
Trophic resources and mercury exposure of two silvertip shark populations in the northeast Pacific Ocean

Le Croizier Gaël ^{1,2,*}, Lorrain Anne ², Schaal Gauthier ², Ketchum James ^{3,4}, Hoyos-Padilla Mauricio ^{3,4,5}, Besnard Lucien ², Munaron Jean-Marie ², Le Loch Francois ², Point David ¹

¹ Géosciences Environnement Toulouse (GET), Observatoire Midi Pyrénées (OMP), UMR 5563 CNRS/IRD/Université Paul Sabatier, 14 Avenue Edouard Belin, 31400, Toulouse, France

² Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280, Plouzané, France

³ Pelagios Kakunjá A.C., Sinaloa 1540, Las Garzas, 23070, La Paz, Baja California Sur, Mexico

⁴ Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Baja California Sur, 23096, Mexico

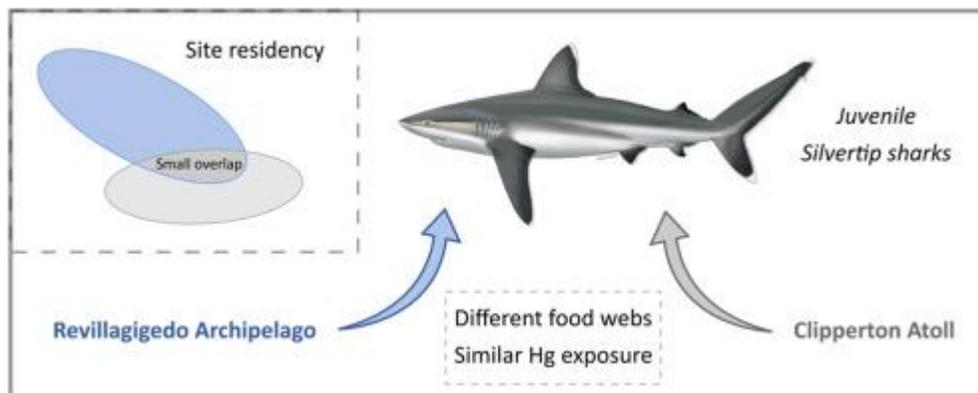
⁵ Fins Attached Marine Conservation, Colorado Springs, USA

* Corresponding author : Gaël Le Croizier, email address : gael.lecroizier@ird.fr

Abstract :

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

Graphical abstract



Highlights

- ▶ Silvertip sharks fed on both pelagic and benthic food webs at Revillagigedo.
- ▶ The population from Clipperton relied only on benthic food webs.
- ▶ Hg levels do not seem to vary between sites or food webs.
- ▶ Weak niche overlap between populations reflected site residency of silvertip sharks.

Keywords : Top-predators ; Mercury transfer ; Food webs ; Foraging habitat ; Stable isotopes ; MPAs

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 δ 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 (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 SEA_B constitutes a proxy of the feeding
175 niche occupied by sharks in one site while the overlap between SEA_B quantifies the trophic
176 overlap between shark populations. The 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‰) (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 ($\text{TA} = 2.34 \text{ ‰}^2$ in
216 Revillagigedo versus 1.55 ‰^2 in Clipperton) and standard ellipse area (SEA_B with 95%
217 credible interval = 3.92 ‰^2 versus 2.66 ‰^2) (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 (Vokshoori 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 (Fourrière 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 (Fourrière 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 for 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

384 **Acknowledgments:**

385 Gaël Le Croizier was supported by a postdoctoral grant from the French National Research
386 Institute for Sustainable Development (IRD). Fieldwork was supported by Alianza
387 WWF/Telmex-Telcel, Chris Fischer Productions/National Geographic. The authors thank

388 Southern Sport and Quino El Guardián for providing space in their boats. This work was
389 financially supported by the French National Research Agency project ANR-17-CE34-0010
390 MERTOX. This research was carried out under permits from the Secretaría de Agricultura,
391 Ganadería, Desarrollo Rural, Pesca y Alimentación (DGOPA.06668.150612.1691) and
392 Comisión Nacional de Areas Naturales Protegidas (F00.DRPBCPN-APFFCSL.REBIARRE-102/13)
393 of Mexico. We are also grateful to Secretaría del Medio Ambiente y Recursos Naturales and
394 Dirección del Parque Nacional Revillagigedo for providing necessary permits to conduct
395 research at the Revillagigedo National Park, a UNESCO World Heritage Site. We thank Laure
396 Laffont for expert management of the OMP mercury facilities.

