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

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13

14 **Abstract**

15 Ecologists primarily use $\delta^{15}\text{N}$ values to estimate the trophic level of organisms, while
16 $\delta^{13}\text{C}$, and even recently $\delta^{15}\text{N}$, are utilized to delineate foraging habitats. However, many
17 factors can influence the stable isotopic composition of consumers, e.g. age, starvation or
18 isotopic signature of primary producers. Such sources of variability make the interpretation of
19 stable isotope data rather complex. To examine these potential sources of variability, muscle
20 tissues of yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*) of various
21 sizes were sampled between 2001 and 2004 in the western Indian Ocean during different
22 seasons and along a latitudinal gradient (23°S to 5°N). Size and latitude effects on $\delta^{15}\text{N}$ and
23 $\delta^{13}\text{C}$ were investigated using linear models. Both latitude and size significantly affect the
24 stable isotope values of the studied species but variations were much more pronounced for
25 $\delta^{15}\text{N}$. We explain the latitudinal effect by differences in nitrogen dynamics existing at the base
26 of the food web and propagating along the food chain up to top predators. This spatial pattern
27 suggests that yellowfin and swordfish populations exhibit a relatively unexpected resident
28 behaviour at the temporal scale of their muscle tissue turnover. The size effect is significant
29 for both species and indicates an increase in prey size through ontogeny. However, this effect
30 is more pronounced in swordfish as a consequence of their different foraging strategies,
31 reflecting specific physiological abilities. Swordfish adults are able to reach very deep water
32 and have access to a larger size range of prey than yellowfin tuna. In contrast, yellowfin
33 juveniles and adults spend most of their time in the surface waters and large yellowfin tuna
34 continue to prey on small organisms. Consequently, nitrogen isotopic signatures of swordfish
35 tissues are higher than those of yellowfin tuna and provide evidence for different trophic
36 levels between these species. Thus, in contrast to $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ analyses of tropical Indian Ocean
37 marine predators allow the investigation of complex vertical and spatial segregation, both
38 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 $\delta^{15}\text{N}$ values and to
40 correct for any size or latitude differences in future food web studies.

41 **Introduction**

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

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

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

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

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

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

Materials and methods

Sample collection

Fish were caught by industrial purse seiners with scientific observers onboard; a 20-m research longliner “Amitié” of the Seychelles Fishing Authority, and the French 24-m industrial longliner “Cap Morgane”. Samples were collected from 2001 to 2004 in the western Indian Ocean along a latitudinal gradient (23°S to 5°N, Fig. 1). A total of 245 yellowfin tuna (*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 Europa Scientific ANCA-NT 20-20 Stable Isotope Analyser with ANCA-NT Solid/Liquid Preparation Module (PDZ Europa Ltd., Crews, UK). Replicate measurements of internal laboratory standards indicate measurement errors of $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. 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 $\delta^{15}\text{N}$ and VPDB Belemnite for $\delta^{13}\text{C}$:

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

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

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. $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ and C/N mass ratios (3.62 and 3.70 for yellowfin tuna and swordfish, respectively). The resulting

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

Statistical analysis

Linear regressions were used on the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data for each species to test the covariates of interest, i.e. latitude and body size. However, all the individuals of one species are not independent and the sampling scheme is clearly unbalanced. The individuals can be grouped according to different factors (e.g. cruise, year, season, etc.; Table 1). We use the two main seasons of the monsoon system to group the individuals of each species caught during the cruises carried out from 2001 to 2004. Indeed, the ocean circulation in the West Indian Ocean is strongly related to the wind monsoon regime, which in turn strongly affects biological productivity (Tomczak and Godfrey 1994; Longhurst 1998; Schott and McCreary 2001). The Northeast (NE) monsoon becomes established in boreal winter (December to March). It is characterized by winds blowing from the Asian continent to the equatorial zone, a weak circulation north of the equator and a well marked counter-current flowing East between 2°S and 7°S . The Southwest (SW) monsoon becomes established in boreal summer (June-September), and is characterized by a reversal of the winds in the northern Indian Ocean, the development of the northward-flowing Somali Current, and an eastward flow that dominates the northern Indian Ocean. Therefore, each observation can be classified according to the season on which it was made (NE or SW monsoon, Table 1). The 5 cruises which took place during the inter-monsoons are relocated in their nearest monsoon: October and May in the SW monsoon, and November in the NE monsoon. A classification based on the 4 seasons (including the 2 additional inter-monsoon seasons) was also tested but not retained as the various models fit to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values gave similar results to the monsoon only 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ values for yellowfin tuna ranged from 10.2 to 15.2‰ and from 11.8 to 16.2‰ for swordfish (Fig. 2). The $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values is therefore much more reduced than the $\delta^{15}\text{N}$ range ($\approx 2\text{‰}$ vs. 5‰).

