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► **To cite this version:**

Gaël Le Croizier, Anne Lorrain, Jeroen Sonke, E. Mauricio Hoyos-Padilla, Felipe Galván-Magaña, et al.. The Twilight Zone as a Major Foraging Habitat and Mercury Source for the Great White Shark. Environmental Science and Technology, 2020, 54 (24), pp.15872-15882. 10.1021/acs.est.0c05621 . hal-03126762

HAL Id: hal-03126762

<https://hal.univ-brest.fr/hal-03126762>

Submitted on 11 May 2023

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The Twilight Zone as a Major Foraging Habitat and Mercury Source for the Great White Shark

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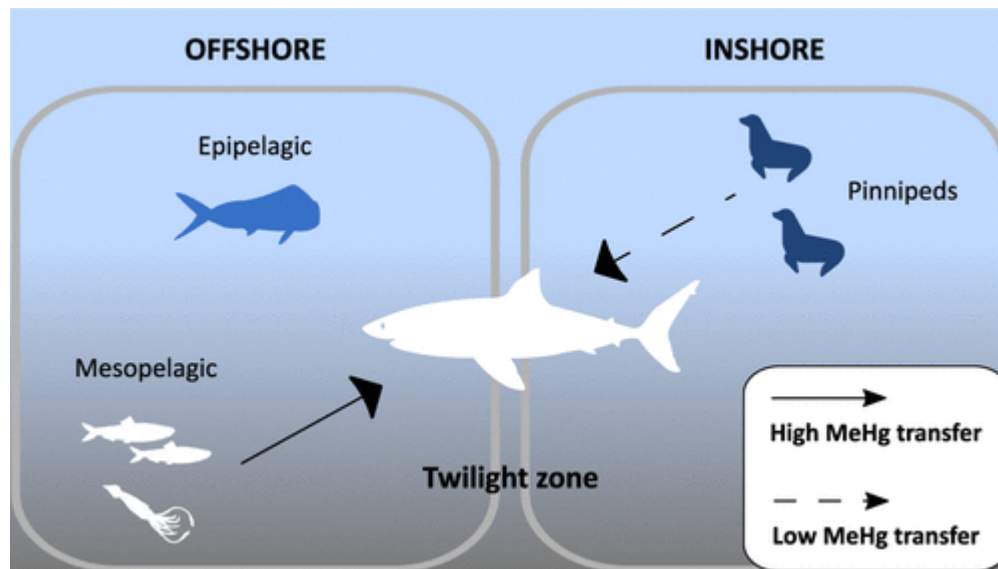
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Abstract

The twilight zone contains the largest biomass of the world's ocean. Identifying its role in the trophic supply and contaminant exposure of marine megafauna constitutes a critical challenge in the context of global change. The white shark (*Carcharodon carcharias*) is a threatened species with some of the highest concentrations of neurotoxin methylmercury (MeHg) among marine top predators. Large white sharks migrate seasonally from coastal habitats, where they primarily forage on pinnipeds, to oceanic offshore habitats. Tagging studies suggest that while offshore, white sharks may forage at depth on mesopelagic species, yet no biochemical evidence exists. Here, we used mercury isotopic composition to assess the dietary origin of MeHg contamination in white sharks from the Northeast Pacific Ocean. We estimated that a minimum of 72% of the MeHg accumulated by white sharks originates from the consumption of mesopelagic prey, while a maximum of 25% derives from pinnipeds. In addition to highlighting the potential of mercury isotopes to decipher the complex ecological cycle of marine predators, our study provides evidence that the twilight zone constitutes a crucial foraging habitat for these large predators,

which had been suspected for over a decade. Climate change is predicted to expand the production of mesopelagic MeHg and modify the mesopelagic biomass globally. Considering the pivotal role of the twilight zone is therefore essential to better predict both MeHg exposure and trophic supply to white sharks, and effectively protect these key vulnerable predators.

Graphical abstract



20 Introduction

21 Many shark populations are declining worldwide in the Anthropocene ¹⁻³, with
22 potential large-scale cascading effects such as changes in abundance, distribution and
23 behavior of prey, that may impact the structure and function of marine ecosystems ⁴⁻⁶. As an
24 apex predator, the white shark (*Carcharodon carcharias*) is a key species that exists in low
25 abundance, implying low capacity for population recovery ^{7,8}. Consequently, white sharks
26 are particularly vulnerable to extinction, along with their ecosystem role as apex predators ⁶.
27 As white sharks experience different levels of protection during their migrations (e.g. areas
28 within and beyond national jurisdictions) ⁹, understanding more about how they use ocean
29 ecosystems is vital to their protection.

30 Mercury (Hg) is a global pollutant of both anthropogenic and natural origin, of which
31 80% of atmospheric emissions are deposited in the ocean ¹⁰. Once in seawater, a fraction of
32 deposited inorganic Hg is converted through microbial activity to toxic methylmercury (MeHg)
33 ¹¹, which is bioaccumulated by aquatic organisms and biomagnified along trophic webs. Due
34 to their long lifespans and high trophic positions, apex predators are particularly prone to
35 MeHg contamination, potentially causing adverse effects on their reproduction,
36 development, behavior and nervous system function ¹²⁻¹⁴. Although the impact of MeHg
37 exposure on shark neurophysiology is still poorly understood ¹⁵, white sharks display some of
38 the highest MeHg concentrations among shark species ¹⁶. MeHg accumulation in white
39 sharks may thus exceed neurotoxicity thresholds proposed for other marine predators ^{13,14}
40 and potentially pose an additional threat to this vulnerable species.

41 Large white sharks are known to aggregate near coastal seal colonies across the
42 global oceans ¹⁷. In the Northeastern Pacific, reproductively mature individuals migrate

43 seasonally from aggregation areas in the productive ecosystem of the California Current (e.g.
44 Guadalupe Island in Mexico and Central California in the USA)¹⁸, to oceanic habitats in the
45 oligotrophic waters of the North Pacific Gyre^{19,20}. While the hunting behavior of white
46 sharks on seals in coastal environments has been widely documented^{21–23}, little is known
47 about their feeding ecology in the open ocean^{24,25}. Recently, offshore movements of blue
48 and white sharks in the Atlantic Ocean have been linked to oceanic processes and more
49 particularly to mesoscale eddies^{26,27}. The vertical mixing dynamics associated with these
50 structures may facilitate access to deep mesopelagic prey. In the Northeast Pacific Ocean,
51 tagging studies revealed that white sharks perform offshore dives in the mesopelagic zone
52^{20,28}. Foraging in these depths, also called the twilight zone (i.e. between 200 and 1000m
53 deep), enables access to the largest fish biomass in the global ocean²⁹. Despite the growing
54 number of studies suggesting that it constitutes a crucial foraging habitat for large pelagic
55 predators, no direct evidence of deep water feeding by white sharks has been provided to
56 date in the Northeastern Pacific.

57 As MeHg production by bacterial transformation is enhanced in deep low oxygen
58 waters³⁰, MeHg exposure increases with foraging depth in pelagic consumers at both the
59 interspecific³¹ and intraspecific scale^{32,33}, when feeding on mesopelagic prey³⁴. Pinnipeds,
60 such as the northern elephant seal (*Mirounga angustirostris*) targeted by white sharks in the
61 Northeastern Pacific, are predators themselves and can display high MeHg concentrations
62^{33,35}, generally exceeding MeHg levels in pelagic fish, squid^{36,37}, and other mesopelagic prey
63³⁸. The high MeHg concentrations found both in pinnipeds and in potential offshore prey
64 raise the question of the relative MeHg exposure associated with different prey, and
65 different foraging depths, during the migratory cycle of white sharks between inshore and
66 offshore habitats.

67 Mercury (Hg) isotopes present multiple useful signatures due to classical mass-
68 dependent isotope fractionation (MDF, reported as $\delta^{202}\text{Hg}$) and unique photochemical mass-
69 independent fractionation (MIF, reported as $\Delta^{199}\text{Hg}$). These properties enable tracing MeHg
70 sources in marine environments ^{39–41}. While Hg MDF is the result of various abiotic (e.g.
71 photoreduction, volatilization) ^{42,43} and biotic processes (e.g. methylation, demethylation) ^{44–}
72 ⁴⁶, Hg MIF occurs predominantly during photochemical reactions ⁴². In seawater, solar
73 radiations induce a MIF gradient from the surface to depths, which leads to higher $\Delta^{199}\text{Hg}$
74 values in the photic or epipelagic zone (between 0 and 200m deep) than in the twilight or
75 mesopelagic zone (between 200 and 1000m deep) where light penetration varies from weak
76 to zero ^{30,47}. Thus, $\Delta^{199}\text{Hg}$ values constitute a powerful tool to trace the feeding depth of
77 marine predators, for instance discriminating epipelagic from mesopelagic foraging habitats
78 ^{32,46}. Importantly, $\Delta^{199}\text{Hg}$ values are conserved between prey and predators, due to the
79 absence of Hg MIF during trophic transfers or metabolic processes ^{40,44,48,49}, which reveals
80 MeHg dietary transfers and therefore predator-prey interactions.

81 Climate change is predicted to increase MeHg contamination in marine predators,
82 due to increases in seawater temperature and deoxygenation ⁵⁰. A proper characterization
83 of trophic MeHg pathways is therefore needed to foresee the evolution of neurotoxicant
84 levels in species, particularly in predators that influence the function of marine ecosystems.
85 In this context, this study sought to evaluate the contribution of different prey groups to
86 MeHg contamination in the white shark. Additionally, our aim was to estimate shark foraging
87 depths and assess the existence of trophic interactions between white sharks and
88 mesopelagic prey. To achieve these objectives, we collected dermis and muscle samples
89 from 95 Northeastern Pacific white sharks in the waters surrounding the aggregation site of
90 Guadalupe Island (Mexico), as well as hair samples from juvenile northern elephant seals,

91 which are a primary prey of white sharks foraging in this region ^{23,51}. We measured Hg
92 isotope signatures from shark and seal samples, and compared those with potential prey for
93 white sharks obtained from published studies in the Central North Pacific ³⁰ and Northeast
94 Pacific ³². We used a Bayesian mixing model based on Hg isotopes to determine both the
95 trophic MeHg sources and the vertical foraging habitat of white sharks. This innovative
96 chemical tracer approach provides an understanding of contaminant exposure, as well as
97 new insights in the trophic ecology of a key marine top predator.