397

398 REFERENCES

- 399 Allen, G.R., Robertson, R., 1997. An annotated checklist of the fishes of Clipperton Atoll, tropical
400 eastern Pacific. 1 813–843.
- 401 Andrews, K.S., Williams, G.D., Levin, P.S., 2010. Seasonal and Ontogenetic Changes in Movement
402 Patterns of Sixgill Sharks. PLOS ONE 5, e12549.
403 <https://doi.org/10.1371/journal.pone.0012549>
- 404 Bird, C.S., Veríssimo, A., Magozzi, S., Abrantes, K.G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea,
405 D.M., Biais, G., Borrell, A., Bouchoucha, M., Boyle, M., Brooks, E.J., Brunnschweiler, J.,
406 Bustamante, P., Carlisle, A., Catarino, D., Caut, S., Cherel, Y., Chouvelon, T., Churchill, D.,
407 Ciancio, J., Claes, J., Colaço, A., Courtney, D.L., Cresson, P., Daly, R., Necker, L. de, Endo, T.,
408 Figueiredo, I., Frisch, A.J., Hansen, J.H., Heithaus, M., Hussey, N.E., Iitembu, J., Juanes, F.,
409 Kinney, M.J., Kiszka, J.J., Klarian, S.A., Kopp, D., Leaf, R., Li, Y., Lorrain, A., Madigan, D.J.,
410 Maljković, A., Malpica-Cruz, L., Matich, P., Meekan, M.G., Ménard, F., Menezes, G.M.,
411 Munroe, S.E.M., Newman, M.C., Papastamatiou, Y.P., Pethybridge, H., Plumlee, J.D., Polo-
412 Silva, C., Quaeck-Davies, K., Raoult, V., Reum, J., Torres-Rojas, Y.E., Shiffman, D.S., Shipley,
413 O.N., Speed, C.W., Staudinger, M.D., Teffer, A.K., Tilley, A., Valls, M., Vaudo, J.J., Wai, T.-C.,
414 Wells, R.J.D., Wyatt, A.S.J., Yool, A., Trueman, C.N., 2018. A global perspective on the trophic
415 geography of sharks. *Nature Ecology & Evolution* 2, 299–305.
416 <https://doi.org/10.1038/s41559-017-0432-z>
- 417 Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production
418 below the mixed layer in the North Pacific Ocean. *Nature Geosci* 6, 879–884.
419 <https://doi.org/10.1038/ngeo1918>
- 420 Bond, M.E., Tolentino, E., Mangubhai, S., Howey, L.A., 2015. Vertical and horizontal movements of a
421 silvertip shark (*Carcharhinus albimarginatus*) in the Fijian archipelago. *Animal Biotelemetry* 3,
422 19. <https://doi.org/10.1186/s40317-015-0055-6>
- 423 Briand, M.J., Bonnet, X., Guillou, G., Letourneur, Y., 2016. Complex food webs in highly diversified
424 coral reefs: Insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes. *Food Webs* 8, 12–22.
425 <https://doi.org/10.1016/j.fooweb.2016.07.002>
- 426 Carlisle, A.B., Kim, S.L., Semmens, B.X., Madigan, D.J., Jorgensen, S.J., Perle, C.R., Anderson, S.D.,
427 Chapple, T.K., Kanive, P.E., Block, B.A., 2012. Using Stable Isotope Analysis to Understand the
428 Migration and Trophic Ecology of Northeastern Pacific White Sharks (*Carcharodon*
429 *carcharias*). PLOS ONE 7, e30492. <https://doi.org/10.1371/journal.pone.0030492>
- 430 Carlisle, A.B., Tickler, D., Dale, J.J., Ferretti, F., Curnick, D.J., Chapple, T.K., Schallert, R.J., Castleton,
431 M., Block, B.A., 2019. Estimating Space Use of Mobile Fishes in a Large Marine Protected
432 Area With Methodological Considerations in Acoustic Array Design. *Front. Mar. Sci.* 6.
433 <https://doi.org/10.3389/fmars.2019.00256>
- 434 Charpy, L., 2009. Clipperton: environnement et biodiversité d'un microcosme océanique. Publ.
435 scientifiques du Muséum National d'Histoire Naturelle, Paris.
- 436 Chen, C.Y., Folt, C.L., 2005. High Plankton Densities Reduce Mercury Biomagnification. *Environ. Sci.*
437 *Technol.* 39, 115–121. <https://doi.org/10.1021/es0403007>
- 438 Cherel, Y., Ducatez, S., Fontaine, C., Richard, P., Guinet, C., 2008. Stable isotopes reveal the trophic
439 position and mesopelagic fish diet of female southern elephant seals breeding on the
440 Kerguelen Islands. *Marine Ecology Progress Series* 370, 239–247.
441 <https://doi.org/10.3354/meps07673>
- 442 Chin, A., Heupel, M.R., Simpfendorfer, C.A., Tobin, A.J., 2013. Ontogenetic movements of juvenile
443 blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and
444 coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23, 468–474.
445 <https://doi.org/10.1002/aqc.2349>
- 446 Chouvelon, T., Cresson, P., Bouchoucha, M., Brach-Papa, C., Bustamante, P., Crochet, S., Marco-
447 Miralles, F., Thomas, B., Knoery, J., 2018. Oligotrophy as a major driver of mercury

