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Isotopic evidence of distinct foraging ecology and movement pattern in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean

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Abstract

Ecologists primarily use $\delta^{15}N$ values to estimate the trophic level of organisms, while $\delta^{13}C$, and even recently $\delta^{15}N$, are utilized to delineate foraging habitats. However, many factors can influence the stable isotopic composition of consumers, e.g. age, starvation or isotopic signature of primary producers. Such sources of variability make the interpretation of stable isotope data rather complex. To examine these potential sources of variability, muscle tissues of yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*) of various sizes were sampled between 2001 and 2004 in the western Indian Ocean during different seasons and along a latitudinal gradient (23°S to 5°N). Size and latitude effects on $\delta^{15}N$ and $\delta^{13}C$ were investigated using linear models. Both latitude and size significantly affect the stable isotope values of the studied species but variations were much more pronounced for $\delta^{15}N$. We explain the latitudinal effect by differences in nitrogen dynamics existing at the base of the food web and propagating along the food chain up to top predators. This spatial pattern suggests that yellowfin and swordfish populations exhibit a relatively unexpected resident behaviour at the temporal scale of their muscle tissue turnover. The size effect is significant for both species and indicates an increase in prey size through ontogeny. However, this effect is more pronounced in swordfish as a consequence of their different foraging strategies, reflecting specific physiological abilities. Swordfish adults are able to reach very deep water and have access to a larger size range of prey than yellowfin tuna. In contrast, yellowfin juveniles and adults spend most of their time in the surface waters and large yellowfin tuna continue to prey on small organisms. Consequently, nitrogen isotopic signatures of swordfish tissues are higher than those of yellowfin tuna and provide evidence for different trophic levels between these species. Thus, in contrast to $\delta^{13}C$, $\delta^{15}N$ analyses of tropical Indian Ocean marine predators allow the investigation of complex vertical and spatial segregation, both within and between species, even in the case of highly opportunistic feeding behaviours. The

39 linear models developed in this study allow us to make predictions of $\delta^{15}N$ values and to

40 correct for any size or latitude differences in future food web studies.

Introduction

Catches of tunas and billfishes have increased dramatically the past twenty years in the western Indian Ocean, very likely altering the structure and functioning of the ecosystems through trophic cascades (Essington et al. 2002; FAO 2006). Concomitantly to these top-down controls, bottom-up effects, via environmental and climatic changes, are also controlling abundance and spatial dynamics of top predators that depend on food availability (Cury et al. 2003; Franck et al. 2006; Frederiksen et al. 2006). Therefore, studies based on trophic ecology and movements of top predators are useful to assess the impact of fisheries and climate on marine resources, and to provide basic elements for an ecosystem approach to fisheries management (Sinclair and Valdimarsson 2003; FAO 2003). Unlike the Pacific and Atlantic oceans, few studies have investigated the diet of tunas and tuna-like species from stomach content analyses in the Indian Ocean (Watanabe 1960; Kornilova 1981; Roger 1994; Maldeniya 1996; Potier et al. 2004, 2007). Furthermore, stomach content analyses only reflect the composition of the most recent meal and limit our ability to address spatial and temporal variability of feeding behaviours.

Small- and large-scale movements of top predators are now assessed using conventional and electronic tagging programs combined with catch statistics (e.g., Block et al. 2005). A tagging programme, the Regional Tuna Tagging Programme of the Indian Ocean Tuna Commission (RTTP-IO, http://www.rttp-io.org/en/about/) is underway in the Indian Ocean. So far, few tag returns are available and catch statistics themselves do not reflect the real movement patterns (Hilborn and Walters 1992; Walters 2003). The knowledge of the spatial dynamics of tuna in the Indian Ocean is therefore still minimal.

Additional information on dietary sources, trophic levels, foraging strategies or movement patterns of migratory species can be obtained from stable isotope analyses of animal tissues (Rau et al. 1983; Fry 1988; Kelly 2000; Rubenstein and Hobson 2004; Cherel and Hobson,

66 2005, 2007). The stable isotope composition of an organism depends on its diet, its trophic
67 level, but also on the isotopic signature at the base of the food web (DeNiro and Epstein,
68 1978, 1981; Post 2002; Fry 2006). $\delta^{15}N$ measurements mainly serve as indicators of
69 consumer's trophic position, while $\delta^{13}C$ values are used to determine primary sources, inshore
70 versus offshore or pelagic versus benthic contribution to food intake (Hobson 1999). Indeed,
71 different oceanic processes affect isotopic baselines of $\delta^{15}N$ and $\delta^{13}C$ in marine pelagic food
72 webs (Rau et al. 1982; Altabet et al. 1995; Gruber and Sarmiento 1997; Lourey et al. 2003).
73 $\delta^{13}C$ values of phytoplankton decrease from low to high latitudes (Lourey et al. 2003) while
74 $\delta^{15}N$ of particulate organic matter is driven by nutrient utilization and the nitrogen source
75 used by primary producers (nitrate, ammonium, N_2 gas; Wada and Hattory 1991). The
76 resulting spatial and temporal variability in the isotopic baseline has been shown to be
77 incorporated and conserved through several trophic levels (up to pelagic consumers) across
78 ocean basins (Takai et al. 2000; Wallace et al. 2006) or within a region of a single basin
79 (Schell et al. 1989; Lesage et al. 2001; Quillfeldt et al. 2005; Cherel and Hobson 2005, 2007;
80 Cherel et al. 2005). Hobson (1999) illustrated this approach by the new maxim "you are what
81 you swim in" that complements the well-known dogma of stable isotopy "you are what you
82 eat." Consequently, the stable isotope ratios of animal tissues have the potential of
83 characterizing the isotopically distinct regions crossed by migrating fish and investigating
84 their foraging ecology. Graham et al. (2006) successfully applied this approach to yellowfin
85 tunas (*Thunnus albacares*) of the Pacific Ocean. One objective of the present study is
86 therefore to investigate the relationships between the isotopic signature of yellowfin tuna and
87 swordfish (*Xiphias gladius*) versus latitude in the western Indian Ocean, and their relative
88 degree of residency. Indeed, for migratory species, the variability of the isotopic signature in
89 their tissue is supposed to be low if the migration rate is quicker than isotopic tissue turnover.
90 Conversely, for more resident species, stable isotope ratios of tissues would reflect the

91 isotopic patterns at the base of the food web (Fry 2006; Graham et al. 2006; Popp et al. in
92 press). A second objective was to document the foraging ecology of yellowfin tuna and
93 swordfish, and potential ontogenetic effects on their trophic status. Ontogenetic shifts in tuna
94 and swordfish foraging behaviour are also expected as larger fish usually expand their
95 foraging habitat and exploit a larger size range of prey in the environment (Ménard et al.
96 2006; Young et al. 2006; Graham et al. 2007).

