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

Fany Sardenne, N'Guessan Constance Diaha, Monin Justin Amande, Iker Zudaire, Lydie I.E. Couturier, Luisa Metral, Fabienne Le Grand, Nathalie Bodin

Canadian Journal of Fisheries and Aquatic Sciences
2019, Volume 76, Issue 1, Pages 69-80
http://dx.doi.org/10.1139/cjfas-2017-0368
http://archimer.ifremer.fr/doc/00436/54796/

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

Sardenne Fany [1, 2, *], Diaha N'guessan Constance [3], Amandé Monin Justin [3], Zudaire Iker [4, 5], Couturier Lydie I. E. [2], Metral Luisa [6], Le Grand Fabienne [2], Bodin Nathalie [1, 7]

[1] Research Institute for Sustainable Development (IRD), UMR MARBEC IRD/CNRS/Ifremer/UM, Centre de Recherche Halieutique, Sète, France
[2] University of Western Brittany (UBO), UMR LEMAR CNRS/UBO/IRD/Ifremer, Brest, France
[3] Centre de Recherches Océanologiques , Abidjan, Côte d'Ivoire
[4] Institut de recherche pour le developpement France-Sud, 98751, UMR MARBEC, Sète, France
[5] IKERBASQUE, Basque Foundation for Science, Bilbao, Spain
[6] IFREMER, UMR MARBEC IRD/CNRS/Ifremer/UM, Centre de Recherche Halieutique, Sète, France
[7] Seychelles Fishing Authority, 280177, Victoria, Mahe, Seychelles

* Corresponding author : Fany Sardenne, email address : fany.sardenne@hotmail.fr

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 δ15N values and high proportions of mono-unsaturated fatty acids). The trophic position of YFT decreased slightly in the last 15 years (δ15N 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

1. INTRODUCTION

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

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

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

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

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

2. MATERIAL & METHODS

2.1. Tunas and tissue sampling

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

2.2. Ecological tracers analysis

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

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

2.2.1. Stable isotope analysis and lipid content determination

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

2.2.2. Fatty acid analysis

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

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

2.3. Data analysis

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

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

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

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

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

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

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

3.2. Comparison of tropical tuna feeding niches

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

4. DISCUSSION

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

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

4.1. Trophic position of yellowfin decreases in the Atlantic Ocean

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

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

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

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

4.2. Large overlap in the tropical tuna feeding niches

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

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

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

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

4.3. Ontogenic changes are limited

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

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

4.4. Body condition of tropical tuna

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

4.5. Future directions

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

ACKNOWLEDGMENTS

We thank the CRO-IRD-IEO team in charge of tropical tunas purse-seine fisheries monitoring in Abidjan (Ivory Coast) for their help with tunas sampling: B.D.S. Barrigah, Y.D. Irié, D.A. Gbeazere, D. Kouadio, P. Dewals and E. Chassot. We also thank the cannery "Pêche et Froid" and the European purse-seiners for providing fish. We are also very grateful to Noémie Guyot (IRD Representation, Abidjan, Ivory Coast) who kindly helped with the transport of samples between Ivory Coast and France. We thank an anonymous reviewer and the associate editor for comments and detailed suggestions that greatly improved the manuscript. This work is a contribution of the research projects ANR EMOTION and MANTUNA. It was co-funded by the French Research Institute for Sustainable Development (IRD), the Centre de Recherches Océanologiques (CRO) and the European Data Collection Framework (DCF, Reg 199/2008 and 665/2008). FS was funded by the French organization France Fillière Pêche (FFP). LC was supported by the LabexMER (ANR-10-LABX-19) and co-funded by a grant from the French government ("Investissements d'Avenir" program), by a grant from the Regional Council of Brittany (SAD program), and by the EU FP7 Marie Curie actions (PCOFUND-GA-2013-609102), through the PRESTIGE program.

406 **REFERENCES**

407 Arrizabalaga, H., Pereira, J.G., Royer, F., Galuardi, B., Goni, N., Artetxe, I., Arregi, I., and Lutcavage,
408 M. 2008. Bigeye tuna (*Thunnus obesus*) vertical movements in the Azores Islands determined
409 with pop-up satellite archival tags. Fish. Oceanogr. **17**(2): 74–83.

410 Aryeetey, E.B.-D. 2002. 23 Socio-economic aspects of artisanal marine fisheries management in West
411 Africa. Large Mar. Ecosyst. **11**: 323–344. doi:10.1016/S1570-0461(02)80045-3.

412 Bard, F.-X., Kouamé, B., and Hervé, A. 2002. Schools of large yellowfin (*Thunnus albacares*)
413 concentrated by foraging on a monospecific layer of *Cubiceps pauciradiatus*, observed in the
414 eastern tropical Atlantic. Col Vol Sci Ap ICCAT **54**: 33–41.

415 Budge, S.M., Penney, S.N., and Lall, S.P. 2012. Estimating diets of Atlantic salmon (*Salmo salar*)
416 using fatty acid signature analyses; validation with controlled feeding studies. Can. J. Fish.
417 Aquat. Sci. **69**(6): 1033–1046. doi:10.1139/f2012-039.

418 Champalbert, G.A., Kouamé, B., Pagano, M., and Marchal, E. 2008. Feeding behavior of adult
419 *Vinciguerria nimbaria* (Phosichthyidae), in the tropical Atlantic (0°–4°N, 15°W). Mar. Biol.
420 **156**(1): 79. doi:10.1007/s00227-008-1067-z.