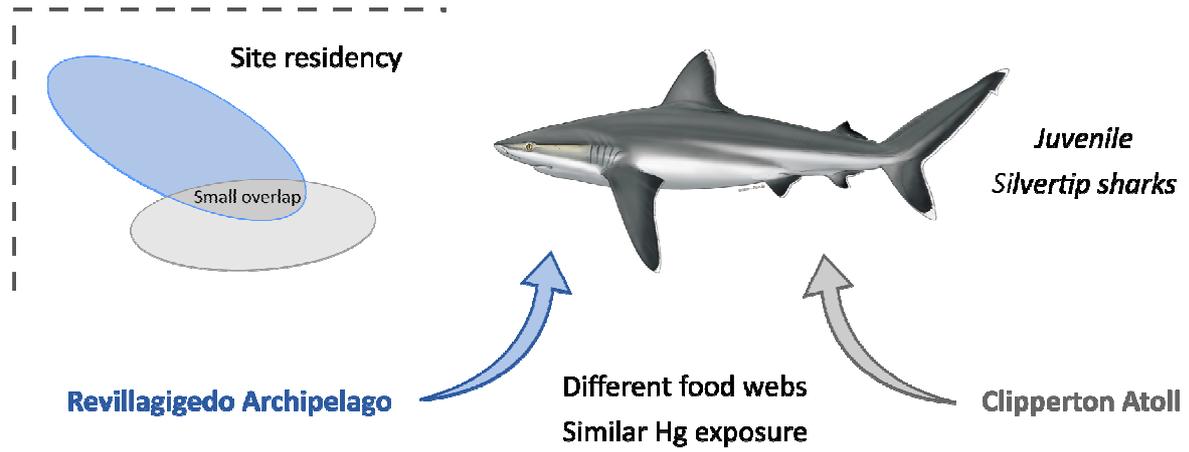
- 448 bioaccumulation in medium-to high-trophic level consumers: A marine ecosystem-
449 comparative study. *Environmental Pollution* 233, 844–854.
450 <https://doi.org/10.1016/j.envpol.2017.11.015>
- 451 Choy, C.A., Popp, B.N., Kaneko, J.J., Drazen, J.C., 2009. The influence of depth on mercury levels in
452 pelagic fishes and their prey. *PNAS* 106, 13865–13869.
453 <https://doi.org/10.1073/pnas.0900711106>
- 454 Clarke, S., 2004. Understanding pressures on fishery resources through trade statistics: a pilot study
455 of four products in the Chinese dried seafood market. *Fish and Fisheries* 5, 53–74.
456 <https://doi.org/10.1111/j.1467-2960.2004.00137.x>
- 457 Compagno, L., Dando, M., Fowler, S., 2005. *Sharks of the world*. Princeton University Press,
458 Princeton.
- 459 Curnick, D.J., Carlisle, A.B., Gollock, M.J., Schallert, R.J., Hussey, N.E., 2019. Evidence for dynamic
460 resource partitioning between two sympatric reef shark species within the British Indian
461 Ocean Territory. *Journal of Fish Biology* 94, 680–685. <https://doi.org/10.1111/jfb.13938>
- 462 Dicken, M.L., Hussey, N.E., Christiansen, H.M., Smale, M.J., Nkabi, N., Cliff, G., Wintner, S.P., 2017.
463 Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters.
464 *PLOS ONE* 12, e0177897. <https://doi.org/10.1371/journal.pone.0177897>
- 465 Driscoll, C.T., Mason, R.P., Chan, H.M., Jacob, D.J., Pirrone, N., 2013. Mercury as a Global Pollutant:
466 Sources, Pathways, and Effects. *Environ. Sci. Technol.* 47, 4967–4983.
467 <https://doi.org/10.1021/es305071v>
- 468 Ebert, D., Fowler, S., Dando, M., 2018. *SHARKS OF THE WORLD: a fully illustrated guide*. WILD
469 NATURE Press, Place of publication not identified.
- 470 Endo, T., Kimura, O., Ohta, C., Koga, N., Kato, Y., Fujii, Y., Haraguchi, K., 2016. Metal Concentrations in
471 the Liver and Stable Isotope Ratios of Carbon and Nitrogen in the Muscle of Silvertip Shark
472 (*Carcharhinus albimarginatus*) Culled off Ishigaki Island, Japan: Changes with Growth. *PLOS*
473 *ONE* 11, e0147797. <https://doi.org/10.1371/journal.pone.0147797>
- 474 Espinoza, M., Heupel, Michelle.R., Tobin, A.J., Simpfendorfer, C.A., 2015. Movement patterns of
475 silvertip sharks (*Carcharhinus albimarginatus*) on coral reefs. *Coral Reefs* 34, 807–821.
476 <https://doi.org/10.1007/s00338-015-1312-0>
- 477 Every, S.L., Pethybridge, H.R., Crook, D.A., Kyne, P.M., Fulton, C.J., 2016. Comparison of fin and
478 muscle tissues for analysis of signature fatty acids in tropical euryhaline sharks. *Journal of*
479 *Experimental Marine Biology and Ecology* 479, 46–53.
480 <https://doi.org/10.1016/j.jembe.2016.02.011>
- 481 Ferretti, F., Curnick, D., Liu, K., Romanov, E.V., Block, B.A., 2018. Shark baselines and the conservation
482 role of remote coral reef ecosystems. *Science Advances* 4, eaaq0333.
483 <https://doi.org/10.1126/sciadv.aaq0333>
- 484 Fiedler, P.C., Talley, L.D., 2006. Hydrography of the eastern tropical Pacific: A review. *Progress in*
485 *Oceanography, A Review of Eastern Tropical Pacific Oceanography* 69, 143–180.
486 <https://doi.org/10.1016/j.pocean.2006.03.008>
- 487 Fourri re, M., Reyes-Bonilla, H., Ayala-Bocos, A., Ketchum, J.A., Ch vez-Comparan, J.C., 2016.
488 Checklist and analysis of completeness of the reef fish fauna of the Revillagigedo
489 Archipelago, Mexico. *Zootaxa* 4150, 436–466. <https://doi.org/10.11646/zootaxa.4150.4.4>
- 490 Fourri re, M., Reyes-Bonilla, H., Galv n-Villa, C.M., Bocos, A.A., Rodr guez-Zaragoza, F.A., 2019. Reef
491 fish structure assemblages in oceanic islands of the eastern tropical Pacific: Revillagigedo
492 Archipelago and Clipperton atoll. *Marine Ecology* 40, e12539.
493 <https://doi.org/10.1111/maec.12539>
- 494 Friedlander, A.M., Giddens, J., Ballesteros, E., Blum, S., Brown, E.K., Caselle, J.E., Henning, B., Jost, C.,
495 Salinas-de-Le n, P., Sala, E., 2019. Marine biodiversity from zero to a thousand meters at
496 Clipperton Atoll ( le de La Passion), Tropical Eastern Pacific. *PeerJ* 7, e7279.
497 <https://doi.org/10.7717/peerj.7279>