Linear regression models with latitude and size added sequentially were significant ($p = 0.026$ for $\delta^{15}\text{N}$ and $p < 0.001$ for $\delta^{13}\text{C}$ for yellowfin tuna; $p < 0.001$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ may differ between seasons.

Linear mixed-effects models (lme models) were fitted to the muscle $\delta^{15}\text{N}$ 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 ($p =$

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

Discussion

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

strongly than $\delta^{13}\text{C}$ values. Model predictions at the population level allow us to analyse these effects separately. Fig. 5A illustrates $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in marine food webs.

Latitudinal effect

The range of variation for the $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ (0.8 and 0.7‰ for yellowfin tuna and swordfish, respectively). Three hypotheses can be put forward to explain the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increase from the Mozambique Channel to the Somali basin: 1) dietary changes, 2) starvation and 3) a shift in $\delta^{15}\text{N}$ 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) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ values of POM might occur. In particular, the Somali region

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

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

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

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

different ways: (i) yellowfin tuna are more resident than swordfish, (ii) swordfish have a slower turnover rate or tissue growth than yellowfin tuna, (iii) swordfish do not migrate to highly ^{15}N depleted areas such as the Arabian Sea, which the very low catch records of this species in this region suggests (Fonteneau 1997). The third hypothesis seems the most plausible given our present knowledge; however, we cannot preclude a mixed influence of the three hypotheses.

Seasonal effect

In the mixed-effects models implemented in this paper for $\delta^{15}\text{N}$ values, the seasonal effect is random and induced by the grouping of the data. Only intercepts differ between NE and SW monsoon predictions: compared to the SW monsoon, the NE monsoon intercepts are 0.36 and 0.67‰ higher for yellowfin tuna and swordfish, respectively. During the NE monsoon, the waters of the Arabian sea are advected to the South and invade the Somali basin (where part of our data collection was undertaken), potentially increasing the $\delta^{15}\text{N}$ values of the baseline of this zone compared to SW monsoon (Davis 2005). Conversely, during the SW monsoon, there is a broad equatorward flow of waters from the South Equatorial Current (SEC) along the East African Coast reaching the Somali region (Tomczak and Godfrey 1994; Schott and McCreary 2001; Davis 2005). Further studies involving measurements of the $\delta^{15}\text{N}$ of the POM over an annual cycle should be investigated to shed some light on the seasonal variations that may occur in the western Indian Ocean.

Interestingly, the seasonal effect is not significant for $\delta^{13}\text{C}$ values. We believe that seasonal changes in the monsoon regime do not have strong consequences on the carbon isotopes ratios in the sampled areas. In addition, the $\delta^{13}\text{C}$ ranges we observed in our data were low compared to the intra-individual variability. Our results suggest that muscle $\delta^{13}\text{C}$ values of fish in these open sea ecosystems of the western Indian Ocean might not be useful to

document seasonal changes, to delineate foraging locations or to track fish movement. This is in contrast to studies conducted in the southern Indian Ocean where $\delta^{13}\text{C}$ has been shown to be a useful tool (Cherel and Hobson 2005, 2007).