98

99 **Materials and methods**

100 **Sample collection**

101 White sharks (n = 95) and northern elephant seals (NES, n = 10) were sampled at
102 Guadalupe Island in the Mexican Pacific, between the months of September and November.
103 Shark samples were collected in 2016, 2017 and 2018, and seal samples in 2018. Free-
104 swimming white sharks were attracted with dead baits (*Thunnus albacares*) near the
105 scientific boat. Samples (dermis and muscle) were taken using a biopsy probe (1 cm
106 diameter) targeting the tissue directly below the dorsal fin ⁵². The same device was used to
107 collect NES hair on one of the island's beaches. The biopsy probe was cleaned and rinsed
108 with alcohol before and between samples. After collection, tissue samples were immediately
109 transferred to a -20 °C freezer onboard the vessel. Individual sharks were sexed (based on
110 the presence or absence of claspers) and sized to the nearest 10 cm using visual size
111 estimates. White sharks ranged from 2m to 5m total length (TL) and were composed of
112 juveniles (< 3m TL), subadults (3-3.6m TL for males and 3-4.8m TL for females) and adults (>
113 3.6m TL for males and > 4.8m TL for females) ⁵³ (SI Appendix, Table S3). Samples were
114 collected from different individuals including 54 females, 34 males and 7 unsexed sharks.
115 Dermis and muscle tissues come from different sharks. Sex and maturity stage of seals were
116 visually determined. Most seals were juveniles and subadults (SI Appendix, Table S3).

117 **Mercury analyzes**

118 Total Hg (THg) is known to be predominantly in the MeHg form in the dermis and
119 muscle of various shark species ^{46,54-58}, aquatic and marine mammal hair ⁵⁹⁻⁶¹, as well as in
120 pelagic fish muscle and squid mantle ^{30,32}. THg was thus used as a proxy for MeHg
121 concentrations in all the species studied here. Moreover, THg isotope ratios in sharks and

122 seals analyzed in this work, or obtained in pelagic organisms from previous studies ^{30,32},
123 mainly reflect the isotopic signature of MeHg. Consequently, considering that MeHg (unlike
124 inorganic mercury) is the main Hg form transferred between prey and predators ^{62,63}, we
125 refer throughout the text to MeHg, although MeHg fraction was not measured in our
126 samples.

127 Blubber and muscle constitute most of the tissues ingested by sharks when eating a
128 seal, and these tissues may have different integration time than hair. However, NES only
129 feed during offshore foraging trips, fasting completely from food and water when at
130 rookeries, such as Guadalupe Island ⁶⁴. This onshore fasting implies that MeHg in all seal
131 tissues may come from the same offshore dietary sources ⁶⁵. Moreover, as MeHg isotope
132 ratios are similar between different seal tissues fed a constant diet ⁴⁴, and MeHg fraction is
133 high in seal hair ⁶⁰, $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values of THg in NES hair represent a relevant proxy for
134 MeHg isotopic signature in other tissues (e.g. blubber and muscle) ⁶⁰.

135 - **Total Hg concentrations**

136 Once in the laboratory, samples were lyophilized and homogenized using an electric
137 grinder that was rinsed with alcohol between samples. THg determination was carried out
138 on aliquots (around 10 mg) of homogenized shark and seal samples by combustion, gold
139 trapping and atomic absorption spectrophotometry detection using a DMA80 analyzer
140 (Milestone, USA). THg concentrations in samples are expressed on a dry weight basis ($\text{ng}\cdot\text{g}^{-1}$
141 dw). Only one analysis was performed per sample, but the accuracy and reproducibility of
142 the method were established using two freeze-dried certified biological material: a tuna fish
143 flesh homogenate reference material (IAEA 436, IRMM) and a lobster hepatopancreas
144 reference material (TORT 3, NRCC). The certified values for IAEA 436 ($4.19 \pm 0.36 \mu\text{g}\cdot\text{g}^{-1}$ dw,

145 n = 10) were reproduced (measured value: $4.33 \pm 0.19 \mu\text{g}\cdot\text{g}^{-1}$ dw) within the confidence
146 limits. The certified values for TORT 3 ($0.292 \pm 0.022 \mu\text{g}\cdot\text{g}^{-1}$ dw) were also reproduced
147 (measured value: $0.286 \pm 0.024 \mu\text{g}\cdot\text{g}^{-1}$ dw, n = 10) within the confidence limits. The detection
148 limit was $0.005 \mu\text{g}\cdot\text{g}^{-1}$ dw.

149 - Hg isotopes

150 Aliquots of approximately 10 mg of dry muscle or 20 mg of dry dermis were left over
151 night at room temperature in 3 mL of concentrated bi-distilled nitric acid (HNO_3). Samples
152 were then digested on a hotplate for 6h at 85°C in pyrolyzed glass vessels closed by Teflon
153 caps. One mL of hydrogen peroxide (H_2O_2) was added and digestion was continued for
154 another 6h at 85°C . One hundred μL of BrCl was then added to ensure a full conversion of
155 MeHg to inorganic Hg. The digest mixtures were finally diluted in an inverse aqua regia (3
156 HNO_3 : 1 HCl , 20 vol.% MilliQ water) to reach a nominal Hg concentration of $1 \text{ ng}\cdot\text{g}^{-1}$. Two
157 types of certified reference materials (NRC TORT-3 and ERM-BCR-464) and blanks were
158 prepared in the same way as tissue samples. Mercury isotope compositions were measured
159 by multi-collector inductively coupled plasma mass spectrometry (MC-ICP-MS, Thermo
160 Finnigan Neptune Plus) with continuous-flow cold vapor (CV) generation using Sn (II)
161 reduction (CETAC HGX-200). Hg isotope composition is expressed in δ notation and reported
162 in parts per thousand (‰) deviation from the NIST SRM 3133 standard, which was
163 determined by sample-standard bracketing according to the following equation: $\delta^{\text{xxx}}\text{Hg}$ (‰)
164 = $[((^{\text{xxx}}\text{Hg}/^{198}\text{Hg})_{\text{sample}} / (^{\text{xxx}}\text{Hg}/^{198}\text{Hg})_{\text{NIST 3133}}) - 1] \times 1000$ where xxx represents the mass of
165 each mercury isotope. $\delta^{202}\text{Hg}$ represents Hg MDF, and Δ notation is used to express Hg MIF
166 by the following equation:

$$167 \Delta^{\text{xxx}}\text{Hg} (\text{‰}) = \delta^{\text{xxx}}\text{Hg} - (\delta^{202}\text{Hg} \times a)$$

168 , where $a = 0.252, 0.502$ and 0.752 for isotopes 199, 200 and 201, respectively.

169 Total Hg in the diluted solutions was monitored by MC-ICP-MS using ^{202}Hg signals: mean
170 recoveries of $101 \pm 13\%$ ($n = 105$) for samples and $95 \pm 7\%$ ($n = 16$) for certified reference
171 materials were found. Hg levels in blanks were below the detection limit. Reproducibility of
172 Hg isotope measurements was assessed by analyzing UM-Almadén ($n = 20$), ETH-Fluka
173 ($n = 20$) and the biological tissue procedural standards NRC TORT-3 ($n = 6$) and ERM-BCR-464
174 ($n = 10$) (SI Appendix, Table S1). Duplicate analyzes were performed on a subset of 15 shark
175 samples to assess $\delta^{202}\text{Hg}$ (2SD = 0.12%) and $\Delta^{199}\text{Hg}$ (2SD = 0.10%) long-term
176 reproducibility. Measured isotope signatures as well as analytical reproducibility of
177 standards were found to be in agreement with previously published values ^{30,66–68} (SI
178 Appendix, Table S1).

179 **Data treatment**

180 Two previous studies analyzed Hg isotopes from pelagic biota in the foraging habitat
181 of Northeast Pacific white sharks (i.e. Central North Pacific ³⁰ and Northeast Pacific ³²) (Figure
182 1). As Hg isotope ratios decrease with increasing foraging depth ³², these potential prey were
183 classified in groups according to their vertical feeding habitat based on individual $\Delta^{199}\text{Hg}$ and
184 $\delta^{202}\text{Hg}$ values (SI Appendix, Table S2), using a K-means cluster analysis ⁶⁹. This clustering
185 method delineates groups in the dataset by minimizing the sum of the within-group sums of
186 squared-distances, based on Euclidean distance. The number of groups for the partition was
187 defined using the Caliński-Harabasz criterion ⁷⁰. Two groups were identified (SI Appendix,
188 Table S2 and Figure S1): a first with higher $\Delta^{199}\text{Hg}$ ($2.69 \pm 0.45 \%$) and $\delta^{202}\text{Hg}$ (0.83 ± 0.18
189 $\%$) representing epipelagic species (“EPI”, $n = 21$), a second group with lower $\Delta^{199}\text{Hg}$ ($1.60 \pm$
190 0.31%) and $\delta^{202}\text{Hg}$ ($0.40 \pm 0.24 \%$) gathering mesopelagic organisms (“MES”, $n = 35$). These

191 groups contain fish and squid species which may be targeted by white sharks or which are
192 representative of a certain foraging depth. As the Hg isotope signature reflects the feeding
193 depth (i.e. where Hg is trophically assimilated), the vertical classification of some species
194 may differ from the literature which uses either the median depth of occurrence³⁰ or to the
195 depth of maximum occurrence³². Flying fish were not included in the analysis since only
196 three individuals from a single species would have formed a fourth group due to outlying
197 $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values caused by direct proximity with the surface ³⁰. Crustaceans were
198 excluded because of their low MeHg fraction which could have biased Hg isotope analyzes ³²,
199 as well as juvenile Pacific bluefin tunas whose signature partially reflect the western Pacific
200 Ocean (outside the white shark distribution) due to recent migration from west to eastern
201 Pacific Ocean waters ³².

