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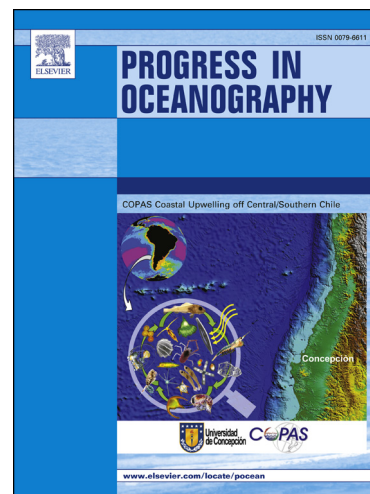
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1 **Trophic niches of sympatric tropical tuna in the Western Indian Ocean inferred by**
2 **stable isotopes and neutral fatty acids**

3

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18 **Highlights**

19 • Sympatric tropical tuna (bigeye, yellowfin and skipjack tuna) were sampled in the Indian
20 Ocean;

21 • Trophic niche partitioning was quantitatively assessed using time-integrated tracers;

22 • Intra- and inter-species resource overlap in three tropical tuna species was detected;

23 • Diet shifts at ~ 100 cm fork length were detected in the larger tuna species (bigeye and
24 yellowfin);

25 • New insights into the mechanisms involved in tropical tuna coexistence are provided.

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33 **ABSTRACT**

34 This study examined the trophic ecology of three sympatric tropical tuna species (bigeye
35 BET, skipjack SKJ, and yellowfin YFT) sampled in the Western Indian Ocean throughout
36 2013. Specifically we explored inter-specific resource partitioning and ontogenetic variability
37 using neutral fatty acids and stable isotope analysis of liver and muscle from small (≤ 100 cm
38 fork length, FL) and large (> 100 cm FL) tuna collected in mixed schools at the surface by
39 purse-seine. Both biochemical tracers were used to calculate trophic niche indices that
40 collectively revealed high potential for resource overlap, especially among small tuna.
41 Resource overlap appeared strongest between BET and YFT, with SKJ tissues having high
42 carbon isotope ($\delta^{13}\text{C}$) values ($-17 \pm 0.3\text{‰}$), lower nitrogen isotope ($\delta^{15}\text{N}$) values ($11.4 \pm 0.6\text{‰}$),
43 and higher relative proportion of poly-unsaturated fatty acids (PUFA) than the two other
44 species, indicating a different diet. Size was found to be a strong predictor for most
45 biochemical tracers in the three species with $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and total lipid content in the liver. In
46 the larger species (YFT and BET), proportions of mono-unsaturated fatty acids typically
47 increased with size, while quantities of PUFA decreased. In addition to ontogenetic
48 variability, trophic markers were shown to vary between sampling area and season: higher
49 lipid reserves and $\delta^{15}\text{N}$ values, and lower $\delta^{13}\text{C}$ values occurred during monsoon periods
50 around Seychelles than in the Mozambique Channel (parted from about 1500 km). Our multi-
51 tracer approach reveals the magnitude of potential competitive interactions in mixed tropical
52 tuna schools at both small and large sizes and demonstrates that ontogenetic niche
53 differentiation acts as a major factor of coexistence in tropical tuna.

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55 **Keywords:** niche area; resource overlap; mixed-school; ontogenetic changes; trophic tracers.

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66 **1. INTRODUCTION**

67 Three principal market tropical tuna species, bigeye (*Thunnus obesus*; BET), skipjack
68 (*Katsuwonus pelamis*; SKJ) and yellowfin (*T. albacares*; YFT), occur in the pelagic
69 environment in schools, often mixed, that are largely targeted by industrial tuna fisheries
70 including purse seine. In all oceans, tropical tuna schools display specific compositions with
71 SKJ, whose size does not exceed one meter, generally recovered with juvenile BET and YFT,
72 while adults of these two species (>100 cm) can be found together (Fonteneau et al., 2000;
73 Hare et al., 2015). Indeed, diving abilities increase with size in BET and YFT and result in
74 deeper vertical distribution with age, whereas SKJ is more vertically confined to the surface
75 layers due to the lack of swim-bladder and higher oxygen requirement (Graham and Dickson,
76 2004). In the purse seine fishery of the Western Indian Ocean, small tuna (fork length;
77 FL≤100 cm) mainly aggregate under floating objects in mixed schools and large tuna
78 (FL>100 cm) mainly form free-swimming schools, although some large fishes are also
79 associated with floating objects (Chassot et al., 2015). Sympatry of tropical tuna in mixed
80 schools suggests possible competition for trophic resources, particularly where resources are
81 limited.

82 The trophic ecology of tropical tuna has mainly been investigated through stomach content
83 analysis which suggests that all species collectively display opportunistic predatory
84 behaviour, feeding during the day on a large diversity of prey composed of small fish,
85 crustaceans and cephalopods (Potier et al., 2004; Olson et al., 2014). Globally, diet
86 composition has been shown to be influenced by local prey availability, fishing gear that
87 corresponds to specific environmental characteristics (e.g. depth, time of the catch), and
88 environmental conditions (e.g. season, geographical area) (Young et al., 2010b; Olson et al.,
89 2014). In the Indian Ocean, crustaceans, mainly the swimming crab *Charybdis smithii* and the
90 stomatopod *Natosquilla investigatoris*, were found to be the main prey of the three species,
91 especially during the day time in September-October (Romanov et al. 2009), followed by
92 small fish like *Cubiceps pauciradiatus* and small scombridae (Potier et al., 2001, 2004;
93 Grande, 2013; Zudaire et al., 2015). Cephalopods, especially the ommastrephids *Sthenoteuthis*
94 *oualaniensis* and *Ornithoteuthis volatilis*, occurred mainly in BET and YFT diet (Potier et al.,
95 2001; Ménard et al., 2013). In addition, feeding habits of tuna have been shown to vary
96 between large individuals that are shallow and deep-dwelling (Potier et al., 2004). While large
97 BET and YFT continue to feed on small prey, at equal size, BET hunt on larger prey than
98 YFT (Ménard et al., 2006), and the average prey size increases with predator size in the
99 tropical tuna (Jaquemet et al., 2011). Limited information is available on diet shift in tropical

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100 tuna, globally, with the exception of a study by Graham et al. (2006) who detected an
101 ontogenetic shift in coastal YFT from Hawaii at around 50 cm FL.

102 Since stomach content analysis only provides a snapshot of the animal's diet (Cortés, 1997),
103 alternative techniques capable of examining trophic relationships over longer time periods
104 have been progressively introduced. Stable isotopes (SI) and fatty acids (FA) are two of the
105 main trophic tracers currently used in trophic ecology as they have the advantage of reflecting
106 nutrients assimilated over period of weeks to multi-years, depending on the rate at which they
107 are incorporated from diet into consumer tissues and the turn-over of the tissues (Dalsgaard et
108 al., 2003; Buchheister and Latour, 2010). SI of carbon (expressed as $\delta^{13}\text{C}$, ‰) details the
109 origins of primary producers' with different values allowing primary feeding habitats to be
110 differentiated (i.e., continental vs. near shore marine vs. offshore marine; Clementz and Koch,
111 2001). Within an ecosystem, SI of nitrogen (expressed as $\delta^{15}\text{N}$, ‰) provides a proxy of an
112 animal's trophic position due to a predictable stepwise enrichment from the heavy to the light
113 isotope between trophic levels. Profiles of FA can be used to examine the dynamics of
114 predator-prey relationships, food web structure and energy fluxes (Iverson et al., 2004).
115 Increasingly the importance for dietary studies to focus on FA stemming from storage lipids
116 (i.e. neutral fatty acids, NFA) has been emphasized (Lee et al., 2006; Pethybridge et al., 2014)
117 as they provide fuel for energetic demands and are transferred with limited modifications
118 from prey to predator in comparison to structural lipids or other nutrients (Robin et al., 2003).

119 Trophic niche metrics (including nestedness, total niche area, niche widths, and niche
120 overlap) derived from functional ecology have been recently adapted to stable isotope ecology
121 (Layman et al., 2007; Cucherousset and Villéger, 2015) and have also been explored using FA
122 (Pethybridge et al., 2014). Several species-specific studies have used SI or FA to investigate
123 either tuna's trophic ecology (SI: Graham et al., 2006; Ménard et al., 2007; Zudaire et al.,
124 2015 ; FA: Saito et al., 1996; Parrish et al., 2013) or the effect of environmental changes
125 (Lorrain et al., 2015; Pethybridge et al., 2015b, 2015a). To our knowledge, no study has
126 undertaken inter-specific comparisons of the three tropical tuna' diet at the same time (their
127 niche partitioning) despite the ecological and economic significance of them co-occurring in
128 mixed schools. This study aimed to examine the extent of resource partitioning among
129 sympatric tropical tuna and with ontogeny for a given species in the Western Indian Ocean.
130 By using a multi-tracer (SI and NFA) and multi-tissue (muscle and liver) approach, our
131 comparative study provides valuable insights into how these co-occurring marine top-
132 predators compete or partition space and prey resources.

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134 2. MATERIAL AND METHODS

135 2.1. Tuna and tissue collection

136 Tuna sampling was conducted throughout 2013 in the Western Indian Ocean during the
137 unloading of the purse seiners at Victoria port, Seychelles. Fish selection was based on two
138 criteria: (i) the capture area from January to December to cover possible geographic and
139 seasonal trophic changes (sampling realized according to the information provided by the
140 purse-seine logbook; the mean coordinates were used when several activities, always
141 comprised within a maximum of 5° square, were grouped in purse-seine wells); and (ii) tuna
142 size, to examine ontogenetic dietary shifts. A total of 81 BET, 94 SKJ and 93 YFT were
143 collected and processed at the laboratory where FL (in cm, taken from the tip of the snout to
144 the fork of the tail), and sex (Indeterminate, I; Female, F; Male, M) were recorded for each
145 individual. Maturity stage was based on macroscopic examination of the gonads and was used
146 to group fish into two phases: developing (Dev, i.e., immature to developing fish), and
147 spawning (Spa, i.e., spawning capable to resting fish; Brown-Peterson et al., 2011). Table S1
148 gives details of the number of samples analyzed for each fish descriptor, i.e. size class, sex,
149 season, capture area and maturity stage. Two sub-samples of frozen fish of around 2 g (wet
150 weight, ww) were taken from the dorsal white muscle (sampled under the dorsal spine on the
151 left side) and the liver of each fish, and frozen within 20 min. All samples were stored at -
152 80°C until further analyses.

153 154 2.2. Trophic tracer analyses

155 The detailed procedures are presented in the Supplementary material.

156 A total of 518 samples (250 livers and 268 muscles) were analyzed for total lipid content
157 (TLC), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ according to the methods of Bodin et al. (2009) and Sardenne et al.
158 (2015b). Briefly, TLC of each sample, expressed in % of dry weight (dw), was estimated by
159 Accelerated Solvent Extraction with dichloromethane. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed together
160 on dried lipid-free samples using a Delta V Advantage isotope ratio mass spectrometer
161 interfaced to a Flash EA 1112 elemental analyzer (Thermo Scientific). Analytical precision
162 for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was <0.15‰ based on replicate measurements of internal laboratory
163 standard (acetanilide and peptone, Thermo Scientific).

164 A total of 367 samples (180 livers and 187 muscles) were selected for the analysis of NFA, to
165 cover a range of sizes. Compounds were separated on a TRACE 1310 gas chromatograph
166 equipped with a FAMEWAXTM column (30 m, 0.32 mm internal diameter, Restek) and a

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167 flame-ionization detector (Thermo Scientific). NFA results were expressed in % as a relative
168 abundance of total identified compounds.

169

170 **2.3. Data analyses**

171 Variations in TLC, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and NFA among tuna species were investigated to
172 test the effects of fish size, habitat (i.e., fishing area) and season. Two distinct size classes
173 based on the aggregative behavior were considered (FL ≤ 100 cm and >100 cm; Chassot et al.,
174 2015), with the second class only including BET and YFT. As previous studies highlighted
175 the peculiarity of the Mozambique Channel (MOZ) in term of productivity (Potier et al.,
176 2014), this sampling area was analyzed separately from the Western-Central Indian Ocean
177 (WCIO; Fig. 1). Finally, the monsoon circulation results in a strong seasonal variability in
178 oceanographic features and biological productivity in the Indian Ocean (Schott and
179 McCreary, 2001), with subsequent effects on tuna prey such as mesopelagic fishes (Vipin et
180 al., 2012). Hence, four distinct seasons were considered in subsequent analyses: North-
181 Eastern Monsoon (NEM) from mid-November to mid-March, South-Western Monsoon
182 (SWM) from mid-May to mid-September, Spring Inter-Monsoon (SIM) from mid-March to
183 mid-May, and Autumn Inter-Monsoon (AIM) from mid-September to mid-November.
184 However, season was excluded from area/season interaction tests because the sampling was
185 unbalanced between these two variables (Table S1) in relation to tropical tuna seasonal
186 migration (Kaplan et al., 2014).

