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Seasonal habitat and length influence on the trophic niche of co-occurring tropical tunas in the eastern Atlantic Ocean

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Abstract :

In the Gulf of Guinea, bigeye *Thunnus obesus* (BET) and yellowfin tuna *Thunnus albacares* (YFT) are important for commercial fisheries and play a prominent ecological role as top predators. Using fatty acid profiles and carbon and nitrogen stable isotopes we examined their niche partitioning in this understudied region. Niche overlap was high (>70%), similar to percentages in other ocean basins. BET occupied a higher trophic position than YFT and fed on deeper prey (high $\delta^{15}\text{N}$ values and high proportions of mono-unsaturated fatty acids). The trophic position of YFT decreased slightly in the last 15 years ($\delta^{15}\text{N}$ values decrease ~ 0.5 ‰) suggesting a change in epipelagic communities, as observed in the eastern Pacific Ocean. Ontogenic changes were limited to BET. For both species, the dietary proportion of the diatoms marker (20:5n-3) increased in the seasonal upwelling area, highlighting the seasonal habitat influence on tunas diet. The relatively lipid-rich muscle (~ 6 % dry weight) of Atlantic tropical tunas suggested a richer diet in this region than for Indian Ocean tropical tunas and/or differences in energy allocation strategies.

Keywords : niche overlap, fatty acids, stable isotopes, body condition, pelagic predators

32 1. INTRODUCTION

33 Bigeye *Thunnus obesus* (BET) and yellowfin tuna *Thunnus albacares* (YFT) are oceanic
34 predators co-occurring in tropical waters worldwide. In the eastern Atlantic Ocean, around
35 200 000 tons of BET and YFT are caught each year, leading to an overexploitation of these
36 species (ICCAT 2015). Tunas occupy high trophic positions in pelagic habitats and their
37 biomass reduction induced by fishing raises concerns about the health of both tuna
38 populations and pelagic ecosystems, especially in a global change context (Chust et al. 2014,
39 Duffy et al. 2017, Hobday et al. 2017). This is a topical issue within the Gulf of Guinea, a
40 productive ecosystem that supports complex food webs, which has been subject to increased
41 pressure from commercial fisheries, human population growth and pollution from domestic
42 and industrial sources in the adjacent countries (Aryeetey 2002, Ukwe et al. 2006).

43 Information on the trophic ecology of tuna in the Gulf of Guinea is limited, especially those
44 relating to ecological tracers (Olson et al. 2016). Ecological tracers are biochemically stable
45 compounds within organisms, including stable isotopes (SI) of carbon and nitrogen and fatty
46 acids (FA). They provide time-integrated information on food assimilated in consumers'
47 tissues (Ramos and González-Solís 2012) over a period of several weeks to years in fish
48 (Iverson et al. 2004, Madigan et al. 2012). Predictable increase from prey to predator in the
49 nitrogen isotope ratio ($^{15}\text{N}/^{14}\text{N}$ expressed as $\delta^{15}\text{N}$ values) allows the determination of trophic
50 position (Vander Zanden et al. 1997). Changes in the carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$ expressed
51 as $\delta^{13}\text{C}$ values) are linked to modifications of the forage habitat (i.e., coastal vs. open ocean)
52 (France 1995). FA are lipid constituents necessary for physiological functions, some of which
53 cannot be readily synthesized by all consumers and are transferred conservatively in food
54 webs. Some 'essential' FA, such as docosahexaenoic acid (22:6n-3), eicosapentaenoic acid
55 (20:5n-3) and arachidonic acid (20:4n-6) are best preserved during trophic transfer (Tocher
56 2003). The profile of the FA transferred from prey to predator may inform on the forage taxa

57 (Dalsgaard et al. 2003, Budge et al. 2012). For example, in the pelagic environment, 22:6n-3
58 is generally a marker for dinoflagellates, 20:5n-3 is a marker for diatoms (Dalsgaard et al.
59 2003) and 18:1n-9 is a marker for deep-copepods (Teuber et al. 2014). In the highest trophic
60 levels, transferred FA are better preserved in storage lipids than in structural lipids (Robin et
61 al. 2003, Budge et al. 2012). The quantification of these ecological tracers also allows the
62 estimation of feeding niche extent (niche space) and provides insights into resource
63 partitioning (niche overlap) between co-occurring species (Jackson et al. 2011, Layman et al.
64 2012) including tunas (Teffer et al. 2015, Sardenne et al. 2016).

65 Given their bioenergetics (i.e. regional heterotherms, fast swim), tunas have adapted a
66 generalist foraging strategy in oligotrophic waters worldwide, consuming small fishes,
67 crustaceans, and cephalopods (Olson et al. 2016). In the eastern Atlantic Ocean, more than
68 160 prey taxa have been identified in their stomach content (Dragovich 1970, Dragovich and
69 Potthoff 1972) indicating that diet variability is linked to environmental conditions (e.g. sea
70 surface temperature and mixed-layer depth) (Weng et al. 2009, Parrish et al. 2015, Duffy et al.
71 2017). In the Atlantic Ocean, tropical tunas take advantage of prey aggregations, such as the
72 mesopelagics lightfish *Vinciguerria nimbaria* (Ménard and Marchal 2003) and the cigarfish
73 *Cubiceps pauciradiatus* (Ménard et al. 2000, Bard et al. 2002). The different tuna species
74 share a common habitat and often form schools, but BET feeds more on vertically migrating
75 Ommastrephidae squids than YFT (Cherel et al. 2007, Young et al. 2010b, Logan and
76 Lutcavage 2013). Resource partitioning between BET and YFT is however not quantified for
77 tuna populations from the eastern Atlantic. Olson et al. (2016) provided the first bulk isotopic
78 values for tropical tunas in this area, suggesting a slightly higher trophic level of BET
79 compared to other species (i.e., $\delta^{15}\text{N}$ of 12.7 ± 0.9 ‰ for BET and of 12.2 ± 1.0 ‰ for YFT,
80 between 2000 and 2004). They suggested that these values were affected by a size sampling
81 bias or unaccounted for habitat effects.

82 To build upon this research, we aimed to (i) determine whether seasonal upwelling, length
83 and sex (male vs. female) have an effect on BET and YFT diet using SI and FA; and (ii)
84 quantify feeding niches and partitioning of tunas (i.e. niches extent and overlap).

85 **2. MATERIAL & METHODS**

86 **2.1. Tunas and tissue sampling**

87 BET and YFT were caught by purse-seiners operating in the Gulf of Guinea, eastern
88 equatorial Atlantic Ocean, between July 2013 and September 2014. Samples were collected at
89 the landing site (fishing port for BET and “Pêche et froid” cannery for YFT) in Abidjan Port,
90 Ivory Coast (Fig. 1). Fishing dates (Julian days) and coordinates of fishing locations were
91 recovered from vessel logbooks, corresponding to the catch location or catch estimates. Catch
92 estimates are mean data computed from logbooks when anglers have grouped fish from
93 several fishing activities in the brine freezing wells of purse-seiners (maximum uncertainty of
94 33 days and 7.4° square). Catch dates covered July-September and January-February, i.e.
95 seasonal upwelling and non-upwelling periods, respectively. Fork length (FL measured with
96 calliper to the nearest 0.1 cm), sex and macroscopic identification of gonad maturity (visual
97 examination according to Diaha et al. 2016) were determined for each fish. Forty-five BET
98 (22 females, 23 males) and 50 YFT (19 females, 31 males) were selected. Length ranges were
99 111.3±25.8 cm FL for BET and 124.6±22.6 cm FL for YFT and included only developing fish
100 (male and female of gonad macroscopic stage 1–2) as tunas diet may change during the
101 spawning process (Zudaire et al. 2015). Around 2g of front dorsal white muscle tissue and
102 liver were sampled on each fish and stored frozen prior to analyses (-20°C during four months
103 after sampling then -80°C for two years).