202 For comparison of Hg isotope ratios between groups, data were first checked for normality
203 (Shapiro–Wilk tests) and homogeneity of variances (Bartlett tests). One-way analyses of
204 variance (ANOVAs) were applied when these conditions were met, followed by Tukey’s HSD
205 tests when more than two groups were compared. In the absence of homoscedasticity
206 Welch's ANOVAs with Games-Howell post hoc test were used. When variables followed a
207 normal distribution, Pearson correlation tests were used to investigate the link between
208 shark length and Hg isotope ratios. In the absence of normality, Spearman correlation tests
209 were applied. To assess the relationship between Hg isotope ratios and depth, individual
210 $\Delta^{199}\text{Hg}$ values in potential pelagic prey (i.e. fish and squids from EPI and MES groups, n = 56)
211 were modeled using a logarithmic regression with depth as explanatory variable. Estimated
212 species depths were taken from previous studies ^{30,32} and correspond either to the median
213 depth of occurrence ³⁰ or to the depth of maximum occurrence ³² (SI Appendix, Table S2).

214 Bayesian stable isotope mixing models were constructed with $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values to
215 estimate the relative contribution of different prey groups to the MeHg burden in white
216 sharks using the “simmr” package ⁷¹ in R. Bayesian approaches use statistical distributions to
217 characterize the uncertainties in food source and consumer isotopic values and in estimated
218 source contributions. Complete formulation of the models is available in the literature ^{72,73}.
219 Because $\Delta^{199}\text{Hg}$ values are conserved between diet and consumer fish ^{48,49,74} and following
220 prior studies ³², no trophic discrimination factor (TDF) for $\Delta^{199}\text{Hg}$ was incorporated in the
221 models. However, MeHg demethylation has recently been suggested in shark species,
222 leading to an increase in $\delta^{202}\text{Hg}$ values in sharks compared to their prey ⁴⁶. Although this
223 $\delta^{202}\text{Hg}$ TDF is poorly characterized to date, our models considered different $\delta^{202}\text{Hg}$ TDF
224 ranging from 0 to 1‰, based on previous studies on sharks and aquatic mammals ^{44,46,75,76}.
225 The source data were incorporated in the mean \pm SD form. Models were run with generalist
226 prior distributions and Markov Chain Monte Carlo (MCMC) simulation methods (number of
227 iterations = 100000, size of burn-in = 10000, amount of thinning = 100 and number of MCMC
228 chains = 4). Convergence of the models was checked using Gelman-Rubin diagnostics. In all
229 cases, the Gelman-Rubin diagnostic was 1, indicating good convergence.

230 All statistical analyses were performed using the open source software R (version 3.6.2, R
231 Core Team, 2020).

232

233

234 Results and Discussion

235 MeHg exposure during the nearshore season

236 In white sharks sampled at Guadalupe Island, Hg isotope values were higher in dermis
237 ($\Delta^{199}\text{Hg} = 1.66 \pm 0.22\text{‰}$ and $\delta^{202}\text{Hg} = 1.15 \pm 0.27\text{‰}$) compared to muscle ($\Delta^{199}\text{Hg} = 1.54 \pm$
238 0.18‰ and $\delta^{202}\text{Hg} = 0.88 \pm 0.25\text{‰}$) (Figure 2, Figure 3). While $\delta^{202}\text{Hg}$ can vary between
239 tissues due to Hg metabolism^{76,77}, $\Delta^{199}\text{Hg}$ values are not affected by trophic transfer or
240 biological processes, leading to similar $\Delta^{199}\text{Hg}$ values between the different tissues of a
241 consumer with a constant diet^{44,48,74,76}. However, $\Delta^{199}\text{Hg}$ values may fluctuate between
242 organs if MeHg exposure changes over time and if tissues exhibit contrasting integration
243 times due to different turnover rates. For instance, arctic seabirds displayed higher $\Delta^{199}\text{Hg}$
244 values in feathers compared to blood, reflecting seasonal dietary changes and different
245 integration times for MeHg exposure among tissues⁷⁸. In the Northeast Pacific, white sharks
246 are primarily concentrated along the west coast of North America from late summer to early
247 winter while the rest of the year they migrate into oceanic habitats^{19,24,28,79}. In aggregation
248 sites such as Guadalupe Island, white sharks have been shown to feed mainly on pinniped
249 species such as sea lions, fur seals and elephant seals^{21,23} while in the open Pacific ocean
250 they are thought to consume pelagic prey^{79,80}, even if targeted species remain largely
251 unidentified^{24,25}. Using carbon and nitrogen stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), previous studies
252 suggested that muscle and dermis have different turnover rates in sharks^{79,81,82}. Moreover,
253 dermis $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of white sharks sampled along the coast of California closely
254 resembled isotopic composition of local pinnipeds, suggesting that dermis displays a faster
255 incorporation rate from prey than muscle tissues, and reflects more recent foraging activity
256⁷⁹. Here, $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values in white shark tissues were significantly lower than in

257 northern elephant seal (NES) (Figure 2, Figure 3). However, Bayesian mixing models
258 estimated that the NES contribution to shark MeHg exposure was higher in dermis than in
259 muscle (e.g. 46% versus 25% without $\delta^{202}\text{Hg}$ TDF, respectively) (Figure 4). In accordance with
260 previous conclusions based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values⁷⁹, Hg isotopes support the hypothesis of
261 a shorter integration time in dermis compared to muscle, as dermis Hg isotope values
262 indicate these tissues are more influenced by the recent consumption of pinnipeds at
263 Guadalupe Island. Importantly, these results reveal that seals represent a significant source
264 of MeHg exposure for white sharks during the nearshore season, accounting for half of
265 MeHg in dermis.

266 **MeHg origin at the scale of the entire migration cycle**

267 Skeletal muscle tissue is believed to integrate dietary MeHg over durations of
268 approximately 1,000 days based on $\Delta^{199}\text{Hg}$ values of captive Pacific bluefin tuna (*Thunnus*
269 *orientalis*), which were fed a controlled diet⁴⁹. This slow turnover time, in a metabolically
270 active fish species with similar physiology traits to white sharks^{83,84}, enables determining the
271 average origin of MeHg exposure across the entire migratory cycle of white sharks, including
272 both oceanic and coastal seasons. Using muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, it has been previously
273 suggested that during the coastal season, northeast Pacific white sharks in California have
274 approximately twice the prey consumption rate compared to when they are offshore⁷⁹.
275 Despite previous results suggesting juvenile elephant seals (NES) are one of the main prey
276 for white sharks near pinniped colonies such as Guadalupe Island^{21,23,51,85}, their Hg signature
277 differed significantly from that of sharks (Figure 2, Figure 3). Because $\Delta^{199}\text{Hg}$ values decrease
278 with depth, lower $\Delta^{199}\text{Hg}$ values in white sharks may indicate deeper foraging depths
279 compared to juvenile NES⁶⁵. In addition, high $\delta^{202}\text{Hg}$ values are commonly observed in

280 mammals and are thought to reflect *in vivo* demethylation of MeHg^{44,76,77}, which probably
281 sets NES apart from other prey groups and white sharks. Consequently, according to
282 Bayesian mixing models based on Hg isotope tracers, the NES contribution to MeHg levels in
283 shark muscle was estimated to be 25% maximum (Figure 4B). Lipid reserves represent major
284 sources of metabolic energy in marine predators that have very high energetic requirements
285 related to long migrations^{86,87}. To cover energy needs related to undertaking long
286 migrations, white sharks are hypothesized to rely primarily on the blubber of marine
287 mammals during the inshore season^{86,88,89}. Indeed, fat can exceed 40% of the total body
288 mass in juvenile NES⁶⁴, which are believed to be a preferred prey for white sharks due to
289 their high energy supply^{51,85}. As MeHg primarily binds to thiol-containing amino acids in
290 proteins^{90–92}, blubber which is mainly composed of lipids generally contains low MeHg levels
291 in seals⁹³. Thus, despite a presumed high feeding rate during the inshore season⁷⁹, low
292 MeHg levels in pinniped blubber may be responsible for the limited contribution of NES to
293 the global MeHg exposure for white sharks (Figure 4B).

294 Electronic tags have rapidly increased our knowledge on marine predator movements
295^{94–96} and revealed that many perform large migrations from forage rich coastal realms to
296 offshore oceanic areas traditionally considered deserts^{20,24}. Recently, these types of
297 movements have been linked to ocean physics and more specifically to mesoscale eddies,
298 which induce regional penetration of warm surface waters to depths of up to 800m²⁶.
299 Mesoscale eddies are hypothesized to improve access to deep-sea mesopelagic prey for blue
300 sharks (*Prionace glauca*)²⁶ and white sharks²⁷ in the Atlantic Ocean, by releasing them from
301 thermal constraints and reducing the physiological costs of thermoregulation, respectively.
302 Although the twilight zone contains the largest fish biomass in the global ocean²⁹, so far
303 there has not been direct evidence of trophic connections between white sharks and

304 mesopelagic organisms in the Pacific Ocean. Here, $\Delta^{199}\text{Hg}$ values in white shark tissues were
305 similar to mesopelagic (MES) prey (Figure 2, Figure 3), which we estimated to be the main
306 MeHg source for white sharks, accounting for a minimum of 52% of dermis MeHg and 72%
307 of muscle MeHg (Figure 4A and 4B). These results align with previous observations revealing
308 higher MeHg exposure associated with deeper foraging depths in pelagic fish from the
309 Pacific Ocean^{31,32}. Indeed, MeHg concentrations in Pacific waters are known to increase with
310 depth^{99,100}, driven by the production of MeHg below the mixed layer³⁰. As $\Delta^{199}\text{Hg}$ values are
311 not modified during MeHg trophic transfer (29–32), our results demonstrate strong evidence
312 that white sharks actively feed on mesopelagic organisms, revealing the existence of trophic
313 interactions that have been suspected for over a decade^{24,25}. Finally, $\Delta^{199}\text{Hg}$ values in white
314 shark muscle indicate an exposure to MeHg having undergone weak photochemical
315 degradation in the twilight zone (i.e. low values, Figure 5). As NES are not the main
316 contributor to overall MeHg exposure (Figure 4B), and as white shark distribution during the
317 coastal season is confined bathymetrically primarily to the photic zone (i.e. above 200m)
318^{20,24,28,89}, the low Hg MIF observed in shark tissues strongly suggests a dominant MeHg origin
319 from offshore deep waters. This conclusion is supported by observed diving behaviors in
320 oceanic habitats, where white sharks frequently reached 500m^{20,28} and occasionally 1,000m
321^{24,27,101}.