97 Inter-specific, spatial and ontogenetic differences in the stable isotope composition of
98 muscle tissues were thus investigated for these two migratory top predators of the western
99 Indian Ocean. Linear models and linear mixed-effects models were developed to test and
100 disentangle potential latitudinal and size effects on the stable isotope values ($\delta^{15}N$ and $\delta^{13}C$)
101 of each species. According to the model predictions, the trophic positions of individuals of
102 different sizes caught in different oceanic regions can then be compared. It is indeed a
103 prerequisite to understand these geographical and ontogenetic variations before determining
104 the trophic position of these species. This paper is however not intended to provide a
105 comprehensive study of the pelagic food web of the western Indian Ocean. Rather, we
106 implement the isotope approach to gain insight into the foraging ecology and movement
107 patterns on the studied predators, the first initiative of this nature in the Indian Ocean.

108

109 **Materials and methods**

110 *Sample collection*

111 Fish were caught by industrial purse seiners with scientific observers onboard; a 20-m
112 research longliner "Amitié" of the Seychelles Fishing Authority, and the French 24-m
113 industrial longliner "Cap Morgane". Samples were collected from 2001 to 2004 in the western
114 Indian Ocean along a latitudinal gradient (23°S to 5°N, Fig. 1). A total of 245 yellowfin tuna
115 (*Thunnus albacares*) and 136 swordfish (*Xiphias gladius*) from various sizes were collected

during these cruises. Fork length (FL) ranged from 40 to 160 cm for yellowfin tuna (mean = 103 cm and median = 108 cm) and Lower Jaw Fork length (LJFL) for swordfish ranged from 68 to 225 cm (mean = 135 cm and median = 133 cm). LJFL is a reliable measure of swordfish body size that allows comparisons with tunas by reducing the bias due to the bill. Table 1 displays all the sample characteristics. Muscle tissues from the dorsal region were collected onboard from freshly caught fishes and were stored frozen at -20°C until processing.

Sample preparation and analysis

Samples were freeze dried and ground to a fine powder. Lipid extraction was performed using 20 ml of cyclohexane on powder aliquots of about 1 g, and the lipid-extracted sample was dried at 60°C before processing. One milligram sample was then placed into 8×5 mm tin cups for CF-IRMS analysis, using a Europea Scientific ANCA-NT 20-20 Stable Isotope Analyser with ANCA-NT Solid/Liquid Preparation Module (PDZ Europa Ltd., Crewz, UK). Replicate measurements of internal laboratory standards indicate measurement errors of ± 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Triplicate analyses performed on some samples confirmed that analytical reproducibility was very good (0.2‰ maximum variation). Isotopic ratios are expressed in the conventional δ notation as parts per thousand (‰) deviation from the international standards: atmospheric nitrogen for $\delta^{15}N$ and VPDB Belemnite for $\delta^{13}C$:

$$\delta X = (R_{sample} / R_{standard} - 1) \times 1000,$$

where X is ^{15}N or ^{13}C and R the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$.

Lipid content in tuna and swordfish muscles may be high (greater than 50%, unpublished data). As lipids are highly depleted in ^{13}C (Tieszen et al. 1983), C/N mass ratios were used to check the lipid extraction process. $\delta^{13}C$ outliers (15 for yellowfin tuna and 33 for swordfish) were removed from the analyses according to the distributions of C/N values for each species. We estimated the corresponding thresholds to suppress any relationships between $\delta^{13}C$ and C/N mass ratios (3.62 and 3.70 for yellowfin tuna and swordfish, respectively). The resulting

141 distributions of C/N were normal (mean ± standard deviation of 3.36 ± 0.11
142 and 3.50 ± 0.11 for yellowfin tuna and swordfish, respectively) and the sampling ranges
143 of latitude and body size were not reduced for both species.

144 *Statistical analysis*

145 Linear regressions were used on the $\delta^{15}N$ and $\delta^{13}C$ data for each species to test the
146 covariates of interest, i.e. latitude and body size. However, all the individuals of one species
147 are not independent and the sampling scheme is clearly unbalanced. The individuals can be
148 grouped according to different factors (e.g. cruise, year, season, etc.; Table 1). We use the two
149 main seasons of the monsoon system to group the individuals of each species caught during
150 the cruises carried out from 2001 to 2004. Indeed, the ocean circulation in the West Indian
151 Ocean is strongly related to the wind monsoon regime, which in turn strongly affects
152 biological productivity (Tomczak and Godfrey 1994; Longhurst 1998; Schott and McCreary
153 2001). The Northeast (NE) monsoon becomes established in boreal winter (December to
154 March). It is characterized by winds blowing from the Asian continent to the equatorial zone,
155 a weak circulation north of the equator and a well marked counter-current flowing East
156 between 2°S and 7°S. The Southwest (SW) monsoon becomes established in boreal summer
157 (June-September), and is characterized by a reversal of the winds in the northern Indian
158 Ocean, the development of the northward-flowing Somali Current, and an eastward flow that
159 dominates the northern Indian Ocean. Therefore, each observation can be classified according
160 to the season on which it was made (NE or SW monsoon, Table 1). The 5 cruises which took
161 place during the inter-monsoons are relocated in their nearest monsoon: October and May in
162 the SW monsoon, and November in the NE monsoon. A classification based on the 4 seasons
163 (including the 2 additional inter-monsoon seasons) was also tested but not retained as the
164 various models fit to the $\delta^{15}N$ and $\delta^{13}C$ values gave similar results to the monsoon only
165 scenario. To test this grouping, the seasonal effect was treated as random variations around a

population mean, and the body size and the latitude were assessed as two fixed continuous covariates, using linear mixed-effects models (lme models; Pinheiro and Bates 2000). These lme models combine a random-effects analysis of variance model (variability amongst seasons) with a linear regression model. Lme models were tested against simple linear regression models using likelihood ratio tests. Population predicted values (obtained by setting the random effects to zero in the lme models) were used to compare latitude and body size effects for yellowfin tuna, for swordfish, and between the two species. All the computations and tests were performed on S-Plus (Insightful 2005).

Results

Muscle $\delta^{15}N$ and $\delta^{13}C$ values for yellowfin tuna and swordfish plotted versus body size, latitude and season (NE and SW monsoons) are shown in Figs. 2 and 3. The $\delta^{15}N$ values for yellowfin tuna ranged from 10.2 to 15.2‰ and from 11.8 to 16.2‰ for swordfish (Fig. 2). The $\delta^{13}C$ values for yellowfin tuna ranged from −17.4 to −15.2 ‰ and from −17.4 to −15.0‰ for swordfish (Fig. 3). The range of variation for the $\delta^{13}C$ values is therefore much more reduced than the $\delta^{15}N$ range (≈ 2‰ vs. 5‰).

Linear regression models with latitude and size added sequentially were significant ($p = 0.026$ for $\delta^{15}N$ and $p < 0.001$ for $\delta^{13}C$ for yellowfin tuna; $p < 0.001$ for $\delta^{15}N$ and $\delta^{13}C$ for swordfish). However, deviations from the models suggest that other models might be appropriate. For example, Fig. 2 reveals that intercepts of the models for $\delta^{15}N$ may differ between seasons.

