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## **Trophic resources and mercury exposure of two silvertip shark populations in the Northeast Pacific Ocean**

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## ABSTRACT

1 Worldwide shark populations have experienced rapid declines over the last decades, mainly  
2 due to overfishing. Marine protected areas (MPAs) have thus become an indispensable tool  
3 for the protection of these marine predators. Two recently-created MPAs in the Northeast  
4 Pacific Ocean, the Revillagigedo National Park and Clipperton atoll, are characterized by  
5 different trophic structures potentially influencing trophic niche and contaminant exposure  
6 for resident sharks in these two sites. In this context, we used carbon ( $\delta^{13}\text{C}$ ) and nitrogen  
7 ( $\delta^{15}\text{N}$ ) stable isotope analyzes as well as total mercury concentrations ([THg]) to assess the  
8 role of foraging site on the trophic niche and Hg levels of juvenile ST sharks *Carcharhinus*  
9 *albimarginatus*. Analyzing fin clip samples from both Revillagigedo and Clipperton, we found  
10 that shark  $\delta^{15}\text{N}$  varied spatially in relation to  $\delta^{15}\text{N}$  baselines, suggesting similar trophic  
11 position in both MPAs. Moreover,  $\delta^{13}\text{C}$  values indicated that ST sharks from Revillagigedo  
12 would feed on different food webs (*i.e.* both benthic and pelagic) while individuals from  
13 Clipperton would only rely on benthic food webs. These differences between MPAs led to a  
14 weak overlap of isotopic niche between the two populations, highlighting site residency for  
15 juvenile ST sharks. Within populations, [THg] was not correlated to trophic tracers ( $\delta^{15}\text{N}$  and  
16  $\delta^{13}\text{C}$ ) and was also similar between populations. This study revealed no influence of site or  
17 food web in [THg] and raises the question of the origin of Hg exposure for reef shark  
18 populations in the Northeast Pacific Ocean.

19

## 20 INTRODUCTION

21 Remote oceanic islands are generally characterized by large biodiversity and abundance of  
22 marine species, including sharks that can be found in high density (Ferretti et al., 2018;  
23 Fourrière et al., 2019; Mourier et al., 2016). In the eastern tropical Pacific (ETP), the  
24 Revillagigedo Archipelago and Clipperton Atoll (Figure 1) are home to diverse marine  
25 species, some of which are endemic (Fourrière et al., 2016; Friedlander et al., 2019). For  
26 instance, Revillagigedo is considered a hot spot for the observation of oceanic manta rays  
27 *Manta birostris* (Stewart et al., 2016a, 2016b) and Clipperton is supposed to be an important  
28 stepping stone for dispersal of marine organisms in the eastern Pacific (Friedlander et al.,  
29 2019; Ketchum and Reyes Bonilla, 2001; Romero-Torres et al., 2018). In order to protect  
30 these unique ecosystems from anthropogenic pressures such as industrial fishing, a no-take  
31 marine reserve of 12 nautical miles around Clipperton was created in 2016 while  
32 Revillagigedo was added to UNESCO world heritage sites (UNESCO, 2016) and became North  
33 America's largest marine reserve in 2017, at nearly 150,000 square kilometers (MPAtlas,  
34 2017). The two marine protected areas (MPAs) are located off the coast of Mexico (644 km  
35 for Revillagigedo and 1,280 km for Clipperton) and present different site characteristics.  
36 While the Revillagigedo Archipelago is composed of four volcanic islands (Socorro, Clarion,  
37 San Benedicto and Roca Partida), which can be up to 400 km apart, Clipperton is constituted  
38 of a single atoll enclosing a lagoon without connection with the ocean. Recently, trophic  
39 structure and composition of reef fish assemblages from Revillagigedo and Clipperton MPAs  
40 have been evaluated (Fourrière et al., 2019). Despite ecological redundancy, differences  
41 were found between communities such as higher trophic level variability in Revillagigedo  
42 and the presence of endemic species in Clipperton. These ecosystem features may imply

43 different trophic inputs for predators inhabiting both areas which may forage on different  
44 prey.

45 The silvertip (ST) shark *Carcharhinus albimarginatus* is one of the most abundant predator  
46 species found in both MPAs in the ETP (Allen and Robertson, 1997; Lara-Lizardi, 2018). This is  
47 a large slow-growing shark, from 0.63-0.68 m in total length (TL) at birth to a maximum body  
48 size of 3 m TL. Males mature between 1.6-1.8 m TL and females between 1.6-2.0 m TL  
49 (Compagno et al., 2005). This species is widely distributed throughout the tropical Indian and  
50 Pacific Oceans, but showing a patchy distribution and population fragmentation due to  
51 minimal dispersion (Ebert et al., 2018). ST sharks inhabit continental or insular shelves and  
52 recent studies have shown small-scale movements between multiple coral reefs within the  
53 same area (Bond et al., 2015; Carlisle et al., 2019; Espinoza et al., 2015). This reef-associated  
54 behavior potentially prevents them from being caught as commercial tuna fisheries bycatch,  
55 but this species can be targeted in subsistence and artisanal fisheries (White, 2007).  
56 Consequently, Silvertip shark population in the remote Chagos archipelago (Indian Ocean)  
57 has been estimated to be only at 7% of its baseline level, mostly due to illegal fishing  
58 (Ferretti et al., 2018). Despite limited excursions outside the large Chagos MPA (Carlisle et  
59 al., 2019), ST sharks were characterized by feeding on both pelagic and reef sources (Curnick  
60 et al., 2019).

61 Stable isotope analyzes have been extensively used to track the foraging habitat of sharks  
62 species (Bird et al., 2018; Carlisle et al., 2012; Young et al., 2015). Stable isotopes of nitrogen  
63 ( $\delta^{15}\text{N}$ ) are known to vary spatially according to varying nitrogen sources at the base of  
64 marine food webs (Michener and Lajtha, 2008; Olson et al., 2010). Moreover, as  $\delta^{15}\text{N}$   
65 increases predictably between prey and consumers, this tracer has been commonly used as

66 a proxy of relative or absolute (i.e. taking into account ecosystem isotopic baselines) trophic  
67 position (Cherel et al., 2008; Hussey et al., 2015; Lorrain et al., 2015). On the other hand,  
68 primary producers display characteristic carbon isotope signatures ( $\delta^{13}\text{C}$ ), due to the  
69 different carbon sources and / or metabolic pathways used during photosynthesis (Fry and  
70 Sherr, 1989). Thus,  $\delta^{13}\text{C}$  allows to discriminate marine food webs based on different primary  
71 producers and thereby to characterize the feeding habitat of consumers (Le Croizier et al.,  
72 2019; McMahon et al., 2016). Overall, the combination of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  constitutes a  
73 relevant proxy of the trophic niche, allowing the evaluation of the feeding overlap between  
74 predator populations or species (Giménez et al., 2017; Trystram et al., 2016).

