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Mercury stable isotopes suggest reduced foraging depth in oxygen minimum zones for blue sharks

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1 **Abstract** (150 words)

2 Oxygen minimum zones (OMZs) are currently expanding across the global ocean due to
3 climate change, leading to a compression of usable habitat for several marine species.
4 Mercury stable isotope compositions provide a spatially and temporally integrated view of
5 marine predator foraging habitat and its variability with environmental conditions. Here, we
6 analyzed mercury isotopes in blue sharks *Prionace glauca* from normoxic waters in the
7 northeastern Atlantic and from the world's largest and shallowest OMZ, located in the
8 northeastern Pacific (NEP). Blue sharks from the NEP OMZ area showed higher $\Delta^{199}\text{Hg}$ values
9 compared to sharks from the northeastern Atlantic, indicating a reduction in foraging depth
10 of approximately 200 meters. Our study suggests for the first time that blue shark feeding
11 depth is altered by expanding OMZs and illustrates the use of mercury isotopes to assess the
12 impacts of ocean deoxygenation on the vertical foraging habitat of pelagic predators.

13 **1. Introduction**

14 The global ocean includes permanent oxygen minimum zones (OMZs) where dissolved
15 oxygen reaches low levels, resulting in hypoxic conditions in the intermediate layers of the
16 water column [1]. During the last decades, ocean deoxygenation caused by global change
17 has led to the extension and shoaling of OMZs [2–4]. Spatial movement studies have
18 observed a reduction in dive depth associated with OMZs for large pelagic predators, such as
19 billfishes and sharks [5–7]. Hypoxic conditions may prevent these species from foraging in
20 the mesopelagic zone (from 200 to 1000 m depth), both as a direct consequence of unmet
21 oxygen requirements at depth [8] and indirectly through changes in prey distribution [9].
22 However, tracking methods provide little information on trophic behaviors, and the
23 potential impact of habitat compression caused by OMZs on predator foraging depth has not
24 yet been investigated.

25 The recent development of mercury (Hg) isotope analyses now makes it possible to trace the
26 vertical foraging habitat of pelagic species, thanks to the unique photochemical mass-
27 independent fractionation of Hg isotopes (reported as $\Delta^{199}\text{Hg}$) [10,11]. As fish Hg intake
28 come primarily from dietary methyl-Hg (MeHg), the $\Delta^{199}\text{Hg}$ gradient with light attenuation
29 along the water column leads to lower $\Delta^{199}\text{Hg}$ values in deeper feeding predators [11,12].
30 The $\Delta^{200}\text{Hg}$ signature, related to upper atmospheric Hg photochemistry but not to aqueous
31 marine photochemistry, provides information on atmospheric Hg deposition pathways and
32 terrestrial Hg supply to coastal food webs [13]. As $\Delta^{200}\text{Hg}$ values usually vary between
33 coastal and offshore habitats, the $\Delta^{200}\text{Hg}$ signature provides an additional proxy for
34 horizontal foraging habitat [14]. Since Hg turnover is slow in muscle tissues, muscle $\Delta^{199}\text{Hg}$
35 and $\Delta^{200}\text{Hg}$ values reflect predator foraging habitat integrated over several months prior to

36 analysis [15]. Finally, the strong influence of metabolism on $\delta^{202}\text{Hg}$ values in marine
37 predators makes it a tool for evaluating *in vivo* detoxification of MeHg [16,17].

38 The blue shark (*Prionace glauca*) is a widely distributed oceanic predator that forages on epi-
39 and mesopelagic prey and occupies the water column from the surface to depths up to
40 ~1000 m [18,19]. The spatial distribution of blue sharks encompasses hypoxic areas, such as
41 the world's largest and shallowest OMZ located in the northeastern Pacific (NEP) off Mexico,
42 where low oxygen waters can locally rise to ~50 m below the surface [4,20]. As shown in
43 other regions, hypoxic conditions likely limit the depth, frequency and duration of dives
44 performed by blue sharks in the mesopelagic zone of the NEP OMZ [7]. The high mobility of
45 blue sharks implies a non-permanent use of hypoxic waters [7,21] and raises the question of
46 the impact of local OMZs on long-term trophic inputs for these predators.