Size effect

Figure 5A indicates changes in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ model predictions along a gradient of body size, for fish caught at two different latitudes. In each case, the $\delta^{15}\text{N}$ values exhibited a stronger size effect for swordfish than for yellowfin tuna. The isotopic difference between large (200 cm) and small (80 cm) swordfish was about 2‰, whereas it was less than 0.5‰ for yellowfin tuna of 40 to 160 cm. The same pattern is supported by $\delta^{13}\text{C}$ values, but isotopic differences are much more reduced (0.8 and 0.4‰ for swordfish and yellowfin tuna, respectively). The lower differences for $\delta^{13}\text{C}$ are not surprising given that $\delta^{15}\text{N}$ is known to increase much more with trophic levels than $\delta^{13}\text{C}$ (DeNiro and Epstein, 1981). Body size is indeed known to play a crucial role in predator-prey interactions (Sheldon et al. 1977; Cury et al. 2003). Analyses of stomach contents and nitrogen isotope ratios conducted on fish communities in different marine ecosystems have shown that prey size and trophic level generally increase with increasing predatory body size (Scharf et al. 2000; Jennings et al. 2002). In open-sea ecosystems, few studies have yet dealt specifically with size-based predation. Ménard et al. (2006) have shown that the maximum size of the prey consumed by yellowfin tunas tends to increase with tuna body length, but that large yellowfin tunas continue to consume small prey in great proportions. In addition, both adults and juveniles of yellowfin tuna generally show only minor differences in depth distributions (Brill et al. 1999, 2005). Yellowfin tuna spend most of their time in the surface layer, even if some exceptional deep dives have been evidenced by one archival tag (Dagorn et al. 2006). The diet of yellowfin tunas is then mainly composed of organisms present in the upper 100 m (Moteki et

al. 2001; Bertrand et al. 2002; Potier et al. 2004, 2007), with no major ontogenetic changes (Ménard et al. 2006). An outstanding diet shift was revealed by Graham et al. (2007) but this study only concerned small juveniles of yellowfin tunas ranging around 45 cm and caught in areas surrounding Hawaiian Islands. Therefore, we conclude that the size of yellowfin tuna does not have a strong impact on its $\delta^{15}\text{N}$ values. On the other hand, large swordfish mainly consume cephalopods (Hernandez-Garcia 1995; Markaida and Hochberg 2005; Young et al. 2006; Potier et al. 2007), while smaller swordfish have a diet focused on mesopelagic fish such as myctophids (Young et al. 2006; Potier et al. 2007). This shift in the dominant prey items has consequences on the $\delta^{15}\text{N}$ values because mesopelagic fish such as myctophids and paralepidids have shown lower mean $\delta^{15}\text{N}$ values than cephalopods (Young et al. 2006). In addition, swordfish can catch larger prey specimens as they grow, due to an increase of mouth-gape size, chasing predation, and diving capability (Carey and Robinson 1981). Therefore, we fully confirm that body size influences the $\delta^{15}\text{N}$ values of swordfish, as already shown by Young et al. (2006) with much fewer data. This influence is much more pronounced than for yellowfin tuna, due to the change in the foraging ecology of swordfish through its ontogeny.

Trophic level differences

Over the body sizes and latitudes common to both species, and for a similar size or latitude, the $\delta^{15}\text{N}$ values of swordfish were about 0.7 to 2.8‰ higher than those of yellowfin tuna (Fig. 5). The greatest $\delta^{15}\text{N}$ differences were found in large fish (160 cm) sampled in the south (25°S), while the smallest differences occurred in small fish (80 cm) sampled in the north (5°N). In a recent study conducted in the same area, Potier et al. (2007) established that (i) the diet composition of swordfish was dominated by mesopelagic cephalopods (Ommastrephidae and to a lesser extent Onychoteuthidae) and by mesopelagic fish

(Nomeidae and Diretmidae), while epipelagic prey dominated the diet of yellowfin tuna, (ii) swordfish catch larger specimens of the same prey species than yellowfin tuna. This general diet pattern reflects a well-known resource partitioning between both species. Swordfish undertake large vertical migrations, allowing them to prey actively at great depth, while both adult and juvenile yellowfin tuna spend the vast majority of their time in the surface layer and prey on small organisms (Brill et al. 2005; Ménard et al. 2006; Potier et al. 2007). Consequently, swordfish have access to a larger size range of prey in the environment than yellowfin tuna, and can feed on the predators of yellowfin tuna's prey. Thus, the observed differences in $\delta^{15}\text{N}$ values of swordfish and yellowfin tuna, once the size and latitudinal effects are removed, illustrate different trophic levels between both species due to distinct foraging strategies. Graham et al. (2007) hypothesized that mesopelagic prey might have $\delta^{15}\text{N}$ values higher than epipelagic species. This assumption could strengthen the $\delta^{15}\text{N}$ differences between both species, but further investigations should be carried out on the isotopic values of the forage fauna of large pelagics.

