all pair of comparisons, after  
361 the incorporation of  $\Delta^{199}\text{Hg}$ , demonstrates that differences in foraging depth better explain trophic  
362 niche partitioning between shark species.

#### 363 **3.4. Influence of foraging depth on mercury exposure**

364 Muscle THg (Table 1) significantly differed among the three species ( $X^2_{35,2} = 15.2$ ,  $p < 0.001$ ).  
365 Blue sharks presented higher THg compared to shortfin mako (Dunn's test,  $p < 0.05$ ) and smooth  
366 hammerhead sharks (Dunn's test,  $p < 0.001$ ), as already observed in a previous study in the area (Maz-  
367 Courrau et al., 2012). The blue shark was the species presenting both higher THg and lower  $\Delta^{199}\text{Hg}$ .  
368 Regardless of the species, THg was higher for individuals foraging on the deepest mesopelagic prey  
369 (i.e. exhibiting the lowest  $\Delta^{199}\text{Hg}$ ) as shown by the significant and negative correlation between the  
370 two variables (Figure 3). In the open Pacific Ocean, MeHg, the most bioavailable form of mercury, is  
371 mainly produced in the mesopelagic layer and especially in the Oxygen Minimum Zone (Blum et al.,  
372 2013; Fitzgerald et al., 2007). As MeHg is trophically incorporated in food webs, sharks feeding in the  
373 mesopelagic zone will be exposed to higher MeHg levels compared to shallow feeding sharks, as  
374 highlighted by our results. This is in agreement with previous observation on fish (Monteiro et al.,  
375 1996), sea birds (Thompson et al., 1998) and pelagic predators (Choy et al., 2009; Houssard et al.,

376 2019; Le Bourg et al., 2019; Madigan et al., 2018) that demonstrated higher mercury contamination  
377 in deeper foraging individuals or species.

378 In generalized linear models (GLMs),  $\Delta^{199}\text{Hg}$  and species were the main factor explaining shark THg  
379 compared to other variables (Table S3), confirming that foraging depth was a key driver of shark  
380 mercury concentration in our dataset. Foraging depth has rarely been assessed in THg accumulation  
381 studies of marine predators except by qualitative approaches such as attributing a median depth of  
382 occurrence (Choy et al., 2009) or habitat preference (Le Bourg et al., 2019) to the studied species. It  
383 is interesting to note that this approach would not have been relevant for blue, shortfin mako and  
384 smooth hammerhead sharks that remain in the upper oceanic layers and occasionally undergo deep  
385 bounce dives to feed on mesopelagic prey (Abascal et al., 2011; Campana et al., 2009; Queiroz et al.,  
386 2010; Sepulveda et al., 2004). In our study, mercury isotopic composition offers new opportunities to  
387 implement quantitative approaches of foraging depth. As  $\Delta^{199}\text{Hg}$  was the main driver of THg (along  
388 with species), we suggest that this factor should be investigated in future research regarding mercury  
389 accumulation patterns in elasmobranchs.

390 In shark species, the pattern observed for THg in muscular tissue has been generally linked to  
391 changes in trophic level, generally estimated through  $\delta^{15}\text{N}$  values (Biton-Porsmoguer et al., 2018; Le  
392 Bourg et al., 2019). Here,  $\delta^{15}\text{N}$  did not explain THg variation. Although the limited number of samples  
393 may not cover the entire spectrum of length and trophic levels for all shark species, influence of such  
394 small  $\delta^{15}\text{N}$  spectrum on THg has been previously demonstrated (Le Croizier et al., 2019). This  
395 therefore implies that foraging depth could affect more significantly THg in pelagic shark species than  
396 their respective trophic levels, but further investigations at a specific level or with broader size and  
397  $\delta^{15}\text{N}$  range are needed to confirm this effect.