421 Cherel, Y., Sabatie, R., Potier, M., Marsac, F., and Ménard, F. 2007. New information from fish diets
422 on the importance of glassy flying squid (*Hyaloteuthis pelagica*)(Teuthoidea:
423 Ommastrephidae) in the epipelagic cephalopod community of the tropical Atlantic Ocean.
424 Fish. Bull. **105**(1): 147–152.

425 Chust, G., Allen, J.I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M.,
426 Cannaby, H., Dadou, I., Daewel, U., Wakelin, S.L., Machu, E., Pushpadas, D., Butenschon,
427 M., Artioli, Y., Petihakis, G., Smith, C., Garçon, V., Goubanova, K., Le Vu, B., Fach, B.A.,
428 Salihoglu, B., Clementi, E., and Irigoien, X. 2014. Biomass changes and trophic amplification
429 of plankton in a warmer ocean. Glob. Change Biol. **20**(7): 2124–2139. doi:10.1111/gcb.12562.

430 Dalsgaard, J., John, M.S., Kattner, G., Müller-Navarra, D., and Hagen, W. 2003. Fatty acid trophic
431 markers in the pelagic marine environment. Adv. Mar. Biol. **46**: 225–340.

432 Del Raye, G., and Weng, K.C. 2015. An aerobic scope-based habitat suitability index for predicting
433 the effects of multi-dimensional climate change stressors on marine teleosts. Deep Sea Res.
434 Part II Top. Stud. Oceanogr. **113**: 280–290. doi:10.1016/j.dsr2.2015.01.014.

435 Diaha, N.C., Zudaire, I., Chassot, E., Barrigah, B.D., Irié, Y.D., Gbeazere, D.A., Kouadio, D.,
436 Pecoraro, C., Romeo, M.U., and Murua, H. 2016. Annual monitoring of reproductive traits of
437 female yellowfin tuna (*Thunnus albacares*) in the eastern Atlantic Ocean. Collect Vol Sci Pap
438 ICCAT **72**: 534–548.

439 Dickson, K.A. 1996. Locomotor muscle of high-performance fishes: what do comparisons of tunas
440 with ectothermic sister taxa reveal? Comp. Biochem. Physiol. A Physiol. **113**(1): 39–49.
441 doi:10.1016/0300-9629(95)02056-X.

442 Dragovich, A. 1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. Fish. Bull. **68**(3):
443 445–460.

444 Dragovich, A., and Potthoff, T. 1972. Comparative study of food of skipjack and yellowfin tunas off
445 the coast of West Africa. Fish. Bull. **70**(4): 1087–1110.

446 Duffy, L.M., Kuhnert, P., Pethybridge, H.R., Young, J.W., Olson, R.J., Logan, J.M., Goñi, N.,
447 Romanov, E., Allain, V., Staudinger, M., Abecassis, M., Choy, C.A., Hobday, A.J., Simier,
448 M., Galván-Magaña, F., Potier, M., and Ménard, F. 2017. Global trophic ecology of yellowfin,
449 bigeye, and albacore tunas: understanding predation on micronekton communities at ocean-
450 basin scales. Deep Sea Res. Part II Top. Stud. Oceanogr. doi:10.1016/j.dsr2.2017.03.003.

451 France, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb
452 implications. Mar. Ecol. Prog. Ser. **124**: 307–312. doi:10.3354/meps124307.

453 Gruber, N., and Sarmiento, J.L. 1997. Global patterns of marine nitrogen fixation and denitrification.
454 Glob. Biogeochem. Cycles **11**(2): 235–266. doi:10.1029/97GB00077.

455 Hobday, A.J., Arrizabalaga, H., Evans, K., Scales, K.L., Senina, I., and Weng, K.C. 2017.
456 International collaboration and comparative research on ocean top predators under CLIOTOP.
457 Deep Sea Res. Part II Top. Stud. Oceanogr. **140**: 1–8. doi:10.1016/j.dsr2.2017.03.008.

458 Houssard, P., Lorrain, A., Tremblay-Boyer, L., Allain, V., Graham, B.S., Menkès, C., Pethybridge, H.,
459 Couturier, L.I.E., Point, D., Leroy, B., Receveur, A., Hunt, B.P.V., Vourey, E., Bonnet, S.,
460 Rodier, M., Raimbault, P., Feunteun, E., Kuhnert, P.M., Munaron, J.-M., Lebreton, B., Otake,
461 T., and Letourneur, Y. 2017. Trophic position increases with thermocline depth in yellowfin
462 and bigeye tuna across the Western and Central Pacific Ocean. Prog. Oceanogr. **154**: 49–63.
463 doi:10.1016/j.pocean.2017.04.008.

464 ICCAT. 2015. ICCAT stock assessments. Available from https://www.iccat.int/en/assess.htm
465 [accessed 19 April 2017].

466 Iverson, S.J., Field, C., Don Bowen, W., and Blanchard, W. 2004. Quantitative fatty acid signature: a
467 new method of estimating predator diets. Ecol. Monogr. **74**(2): 211–235. doi:10.1890/02-
468 4105.

469 Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths among
470 and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. **80**(3):
471 595–602.

472 Kelly, J., and Scheibling, R. 2012. Fatty acids as dietary tracers in benthic food webs. Mar. Ecol. Prog.
473 Ser. **446**: 1–22. doi:10.3354/meps09559.