Summary and conclusion

This study revealed body size and latitudinal effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of two migratory highly opportunistic predators: yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*). However, in these open sea ecosystems of the western Indian Ocean, $\delta^{15}\text{N}$ was much more useful than $\delta^{13}\text{C}$ to delineate trophic relationships and to track fish movements. Linear mixed-effects models developed here will allow us to make predictions of $\delta^{15}\text{N}$ values and to correct for any size or latitude differences in future food web studies. This study also confirmed that baseline $\delta^{15}\text{N}$ isotopic variations can be conserved through several trophic levels, and even up to high trophic levels such as tunas and swordfish. These spatial 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ of marine pelagic fish should be considered when using $\delta^{15}\text{N}$ to detect trophic-level variation in natural communities.

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575

576 Table 1. Sample characteristics of yellowfin tuna and swordfish
577

Cruise	Time period	Year	Group	Swordfish					Yellowfin				
				N	Size		Latitude		N	Size		Latitude	
					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

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

Coefficients		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
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 $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from the linear models (linear mixed-effects models for $\delta^{15}\text{N}$ and simple linear models for $\delta^{13}\text{C}$) for swordfish (dashed line) and yellowfin tuna (full line) plotted versus size (A) considering two different fixed latitudes (0°N or 10°S); and plotted versus latitude (B) for two different sizes (80cm or 160cm).