75 Diet is considered as the main exposure pathway to mercury (Hg) for marine organisms  
76 (Wang and Wong, 2003). This global pollutant, present as a gaseous element in the  
77 atmosphere, can be deposited far from emission sources. Combined with the aquatic  
78 transport of Hg by rivers and ocean currents, this can lead to the Hg exposure of remote  
79 areas without nearby anthropogenic influence (Driscoll et al., 2013). In marine ecosystems,  
80 Hg can be converted by microorganisms into organic monomethylmercury (MMHg) (Gilmour  
81 et al., 2013; Podar et al., 2015) before being assimilated by phytoplankton and transferred  
82 along trophic webs. The bioaccumulation (*i.e.* increase in contaminant over time) and  
83 biomagnification (*i.e.* increase in contaminant with trophic position) properties of MMHg  
84 generally lead to high levels of this potent neurotoxin in top-predators (Le Bourg et al., 2019;  
85 McKinney et al., 2016). MMHg basal concentrations can vary between marine habitats due  
86 to several biotic and abiotic factors such as deposition rate of atmospheric Hg (Gworek et al.,  
87 2016), variations in methylation and demethylation rates (Munson et al., 2018), ecosystem  
88 productivity (Chouvelon et al., 2018) as well as density and composition of phytoplankton  
89 communities (Chen and Folt, 2005; Heimbürger et al., 2010). Thereby, in addition to the

90 influence of trophic level, MMHg exposure in marine consumers is closely linked to their  
91 foraging habitat (Le Bourg et al., 2019; Le Croizier et al., 2019).

92 Various types of shark tissues have been used for ecological tracers analyzes, providing  
93 different time integration according to tissue turnover rate, from few months (plasma and  
94 liver) to approximately one year (muscle) (Sora Lee Kim et al., 2012; Malpica-Cruz et al.,  
95 2012). Generally sampled for genetic analyzes, fin clips have recently been employed in  
96 stable isotope and fatty acid analyses in sharks (Every et al., 2016; Rangel et al., 2019),  
97 revealing feeding habits and habitat use over long periods of time (*i.e.* more than a year)  
98 (Malpica-Cruz et al., 2012). Similarly, Hg concentrations in fins were strongly correlated to  
99 Hg levels in other tissues such as liver and muscle, thus representing a minimally invasive  
100 method for estimating Hg contamination (O'Bryhim et al., 2017).

101 In the present study, we analyzed carbon and nitrogen stable isotopes together with total Hg  
102 concentrations ([THg]) in fin clips of ST sharks from the Revillagigedo Archipelago and  
103 Clipperton atoll, where to date there is no data on Hg levels in both benthic and pelagic  
104 marine organisms. The objectives of this study were to evaluate the influence of site-specific  
105 trophic structure and habitat features on the feeding niche and Hg concentrations of  
106 resident top predators in these oceanic MPAs. Specifically, we sought to determine whether  
107 the higher trophic level diversity previously found in the fish assemblage at Revillagigedo  
108 resulted in greater variability in trophic levels and Hg concentrations in ST sharks than those  
109 present at Clipperton. Silvertips being one of the most abundant shark species in these  
110 remote reef ecosystems.

111

## 112 **MATERIALS AND METHODS**

113           **Sampling**

114 Juvenile ST sharks were captured in the Revillagigedo Archipelago (from 2006 to 2016, n=26)  
115 and Clipperton Atoll (2017, n=28) using hook and line (Figure 1). Biometric data (e.g. total  
116 length [TL], sex) was recorded and a fin clip sample was taken from the free rear tip of the  
117 second dorsal fin for each individual. All sharks were immature (Compagno et al., 2005),  
118 ranging from 0.69 to 1.52 m TL in Revillagigedo and from 0.7 to 0.97 m TL in Clipperton,  
119 which corresponds to young-of-the-year to 5-year-old sharks (Smart et al., 2017). Tissue  
120 samples were immediately transferred to a -20 °C freezer onboard the boat. Once at the  
121 laboratory, entire (i.e. including skin, subdermal tissue and cartilage) fin clip samples (~1 cm)  
122 were lyophilized and homogenized.

123           **Total Hg concentration**

124 As total Hg (THg) is strongly correlated with monomethylmercury (MMHg) in fish tissues  
125 including shark fins (Nalluri et al., 2014), THg was used as a proxy of MMHg concentrations in  
126 silvertip shark tissues. THg determination was carried out on an aliquot (around 10 mg) of  
127 sample powder by combustion, amalgamation and atomic absorption spectrophotometry  
128 detection using a DMA80 analyzer (Milestone, USA). Total mercury concentrations ([THg]) in  
129 samples are expressed on a wet weight basis ( $\text{ng}\cdot\text{g}^{-1}$  ww) by applying a correction factor of  
130 0.25 to the dry weight (dw) values, based on previous information on shark fins (Clarke,  
131 2004). The accuracy and reproducibility of the method were established using a freeze-dried  
132 certified biological material (lobster hepatopancreas; TORT 3, NRCC). The certified values for  
133 TORT 3 ( $0.292 \pm 0.022 \mu\text{g}\cdot\text{g}^{-1}$  dw) were reproduced (measured value:  $0.286 \pm 0.024 \mu\text{g}\cdot\text{g}^{-1}$   
134 dw) within the confidence limits. The detection limit was  $0.005 \mu\text{g}\cdot\text{g}^{-1}$  dw.

135           **C and N isotopes**

136 Before isotope analyzes, urea and lipid extractions were applied on powdered samples  
137 according to (Li et al., 2016). Briefly, for urea removal, each sample was vortexed in  
138 deionized water for 1 min and soaked for 24 h at room temperature. Each sample was then  
139 centrifuged for 5 min and the water removed with a medical syringe. This process was  
140 repeated three times before the samples were dried again using a Genevac centrifugal  
141 evaporator. For lipid extraction, each urea-free sample was soaked in a 2:1  
142 chloroform/methanol mixture, vortexed for 1 min, left overnight at room temperature,  
143 centrifuged for 10 min and decanted. This process was also repeated three times and the  
144 samples re-dried to eliminate excess solvent.