398 THg in marine organisms depends not only on trophic features (Ferriss and Essington, 2014; Le Bourg  
399 et al., 2019; Thompson et al., 1998) but also on species physiological characteristics such as longevity,  
400 metabolic, growth and feeding rates and/or possible detoxication processes (Bolea-Fernandez et al.,

2019; Houssard et al., 2019; Li et al., 2020; Senn et al., 2010). This can be seen in our results as the best-fitted model incorporated species as a key variable explaining THg (along with  $\Delta^{199}\text{Hg}$ ). However, all these parameters could not be tested in this study, except for longevity and demethylation mechanisms which are known to increase  $\delta^{202}\text{Hg}$  values (Bolea-Fernandez et al., 2019; Senn et al., 2010). Here,  $\delta^{202}\text{Hg}$  values varied significantly between species (Table 1;  $F_{35,2} = 4.4$ ,  $p < 0.05$ ), as previously observed for other co-occurring shark species (Le Croizier et al., 2020b). Still,  $\delta^{202}\text{Hg}$  variations did not affect THg in GLMs (as it can also be seen in the relation between the two variables in Figure S2) showing no link between mercury contamination and the demethylation process previously highlighted by the absence of correlation between  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  (Figure S1). Age was also not affecting THg while differences between species were also significant ( $F_{35,2} = 8.6$ ,  $p < 0.001$ ), with blue sharks encompassing the oldest individuals and shortfin mako sharks the youngest (Table S5). Overall, the fact that metabolic demethylation and individual age did not critically affect THg strengthens the hypothesis that ecological characteristics were mainly driving muscle mercury contamination in all shark species. As all physiological characteristics could not be analyzed in this study, future investigations on physiological intra-specific differences between blue, shortfin mako and smooth hammerhead sharks might help to identify the entire mechanisms behind their THg.

#### 3.4. Insights into mercury cycle

In the northeastern Pacific region, atmospheric mercury deposition dominates mercury inputs to the water column as river influence appears negligible (Masbou et al., 2018; Zhang et al., 2014). This deposition at the atmosphere/ocean interface has two different origins: inorganic mercury (iHg) via precipitation and atmospheric gaseous mercury ( $\text{Hg}(0)$ ) through dissolution (Gratz et al., 2010; Zhang et al., 2014). While the mechanisms causing mass-independent isotopic fractionation (MIF) of even-mass Hg isotopes are still poorly understood, processes such as photo-oxidation of  $\text{Hg}(0)$  to iHg in the atmosphere (e.g. tropopause) may be involved leading to isotopic fractionation (Chen et al., 2012). Therefore, iHg deposition by precipitation presents slightly different

426  $\Delta^{200}\text{Hg}$  signatures ranging from 0 to 0.3 ‰ than atmospheric Hg(0) dissolution characterized by  
427  $\Delta^{200}\text{Hg}$  between  $-0.11$  and  $-0.01$  ‰ (Enrico et al., 2016; Gratz et al., 2010). Once in the water  
428 column,  $\Delta^{200}\text{Hg}$  values are conserved, making it a good tracer of atmospheric deposition pathways  
429 even when analyzed in top-predator species (Enrico et al., 2016; Le Croizier et al., 2020b). Here,  
430  $\Delta^{200}\text{Hg}$  values ranged from  $-0.07$  to  $0.14$  ‰ with no significant differences between species ( $F_{35,2} =$   
431  $1.4$ ,  $p > 0.05$ ; i.e.  $0.05 \pm 0.05$  ‰ for blue and smooth hammerhead sharks and  $0.02 \pm 0.05$  ‰ for  
432 shortfin mako sharks). These values are similar to those observed in bottomfish from Hawaii, i.e.  
433  $-0.04$  to  $0.10$  ‰ (Sackett et al., 2017), and to other coastal shark species sampled off La Réunion  
434 Island, i.e.  $0.08 \pm 0.04$  ‰ in bull sharks, *Carcharhinus leucas*, and  $0.06 \pm 0.04$  ‰ in tiger sharks,  
435 *Galeocerdo cuvier* (Le Croizier et al., 2020b). For the three shark species,  $\Delta^{200}\text{Hg}$  values suggest a  
436 common origin in the mercury precursors of MeHg in shark tissues, probably from a combined  
437 source of both iHg and Hg(0) because of both positive and negative  $\Delta^{200}\text{Hg}$  compositions (Le Croizier  
438 et al., 2020b).