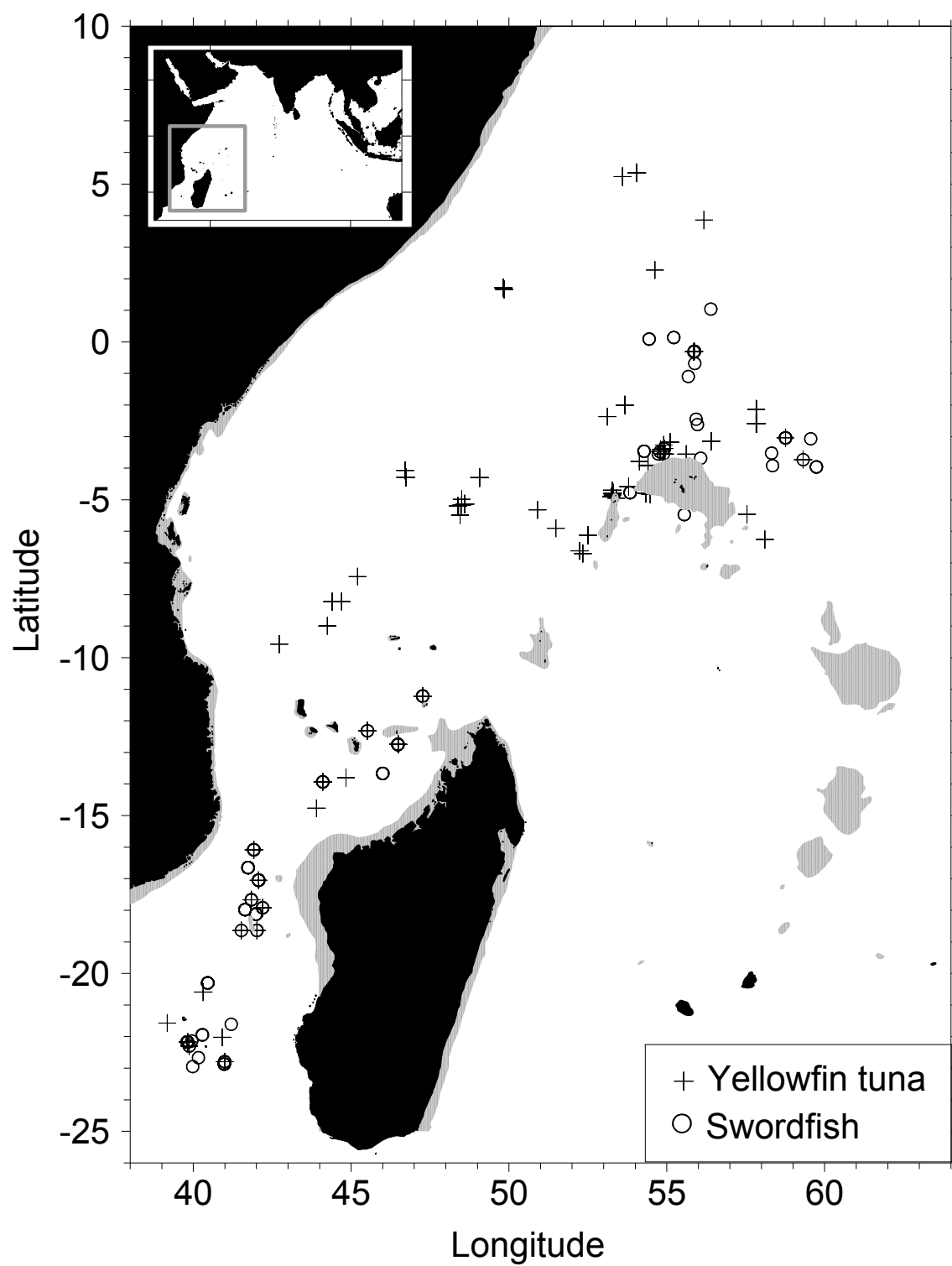


Figure 1. Muscle sample collection sites of swordfish (open circles) and yellowfin tuna (crosses) in the western Indian Ocean.