322 **Hg isotopes to interpret white shark movements and habitat use**

323 Contrasting habitat use was previously identified between juvenile and adult white
324 sharks at Guadalupe Island⁸⁹, which could potentially influence MeHg exposure and
325 therefore Hg isotope signatures. Juvenile white sharks at Guadalupe Island remained close
326 to the shore and in shallow water (i.e. primarily between the surface and 50m depth),

327 probably to avoid adults patrolling in deeper water (up to 200m depth) in search for an
328 opportunity to attack seals ⁸⁹. Moreover, juveniles and adults have different thermal
329 preferences, with adults being more tolerant to colder waters, likely due to an increase in
330 thermal inertia and thermoregulatory abilities with ontogeny ^{89,96,102}. This higher thermal
331 tolerance could result in vertical niche expansion for adult sharks, increasing exposure to
332 MeHg with lower isotope ratios ³⁰. Although both juvenile and adult sharks were considered
333 in our study (SI Appendix, Table S3), $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values did not vary with body length
334 for any of the two tissues analyzed (Pearson or Spearman correlation tests, $p > 0.05$). Thus,
335 our results do not provide support for an effect of habitat use or thermal tolerance on
336 foraging depth, and subsequent MeHg exposure, for white sharks over 2 meters in total
337 length. Alternatively, both juveniles and adult sharks could have access to the same
338 mesopelagic prey that migrate to the surface at night, facilitated by the very steep
339 bathymetry and oceanic nature of Guadalupe Island ⁸⁹.

340 During the seasonal offshore migration, northeast Pacific white sharks occupy a
341 pelagic zone referred to as the “White Shark Café”, also known as “Shared Offshore foraging
342 Area” (SOFA), located in the North Pacific Sub-Tropical Gyre halfway between Hawaii and
343 the coasts of Mexico ^{19,24,101}. The reason why a large number of white sharks congregate in
344 this area remains unanswered, and the two main hypotheses proposed relate to
345 reproduction or feeding ^{20,28,53}. Pronounced sex-based structure in the diving behavior of
346 white sharks has been identified within the Café ²⁰. If foraging was the only activity, the
347 significant differences in depth occupancy between sexes ²⁰ should be reflected by
348 contrasting $\Delta^{199}\text{Hg}$ values. Indeed, in the Café region, females mainly perform diel vertical
349 migrations (DVM) peaking in the upper 200 meters during the night, while they occupy a
350 water layer between 350 and 500m depth during the day (Figure 5). By contrast, males

351 initially exhibit a mix of DVM and rapid oscillatory diving (ROD) behavior, then increasingly
352 focus on ROD at depths between the surface and 200m (day and night), before returning to
353 the coast ^{19,20}. We found that muscle $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values did not differ between sexes
354 (ANOVAs, $p > 0.05$), suggesting no difference in mean foraging depth between females and
355 males at the scale of the entire migration cycle. Only a slight difference in $\Delta^{199}\text{Hg}$ values was
356 found in the more rapidly integrating dermis tissue, with lower values for females compared
357 to males (ANOVA, $p = 0.048$). Since none of the previous studies has identified differences in
358 diving behavior between males and females at Guadalupe Island ^{24,25,89} or along the
359 California coast ^{20,28,103}, the lower $\Delta^{199}\text{Hg}$ values in the females' dermis likely reflects the fact
360 that females arrive later at Guadalupe Island compared to males ^{24,89}. At the moment of
361 sample collection, females had spent less time in the insular habitat. Their dermis, which is
362 mainly influenced by recent MeHg exposure, would therefore reflect to a stronger degree
363 the offshore season, during which both sexes dive deeper and may assimilate MeHg with
364 lower $\Delta^{199}\text{Hg}$ values than in the waters surrounding Guadalupe Island ^{24,25}. Regarding DVM
365 performed by both sexes, previous studies agree that it may reflect a foraging behavior
366 following the diel vertical migration of the deep scattering layer (DSL), a community of
367 mesopelagic fish and squid that rise near the surface at night and occupy the twilight zone
368 during the day ^{20,25}. In the Café, the estimated depth at the top of this layer is 460m during
369 the day ¹⁰¹, which corresponds both to the layer occupied by white sharks engaged in
370 daytime DVM ²⁰ and matches the $\Delta^{199}\text{Hg}$ values found in white shark tissues (Figure 5). The
371 White Shark Café is thought to support considerable mesopelagic biomass ⁵³. Although DVM
372 is not restricted to the Café and is performed throughout the entire offshore range of white
373 sharks ²⁰, they may preferentially use this offshore ecosystem to target deep mesopelagic
374 prey, as suggested in other regions ²⁷. While through ROD behavior males could also target

375 the DSL which rises to the 200m zone at night ²⁰, daytime ROD appears incompatible with
376 the $\Delta^{199}\text{Hg}$ values found in white shark tissues (e.g. around 1.5 ‰ in muscle), which would
377 correspond to a daytime feeding depth of over 350m (Figure 5). Alternatively, this behavior
378 is similar to the vertical movements of Atlantic Bluefin tuna (*Thunnus thynnus*) at their
379 breeding grounds ¹⁰⁴ and has previously been proposed as a potential mating activity ^{20,28}.
380 Overall, Hg isotopes confirm that mesopelagic foraging occurs in the Café, but do not
381 exclude the possibility that other behaviors such as mating could take place in this area.

382 In the context of climate change, global warming is expected to expand oxygen-
383 minimum zones (OMZs) by reducing oxygen supply to the ocean ^{105,106}. Microbial MeHg
384 production is enhanced in mesopelagic zones, which are located in sub-thermocline oceanic
385 waters, where oxygen concentration is low and organic matter is intensively remineralized
386 ^{30,107,108}. Thus, the expansion of the MeHg production zone suggests that MeHg exposure
387 could increase for mesopelagic organisms and consequently for their predators such as
388 white sharks. In addition, strong modifications in global mesopelagic biogeographic structure
389 are predicted by the end of this century. More precisely, the mesopelagic biomass is
390 expected to decrease in the North Pacific Tropical Gyre, including the offshore foraging
391 habitat of northeast Pacific white sharks ¹⁰⁹. This study highlights the importance of the
392 mesopelagic compartment in the diet of marine apex predators, such as white sharks. A
393 reduction in the mesopelagic biomass could therefore alter trophic supply to sharks and / or
394 lead to a modification of their migration patterns towards more productive offshore areas,
395 which could alter the location or function of their potential mating area. These climate-
396 driven changes should be carefully considered to avoid potential extinction of white sharks
397 and their ecological roles over the next century ⁶.

398 **Acknowledgments**

399 Gaël Le Croizier was supported by a postdoctoral grant from the French National Research
400 Institute for Sustainable Development (IRD) and the ISblue "Interdisciplinary graduate School
401 for the blue planet" project (ANR-17-EURE-0015). The project was funded by Alianza WWF-
402 TELCEL, The Annenberg Foundation, International Community Foundation, Fins Attached
403 Marine Research and Conservation, The Watermen Project, Pflieger Institute of
404 Environmental Research and Shark Diver. Field work was greatly facilitated through
405 courtesies extended to us by personnel of the University of California, Davis, Centro
406 Interdisciplinario de Ciencias Marinas (CICIMAR), Secretaria de Marina, Comisión de Areas
407 naturales Protegidas (CONANP), Island Conservation (GECI), Horizon Charters, Islander
408 Charters, Solmar V, Club Cantamar and local fishermen from Guadalupe Island. The
409 laboratory analyses were financially supported by the French National Research Agency
410 project ANR-17-CE34-0010 MERTOX (PI David Point). White shark and elephant seal samples
411 were collected under permits from the Secretaría del Medio Ambiente y Recursos Naturales
412 (SEMARNAT): OFICIO NUM.SGPA/DGVS/07052/16 in 2016, OFICIO
413 NUM.SGPA/DGVS/06673/17 in 2017 and OFICIO NUM.SGPA/DGVS/004284/18 in 2018.
414 White shark samples were exported from Mexico under the CITES permit (number MX007)
415 of the Universidad Nacional Autónoma de México and imported in France under the CITES
416 permit (number FR75A) of the Muséum National d'Histoire Naturelle. We thank Laure
417 Laffont and Jérôme Chmeleff for expert management of the OMP mercury and mass
418 spectrometry facilities. Felipe Galvan-Magaña thanks the Instituto Politécnico Nacional (IPN)
419 for the COFAA and EDI fellowships.

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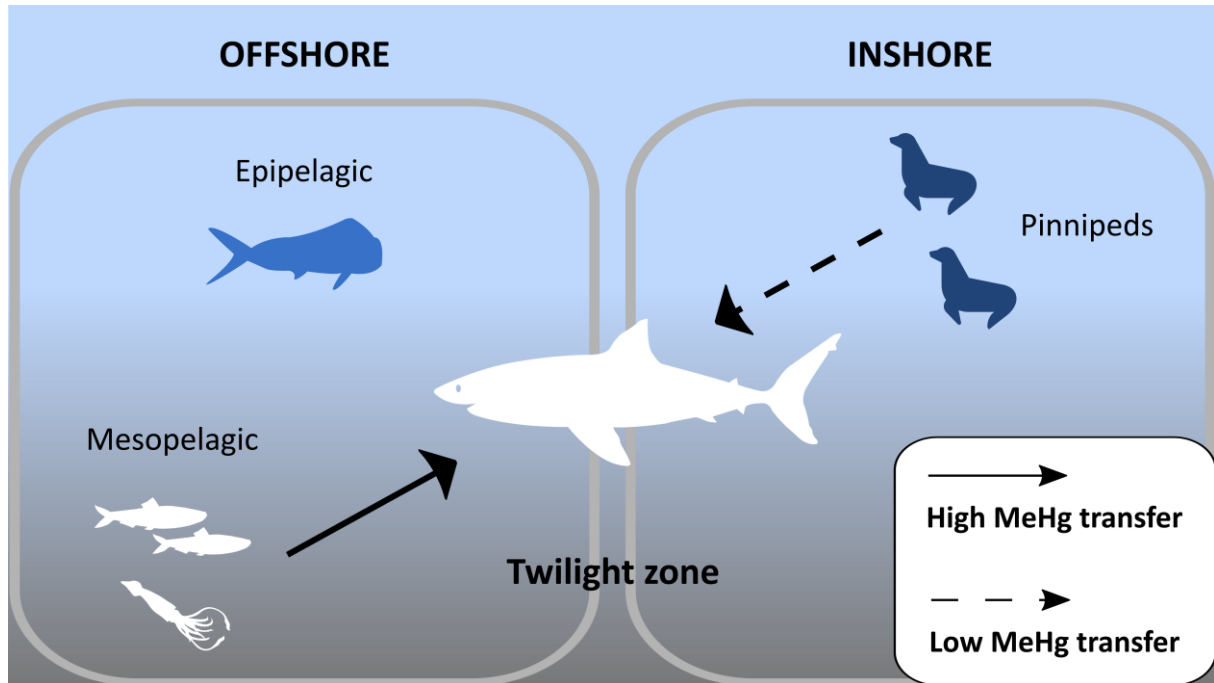
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Tables and figures