- 498 Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E., Hobbs, J.-P.A.,
499 2016. Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs*
500 35, 459–472. <https://doi.org/10.1007/s00338-016-1415-2>
- 501 Fry, B., Sherr, E.B., 1989. $\delta^{13}\text{C}$ Measurements as Indicators of Carbon Flow in Marine and Freshwater
502 Ecosystems. *SpringerLink* 196–229. https://doi.org/10.1007/978-1-4612-3498-2_12
- 503 Gilmour, C.C., Podar, M., Bullock, A.L., Graham, A.M., Brown, S.D., Somenahally, A.C., Johs, A., Hurt,
504 R.A., Bailey, K.L., Elias, D.A., 2013. Mercury Methylation by Novel Microorganisms from New
505 Environments. *Environ. Sci. Technol.* 47, 11810–11820. <https://doi.org/10.1021/es403075t>
- 506 Giménez, J., Cañadas, A., Ramírez, F., Afán, I., García-Tiscar, S., Fernández-Maldonado, C., Castillo,
507 J.J., Stephanis, R. de, 2017. Intra- and interspecific niche partitioning in striped and common
508 dolphins inhabiting the southwestern Mediterranean Sea. *Marine Ecology Progress Series*
509 567, 199–210. <https://doi.org/10.3354/meps12046>
- 510 Glynn, P.W., Veron, J.E.N., Wellington, G.M., 1996. Clipperton Atoll (eastern Pacific): oceanography,
511 geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* 15, 71–99.
512 <https://doi.org/10.1007/BF01771897>
- 513 Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2010. Using Isoscapes to
514 Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems, in:
515 West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), *Isoscapes: Understanding Movement,*
516 *Pattern, and Process on Earth through Isotope Mapping.* Springer Netherlands, Dordrecht,
517 pp. 299–318. https://doi.org/10.1007/978-90-481-3354-3_14
- 518 Grubbs, R., 2010. Ontogenetic Shifts in Movements and Habitat Use, in: *Sharks and Their Relatives II.*
519 CRC Press, pp. 319–350. <https://doi.org/10.1201/9781420080483-c7>
- 520 Gworek, B., Bemowska-Kałabun, O., Kijeńska, M., Wrzosek-Jakubowska, J., 2016. Mercury in Marine
521 and Oceanic Waters—a Review. *Water Air Soil Pollut* 227, 371.
522 <https://doi.org/10.1007/s11270-016-3060-3>
- 523 Heimbürger, L.-E., Cossa, D., Marty, J.-C., Migon, C., Averty, B., Dufour, A., Ras, J., 2010. Methyl
524 mercury distributions in relation to the presence of nano- and picophytoplankton in an
525 oceanic water column (Ligurian Sea, North-western Mediterranean). *Geochimica et*
526 *Cosmochimica Acta* 74, 5549–5559. <https://doi.org/10.1016/j.gca.2010.06.036>
- 527 Hoen, D.K., Kim, S.L., Hussey, N.E., Wallsgrove, N.J., Drazen, J.C., Popp, B.N., 2014. Amino acid ^{15}N
528 trophic enrichment factors of four large carnivorous fishes. *Journal of Experimental Marine*
529 *Biology and Ecology* 453, 76–83. <https://doi.org/10.1016/j.jembe.2014.01.006>
- 530 Houssard, P., Point, D., Tremblay-Boyer, L., Allain, V., Pethybridge, H., Masbou, J., Ferriss, B.E., Baya,
531 P.A., Lagane, C., Menkes, C.E., Letourneur, Y., Lorrain, A., 2019. A Model of Mercury
532 Distribution in Tuna from the Western and Central Pacific Ocean: Influence of Physiology,
533 Ecology and Environmental Factors. *Environ. Sci. Technol.* 53, 1422–1431.
534 <https://doi.org/10.1021/acs.est.8b06058>
- 535 Hoyos-Padilla, E.M., Ketchum, J.T., Klimley, A.P., Galván-Magaña, F., 2014. Ontogenetic migration of a
536 female scalloped hammerhead shark *Sphyrna lewini* in the Gulf of California. *Animal*
537 *Biotelemetry* 2, 17. <https://doi.org/10.1186/2050-3385-2-17>
- 538 Hussey, N.E., MacNeil, M.A., Siple, M.C., Popp, B.N., Dudley, S.F.J., Fisk, A.T., 2015. Expanded trophic
539 complexity among large sharks. *Food Webs* 4, 1–7.
540 <https://doi.org/10.1016/j.fooweb.2015.04.002>
- 541 Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and
542 within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*
543 80, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- 544 Ketchum, J.T., Reyes Bonilla, H., 2001. Taxonomy and distribution of the hermatypic corals
545 (Scleractinia) of the Revillagigedo Archipelago, Mexico. *Rev. Biol. Trop.* 49, 803–848.
- 546 Kim, Sora Lee, Rio, C.M. del, Casper, D., Koch, P.L., 2012. Isotopic incorporation rates for shark tissues
547 from a long-term captive feeding study. *Journal of Experimental Biology* 215, 2495–2500.
548 <https://doi.org/10.1242/jeb.070656>