474 Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich,
475 P., Rosenblatt, A.E., Vaudo, J.J., and Yeager, L.A. 2012. Applying stable isotopes to examine
476 food-web structure: an overview of analytical tools. Biol. Rev. **87**(3): 545–562.

477 Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M., and Maury, O. 2015. Spatial and body-size
478 dependent response of marine pelagic communities to projected global climate change. Glob.
479 Change Biol. **21**(1): 154–164. doi:10.1111/gcb.12679.

480 Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., and Lutcavage, M.E. 2008. Lipid
481 corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction
482 and modelling methods. J. Anim. Ecol. **77**(4): 838–846. doi:10.1111/j.1365-
483 2656.2008.01394.x.

Logan, J.M., and Lutcavage, M.E. 2013. Assessment of trophic dynamics of cephalopods and large pelagic fishes in the central North Atlantic Ocean using stable isotope analysis. Deep Sea Res. Part II Top. Stud. Oceanogr. **95**: 63–73. doi:10.1016/j.dsr2.2012.07.013.

Lorrain, A., Graham, B.S., Popp, B.N., Allain, V., Olson, R.J., Hunt, B.P.V., Potier, M., Fry, B., Galván-Magaña, F., Menkes, C.E.R., Kaehler, S., and Ménard, F. 2015. Nitrogen isotopic baselines and implications for estimating foraging habitat and trophic position of yellowfin tuna in the Indian and Pacific Oceans. Deep Sea Res. Part II Top. Stud. Oceanogr. **113**: 188–198. doi:10.1016/j.dsr2.2014.02.003.

Madigan, D.J., Litvin, S.Y., Popp, B.N., Carlisle, A.B., Farwell, C.J., and Block, B.A. 2012. Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific bluefin tuna (*Thunnus orientalis*). PLoS ONE **7**(11): e49220. doi:10.1371/journal.pone.0049220.

Ménard, F., Benivary, H.D., Bodin, N., Coffineau, N., Le Loc'h, F., Mison, T., Richard, P., and Potier, M. 2014. Stable isotope patterns in micronekton from the Mozambique Channel. Deep Sea Res. Part II Top. Stud. Oceanogr. **100**: 153–163. doi:10.1016/j.dsr2.2013.10.023.

Ménard, F., Labrune, C., Shin, Y.-J., Asine, A.-S., and Bard, F.-X. 2006. Opportunistic predation in tuna: a size-based approach. Mar. Ecol. Prog. Ser. **323**: 223–231.

Ménard, F., Lorrain, A., Potier, M., and Marsac, F. 2007. Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. Mar. Biol. **153**(2): 141–152. doi:10.1007/s00227-007-0789-7.

Ménard, F., and Marchal, E. 2003. Foraging behaviour of tuna feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic Ocean. Aquat. Living Resour. **16**(03): 231–238. doi:10.1016/S0990-7440(03)00040-8.

Ménard, F., Stéquert, B., Rubin, A., Herrera, M., and Marchal, É. 2000. Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. Aquat. Living Resour. **13**(4): 233–240.

Mourente, G., Megina, C., and Díaz-Salvago, E. 2001. Lipids in female northern bluefin tuna (*Thunnus thynnus thynnus* L.) during sexual maturation. Fish Physiol. Biochem. **24**(4): 351–363. doi:10.1023/A:1015011609017.

Olson, R.J., Duffy, L.M., Kuhnert, P.M., Galván-Magaña, F., Bocanegra-Castillo, N., and Alatorre-Ramírez, V. 2014. Decadal diet shift in yellowfin tuna *Thunnus albacares* suggests broad-scale food web changes in the eastern tropical Pacific Ocean. Mar. Ecol. Prog. Ser. **497**: 157–178.

Olson, R.J., Young, J.W., Ménard, F., Potier, M., Allain, V., Goñi, N., Logan, J.M., and Galván-Magaña, F. 2016. Bioenergetics, Trophic Ecology, and Niche Separation of Tunas. *In* Advances in Marine Biology. *Edited by* B.E. Curry. Academic Press. pp. 199–344. Available from http://www.sciencedirect.com/science/article/pii/S0065288116300049 [accessed 30 September 2016].

Parrish, C.C., Pethybridge, H., Young, J.W., and Nichols, P.D. 2015. Spatial variation in fatty acid trophic markers in albacore tuna from the southwestern Pacific Ocean—A potential 'tropicalization' signal. Deep Sea Res. Part II Top. Stud. Oceanogr. **113**: 199–207. doi:10.1016/j.dsr2.2013.12.003.

526 Pfennig, K.S., and Pfennig, D.W. 2009. Character Displacement: Ecological and Reproductive
527 Responses to a Common Evolutionary Problem. Q. Rev. Biol. **84**(3): 253–276.
528 doi:10.1086/605079.

529 Pinnegar, J.K., and Polunin, N.V.C. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish
530 tissues: implications for the study of trophic interactions. Funct. Ecol. **13**(2): 225–231.

531 Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007.
532 Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in
533 stable isotope analyses. Oecologia **152**(1): 179–189. doi:10.1007/s00442-006-0630-x.

534 Robin, J.., Regost, C., Arzel, J., and Kaushik, S.. 2003. Fatty acid profile of fish following a change in
535 dietary fatty acid source: model of fatty acid composition with a dilution hypothesis.
536 Aquaculture **225**(1–4): 283–293. doi:10.1016/S0044-8486(03)00296-5.