Graphical abstract

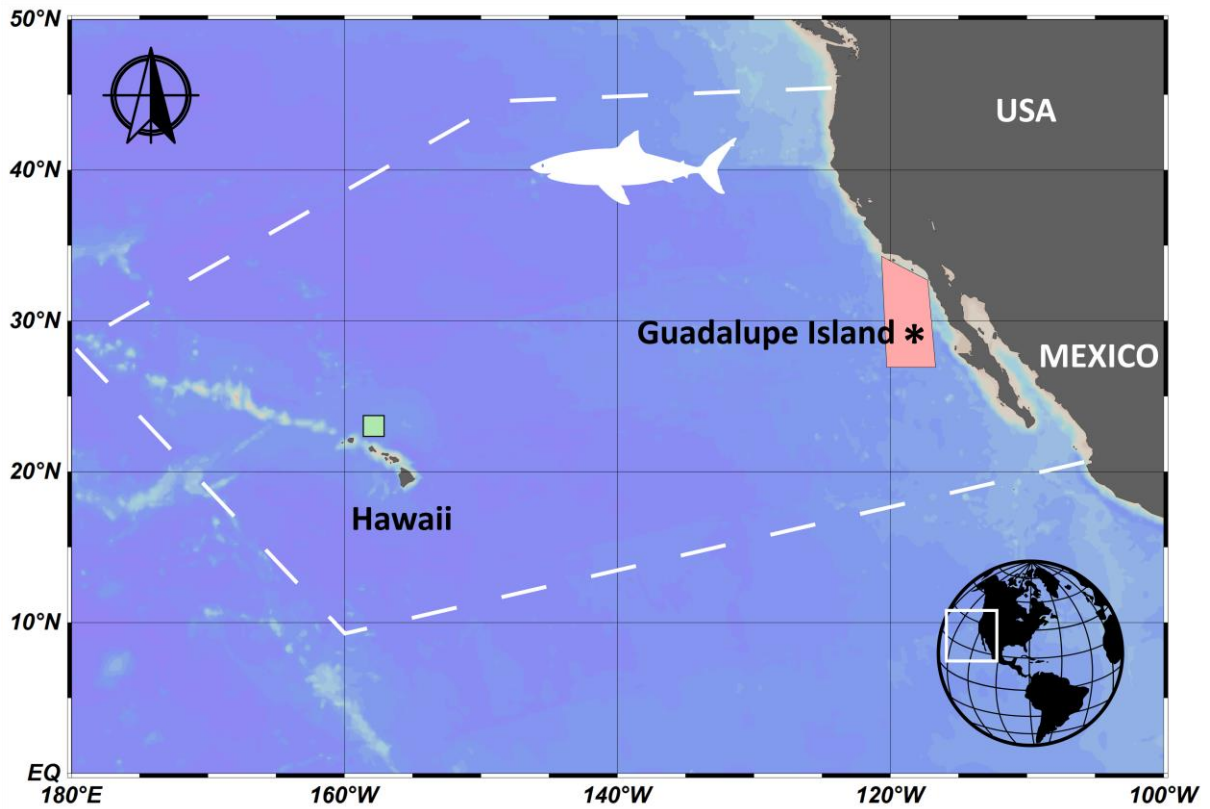


Figure 1: Map of the spatial distribution of white sharks (white hatched lines) in the Northeast Pacific Ocean. White shark and northern elephant seal samples were collected at Guadalupe Island (*) for the present study. Hg isotope signatures in pelagic organisms were obtained from two previous studies: green and red sampling locations for Blum et al. (2013)³⁰ and Madigan et al. (2018)³², respectively.

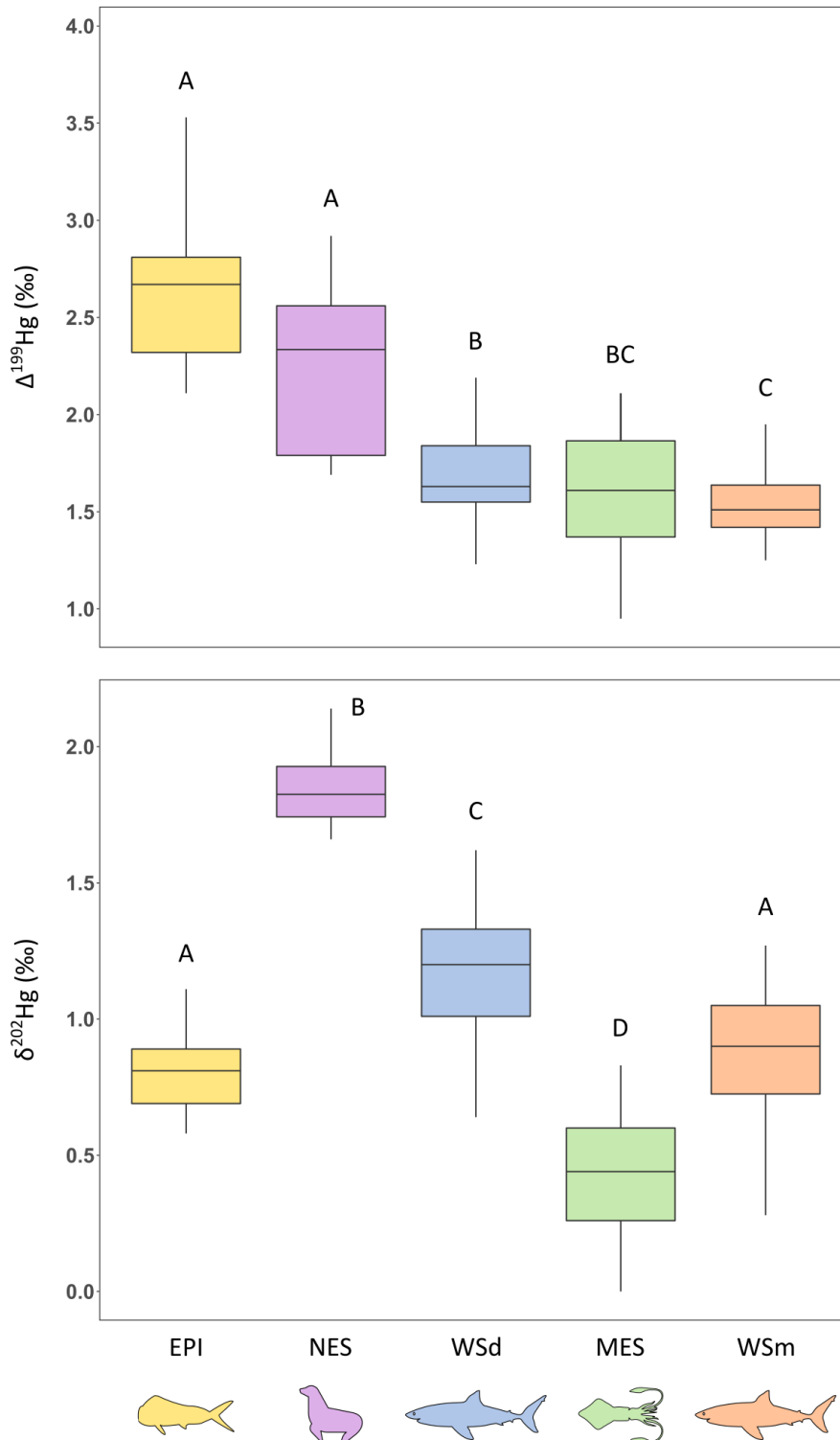


Figure 2: Boxplots of Hg isotope values in white shark tissues and potential prey groups: epipelagic prey (EPI, n = 21), mesopelagic prey (MES, n = 35), northern elephant seals (NES, n = 10), white shark dermis (WSd, n = 65) and white shark muscle (WSm, n = 30). Groups are ordered by decreasing $\Delta^{199}\text{Hg}$ values. Different letters indicate significant differences between groups ($\Delta^{199}\text{Hg}$: Welch's ANOVA with Games-Howell post hoc test, $\delta^{202}\text{Hg}$: ANOVA followed by Tukey's HSD test; $p < 0.05$).