439 Due to solar radiation, photodemethylation can transform dissolved MeHg into iHg and  
440 photoreduction can convert iHg into Hg(0) in the water column. Both of these reactions are  
441 characterized by a  $\Delta^{199}\text{Hg}/\Delta^{201}\text{Hg}$  ratio of respectively 1.36 and 1.00 (Bergquist and Blum, 2007). All  
442 shark species considered,  $\Delta^{199}\text{Hg}/\Delta^{201}\text{Hg}$  slope was 1.16 (Figure S3), not clearly indicating the  
443 prevalence of one reaction over another. Surprisingly this is not in accordance with previous studies  
444 reporting the dominance of MeHg demethylation in oceanic island marine ecosystems (Le Croizier et  
445 al., 2020b; Sackett et al., 2017). Indeed, the ratio observed here seems to represent a mixed  
446 signature of both phenomena. Interestingly, in Hawaii, deep-foraging species exhibit a flatter  
447  $\Delta^{199}\text{Hg}/\Delta^{201}\text{Hg}$  slope (1.05 ratio) compared to shallower species (1.21 ratio) (Blum et al., 2013;  
448 Masbou et al., 2018). The intermediate slope in this study is therefore consistent with shark species  
449 foraging on mesopelagic prey exhibiting a flatter slope than epipelagic ones, reinforcing the  
450 conclusion that all three shark species foraged mainly at depth.

## 451 **Conclusions**

452           Based on  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\Delta^{199}\text{Hg}$ , this study provided new information on the trophic ecology  
453 of blue, shortfin mako and smooth hammerhead sharks in the eastern Pacific region. Mesopelagic  
454 prey appeared as a major component in the diet of the three species. Our study demonstrated the  
455 importance of considering foraging depth when studying resource partitioning between co-occurring  
456 pelagic predators. In the northeastern Pacific, blue sharks appeared to forage deeper than mako and  
457 smooth hammerhead sharks and these foraging strategies seemed to reduce trophic competition  
458 between them. Since carbon and nitrogen isotopes did clearly underestimate resource partitioning,  
459 this study confirmed the usefulness of multi-isotopic approaches to help fine scaling resource  
460 partitioning in top-predators depending on the ecology of the studied species. Our results highlighted  
461 the underexploited potential of mercury stable isotopes for marine ecology studies. This new tool  
462 has the potential to elucidate possible ontogenetic variation in depth utilization for these species, as  
463 deep diving at early life stages is a rare pattern for blue and shortfin mako sharks (Nosal et al., 2019)  
464 and could be limited inside shallow coastal nursery areas for smooth hammerhead sharks (Francis,  
465 2016; Santos and Coelho, 2018). Moreover, there are increasing evidences of vertical habitat  
466 partitioning between different predator species in other pelagic ecosystems (Madigan et al., 2020)  
467 and mercury stable isotopes could help to precise the mechanisms behind such vertical structuring.  
468 As foraging depth appeared a key factor influencing mercury exposure for the three species, it should  
469 be more extensively studied to understand mercury accumulation in top predators. In the context of  
470 climate change, Oxygen Minimum Zones are observed at shallower depth in tropical and subtropical  
471 regions, acting as a physical barrier and preventing sharks to forage deeper in the water column  
472 (Vedor et al., 2021), particularly in the tropical eastern Pacific (Trucco-Pignata et al., 2019). This  
473 habitat compression could therefore limit the possibility for co-occurring shark species to forage at  
474 significant different depths and could lead to new competition processes between pelagic predators  
475 that should be carefully monitored.