- 549 Kim, Sora L., Tinker, M.T., Estes, J.A., Koch, P.L., 2012. Ontogenetic and Among-Individual Variation in
550 Foraging Strategies of Northeast Pacific White Sharks Based on Stable Isotope Analysis. *PLOS*
551 *ONE* 7, e45068. <https://doi.org/10.1371/journal.pone.0045068>
- 552 Kiszka, J.J., Aubail, A., Hussey, N.E., Heithaus, M.R., Caurant, F., Bustamante, P., 2015. Plasticity of
553 trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by
554 stable isotope and mercury analyses. *Deep Sea Research Part I: Oceanographic Research*
555 *Papers* 96, 49–58. <https://doi.org/10.1016/j.dsr.2014.11.006>
- 556 Kolasinski, J., Rogers, K., Cuét, P., Barry, B., Frouin, P., 2011. Sources of particulate organic matter at
557 the ecosystem scale: a stable isotope and trace element study in a tropical coral reef. *Marine*
558 *Ecology Progress Series* 443, 77–93. <https://doi.org/10.3354/meps09416>
- 559 Lara-Lizardi, F., 2018. Distribution patterns of sharks in the Revillagigedo archipelago and their
560 connectivity in the eastern tropical Pacific.
- 561 Lara-Lizardi, F., Hoyos-Padilla, M., Hearn, A., Klimley, A.P., Galván-Magaña, F., Arauz, R., Bessudo, S.,
562 Castro, E., Clua, E., Espinoza, E., Fischer, C., Peñaherrera-Palma, C., Steiner, T., Ketchum, J.T.,
563 2020. Shark movements in the Revillagigedo Archipelago and connectivity with the Eastern
564 Tropical Pacific. *bioRxiv* 2020.03.02.972844. <https://doi.org/10.1101/2020.03.02.972844>
- 565 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. CAN STABLE ISOTOPE RATIOS
566 PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE? *Ecology* 88, 42–48.
567 [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
- 568 Le Bourg, B., Kiszka, J.J., Bustamante, P., Heithaus, M.R., Jaquemet, S., Humber, F., 2019. Effect of
569 body length, trophic position and habitat use on mercury concentrations of sharks from
570 contrasted ecosystems in the southwestern Indian Ocean. *Environmental Research* 169, 387–
571 395. <https://doi.org/10.1016/j.envres.2018.11.024>
- 572 Le Croizier, G., Schaal, G., Point, D., Le Loc’h, F., Machu, E., Fall, M., Munaron, J.-M., Boyé, A., Walter,
573 P., Laë, R., Tito De Morais, L., 2019. Stable isotope analyses revealed the influence of foraging
574 habitat on mercury accumulation in tropical coastal marine fish. *Science of The Total*
575 *Environment* 650, 2129–2140. <https://doi.org/10.1016/j.scitotenv.2018.09.330>
- 576 Li, M., Sherman, L.S., Blum, J.D., Grandjean, P., Mikkelsen, B., Weihe, P., Sunderland, E.M., Shine, J.P.,
577 2014. Assessing Sources of Human Methylmercury Exposure Using Stable Mercury Isotopes.
578 *Environ. Sci. Technol.* 48, 8800–8806. <https://doi.org/10.1021/es500340r>
- 579 Li, Y., Zhang, Y., Hussey, N.E., Dai, X., 2016. Urea and lipid extraction treatment effects on $\delta^{15}\text{N}$ and
580 $\delta^{13}\text{C}$ values in pelagic sharks. *Rapid Communications in Mass Spectrometry* 30, 1–8.
581 <https://doi.org/10.1002/rcm.7396>
- 582 López-Ibarra, G.A., Bode, A., Hernández-Trujillo, S., Zetina-Rejón, M.J., Arreguín-Sánchez, F., 2018.
583 Trophic position of twelve dominant pelagic copepods in the eastern tropical Pacific Ocean.
584 *Journal of Marine Systems* 187, 13–22. <https://doi.org/10.1016/j.jmarsys.2018.06.009>
- 585 Lorrain, A., Graham, B.S., Popp, B.N., Allain, V., Olson, R.J., Hunt, B.P.V., Potier, M., Fry, B., Galván-
586 Magaña, F., Menkes, C.E.R., Kaehler, S., Ménard, F., 2015. Nitrogen isotopic baselines and
587 implications for estimating foraging habitat and trophic position of yellowfin tuna in the
588 Indian and Pacific Oceans. *Deep Sea Research Part II: Topical Studies in Oceanography,*
589 *Impacts of climate on marine top predators* 113, 188–198.
590 <https://doi.org/10.1016/j.dsr2.2014.02.003>
- 591 Lyons, K., Carlisle, A., Preti, A., Mull, C., Blasius, M., O’Sullivan, J., Winkler, C., Lowe, C.G., 2013.
592 Effects of trophic ecology and habitat use on maternal transfer of contaminants in four
593 species of young of the year lamniform sharks. *Marine Environmental Research* 90, 27–38.
594 <https://doi.org/10.1016/j.marenvres.2013.05.009>
- 595 Magozzi, S., Yool, A., Zanden, H.B.V., Wunder, M.B., Trueman, C.N., 2017. Using ocean models to
596 predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* 8, e01763.
597 <https://doi.org/10.1002/ecs2.1763>
- 598 Malpica-Cruz, L., Herzka, S.Z., Sosa-Nishizaki, O., Lazo, J.P., 2012. Tissue-specific isotope trophic
599 discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling
600 results. *Can. J. Fish. Aquat. Sci.* 69, 551–564. <https://doi.org/10.1139/f2011-172>

- 601 McKinney, M.A., Dean, K., Hussey, N.E., Cliff, G., Wintner, S.P., Dudley, S.F.J., Zungu, M.P., Fisk, A.T.,
602 2016. Global versus local causes and health implications of high mercury concentrations in
603 sharks from the east coast of South Africa. *Science of The Total Environment* 541, 176–183.
604 <https://doi.org/10.1016/j.scitotenv.2015.09.074>
- 605 McMahon, K.W., Thorrold, S.R., Houghton, L.A., Berumen, M.L., 2016. Tracing carbon flow through
606 coral reef food webs using a compound-specific stable isotope approach. *Oecologia* 180,
607 809–821. <https://doi.org/10.1007/s00442-015-3475-3>
- 608 Michener, R., Lajtha, K., 2008. *Stable Isotopes in Ecology and Environmental Science*. John Wiley &
609 Sons.
- 610 Mourier, J., Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M.L., Planes, S., 2016. Extreme
611 Inverted Trophic Pyramid of Reef Sharks Supported by Spawning Groupers. *Current Biology*
612 26, 2011–2016. <https://doi.org/10.1016/j.cub.2016.05.058>
- 613 Munson, K.M., Lamborg, C.H., Boiteau, R.M., Saito, M.A., 2018. Dynamic mercury methylation and
614 demethylation in oligotrophic marine water. *Biogeosciences* 15, 6451–6460.
615 <https://doi.org/10.5194/bg-15-6451-2018>
- 616 Munson, K.M., Lamborg, C.H., Swarr, G.J., Saito, M.A., 2015. Mercury species concentrations and
617 fluxes in the Central Tropical Pacific Ocean. *Global Biogeochemical Cycles* 29, 656–676.
618 <https://doi.org/10.1002/2015GB005120>
- 619 Muntaner López, G., 2016. Movement patterns and habitat use of the silver tip shark (“*Carcharhinus*
620 *albimarginatus*”) at the Revillagigedo Archipelago.
- 621 Nalluri, D., Baumann, Z., Abercrombie, D.L., Chapman, D.D., Hammerschmidt, C.R., Fisher, N.S., 2014.
622 Methylmercury in dried shark fins and shark fin soup from American restaurants. *Science of*
623 *The Total Environment* 496, 644–648. <https://doi.org/10.1016/j.scitotenv.2014.04.107>
- 624 O’Byrhim, J.R., Adams, D.H., Spaet, J.L.Y., Mills, G., Lance, S.L., 2017. Relationships of mercury
625 concentrations across tissue types, muscle regions and fins for two shark species.
626 *Environmental Pollution* 223, 323–333. <https://doi.org/10.1016/j.envpol.2017.01.029>
- 627 Olson, R.J., Popp, B.N., Graham, B.S., López-Ibarra, G.A., Galván-Magaña, F., Lennert-Cody, C.E.,
628 Bocanegra-Castillo, N., Wallsgrove, N.J., Gier, E., Alatorre-Ramírez, V., Ballance, L.T., Fry, B.,
629 2010. Food-web inferences of stable isotope spatial patterns in copepods and yellowfin tuna
630 in the pelagic eastern Pacific Ocean. *Progress in Oceanography, CLimate Impacts on Oceanic*
631 *TOp Predators (CLIOTOP)* 86, 124–138. <https://doi.org/10.1016/j.pocean.2010.04.026>
- 632 Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source Partitioning Using Stable Isotopes:
633 Coping with Too Much Variation. *PLoS ONE* 5, e9672.
634 <https://doi.org/10.1371/journal.pone.0009672>
- 635 Podar, M., Gilmour, C.C., Brandt, C.C., Soren, A., Brown, S.D., Crable, B.R., Palumbo, A.V.,
636 Somenahally, A.C., Elias, D.A., 2015. Global prevalence and distribution of genes and
637 microorganisms involved in mercury methylation. *Science Advances* 1, e1500675.
638 <https://doi.org/10.1126/sciadv.1500675>
- 639 Rangel, B. de S., Hussey, N.E., Gomes, A.D., Rodrigues, A., Martinelli, L.A., Moreira, R.G., 2019.
640 Resource partitioning between two young-of-year cownose rays *Rhinoptera bonasus* and *R.*
641 *brasiliensis* within a communal nursery inferred by trophic biomarkers. *Journal of Fish*
642 *Biology* 94, 781–788. <https://doi.org/10.1111/jfb.13958>
- 643 Renedo, M., Amouroux, D., Pedrero, Z., Bustamante, P., Cherel, Y., 2018. Identification of sources and
644 bioaccumulation pathways of MeHg in subantarctic penguins: a stable isotopic investigation.
645 *Sci Rep* 8, 8865. <https://doi.org/10.1038/s41598-018-27079-9>
- 646 Reyes-Bonilla, H., 2003. Coral reefs of the Pacific coast of México, in: Cortés, J. (Ed.), *Latin American*
647 *Coral Reefs*. Elsevier Science, Amsterdam, pp. 331–349. [https://doi.org/10.1016/B978-](https://doi.org/10.1016/B978-044451388-5/50015-1)
648 [044451388-5/50015-1](https://doi.org/10.1016/B978-044451388-5/50015-1)
- 649 Romero-Torres, M., Treml, E.A., Acosta, A., Paz-García, D.A., 2018. The Eastern Tropical Pacific coral
650 population connectivity and the role of the Eastern Pacific Barrier. *Sci Rep* 8, 1–13.
651 <https://doi.org/10.1038/s41598-018-27644-2>