Linear mixed-effects models (lme models) were fitted to the muscle $\delta^{15}N$ values grouped by season. The most parsimonious model for swordfish was obtained with both latitude and size as fixed-effect covariates ($p < 0.0001$). For yellowfin tuna, when body size was added to a lme model containing latitude only, the fit was only marginally improved (p =

191 0.092). This p-value evidences the low significance of body size for yellowfin tuna $\delta^{15}N$
192 values, a result already exhibited in Fig. 2. According to the likelihood ratio test, lme models
193 for both species provided a much better description of the $\delta^{15}N$ data than the linear regression
194 models did ($p < 0.0007$ and $p < 0.0001$ for yellowfin tuna and swordfish, respectively). Fig. 4
195 displays the predicted lines for each season (using the estimated random effects) and the
196 original data for model checking. These plots exhibit the large variability of the $\delta^{15}N$ values
197 for each season, and confirm that latitude was the strongest linear fixed-effect for yellowfin
198 tuna, while body size was the most significant fixed-effect for swordfish. For both species, the
199 random effects were associated with the intercepts only. Therefore within-season intercept
200 estimates for $\delta^{15}N$ data were different, while slopes were identical. Interestingly, within-
201 season intercepts exhibited a similar pattern whatever the species: the NE monsoon intercept
202 was always greater than the SW monsoon intercept (difference estimated at 0.37 and 0.67‰
203 for yellowfin tuna and swordfish, respectively). The assumption of normality and
204 independence for the random effect and the residuals were graphically assessed (not shown).
205 On the other hand, lme models fit to the fish muscle $\delta^{13}C$ values were not significantly better
206 than the linear regression models ($p > 0.50$ for yellowfin tuna and $p = 0.33$ for swordfish).
207 Table 2 lists the coefficients and standard errors estimated by the most parsimonious models
208 fit to the $\delta^{15}N$ and $\delta^{13}C$ data.
209

210 **Discussion**

211 Our results provide evidence for a genuine relationship between latitude and body size
212 with $\delta^{15}N$ and $\delta^{13}C$ values of yellowfin tuna and swordfish. Linear mixed-effects models were
213 used for $\delta^{15}N$ data and provided identical slopes with different intercepts between the two
214 seasons for both latitude and body size. Simple linear models with no seasonal effect were
215 selected for $\delta^{13}C$ data. Both size and latitude influence $\delta^{15}N$ values of the two species more

strongly than $\delta^{13}C$ values. Model predictions at the population level allow us to analyse these effects separately. Fig. 5A illustrates $\delta^{15}N$ and $\delta^{13}C$ predicted values of yellowfin tuna and swordfish as a function of varying sizes for fish caught at different latitudes (-10° and 0°). In the same way, Fig. 5B represents $\delta^{15}N$ and $\delta^{13}C$ predicted values for fish of different sizes (80 and 160 cm) as a function of a latitudinal gradient. We now attempt to examine some hypotheses supported by our results with respect to the trophic ecology of yellowfin tuna and swordfish, and to the oceanic processes affecting the isotopic baseline of $\delta^{15}N$ and $\delta^{13}C$ in marine food webs.

Latitudinal effect

The range of variation for the $\delta^{15}N$ values of yellowfin tuna and swordfish is of 2‰ along a latitudinal gradient of 30° (2.4 and 1.1‰ for yellowfin tuna and swordfish, respectively, Fig 5B), whereas those variations are less than 1‰ for $\delta^{13}C$ (0.8 and 0.7‰ for yellowfin tuna and swordfish, respectively). Three hypotheses can be put forward to explain the $\delta^{15}N$ and $\delta^{13}C$ increase from the Mozambique Channel to the Somali basin: 1) dietary changes, 2) starvation and 3) a shift in $\delta^{15}N$ baseline. Trophic level differences or starvation of the northern individuals seem highly unlikely given the regularity of the observed variations, and are not supported by any ecological data. We argue that this spatial pattern results from different oceanic processes at the base of the food web that vary by region in the western Indian Ocean, and that are conserved through different trophic levels up to top predators.

Particulate organic matter (POM) $\delta^{15}N$ and $\delta^{13}C$ isotopic values are not available in the western Indian Ocean to document a latitudinal pattern at the base of the food chain. However, knowledge of nitrogen dynamics in several zones of the western Indian Ocean suggests that differences in $\delta^{15}N$ values of POM might occur. In particular, the Somali region

241 should have higher $\delta^{15}N$ baseline values compared to Mozambique Channel. This is because
242 the Arabian Sea is a major area of anoxia (Gruber and Sarmiento 1997), and is characterized
243 by intensive denitrification that leads to an accumulation of isotopically enriched nitrate in
244 subsurface waters (Gaye-Haake et al. 2005; Naqvi et al. 2006). Conversely, different tracers
245 and biological indicators in the surface waters of the South Indian subtropical gyre (around
246 20°S, 57°E) have shown a prevailing N_2 fixation, known to generate lower $\delta^{15}N$ values for
247 phytoplankton (Capone and Carpenter 1982; Carpenter 1983; Gruber and Sarmiento 1997).
248 Gruber and Sarmiento (1997) also found a latitudinal gradient between the Arabian Sea and
249 25°S in the western Indian Ocean with decreasing denitrification and increasing N_2 fixation
250 from North to South. We did not sample the core of the South Indian subtropical gyre, nor the
251 Arabian Sea; however, the northern and southern edges of our sampling zone are connected
252 through the current system to the two most contrasted zones of denitrification (the Arabian
253 Sea) and N_2 fixation (subtropical gyre, Tomczak and Godfrey 1994; Schott and McCreary
254 2001, Davis 2005). Therefore, the $\delta^{15}N$ baseline values of the Somali region are likely to be
255 strongly influenced by the Arabian Sea while those of the Mozambique Channel are under the
256 influence of the subtropical gyre (Davis 2005).