104 **2.2. Ecological tracers analysis**

105 SI analyses were performed on white muscle, the less variable tissue and the most extensively
106 used in fish ecology (Pinnegar and Polunin 1999), while FA profiles were examined from

107 liver tissue, the richest tissue in storage lipids in tropical tunas (Sardenne et al. 2017). In
108 addition, we recorded the muscle lipid content as a proxy of fish body condition (Tocher
109 2003), thereafter included in the term ‘ecological tracers’.

110 **2.2.1. Stable isotope analysis and lipid content determination**

111 Carbon and nitrogen SI and lipid content were analyzed on 92 freeze-dried muscle samples of
112 tunas (45 BET and 47 YFT, three YFT samples have been lost during lab analysis). Samples
113 were ground up to a fine homogeneous powder with a ball mill MM200 (Retsch). They were
114 then treated with dichloromethane using a Dionex Accelerated Solvent Extractor (ASE 200),
115 as described by Bodin et al. (2009) to remove naturally ^{13}C -depleted lipids that affect $\delta^{13}\text{C}$
116 values (Sardenne et al. 2015). Lipid extracts were dried to a constant weight and weighed to
117 the nearest 0.1 mg to determine total lipid content (TLC, in % of dry weight (dw) sample).
118 Lipid-free powders were analyzed for SI using an Elemental Analyser (Flash EA 1112;
119 Thermo Scientific) coupled to an Isotope Ratio Mass Spectrometer (Delta V Advantage with
120 a ConFlo IV interface; Thermo Scientific) at the LIENSs Stable Isotope facility (La Rochelle,
121 France). Results were reported in the δ unit notation and expressed as parts per thousand (‰)
122 relative to international standards (atmospheric N_2 for nitrogen and Vienna-Pee Dee
123 Belemnite for carbon). Calibration was completed using reference materials (IAEA- N_2 , $-\text{NO}_3^-$,
124 -600 for nitrogen; USGS-24, IAEA-CHE, -600 for carbon). Analytical precision based on
125 replicate measurements of internal laboratory standard (acetanilide, Thermo Scientific) was
126 <0.15 ‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The effectiveness of the chemical extraction of the lipid-free
127 samples was checked by examining the C:N ratio from the percent element weight (C:N $<$
128 3.5; Post et al. 2007).

129 **2.2.2. Fatty acid analysis**

130 FA were determined on total lipid extracts of fresh liver samples (45 BET and 50 YFT).
131 Around 165 ± 35 mg of tissue were extracted using a mixture of dichloromethane and methanol

132 (2:1, v/v) with a potter homogenizer (glass/teflon). A known amount of 23:0 fatty acid was
133 added as an internal standard, and extracts were then trans-esterified with sulphuric acid
134 (3.8 % in methanol) at 100°C for 10 min. After addition of 800 μ L of hexane and three
135 washes with hexane-saturated distilled water, the fatty acid methyl esters (FAME) were
136 separated and quantified on a Varian CP8400 gas chromatography equipped with a Zebron
137 ZB-WAX column (30 m in length, 0.25 mm internal diameter, 0.25 μ m film thickness;
138 Phenomenex) and a flame ionisation detector at the LEMAR Lipidocean facility (Brest,
139 France). Samples were injected in splitless mode at 280°C and carried by hydrogen gas. The
140 oven temperature was raised from 60°C to 150 °C at 50°C/min, to 170 °C at 3.5 °C/min, to
141 185 °C at 1.5 °C/min, to 225 °C at 2.4 °C/min and then to 250°C at 5.5°C/min.. FAMES were
142 identified by comparing sample retention times to those of a commercial standard mixture
143 (37-components FAME Mix; Sigma) and lab-made standards using Galaxie 1.9.3.2 software
144 (Varian). Individual FA results were expressed as percentage of the total identified FA.
145 Finally, only FA accounting for >1% in at least two samples (n=20) were kept for statistical
146 analyses (Table 1).

147 2.3. Data analysis

148 We used linear regressions or multivariate analyses to examine the relative importance of
149 spatiotemporal (fishing longitude and date) and biological variables (species, length, and sex)
150 on ecological tracers ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, TLC and FA profile). There was no collinearity among
151 the five factors (variance inflation factors ranking 1.1 to 4.3). We added to our models the
152 interaction of species*length interaction to detect inter-specific differences in diet shift. For
153 isotopic data and TLC, covariate selection was based on the Akaike Information Criterion
154 (AIC). ANOVA on multiple regressions and post-hoc t-tests (with t the test value) were then
155 applied on scaled data, and normality of the residuals checked on Q-Q plots (based on the Q-
156 Q plot, one TLC outlier of 53.5% was removed from the dataset). For the multivariate FA

157 data, we tested for the equality of variances (using the function *Betadisper*, an analogous to
158 Levene's test available in the R package *vegan*). We then used Permutational multivariate
159 analysis of variance (PERMANOVA; non-parametric) based on the Bray-Curtis distance
160 matrix of the untransformed % FA to test the effect of candidate variables. Untransformed %
161 FA were used to avoid giving artificial weight to FA present in small quantities (Kelly and
162 Scheibling 2012). Differences in individual FA were assessed using Wilcoxon's tests (with *W*
163 the test value) for categorical variables (i.e., species and sex) and linear regressions for
164 continuous ones (i.e., longitude, date, and length).

165 Then, we compared tunas' feeding niches using the R package *SIBER* (Stable Isotope
166 Bayesian Ellipses in R) (Jackson et al. 2011) on biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and of
167 individual coordinates from dimension 1 and 2 of the principal components analysis (PCA)
168 for the untransformed % FA. For each species, we computed standard ellipses encompassing
169 95% of the data and calculated the Bayesian standard ellipse areas (SEA_B) and their credible
170 intervals (50%, 75% and 95%). The SEA_B is used as a proxy of the extent of the feeding
171 niche, parallel to the isotopic niche of Layman et al. (2012) and the credible intervals
172 represent the uncertainty surrounding the metric. The SEA_B quantifies the feeding niche
173 occupied by each species (i.e., intra-specific) while the overlap between SEA_B quantify the
174 feeding niche share by the two species (i.e., inter-specific). We computed a Bayesian estimate
175 for the overlap between the two SEA_B and an overlap coefficient (OC, express in %) to
176 quantify the proportion of feeding niche overlap. OC is the ratio between the Bayesian
177 estimates for the overlap and the minimal SEA_B filled by a species (similar to the Jaccard
178 similarity coefficient). OC of 0% corresponds to no overlap and of 100 % to a full SEA_B
179 overlap. All statistical analyses were performed with R 3.0.2 software.