- 652 Sackett, D.K., Drazen, J.C., Popp, B.N., Choy, C.A., Blum, J.D., Johnson, M.W., 2017. Carbon, Nitrogen,
653 and Mercury Isotope Evidence for the Biogeochemical History of Mercury in Hawaiian
654 Marine Bottomfish. *Environ. Sci. Technol.* 51, 13976–13984.
655 <https://doi.org/10.1021/acs.est.7b04893>
- 656 Senn, D.B., Chesney, E.J., Blum, J.D., Bank, M.S., Maage, A., Shine, J.P., 2010. Stable isotope (N, C, Hg)
657 study of methylmercury sources and trophic transfer in the northern gulf of Mexico. *Environ.*
658 *Sci. Technol.* 44, 1630–1637. <https://doi.org/10.1021/es902361j>
- 659 Smart, J.J., Chin, A., Baje, L., Tobin, A.J., Simpfendorfer, C.A., White, W.T., 2017. Life history of the
660 silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea. *Coral Reefs* 36, 577–
661 588. <https://doi.org/10.1007/s00338-016-1533-x>
- 662 Stewart, J.D., Beale, C.S., Fernando, D., Sianipar, A.B., Burton, R.S., Semmens, B.X., Aburto-Oropeza,
663 O., 2016a. Spatial ecology and conservation of *Manta birostris* in the Indo-Pacific. *Biological*
664 *Conservation* 200, 178–183. <https://doi.org/10.1016/j.biocon.2016.05.016>
- 665 Stewart, J.D., Hoyos-Padilla, E.M., Kumli, K.R., Rubin, R.D., 2016b. Deep-water feeding and behavioral
666 plasticity in *Manta birostris* revealed by archival tags and submersible observations. *Zoology*
667 119, 406–413. <https://doi.org/10.1016/j.zool.2016.05.010>
- 668 Sunderland, E.M., Krabbenhoft, D.P., Moreau, J.W., Strode, S.A., Landing, W.M., 2009. Mercury
669 sources, distribution, and bioavailability in the North Pacific Ocean: Insights from data and
670 models: MERCURY IN THE NORTH PACIFIC OCEAN. *Global Biogeochem. Cycles* 23, n/a-n/a.
671 <https://doi.org/10.1029/2008GB003425>
- 672 Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., Reist, J.D., 2015. A new probabilistic
673 method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* 96, 318–
674 324. <https://doi.org/10.1890/14-0235.1>
- 675 Trueman, C.N., St John Glew, K., 2019. Chapter 6 - Isotopic Tracking of Marine Animal Movement, in:
676 Hobson, K.A., Wassenaar, L.I. (Eds.), *Tracking Animal Migration with Stable Isotopes (Second*
677 *Edition)*. Academic Press, pp. 137–172. [https://doi.org/10.1016/B978-0-12-814723-8.00006-](https://doi.org/10.1016/B978-0-12-814723-8.00006-4)
678 4
- 679 Trystram, C., Rogers, K.M., Soria, M.M., Jaquemet, S., 2016. Feeding patterns of two sympatric shark
680 predators in coastal ecosystems of an oceanic island. *Canadian Journal of Fisheries and*
681 *Aquatic Sciences*. <https://doi.org/10.1139/cjfas-2016-0105>
- 682 Vokshoori, N.L., McCarthy, M.D., 2014. Compound-Specific $\delta^{15}\text{N}$ Amino Acid Measurements in
683 Littoral Mussels in the California Upwelling Ecosystem: A New Approach to Generating
684 Baseline $\delta^{15}\text{N}$ Isoscapes for Coastal Ecosystems. *PLOS ONE* 9, e98087.
685 <https://doi.org/10.1371/journal.pone.0098087>
- 686 Wang, W., Wong, R.S.K., 2003. Bioaccumulation kinetics and exposure pathways of inorganic
687 mercury and methylmercury in a marine fish, the sweetlips *Plectorhinchus gibbosus*. *Mar*
688 *Ecol Prog Ser* 261, 257–268. <https://doi.org/10.3354/meps261257>
- 689 White, W.T., 2007. Catch composition and reproductive biology of whaler sharks (Carcharhiniformes:
690 Carcharhinidae) caught by fisheries in Indonesia. *Journal of Fish Biology* 71, 1512–1540.
691 <https://doi.org/10.1111/j.1095-8649.2007.01623.x>
- 692 Young, J.W., Hunt, B.P.V., Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccarelli, D., Lorrain,
693 A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloser, R.J.,
694 Arrizabalaga, H., Anela Choy, C., 2015. The trophodynamics of marine top predators: Current
695 knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in*
696 *Oceanography, Impacts of climate on marine top predators* 113, 170–187.
697 <https://doi.org/10.1016/j.dsr2.2014.05.015>
698