145 Approximately 350 µg of sample powder was then weighed in tin capsules for isotopic  
146 analysis. The samples were analyzed by continuous flow on a Thermo Scientific Flash EA  
147 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer at the Pôle  
148 Spectrométrie Océan (Plouzané, France). Results are expressed in standard  $\delta$  notation based  
149 on international standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  
150  $\delta^{15}\text{N}$ ) following the equation  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$  (in ‰), where R  
151 is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . International isotopic standards of known  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were analyzed:  
152 IAEA-600 Caffeine, IAEA-CH-6 Sucrose, IAEA-N-1 and IAEA-N-2 Ammonium Sulphate. A home  
153 standard (Thermo Acetanilide) was used for experimental precision (based on the standard  
154 deviation of the replicates of the internal standard) and indicated an analytical precision of  $\pm$   
155 0.11‰ for  $\delta^{13}\text{C}$  and  $\pm$  0.07‰ for  $\delta^{15}\text{N}$ . C:N ratios were comprised between 2.8 and 3 (Table  
156 1), in accordance with previous results obtained on various shark species following urea and  
157 lipid extraction (Li et al., 2016).

158 **Data treatment**

159  $\delta^{15}\text{N}$  baselines for the Revillagigedo Archipelago and Clipperton Atoll (i.e. 10.5‰ and 9‰,  
160 respectively) were obtained using estimated  $\delta^{15}\text{N}$  values of omnivorous copepods in the area  
161 (Olson et al., 2010). Discrimination factor (i.e.  $\Delta^{15}\text{N}$ : difference in  $\delta^{15}\text{N}$  between a consumer  
162 and its prey) is variable between shark species (e.g. from 2.1 to 4.0‰ in muscle) (Hoen et al.,  
163 2014) and is unknown for fin tissue. We thus calculated for each site the isotopic distance  
164 between ST sharks and the copepod-baseline ( $\Delta^{15}\text{N}_{\text{ST-COP}} = \delta^{15}\text{N}_{\text{ST}} - \delta^{15}\text{N}_{\text{COP}}$ ) rather than their  
165 absolute trophic position. This baseline-to-predator difference is considered as a proxy of  
166 the predator trophic position. For site comparisons, data was first checked for normality  
167 (Shapiro–Wilks test) and homogeneity of variances (Bartlett’s test). When these conditions  
168 were met, one-way ANOVAs were performed to test for differences between sites.  
169 Otherwise, non-parametric analogues were used, i.e. Kruskal–Wallis tests (KW). Depending  
170 on data distribution (Shapiro–Wilks test), Pearson or Spearman correlation tests were  
171 applied to investigate the correlation between variables (total length, THg,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ).

172 Standard ellipse areas encompassing 95% of the data ( $\text{SEA}_B$ , Bayesian SEA) were performed  
173 using the package “SIBER” based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , to quantify the niche width and overlap  
174 between the two sites (Jackson et al., 2011). The  $\text{SEA}_B$  constitutes a proxy of the feeding  
175 niche occupied by sharks in one site while the overlap between  $\text{SEA}_B$  quantifies the trophic  
176 overlap between shark populations. The  $\text{SEA}_B$  overlap is expressed as a proportion of the  
177 non-overlapping area of the two ellipses.

178 Layman’s metrics (Layman et al., 2007) were calculated to compare isotopic niche between  
179 sites using the package “SIAR” (Parnell et al., 2010). The mean distance to centroid (CD)  
180 describes the average degree of trophic diversity, considering the trophic-level diversity  
181 ( $\delta^{15}\text{N}$  range) and the organic matter source diversity ( $\delta^{13}\text{C}$  range) diversities. The nearest

182 neighbour distance (NND) measures the mean trophic similarity between individuals and the  
183 total area (TA) represents the niche space encompassing all individuals in the population.

184 With THg,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, the “nicheROVER” package was used for defining niche  
185 region (NR) and niche overlap (NO) between sharks from the two sites (Swanson et al.,  
186 2015). NR was defined as the 95% probability region in multivariate space, while NO is  
187 calculated as the probability that an individual from site 1 is found in the NR of site 2.  
188 Overlap uncertainty was accounted for by performing 1000 elliptical projections of NR  
189 through Bayesian statistics.

190 All statistical analyses were performed using the open source software R (version 3.6.1, R  
191 Core Team, 2019).

192

## 193 **RESULTS**

### 194 **Site comparison**

195 We found that absolute  $\delta^{15}\text{N}$  was higher ( $p < 0.001$ ) in ST sharks from Revillagigedo ( $\delta^{15}\text{N} =$   
196  $15.40 \pm 0.57\text{‰}$ ) compared to Clipperton ( $\delta^{15}\text{N} = 13.92 \pm 0.36\text{‰}$ ) (Table 1, Figure 2A), but  
197 isotopic distance of sharks compared to the copepod-baseline ( $\Delta^{15}\text{N}_{\text{ST-COP}}$ ) was similar  
198 between sites ( $p > 0.05$ ) (Table 1). Conversely,  $\delta^{13}\text{C}$  was significantly higher ( $p < 0.001$ ) in ST  
199 sharks from Clipperton ( $\delta^{13}\text{C} = -14.02 \pm 0.44\text{‰}$ ) compared to Revillagigedo ( $\delta^{13}\text{C} = -14.69 \pm$   
200  $0.47\text{‰}$ ) (Table 1, Figure 2B). Mercury concentrations did not vary spatially, since THg was  
201 similar ( $p > 0.05$ ) in ST sharks from Clipperton (THg =  $63 \pm 48 \mu\text{g}\cdot\text{g}^{-1}$  ww) and Revillagigedo  
202 (THg =  $56 \pm 32 \mu\text{g}\cdot\text{g}^{-1}$  ww) (Table 1, Figure 2C).

### 203 **Correlations between variables**

204 Regarding associations between tracers, nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) stable isotopes  
205 were negatively correlated in Revillagigedo ( $R^2 = 0.45$ ;  $p < 0.001$ ) while no correlation was  
206 found between these variables in Clipperton ( $p > 0.05$ ) (Figure 3). Although total length was  
207 higher in Revillagigedo than in Clipperton ( $p < 0.01$ ) (Table 1), no influence of shark size was  
208 detected on the different tracers since  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and THg were not correlated to total  
209 length in either site ( $p > 0.05$ ). Isotopic tracers did not explain Hg concentrations since THg  
210 was not correlated with  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  for any of the shark populations.