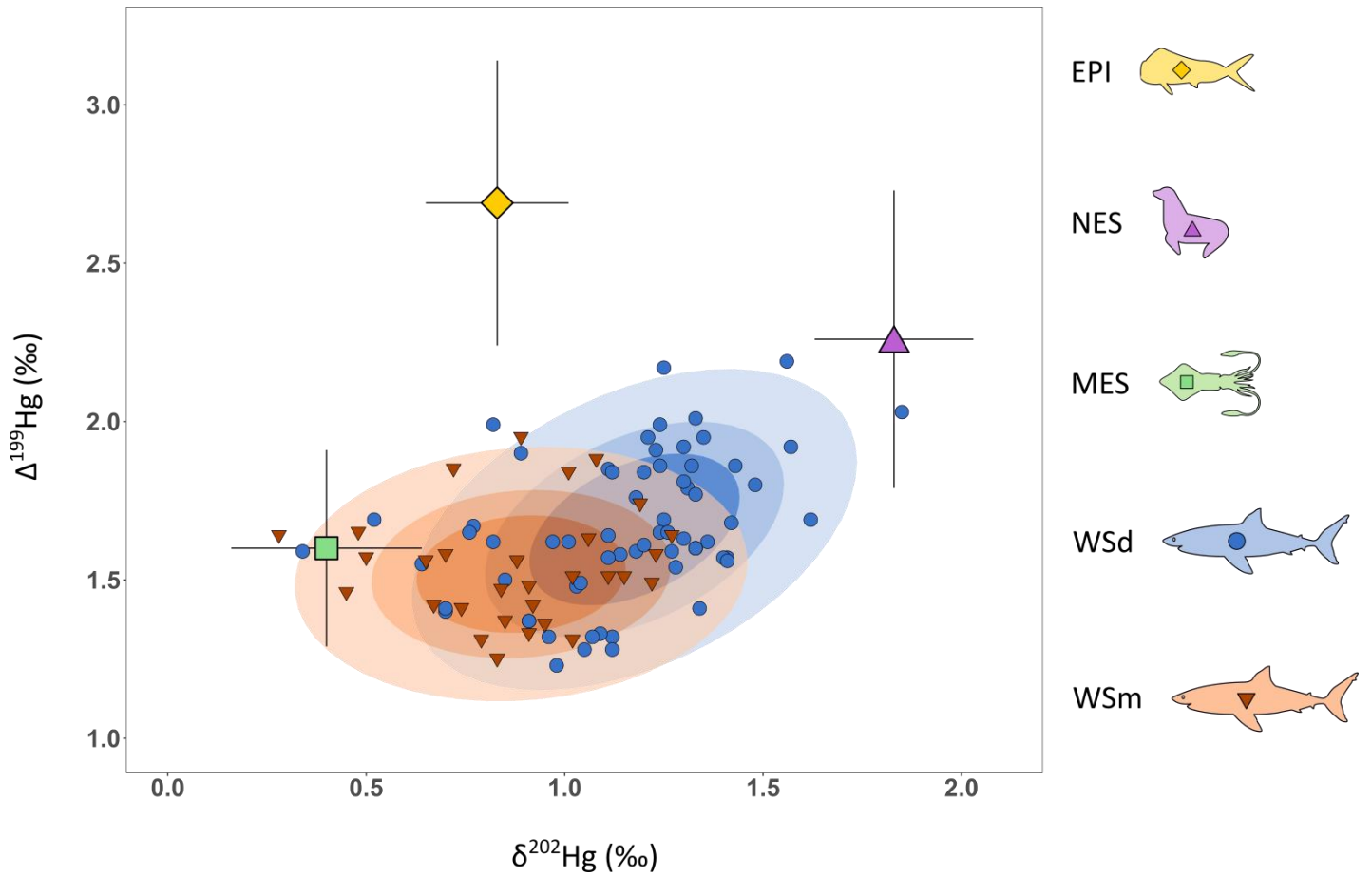


Figure 3: Individual $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values for white shark dermis (WSd, $n = 65$) and muscle (WSm, $n = 30$). Standard ellipse areas at 50%, 75% and 95% are figured. Hg isotope compositions of potential prey groups are displayed as mean (\pm SD): epipelagic prey (EPI, $n = 21$), mesopelagic prey (MES, $n = 35$) and northern elephant seals (NES, $n = 10$).

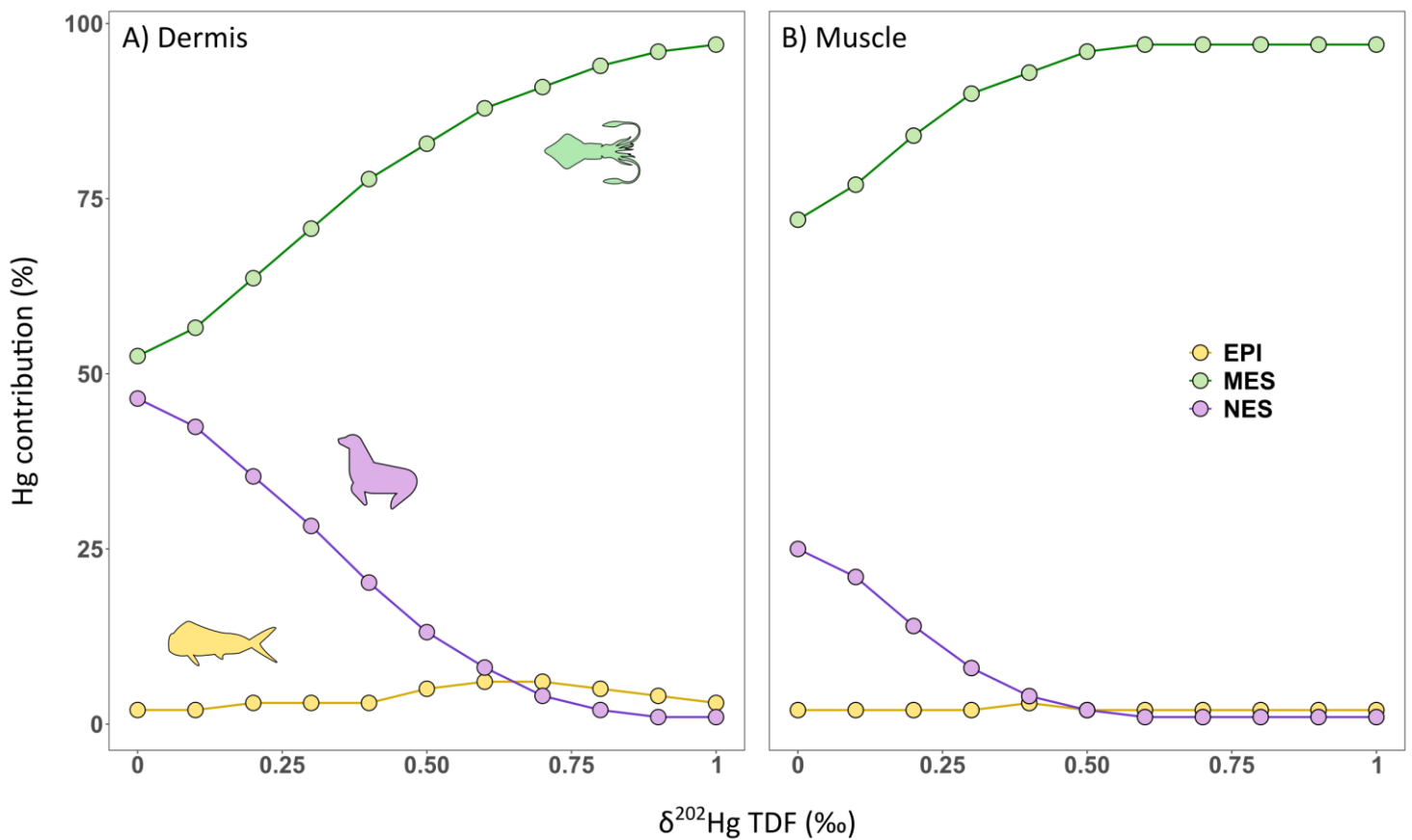


Figure 4: Estimated contributions (%) based on Hg isotope values of different prey groups in the Hg burden in A) dermis and B) muscle of white sharks. Hg contributions were evaluated by considering different trophic discrimination factors (TDF) for $\delta^{202}\text{Hg}$ ranging from 0 to 1 ‰. EPI: epipelagic prey; MES: mesopelagic prey; NES: northern elephant seals. Bayesian mixing models indicated a minimum Hg contribution of 52% from MES in shark dermis (A) and 72% in shark muscle (B). Maximum Hg contribution from NES was 46% in shark dermis (A) and 25% in shark muscle (B). Maximum Hg contribution from EPI was 6% in shark dermis (A) and 3% in shark muscle (B).