180 3. RESULTS

181 3.1. Inter- and intra-specific variability of ecological tracers

182 Muscle $\delta^{15}\text{N}$ values were more variable than $\delta^{13}\text{C}$ values for both species (BET $\delta^{15}\text{N}$:
 183 min–max=11.6–14.2 ‰, Coefficient of variation CV=5.0 %; $\delta^{13}\text{C}$: -17.6–-16.5 ‰; CV=1.1 %
 184 and YFT $\delta^{15}\text{N}$: 10.1–13.2 ‰, CV= 7.8 %; $\delta^{13}\text{C}$: -17.8–-16.4 ‰; CV=1.7 %). The total lipid
 185 content in muscle showed large variations in BET (1.6–36.2% dw, CV=123 %) and YFT
 186 (0.5–18.2 % dw, CV=82.6 %). In liver tissue, the three most abundant FA in both BET and
 187 YFT were the saturated FA (SFA) 16:0 (BET: 17.4–31.7 %; YFT: 18.0–32.4 %), the poly-
 188 unsaturated FA (PUFA) 22:6n-3 (BET: 15.9–29.8 %; YFT: 12.9–32.0 %) and the mono-
 189 unsaturated FA (MUFA) 18:1n-9 (BET: 6.9–25.4 %; YFT: 4.4–24.2 %). Major FA in the
 190 two species also included PUFA 20:5n-3 (BET: 3.3–8.8 %; YFT: 3.4–10.4%) and 20:4n-6
 191 (BET: 2.3–8.3 %; YFT: 2.0–6.7 %); MUFA 18:1n-7 (BET: 0.8–4.1 %; YFT: 1.2–4.0%) and
 192 16:1n-7 (BET: 1.2–4.1 %; YFT: 1.1–3.8%); SFA 18:0 (BET: 6.1–11.7 %; YFT: 7.9–13.9%)
 193 and 17:0 (BET: 1.5–3.0 %; YFT: 1.0–2.0%). Overall, elevated proportions of PUFA n-3
 194 (>30 %) compared to PUFA n-6 (<10 %) were found for both species (Table 1).

195 ‘Species’ and to a lesser extent ‘length’ had the largest influence on the ecological
 196 tracers, especially on $\delta^{15}\text{N}$ values, TLC and FA profiles (highest F and Pseudo-F; Table 2).
 197 The spatiotemporal variables ‘longitude’ affected only FA while ‘fishing date’ has no
 198 influence on ecological tracers. First, inter-specific differences were noted with higher $\delta^{15}\text{N}$
 199 values in BET than YFT (mean \pm SD = 12.8 \pm 0.7 ‰ vs. 11.7 \pm 0.9 ‰; $t = -7.8$, $p < 0.001$) while
 200 a larger intra-specific variability was found in YFT’s values (CV = 5 % for BET vs. 8 % for
 201 YFT). TLC was also higher for BET ($t = 2.0$, $p < 0.05$) despite a larger intra-specific
 202 variability (CV = 133 % for BET vs. 83 % for YFT). Overall, FA profiles and levels of
 203 several individual FA were generally different between species (Pseudo-F = 10.5, $p < 0.001$
 204 and Table 1). Main differences concerned 18:1n-9 (ca. 14 \pm 5 % for BET vs. 11 \pm 6 % for YFT),
 205 18:0 (ca. 9 \pm 1 % for BET vs. 11 \pm 2 % for YFT) and 20:4n-6 (ca. 5 \pm 2 % for BET vs. 4 \pm 1 % for
 206 YFT). In contrast, no inter-specific differences were observed for the two other essential FA,

207 i.e. 22:6n-3 ($W = 873$, $p = 0.06$) and 20:5n-3 ($W = 1090$, $p = 0.80$). Regarding the main FA
 208 classes, SFA were in higher proportions in YFT than BET (ca. 39 ± 3 % vs. 36 ± 5 %; $W = 662$,
 209 $p < 0.001$), MUFA were higher in BET than YFT (ca. 23 ± 6 % vs. 18 ± 7 %; $W = 1625$, $p <$
 210 0.001) and no difference was observed for PUFA (40 ± 6 %; $W = 882$, $p = 0.07$) (Table 1).

211 Second, BET length explained 33% and 19% of the variance in $\delta^{15}\text{N}$ values and TLC,
 212 respectively. The $\delta^{15}\text{N}$ values linearly increased with length in BET from 12.7 ± 0.4 ‰ under
 213 80 cm to 13.5 ± 0.3 ‰ above 130 cm but no significant increase was observed for YFT (Fig.
 214 2a). TLC and its intra-specific variability also increased with length in BET, from 2.5 ± 0.8 %
 215 dw (CV = 30 %) for individuals under 80 cm to 13.1 ± 12.6 % dw (CV = 96 %) above 130 cm,
 216 while it remained constant in YFT (around 4.5 ± 3.7 % dw; Fig. 2c). Length influenced FA
 217 profiles (PERMANOVA, Pseudo-F = 5, $p < 0.05$) for both species, but results were different
 218 for each individual FA and generally unclear because of large variability within species. For
 219 example, the proportion of essential n-3 PUFA 20:5n-3 increased with length in BET, from
 220 5.0 ± 1.5 % of total FA under 80 cm to 7.7 ± 1.2 % above 130 cm but remained constant in YFT
 221 (6.2 ± 1.6 %; CV = 26 %) (Fig. 3a). In contrast, the proportion of essential n-6 PUFA 20:4n-6
 222 tended to decrease with length in both species, from 4.9 ± 1.5 % under 80 cm to 3.9 ± 1.1 %
 223 above 130 cm (mean \pm SD for the two species) but the relationship was poor ($r^2 = 0.12$)
 224 (Fig. 3b). For some other important FA trophic markers, such as 22:6n-3 and 18:1n-9, no
 225 relationship with ‘length’ was detected (Fig. 3c and 3d).

226 Finally, longitude influenced the FA profiles (Table 2). The addition of ‘longitude’ as an
 227 illustrative variable on PCA indicated an increasing proportion of 20:5n-3, 20:4n-3 and 18:2n-
 228 6 and a decreasing proportion of 20:4n-6 in tunas’ liver with the longitude value. Between
 229 17.6°W and 4°E , the proportion of 20:5n-3 increased similarly in both species from 5.2 ± 0.8 %
 230 to 6.7 ± 1.6 % (mean \pm SD for the two species; Fig. 4a) and the 20:4n-3 proportion increased
 231 from 0.3 ± 0.1 % to 0.2 ± 0.6 % (Fig 4b). Within this longitude range, the increase of the 18:2n-6

232 proportion was more restricted (mean ranging from 0.8 to 1%; $p < 0.05$, $r^2=0.06$). A large
233 decrease in the 20:4n-6 proportion was observed in BET only, (mean ranging from 6.7% to
234 3.8% ; $p < 0.001$, $r^2=0.28$; Fig. 4b). Carbon isotopic values were unaffected by the five tested
235 factors (Table 2). Fish 'sex' affected only TLC, females being leaner than males ($4.6\pm 5.5\%$
236 vs. $7.1\pm 8.0\%$; $t=2.7$, $p < 0.01$). 'Fishing date' had no effect on any of the ecological tracers
237 analyzed.