187 A total of 27 NFA accounting each for $>0.8\%$ in all samples cumulated (i.e., the most
188 representative) were kept for statistical analyses and arc-sinus root squared transformed to
189 improve normality and homoscedasticity (Underwood, 1997). Permutational multivariate
190 analyses of variance (PERMANOVA) based on Euclidean distance matrix were first
191 performed on NFA profiles of muscle and liver separately to test the effects of species, size
192 class, area and season. Non-metric multidimensional scaling (NMDS), also based on the
193 Euclidean distance matrix, was then used to compare the samples through the relative
194 dissimilarity in NFA profiles among tested groups. NMDS is a rank-based approach that aims
195 to summarize the information provided by a large set of dimensions. Here, a set of three
196 dimensions was considered and an optimal configuration of the individuals was based on a
197 maximum limit value of 0.1 for the stress (i.e., goodness-of-fit index). The samples
198 coordinates in the three dimensions of the NMDS were subsequently used to investigate the
199 ontogenetic changes in NFA composition in each tuna species. Differences in individual NFA
200 compounds were assessed using Wilcoxon's tests, pairwise tests being used when more than

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201 two means were compared. Analysis of variance (ANOVA) was finally performed on $\delta^{13}\text{C}$,
202 $\delta^{15}\text{N}$ and TLC, and followed by Tukey's honestly significant difference (HSD) post hoc tests.
203 Ontogenetic changes in trophic tracers in each tissue were investigated for each species using
204 Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990). FL was used as a proxy
205 of age because of the difficulties associated with age estimation in tropical tuna (Sardenne et
206 al., 2015a). Sex of the fish (S) and maturity stage (D) were included in the model in addition
207 to sampling area (A) and season (M) following:

$$208 \quad T_i = a + s(FL_i) + A_i + M_i + S_i + D_i + \varepsilon_i,$$

209 with T is the trophic tracer ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, TLC or NMDS scores of NFA profiles), a the
210 intercept, s the spline function smoother (with no preset value concerning the amount of
211 smoothing), i indicates individual fish of a given species, and ε is the random noise term
212 assumed to be normally distributed with mean zero and constant variance. The best model
213 was selected using Akaike Information Criterion (AIC), and ANOVAs were used to detect
214 significant effects of covariates. When a significant size effect was detected on NFA profiles
215 in a given tissue, the initial model was also applied on the three main NFA families (mono-
216 unsaturated FA, MUFA; poly-unsaturated FA, PUFA; and saturated FA, SFA) and essential
217 NFA (i.e. 22:6 ω 3 (DHA); 20:5 ω 3 (EPA); 20:4 ω 6 (AA); 18:2 ω 6; 18:3 ω 3; Arts et al., 2001) to
218 investigate how they vary with size.

219 Species-specific indices of nestedness based on SI or NFA (i.e. convex hull areas or volumes)
220 were calculated to compare tuna' trophic niches as described in Cucherousset and Villéger
221 (2015). Convex hull allows integration of organisms positioned at the edge of SI or NFA
222 niches. The indice of nestedness is the ratio between the niche volume shared and the minimal
223 volume filled by a group. It ranges between 0 and 1 with 0 indicating no overlap between the
224 trophic niches and 1 indicating a perfect overlap or a full inclusion of the lowest volume in the
225 larger one. It was computed on an isotopic two-dimensional standardized space, where each
226 axis was scaled to have the same range (e.g. 0–1) for each stable isotope (INes; Cucherousset
227 and Villéger, 2015), and on a NFA three-dimensional space (FANes), based on NMDS
228 coordinates. These two indices were calculated to compare species trophic niches, according
229 to size class and sampling area, using bootstrapping to overcome differences in the number of
230 individuals per species.

231 All statistical analyses were performed using R 3.0.2 software. The *vegan* library (Oksanen et
232 al., 2015) was used for PERMANOVA and NMDS and the *mgcv* library (Wood and Wood,

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233 2015) was used for fitting GAMs. Indices of nestedness were calculated using the published R
234 code of Cucherousset and Villéger (2015).

235

236 3. RESULTS

237 3.1. Inter-specific differences

238 3.1.1. Total lipid content comparisons

239 TLC was significantly higher in liver ($15\pm 8\%$) than muscle ($3\pm 2\%$, Tukey HSD, $P<0.0001$;
240 Table 1). Muscle TLC did not vary with season, area, size class or species (Table 2). Liver
241 TLC significantly varied with size class and season, but similarly to muscle, no inter-specific
242 differences were highlighted in liver samples either (Table 1). According to post-hoc Tukey
243 HSD comparisons, large tuna presented higher lipid-rich livers than small tuna (TLC =
244 $22\pm 11\%$ and $14\pm 6\%$, respectively, $P<0.0001$). Tuna liver was also characterized by
245 significant lower TLC during SIM than during the monsoon periods with tuna sampled during
246 this period being $4\pm 7\%$ leaner than during NEM ($P<0.05$) and $5\pm 2\%$ leaner than during SWM
247 ($P<0.001$). While ANOVA showed that there was a significant influence of area on TLC in
248 both tissues in each size class (Table 2), post-hoc tests detected no TLC differences between
249 area in each size class in liver (small and large size classes, $P=0.80$ and $P=0.29$ respectively)
250 and muscle ($P=0.12$ and $P=0.05$ respectively).

251

252 3.1.2. Neutral fatty acids profiles

253 NFA profiles for all tuna were consistently dominated by saturated compounds (means
254 ranging from 42 to 49%, Table 1), that remained constant across size classes. However,
255 varying importance of PUFA (17–37%) and MUFA (13–35%, Table 1) was observed. Among
256 the species, the most common NFA in both tissues, in decreasing order of importance, were
257 typically: 16:0 ($32\pm 7\%$), 22:6 ω 3 (DHA; $19\pm 7\%$), 18:1 ω 9 ($13\pm 7\%$) and 18:0 ($11\pm 3\%$). There
258 were significant differences in NFA profiles between tissues, with muscle having higher
259 proportions of PUFA and especially of DHA than liver (PUFA: $33\pm 9\%$ vs. $29\pm 9\%$, $W=13379$,
260 $P<0.001$; DHA: $21\pm 7\%$ vs. $17\pm 6\%$, $W=10364$, $P<0.0001$).

261 For both tissues, differences in NFA profiles were observed among size classes, species, areas
262 and seasons, in decreasing order of importance. Interactions among size classes and species
263 and among species and area were also detected in muscle (both $P<0.05$), when a significant
264 interaction between size classes and area was detected in liver ($P<0.01$; Table 2).

265 In both tissues, small tuna (≤ 100 cm FL) generally had higher proportions of PUFA ($32\pm 8\%$
266 in liver and $35\pm 9\%$ in muscle, the three species combined) than larger tuna (PUFA: $22\pm 10\%$

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267 in liver and $29\pm 8\%$ in muscle, YFT and BET combined; both $p < 0.0001$), and especially of
268 essential PUFA (e.g. in liver: DHA: $18\pm 5\%$ vs. $12\pm 6\%$; EPA: $5\pm 2\%$ vs. $3\pm 2\%$ and AA: $4\pm 1\%$
269 vs. $3\pm 2\%$). In contrast, MUFA were higher in large tuna, within both liver ($32\pm 10\%$ vs.
270 $21\pm 8\%$, $W=5315$, $p < 0.0001$) and muscle ($25\pm 6\%$ vs. $18\pm 6\%$, $W=5442$, $P < 0.0001$). Levels of
271 SFA remained similar between size class: $46\pm 7\%$ in liver ($W=2954$, $P=0.28$) and $47\pm 9\%$ in
272 muscle ($W=2886$, $P=0.16$), with limited differences in individual SFA (mean difference $< 2\%$
273 for 15:0 and 17:0 in liver and 14:0, 18:0 and 20:0 in muscle).

274 Among the species, higher PUFA proportions were found in SKJ liver and muscle ($32\pm 8\%$
275 and $37\pm 9\%$, respectively) than in the two other species (on average $27\pm 9\%$ and $31\pm 8\%$ for
276 liver and muscle respectively for YFT and BET, small and large specimens combined, all
277 $P < 0.0001$). DHA mainly contributed to these inter-specific discriminations, with higher
278 proportions in SKJ ($19\pm 6\%$ and $24\pm 6\%$ in liver and muscle, respectively), while BET and
279 YFT had similar proportions (on average $15\pm 6\%$ and $20\pm 6\%$ in liver and muscle,
280 respectively). In contrast, regardless of size class, in both tissues MUFA proportions were
281 highest in BET followed by YFT then SKJ (e.g. in liver, $30\pm 10\%$ in BET, $25\pm 11\%$ in YFT
282 and $18\pm 5\%$ SKJ, small and large specimens combined for BET and YFT, all $P < 0.05$). Those
283 differences were mainly attributed to 18:1 ω 9, 18:1 ω 7 and 20:1 ω 9 (Table 1). Overall, SFA
284 were in comparable proportions among species, despite some specific differences in liver (e.g.
285 16:0 was higher, $36\pm 7\%$ in SKJ compared to $34\pm 5\%$ in YFT and $31\pm 5\%$ in BET small and
286 large specimens combined for BET and YFT).

287 The influence of sampling area on tuna's NFA was highlighted by post-hoc Wilcoxon's tests,
288 but different results were obtained for each tissue. Slightly higher proportions of SFA were
289 found in muscle of tuna from WCIO ($47\pm 9\%$) than those from MOZ ($44\pm 9\%$; $W=4043$,
290 $P < 0.05$), while proportions of PUFA and MUFA were similar ($P=0.15$ and $P=0.10$). In tuna'
291 liver, proportions of PUFA were higher in MOZ ($34\pm 7\%$) than in WCIO ($28\pm 10\%$; $W=1927$,
292 $P < 0.005$), mainly driven by changes in DHA ($W=3714$, $P < 0.01$) but not EPA ($P=0.09$), the
293 second most relevant PUFA. In contrast, MUFA were higher in WCIO ($25\pm 11\%$) than in
294 MOZ ($20\pm 8\%$; $W=3765$, $P < 0.005$) while proportions of SFA were the same ($P=0.718$).

295 Seasonal effects were observed in tuna' liver due to variations in ω 6 proportions between SIM
296 ($7\pm 2\%$) and SWM ($6\pm 2\%$; $P < 0.01$) and in EPA proportions between AIM ($6\pm 2\%$) and NEM
297 ($5\pm 2\%$; $P < 0.05$). Seasonal effects were also observed in tuna' muscle largely due to
298 differences in MUFA proportions between SIM ($22\pm 6\%$) and NEM ($18\pm 7\%$; $P < 0.01$).

299 Several interactions among factors influenced tissue NFA profiles. In liver, only an
300 interaction between size class and area was detected (Table 2). Thus, large YFT in the WCIO

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301 had significantly different liver NFA profiles than similar sized YFT in the MOZ
 302 (PERMANOVA, Pseudo-F=16.9, $P<0.001$), with on average 14% more MUFA than YFT
 303 from MOZ (W=20, $P<0.005$), mainly attributed to 18:1 ω 9 (12% more; W=18, $P<0.005$), but
 304 on average 15% less PUFA (W=137, $P<0.001$). In contrast, in the liver of small tuna almost
 305 no differences between areas were detected: only ω 6-PUFA family was found higher of 1% in
 306 MOZ (MOZ: $8\pm 1\%$, WCIO: $7\pm 1\%$; W=2096, $P<0.001$).