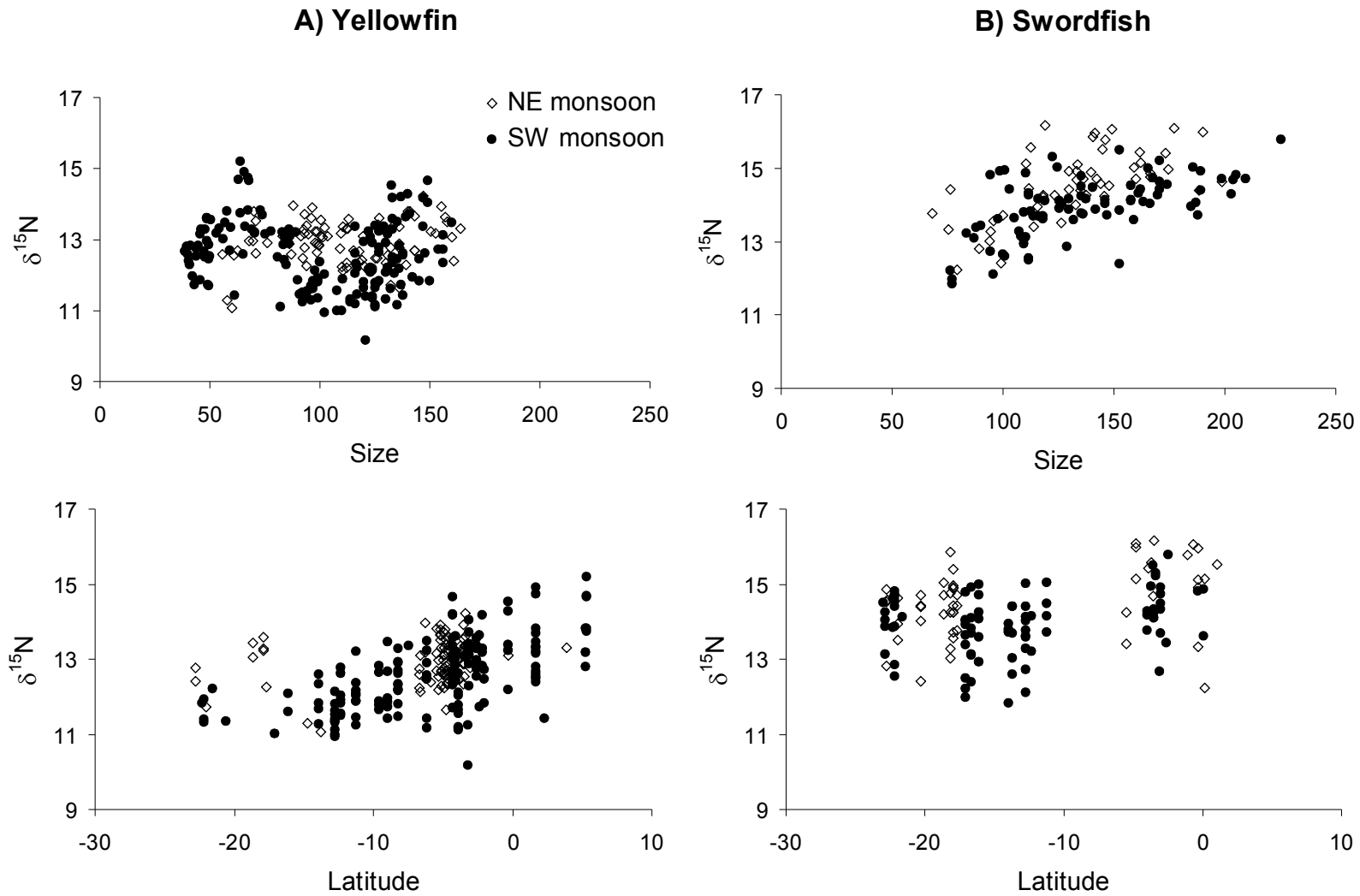


Figure 2. Muscle $\delta^{15}\text{N}$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

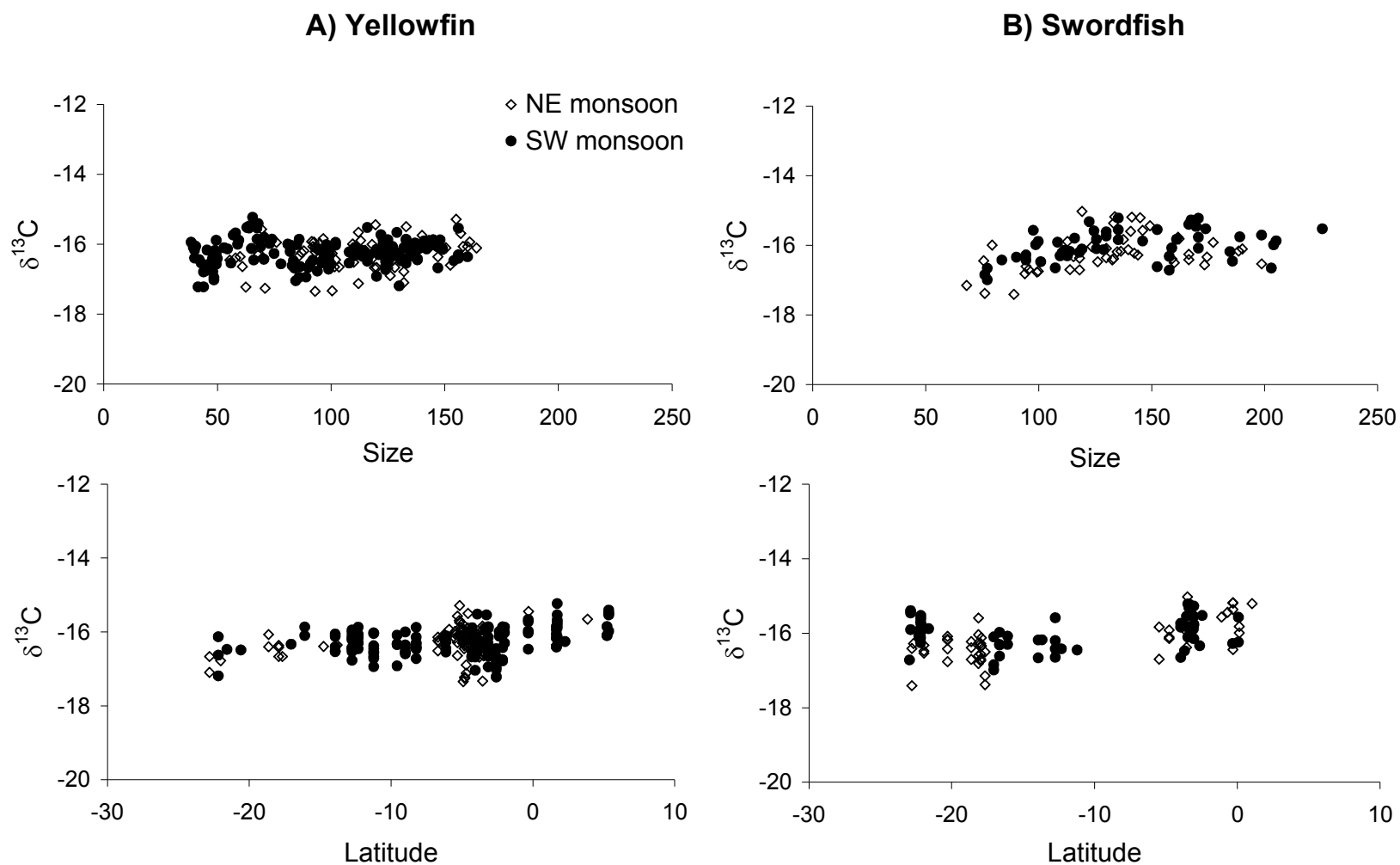


Figure 3. Muscle $\delta^{13}\text{C}$ values from yellowfin tuna (A) and swordfish (B) plotted versus size or latitude according to the considered season: SW monsoon (full symbols) and NE monsoon (open symbols).