238 3.2. Comparison of tropical tuna feeding niches

239 First, feeding niches of BET and YFT mostly overlapped according to both isotopic and FA
240 data. Despite the slightly higher $\delta^{15}\text{N}$ values of BET, the isotopic feeding niches of the two
241 species overlapped of $\text{OC} = 76.8\pm 13.7\%$ (Fig. 5a). This result was in accordance with FA
242 feeding niches of the species, that also had an important overlap ($\text{OC} = 70.2\pm 8.2\%$; Fig. 5b).
243 FA feeding niches were only discriminated on the PCA-Dimension 2 which explained 21.3%
244 of the total variability in FA profiles, and was mainly driven by 20:5n-3 and by minors FA
245 such 24:1n-9, 17:0 18:2n-6 and 22:4n-6 and to a lesser extent by 20:1n-9 and 18:1n-9 (Fig.
246 5b). Second, the extent of tuna feeding niches (proxy of the intra-specific variability) varied
247 across tracers. The isotopic niche extent was smaller for BET than for YFT ($t=-192$, $p < 0.001$
248 with all posterior estimates smaller for BET than for YFT; Fig. 5a) while the FA niche extent
249 was larger for BET than for YFT ($t=74$, $p < 0.001$ with 89 % of the posterior estimates larger
250 for BET than for YFT; Fig. 5b). Finally, the variability in FA profiles was mainly explained
251 by individual variability among all fish rather than the difference between species (31.1 % of
252 the explained variability was observed on PCA-Dimension 1 while the two species were
253 discriminated on the PCA-Dimension 2; Fig. 5b).

254 4. DISCUSSION

255 Using SI and FA ecological tracers, we quantified for the first time the feeding niches of BET
256 and YFT and their overlap in the eastern Atlantic Ocean. Overall, there was a large overlap in

257 the feeding niches of tropical tunas, despite BET occupying a slightly higher trophic position
258 (higher $\delta^{15}\text{N}$ values). The fish length appeared to be the most influencing factor for ecological
259 tracers in BET. Spatiotemporal variables had no influence on SI values, while higher
260 proportions of diatoms' FA marker (20:5n-3) were observed in the liver tissue of tunas caught
261 beyond 5°E during the seasonal upwelling. Essential FA such as 20:5n-3 could therefore be
262 interesting tracers for the monitoring of tuna's trophic ecology over large spatial scales. Large
263 datasets of SI and FA should allow future studies to consider the effect of other biological and
264 environmental factors (e.g. tuna maturity, sea surface temperature, oxygen conditions) and
265 their interactions that we could not integrate here.

266 **4.1. Trophic position of yellowfin decreases in the Atlantic Ocean**

267 Spatial changes in baseline nitrogen composition preclude any direct comparison of tuna
268 isotopic values among oceans (Lorrain et al. 2015). In the Indian and Pacific Oceans, the
269 baseline $\delta^{15}\text{N}$ values change with latitude, probably related to denitrification process in
270 reduced oxygen conditions (Ménard et al. 2007, Lorrain et al. 2015) or diazotrophy in highly
271 oligotrophic areas (Houssard et al. 2017). In the tropical Atlantic Ocean, denitrification occurs
272 in the Caribbean Sea (Gruber and Sarmiento 1997) and upwelling occurs on the African coast,
273 suggesting possible baseline differences between the eastern and western Atlantic Ocean.
274 However, in the Gulf of Guinea, we assumed that the isotopic baseline is similar for these two
275 co-occurring tunas as fishing date and longitude had no effect on tuna isotopic values in our
276 study. BET and YFT are closely related (same genus; Dickson 1996), and because selected
277 individuals were at similar maturity stage and of similar length, we presume that differences
278 in $\delta^{15}\text{N}$ values did not result from physiological specificities. We concluded that higher
279 $\delta^{15}\text{N}$ values for BET indicate its slightly higher trophic position than YFT (difference of ca.
280 1.1 ‰), with less than one trophic level between the two species (i.e. difference < 3.4 ‰; Post
281 2002). Olson et al. (2016) obtained a smaller difference between the two species in the same

282 region (i.e. 0.5 ‰) due to higher $\delta^{15}\text{N}$ values for YFT in the past (12.2 ± 1.0 ‰ in 2000-2004
283 vs. 11.7 ± 0.9 ‰ here in 2013-2014). Regardless of possible fish length differences between
284 studies (no length effect detected for YFT here), it appears that the trophic level of YFT has
285 been decreasing over the last ten years. This suggests that either (i) YFT has a high trophic
286 plasticity related to a flexible and opportunistic diet all year round, and thus it is affected by
287 the random sampling; or (ii) as in the eastern Pacific Ocean, a decadal diet shift occurs in
288 YFT with changes in mid-trophic level communities, from large epipelagic fish (0-200 m) to
289 smaller mesopelagic species (200-1000 m), especially crustaceans (Olson et al. 2014). BET
290 feeds at greater depth on mesopelagic species and its trophic level has remained similar across
291 the two studies ($\delta^{15}\text{N}$ values of 12.7 ± 0.9 ‰ in 2000-2004 vs. 12.8 ± 0.6 ‰ here) suggesting a
292 decline in the trophic level of YFT prey over the last 15 years in the epipelagic ecosystem of
293 the Gulf of Guinea. Changes in the epipelagic communities can have a broader implication on
294 food web balance and stability and should be monitored in the Atlantic Ocean. For example, it
295 may increase predation on mesopelagic communities and favor competition among large
296 predators already suspected to be less resilient to climate change than previously assumed
297 (Lefort et al. 2015, Del Raye and Weng 2015). It might also affect tuna diving behaviour as
298 BET seems to dive according to the food availability in the upper layers (Arrizabalaga et al.
299 2008) and to the thermocline depth (Houssard et al. 2017).

300 Unfortunately, $\delta^{13}\text{C}$ values could not be compared with bulk values of Olson et al. (2016)
301 because lipid correction models require bulk C:N ratios (Logan et al. 2008) but changes in
302 carbon sources (forage habitats and phytoplankton taxa) during the last decades should be
303 explored. In the eastern Atlantic Ocean, a reduction of phytoplankton biomass might indeed
304 propagate into the food web through a bottom-up control by the end of the 21st century (Chust
305 et al. 2014). Here, we detected changes in the phytoplankton taxa with an increase of 20:5n-3
306 proportions in tunas collected after the upwelling period started (~ August) between 0° and

307 10°E. This change is consistent with the 20:5n-3-rich diatoms development favored by cool
308 upwelling waters (20–25 °C) in the eastern Gulf of Guinea (Wiafe et al. 2016). FA might thus
309 be an efficient tool to monitor forage taxa of tuna across seasons and years.

310 4.2. Large overlap in the tropical tuna feeding niches

311 Both SI and FA detected large overlaps (>70 %) in tuna feeding niches. Trophic position
312 derived from $\delta^{15}\text{N}$ values was the main source of difference in tuna feeding niche (see section
313 4.1). The highest trophic position of BET coincides with the $\delta^{15}\text{N}$ values from the Indian
314 Ocean: ca. 1 ‰ higher in BET than in YFT (Sardenne et al. 2016). Stomach content analyses
315 confirm this trend and shows that BET feeds more on high trophic level prey, such as squids,
316 than YFT (Cherel et al. 2007, Logan and Lutcavage 2013).