307 In muscle, inter-specific size-relevant differences from both areas were detected. In small tuna
 308 from WCIO, higher proportions of MUFA were reported in BET compared to YFT (mean
 309 difference of 5%, $P<0.05$) and SKJ (mean difference of 9%, $P<0.001$). Such differences were
 310 mainly attributed to 18:1 ω 9 ($P<0.001$). No significant inter-specific differences were detected
 311 among small tuna for PUFA, ω 3- and ω 6-PUFA families, however there were significantly
 312 higher contributions of EPA, DHA, AA, and 22:5 ω 6 observed in SKJ compared to both YFT
 313 and BET ($P<0.05$) which showed similar profiles. Only one SFA, 18:0, was found to differ
 314 among muscle of small tuna, with lowest proportions found in BET (12% of total NFA) than
 315 in SKJ (14%, $P<0.05$) and YFT (14%, $P<0.05$). For large tuna in the WCIO, no differences in
 316 NFA profiles were noted among species (PERMANOVA, Pseudo-F=1.0, $P=0.36$): only
 317 18:3 ω 3 was found to differ inter-specifically in the muscle. Similar inter-specific size-
 318 comparable differences were also detected among tuna sampled in the MOZ, with lower
 319 proportions of PUFA recorded in BET muscle compared to SKJ (mean difference of 14%,
 320 $P<0.001$) and YFT (mean difference of 8%, $P<0.005$), the highest proportions being measured
 321 in SKJ muscle (e.g. DHA on average 8% and 5% lower in BET than SKJ and YFT
 322 respectively). The highest MUFA proportions were observed in BET and the lowest in SKJ,
 323 mainly attributed to the 18:1 ω 9, on average 5% higher in BET than in SKJ for muscle
 324 ($P<0.05$).

325

326 3.1.3. Stable isotope values

327 $\delta^{13}\text{C}$ values varied with area and size class in liver and by size class, species and season in
 328 muscle. $\delta^{15}\text{N}$ values significantly varied with area, season, species and according to a species-
 329 area interaction in both tissues, but varied with size class in muscle only and with a size class-
 330 species interaction in liver (Table 2).

331 Muscle $\delta^{13}\text{C}$ values were slightly lower during NEM ($-17.1\pm 0.2\text{‰}$) than AIM ($-16.8\pm 0.2\text{‰}$)
 332 and SWM ($-16.9\pm 0.4\text{‰}$) ($P<0.05$) but no difference was observed in liver. $\delta^{15}\text{N}$ values in tuna
 333 muscle were significantly higher in WCIO ($12.2\pm 0.9\text{‰}$) than in MOZ ($10.2\pm 1.3\text{‰}$, $P<0.001$),
 334 with a similar trend displayed in the liver (WCIO: $11.4\pm 0.7\text{‰}$; MOZ: $9.3\pm 1.2\text{‰}$, $P<0.001$).

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335 $\delta^{15}\text{N}$ values in both tissues were lower during SIM than during the other seasons (i.e. in liver:
336 mean value in SIM was 1.9‰ lower than AIM, 1.8‰ lower than NEM and 1.6‰ lower than
337 SWM, $P<0.001$; and in muscle: mean value in SIM was 1.3‰ lower than AIM, 1.0‰ lower
338 than NEM and 1.5‰ lower than SWM, $P<0.001$).

339 Size-class differences were reported for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle with higher
340 values reported in large tuna in comparison to small tuna (mean difference of 0.2‰ and 0.8‰
341 respectively, $P<0.001$). In liver, $\delta^{13}\text{C}$ values were significantly higher in large tuna than in
342 small tuna (mean difference of 0.3‰, $P<0.001$), but no difference in $\delta^{15}\text{N}$ values was
343 observed ($P=0.784$).

344 Inter-specific size-comparable differences from the WCIO were found using post-hoc Tukey
345 HSD comparisons. In small tuna, $\delta^{13}\text{C}$ values were slightly lower in BET compared to YFT
346 and SKJ in muscle (mean difference of 0.2‰, $P<0.01$), while no inter-specific differences
347 were detected in liver (both $P>0.1$). In contrast, $\delta^{15}\text{N}$ values were significantly higher in BET,
348 closely followed by YFT, and finally SKJ in both tissues (Table 1), with mean differences
349 among species ranging from 0.3 to 1.1‰ ($P<0.05$, except between BET and YFT in muscle:
350 $P=0.12$). In large tuna, significantly lower $\delta^{13}\text{C}$ values were found in BET muscle than in
351 YFT muscle (on average 0.5‰, $P<0.001$), while the low differences (of 0.2‰) in liver were
352 not significant ($P=0.09$). BET presented significantly higher $\delta^{15}\text{N}$ values than YFT for both
353 tissues (on average 1‰ and 0.8‰ higher, respectively, $P<0.001$). In MOZ, $\delta^{13}\text{C}$ values were
354 slightly lower in small BET compared to small YFT and SKJ, as in WCIO (mean difference
355 of 0.2‰, $P<0.05$). On the contrary, small BET had higher muscle $\delta^{15}\text{N}$ values (1.7‰ higher)
356 than YFT ($P<0.005$) and SKJ ($P<0.001$), while small YFT and SKJ exhibited similar muscle
357 $\delta^{15}\text{N}$ values ($P=0.986$). In liver, the highest $\delta^{15}\text{N}$ values were recorded for small BET
358 followed by small YFT and finally SKJ, with mean differences ranging from 0.7 to 1.9‰
359 ($P<0.05$). Post-hoc Tukey HSD comparisons revealed significantly lower $\delta^{15}\text{N}$ values in large
360 YFT from MOZ than in large YFT from WCIO in muscle and liver (mean difference of
361 2.3‰, $P<0.001$ and 1.9‰, $P<0.001$, respectively). $\delta^{13}\text{C}$ values in muscle of large YFT were
362 also lower in MOZ than in WCIO (mean difference of 0.3‰, $P<0.001$), while no difference
363 was detected in liver ($P=0.386$).

364

365 **3.1.4. Biochemical trophic niche metrics**

366 Trophic niche overlap based on SI (INes) and FA (FANes) was explored among the three tuna
367 species differentiating patterns between tissues, size classes and sampling areas. In WCIO,
368 index values showed less variation in liver (ranging from 0.30 to 0.81) than in muscle (0.09 to

369 0.81, Table 3), while they were similar in MOZ (from 0.08 to 0.73 in liver and from 0.06 to
370 0.63 in muscle). Although some differences were evident between INes and FANes, the
371 degree of overlap among species agreed, with the lowest trophic space shared by BET and
372 SKJ.

373 According to these indices in both tissues of small tuna, and in particular muscle, SKJ and
374 BET shared limited trophic space, whereas the highest niche overlap was between BET and
375 YFT. Indeed, in muscle of small tuna sampled in the WCIO, the NFA niche volume defined
376 for YFT overlapped with that of BET, while the niche area of SKJ differed mainly due to
377 PUFA (Fig. 2a). A similar pattern was observed for INes in liver, with large overlap between
378 YFT and BET (0.81) due to higher $\delta^{15}\text{N}$ values compared to SKJ (Fig. 3a). However, in
379 muscle, the highest INes was observed between small YFT and SKJ (0.81). In large tuna,
380 FANes in both tissues showed quite large trophic overlaps between BET and YFT (Table 3,
381 Fig. 2b). On the contrary, differences in INes were apparent with no overlap of trophic space
382 between large BET and YFT in muscle (INes=0.0) and a limited overlap in liver (INes=0.34)
383 (Fig. 3b).

384 In MOZ, SKJ and small YFT shared most of their trophic space, while small BET and small
385 YFT shared almost a third of their trophic space (with FANes and INes in both tissues ranging
386 from 0.40 to 0.73 and 0.29 to 0.44, respectively, Table 3). In comparison, small BET and SKJ
387 exhibited reduced overlaps according to both FANes and INes in both tissues.

388

389 **3.2. Intra-specific variability focusing on ontogenetic and sexual shifts**

390 **3.2.1. Bigeye tuna**

391 GAM predicted TLC in BET remained constant in muscle (3 ± 2 % dw) while it generally
392 increased in liver with size from around 10 to 20% dw between 29.5 and 160.8 cm FL, with
393 no influence of other tested variables, as sex (Table S2). The dominance of the predicted
394 proportions of MUFA and PUFA (predominantly represented by 18:1 ω 9 and DHA
395 respectively) were reversed in liver at 91 cm FL with MUFA higher in larger individuals (Fig.
396 4a). Proportions of MUFA increased linearly with size, while PUFA proportions decreased
397 (23.6% of deviance explained with size alone), mainly due to a decrease of DHA proportion
398 in comparison to other essential NFA (Fig. 4b). No change was observed for SFA in liver,
399 which remained the main NFA class throughout the BET size range. Finally, deviance
400 explained for the main NFA families in BET muscle was poor (ranging from 5.3% for PUFA
401 to 23.4% for MUFA), but there was also a slight increase of MUFA proportion with size. No
402 influence of maturity or sex was observed in NFA in either tissues (Table S3a and S3b).

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403 Predicted values of both isotopes were mainly affected by size and area in both BET tissues
404 (Table S2). Season also influenced $\delta^{13}\text{C}$ values in both tissues, but no influence of sex or
405 maturity on isotopic data was observed. No clear pattern with size was obtained for liver $\delta^{13}\text{C}$
406 values, with a mean increase from around $-18.2\pm 0.2\text{‰}$ to $-17.4\pm 0.2\text{‰}$ between 30 and 76 cm
407 FL before oscillating around $-17.4\pm 0.5\text{‰}$ until 160 cm FL (Fig. 5a). $\delta^{13}\text{C}$ values in muscle
408 displayed an increase from 30 to 77 cm FL (from around $-17.5\pm 0.1\text{‰}$ to $-17.0\pm 0.1\text{‰}$) and
409 then remained constant at $-17\pm 0.1\text{‰}$ until 160 cm FL (Fig. 5b). Liver $\delta^{15}\text{N}$ values slowly
410 increased with BET size between 30 and 69 cm FL (i.e. mean increase of 0.7‰ in 39 cm,
411 from around $11.3\pm 0.2\text{‰}$ to $12\pm 0.1\text{‰}$), then remained stable until 160 cm FL (Fig. 5a). In
412 muscle, the main variation of $\delta^{15}\text{N}$ was observed from 30 to 54 cm FL (i.e. mean increase of
413 1.7‰ in 24 cm, from around 11.0 ± 0.2 to $12.7\pm 0.2\text{‰}$), followed by relatively constant values
414 until 140 cm and a slight increase between 140 and 160 cm (i.e. from around $13.4\pm 0.2\text{‰}$ to
415 $13.7\pm 0.3\text{‰}$; Fig. 5b).

416

417 3.2.2. *Yellowfin tuna*

418 TLC in YFT muscle and liver was affected by size (Table S2) but with unpredictable trends,
419 and the fitted GAM performed poorly for muscle with only 11.6% of deviance explained. In
420 liver, TLC oscillated with size, and males had a slightly higher TLC than females and
421 indeterminate individuals combined ($23\pm 11\%$ vs. $15\pm 8\%$, $P<0.05$). NFA profiles were mainly
422 affected by size (Table S3a). In liver, the mean proportions of MUFA and PUFA were
423 reversed at 109 cm FL (Fig. 4a): MUFA increased by about 20% from 109 to 160 cm FL
424 (from around 50% to 70%), when PUFA subsequently decreased (from around 55% to 35%).
425 Size explained 38% of MUFA and 51.5% of PUFA variability in liver, but showed minor
426 influence on SFA (Table S3b). Among PUFA, three essential NFA contributed strongly to the
427 observed PUFA decrease with size in liver: DHA, EPA and AA (Fig. 4b). Although minor
428 contributors, 18:3 ω 3 and 18:2 ω 6 also significantly decreased with size ($P<0.0001$). In muscle,
429 PUFA and SFA generally remained constant with size ($38\pm 3\%$ and $44\pm 5\%$, respectively). In
430 contrast, size explained 58.4% of MUFA variability in muscle with proportions showing a
431 progressive increase from $14\pm 2\%$ at 32 cm FL to $29\pm 2\%$ at 157 cm FL. Despite a maturity
432 influence in NFA profiles of liver and muscle, no influence was detected when considering
433 the main NFA families individually (Table S3b). Isotopic compositions in both tissues were
434 influenced by all tested variables, with the exception of sex. In liver, GAM predicted $\delta^{13}\text{C}$
435 values increased ca. $-17.7\pm 0.1\text{‰}$ to $-16.6\pm 0.2\text{‰}$, and $\delta^{15}\text{N}$ values from ca. $12.1\pm 0.2\text{‰}$ to
436 $12.5\pm 0.3\text{‰}$ between 29 and 157 cm FL (Fig. 5a). In muscle, minor variations of $\delta^{13}\text{C}$

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437 values were observed over the range size (<0.6‰), while $\delta^{15}\text{N}$ values strongly increased
438 between 29 and 53 cm (from $10.7\pm 0.3\text{‰}$ to $12.9\pm 0.3\text{‰}$), then progressively increased until
439 157 cm to reach $13.9\pm 0.4\text{‰}$, with a stronger increase between 140 and 157 cm (Fig. 5b).
440 Muscle $\delta^{13}\text{C}$ values were also highest in YFT spawning ($-16.5\pm 0.2\text{‰}$) compared to those
441 developing ($-17\pm 0.3\text{‰}$, $P<0.001$).