47 Stable isotopes of carbon and nitrogen are classically used in trophic ecology and suggest
48 that blue sharks collected in the NEP OMZ integrate the chemical signature of their sampling
49 region, reflecting trophic reliance on the OMZ area [22]. However, these tracers poorly
50 describe the vertical habitat of predators [23] and have so far not made it possible to assess
51 whether the feeding depth of blue sharks is altered in OMZ areas. To fill this knowledge gap,
52 we compared Hg isotope signatures in the muscle of blue sharks collected in the NEP OMZ
53 and in normoxic waters of the northeastern Atlantic. Specifically, we sought to assess
54 whether the influence of the OMZ resulted in increased $\Delta^{199}\text{Hg}$ values in blue sharks,
55 suggesting a reduction in their foraging depth.

56 **2. Materials and methods**

57 Blue sharks were caught by longline fisheries operating in the northeastern Pacific and
58 northeastern Atlantic (n = 23 in 2016 and n = 18 in 2008 for Pacific and Atlantic, respectively)
59 (Table 1). The Pacific sampling site is located within the OMZ area off Mexico, while the
60 Atlantic site off France is characterized by normoxic conditions (Figure S1). At landing points
61 (Punta Lobos, Baja California Sur in Mexico and Les Sables-d'Olonne in France), sex and total
62 length (TL) were recorded, and white muscle was sampled from the dorsal region between
63 the first dorsal fin and the snout, using scalpels and scissors cleaned and rinsed with alcohol
64 before and between samples. Tissues were stored frozen into plastic vials and lyophilized
65 prior to Hg isotope analysis according to a previously published protocol [11,16]. A detailed
66 version of the analytical method is provided in the supplementary electronic material.

67 Data were checked for normality (Shapiro-Wilks tests) and variance homogeneity (Bartlett's
68 tests). As these conditions were not met, non-parametric Mann-Whitney U tests were
69 performed to evaluate differences in mercury isotope compositions of blue sharks between
70 regions.

71 We compiled published data from pelagic biota in the northeastern and central Pacific (n =
72 73, Table S2) to assess the depth profile of $\Delta^{199}\text{Hg}$ values, as done elsewhere [11,24,25]. We
73 used the equation of the linear regression line between $\log(\Delta^{199}\text{Hg})$ and the feeding depth of
74 pelagic species provided by previous studies [10,12,26,27], to estimate the foraging depth of
75 blue sharks in an OMZ area (northeastern Pacific) and in normoxic waters (northeastern
76 Atlantic). This approach is subject to the difficulty of assigning a precise feeding depth for
77 pelagic species that may cover large vertical distances, occupy different depths between day
78 and night, and show inter-individual variability in vertical habitat use.

79 3. Results and discussion

80 A decrease in $\delta^{202}\text{Hg}$ values with depth was previously found in pelagic teleost fishes from
81 the central and northeastern Pacific (NEP) [10,12], allowing the potential use of the $\delta^{202}\text{Hg}$
82 tracer to assess vertical habitat in these species. However, *in vivo* hepatic demethylation of
83 mercury (Hg) has been shown to significantly alter the $\delta^{202}\text{Hg}$ signature in sharks [11,16],
84 thus complicating its use as an ecological tracer. Discrepancies in $\delta^{202}\text{Hg}$ values between
85 sympatric shark species are believed to reflect differences in MeHg metabolism, with higher
86 $\delta^{202}\text{Hg}$ values in sharks showing higher demethylation [16]. In our study, Pacific and Atlantic
87 blue sharks displayed similar $\delta^{202}\text{Hg}$ values (Figure 1A), likely reflecting homogeneity in Hg
88 metabolism at the species level.