Graphical abstract

Journal Pre-proof

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 (‰ ²)	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

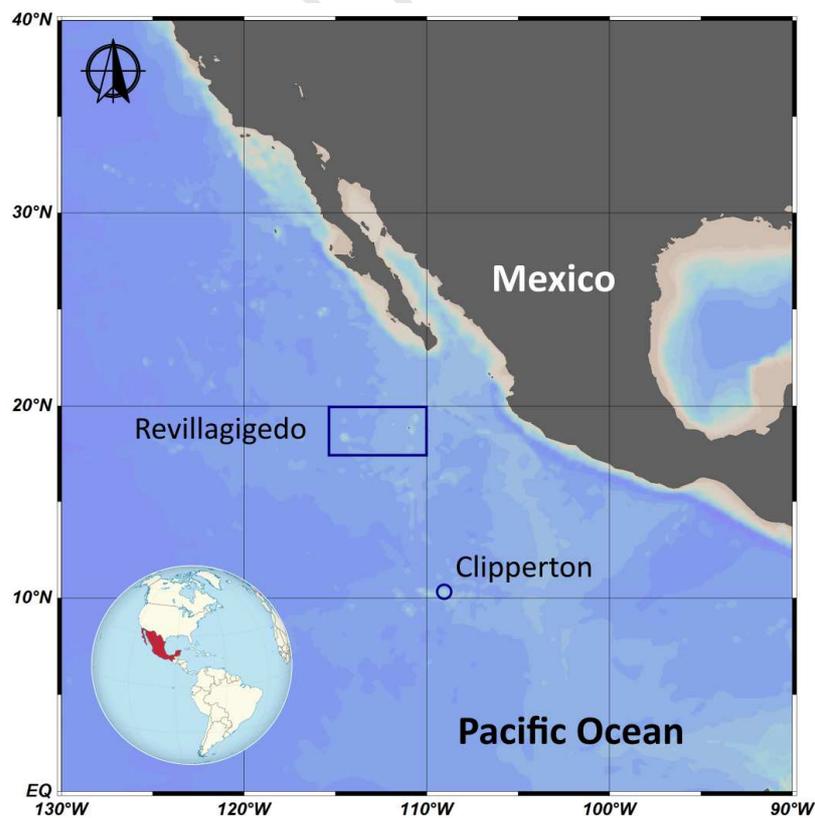


Figure 1: Map of the Northeast Pacific Ocean including the two sampling sites, the Revillagigedo Archipelago (Mexico) and Clipperton Island (France), which are both marine protected areas (MPAs).