442

443 3.2.3. Skipjack tuna

444 GAM predicted TLC was not affected by any of the tested variables in muscle of SKJ (Table
445 S2) but varied with size in liver (min–max=2–30% dw), despite no obvious trend observed. In
446 SKJ tissues, differences in NFA profiles were mainly attributed to sex and area, whereas size
447 had no significant influence in muscle and a limited influence in liver (Table S3a). There was
448 also no influence of maturity in both tissues (Table S3a). Wilcoxon tests revealed that the
449 liver of females contained more SFA ($53\pm 7\%$ vs. $46\pm 7\%$; $W=218$, $P<0.05$), mainly 16:0
450 ($W=238$, $P<0.005$), and more MUFA than males ($21\pm 5\%$ vs. $15\pm 5\%$; $W=240$, $P<0.005$)
451 mainly 16:1 ω 7 ($W=250$, $P<0.001$) and 18:1 ω 9 ($W=234$, $P<0.01$) (Table S4). In contrast, liver
452 of males had higher relative amounts of essential NFA including EPA, DHA and AA (all
453 $P<0.01$; Table S4) than females: mean differences between males and females ranged from
454 1% for 22:5 ω 6 to 8% for DHA (Table S4). PUFA proportion in liver was higher in males and
455 indeterminate individuals ($W=201$, $P<0.05$) than in females ($W=173$, $P<0.001$, Table S4).
456 In contrast, no differences in isotopic compositions were observed between sexes in either
457 tissue (Table S4). No clear trend was observed for $\delta^{13}\text{C}$ values which remains overall constant
458 (around -17.5‰ in liver and -17‰ in muscle), whereas $\delta^{15}\text{N}$ values increased by 2.0‰ in
459 muscle from 11‰ , and by 1.1‰ in liver from 11.1‰ between 30 and 78 cm FL (Fig. 5). For
460 both isotopic values in both tissues, no influence of maturity was noted (Table S2).

461

462 4. DISCUSSION

463 Using complementary trophic tracers, this study provides greater understanding of trophic
464 relationships and food partitioning among tropical tuna from the Western Indian Ocean. Due
465 to their biological proximity and habitat sharing, overlaps in their trophic niches were
466 detected, especially in NFA compositions of large individuals (Fig. 2b). However, significant
467 inter- and intra-specific differences were also noticed: higher PUFA proportions in SKJ than
468 in small BET and YFT (Fig. 2a); separated isotopic niches occupied by large YFT and BET
469 (Fig. 3b); increased MUFA proportions with size in the liver of BET and YFT (Fig. 4), while
470 a difference between sexes was observed only in SKJ (higher PUFA proportions in males).

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471

472 **4.1.FA and SI compositions of tuna prey**

473 The origins of these inter-specific differences are likely explained through the FA and SI
474 compositions of their main prey and this section gives an overview of these compositions,
475 used in the following sections. Only a few studies report NFA profiles for tuna prey in the
476 Western Indian Ocean, but some information exists for other oceans. High MUFA proportions
477 are characteristic of myctophid fishes (Saito and Murata, 1998), including in tropical waters
478 (Sebastine et al., 2011; Baby et al., 2014), due to their high consumption of copepods rich in
479 20:1 MUFA (Saito and Kotani, 2000). Myctophids are small pelagic fishes, inhabiting deep
480 layers (over 400 m) during the day and that migrate to surface layers (around 5-100 m) each
481 night to feed (Vipin et al., 2012). They are important prey of squids. Indeed, middle-sized
482 squid *Sthenoteuthis oualaniensis*, a common tuna prey in the region under study (Ménard et
483 al., 2013), ascends between the surface and 100 meters depth only at night to feed on
484 myctophids (Shulman et al., 2002). Despite *S. oualaniensis* feed on myctophids rich in
485 MUFA, its mantle contains high proportions of DHA (Shulman et al., 2002) and PUFA (52%
486 of total FA; Young et al., 2010a). Cigarfish *C. pauciradiatus* is another small fish prey rich in
487 MUFA (Young et al., 2010a), on which YFT mainly forage during the NEM period in WCIO
488 (Zudaire et al., 2015). Globally, less information is available concerning the FA profile of
489 crustaceans, including the swimming crab *Charybdis smithii* and the stomatopod *Natosquilla*
490 *investigatoris*, that are also known prey of tropical tuna (Potier et al., 2004). In the Pacific
491 Ocean a related crab species, *Charybdis hawaiiensis*, is reported to be mainly composed of
492 PUFA (42% of total FA) (Piché et al., 2010). In addition, *C. smithii* come up in surface layers
493 mainly at night in the Indian Ocean (Romanov et al., 2009), while *N. investigatoris* was
494 occasionally found in surface layers at daytime (Losse and Merrett, 1971).

495 In contrast to NFA profiles, isotopic data of the main tuna prey groups were available for the
496 Western Indian Ocean, but more so for the Mozambique Channel. Squids and small fishes
497 have been shown to occupy similar trophic levels with mean $\delta^{15}\text{N}$ values around $9.4\pm 0.8\text{‰}$
498 and $9.5\pm 1.6\text{‰}$, respectively, while crustaceans occupy a slightly lower trophic level with
499 mean $\delta^{15}\text{N}$ values around $8.7\pm 1.3\text{‰}$ (Ménard et al., 2014). However, a great variability was
500 observed among the small fishes: cigarfish had lower mean $\delta^{15}\text{N}$ values ($9.0\pm 2.2\text{‰}$) than most
501 myctophids such as *Diaphus metopoclampus* with higher $\delta^{15}\text{N}$ values ($12.2\pm 0.4\text{‰}$) but lower
502 $\delta^{13}\text{C}$ values ($-19.3\pm 0.2\text{‰}$; Ménard et al., 2014). $\delta^{15}\text{N}$ values of main tuna prey have also been
503 shown to increase with size (in myctophids, the cigarfish and squid *S. oualaniensis*; Parry,
504 2007; Ménard et al., 2014). However, limited variability in $\delta^{13}\text{C}$ values are displayed among

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505 tuna prey with mean values ranging from $-18.6 \pm 0.4\text{‰}$ in small fish to $-18.2 \pm 0.6\text{‰}$ in
506 crustaceans. This suggests that any differences in $\delta^{13}\text{C}$ values in tuna from this area should be
507 interpreted with caution.

508

509 **4.2. Trophic partitioning in tuna aggregations**

510 Total lipid content data suggests that none of the three tuna species appears to store lipids in
511 muscle, as TLC values remained low and did not vary with the considered factors. The liver
512 showed more variability in TLC, which was mainly explained by season and size class
513 differences, suggesting this organ could be used to store lipids. In the three species, fattest
514 livers were sampled during the two monsoon periods; however, modest seasonal differences
515 were detected in SKJ. This could be related to a specific diet during monsoons, as YFT have
516 been recorded to forage predominantly on fatty small fishes (7-39% dw of lipids; Young et
517 al., 2010a), such as *C. pauciradiatus* during NEM in the studied region (Zudaire et al., 2015).

518 Partial niche overlaps were observed in the liver of small tuna (Fig. 2a and 3a). As tuna still
519 form multispecific schools, partial trophic sharing does not appear to reduce the advantages of
520 schooling behavior (e.g. reduced predation, faster food detection; Pavlov and Kasumyan,
521 2000). When trophic niches are large (i.e., diet behaviors of individuals are diverse in each
522 species), diet overlap among species does not really increase the competition intensity among
523 them, because only a few individuals in each species are impacted; Bolnick et al. (2011)
524 called this “niche complementarity”. This phenomenon might reduce predator-prey
525 dependency and dampen consumers-resources oscillations (McCann et al., 1998), which may
526 offer a long-term advantage in nutrient poor habitats such as tropical offshore waters. As these
527 small tuna were caught under drifting fish aggregating devices, the use of which has recently
528 intensified (Chassot et al., 2015) and is thought to act as an ecological trap (e.g. Hallier and
529 Gaertner, 2008), the possibility that devices promote competition among small tuna cannot be
530 excluded (Jaquemet et al., 2011)

531 Calculated FANes showed greater trophic overlap between YFT and BET than between YFT
532 and SKJ, mainly based on differences in MUFA and PUFA proportions. The high proportions
533 of PUFA in SKJ suggest a lower consumption of myctophids, squid consuming myctophids,
534 and small fish in general, but a higher consumption of crustaceans (see section 4.1 for details,
535 and Grande (2013) who investigated stomach contents of SKJ in the Western Indian Ocean).
536 By contrast, PUFA proportions in small BET and in YFT suggest a low consumption of
537 crustaceans that seems to decrease with size with higher proportions of MUFA in large
538 individuals (Fig. 4a). In addition, mean $\delta^{15}\text{N}$ values in both tissues were higher in small BET

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539 than in small YFT and SKJ. This suggests that small BET likely feeding on prey with higher
540 trophic positions and/or of a larger size, as already observed by comparing the size of prey
541 from stomach contents of YFT and BET (Ménard et al., 2006). No studies have specifically
542 focused on tuna prey size distribution in the Indian Ocean, however, Potier et al. (2008)
543 noticed that surface YFT and BET fed more on smaller cigarfish than sub-surface YFT and
544 BET of the same size, and suggested ontogenetic changes in the depth distribution of
545 cigarfish. On the other hand, diving capacities differences among small tuna (further
546 discussed in section 4.3) also suggest the possibility of vertical sharing in mixed schools of
547 small tuna, with small BET occupying the deeper layers of schools.

548 In large tuna, only minor differences in the proportions of individual NFA were observed
549 (Table 1). This suggests that the two species BET and YFT fed on similar proportions of the
550 same prey species, which is in agreement with stomach content analyses of large tuna caught
551 by purse-seine (Potier et al., 2004). However, the stable isotope compositions were different
552 between these two species and suggested a higher trophic level in BET than in YFT (Fig. 3b).

553 As mentioned for small tuna, differences in prey size could explain differences in $\delta^{15}\text{N}$ values
554 between large tuna. These results align with stomach content data from the same area, which
555 showed that squid and cigarfish individuals were larger in the stomachs of BET than similar
556 sized YFT (Potier et al., 2008; Ménard et al., 2013). The present study also reported large
557 MUFA proportions in the tissues of the larger tropical tuna (BET and YFT) which is likely
558 associated to direct consumption of myctophids or indirect myctophid consumption passing
559 through the digestive gland of various squids (Phillips et al., 2002; Pethybridge et al., 2013).

560 Indeed, large BET in deeper water layers have been found to feed more on squids than similar
561 sized YFT (Potier et al., 2004). As indicated by differences in $\delta^{13}\text{C}$ values, we suspect that
562 BET fed, directly or indirectly (i.e., through squids), on specific myctophids, such as
563 *D. metopoclampus*, with lower $\delta^{13}\text{C}$ values. The particular isotopic position of this myctophid
564 species might increase the isotopic position of large BET, which has higher $\delta^{15}\text{N}$ values and
565 lower $\delta^{13}\text{C}$ values than large YFT, in muscle and liver (Fig. 3b). Thus, despite large BET and

566 YFT co-occurring and focusing on similar prey groups in surface waters when caught by
567 purse-seine, in long-term (as integration times of trophic tracers used in the present study
568 approach several months; Budge et al., 2011; Madigan et al., 2012), a specific orientation
569 based on prey size and/or specific myctophids predators could limit their competition. In
570 addition, the same inter-specific differences in isotopic compositions were observed in both
571 tissues with different integration time (Fig. 3a). This suggests that the aggregations of large

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572 individuals in mixed schools are not durable at the scale of isotopic turnover rates (around 6
573 months in muscle and 3 in liver; Madigan et al., 2012).