317 In contrast, $\delta^{13}\text{C}$ values were similar between species, probably because phytoplankton is the
318 major source of primary production in the pelagic systems (absence of coastal macroalgae or
319 plants with different isotopic carbon values). Large overlap (ca. 70%) in FA profiles indicated
320 that BET and YFT feed on similar prey species but in different proportions. The higher
321 MUFA proportion for BET compared to YFT (ca. $23\pm 6\%$ vs. $18\pm 7\%$), especially in 18:1n-9,
322 suggest a higher proportion of mesopelagic prey in the diet. In the tropical eastern Atlantic
323 Ocean, MUFA- and 18:1n-9-rich copepods such as *Megacalanus princeps* are found between
324 400 and 1000 m deep (Teuber et al. 2014) and in the stomachs of small fish ingested by
325 tropical tunas (Dragovich 1970). As a consequence, MUFA are also in great proportion in
326 small fish feeding on mesopelagic copepods such as the myctophids (Saito and Murata 1998)
327 and the cigarfish *Cubiceps pauciradiatus* (Young et al. 2010a), which are typical tuna prey
328 (Bard et al. 2002, Zudaire et al. 2015). In the Indian Ocean, MUFA are also present in great
329 proportion in tropical tunas >100 cm (Sardenne et al. 2016) which have deep dive capacities
330 and commonly swim down to 900 m depth (Schaefer et al. 2011). The tuna FA profiles
331 confirmed that BET generally feed at greater depth than YFT in the Gulf of Guinea, which is

332 consistent with vertical movement patterns recorded worldwide (Schaefer et al. 2009, Weng
333 et al. 2009).

334 The feeding niche overlaps observed here are larger than those observed in large tunas from
335 the Indian Ocean (no overlap for SI feeding niche and 53 % for FA feeding niche in the
336 Indian Ocean using bootstrapped convex hulls; Sardenne et al. 2016) although difference in
337 metrics may explain these dissimilarities (convex hulls vs. SIBER). Convex hulls would
338 provide lower overlaps here (see Fig. 3) but SIBER was preferred to reduce metrics bias
339 related to sample size (Jackson et al. 2011).

340 **4.3. Ontogenic changes are limited**

341 Diet change during ontogeny was relatively limited in the present study for tuna ranging 64–
342 174 cm FL. Only the trophic level of BET (through $\delta^{15}\text{N}$ values) increased linearly with
343 length, but this was not associated with noticeable changes in prey taxa according to FA
344 profiles. No ontogenic change was observed for YFT. Our sampling lacked, however, a robust
345 representation across length classes to detect such early changes. Stomach content analyzes of
346 YFT from the western Atlantic Ocean showed an increase in the proportion of small fish prey
347 in individuals between 70 and 90 cm FL (Vaske et al. 2003). In the Pacific and Indian Oceans,
348 diet changes with length were detected through a fast increase of $\delta^{15}\text{N}$ values for tunas
349 between 25–55 cm FL (Graham et al. 2006, Sardenne et al. 2016). In the Indian Ocean, $\delta^{15}\text{N}$
350 values slowly increased with length in both BET and YFT after 60 cm (ca. 1 ‰ between 60–
351 130 cm) (Ménard et al. 2007, Sardenne et al. 2016) as observed here for BET (Fig. 2a). Due
352 to their opportunist behavior, tunas continue to feed on small prey when larger/adults (Vaske
353 et al. 2003, Ménard et al. 2006), which have lower $\delta^{15}\text{N}$ values than larger prey (Logan and
354 Lutcavage 2013, Ménard et al. 2014), resulting in intermediate $\delta^{15}\text{N}$ values for large tunas and
355 limited changes in trophic level across length classes. Most FA proportions did not change
356 with tuna length, contrary to the observations from the Indian Ocean for 18:1n-9 and 22:6n-3

357 (Sardenne et al. 2016). Future work should focus on small and large-sized tuna (20-60 cm and
358 > 180 cm) to investigate ontogenic changes of foraging strategies in these species.

359 **4.4. Body condition of tropical tuna**

360 Lipids are the primary energy storage form in fish. The lipid content in an individual
361 generally indicates the energy available for vital functions and is therefore a good proxy of
362 fish global condition (Tocher 2003). Tropical tunas face limited seasonal changes in
363 comparison with their temperate counterparts and consequently store fewer lipids in muscle
364 (e.g. TLC~20 % dw in muscle tissue of bluefin tuna *T. thynnus*; Mourente et al. 2001). Yet,
365 muscle lipid content can provide valuable indication to compare general condition of tropical
366 tuna among regions. Here, the total lipid content of white muscle remained constant among
367 seasons (no influence of fishing date). Total lipid content in the Gulf of Guinea is similar to
368 TLC in the western central Pacific (TLC ~ 6.8±4.8 % dw, n=43; Lydie Couturier, unpubl.
369 data) and higher than in the western Indian Ocean (TLC ~ 2.3±1.1 % dw for both species,
370 n=111; Sardenne et al. 2016) although data from the three basins were collected across
371 different seasons. This suggests two non-exclusive assumptions: (i) BET and YFT food
372 sources are richer in the Atlantic and Pacific Oceans (in quality and/or quantity) which favors
373 energy storage in muscle, or (ii) tunas have different energy allocation strategies among world
374 regions. Tuna condition may indeed depend on prey quality, and seasonal upwelling favor the
375 biomass production from phytoplankton to small fishes which might benefit tunas
376 (Champalbert et al. 2008). Extended studies on the energy allocation strategies of tunas and
377 on lipid content in their prey in relation to the environmental condition (e.g. upwelling
378 intensity) are required to elucidate this point and assess its ecological implications (e.g.
379 vulnerability of populations). Reproduction should be further considered as it seasonally
380 affects lipid content (Mourente et al. 2001, Zudaire et al. 2014) and any decrease in energy
381 allocation to the reproductive process might influence tuna demography.

382 **4.5. Future directions**

383 Information about the trophic ecology of skipjack tuna *Katsuwonus pelamis* (over 50% of
384 total catch in the Eastern Atlantic Ocean; ICCAT 2015) sharing schools with small BET and
385 YFT, would improve our understanding of competition among co-occurring species and
386 ontogenic stages. In addition, skipjack tuna and small BET and YFT occur mostly in
387 epipelagic waters and can therefore be an interesting mid-trophic level ‘sampler’ in this
388 stratum (e.g. Cherel et al. 2007). The epipelagic stratum should be more extensively
389 monitored and the use of ecological tracers can be a powerful tool in this context.

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Fig. 1. Location of bigeye (BET; $n=45$) and yellowfin tuna (YFT; $n=50$) caught by purse-seiners in the Gulf of Guinea between July 2013 and September 2014. Major seasonal upwelling (grey area) develops in boreal summer (July–September).