257 In several studies using stable isotopes to delineate foraging locations of marine
258 predators of the southern Ocean, $\delta^{13}C$ displayed strong variations with latitude, whereas $\delta^{15}N$
259 values responded mainly to trophic enrichment (Quillfeldt et al. 2005; Cherel and Hobson
260 2005, 2007). Indeed, in the southern hemisphere, the geographical $\delta^{13}C$ gradient in POM of
261 surface waters is well defined, and ranges from high $\delta^{13}C$ values in warm subtropical waters
262 in the North, to low values in cold Antarctic waters in the South (François et al. 1993; Trull
263 and Armand 2001), with abrupt changes at fronts (Subtropical, Subantarctic and Polar fronts).
264 Gradients in terms of sea temperature are much more reduced in our sampling zone (Tomczak
265 and Godfrey 1994), which could explain the weak $\delta^{13}C$ variations in the western tropical

266 Indian Ocean revealed by our study. Broad $\delta^{15}N$ gradients, as observed in this study, have
267 been found in other open ocean regions. Comparing leatherback turtle $\delta^{15}N$ signatures in the
268 Eastern Tropical Pacific and in the Atlantic Ocean, Wallace et al. (2006) found inter-basin
269 differences of 5‰ between denitrification and N_2 fixation zones. In the Equatorial Pacific,
270 Graham et al. (2006) have shown basin-wide $\delta^{15}N$ differences as high as 11‰ in tuna muscle
271 tissue. In the Indian Ocean, we detected a much lower intra-basin difference (i.e., maximum
272 of 2.4‰ for yellowfin tuna), most probably because our samples did not cover the core areas
273 mentioned earlier. Consequently, even if yellowfin tuna and swordfish are migrating between
274 the two contrasted region (the Arabian Sea versus the subtropical gyre), we are probably
275 observing a diluted effect of this general intra-basin difference. Furthermore, muscle tissues
276 of these species might never be at isotopic equilibrium with their recent diet because of their
277 continuous movement, their opportunistic foraging behaviour and their muscle tissue isotopic
278 turnover (half-life around 50 days, Graham, unpublished data). All these reasons generate
279 variability in the data, reduce the effect of the latitudinal gradient, but do not challenge its
280 occurrence.

281 The observed conservation of the $\delta^{15}N$ baseline characteristics in these top predators
282 has several implications. First, these species are known to be highly migratory and thus such a
283 gradient in the data is not expected. Indeed, these data suggest that yellowfin tuna and
284 swordfish are relatively resident species at the temporal scale of their tissue isotopic turnover,
285 i.e., three months for yellowfin tuna (Graham, unpublished data). However, this does not
286 preclude large basin-wide movement patterns at the temporal scale of their life time.
287 Furthermore, the coexistence of migrating fish among more resident fish might occur and
288 explain the rather high intra-season variability found in our study. Interestingly, the $\delta^{15}N$
289 predictions along the latitudinal gradient varied two times more for yellowfin tuna than for
290 swordfish (differences of 2.4‰ and of 1.2‰, respectively). This can be interpreted in

291 different ways: (i) yellowfin tuna are more resident than swordfish, (ii) swordfish have a
292 slower turnover rate or tissue growth than yellowfin tuna, (iii) swordfish do not migrate to
293 highly ^{15}N depleted areas such as the Arabian Sea, which the very low catch records of this
294 species in this region suggests (Fonteneau 1997). The third hypothesis seems the most
295 plausible given our present knowledge; however, we cannot preclude a mixed influence of the
296 three hypotheses.
297
298 *Seasonal effect*
299 In the mixed-effects models implemented in this paper for $\delta^{15}N$ values, the seasonal
300 effect is random and induced by the grouping of the data. Only intercepts differ between NE
301 and SW monsoon predictions: compared to the SW monsoon, the NE monsoon intercepts are
302 0.36 and 0.67‰ higher for yellowfin tuna and swordfish, respectively. During the NE
303 monsoon, the waters of the Arabian sea are advected to the South and invade the Somali basin
304 (where part of our data collection was undertaken), potentially increasing the $\delta^{15}N$ values of
305 the baseline of this zone compared to SW monsoon (Davis 2005). Conversely, during the SW
306 monsoon, there is a broad equatorward flow of waters from the South Equatorial Current
307 (SEC) along the East African Coast reaching the Somali region (Tomczak and Godfrey 1994;
308 Schott and McCreary 2001; Davis 2005). Further studies involving measurements of the $\delta^{15}N$
309 of the POM over an annual cycle should be investigated to shed some light on the seasonal
310 variations that may occur in the western Indian Ocean.
311 Interestingly, the seasonal effect is not significant for $\delta^{13}C$ values. We believe that
312 seasonal changes in the monsoon regime do not have strong consequences on the carbon
313 isotopes ratios in the sampled areas. In addition, the $\delta^{13}C$ ranges we observed in our data were
314 low compared to the intra-individual variability. Our results suggest that muscle $\delta^{13}C$ values
315 of fish in these open sea ecosystems of the western Indian Ocean might not be useful to

316 document seasonal changes, to delineate foraging locations or to track fish movement. This is
317 in contrast to studies conducted in the southern Indian Ocean where $\delta^{13}C$ has been shown to
318 be a useful tool (Cherel and Hobson 2005, 2007).
319
320 *Size effect*
321 Figure 5A indicates changes in the $\delta^{15}N$ and $\delta^{13}C$ model predictions along a gradient
322 of body size, for fish caught at two different latitudes. In each case, the $\delta^{15}N$ values exhibited
323 a stronger size effect for swordfish than for yellowfin tuna. The isotopic difference between
324 large (200 cm) and small (80 cm) swordfish was about 2‰, whereas it was less than 0.5‰ for
325 yellowfin tuna of 40 to 160 cm. The same pattern is supported by $\delta^{13}C$ values, but isotopic
326 differences are much more reduced (0.8 and 0.4‰ for swordfish and yellowfin tuna,
327 respectively). The lower differences for $\delta^{13}C$ are not surprising given that $\delta^{15}N$ is known to
328 increase much more with trophic levels than $\delta^{13}C$ (DeNiro and Epstein, 1981). Body size is
329 indeed known to play a crucial role in predator-prey interactions (Sheldon et al. 1977; Cury et
330 al. 2003). Analyses of stomach contents and nitrogen isotope ratios conducted on fish
331 communities in different marine ecosystems have shown that prey size and trophic level
332 generally increase with increasing predatory body size (Scharf et al. 2000; Jennings et al.
333 2002). In open-sea ecosystems, few studies have yet dealt specifically with size-based
334 predation. Ménard et al. (2006) have shown that the maximum size of the prey consumed by
335 yellowfin tunas tends to increase with tuna body length, but that large yellowfin tunas
336 continue to consume small prey in great proportions. In addition, both adults and juveniles of
337 yellowfin tuna generally show only minor differences in depth distributions (Brill et al. 1999,
338 2005). Yellowfin tuna spend most of their time in the surface layer, even if some exceptional
339 deep dives have been evidenced by one archival tag (Dagorn et al. 2006). The diet of
340 yellowfin tunas is then mainly composed of organisms present in the upper 100 m (Moteki et