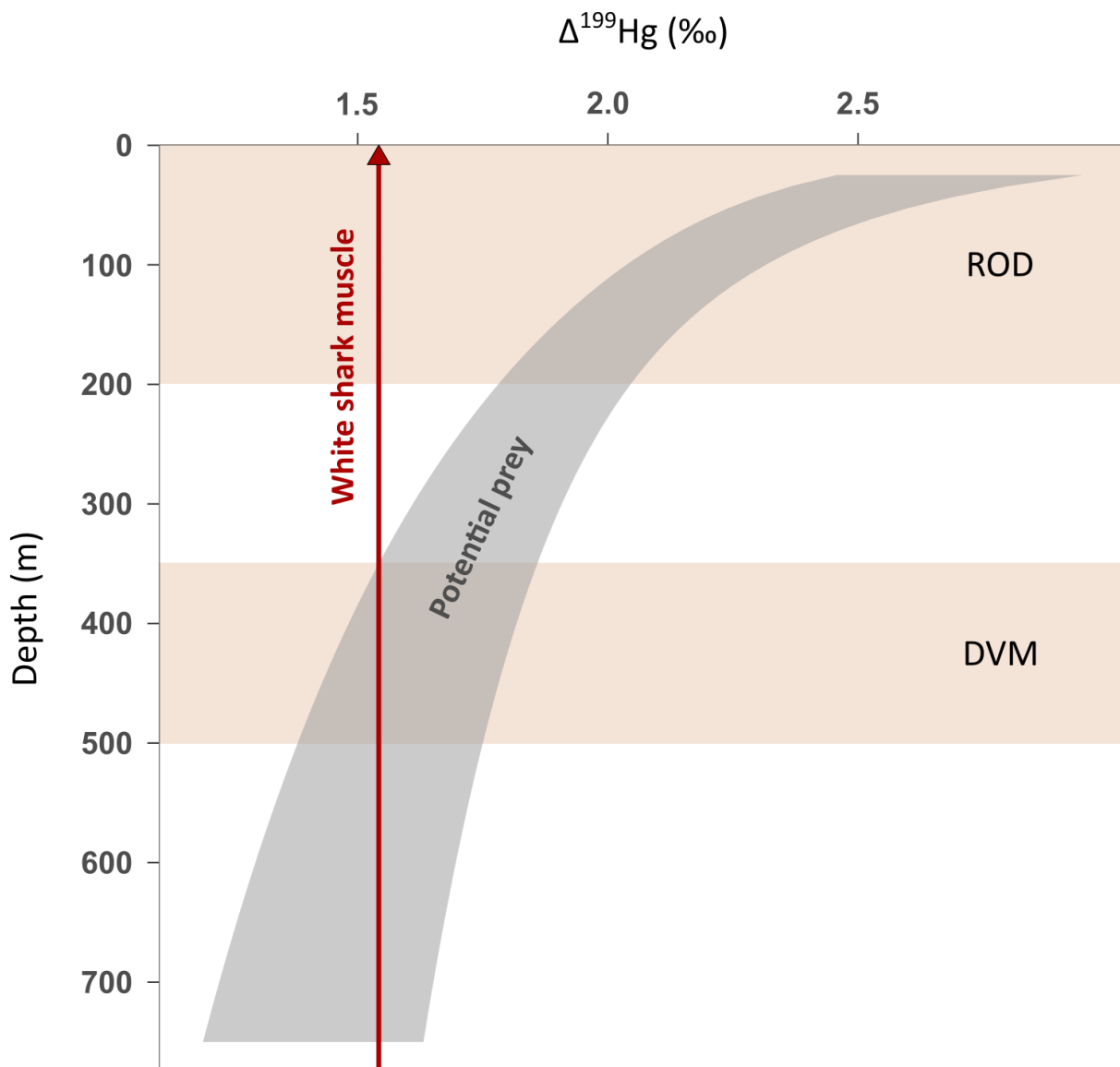


Figure 5: Mean $\Delta^{199}\text{Hg}$ value in white shark muscle from this study ($\Delta^{199}\text{Hg} = 1.54\text{‰}$, $n = 30$, red vertical line) and 95% confidence interval (grey band) from a logarithmic model fitted to $\Delta^{199}\text{Hg}$ values as a function of depth ($R^2 = 0.45$, $p < 0.001$) in potential pelagic prey from the literature^{30,32} (i.e. fish and squids from epipelagic and mesopelagic groups, $n = 56$; SI Appendix, Table S2). Two offshore diving behaviors of white sharks are figured: the “rapid oscillatory diving” (ROD) behavior occurring between 0 and 200m (day and night) and the daytime “diel vertical migration” (DVM) behavior from 350 to 500m²⁰. According to the $\Delta^{199}\text{Hg}$ variation in potential prey, the signature of white shark corresponds to a feeding on organisms living over 350 meters deep during the day, which matches daytime DVM but not daytime ROD.

Supplementary information (SI)

The twilight zone as a major foraging habitat and mercury source for the great white shark.

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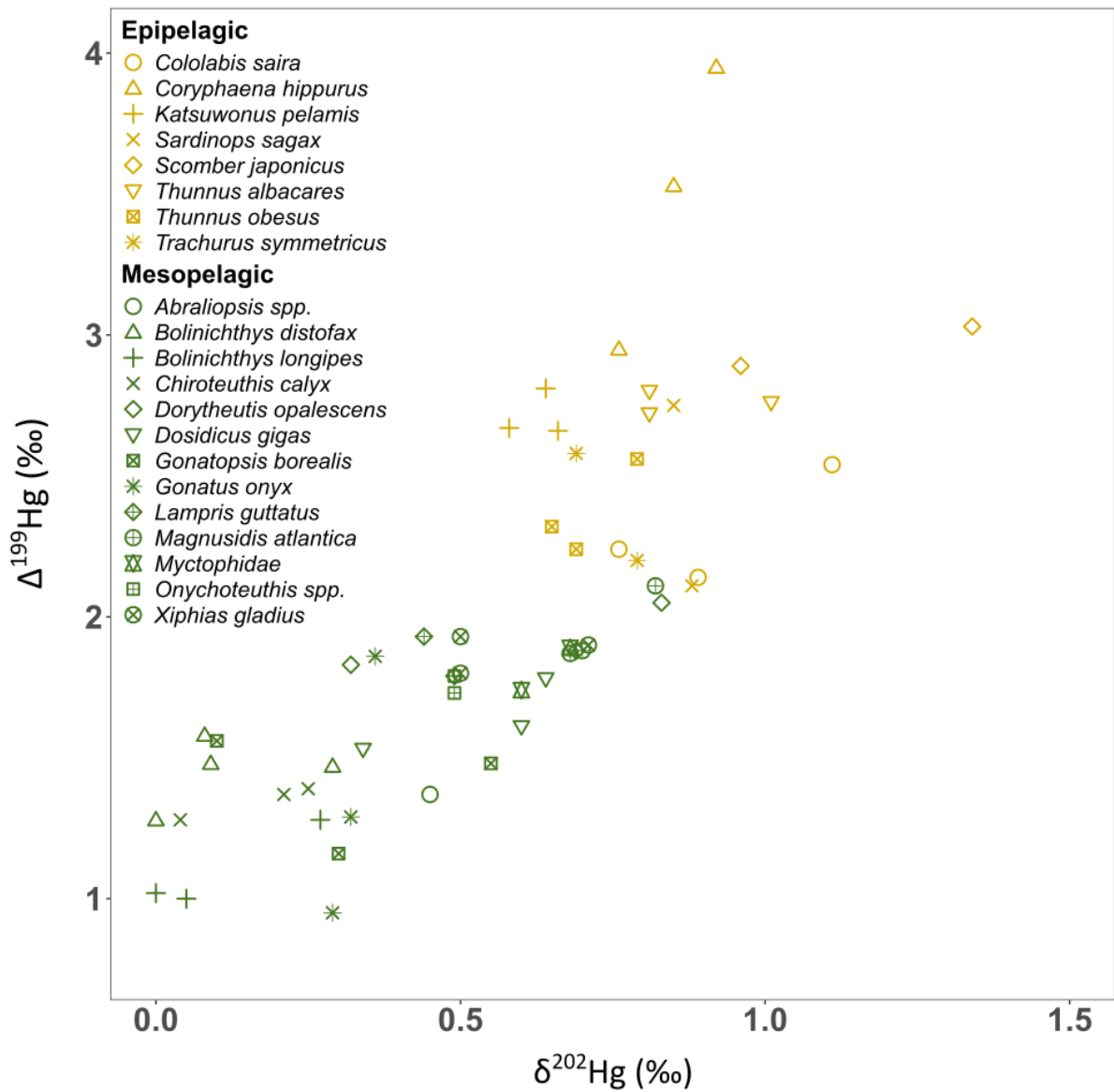


Figure S1: Hg isotope signatures in pelagic fish and squids from the foraging habitat of northeast Pacific white sharks, obtained in previous studies^{30,32}. Species were classified in two groups (i.e. epipelagic or mesopelagic) according to individual $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values.

Table S1: Summary (mean \pm 2SD) of $\delta^{202}\text{Hg}$ and $\Delta^{199}\text{Hg}$ values measured in certified reference materials (CRM).

CRM	n	$\delta^{202}\text{Hg}$ (‰)	$\Delta^{199}\text{Hg}$ (‰)	Reference
UM-Almadén	20	-0.57 ± 0.10	-0.03 ± 0.08	This study
		-0.57 ± 0.05	-0.02 ± 0.03	Blum et al., 2013 ³⁰
ETH-Fluka	20	-1.41 ± 0.12	0.10 ± 0.06	This study
		-1.44 ± 0.12	0.07 ± 0.05	Jiskra et al., 2017 ⁶⁷
BCR 464	10	0.70 ± 0.10	2.29 ± 0.06	This study
		0.73 ± 0.14	2.29 ± 0.09	Masbou et al., 2013 ⁶⁶
		0.69 ± 0.06	2.40 ± 0.06	Blum et al., 2013 ³⁰
TORT 3	6	0.09 ± 0.16	0.65 ± 0.06	This study
		0.13 ± 0.12	0.69 ± 0.10	Li et al., 2016 ⁶⁸

Table S2: Hg isotope signatures in pelagic fish and squids from the foraging habitat of northeast Pacific white sharks, obtained in previous studies ^{30,32}. Species were classified in two groups (i.e. epipelagic or mesopelagic) according to individual $\Delta^{199}\text{Hg}$ and $\delta^{202}\text{Hg}$ values. Estimated species depths of occurrence are presented as described in the literature and correspond either to the median depth of occurrence (Blum et al., 2013) ³⁰ or to the depth of maximum occurrence (Madigan et al., 2018) ³². “n” refers to the number of individuals per species or group.