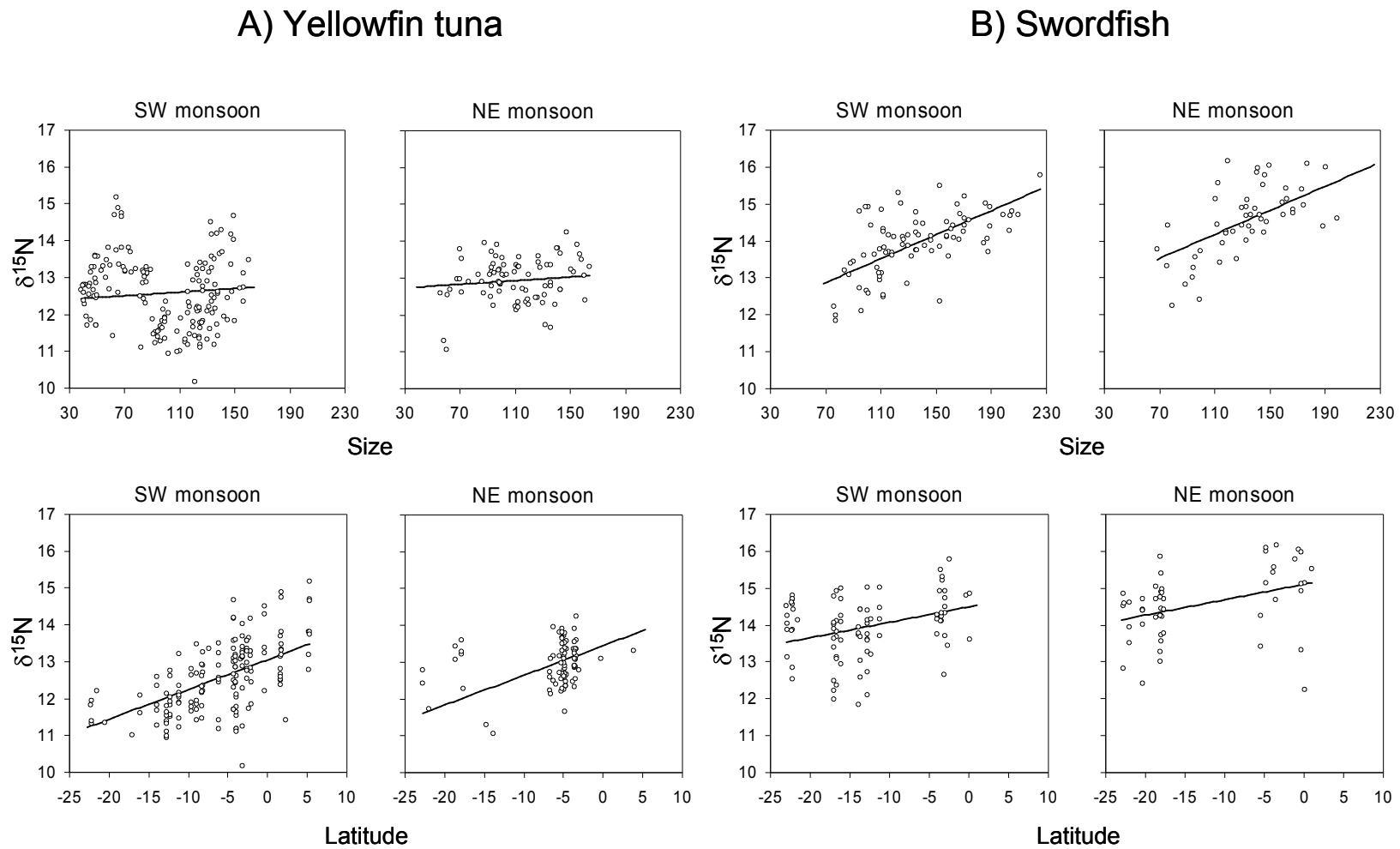


Figure 4. Within-season predicted muscle $\delta^{15}\text{N}$ values (solid lines) from the linear mixed-effects models for yellowfin tuna (A) and swordfish (B) plotted versus size or latitude. The original data (open circles) were superimposed on the predicted lines within each season, SW monsoon (left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