341 al. 2001; Bertrand et al. 2002; Potier et al. 2004, 2007), with no major ontogenetic changes
342 (Ménard et al. 2006). An outstanding diet shift was revealed by Graham et al. (2007) but this
343 study only concerned small juveniles of yellowfin tunas ranging around 45 cm and caught in
344 areas surrounding Hawaiian Islands. Therefore, we conclude that the size of yellowfin tuna
345 does not have a strong impact on its $\delta^{15}N$ values. On the other hand, large swordfish mainly
346 consume cephalopods (Hernandez-Garcia 1995; Markaida and Hochberg 2005; Young et al.
347 2006; Potier et al. 2007), while smaller swordfish have a diet focused on mesopelagic fish
348 such as myctophids (Young et al. 2006; Potier et al. 2007). This shift in the dominant prey
349 items has consequences on the $\delta^{15}N$ values because mesopelagic fish such as myctophids and
350 paralepidids have shown lower mean $\delta^{15}N$ values than cephalopods (Young et al. 2006). In
351 addition, swordfish can catch larger prey specimens as they grow, due to an increase of
352 mouth-gape size, chasing predation, and diving capability (Carey and Robinson 1981).
353 Therefore, we fully confirm that body size influences the $\delta^{15}N$ values of swordfish, as already
354 shown by Young et al. (2006) with much fewer data. This influence is much more
355 pronounced than for yellowfin tuna, due to the change in the foraging ecology of swordfish
356 through its ontogeny.
357
358 *Trophic level differences*
359 Over the body sizes and latitudes common to both species, and for a similar size or
360 latitude, the $\delta^{15}N$ values of swordfish were about 0.7 to 2.8‰ higher than those of yellowfin
361 tuna (Fig. 5). The greatest $\delta^{15}N$ differences were found in large fish (160 cm) sampled in the
362 south (25°S), while the smallest differences occurred in small fish (80 cm) sampled in the
363 north (5°N). In a recent study conducted in the same area, Potier et al. (2007) established that
364 (i) the diet composition of swordfish was dominated by mesopelagic cephalopods
365 (Ommastrephidae and to a lesser extent Onychoteuthidae) and by mesopelagic fish

366 (Nomeidae and Diretmidae), while epipelagic prey dominated the diet of yellowfin tuna, (ii)
367 swordfish catch larger specimens of the same prey species than yellowfin tuna. This general
368 diet pattern reflects a well-known resource partitioning between both species. Swordfish
369 undertake large vertical migrations, allowing them to prey actively at great depth, while both
370 adult and juvenile yellowfin tuna spend the vast majority of their time in the surface layer and
371 prey on small organisms (Brill et al. 2005; Ménard et al. 2006; Potier et al. 2007).
372 Consequently, swordfish have access to a larger size range of prey in the environment than
373 yellowfin tuna, and can feed on the predators of yellowfin tuna's prey. Thus, the observed
374 differences in $\delta^{15}N$ values of swordfish and yellowfin tuna, once the size and latitudinal
375 effects are removed, illustrate different trophic levels between both species due to distinct
376 foraging strategies. Graham et al. (2007) hypothesized that mesopelagic prey might have $\delta^{15}N$
377 values higher than epipelagic species. This assumption could strengthen the $\delta^{15}N$ differences
378 between both species, but further investigations should be carried out on the isotopic values of
379 the forage fauna of large pelagics.
380
381 **Summary and conclusion**
382 This study revealed body size and latitudinal effects on $\delta^{15}N$ and $\delta^{13}C$ values of two
383 migratory highly opportunistic predators: yellowfin tuna (*Thunnus albacares*) and swordfish
384 (*Xiphias gladius*). However, in these open sea ecosystems of the western Indian Ocean, $\delta^{15}N$
385 was much more useful than $\delta^{13}C$ to delineate trophic relationships and to track fish
386 movements. Linear mixed-effects models developed here will allow us to make predictions of
387 $\delta^{15}N$ values and to correct for any size or latitude differences in future food web studies. This
388 study also confirmed that baseline $\delta^{15}N$ isotopic variations can be conserved through several
389 trophic levels, and even up to high trophic levels such as tunas and swordfish. These spatial
390 differences together with differences in the size effects according to species illustrated the

potential of stable isotopes to investigate complex trophic ecology and foraging strategies, both within and between species, even in the case of highly opportunistic feeding behaviours.

To further investigate these spatial and size variations in the $\delta^{15}N$ values of yellowfin tuna and swordfish, isotopic analyses of mesopelagic species together with particulate organic matter from these regions are needed. Spatial and size-based variation in the $\delta^{15}N$ of marine pelagic fish should be considered when using $\delta^{15}N$ to detect trophic-level variation in natural communities.

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Table 1. Sample characteristics of yellowfin tuna and swordfish

				Swordfish					Yellowfin				
				N	Size		Latitude		N	Size		Latitude	
Cruise	Time period	Year	Group		min	max	min	max		min	max	min	max
AM1	Aug. 13-24	2001	SW monsoon	0					18	108	156	-4	2
AM2	Oct. 16-26	2001	SW monsoon	4	94	111	-4	0	5	122	140	0	0
AM6	Jul. 13-30	2002	SW monsoon	13	100	203	-4	-3	1	136	136	-3	-3
AM9	Jul. 4-9	2004	SW monsoon	5	90	226	-4	-2	1	123	123	-3	-3
ECO6	May 5-19	2004	SW monsoon	47	76	209	-17	-11	34	65	156	-17	-11
ECO9	Sept. 11-19	2003	SW monsoon	16	108	205	-23	-22	6	124	150	-22	-21
TG2	May 2 - June 21	2001	SW monsoon	0					32	42	160	-10	-6
GU1	Oct. 6 - Nov. 7	2001	SW monsoon	0					66	39	149	-4	5
AM3	Nov. 19-30	2001	NE monsoon	3	111	190	-5	-5	8	112	136	-5	-4
AM4	Jan. 28 - Feb. 8	2002	NE monsoon	3	113	162	-4	-3	10	102	153	-4	-3
AM5	Feb. 27 - Mar. 12	2002	NE monsoon	3	145	149	-1	1	0				
AM7	Dec. 10-20	2002	NE monsoon	2	114	137	-5	-5	5	88	141	-6	4
AM8	Jan. 29 - Feb. 9	2003	NE monsoon	7	76	162	-4	0	27	56	151	-5	0
ECO7	Nov. 10 - 29	2004	NE monsoon	33	68	199	-23	-18	9	96	160	-23	-18
TAL	March 28 - Apr. 29	2002	NE monsoon	0					2	58	60	-15	-14
AVAD	Feb. 2-10	2003	NE monsoon	0					21	61	164	-7	-5

Table 2. Estimated intercepts and slopes (with standard errors) and within-season standard deviations σ_{season} for the random effects for linear mixed-effects models fit to the $\delta^{15}N$ values of yellowfin tuna and swordfish, and estimated intercepts and slopes (with standard errors) for linear regression models fit to the $\delta^{13}C$ values of yellowfin tuna and swordfish.