537 Saito, H., and Murata, M. 1998. Origin of the monoene fats in the lipid of midwater fishes:
538 relationship between the lipids of myctophids and those of their prey. Mar. Ecol. Prog. Ser.
539 **168**: 21–33.

540 Sardenne, F., Bodin, N., Chassot, E., Amiel, A., Fouché, E., Degroote, M., Hollanda, S., Pethybridge,
541 H., Lebreton, B., Guillou, G., and Ménard, F. 2016. Trophic niches of sympatric tropical tuna
542 in the Western Indian Ocean inferred by stable isotopes and neutral fatty acids. Prog.
543 Oceanogr. **146**: 75–88. doi:10.1016/j.pocean.2016.06.001.

544 Sardenne, F., Kraffe, E., Amiel, A., Fouché, E., Debrauwer, L., Ménard, F., and Bodin, N. 2017.
545 Biological and environmental influence on tissue fatty acid compositions in wild tropical
546 tunas. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. **204**: 17–27.
547 doi:10.1016/j.cbpa.2016.11.007.

548 Sardenne, F., Ménard, F., Degroote, M., Fouché, E., Guillou, G., Lebreton, B., Hollanda, S.J., and
549 Bodin, N. 2015. Methods of lipid-normalization for multi-tissue stable isotope analyses in
550 tropical tuna. Rapid Commun. Mass Spectrom. **29**(13): 1253–1267. doi:10.1002/rcm.7215.

551 Schaefer, K.M., Fuller, D.W., and Block, B.A. 2009. Vertical Movements and Habitat Utilization of
552 Skipjack (*Katsuwonus pelamis*), Yellowfin (*Thunnus albacares*), and Bigeye (*Thunnus*
553 *obesus*) Tunas in the Equatorial Eastern Pacific Ocean, Ascertained Through Archival Tag
554 Data. *In* Tagging and Tracking of Marine Animals with Electronic Devices. Springer,
555 Dordrecht. pp. 121–144. doi:10.1007/978-1-4020-9640-2_8.

556 Schaefer, K.M., Fuller, D.W., and Block, B.A. 2011. Movements, behavior, and habitat utilization of
557 yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean off Baja California, Mexico,
558 determined from archival tag data analyses, including unscented Kalman filtering. Fish. Res.
559 **112**(1–2): 22–37. doi:10.1016/j.fishres.2011.08.006.

560 Teffer, A.K., Staudinger, M.D., and Juanes, F. 2015. Trophic niche overlap among dolphinfish and co-
561 occurring tunas near the northern edge of their range in the western North Atlantic. Mar. Biol.
562 **162**(9): 1823–1840. doi:10.1007/s00227-015-2715-8.

563 Teuber, L., Schukat, A., Hagen, W., and Auel, H. 2014. Trophic interactions and life strategies of epi-
564 to bathypelagic calanoid copepods in the tropical Atlantic Ocean. J. Plankton Res. **36**(4):
565 1109–1123. doi:10.1093/plankt/fbu030.

566 Tocher, D.R. 2003. Metabolism and functions of lipids and fatty acids in teleost fish. Rev. Fish. Sci.
567 **11**(2): 107–184. doi:10.1080/713610925.

568 Ukwe, C.N., Ibe, C.A., and Sherman, K. 2006. A sixteen-country mobilization for sustainable fisheries
569 in the Guinea Current Large Marine Ecosystem. Ocean Coast. Manag. **49**(7): 385–412.
570 doi:10.1016/j.ocecoaman.2006.04.006.

571 Vander Zanden, M.J., Cabana, G., and Rasmussen, J.B. 1997. Comparing trophic position of
572 freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary
573 data. Can. J. Fish. Aquat. Sci. **54**(5): 1142–1158. doi:10.1139/f97-016.

574 Vaske, T., Vooren, C.M., and Lessa, R.P. 2003. Feeding strategy of yellowfin tuna (*Thunnus*
575 *albacares*), and wahoo (*Acanthocybium solandri*) in the Saint Peter and Saint Paul
576 Archipelago, Brazil. Bol. Inst. Pesca São Paulo **29**: 173–181.

577 Weng, K.C., Stokesbury, M.J.W., Boustany, A.M., Seitz, A.C., Teo, S.L.H., Miller, S.K., and Block,
578 B.A. 2009. Habitat and behaviour of yellowfin tuna *Thunnus albacares* in the Gulf of Mexico
579 determined using pop up satellite archival tags. J. Fish Biol. **74**(7): 1434–1449.

580 Wiafe, G., Dovlo, E., and Agyekum, K. 2016. Comparative productivity and biomass yields of the
581 Guinea Current LME. Environ. Dev. **17**: 93–104. doi:10.1016/j.envdev.2015.07.001.

582 Young, J.W., Guest, M.A., Lansdell, M., Phleger, C.F., and Nichols, P.D. 2010a. Discrimination of
583 prey species of juvenile swordfish *Xiphias gladius* (Linnaeus, 1758) using signature fatty acid
584 analyses. Prog. Oceanogr. **86**(1–2): 139–151. doi:10.1016/j.pocean.2010.04.028.

585 Young, J.W., Lansdell, M.J., Campbell, R.A., Cooper, S.P., Juanes, F., and Guest, M.A. 2010b.
586 Feeding ecology and niche segregation in oceanic top predators off eastern Australia. Mar.
587 Biol. **157**(11): 2347–2368. doi:10.1007/s00227-010-1500-y.