574 As noticed by Young et al. (2010b) in the Pacific Ocean for large individuals, diet differences
575 reflect diel variations in foraging among tuna, with large BET thought to feed more at night
576 than YFT, when myctophids and squids ascend from deeper layers (see section 4.1). In
577 contrast, SKJ feed mainly during the day, but night foraging has been reported (Romanov et
578 al., 2009; Grande, 2013). Such diel foraging behaviors may be reflected in the biochemical
579 signatures and suggest limited tuna competition. Indeed, considering the main tuna prey,
580 myctophids, squids and the crab *C. smithii* come up in surface layers mainly at night in the
581 Indian Ocean), whereas the stomatopod, *N. investigatoris*, could be found in surface layers at
582 daytime (see section 4.1) and in stomach content of surface tuna in Indian Ocean (Potier et al.,
583 2008; Grande, 2013). Thus, a myctophid dominant diet, as suggested in BET with the high
584 MUFA proportions, is probably more related to nocturnal feeding and/or twilight feeding.

585 Environmental variables (i.e., fishing area and season) influenced trophic tracers in both
586 tissues, attesting to their non-negligible impacts on tuna diet. For example, the cigarfish
587 constitutes most of the tuna diet in the Indian Ocean especially during NEM (Fonteneau et al.,
588 2008; Potier et al., 2008) and appears to be an important energy source in the reproduction of
589 YFT in WCIO (Zudaire et al., 2015). Although this could explain the higher MUFA
590 proportion in the liver of tuna from WCIO than from MOZ, the large variability among
591 individuals does not allow to properly characterizing these environmental influences.

592 Lower $\delta^{15}\text{N}$ values were found in tuna from MOZ than from WCIO, as reported in previous
593 studies (Ménard et al., 2007; Zudaire et al., 2015). This is generally attributed to a lower base
594 line in Mozambique Channel (Ménard et al., 2007), due to diazotrophic organisms that lower
595 the $\delta^{15}\text{N}$ value of particulate organic matter (Dupuy et al., 2016). An influence on NFA
596 profiles was also possible, as diatoms, with high EPA biosynthesis capacities, have been
597 shown to predominate in mesoscale eddies (e.g. Brown et al. (2008) in subtropical Pacific),
598 which are abundant in MOZ (Potier et al., 2014). In contrast, higher proportions of DHA,
599 characteristic of dinoflagellates, were found in liver of tuna from MOZ, suggesting a more
600 complex response to mixing events of nutrient, and overall a mixing signal through multiple
601 trophic levels from phytoplankton to higher trophic levels (Kainz et al., 2004).

602

603 **4.3. Diet changes during tuna ontogeny**

604 Patterns of NFA and SI observed in each tuna species were slightly different with size,
605 probably related to diet differences but also to physiological differences. For the three species,

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606 the liver was found to be more informative than the white muscle to detect intra-specific
607 changes, as it is a reactive tissue to rapid diet changes in relation with fast turnover rates
608 (around 6 months in muscle and 3 months in liver for stable isotopes; Madigan et al., 2012).
609 In addition, TLC was relatively lower in white muscle than in liver, attesting to the known
610 role of liver in energy storage. Therefore, NFA profiles in muscle appear to be less
611 informative for ontogenetic studies in leaner fish such as these tropical tuna. By contrast,
612 NFA profiles in liver were found to be of valuable interest when examining dietary changes
613 with size.

614 In both BET and YFT, PUFA proportions decreased in liver with size while MUFA
615 concurrently increased (at around 91 and 109 cm in BET and YFT; Fig. 4a). In contrast, no
616 changes were observed with size in SKJ, but differences between sexes were noticed,
617 especially in liver, with higher PUFA proportion in males (Table S4). Two main hypotheses
618 could support differences among the tuna species: a biological process response (e.g.
619 reproduction) and/or a change of habitat (e.g. from surface to deeper layers). First, concerning
620 reproduction, the size at which 50% of the population matures was estimated at 100 cm FL
621 for BET in the Pacific Ocean (Farley et al., 2006), 75 cm for YFT (Zudaire et al., 2013) and
622 39 cm for SKJ (Grande et al., 2014), both studies from the Western Indian Ocean. Thereby,
623 PUFA of mature fish would be allocated to germinal cell production, especially in females.
624 Indeed, vitellogenin synthesis in ovary has been shown to require higher quantities of PUFA,
625 especially in EPA and DHA (Silversand and Haux, 1995). However, no significant influence
626 of maturity on the proportions of the main NFA classes was detected in this study. The
627 influence of reproduction on NFA profiles is however more likely in SKJ, as it has been
628 shown to be an income-breeder species, i.e. which reinvest the majority of its acquired energy
629 to reproduction, and breeding all year round (Grande et al., 2014). This suggests that in
630 females, PUFA from liver are rapidly allocated to the ovary after acquisition; while males
631 have fewer PUFA requirements and can store them into the liver explaining the higher
632 proportion of PUFA in males than in females SKJ observed in the present study, and,
633 potentially explaining higher TLC in liver of males. In the same way, in liver, PUFA
634 proportion was found to be higher in indeterminate individuals (i.e. the smaller fishes) than in
635 females (Table S4). Indeed, according to this assumption, PUFA would be allocated to the
636 gonads. These differences between sexes could also make females SKJ more sensitive to
637 environmental changes, especially if dietary essential PUFA become less available, as
638 predicted for the south west Pacific Ocean (Pethybridge et al., 2015a).

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639 Concerning habitat usage, the shift in main NFA families in BET and YFT could correspond
640 to a habitat change for deeper environments providing rich-MUFA prey as myctophids or the
641 myctophids-predators squids, which inhabit deeper layers (see section 4.1). Indeed, this shift
642 could correspond to the sufficient development of the swim bladder and regional endothermy
643 (Graham and Dickson, 2004), allowing BET and YFT to reach deeper layers with size, while
644 SKJ is restricted to the surface due to the lack of swim bladder. Magnuson (1973) observed an
645 allometric growth of swim bladder for YFT until 8-10 kg, corresponding approximately to a
646 70-75 cm FL fish. Bertrand and Josse (2000), who observed larger swim bladder in BET than
647 in YFT at similar size, observed also an increase in the swim bladder volume over 120 cm FL
648 in BET. This would suggest that BET could reach deeper layers at smaller size than YFT, as
649 emphasized with the earlier shift in NFA profile observed in BET than in YFT (i.e., 91 vs. 109
650 cm FL).

651 $\delta^{15}\text{N}$ values should be interpreted in context of specific differences in amino acids
652 composition that are nitrogen compounds (i.e. slow turnover of essential amino acids; Popp et
653 al., 2007), the tissue growth and the turnover rate (Martinez del Rio et al., 2009). Indeed, the
654 fast increase with size of $\delta^{15}\text{N}$ values in muscle of the three species highlighted the influence
655 of metabolic process and the importance of selected tissue for the trophic level estimation in
656 food webs studies. In juvenile bluefin tuna, *T. orientalis*, Madigan et al. (2012) showed that
657 the half-lives of ^{15}N in white muscle and liver were 167 and 86 days respectively, and 255 and
658 162 days for ^{13}C , respectively, highlighting influences of turn-over on isotopic composition.
659 In addition, in different marine fish, a growth rate increase promotes a decrease of $\delta^{15}\text{N}$ values
660 in muscle, and high metabolic levels promote a faster equilibration with diet (Trueman et al.,
661 2005).

662 In the three species, limited variations of $\delta^{13}\text{C}$ values in muscle indicated no change of carbon
663 sources through life cycle. However, $\delta^{13}\text{C}$ values in liver were more difficult to interpret due
664 to irregular variations, which could be related to metabolic activities as previously mentioned.

665 In both tissues, an increase in $\delta^{15}\text{N}$ values with size was observed in the three species with a
666 strongest signal in muscle (Fig. 5). This increase could be linked to slowdown in growth rate
667 and/or to an increase of prey size. Indeed, tropical tuna are opportunistic feeders and the mean
668 size of their prey increased with tuna size (Ménard et al., 2006; Jaquemet et al., 2011),
669 besides, $\delta^{15}\text{N}$ values of prey also increase with prey size (Ménard et al., 2014). Finally, in
670 BET and YFT, no breakpoints in isotopic values matched specific maturity or growth events,
671 although Zudaire et al. (2015) observed higher $\delta^{15}\text{N}$ values in liver of spawning YFT.

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673 **Conclusion**

674 This study provides a greater understanding of trophic interactions among and within three
675 prominent tropical tuna species. We found that there is a resource partitioning among
676 sympatric tuna and particularly among tuna ≤ 100 cm FL. Based on the biochemical tracers,
677 we show evidence of ontogenetic dietary shifts in the larger tuna species (i.e. BET and YFT).
678 Generally, larger tuna individuals were shown to have higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than
679 smaller individuals, suggesting higher trophic positions for the larger individuals, and higher
680 proportions of MUFA commonly high in myctophid fish. Future work should focus on
681 reporting of NFA profiles for potential prey in the Western Indian Ocean that to date was
682 particularly scarce of such data, and detailing specific turnover rates of tissues and
683 compounds (SI as NFA).

684

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694

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937 **FIGURE CAPTION**

938 **Figure 1.** Location of skipjack tuna (SKJ), yellowfin tuna (YFT) and bigeye tuna (BET)
 939 caught in the Western Indian Ocean throughout 2013. The limit of the two study areas,
 940 Mozambique Channel (MOZ) and Western-Central Indian Ocean (WCIO), is indicated with a
 941 dashed line.

942 **Figure 2.** Scatterplots and associated convex hull of three-dimensional nonmetric
 943 multidimensional scaling (NMDS) using Euclidean distance matrix for neutral fatty acid
 944 profiles in the muscle of skipjack tuna (SKJ), yellowfin tuna (YFT) and bigeye tuna (BET)
 945 caught in the Western-Central Indian Ocean (WCIO), according to size class: (a) fish with
 946 fork length less than 100 cm ($FL \leq 100$ cm) and (b) fish with fork length longer than 100 cm
 947 ($FL > 100$ cm). Arrows are significant variables ($P < 0.05$) correlated with the ordination. Dim:
 948 dimension.

949 **Figure 3.** Two-dimensional scaled isotopic space ($\delta^{15}N$ and $\delta^{13}C$) in the muscle and liver of
 950 skipjack tuna (SKJ), yellowfin tuna (YFT) and bigeye tuna (BET) caught in the Western-
 951 Central Indian Ocean (WCIO), according to size class: (a) fish with fork length less than
 952 100 cm ($FL \leq 100$ cm), (b) fish with fork length longer than 100 cm ($FL > 100$ cm).

953 **Figure 4.** Smoother plots illustrating the relationship between observed fork length (FL) and
 954 GAM predicted values for (a) the main fatty acid (FA) families (b) six individuals neutral
 955 fatty acid (NFA) of which five are essential (DHA, EPA, AA, 18:3 ω 3 and 18:2 ω 6) in the liver
 956 of BET and YFT sampled in the Western-Central Indian Ocean throughout 2013. Vertical
 957 dashed lines represent the size at which a proportion change in the main FA families occurs
 958 (91 and 109 cm FL for BET and YFT respectively). Solid areas showed the confidence
 959 interval ($1.96 * \text{standard error}$) around the predicted value (line). Short vertical lines on the x-
 960 axis represent the sampled values; BET: Bigeye; SKJ: Skipjack; YFT: Yellowfin; EPA:
 961 Eicosapentaenoic acid (20:5 ω 3); DHA: Docosahexaenoic acid (22:6 ω 3); AA: Arachidonic acid
 962 (20:4 ω 6).

963 **Figure 5.** Smoother plots illustrating the relationship between observed fork length (FL) and
 964 GAM predicted values for stable isotopes values ($\delta^{13}C$ in blue and $\delta^{15}N$ in black) in (a) liver
 965 and (b) muscle of bigeye (BET), yellowfin (YFT) and skipjack (SKJ) from Western-Central
 966 Indian Ocean. Solid areas showed the confidence interval ($1.96 * \text{standard error}$) around the
 967 predicted value (line). Short vertical lines on the x-axis represent the sampled values.