Coefficients		$\delta^{15}N$	$\delta^{13}C$
Intercept	Yellowfin tuna	12.995 (0.245)	–16.418 (0.0759)
	Swordfish	12.613 (0.414)	–16.568 (0.162)
Latitude	Yellowfin tuna	0.0807 (0.0085)	0.0266 (0.0042)
	Swordfish	0.0418 (0.0072)	0.0282 (0.0047)
Size	Yellowfin tuna	0.0025 (0.0015)	0.0030 (0.0007)
	Swordfish	0.0163 (0.0016)	0.0060 (0.0011)
σ_{season}	Yellowfin tuna	0.267	-
	Swordfish	0.481	-

Legends of the figures

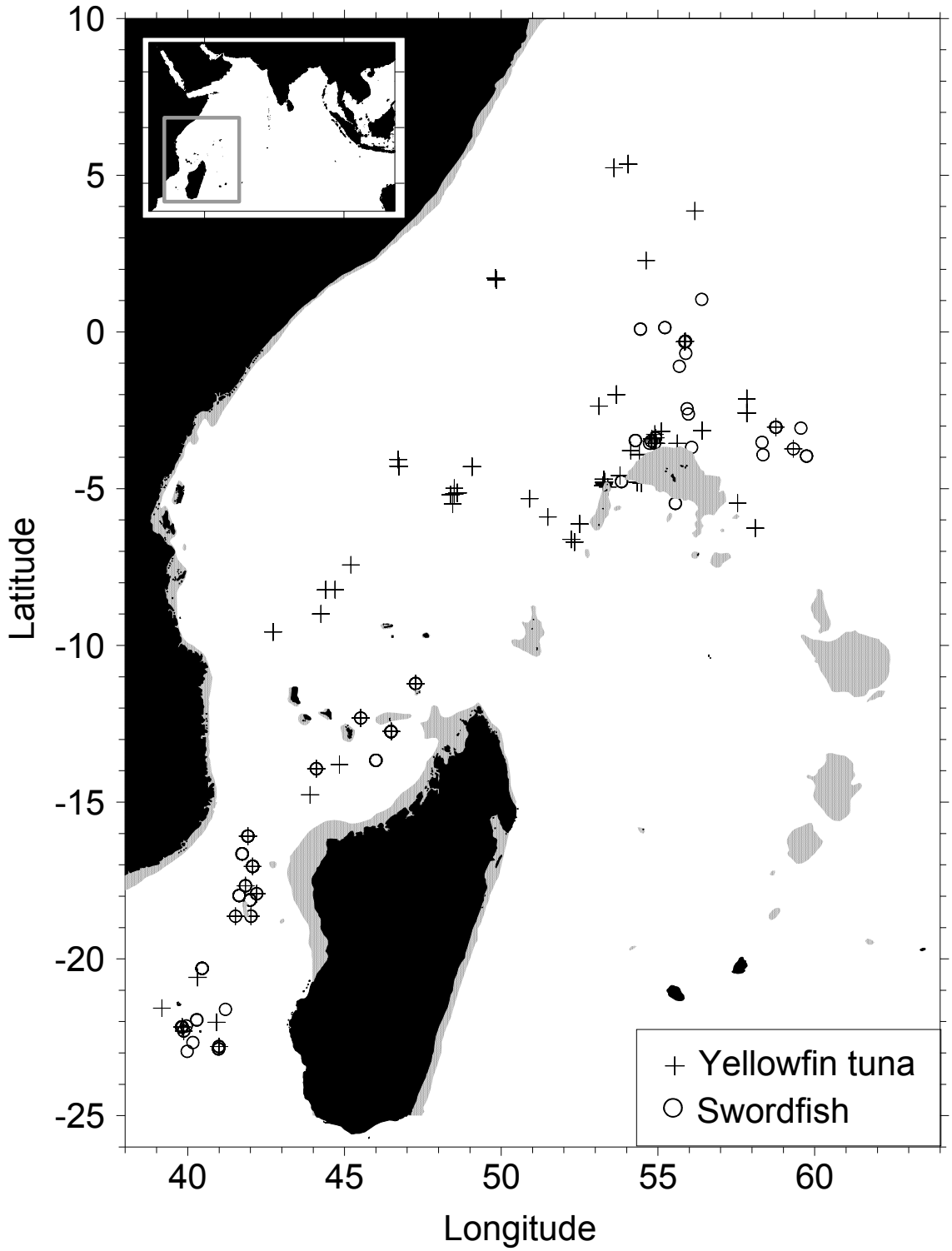
Figure 1. Muscle sample collection sites of swordfish (open circles) and yellowfin tuna (crosses) in the western Indian Ocean.

Figure 2. Muscle $\delta^{15}N$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

Figure 3. Muscle $\delta^{13}C$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

Figure 4. Within-season predicted muscle $\delta^{15}N$ values (solid lines) from the linear mixed-effects models for yellowfin tuna (A) and swordfish (B) plotted versus size or latitude. The original data (open circles) were superimposed on the predicted lines within each season, SW monsoon (left side) and NE monsoon (right side).

Figure 5. Population predicted muscle $\delta^{15}N$ and $\delta^{13}C$ values from the linear models (linear mixed-effects models for $\delta^{15}N$ and simple linear models for $\delta^{13}C$) for swordfish (dashed line) and yellowfin tuna (full line) plotted versus size (A) considering two different fixed latitudes (0°N or l0°S); and plotted versus latitude (B) for two different sizes (80cm or 160cm).