588 Zudaire, I., Murua, H., Grande, M., Goñi, N., Potier, M., Ménard, F., Chassot, E., and Bodin, N. 2015.
589 Variations in the diet and stable isotope ratios during the ovarian development of female
590 yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. Mar. Biol.: 1–15.
591 doi:10.1007/s00227-015-2763-0.

592 Zudaire, I., Murua, H., Grande, M., Pernet, F., and Bodin, N. 2014. Accumulation and mobilization of
593 lipids in relation to reproduction of yellowfin tuna (*Thunnus albacares*) in the Western Indian
594 Ocean. Fish. Res. **160**: 50–59. doi:10.1016/j.fishres.2013.12.010.

595

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).

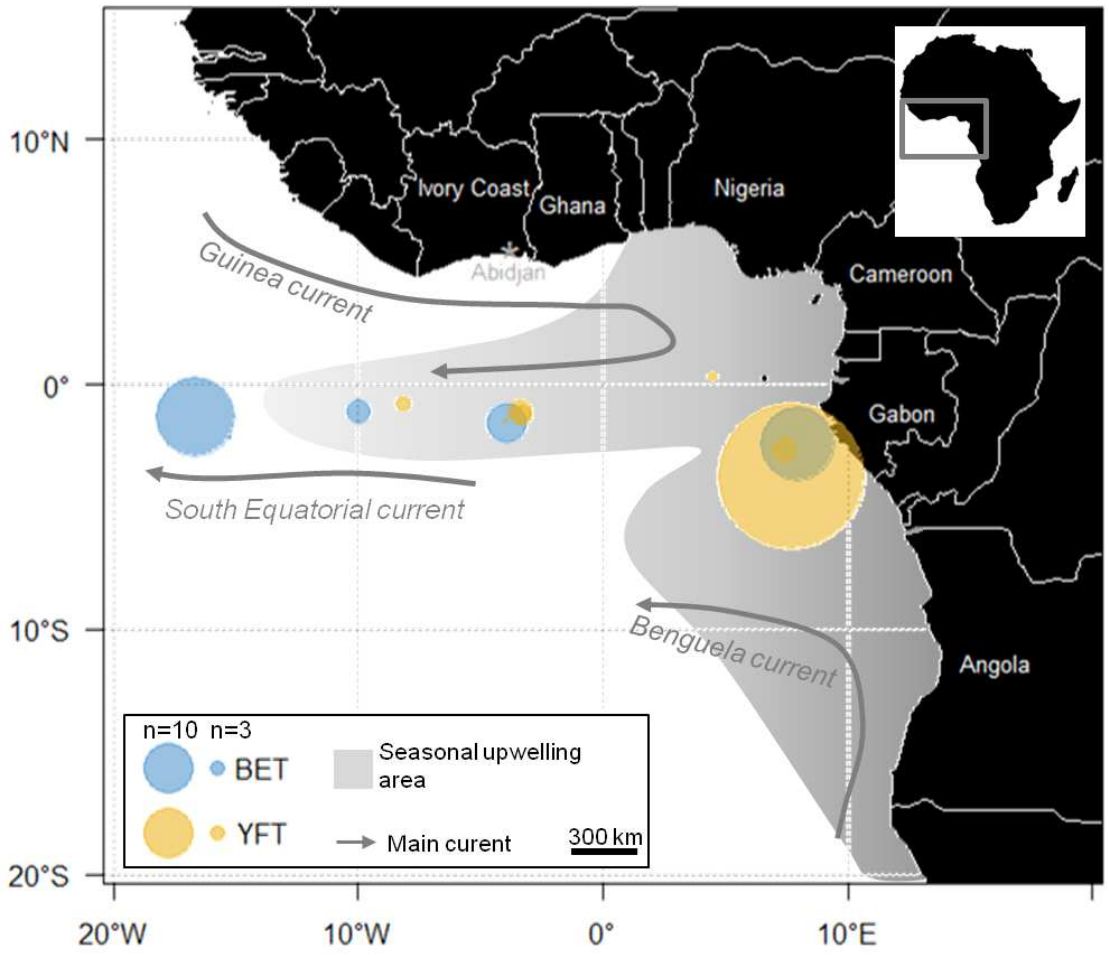

Fig. 2. Length influence on (a) nitrogen stable isotopic values ($\delta^{15}N$), (b) carbon stable isotopic values ($\delta^{13}C$) and (c) total lipid content (TLC) in muscle tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Linear regressions with confidence intervals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