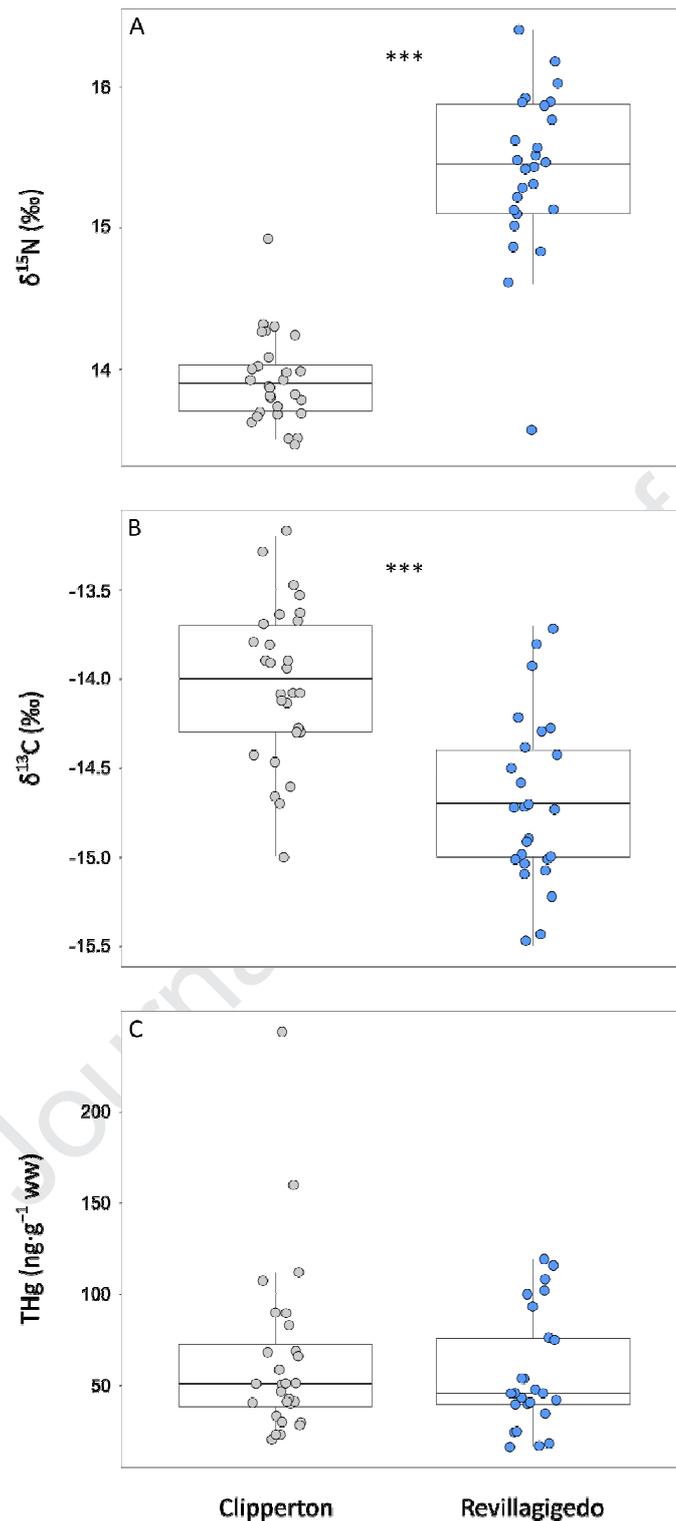


Figure 2: Boxplots of $\delta^{15}\text{N}$ (A), $\delta^{13}\text{C}$ (B) and THg (C) in fin clips of silvertip sharks from the Revillagigedo archipelago and Clipperton atoll. Isotope results are expressed in standard δ notation based on international standards: Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}\text{C}$ 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 *** $p < 0.001$.

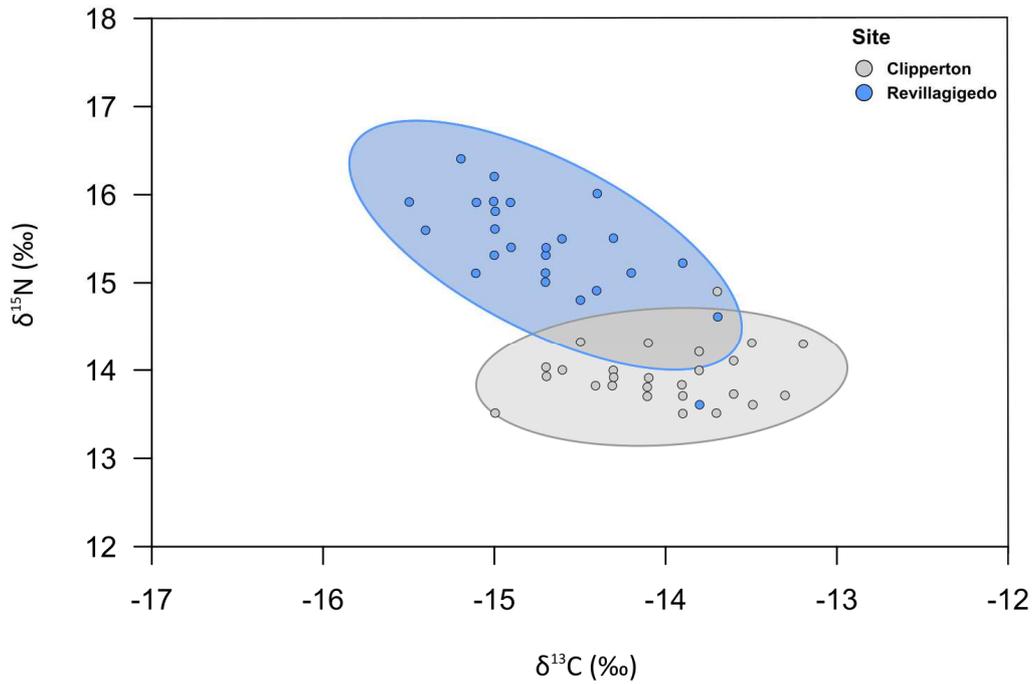


Figure 4: Trophic niche area of Silvertip sharks based on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes. Standards are V-PDB for $\delta^{13}\text{C}$ and air for $\delta^{15}\text{N}$. Isotopic niche area was 2.66 ‰^2 in Clipperton (grey ellipse) and 3.92 ‰^2 in Revillagigedo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

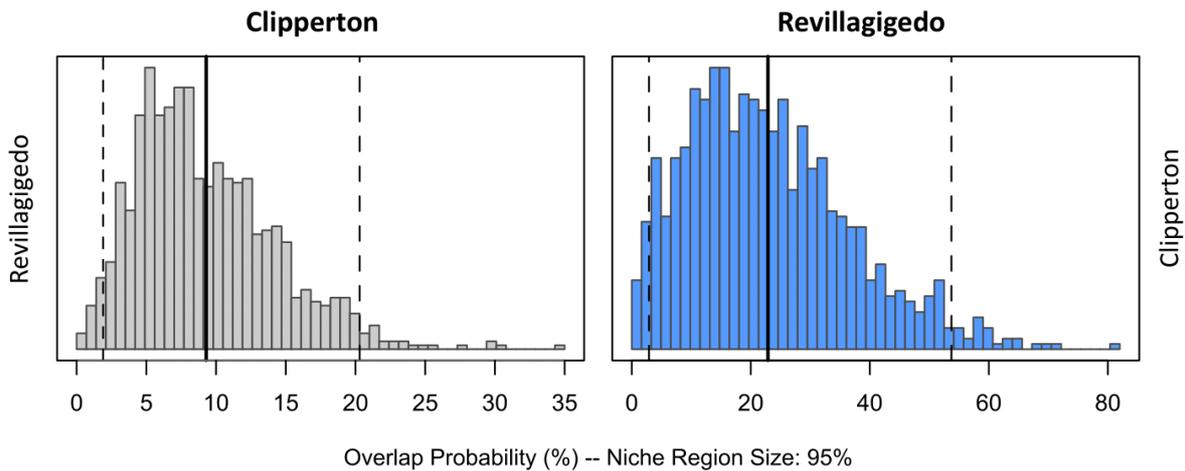


Figure 5: Comparisons of the posterior distributions of the probabilistic niche overlap metrics of 3 biochemical tracers ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and THg) between silvertip sharks from two sites: Clipperton Island (grey) and the Revillagigedo archipelago (blue). Niche overlap is 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%.

Highlights

- Silvertip sharks fed on both pelagic and benthic food webs at Revillagigedo
- The population from Clipperton relied only on benthic food webs
- Hg levels do not seem to vary between sites or food webs
- Weak niche overlap between populations reflected site residency of silvertip sharks

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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