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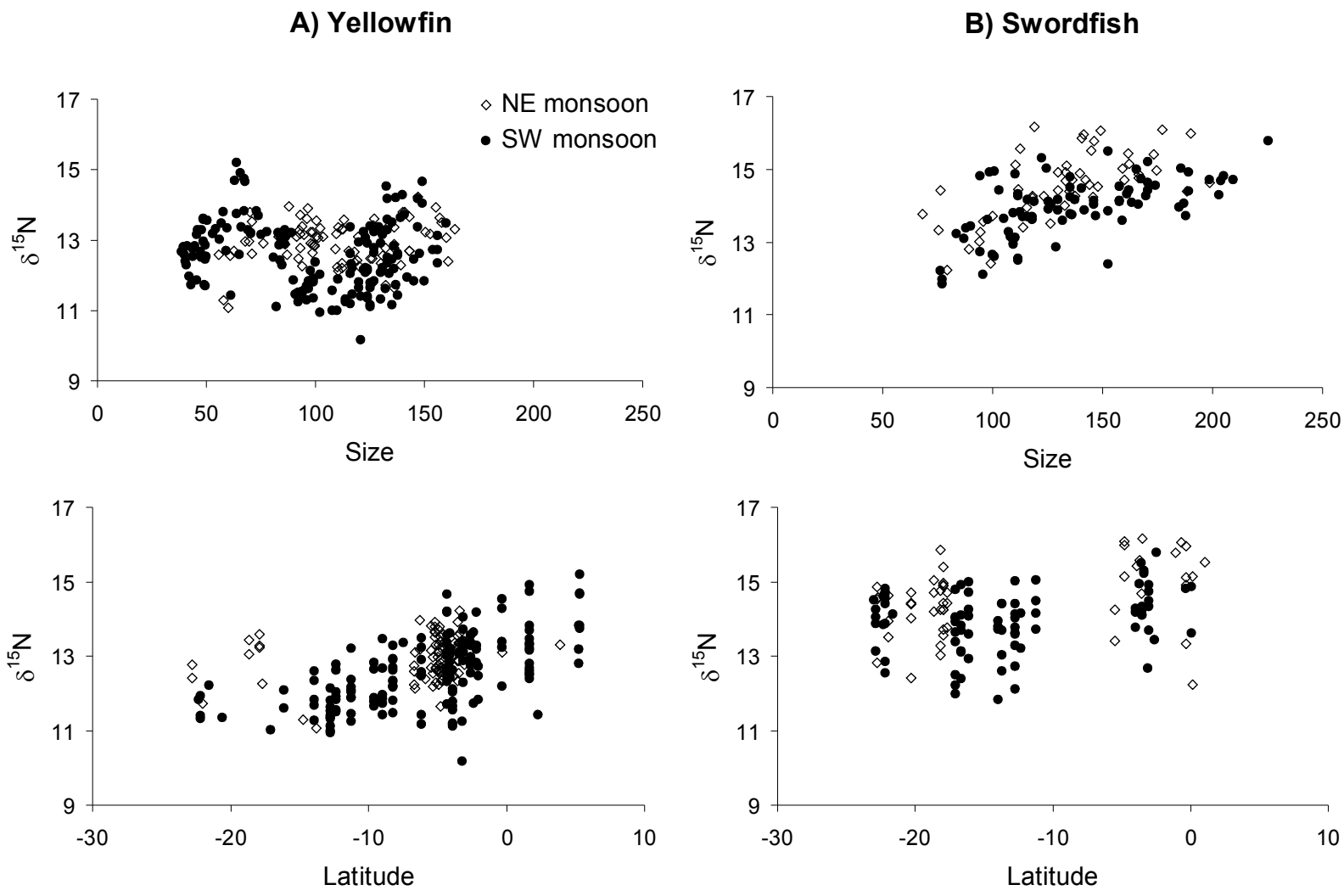


Figure 2. Muscle $\delta^{15}N$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

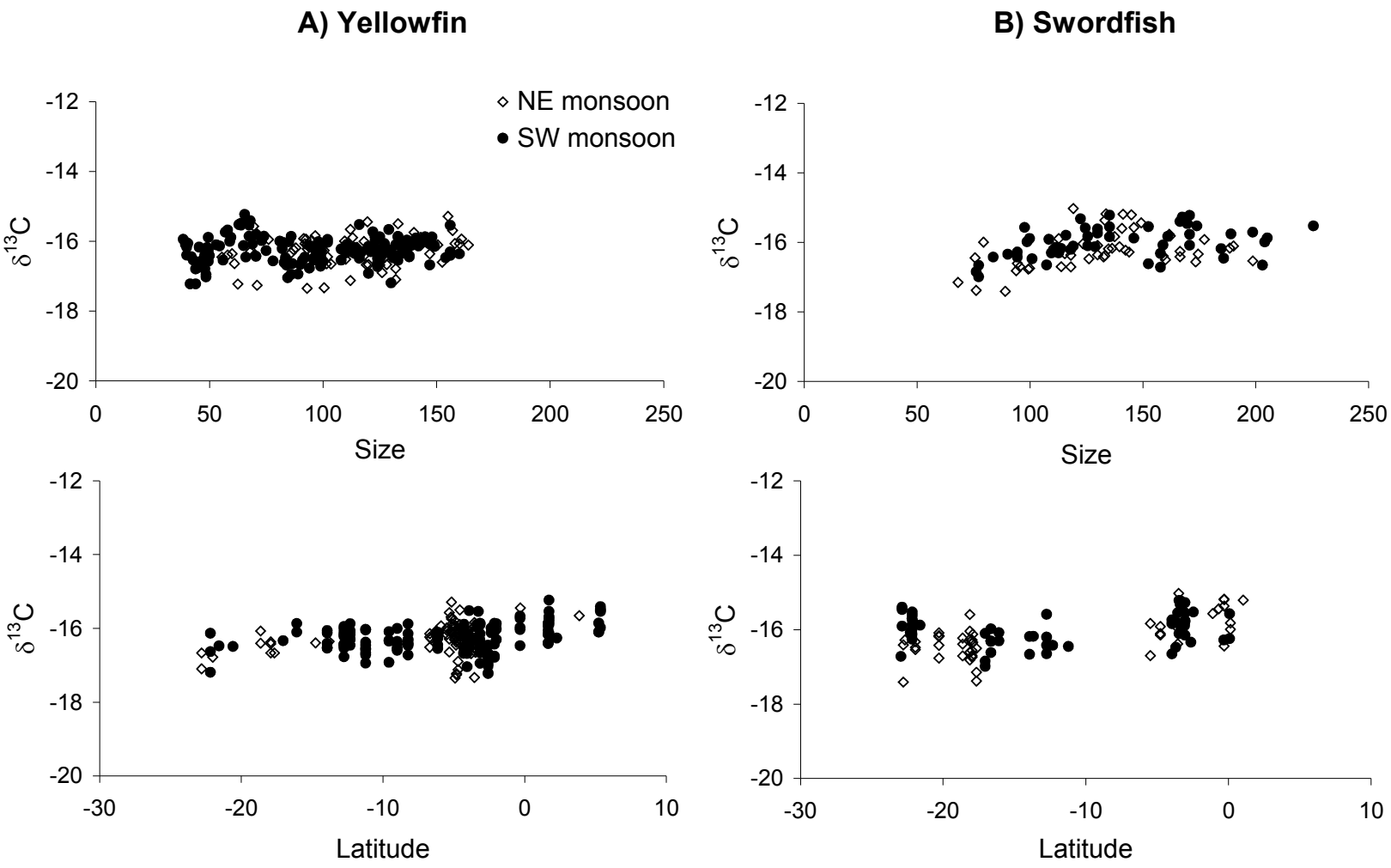


Figure 3. Muscle $\delta^{13}C$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