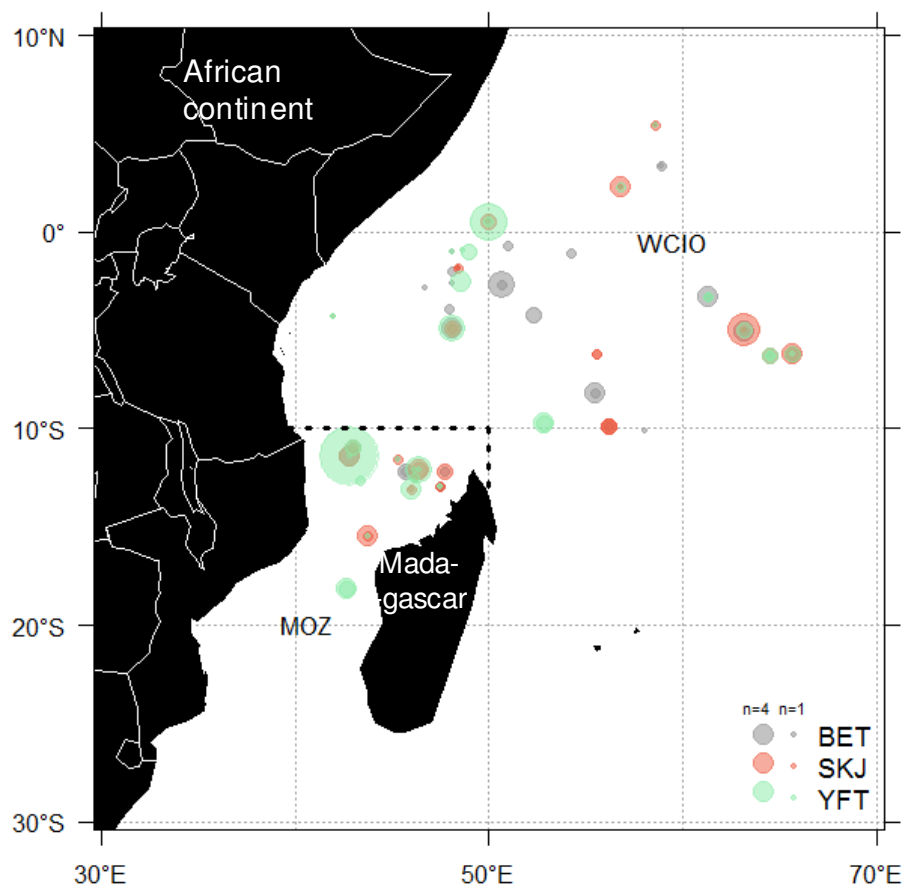
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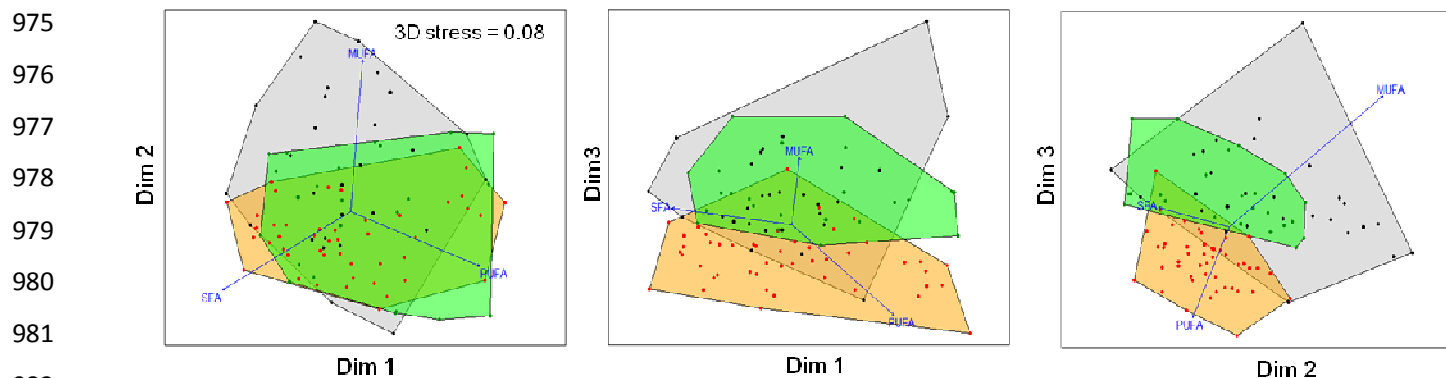
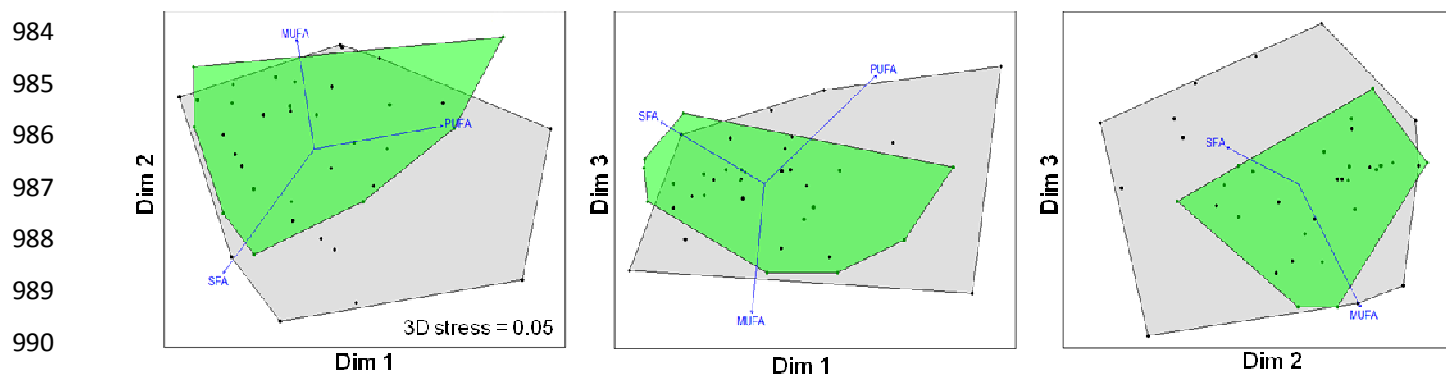
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971 **Figure 1.**

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973 **Figure 2.**974 (a) WCIO – FL ≤ 100 cm983 (b) WCIO – FL > 100 cm

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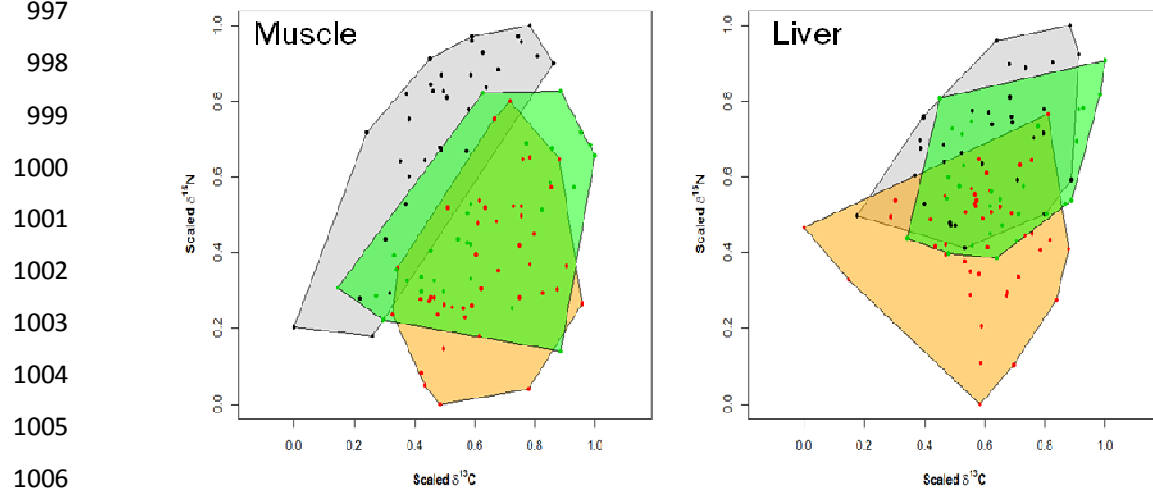
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994 **Figure 3.**

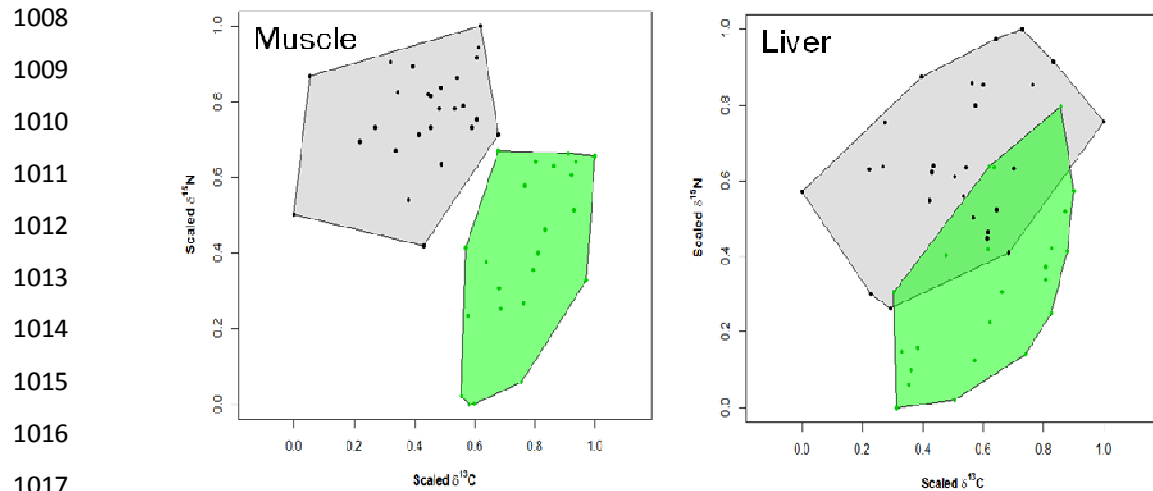
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(a) $FL \leq 100$ cm