89 The $\Delta^{200}\text{Hg}$ signature represents a conservative tracer for atmospheric Hg deposition
90 pathways to the marine environment, which are known to vary between habitats [14,28].
91 Offshore environments show equal contributions of gaseous Hg(0) uptake and inorganic
92 Hg(II) deposition, resulting in $\Delta^{200}\text{Hg}$ values in pelagic biota around 0.05 ‰ [13,26]. In
93 contrast, the $\Delta^{200}\text{Hg}$ signature of coastal food webs is more influenced by the Hg(0) end-
94 member via terrestrial runoff, and is generally characterized by lower, negative $\Delta^{200}\text{Hg}$
95 values close to - 0.05 ‰ [29,30]. In blue sharks from the NEP and northeastern Atlantic, we
96 found positive $\Delta^{200}\text{Hg}$ values of 0.04 ± 0.05 and 0.06 ± 0.03 ‰ respectively (Table 1), thus
97 reflecting reliance on offshore pelagic resources. Variations in $\Delta^{200}\text{Hg}$ were previously
98 observed among distinct populations of white sharks (*Carcharodon carcharias*), likely driven
99 by differences in the use of coastal versus offshore habitats [14]. Here, similar $\Delta^{200}\text{Hg}$ values
100 in Pacific and Atlantic blue sharks (Figure 1B) demonstrate consistency in horizontal foraging
101 habitat across regions.

102 In contrast to the $\Delta^{200}\text{Hg}$ and $\delta^{202}\text{Hg}$ signatures, $\Delta^{199}\text{Hg}$ values in blue sharks varied
103 significantly between regions (Figure 1C), ranging from 1.27 ± 0.06 ‰ in the northeastern
104 Atlantic to 1.59 ± 0.10 ‰ in the NEP (Table 1). In pelagic biota, photodegradation of MeHg in
105 the water column is known to be the only process driving $\Delta^{199}\text{Hg}$ values, which are not
106 altered by trophic transfers and metabolism [12,15,31]. In agreement with many previous
107 studies using the $\Delta^{199}\text{Hg}$ signature as a proxy for feeding depth [10,32,33], lower $\Delta^{199}\text{Hg}$
108 values for NEP blue sharks thus suggest shallower foraging in the OMZ area than in normoxic
109 Atlantic waters (Figure 1C).

110 Given the lack of Hg isotope data in pelagic biota from the northeastern Atlantic, we used a
111 depth profile of $\Delta^{199}\text{Hg}$ values in pelagic species from the central and northeastern Pacific, to
112 provide an estimate of absolute foraging depth for blue sharks. According to the species-
113 specific regression, a $\Delta^{199}\text{Hg}$ shift of 0.3 ‰ between regions would correspond to a reduction
114 in average feeding depth of approximately 200 m for sharks collected in the OMZ area
115 compared to normoxic conditions, with estimated foraging depth decreasing from ~650 to
116 ~450 m depth (Figure 2). Although these estimations match mesopelagic layers in both
117 regions, hypoxic waters are known to reduce i) the time spent at depth, ii) the number of
118 deep dives, and iii) the maximum dive depth for blue sharks [7]. Thus, foraging in the OMZ
119 area may reduce trophic interactions with species from the deeper layers of the mesopelagic
120 zone. Alternatively, some prey species could see their distribution limited to surface waters
121 by the OMZ [9], leading to greater feeding opportunities for pelagic predators in the upper
122 layers and thus increasing the contribution of epipelagic prey to the diet of blue sharks. No
123 previous evidence of the influence of OMZs on the proportion of epi- versus mesopelagic
124 prey in the diet of blue sharks was provided by stomach contents, with mesopelagic
125 cephalopods found as the most abundant prey for blue sharks in both the NEP OMZ and the

126 northeastern Atlantic [19,34], highlighting the capability of the $\Delta^{199}\text{Hg}$ tracer to reveal cryptic
127 changes in foraging depth.

128 Our two-site approach did not allow the impact of dissolved oxygen to be disentangled from
129 that of other confounding environmental parameters such as temperature, which is also
130 known to influence the vertical distribution of blue sharks, with deeper dives generally
131 associated with warmer waters [35,36]. Moreover, although $\Delta^{199}\text{Hg}$ values are primarily
132 driven by photochemical degradation in the water column, Hg isotope analyses in pelagic
133 biota from the northeastern Atlantic region would verify the foraging depth estimate for
134 blue sharks in this ocean basin. Then, diving depth is known to increase during ontogeny in
135 various shark species [37,38], which would result in a decrease in $\Delta^{199}\text{Hg}$ values with size. In
136 our study, since no correlation was found between $\Delta^{199}\text{Hg}$ values and total length (Figure
137 S2), and the size of NEP blue sharks encompassed that of Atlantic individuals, lower values in
138 the latter are unlikely to be related to different life history stages. Finally, climatic events
139 such as El Niño Southern Oscillations (ENSO) are known to influence oxycline (i.e., upper
140 boundary of the OMZ) depth and consequently $\Delta^{199}\text{Hg}$ values in marine predators [39]. Blue
141 sharks from the NEP OMZ were collected in 2016, under strong El Niño conditions with
142 deeper oxycline [40]. Normal ENSO conditions therefore imply a shallower OMZ that would
143 lead to reduced vertical habitat for pelagic predators and increased $\Delta^{199}\text{Hg}$ values in blue
144 sharks, further strengthening the hypothesis put forward in our study.