### 211 **Isotopic niches**

212 Both shark populations (Revillagigedo, Clipperton) displayed similar  $\delta^{13}\text{C}$  range of 1.80 ‰  
213 (Table 2) but sharks in Revillagigedo had higher  $\delta^{15}\text{N}$  range than in Clipperton (i.e. 2.80 and  
214 1.40 ‰, respectively). This difference in  $\delta^{15}\text{N}$  variation led to a wider isotopic niche area for  
215 sharks of Revillagigedo compared to Clipperton, revealed by both total area (TA = 2.34 ‰<sup>2</sup> in  
216 Revillagigedo versus 1.55 ‰<sup>2</sup> in Clipperton) and standard ellipse area (SEA<sub>B</sub> with 95%  
217 credible interval = 3.92 ‰<sup>2</sup> versus 2.66 ‰<sup>2</sup>) (Table 2 and Figure 4). Although  $\delta^{15}\text{N}$  range is  
218 strongly influenced by extreme  $\delta^{15}\text{N}$  values (Figure 2A), the mean distance to centroid (CD)  
219 and nearest neighbour distance (NND) were also higher in Revillagigedo revealing a larger  
220 trophic diversity at the population scale (Table 2).

221 Using  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, the isotopic niche overlap was low between populations (i.e.  
222 11%; Figure 4). Combining stable isotopes and THg, the mean probability for a Revillagigedo  
223 shark to be found in the Clipperton niche was 23%, while the mean probability for a  
224 Clipperton shark to be found in the Revillagigedo niche was 10% (Figure 5).

225

## 226 **DISCUSSION**

### 227 **Habitat isotopic features**

228 In the Northeast Pacific,  $\delta^{15}\text{N}$  is known to vary spatially with latitude in various marine taxa  
229 such as mussels (Vokhshoori and McCarthy, 2014), copepods (López-Ibarra et al., 2018;  
230 Olson et al., 2010) and tunas (Olson et al., 2010). In the present study, the shift in  $\delta^{15}\text{N}$   
231 between copepod-baseline and ST sharks was similar in Revillagigedo and Clipperton (i.e.  
232 around 4.9 ‰; Table 1), suggesting similar trophic position in both sites. This indicates that  
233 the difference in  $\delta^{15}\text{N}$  between the two shark populations (Figure 2A) is mostly explained by  
234 variations in isotopic composition at the base of the food webs, such as previously observed  
235 for tunas in this area (Lorrain et al., 2015; Olson et al., 2010). This result is in total agreement  
236 with a recent assessment of the reef fish structures from the two MPAs, revealing a similar  
237 community mean trophic level between the two sites (Fourrière et al., 2019). The difference  
238 in  $\delta^{15}\text{N}$  baselines between sites is thought to be influenced by the south-to-north increase of  
239  $\delta^{15}\text{N}$  values in the dissolved nitrate pool (Olson et al., 2010). This spatial trend of  $\delta^{15}\text{N}$  is  
240 probably due to the combination of phytoplankton drawdown of upwelled nitrate at the  
241 equator and the denitrification occurring in the oxygen minimum layer further north in the  
242 ETP (Fiedler and Talley, 2006).

243 In contrast to  $\delta^{15}\text{N}$ , previous studies on copepods (López-Ibarra et al., 2018; Olson et al.,  
244 2010), yellowfin tunas (Olson et al., 2010) or ocean models (Magozzi et al., 2017) have found  
245 limited  $\delta^{13}\text{C}$  variation with latitude in this area, suggesting that  $\delta^{13}\text{C}$  oceanic baselines are  
246 homogenous in the surface waters surrounding the islands studied here. The difference in  
247  $\delta^{13}\text{C}$  values between silvertips from the two sites (Figure 2B) may thus reflect local island  
248 production rather than a latitudinal oceanic gradient. Coral reefs are present at both sites

249 but with some differences in species composition and richness (Fourri re et al., 2019; Glynn  
250 et al., 1996). Indeed, 17 different coral species are found in the Revillagigedo Archipelago  
251 against only 8 species at Clipperton Island (Reyes-Bonilla, 2003). Coral reef food webs are  
252 supported by various primary producers such as phytoplankton, macroalgae and coral  
253 (McMahon et al., 2016). The different sources of organic matter are characterized by  
254 contrasted isotopic values (e.g.  $\delta^{13}\text{C}$ ) which ultimately influence the isotopic composition of  
255 top-predators (Briand et al., 2016; Trystram et al., 2016). For instance, according to  $\delta^{13}\text{C}$   
256 values, the blackspot snapper (*Lutjanus ehrenbergii*) relied either on a benthic macroalgal  
257 food web or on a phytoplankton-based food web depending on reef sites in the Red Sea  
258 (McMahon et al., 2016). In the present study, ST sharks differed in  $\delta^{13}\text{C}$  values despite  
259 supposed similar trophic position, with sharks from Clipperton showing higher values (Table  
260 1 and Figure 2B). As food webs supported by coral reef display higher  $\delta^{13}\text{C}$  values than  
261 phytoplankton-based food webs (Briand et al., 2016; Kolasinski et al., 2011), this result could  
262 potentially suggest that Clipperton's food web is mostly supported by coral reef, while that  
263 of Revillagigedo might be more influenced by oceanic inputs of organic matter. This  
264 assumption is in agreement with the greater coral cover observed in Clipperton Atoll  
265 compared to the Revillagigedo Archipelago (Fourri re et al., 2019).

### 266 **Trophic ecology of shark populations**

267  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are generally positively correlated as they both increase with trophic position  
268 in sharks species at both the inter (Hussey et al., 2015) and intraspecific level (Kiszka et al.,  
269 2015), including for ST sharks (Endo et al., 2016). In the present study, ST sharks from  
270 Revillagigedo displayed a decrease in  $\delta^{13}\text{C}$  when increasing  $\delta^{15}\text{N}$  values (Figure 3). A similar  
271 trend has been observed for fish and shark communities in the southwest Pacific coral reefs,

272 with species feeding on the pelagic food web having higher  $\delta^{15}\text{N}$  and lower  $\delta^{13}\text{C}$  compared to  
273 species feeding on benthic food webs (Briand et al., 2016; Frisch et al., 2016). Although  
274 confined to coral reefs and generally with limited offshore displacements (e.g. < 18 km)  
275 (Bond et al., 2015), ST sharks are characterized by a mix of reef-associated and pelagic  
276 behaviors which can result in a diet based on both reef and pelagic food webs. For instance,  
277 in the Indian Ocean it has been estimated that ST sharks were feeding on 60% reef prey and  
278 on 40% oceanic prey (Curnick et al., 2019). Moreover, juvenile and adult ST sharks display  
279 inter-island movements within the Revillagigedo MPA, using diverse habitats ranging from  
280 shallow and calm waters at San Benedicto and Socorro islands to near vertical slopes  
281 influenced by oceanic currents at Roca Partida, a small islet where several schools of pelagic  
282 fish gather to mate and feed (Muntaner López, 2016). The direct exposure to open water in  
283 Roca Partida favors the presence of pelagic fish of higher trophic level, compared to the reef  
284 fish communities of the other islands of the Revillagigedo Archipelago (Fourrière et al.,  
285 2019). Overall, these results suggest that the Revillagigedo shark population is feeding on  
286 both pelagic and benthic food webs, probably due to habitat diversity, resulting in lower  $\delta^{13}\text{C}$   
287 and higher  $\delta^{15}\text{N}$  values for sharks feeding on pelagic prey.