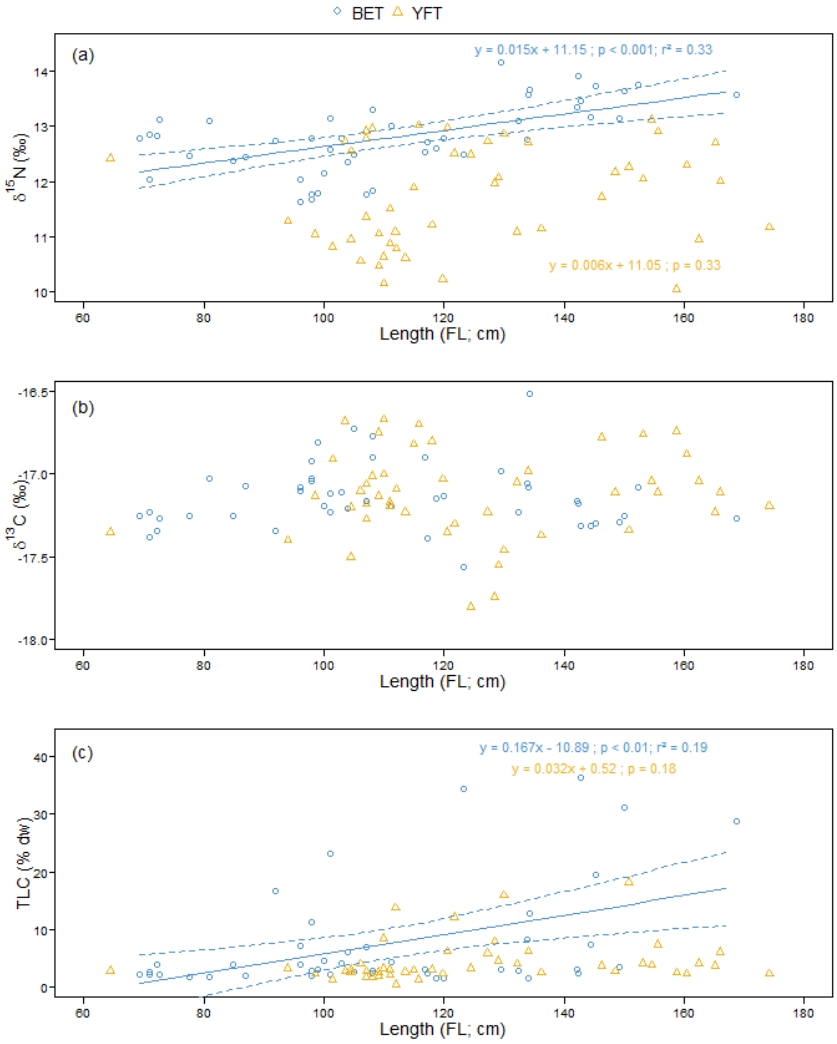

Fig. 3. Length influence on proportions of common fatty acids trophic markers in pelagic environment: (a) 20:5n-3, (b) 20:4n-6, (c) 18:1n-9 and (d) 22:6n-3, in the liver tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Simple linear regressions with confidence intervals 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).