145 This contribution illustrates the $\Delta^{199}\text{Hg}$ signature as a major asset for assessing feeding depth
146 in pelagic predators. As suggested by previous tracking studies, $\Delta^{199}\text{Hg}$ values support the
147 hypothesis of a reduced foraging depth for blue sharks in OMZ areas. The global climate-
148 driven expansion of OMZs could therefore have major implications for trophic fluxes

149 between surface-oriented predators and mesopelagic compartments [41], and also increase
150 the vulnerability of oceanic sharks to epipelagic fisheries [6,7]. Our study calls for a larger
151 scale investigation allowing to decipher the role of various biotic (e.g., mesopelagic prey
152 distribution and abundance) and abiotic factors (e.g., dissolved oxygen and temperature)
153 governing spatial variations in vertical foraging habitat of pelagic predator.

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Graphical abstract

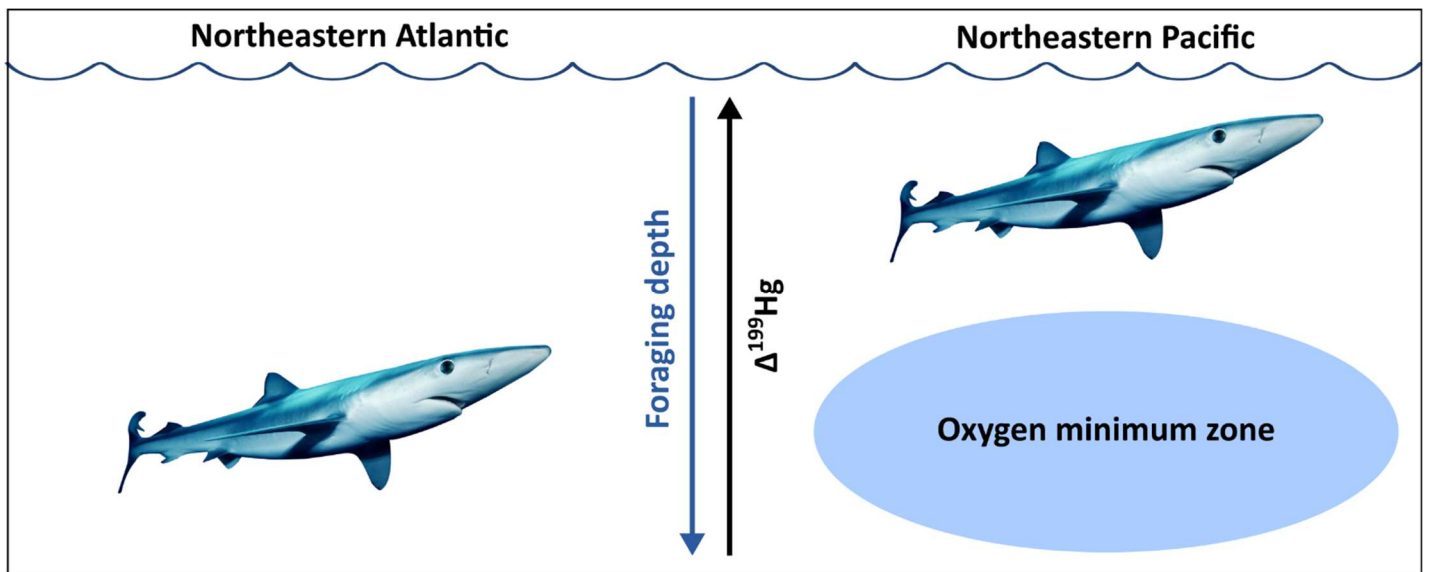


Table 1: Data summary (mean \pm SD) for blue sharks collected in the Northeastern Pacific OMZ and in normoxic waters of the Northeastern Atlantic.