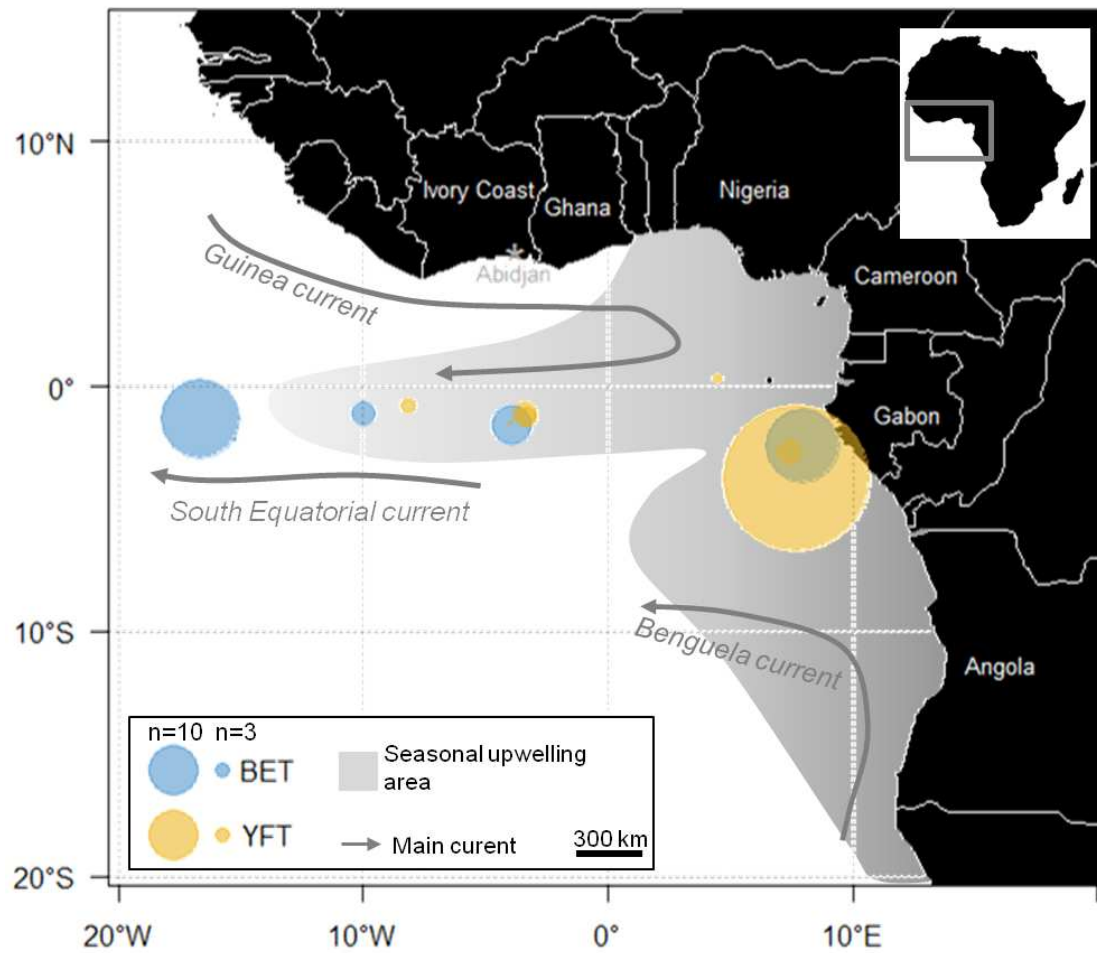


Fig. 2. Length influence on (a) nitrogen stable isotopic values ($\delta^{15}\text{N}$), (b) carbon stable isotopic values ($\delta^{13}\text{C}$) and (c) total lipid content (TLC) in muscle tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Linear regressions with confidence intervals are plotted when the relationship is significant.

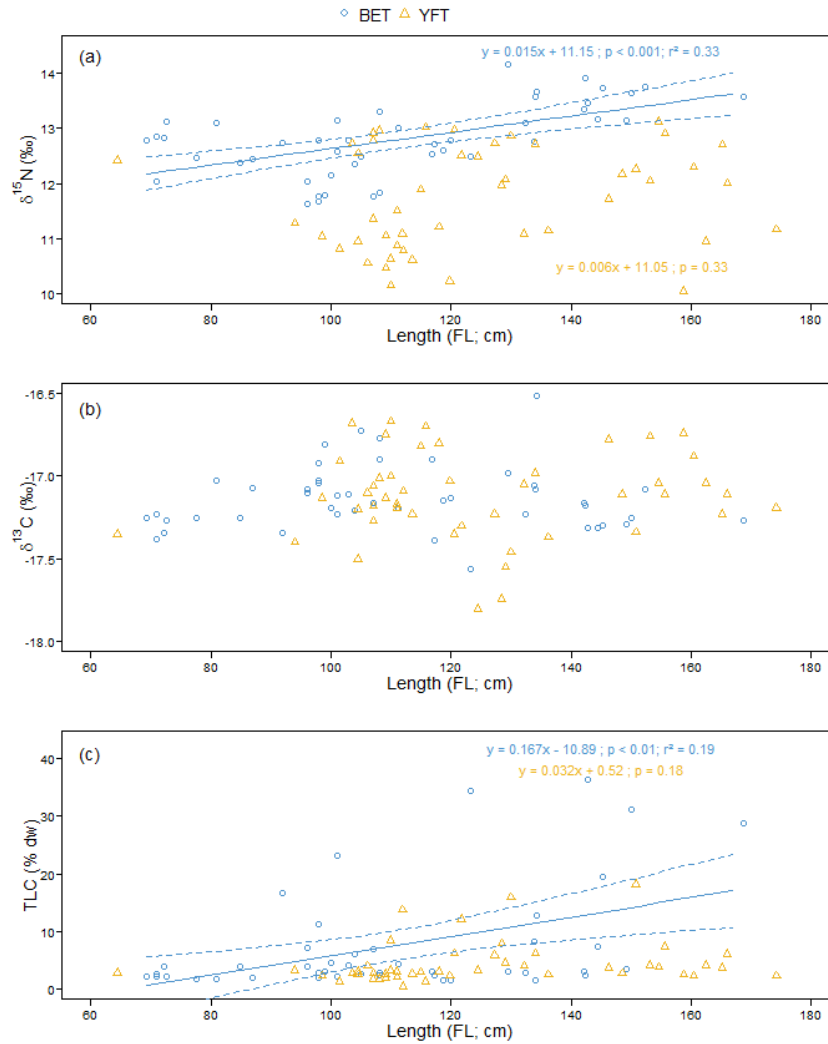


Fig. 3. Length influence on proportions of common fatty acids trophic markers in pelagic environment: (a) 20:5n-3, (b) 20:4n-6, (c) 18:1n-9 and (d) 22:6n-3, in the liver tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Simple linear regressions with confidence intervals are plotted when length influence is detected. The black regression in (b) is adjusted on both BET and YFT data (similar length influence for BET & YFT).