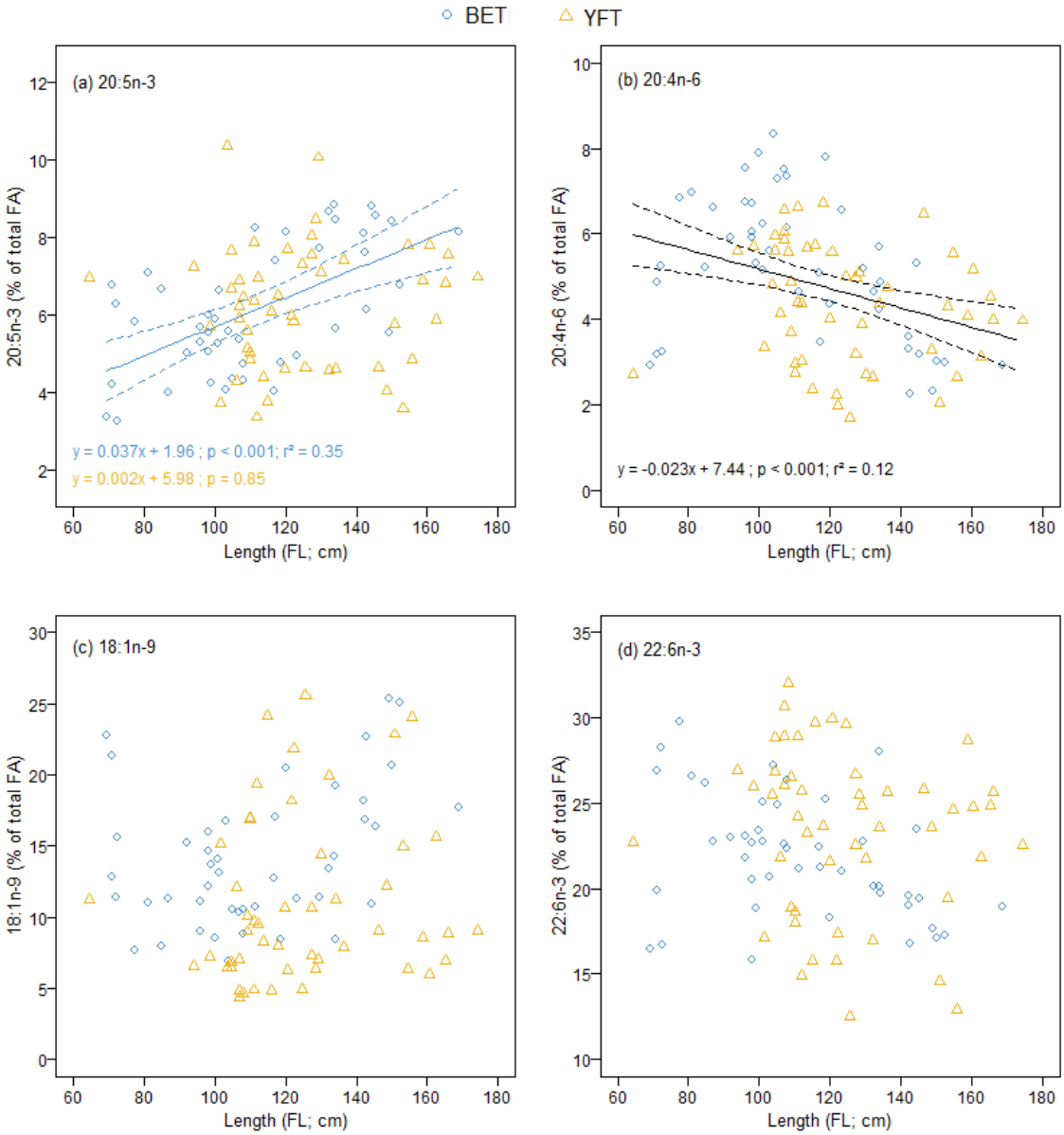

Fig. 4. Longitude influence on the three most affected fatty acids according to PCA: (a) 20:5n-3, (b) 20:4n-3 and (c) 20:4n-6, in liver tissue of bigeye (BET) and yellowfin tuna (YFT) collected from the Gulf of Guinea. Linear regressions with confidence interval are adjusted on both BET and YFT data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

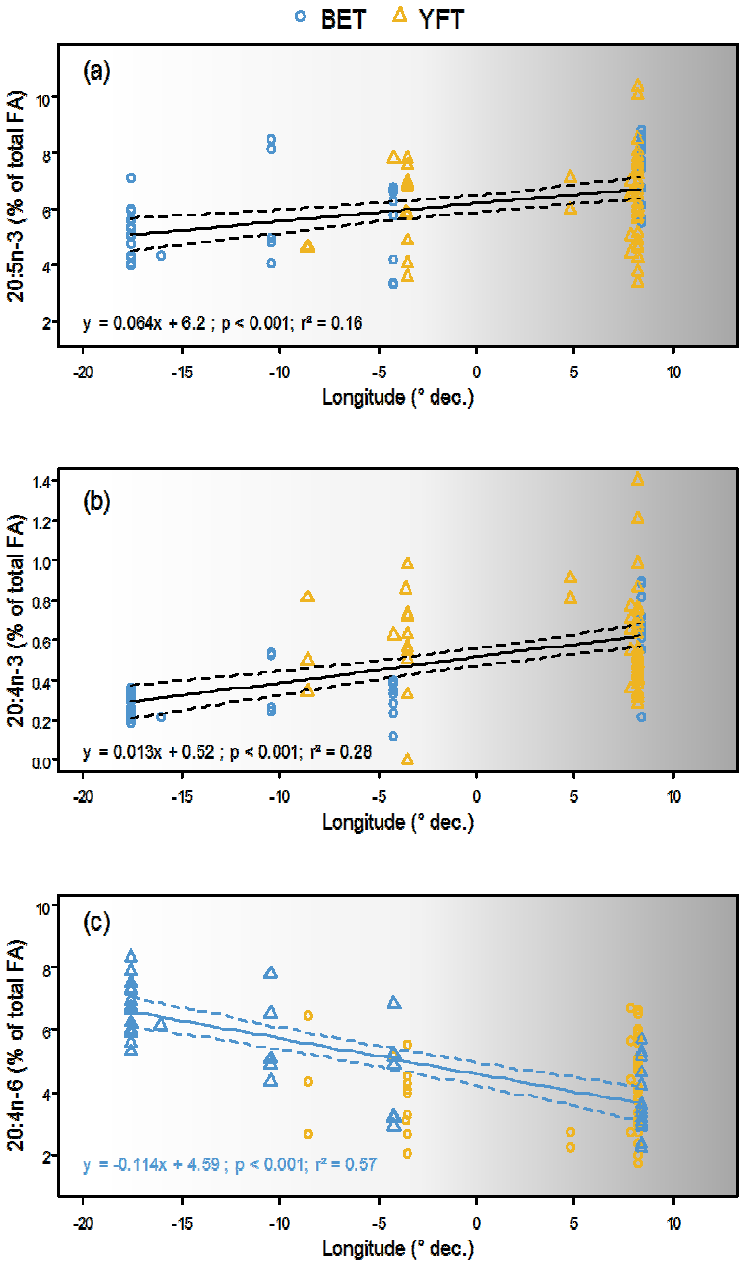

Fig. 5. Feeding niches of bigeye (BET; n=45) and yellowfin tuna (YFT; n=50) from the Gulf of Guinea using *SIBER* on (a) $\delta^{13}C$ and $\delta^{15}N$ values of muscle, and on (b) Principal component analyze (PCA) dimensions of fatty acids (FA) profiles of liver. FA most influential in PCA ($cos^2>0.35$) 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).