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(b) $FL > 100$ cm

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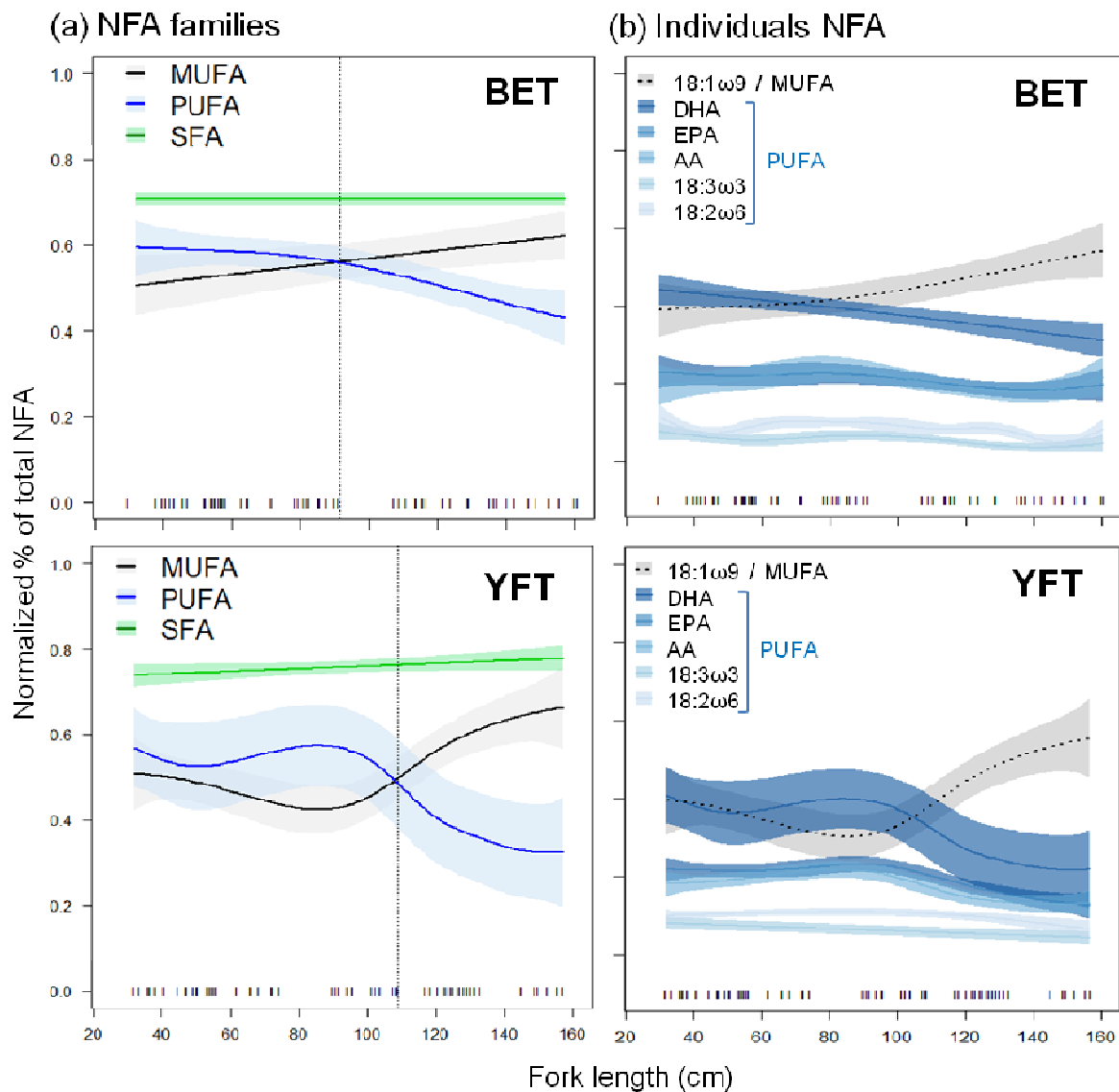
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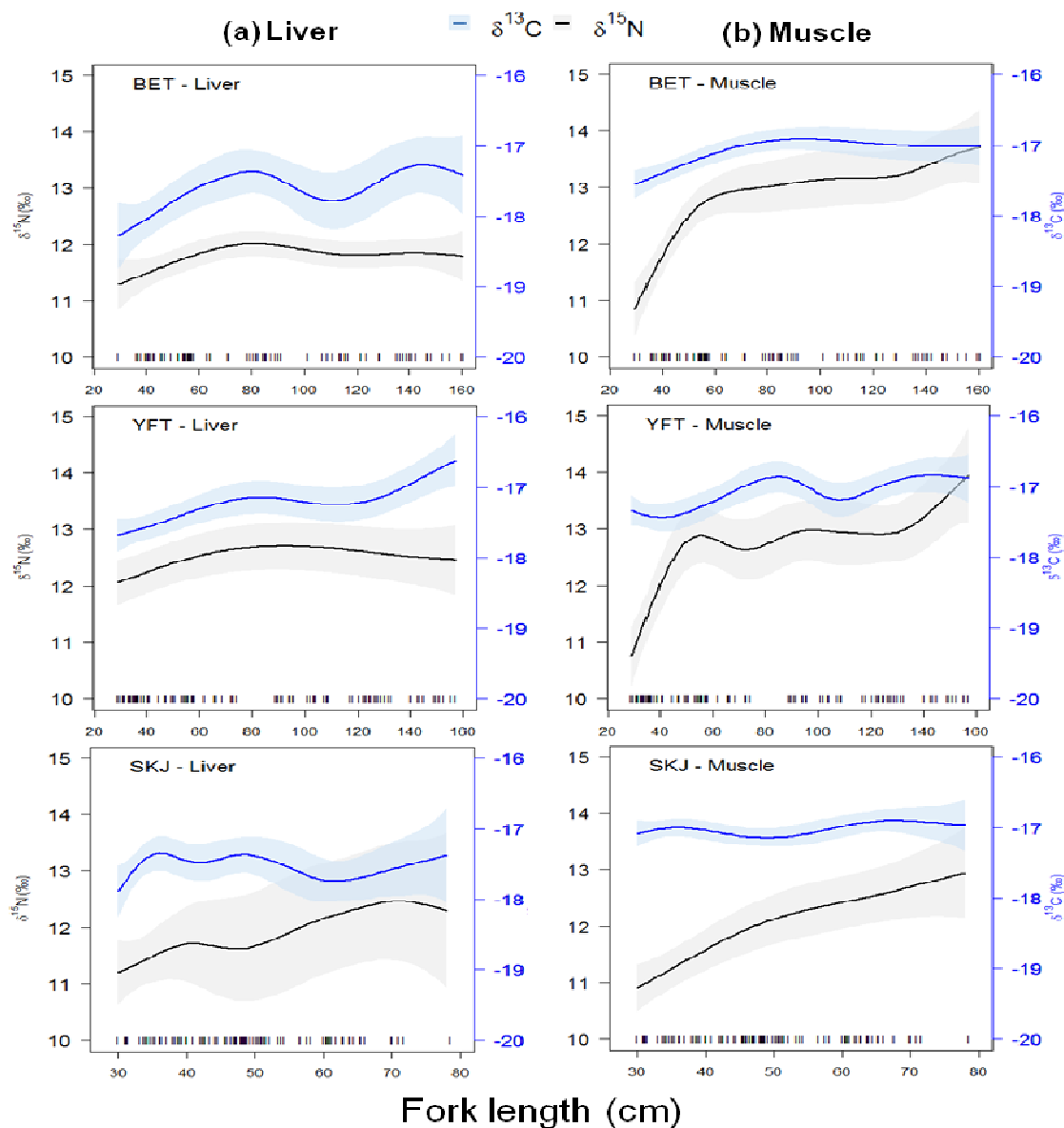
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1027 **Figure 4.**

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1028 **Figure 5.**

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Table 1. Mean values (\pm standard deviation) of carbon and nitrogen isotopic data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰), total lipid content (TLC, % dry weight) and fatty acid profiles (neutral lipids as a % of total fatty acids) of the liver and muscle of skipjack tuna (SKJ), yellowfin tuna (YFT) and bigeye tuna (BET) in the Western-Central Indian Ocean, according to size class (FL \leq 100 cm and FL $>$ 100 cm). N is the number of samples for stable isotopes (SI) and neutral fatty acids (NFA) analyses. Superscripts represent significantly $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, TLC and NFA differences among species (P $<$ 0.05 for Wilcoxon's test): ^B different from BET; ^S different from SKJ; ^Y different from YFT.

N (SI NFA)	Small tunas (FL \leq 100 cm)						Large tunas (FL $>$ 100 cm)			
	Liver			Muscle			Liver		Muscle	
	BET	SKJ	YFT	BET	SKJ	YFT	BET	YFT	BET	YFT
	33 26	43 46	29 24	33 28	43 47	29 23	27 24	23 19	26 21	23 19
$\delta^{13}\text{C}$	-17.6 \pm 0.4	-17.7 \pm 0.4	-17.5 \pm 0.4	-17.2 \pm 0.3 ^{SY}	-17.0 \pm 0.3 ^B	-17.0 \pm 0.4 ^B	-17.4 \pm 0.5	-17.1 \pm 0.5	-17.0 \pm 0.2 ^Y	-16.6 \pm 0.3 ^B
$\delta^{15}\text{N}$	11.8 \pm 0.6 ^{SY}	10.8 \pm 0.6 ^{BY}	11.4 \pm 0.5 ^{BS}	12.5 \pm 0.7 ^{SY}	11.4 \pm 0.6 ^B	11.7 \pm 0.6 ^B	11.8 \pm 0.5 ^B	11.0 \pm 0.5 ^Y	13.4 \pm 0.4 ^Y	12.4 \pm 0.6 ^B
TLC (% dw)	13.8 \pm 5.0	14.4 \pm 5.7	13.9 \pm 8.3	2.7 \pm 1.9	3.1 \pm 3.5	2.0 \pm 1.0	20.0 \pm 8.8 ^B	27.3 \pm 11.2 ^Y	2.2 \pm 1.0	2.5 \pm 1.3
14:0	1.3 \pm 0.9	1.7 \pm 0.9 ^Y	1.2 \pm 0.6 ^S	1.2 \pm 1.2 ^S	0.6 \pm 0.5 ^B	0.7 \pm 0.5	1.1 \pm 0.6	1.4 \pm 0.8	0.8 \pm 0.4	1.1 \pm 0.9
15:0	0.8 \pm 0.4	1.0 \pm 0.4	0.8 \pm 0.4	0.5 \pm 0.4	0.4 \pm 0.4	0.4 \pm 0.3	0.5 \pm 0.4	0.5 \pm 0.3	0.4 \pm 0.3	0.6 \pm 0.4
16:0	30.6 \pm 4.5 ^S	36.1 \pm 7.0 ^B	33.4 \pm 4.7	30.8 \pm 8.0	32.8 \pm 8.7	30.6 \pm 9.4	31.7 \pm 4.0 ^Y	35.7 \pm 4.3 ^B	29.5 \pm 8.8	29.6 \pm 8.8
17:0	1.4 \pm 0.5	1.6 \pm 0.7	1.6 \pm 0.7	1.3 \pm 0.3	1.2 \pm 0.4	1.3 \pm 0.3	1.0 \pm 0.6	1.2 \pm 0.5	1.2 \pm 0.2	1.2 \pm 0.4
18:0	7.6 \pm 1.4 ^Y	8.3 \pm 1.7 ^Y	10.2 \pm 1.3 ^{BS}	12.0 \pm 3.9 ^{SY}	13.8 \pm 2.6 ^B	14.4 \pm 3.1 ^B	8.3 \pm 1.4	8.8 \pm 1.9	12.4 \pm 3.4	11.6 \pm 2.5
20:0	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.4 \pm 0.4	0.3 \pm 0.4	0.3 \pm 0.4	0.1 \pm 0.1	0.2 \pm 0.1	0.6 \pm 0.4	0.6 \pm 0.4
22:0	0.0 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.3	0.2 \pm 0.5	0.3 \pm 0.4	0.0 \pm 0.0	0.0 \pm 0.0	0.4 \pm 0.6	0.3 \pm 0.5
ΣSFA	41.9 \pm 5.3^{SY}	48.9 \pm 7.5^B	47.3 \pm 5.2^B	46.4 \pm 8.4	49.4 \pm 9.1	48.0 \pm 8.9	42.7 \pm 5.0^Y	47.8 \pm 4.3^B	45.2 \pm 8.7	45.0 \pm 8.3
16:1 ω 7	2.9 \pm 1.1	2.9 \pm 1.2	2.4 \pm 1.0	2.2 \pm 1.7	1.6 \pm 0.9	1.3 \pm 1.0	3.9 \pm 1.2	4.2 \pm 1.0	2.2 \pm 1.8	3.5 \pm 2.1
17:1 ω 7	0.7 \pm 0.5 ^{SY}	0.5 \pm 0.4 ^B	0.5 \pm 0.4 ^B	0.7 \pm 0.3 ^{SY}	0.5 \pm 0.3 ^B	0.4 \pm 0.3 ^B	0.8 \pm 0.5	0.7 \pm 0.4	0.6 \pm 0.3	0.7 \pm 0.4
18:1 ω 9	16.4 \pm 7.3 ^{SY}	10.4 \pm 4.2 ^B	12.9 \pm 8.8 ^B	13.1 \pm 4.2 ^{SY}	7.8 \pm 1.5 ^B	10.2 \pm 3.2 ^B	23.8 \pm 10.0	24.0 \pm 6.0	15.0 \pm 5.4	16.1 \pm 2.6
18:1 ω 7	3.2 \pm 0.9 ^{SY}	2.2 \pm 0.7 ^B	2.5 \pm 1.0 ^B	2.8 \pm 0.6 ^{SY}	1.9 \pm 0.4 ^{BY}	2.5 \pm 0.5 ^{BS}	3.6 \pm 0.9	3.4 \pm 0.4	3.2 \pm 0.8	3.2 \pm 0.6
20:1 ω 9	1.0 \pm 0.5 ^{SY}	0.3 \pm 0.2 ^B	0.6 \pm 0.5 ^B	1.0 \pm 0.4 ^{SY}	0.3 \pm 0.3 ^{BY}	0.6 \pm 0.4 ^{BS}	1.0 \pm 0.5	0.8 \pm 0.3	0.9 \pm 0.6	0.8 \pm 0.4
22:1 ω 9	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	2.4 \pm 2.8 ^S	0.9 \pm 0.7 ^{BY}	2.2 \pm 1.3 ^S	0.1 \pm 0.1	0.1 \pm 0.1	2.3 \pm 3.0	2.0 \pm 1.6
24:1 ω 9	2.4 \pm 2.2	2.0 \pm 1.9	2.2 \pm 2.3	0.3 \pm 0.3	0.2 \pm 0.4	0.4 \pm 0.4	1.6 \pm 1.5	0.9 \pm 0.9	0.4 \pm 0.5	0.4 \pm 0.3
ΣMUFA	26.8 \pm 8.5^{SY}	18.2 \pm 5.4^B	21.0 \pm 10.2^B	22.6 \pm 6.7^{SY}	13.3 \pm 2.1^{BY}	17.5 \pm 4.1^{BS}	34.8 \pm 11.0	34.2 \pm 6.9	24.6 \pm 7.8	26.8 \pm 3.9
18:3 ω 3	0.5 \pm 0.2 ^{SY}	0.2 \pm 0.2 ^B	0.3 \pm 0.1 ^B	0.3 \pm 0.3	0.2 \pm 0.2	0.3 \pm 0.2	0.2 \pm 0.1	0.3 \pm 0.2	0.3 \pm 0.4 ^Y	0.4 \pm 0.3 ^B
20:5 ω 3 (EPA)	4.9 \pm 1.4	5.6 \pm 1.9	5.1 \pm 1.6	3.9 \pm 0.7 ^S	5.0 \pm 0.9 ^{BY}	3.8 \pm 0.8 ^S	3.4 \pm 1.5	2.5 \pm 1.3	3.5 \pm 0.9	3.5 \pm 0.9
22:5 ω 3	1.2 \pm 0.5 ^S	0.9 \pm 0.6 ^B	1.0 \pm 0.8	0.7 \pm 0.5	0.4 \pm 0.5	0.9 \pm 0.7	1.0 \pm 0.6	1.1 \pm 0.6	0.7 \pm 0.6	0.8 \pm 0.5
22:6 ω 3 (DHA)	16.6 \pm 5.3	19.1 \pm 5.6	17.6 \pm 4.6	20.1 \pm 5.1 ^S	23.6 \pm 6.2 ^B	22.7 \pm 6.7	12.0 \pm 5.6	9.4 \pm 4.0	18.9 \pm 6.3	16.7 \pm 5.2
18:2 ω 6	0.9 \pm 0.4	0.8 \pm 0.3 ^Y	1.1 \pm 0.3 ^S	1.0 \pm 0.4 ^{SY}	1.1 \pm 0.3 ^{BY}	1.4 \pm 0.4 ^{BS}	0.6 \pm 0.4	0.7 \pm 0.5	1.1 \pm 0.4	1.3 \pm 0.4
18:3 ω 6	0.3 \pm 0.4	0.3 \pm 0.3	0.2 \pm 0.2	0.1 \pm 0.2	0.1 \pm 0.2	0.2 \pm 0.4	0.1 \pm 0.1 ^Y	0.2 \pm 0.1 ^B	0.2 \pm 0.2	0.3 \pm 0.5
20:2 ω 6	0.3 \pm 0.2 ^{SY}	0.1 \pm 0.1 ^B	0.2 \pm 0.1 ^B	0.2 \pm 0.2	0.2 \pm 0.4	0.1 \pm 0.3	0.1 \pm 0.1	0.1 \pm 0.1	0.2 \pm 0.2	0.1 \pm 0.2
20:3 ω 6	0.1 \pm 0.1 ^{SY}	0.1 \pm 0.1 ^B	0.1 \pm 0.1 ^B	0.0 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.3	0.1 \pm 0.1 ^Y	0.1 \pm 0.1 ^B	0.1 \pm 0.1	0.1 \pm 0.3
20:4 ω 6 (AA)	4.5 \pm 1.6	3.7 \pm 1.1	4.2 \pm 1.6	2.9 \pm 0.6 ^S	4.0 \pm 1.1 ^{BY}	2.7 \pm 0.6 ^S	3.4 \pm 1.8 ^Y	1.9 \pm 0.8 ^B	3.1 \pm 0.9	2.6 \pm 1.0
22:2 ω 6	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.2	0.1 \pm 0.2	0.0 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.1	0.1 \pm 0.2
22:4 ω 6	0.4 \pm 0.3 ^S	0.2 \pm 0.2 ^B	0.3 \pm 0.3	0.1 \pm 0.2	0.0 \pm 0.1	0.0 \pm 0.1	0.4 \pm 0.3	0.3 \pm 0.2	0.3 \pm 0.5	0.2 \pm 0.3
22:5 ω 6	1.0 \pm 0.3	1.2 \pm 0.5	1.1 \pm 0.3	1.4 \pm 0.4 ^S	2.2 \pm 0.7 ^{BY}	1.8 \pm 0.5 ^S	0.8 \pm 0.4	0.7 \pm 0.2	1.5 \pm 0.6	1.4 \pm 0.6
$\Sigma\omega$3	23.2 \pm 6.0	25.8 \pm 7.0	24.0 \pm 5.7	24.9 \pm 5.3	29.3 \pm 7.0	27.6 \pm 7.4	16.5 \pm 7.4	13.4 \pm 5.7	23.4 \pm 7.4	21.5 \pm 5.9
$\Sigma\omega$6	7.5 \pm 1.9	6.5 \pm 1.6	7.1 \pm 1.8	5.8 \pm 1.0	7.7 \pm 2.1	6.4 \pm 1.4	5.5 \pm 2.4	4.1 \pm 1.3	6.4 \pm 1.9	6.2 \pm 1.7
ΣPUFA	30.7 \pm 7.6	32.2 \pm 8.3	31.1 \pm 7.4	30.8 \pm 5.8	37.0 \pm 8.5	34.1 \pm 8.1	22.0 \pm 9.6	17.4 \pm 6.9	29.8 \pm 8.9	27.6 \pm 7.4