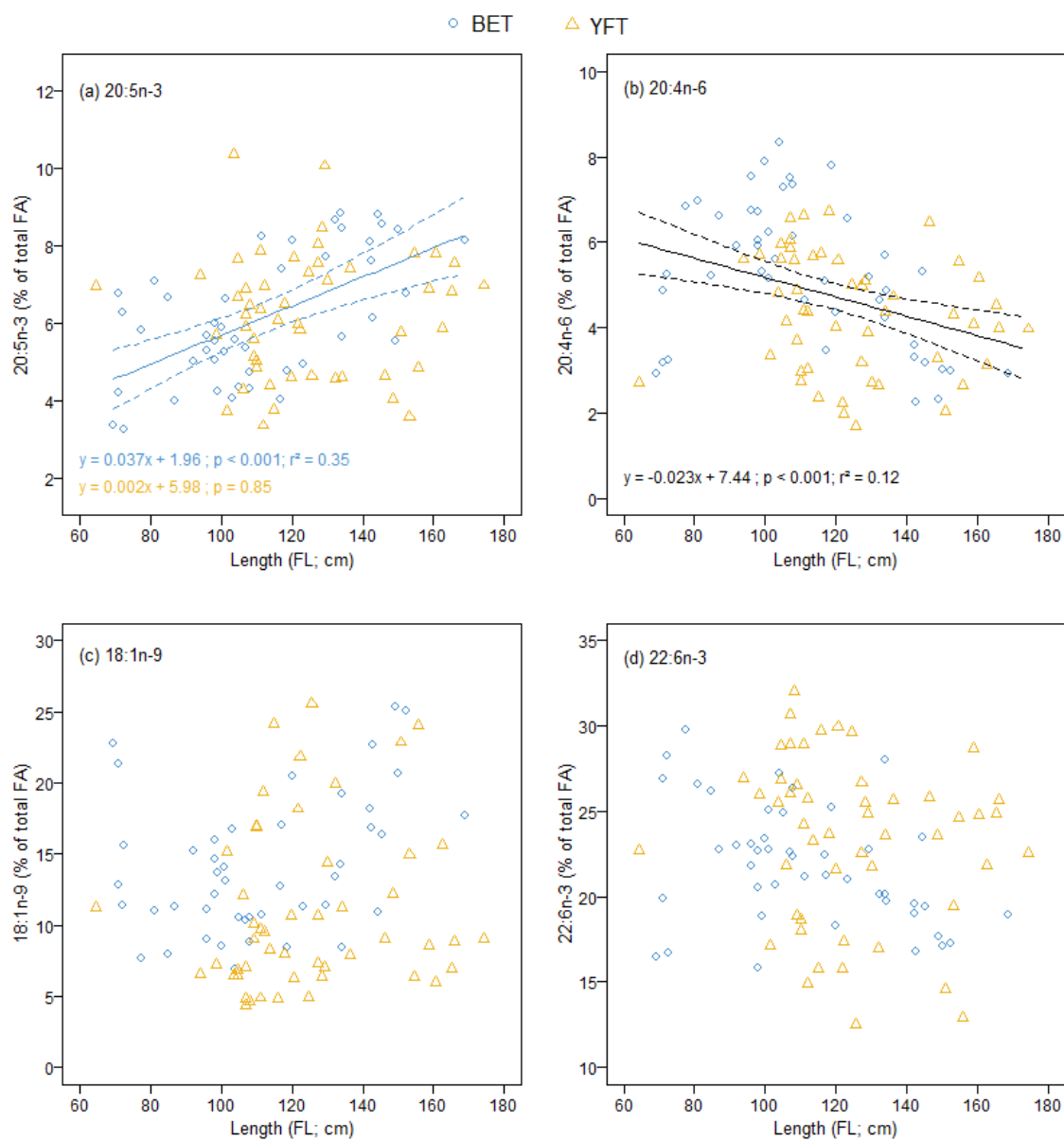


Fig. 4. Longitude influence on the three most affected fatty acids according to PCA: (a) 20:5n-3, (b) 20:4n-3 and (c) 20:4n-6, in liver tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Linear regressions with confidence interval are adjusted on both BET and YFT data (no species difference) (a & b) and for BET only (c). The intensity of the grey in background indicates the seasonal upwelling influence.

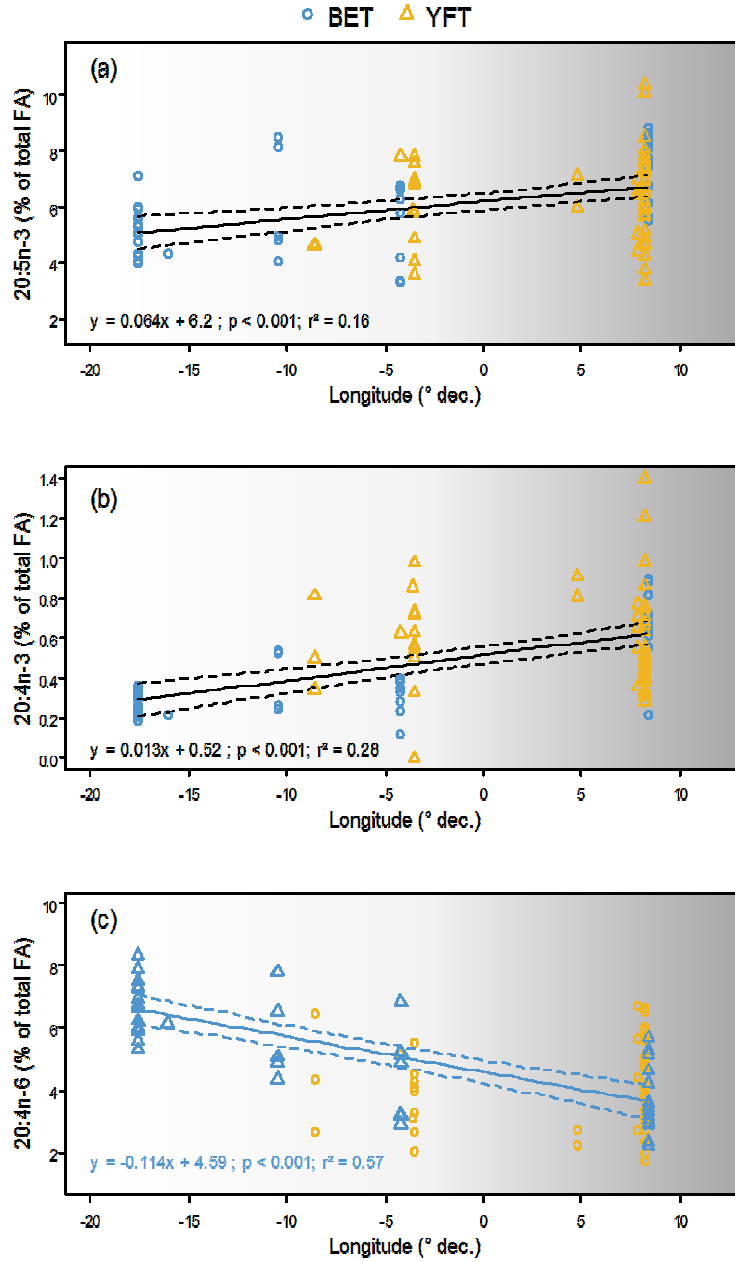


Fig. 5. Feeding niches of bigeye (BET; n=45) and yellowfin tuna (YFT; n=50) from the Gulf of Guinea using *SIBER* on (a) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of muscle, and on (b) Principal component analyze (PCA) dimensions of fatty acids (FA) profiles of liver. FA most influential in PCA ($\text{cos}^2 > 0.35$) are superimposed. Ellipses areas contain 95% of the data; Boxes represent the credible intervals (95, 75 and 50%) for the Bayesian standard ellipses areas and their overlaps (in green).