## 476 **CRedit authorship contribution statement**

477 **Lucien Besnard:** Conceptualization, Methodology, Formal analysis, Investigation, Writing -  
478 Original Draft, Writing - Review & Editing, Visualization. **Gaël Le Croizier:** Methodology, Validation,  
479 Investigation, Writing - Review & Editing, Supervision. **Felipe Galván-Magaña:** Investigation,  
480 Resources, Writing - Review & Editing, Funding acquisition. **David Point:** Resources, Writing - Review  
481 & Editing, Funding acquisition. **Edouard Kraffe:** Resources, Writing - Review & Editing, Funding  
482 acquisition. **James Ketchum:** Resources, Writing - Review & Editing, Funding acquisition. **Raul**  
483 **Octavio Martinez Rincon:** Formal analysis, Resources, Writing - Review & Editing, Funding  
484 acquisition. **Gauthier Schaal:** Resources, Writing - Review & Editing, Supervision, Funding acquisition.

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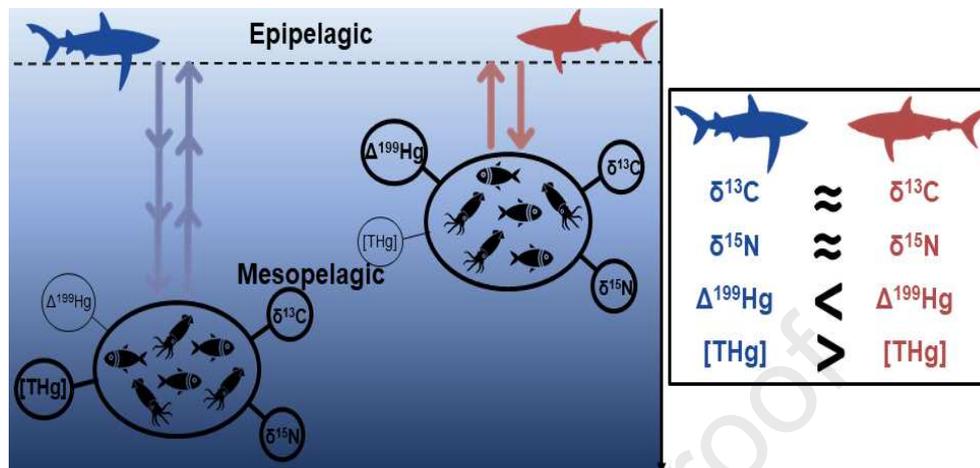
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## FIGURES AND TABLES (Colors should be used for any figures in the print)



## Graphical abstract

## KEYWORDS

Trophic ecology; Top-predator; Mercury stable isotopes; Resource partitioning; Foraging depth; Mercury accumulation