288 The  $\delta^{13}\text{C}$  range of the Clipperton population was similar to that of the Revillagigedo  
289 population (Table 2), but the  $\delta^{15}\text{N}$  range was narrower in Clipperton and no correlation was  
290 observed between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values within this population (Figure 3). In coral reefs,  
291 benthic carbon sources can be differentiated by their  $\delta^{13}\text{C}$  values while they show similar  
292  $\delta^{15}\text{N}$  values, all lower than  $\delta^{15}\text{N}$  values from oceanic sources (Briand et al., 2016). The limited  
293  $\delta^{15}\text{N}$  range in the Clipperton population may thus reflect a lesser extent of pelagic sources in  
294 the shark diet, while the  $\delta^{13}\text{C}$  variation may imply the use of different benthic food webs  
295 (e.g. based on macroalgae and coral) (Charpy, 2009). In addition, the isotopic metrics of

296 trophic diversity that are not strongly influenced by extreme data points (i.e. CD and NND)  
297 confirmed that the Clipperton population is characterized by lower trophic diversity (Table  
298 2). Therefore, ST sharks from Clipperton seem to have access to a lower variety of  
299 isotopically different prey. Clipperton MPA is composed of a single atoll probably offering  
300 limited habitat and food web diversity compared to the Revillagigedo Archipelago.  
301 Moreover, despite the similarity of mean trophic level of fish communities in both MPAs,  
302 Clipperton atoll displayed homogeneous fish abundance per trophic level, while this index  
303 was more variable among the different islands of the Revillagigedo Archipelago (Fourrière et  
304 al., 2019). This observation may indicate that Clipperton's sharks are likely to feed on less  
305 diverse trophic levels, confirmed by the narrower  $\delta^{15}\text{N}$  range and total niche area (TA) (Table  
306 2).

### 307 **Mercury exposure of sharks**

308 In the Pacific Ocean, [THg] can display important geographical contrasts, with significant  
309 latitudinal variations in oceanic species such as tunas (Houssard et al., 2019). For instance, a  
310 ~3-fold THg enrichment was measured in the bigeye tuna *Thunnus obesus* between equator  
311 and 20°S, although it was mainly explained by differences in vertical foraging habitat. In our  
312 study, despite almost 10° of latitude (around 1000 km) between the two MPAs, [THg] was  
313 similar between shark populations (Figure 2C). Hg levels in Pacific seawaters are known to  
314 increase with depth below the 100 meter layer (Munson et al., 2015; Sunderland et al.,  
315 2009) as well as in pelagic fish (Choy et al., 2009) in accordance with the production of  
316 methylmercury (MMHg) in deep water (Blum et al., 2013). In the southwest Pacific (Great  
317 Barrier Reef), the mean depth of occurrence for ST sharks was around 25 m throughout the  
318 year (Espinoza et al., 2015). Similar [THg] may thus indicate that both populations feed at

319 comparable depths, probably shallower than 100 m, preventing them from being submitted to  
320 the MMHg increase in deeper waters. However, THg and MMHg in surface waters have also  
321 been shown to vary with latitude in the central Pacific Ocean, according to spatial  
322 differences in methylation and demethylation rates (Munson et al., 2018). Here, the absence  
323 of Hg variation observed in a shallow water species does not allow for concluding on  
324 differences in MMHg production between MPAs. Furthermore, as MMHg biomagnifies along  
325 food webs, the fact that both shark populations are thought to occupy the same trophic  
326 position implies similar MMHg exposure. In addition, Hg levels found in young-of-the-year  
327 (YOY) sharks can be derived from maternal offloading and therefore be influenced by the  
328 maternal trophic position (Lyons et al., 2013). A previous study on ST sharks did not find  
329 evidence of mother-to-embryo transfer of Hg (Endo et al., 2016). Thus, even in the case of  
330 differences in feeding ecology of adult ST sharks between MPAs, this would probably not  
331 have a strong impact on Hg levels in the YOY sharks, due to apparent limited maternal  
332 transfer of Hg in this species. Finally, within the same population, [THg] was not explained by  
333  $\delta^{15}\text{N}$  nor  $\delta^{13}\text{C}$  values, suggesting that feeding on either pelagic or benthic food webs at  
334 Revillagigedo, or on different benthic food webs at Clipperton, does not induce differences  
335 in Hg exposure for sharks. In addition to the absence of large-scale Hg variation (i.e. between  
336 sites), these results seem to indicate homogeneous Hg concentrations in prey and / or  
337 habitats used by ST sharks within each MPA.

### 338 **Site residency of juvenile ST sharks**

339 As isotopic spatial gradients are conserved from the baseline to the top of food webs, they  
340 allow the tracking of movements of marine predators (Graham et al., 2010; Trueman and St  
341 John Glew, 2019). Here, the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  segregation between the two shark populations

342 (Figure 2A and 2B) is thought to reflect the differences in isotopic baselines between MPAs.  
343 In addition, the estimated trophic overlap between populations was low according to C and  
344 N stable isotopes only (i.e. 11%, Figure 4) as well as combining stable isotopes and [THg]  
345 (23% maximum, Figure 5), suggesting limited trophic connectivity between sites for juvenile  
346 ST sharks. In the Great Barrier Reef (Southwest Pacific), ST sharks showed intermediate  
347 residency index, spending ~50% of the time in the study site (Espinoza et al., 2015). Their  
348 movements between reefs of the Great Barrier did not exceed 50 km, and in the Fijian  
349 archipelago a net offshore displacement of only 18 km was recorded (Bond et al., 2015). In  
350 the British Indian Ocean Territory MPA (Indian Ocean), although silvertips sharks had a wider  
351 space use than other species such as grey reef sharks (*Carcharhinus amblyrhynchos*), the  
352 majority of individuals were detected within 30 km of their tagging location and no silvertip  
353 left the MPA (Carlisle et al., 2019). Thus, although movements of more than 100 km have  
354 been recorded between the islands of the Revillagigedo Archipelago (Muntaner López,  
355 2016), biochemical tracers seem to confirm the site-residency of ST sharks. However, many  
356 shark species display ontogenetic changes in movement patterns, performing larger  
357 displacements and exhibiting a broader habitat use once adults (Andrews et al., 2010; Chin  
358 et al., 2013; Grubbs, 2010; Hoyos-Padilla et al., 2014), which can lead to an expansion of  
359 their trophic niche (Dicken et al., 2017; Sora L. Kim et al., 2012). All ST sharks sampled in our  
360 study were juveniles (Compagno et al., 2005), it is therefore possible that the analysis of  
361 adult sharks may lead to a wider degree of overlap between the populations of Revillagigedo  
362 and Clipperton, reflecting a higher dispersion of adult ST sharks. Finally, other shark species  
363 such as the Galapagos shark *Carcharhinus galapagensis* have been recorded to perform long  
364 distance movements between MPAs including Revillagigedo and Clipperton, realizing  
365 migrations exceeding 3000 km (Lara-Lizardi et al., 2020). In comparison with more resident