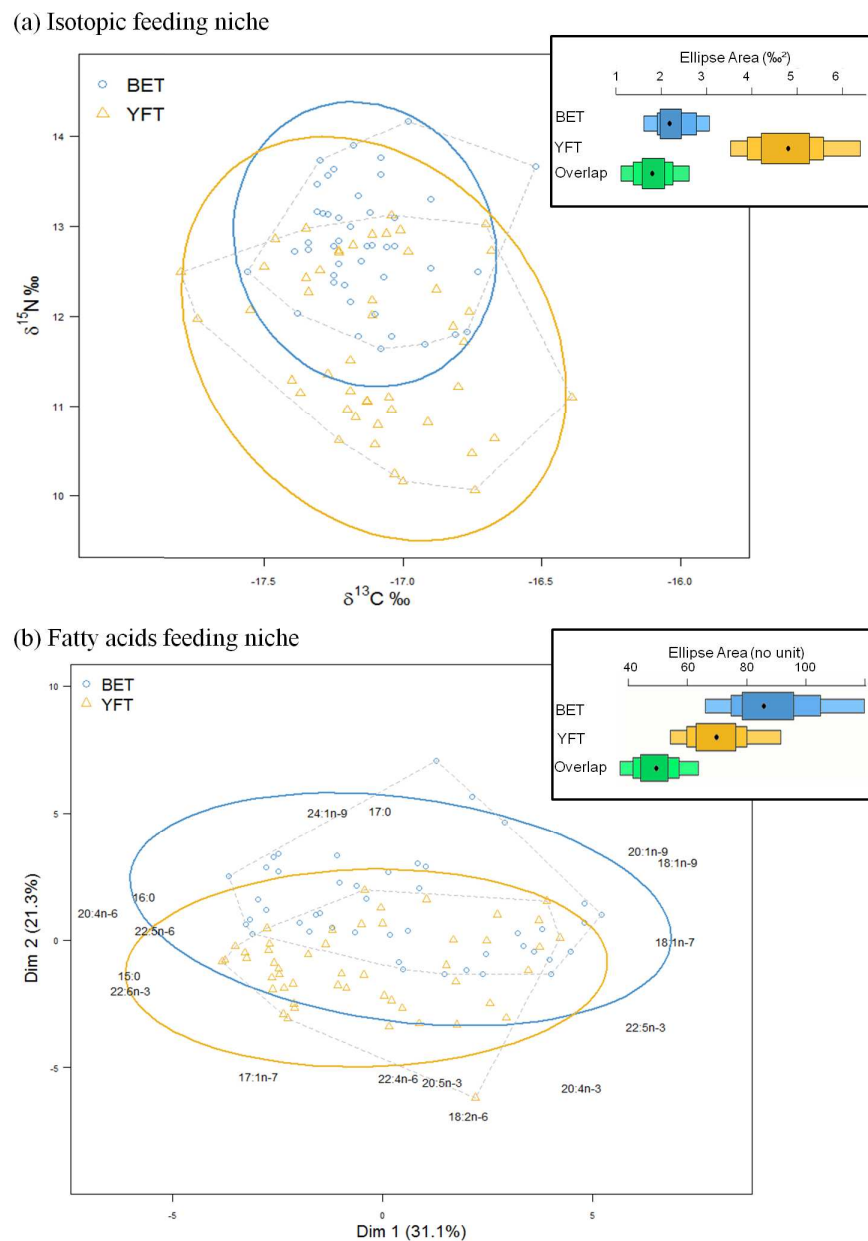


Table 1. Characteristics of fish, stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in ‰) and total lipid content (TLC in % dry weigh) of muscle and fatty acid (FA) distribution (in % of total FA) of liver for bigeye (BET) and yellowfin tuna (YFT) from the Gulf of Guinea. Data are mean \pm SD. *n* denotes sample numbers analyzed. * denotes significant differences between BET and YFT (post-hoc t-tests for stable isotopes and TLC and Wilcoxon tests for fatty acids; $p < 0.05$). SFA: Saturated FA; MUFA: Mono-unsaturated FA; PUFA: Poly-unsaturated FA.

	BET	YFT
Size (cm FL)	111.3 \pm 25.8	124.6 \pm 22.6
Sex ratio (♀ : ♂)	1 : 1.05	1 : 1.63
<i>Muscle</i>		
<i>n</i>	45	47
$\delta^{13}\text{C}$ (‰)	-17.1 \pm 0.2	-17.1 \pm 0.3
$\delta^{15}\text{N}$ (‰)	12.8 \pm 0.6	11.7 \pm 0.9 *
TLC (% dw)	7.6 \pm 9.3	4.5 \pm 3.7 *
<i>Liver</i>		
<i>n</i>	45	50
14:0	0.8 \pm 0.2	0.7 \pm 0.2 *
15:0	0.6 \pm 0.2	0.6 \pm 0.2
16:0	23.3 \pm 4.1	25.0 \pm 2.9 *
17:0	2.0 \pm 0.4	1.5 \pm 0.2 *
18:0	8.7 \pm 1.2	11.0 \pm 1.5 *
Σ SFA	35.5 \pm 4.7	38.9 \pm 3.2 *
16:1n-7	2.4 \pm 0.7	2.1 \pm 0.7 *
17:1n-7	1.0 \pm 0.3	1.2 \pm 0.2 *
18:1n-9	14.1 \pm 4.8	11.0 \pm 5.9 *
18:1n-7	2.7 \pm 0.8	2.3 \pm 0.7 *
20:1n-9	1.4 \pm 0.5	0.9 \pm 0.4 *
20:1n-7	0.4 \pm 0.8	0.1 \pm 0.1 *
24:1n-9	0.8 \pm 0.6	0.3 \pm 0.1 *
Σ MUFA	22.7 \pm 6.3	17.9 \pm 7.0 *
18:2n-6	0.9 \pm 0.2	1.0 \pm 0.2 *
20:4n-6 (ARA)	5.2 \pm 1.7	4.3 \pm 1.4 *
22:4n-6	0.4 \pm 0.2	0.8 \pm 0.4 *
22:5n-6	1.3 \pm 0.4	1.4 \pm 0.4
20:4n-3	0.4 \pm 0.2	0.6 \pm 0.2 *
20:5n-3 (EPA)	6.1 \pm 1.6	6.2 \pm 1.6
22:5n-3	1.7 \pm 0.9	1.7 \pm 0.7
22:6n-3 (DHA)	21.9 \pm 3.5	23.3 \pm 4.9
Σ n-6	7.8 \pm 2.0	7.5 \pm 1.7
Σ n-3	30.2 \pm 3.9	31.8 \pm 5.9
Σ PUFA	38.0 \pm 4.8	39.3 \pm 7.2

Table 2. Summary of factors influencing the ecological tracers of bigeye (BET) and yellowfin tuna (YFT) from the Gulf of Guinea according to ANOVA (after an AIC-based selection, _ denotes the unselected factors) for stable isotopes values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and total lipid content (TLC), and PERMANOVA (based on Bray-Curtis distance matrix and 1000 permutations) for fatty acids profile. P-values in bold denote factors with significant influence on the ecological tracers.

Factors	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			TLC			FATTY ACIDS			
	df	F	p-value	df	F	p-value	df	F	p-value	df	Pseudo-F	r ²	p-value
Fishing longitude	1	3.6	0.060	1	0.6	0.422	–	–	–	1	3.7	0.03	0.027
Fishing date	–	–	–	–	–	–	–	–	–	1	0.3	0.00	0.757
Species	1	3.3	0.071	1	55.1	0.000	1	5.6	0.020	1	10.5	0.10	0.001
Size	1	0.4	0.511	1	8.8	0.004	1	14.4	0.000	1	5.0	0.05	0.013
Sex	–	–	–	–	–	–	1	7.7	0.007	1	0.5	0.00	0.653
Species*Size	1	3.8	0.054	–	–	–	1	5.7	0.019	1	0.6	0.01	0.535