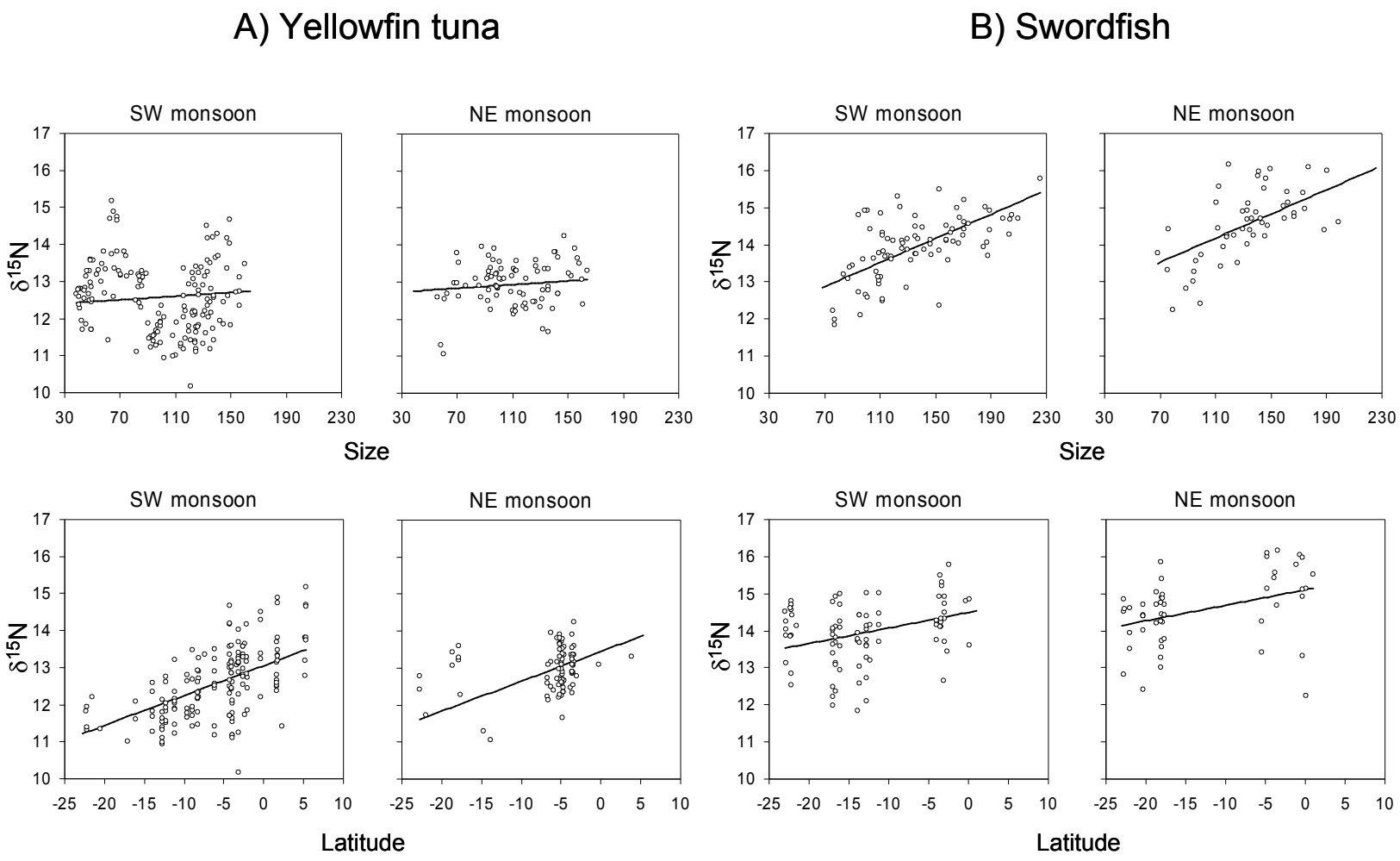
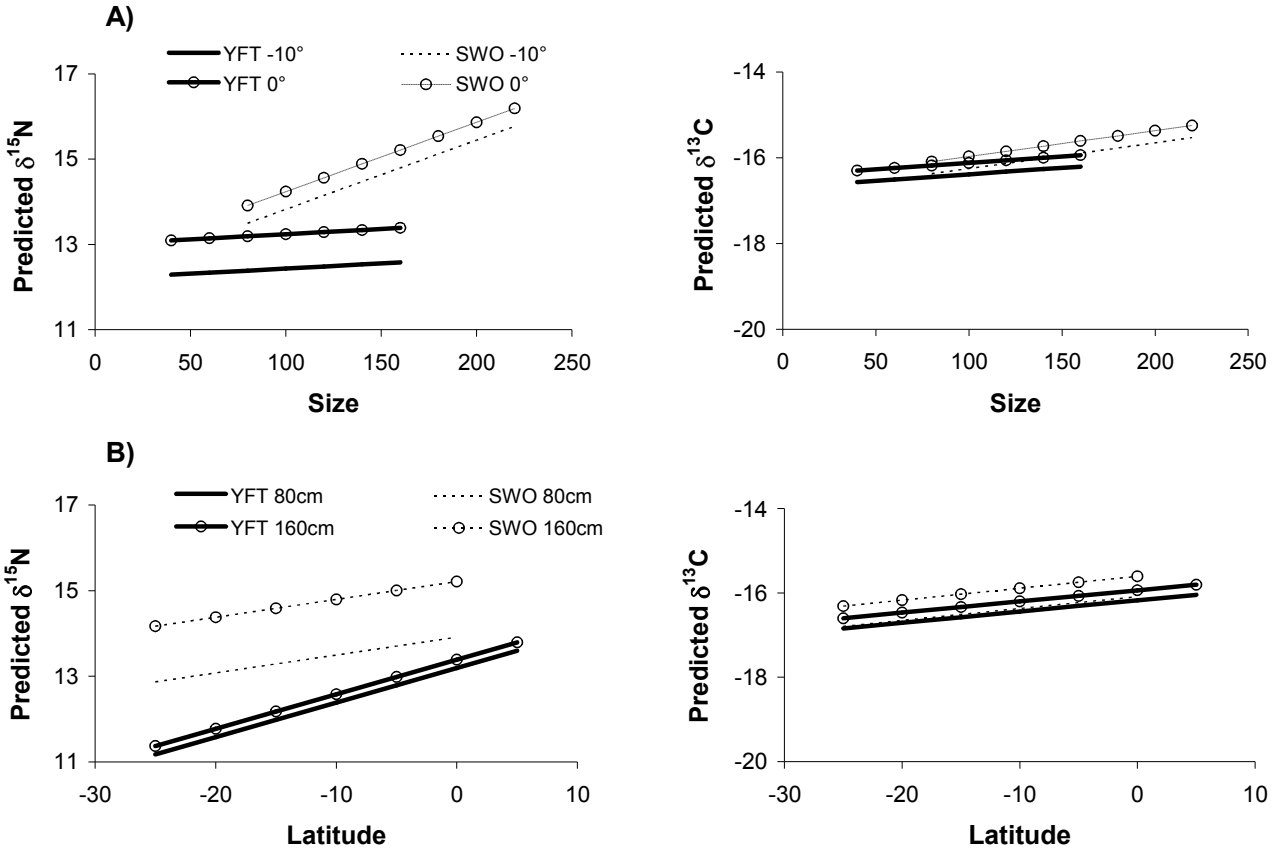


Figure 4. Within-season predicted muscle $\delta^{15}N$ values (solid lines) from the linear mixed-effects models for yellowfin tuna (A) and swordfish (B) plotted versus size or latitude. The original data (open circles) were superimposed on the predicted lines within each season, SW monsoon (left side) and NE monsoon (right side).



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