## HIGHLIGHTS

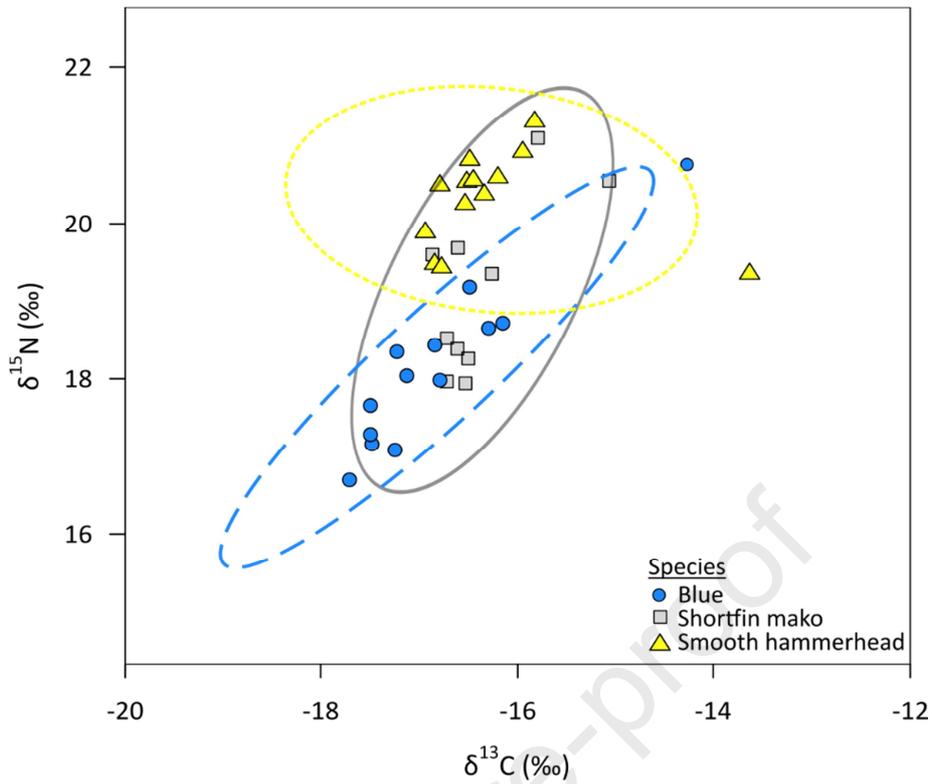
- $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  were determined in three pelagic shark species.
- Hg isotopes suggested shark species foraged on mesopelagic prey.
- $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  overestimated overlaps between trophic niches.
- Differences in foraging depth better explained resource partitioning.
- Foraging depth influenced mercury contamination level.

**Table 1:** Number of individuals, total length, C, N and Hg isotope composition, and total mercury concentration (THg) in muscles of blue, shortfin mako and smooth hammerhead sharks. Data are means ( $\pm$  standard deviation). THg is expressed on a dry weight basis. Different letters indicate significant differences between species for each variable.