Common name	Species	Reference	Depth (m)	Species n	Species $\delta^{202}\text{Hg}$ (‰)	Species $\Delta^{199}\text{Hg}$ (‰)	Group	Group n	Group $\delta^{202}\text{Hg}$ (‰)	Group $\Delta^{199}\text{Hg}$ (‰)
Common dolphinfish	<i>Coryphaena hippurus</i>	Blum et al., 2013	50	3	0.84 ± 0.08	3.48 ± 0.50	Epipelagic (EPI)	21	0.83 ± 0.18	2.69 ± 0.45
Chub mackerel	<i>Scomber japonicus</i>	Madigan et al., 2018	38	2	1.15 ± 0.27	2.96 ± 0.10	Epipelagic (EPI)			
Yellowfin tuna	<i>Thunnus albacares</i>	Blum et al., 2013	50	3	0.88 ± 0.12	2.76 ± 0.04	Epipelagic (EPI)			
Skipjack tuna	<i>Katsuwonus pelamis</i>	Blum et al., 2013	150	3	0.63 ± 0.04	2.71 ± 0.08	Epipelagic (EPI)			
South american pilchard	<i>Sardinops sagax</i>	Madigan et al., 2018	38	2	0.87 ± 0.02	2.43 ± 0.45	Epipelagic (EPI)			
Jack mackerel	<i>Trachurus symmetricus</i>	Madigan et al., 2018	38	2	0.74 ± 0.07	2.39 ± 0.27	Epipelagic (EPI)			
Bigeye tuna	<i>Thunnus obesus</i>	Blum et al., 2013	250	3	0.71 ± 0.07	2.37 ± 0.17	Epipelagic (EPI)			
Pacific saury	<i>Cololabis saira</i>	Madigan et al., 2018	25	3	0.92 ± 0.18	2.31 ± 0.21	Epipelagic (EPI)			
Barracudina	<i>Magnusidid atlantica</i>	Madigan et al., 2018	188	3	0.73 ± 0.08	1.95 ± 0.14	Mesopelagic (MES)	35	0.40 ± 0.24	1.60 ± 0.31
Opalescent inshore squid	<i>Doryteuthis opalescens</i>	Madigan et al., 2018	25	2	0.58 ± 0.36	1.94 ± 0.16	Mesopelagic (MES)			
Swordfish	<i>Xiphias gladius</i>	Blum et al., 2013	375	3	0.57 ± 0.12	1.88 ± 0.07	Mesopelagic (MES)			
Opah	<i>Lampris guttatus</i>	Blum et al., 2013	225	3	0.54 ± 0.13	1.87 ± 0.07	Mesopelagic (MES)			
Lantern fish	Myctophidae indet.	Madigan et al., 2018	63	2	0.64 ± 0.06	1.82 ± 0.11	Mesopelagic (MES)			
Squid	<i>Onychoteuthis spp.</i>	Madigan et al., 2018	300	2	0.49 ± 0.00	1.76 ± 0.04	Mesopelagic (MES)			
Humbolt squid	<i>Dosidicus gigas</i>	Madigan et al., 2018	80	3	0.53 ± 0.16	1.64 ± 0.13	Mesopelagic (MES)			
Lantern fish	<i>Bolinichthys distofax</i>	Blum et al., 2013	590	4	0.12 ± 0.12	1.45 ± 0.13	Mesopelagic (MES)			
Boreopacific armhook squid	<i>Gonatopsis borealis</i>	Madigan et al., 2018	550	3	0.32 ± 0.23	1.40 ± 0.21	Mesopelagic (MES)			
Clawed armhook squid	<i>Gonatus onyx</i>	Madigan et al., 2018	600	3	0.32 ± 0.04	1.37 ± 0.46	Mesopelagic (MES)			
Squid	<i>Abraliopsis spp.</i>	Madigan et al., 2018	450	1	0.45 ± 0.00	1.37 ± 0.00	Mesopelagic (MES)			
Squid	<i>Chiroteuthis calyx</i>	Madigan et al., 2018	750	3	0.17 ± 0.11	1.35 ± 0.06	Mesopelagic (MES)			
Lantern fish	<i>Bolinichthys longipes</i>	Blum et al., 2013	388	3	0.11 ± 0.14	1.10 ± 0.16	Mesopelagic (MES)			

Table S3: Global data set of the shark and seal samples analyzed in this study.

Common name	Species	Tissue	Sex	Total length (m)	Size class	THg (ng/g dw)	$\delta^{202}\text{Hg}$ (‰)	$\Delta^{199}\text{Hg}$ (‰)	$\Delta^{200}\text{Hg}$ (‰)	$\Delta^{201}\text{Hg}$ (‰)
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.3	juvenile	1072	0.96	1.32	0.08	1.05
Great white shark	<i>Carcharodon carcharias</i>	dermis	-	2.5	juvenile	408	0.82	1.99	0.03	1.69
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	2.5	juvenile	941	1.18	1.59	0.03	1.44
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.5	juvenile	1210	0.64	1.55	0.09	1.24
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.5	juvenile	1326	1.30	1.81	-0.03	1.49
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	2.5	juvenile	335	0.91	1.37	0.10	1.25
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.5	juvenile	683	1.41	1.56	0.02	1.44
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	2.5	juvenile	103	1.12	1.32	0.04	1.16
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.7	juvenile	1009	1.56	2.19	0.05	1.80
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	2.7	juvenile	1297	1.25	1.69	0.05	1.33
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	2.8	juvenile	846	0.77	1.67	0.06	1.47
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	418	0.89	1.90	0.07	1.58
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	800	1.21	1.95	0.08	1.68
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	820	0.34	1.59	0.10	1.24
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	829	0.70	1.40	0.11	1.06
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3	subadult	901	1.20	1.61	0.02	1.33
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	1471	1.05	1.28	0.04	1.12
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	1637	1.43	1.86	0.10	1.55
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3	subadult	2217	1.27	1.59	0.00	1.37
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3	subadult	2372	0.82	1.62	0.05	1.29
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	285	0.91	1.37	0.01	1.18
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3	subadult	455	1.03	1.48	0.02	1.06
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.2	subadult	842	1.24	1.99	0.08	1.63
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.2	subadult	1803	1.34	1.41	0.01	1.16
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.2	subadult	2210	1.24	1.65	0.04	1.42
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.2	subadult	2294	1.33	2.01	0.00	1.65

Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.2	subadult	2813	1.48	1.80	0.05	1.46
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.2	subadult	3914	1.57	1.92	0.08	1.61
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.2	subadult	389	1.41	1.57	0.05	1.23
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.2	subadult	916	1.40	1.57	-0.04	1.12
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.5	subadult	654	1.01	1.62	0.06	1.45
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	711	0.52	1.69	0.08	1.23
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.5	subadult	896	0.70	1.41	0.03	1.14
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	920	1.12	1.84	0.10	1.56
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.5	subadult	1180	1.28	1.54	0.12	1.25
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	2098	1.04	1.49	0.08	1.29
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	2129	0.85	1.50	0.04	1.21
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	3.5	subadult	2504	1.18	1.76	0.08	1.40
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	3074	1.30	1.63	0.05	1.34
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.5	subadult	3366	1.23	1.91	0.10	1.63
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	3.7	adult	1197	1.32	1.86	0.07	1.59
Great white shark	<i>Carcharodon carcharias</i>	dermis	-	4	-	660	0.76	1.65	0.11	1.36
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	959	1.09	1.33	0.02	1.06
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	4	adult	980	0.97	1.62	-0.01	1.54
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	1198	1.11	1.85	0.06	1.55
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	1308	1.62	1.69	0.04	1.40
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	4	adult	1544	1.25	2.17	0.09	1.79
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	1726	1.36	1.62	0.10	1.33
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	1882	1.12	1.28	0.04	1.07
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	1921	1.07	1.32	0.04	1.17
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	4	adult	2095	1.14	1.58	0.04	1.39
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	2098	1.30	1.92	0.05	1.64
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	2123	1.24	1.86	0.07	1.53
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	4	adult	4361	1.33	1.77	0.05	1.47
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	5135	1.35	1.95	0.05	1.66
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	4	adult	3135	1.26	1.65	0.13	1.40
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4	subadult	200	1.31	1.79	-0.01	1.46
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	4.5	subadult	4807	1.11	1.64	0.02	1.41
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	5	adult	1771	1.42	1.68	0.01	1.41
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	5	adult	2309	1.33	1.60	0.02	1.36

Great white shark	<i>Carcharodon carcharias</i>	dermis	F	5	adult	2508	1.33	1.60	0.03	1.26
Great white shark	<i>Carcharodon carcharias</i>	dermis	F	5	adult	2759	0.98	1.23	0.02	1.05
Great white shark	<i>Carcharodon carcharias</i>	dermis	M	5	adult	3326	1.85	2.03	0.11	1.71
Great white shark	<i>Carcharodon carcharias</i>	dermis	-	-	-	2301	1.11	1.57	0.07	1.39
Great white shark	<i>Carcharodon carcharias</i>	dermis	-	-	-	1756	1.20	1.84	0.04	1.51
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2	juvenile	8688	0.88	1.56	0.04	1.28
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2	juvenile	7347	0.91	1.48	0.04	1.24
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2	juvenile	10342	0.45	1.46	0.14	1.19
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2	juvenile	8631	0.67	1.42	0.13	1.11
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	2	juvenile	9642	0.72	1.85	0.00	1.42
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	2	juvenile	7606	0.84	1.47	0.08	1.24
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	2.5	juvenile	13075	1.27	1.64	0.03	1.42
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2.5	juvenile	12349	0.95	1.36	0.09	1.10
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2.5	juvenile	10385	0.74	1.41	0.08	1.05
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	2.5	juvenile	10970	0.70	1.58	0.08	1.32
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3	subadult	12728	0.92	1.42	0.04	1.28
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3	subadult	9283	1.02	1.51	0.07	1.20
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3	subadult	12500	0.85	1.37	0.04	1.02
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	3	subadult	13347	1.11	1.51	0.04	1.14
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3	subadult	8048	1.15	1.51	0.02	1.15
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3.2	subadult	15719	1.23	1.58	0.03	1.38
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3.5	subadult	13712	0.91	1.33	0.04	1.03
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3.5	subadult	9767	0.89	1.95	0.02	1.52
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	3.5	subadult	14313	1.02	1.31	0.10	1.13
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	3.75	adult	14051	1.19	1.74	0.05	1.32
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	3.75	subadult	7342	1.06	1.63	0.11	1.52
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	4	adult	10667	0.50	1.57	0.03	1.33
Great white shark	<i>Carcharodon carcharias</i>	muscle	-	4	-	6475	0.28	1.64	0.08	1.33
Great white shark	<i>Carcharodon carcharias</i>	muscle	M	4	adult	11840	0.48	1.65	0.09	1.42
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	4	subadult	9084	1.22	1.49	0.09	1.19
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	4.2	subadult	11713	1.01	1.84	0.07	1.50
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	4.5	subadult	11950	1.08	1.88	0.06	1.53
Great white shark	<i>Carcharodon carcharias</i>	muscle	F	5	adult	11512	0.79	1.31	0.01	1.03
Great white shark	<i>Carcharodon carcharias</i>	muscle	-	-	-	10311	0.65	1.56	0.08	1.26

Great white shark	<i>Carcharodon carcharias</i>	muscle	-	-	-	3983	0.83	1.25	0.08	1.02
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	juvenile	3802	2.05	2.18	0.09	1.82
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	-	-	-	8969	1.79	1.77	0.07	1.47
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	subadult	17943	1.93	2.92	0.11	2.59
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	M	-	juvenile	17939	2.14	2.82	0.02	2.47
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	subadult	6138	1.86	1.76	0.05	1.40
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	M	-	juvenile	9042	1.75	2.58	0.10	2.32
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	subadult	2378	1.74	1.85	0.02	1.44
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	adult	6585	1.45	1.69	0.05	1.49
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	juvenile	15227	1.66	2.50	0.07	2.24
Northern elephant seal	<i>Mirounga angustirostris</i>	hair	F	-	juvenile	22469	1.92	2.49	0.07	1.97