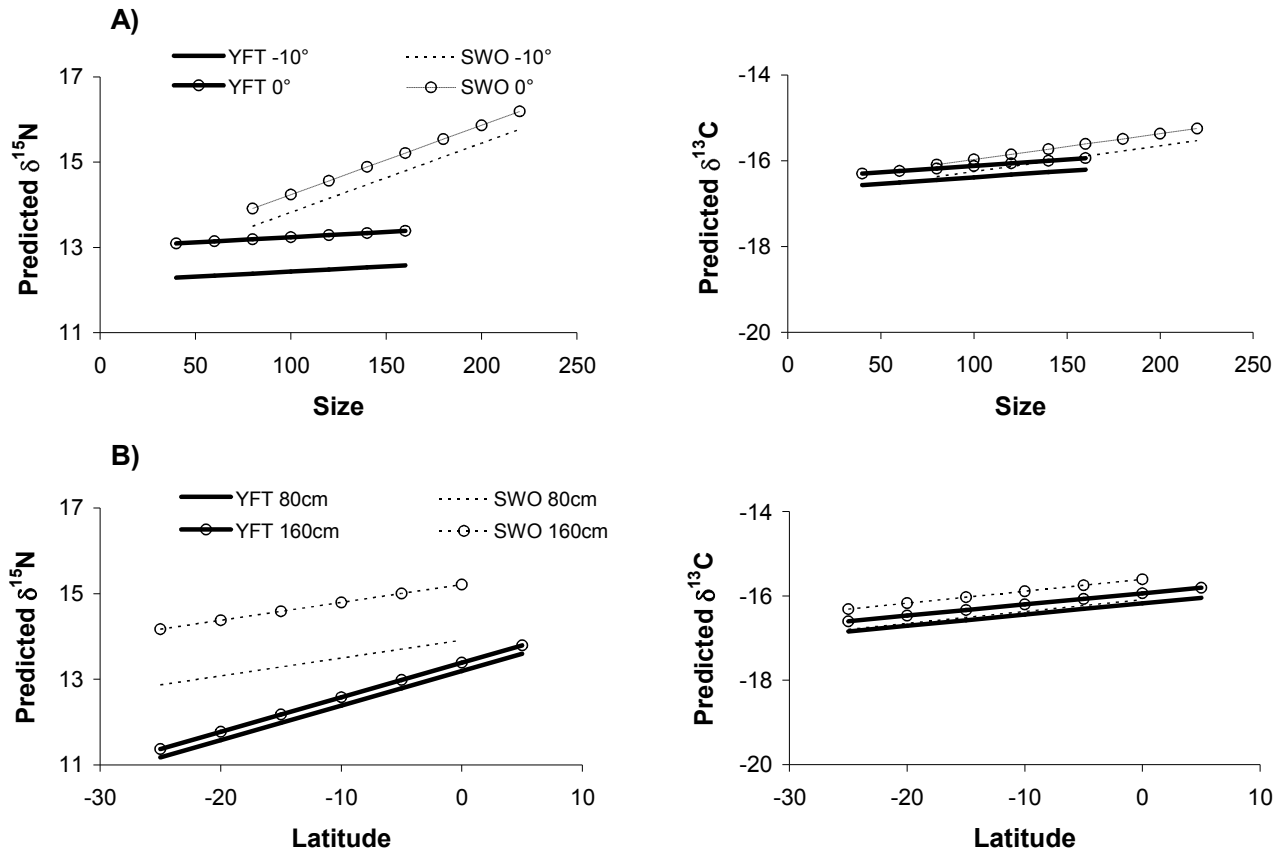


Fig 5. Population predicted muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from the linear models (linear mixed-effects models for $\delta^{15}\text{N}$ and simple linear models for $\delta^{13}\text{C}$) for swordfish (dashed line) and yellowfin tuna (full line) plotted versus size (A) considering two different fixed latitudes (0°N or 10°S); and plotted versus latitude (B) for two different sizes (80cm or 160cm).