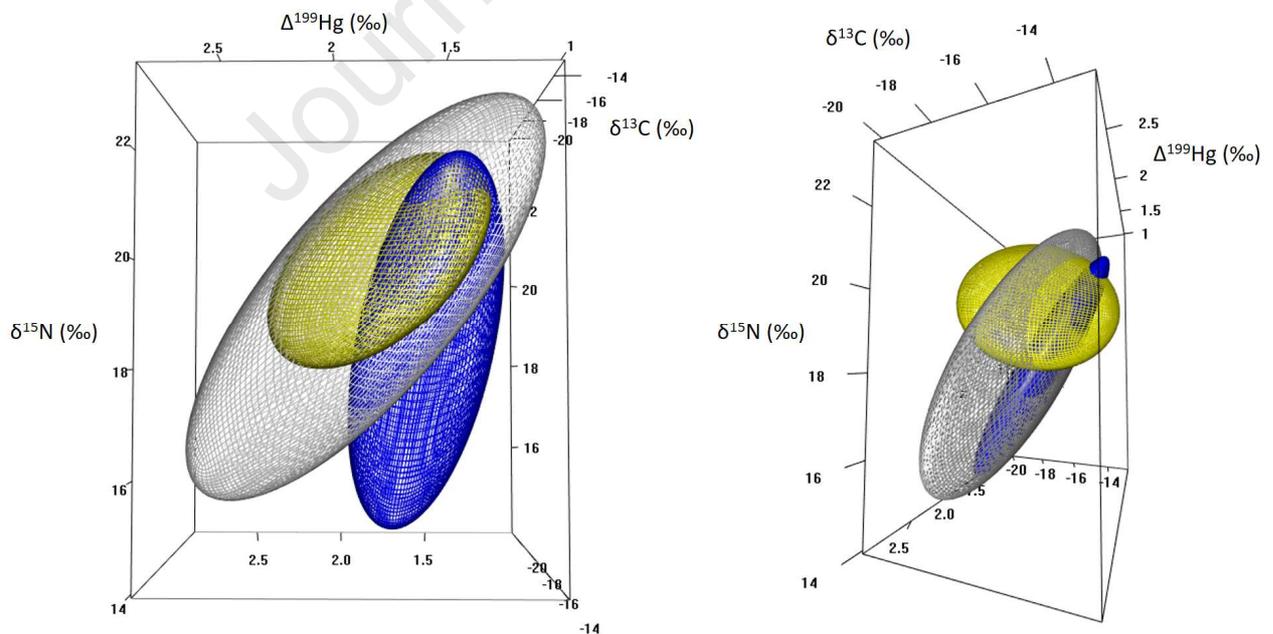
Species	N	Total length (m)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{199}\text{Hg}$ (‰)	$\delta^{202}\text{Hg}$ (‰)	THg ( $\text{ng}\cdot\text{g}^{-1}$ )
Blue	13	1.98 ( $\pm 0.36$ )	-16.81 ( $\pm 0.91$ ) <sup>A</sup>	18.15 ( $\pm 1.07$ ) <sup>A</sup>	1.56 ( $\pm 0.10$ ) <sup>A</sup>	0.63 ( $\pm 0.16$ ) <sup>AB</sup>	7804 ( $\pm 2699$ ) <sup>A</sup>
Shortfin mako	10	1.49 ( $\pm 0.43$ )	-16.36 ( $\pm 0.55$ ) <sup>A</sup>	19.13 ( $\pm 1.10$ ) <sup>B</sup>	1.94 ( $\pm 0.23$ ) <sup>B</sup>	0.53 ( $\pm 0.15$ ) <sup>A</sup>	4772 ( $\pm 3892$ ) <sup>B</sup>
Smooth hammerhead	13	1.67 ( $\pm 0.16$ )	-16.25 ( $\pm 0.85$ ) <sup>A</sup>	20.30 ( $\pm 0.60$ ) <sup>C</sup>	1.82 ( $\pm 0.15$ ) <sup>B</sup>	0.71 ( $\pm 0.12$ ) <sup>B</sup>	3600 ( $\pm 1524$ ) <sup>B</sup>

**Table 2:** Isotopic overlaps between blue, shortfin mako and smooth hammerhead sharks. Comparison is made between the SIBER ellipse metric for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ,  $\text{SEA}_B$  (Jackson et al., 2011), and the ellipsoid approach combining  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\Delta^{199}\text{Hg}$ ,  $\text{SEV}_B$  (Skinner et al., 2019).