Location	Oxygen conditions	Total Length (m)	n	$\delta^{202}\text{Hg}$ (‰)	$\Delta^{199}\text{Hg}$ (‰)	$\Delta^{200}\text{Hg}$ (‰)
Northeastern Pacific	OMZ	1.50 \pm 0.64	23	0.49 \pm 0.22	1.59 \pm 0.10	0.04 \pm 0.05
Northeastern Atlantic	Normoxia	1.81 \pm 0.26	18	0.58 \pm 0.16	1.27 \pm 0.06	0.06 \pm 0.03

Figure 1: Boxplots of Hg isotopic compositions in the muscle of blue sharks from the northeastern Atlantic (normoxia, in dark blue) and northeastern Pacific (OMZ, in light blue). The box length represents the interquartile range, the bar length represents the range, and the horizontal line is the median value and dots are outliers. Significant difference in $\Delta^{199}\text{Hg}$ values between regions is indicated by *** ($p < 0.001$).

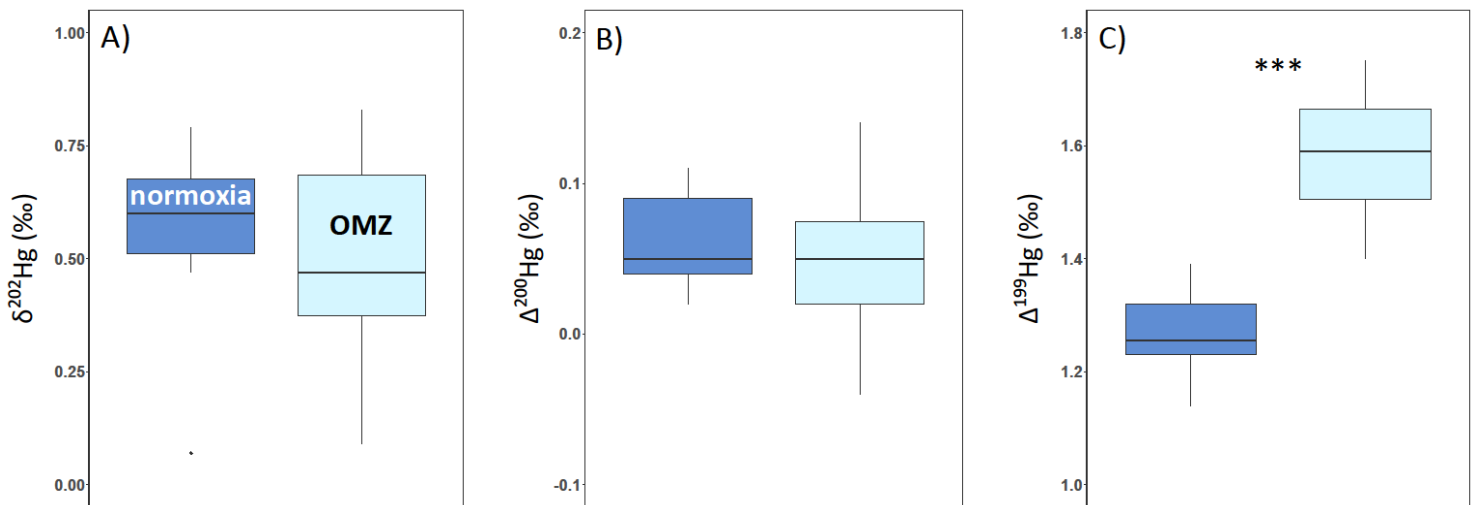


Figure 2: Linear correlation ($R^2 = 0.67$, $p < 0.001$) between $\log(\Delta^{199}\text{Hg})$ values and feeding depth in pelagic species from the northeastern and central Pacific analyzed in previous studies (white dots) [10,12,26,27]. Based on this relationship, mean foraging depth was estimated for blue sharks (colored dots) in the northeastern Pacific (OMZ) and northeastern Atlantic (normoxia).