366 species such as ST sharks, these migratory predators probably provide trophic connectivity  
367 between MPAs in the North Eastern tropical Pacific. This biochemical approach represents a  
368 low-intrusive method complementary to tracking studies and could be used on other shark  
369 species with broad ecological characteristics.

## 370 **CONCLUSION**

371 Carbon and nitrogen stable isotopes revealed that, despite similar trophic position, the two  
372 silvertip shark populations seemed to use different food webs. While the Revillagigedo  
373 population fed on both benthic and pelagic food webs, the Clipperton population relied only  
374 on benthic sources. Hg exposure was not determined by the residence site or the feeding  
375 patterns, suggesting similar Hg concentrations in the different habitats used by ST sharks in  
376 this region. In these remote sites without direct anthropogenic Hg inputs, Hg incorporation  
377 in island food webs may come from the advection of deep oceanic MMHg as well as possible  
378 local MMHg production and/or transformation as previously suggested for coastal fish from  
379 Hawaii (Sackett et al., 2017). In future studies, Hg isotopes could be of great interest to  
380 determine the origin of Hg in these oceanic island ecosystems, since they allow to trace Hg  
381 sources transferred in trophic webs to top-predators (Li et al., 2014; Renedo et al., 2018;  
382 Senn et al., 2010).

383

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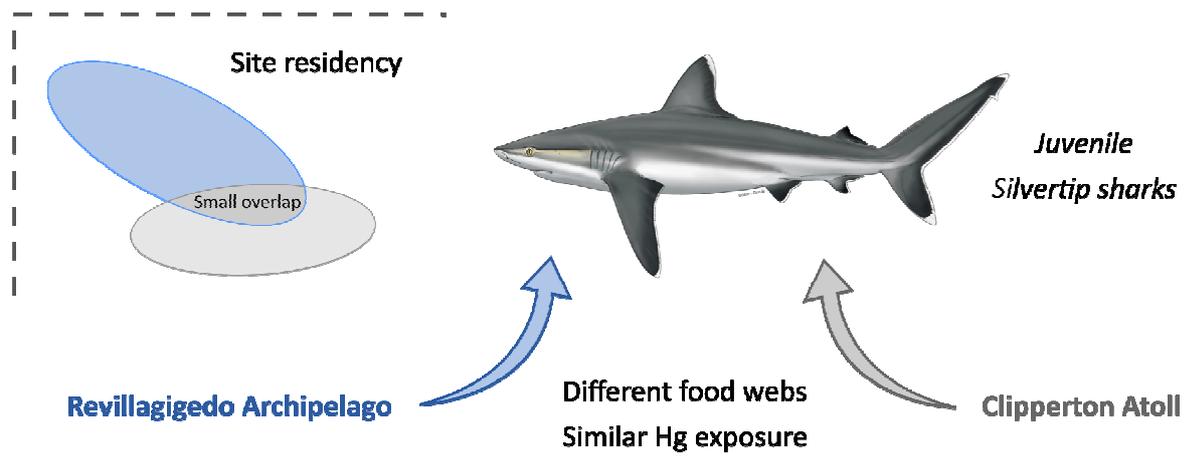
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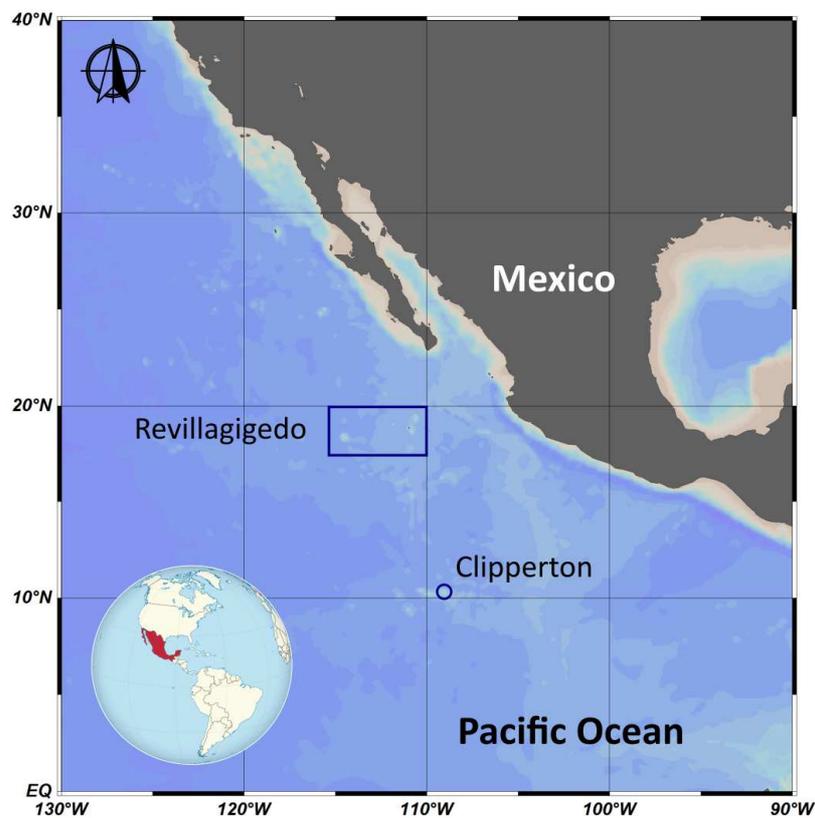
Graphical abstract

Table 1: Summary (mean  $\pm$  standard deviation) of the different variables measured in silvertip sharks from the two sites.  $\Delta^{15}\text{N}_{\text{ST-COP}}$  refers to the relative trophic position of sharks compared to the copepod-baseline in each site. Significant differences between sites are indicated by \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