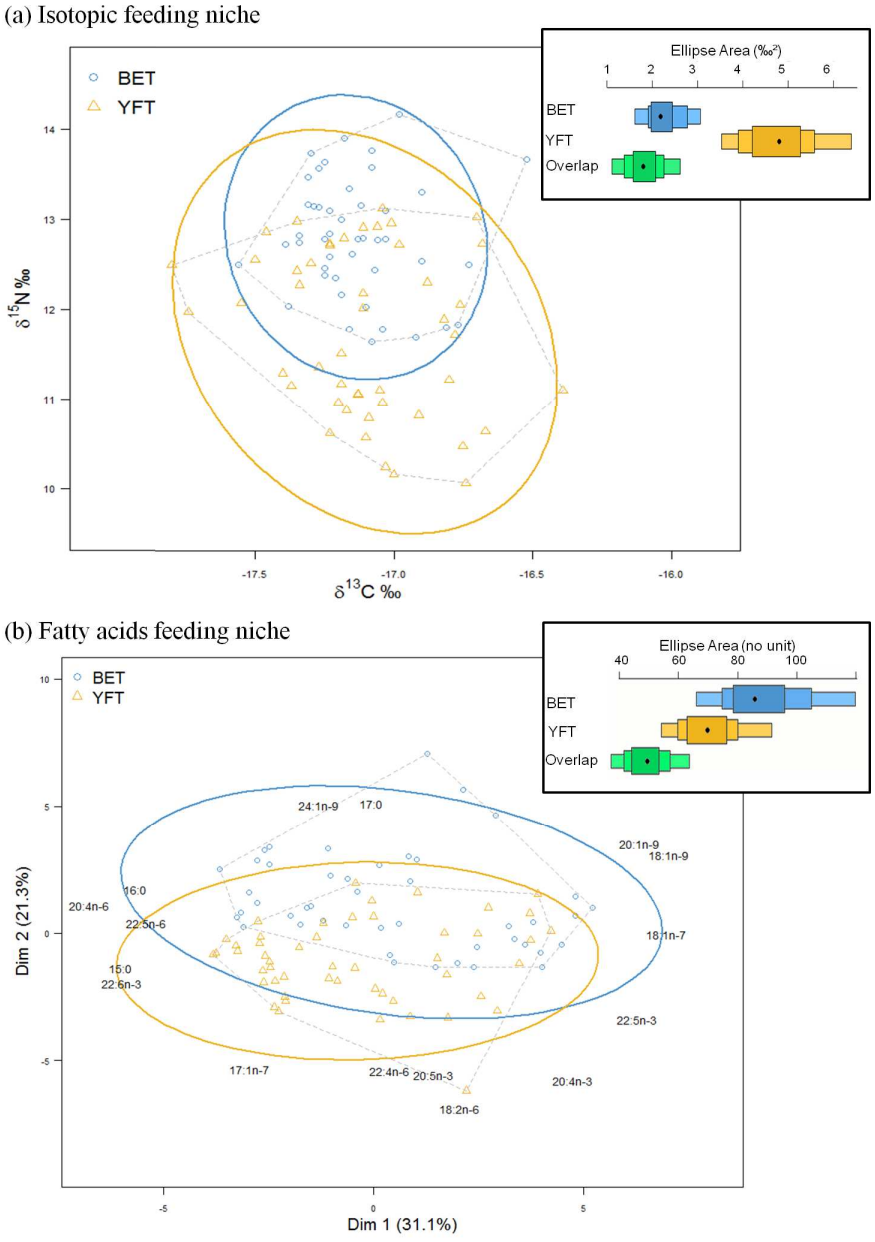

Table 1. Characteristics of fish, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$ values in ‰) and total lipid content (TLC in % dry weigh) of muscle and fatty acid (FA) distribution (in % of total FA) of liver for bigeye (BET) and yellowfin tuna (YFT) from the Gulf of Guinea. Data are mean ± SD. *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 ± 25.8	124.6 ± 22.6	
Sex ratio (♀ : ♂)	1 : 1.05	1 : 1.63	
Muscle			
n	*45*	*47*	
$\delta^{13}C$ (‰)	-17.1 ± 0.2	-17.1 ± 0.3	
$\delta^{15}N$ (‰)	12.8 ± 0.6	11.7 ± 0.9	*
TLC (% dw)	7.6 ± 9.3	4.5 ± 3.7	*
Liver			
n	*45*	*50*	
14:0	0.8 ± 0.2	0.7 ± 0.2	*
15:0	0.6 ± 0.2	0.6 ± 0.2	
16:0	23.3 ± 4.1	25.0 ± 2.9	*
17:0	2.0 ± 0.4	1.5 ± 0.2	*
18:0	8.7 ± 1.2	11.0 ± 1.5	*
Σ SFA	**35.5 ± 4.7**	**38.9 ± 3.2**	*
16:1n-7	2.4 ± 0.7	2.1 ± 0.7	*
17:1n-7	1.0 ± 0.3	1.2 ± 0.2	*
18:1n-9	14.1 ± 4.8	11.0 ± 5.9	*
18:1n-7	2.7 ± 0.8	2.3 ± 0.7	*
20:1n-9	1.4 ± 0.5	0.9 ± 0.4	*
20:1n-7	0.4 ± 0.8	0.1 ± 0.1	*
24:1n-9	0.8 ± 0.6	0.3 ± 0.1	*
Σ MUFA	**22.7 ± 6.3**	**17.9 ± 7.0**	*
18:2n-6	0.9 ± 0.2	1.0 ± 0.2	*
20:4n-6 (ARA)	5.2 ± 1.7	4.3 ± 1.4	*
22:4n-6	0.4 ± 0.2	0.8 ± 0.4	*
22:5n-6	1.3 ± 0.4	1.4 ± 0.4	
20:4n-3	0.4 ± 0.2	0.6 ± 0.2	*
20:5n-3 (EPA)	6.1 ± 1.6	6.2 ± 1.6	
22:5n-3	1.7 ± 0.9	1.7 ± 0.7	
22:6n-3 (DHA)	21.9 ± 3.5	23.3 ± 4.9	
Σ n-6	**7.8 ± 2.0**	**7.5 ± 1.7**	
Σ n-3	**30.2 ± 3.9**	**31.8 ± 5.9**	
Σ PUFA	**38.0 ± 4.8**	**39.3 ± 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 ($\delta^{13}C$ and $\delta^{15}N$) 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	**$\delta^{13}C$**			**$\delta^{15}N$**			**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