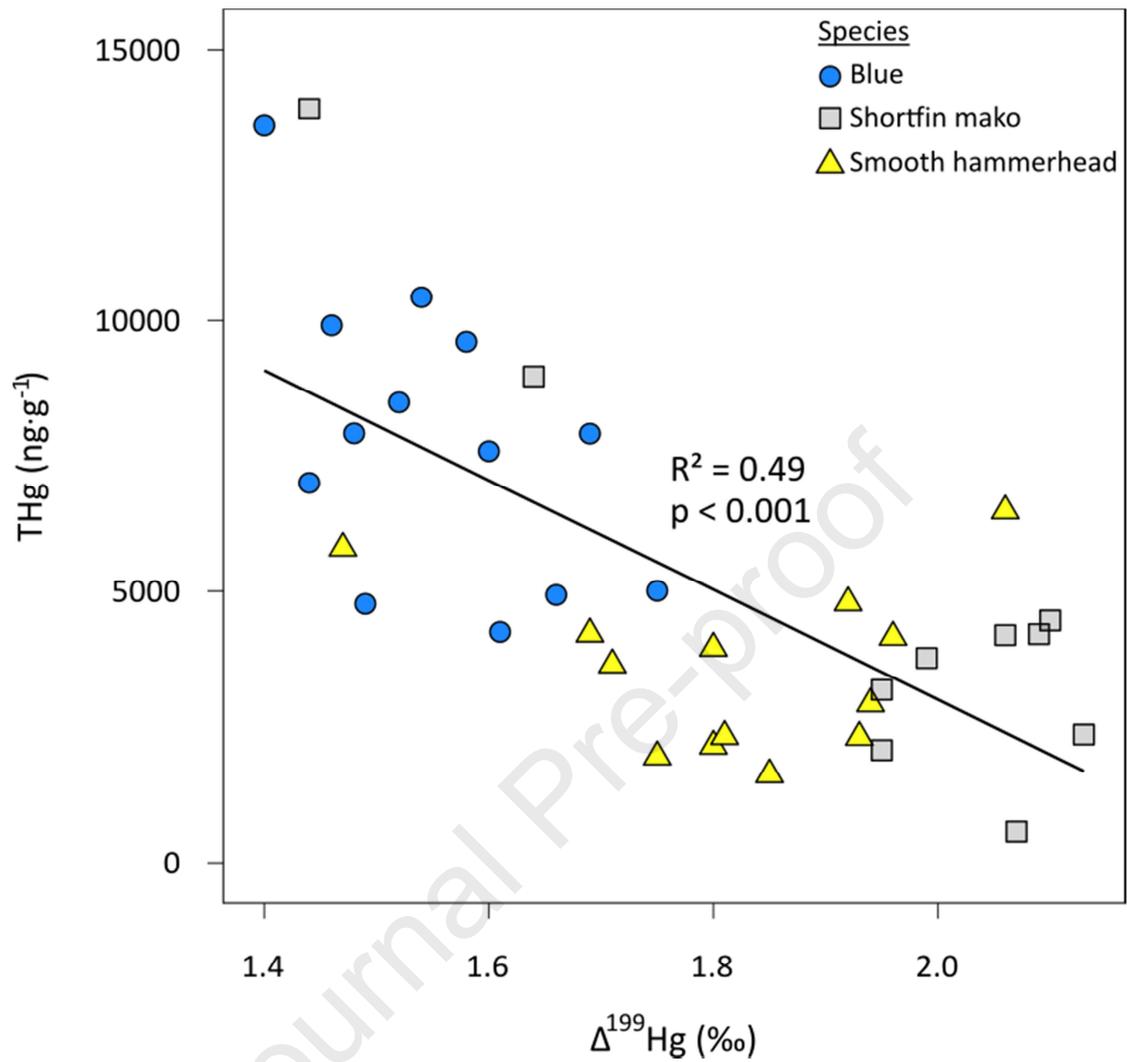
	$\delta^{13}\text{C}/\delta^{15}\text{N}$	$\delta^{13}\text{C}/\delta^{15}\text{N}/\Delta^{199}\text{Hg}$
Blue   Shortfin mako	42.0%	23.0%
Shortfin mako   Smooth hammerhead	33.3%	27.4%
Blue   Smooth hammerhead	16.8%	12.9%



**Figure 1:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of blue (● ----), shortfin mako (□ —), and smooth hammerhead (▲ - - - -) sharks. The represented ellipses encompass 95% of the data.



**Figure 2:** 95% ellipsoids using  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\Delta^{199}\text{Hg}$  for blue, shortfin mako and smooth hammerhead sharks respectively represented in blue, grey and yellow.



**Figure 3:** Variation of THg with  $\Delta^{199}\text{Hg}$  values in the muscle of blue (●), shortfin mako (□) and smooth hammerhead (▲) sharks. Data fit a linear curve. Pearson correlation ( $r^2$  value) was significant as indicated by its p-value.

## HIGHLIGHTS

- $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\Delta^{199}\text{Hg}$  and  $\delta^{202}\text{Hg}$  were determined in three pelagic shark species.
- Hg isotopes suggested shark species foraged on mesopelagic prey.
- $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  overestimated overlaps between trophic niches.
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**Declaration of interests**

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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