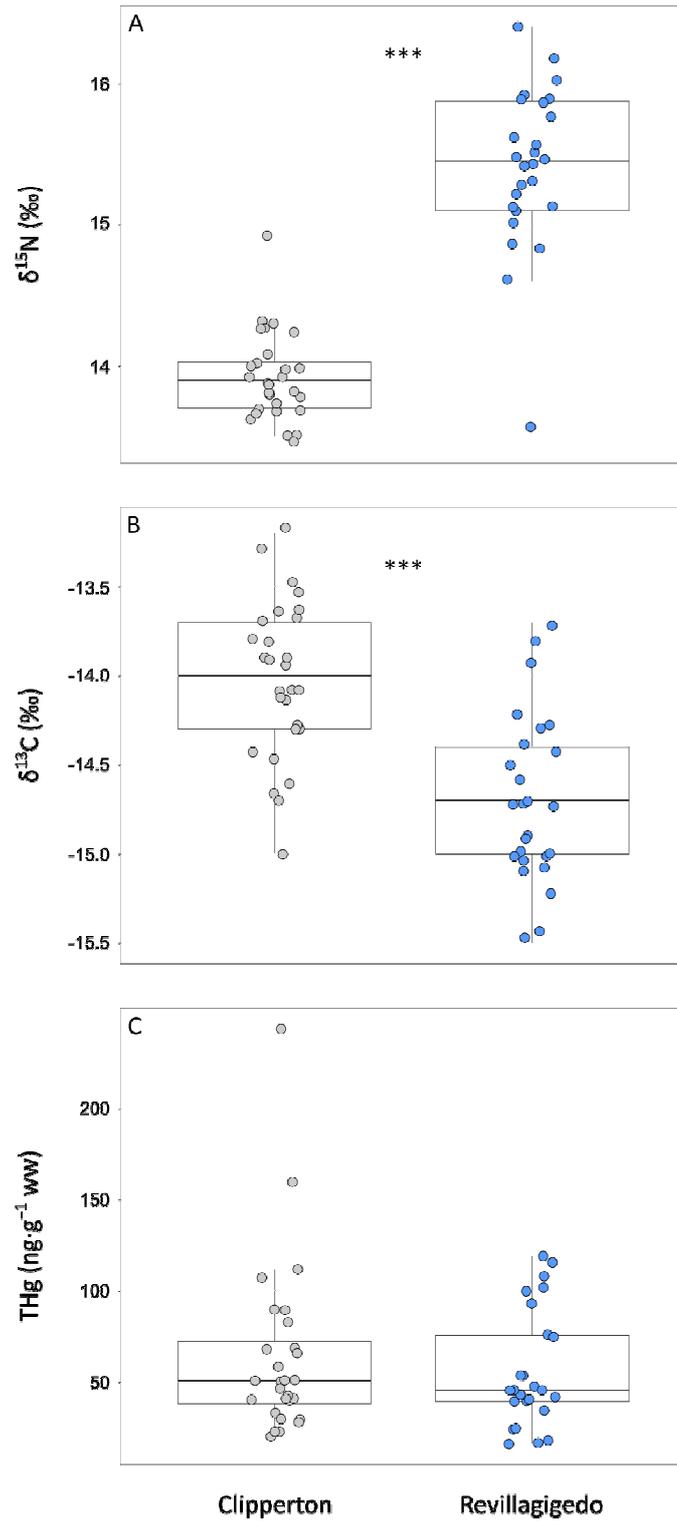
Site	n	Total Length (m)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N	$\Delta^{15}\text{N}_{\text{ST-COP}}$ (‰)	THg ( $\text{ng}\cdot\text{g}^{-1}$ ww)
Revillagigedo	26	1.01 $\pm$ 0.21**	-14.69 $\pm$ 0.47	15.40 $\pm$ 0.57***	2.93 $\pm$ 0.07	4.92 $\pm$ 0.31	56 $\pm$ 32
Clipperton	28	0.83 $\pm$ 0.07	-14.02 $\pm$ 0.44***	13.92 $\pm$ 0.36	2.88 $\pm$ 0.05	4.90 $\pm$ 0.57	63 $\pm$ 48

**Table 2:** Layman's metrics describing the isotopic niche of silvertip sharks in each site: nitrogen stable isotope range ( $\delta^{15}\text{N}$  range), carbon stable isotope range ( $\delta^{13}\text{C}$  range), total area (TA), mean distance to centroid (CD), nearest neighbour distance (NND, mean  $\pm$  standard deviation).

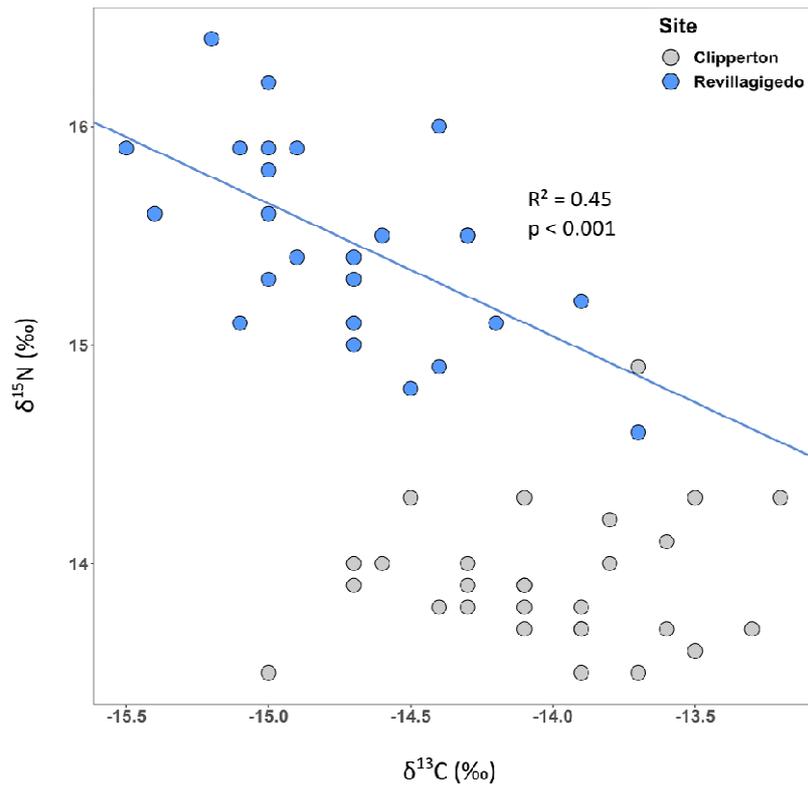
Site	$\delta^{13}\text{C}$ range (‰)	$\delta^{15}\text{N}$ range (‰)	TA (‰ <sup>2</sup> )	CD (‰)	NND (‰)
Revillagigedo	1.80	2.80	2.34	0.60	0.23 $\pm$ 0.21
Clipperton	1.80	1.40	1.55	0.46	0.17 $\pm$ 0.14