SFA: Saturated fatty acids; MUFA: Monounsaturated fatty acids; PUFA: Polyunsaturated fatty acids; EPA: Eicosapentaenoic acid; DHA: Docosahexaenoic acid; AA: Arachidonic acid; ω 3: Omega-3 fatty acids; ω 6: Omega-6 fatty acids.

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Table 2. ANOVA and PERMANOVA results of tests for differences in total lipid content (TLC, % dw), fatty acid profiles (neutral lipids as a % of total fatty acids), and nitrogen and carbon isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, ‰) in the muscle and liver of tropical tuna. Tested factors are season (NEM, SWM, SIM, AIM), area (WCIO or MOZ), size class (FL \leq 100 cm or FL $>$ 100 cm), species (SKJ, YFT and BET) and their interactions when possible. NEM: North-Eastern Monsoon; SWM: South Western Monsoon; SIM: Spring Inter-Monsoon; AIM: Autumn Inter-Monsoon; WCIO: Western-Central Indian Ocean; MOZ: Mozambique channel; BET: Bigeye; SKJ: Skipjack; YFT: Yellowfin. df: freedom degree; sqs: squares, F and Pseudo F: statistics of the tests.

Tissue	Factors	TLC					FATTY ACIDS					$\delta^{15}\text{N}$					$\delta^{13}\text{C}$				
		df	Sums of sqs	Mean sqs	F	P-value	df	Sums of sqs	Mean sqs	Pseudo-F	P-value	df	Sums of sqs	Mean sqs	F	P-value	df	Sums of sqs	Mean sqs	F	P-value
Muscle	Season	3	16.2	5.4	1.1	0.333	3	0.30	0.10	2.43	0.006	3	106.5	35.5	56.8	0.000	3	1.0	0.3	4.9	0.003
	Area	1	1.5	1.5	0.3	0.568	1	0.13	0.13	3.20	0.021	1	150.3	150.3	240.3	0.000	1	0.0	0.0	0.0	0.877
	Size class	1	4.3	4.3	0.9	0.342	1	0.51	0.51	12.37	0.001	1	32.2	32.2	51.5	0.000	1	2.8	2.8	40.2	0.000
	Species	2	3.2	1.6	0.3	0.715	2	0.49	0.24	5.84	0.001	2	79.5	39.7	63.6	0.000	2	3.3	1.6	23.2	0.000
	Size class * Species	1	14.7	14.7	3.1	0.079	1	0.09	0.09	2.25	0.043	1	0.7	0.7	1.1	0.296	1	0.1	0.1	1.2	0.276
	Size class * Area	1	60.9	60.9	12.9	0.000	1	0.07	0.07	1.78	0.120	1	1.7	1.7	2.7	0.103	1	0.5	0.5	6.4	0.012
	Species * Area	2	15.2	7.6	1.6	0.201	2	0.22	0.11	2.66	0.011	2	6.5	3.2	5.2	0.006	2	0.0	0.0	0.3	0.735
	Residuals	254	1198.9	4.7			176	7.32	0.04	0.80		242	151.4	0.6			242	17.0	0.1		
Liver	Season	3	1101.5	367.2	7.8	0.000	3	0.30	0.10	2.85	0.006	3	159.5	53.2	139.0	0.000	3	1.1	0.4	2.5	0.060
	Area	1	199.8	199.8	4.2	0.041	1	0.19	0.19	5.28	0.002	1	109.5	109.5	286.2	0.000	1	1.2	1.2	8.1	0.005
	Size class	1	2508.1	2508.1	53.0	0.000	1	1.27	1.27	35.70	0.001	1	0.0	0.0	0.1	0.760	1	5.3	5.3	34.8	0.000
	Species	2	230.4	115.2	2.4	0.090	2	0.54	0.27	7.56	0.001	2	53.9	26.9	70.4	0.000	2	0.5	0.2	1.5	0.215
	Size class * Species	1	153.6	153.6	3.2	0.073	1	0.03	0.03	0.97	0.334	1	3.0	3.0	7.7	0.006	1	0.0	0.0	0.2	0.646
	Size class * Area	1	689.0	689.0	14.6	0.000	1	0.22	0.22	6.31	0.002	1	0.0	0.0	0.0	0.849	1	0.4	0.4	2.4	0.121
	Species * Area	2	95.9	48.0	1.0	0.365	2	0.05	0.03	0.77	0.583	2	8.7	4.4	11.4	0.000	2	0.6	0.3	1.9	0.149
	Residuals	241	11407.1	47.3			168	5.97	0.04	0.70		227	86.8	0.4			227	34.4	0.2		

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Table 3. Biochemical trophic niches indices (INes for stable isotopes and FANes for neutral fatty acids profiles) calculated for small (≤ 100 cm) and large tuna (> 100 cm), in Western-Central Indian Ocean (WCIO) and Mozambique Channel (MOZ) separately. Values correspond to the degree of overlap among species with 0 = no overlap and 1 = complete overlap. BET: Bigeye; SKJ: Skipjack; YFT: Yellowfin.

Area	Size class	Tissue	Groups	FANes (3D)	INes (2D)
WCIO	FL \leq 100cm	Muscle	BET, SKJ	0.12 \pm 0.07	0.09 \pm 0.03
			BET, YFT	0.62 \pm 0.08	0.37 \pm 0.03
			SKJ, YFT	0.07 \pm 0.10	0.81 \pm 0.05
		Liver	BET, SKJ	0.30 \pm 0.05	0.43 \pm 0.07
			BET, YFT	0.60 \pm 0.08	0.81 \pm 0.04
			SKJ, YFT	0.51 \pm 0.07	0.49 \pm 0.03
	FL $>$ 100cm	Muscle	BET, YFT	0.71 \pm 0.06	0.00 \pm 0.00
		Liver	BET, YFT	0.53 \pm 0.14	0.34 \pm 0.06
MOZ	all sizes	Muscle	BET, SKJ	0.06 \pm 0.08	0.10 \pm 0.02
			BET, YFT	0.29 \pm 0.13	0.36 \pm 0.06
			SKJ, YFT	0.41 \pm 0.07	0.63 \pm 0.05
		Liver	BET, SKJ	0.08 \pm 0.04	0.15 \pm 0.04
			BET, YFT	0.34 \pm 0.22	0.44 \pm 0.13
			SKJ, YFT	0.40 \pm 0.06	0.73 \pm 0.05

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Highlights

- Sympatric tropical tuna (bigeye, yellowfin and skipjack tuna) were sampled in the Indian Ocean;
- Trophic niche partitioning was quantitatively assessed using time-integrated tracers;
- Intra- and inter-species competition in three tropical tuna species were detected;
- Diet shifts at ~ 100 cm FL were detected in the larger tuna species (bigeye and yellowfin);
- New insights into the mechanisms involved in tropical tuna coexistence were provided.

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