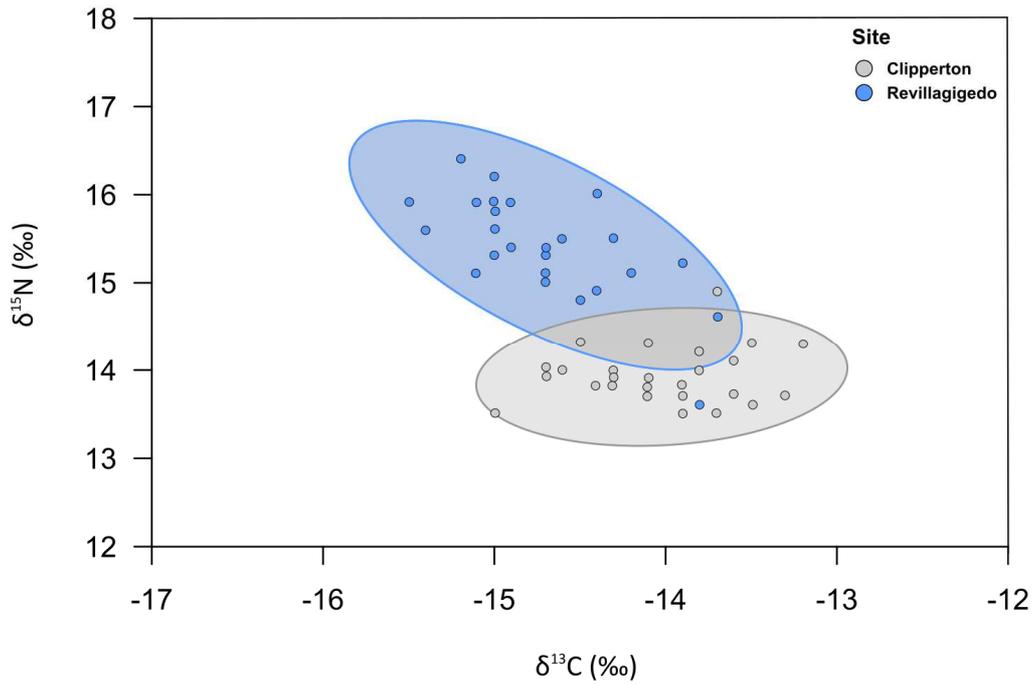
**Figure 1:** Map of the Northeast Pacific Ocean including the two sampling sites, the Revillagigedo Archipelago (Mexico) and Clipperton Island (France), which are both marine protected areas (MPAs).



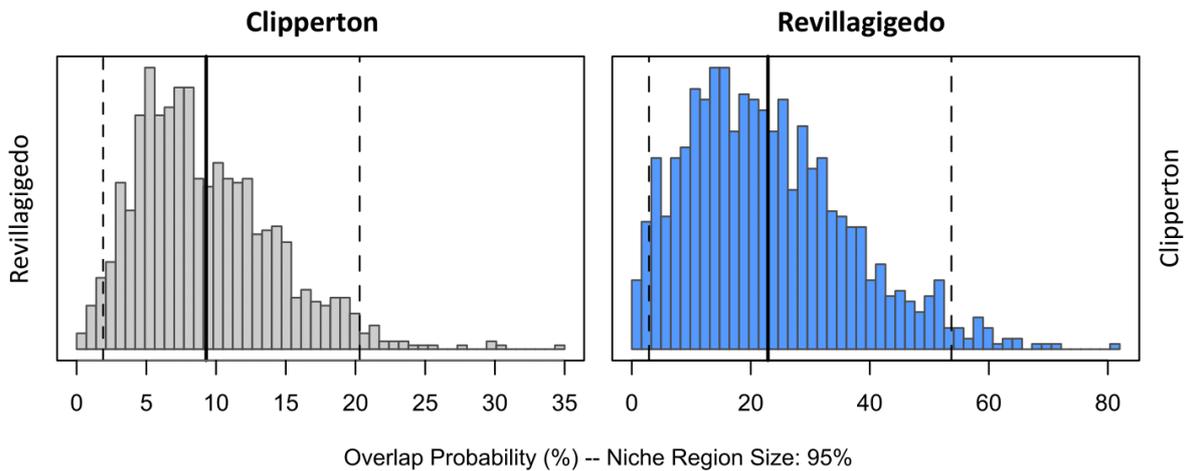
**Figure 2:** Boxplots of  $\delta^{15}\text{N}$  (A),  $\delta^{13}\text{C}$  (B) and THg (C) in fin clips of silvertip sharks from the Revillagigedo archipelago and Clipperton atoll. Isotope results are expressed in standard  $\delta$  notation based on international standards: Vienna Pee Dee Belemnite (V-PDB) for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . The box length represents the interquartile range, the bar length represents the range, and the horizontal line is the median value. Significant differences between sites are indicated by \*\*\*  $p < 0.001$ .



**Figure 3:**  $\delta^{15}\text{N}$  (‰) versus  $\delta^{13}\text{C}$  (‰) in fin clips of Silvertip sharks from the Revillagigedo archipelago and Clipperton atoll. Standards are V-PDB for  $\delta^{13}\text{C}$  and air for  $\delta^{15}\text{N}$ . Data fit a linear regression in Revillagigedo (one outlier removed) while no correlation was found in Clipperton.



**Figure 4:** Trophic niche area of Silvertip sharks based on carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes. Standards are V-PDB for  $\delta^{13}\text{C}$  and air for  $\delta^{15}\text{N}$ . Isotopic niche area was  $2.66 \text{ ‰}^2$  in Clipperton (grey ellipse) and  $3.92 \text{ ‰}^2$  in Revillagigedo (blue ellipse) ( $\text{SEA}_B$  with 95% credible interval). The area overlap between sites was 11%.



**Figure 5:** Comparisons of the posterior distributions of the probabilistic niche overlap metrics of 3 biochemical tracers ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and THg) between silvertip sharks from two sites: Clipperton Island (grey) and the Revillagigedo archipelago (blue). Niche overlap is characterized by the probability that a shark from one site is found within the niche region of the other site. Posterior means and 95% credible intervals are displayed in full and dash line respectively. The mean probability for a shark from Clipperton to be found in the Revillagigedo niche was 10%, while the mean probability for an individual from Revillagigedo to be found in the Clipperton niche was 23%.