Mar Biol (2007) 153:141–152
DOI 10.1007/s00227-007-0789-7

RESEARCH ARTICLE

Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean

Frédéric Ménard · Anne Lorrain ·
Michel Potier · Francis Marsac

Received: 28 May 2007 / Accepted: 8 August 2007 / Published online: 4 September 2007

Abstract Ecologists primarily use δ^{15}N values to estimate the trophic level of organisms, while δ^{13}C, and even recently δ^{15}N, are utilized to delineate feeding 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 body lengths were sampled between 2001 and 2004 in the western Indian Ocean during different seasons and along a latitudinal gradient (23°S to 5°N). Body length and latitude effects on δ^{15}N and δ^{13}C were investigated using linear models. Both latitude and body length significantly affect the stable isotope values of the studied species but variations were much more pronounced for δ^{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 body length effect is significant for both species but this effect is more pronounced in swordfish as a consequence of their different feeding 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 δ^{13}C, δ^{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 linear models developed in this study allow us to make predictions of δ^{15}N values and to correct for any body length or latitude differences in future food web studies.

Introduction

Catches of tunas and billfishes have increased dramatically the past 20 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; Frank 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

---

Communicated by S.A. Poulet.

F. Ménard (✉) · A. Lorrain · F. Marsac
Institut de Recherche pour le Développement,
Centre de Recherche Halieutique Méditerranéenne et Tropicale,
BP 171, 34203 Sète Cedex, France
e-mail: menard@ird.fr

M. Potier
Institut de Recherche pour le Développement, BP 172,
97492 Ste Clotilde Cedex, La Réunion, France

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 thunniform fishes 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 programmes 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, feeding 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 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). δ^{15}N measurements mainly serve as indicators of consumer's trophic position, while δ^{13}C values are used to determine the sources of primary production, inshore versus offshore or pelagic versus benthic contribution to food intake (Hobson 1999). Indeed, different oceanic processes affect isotopic baselines of δ^{15}N and δ^{13}C in marine pelagic food webs (Rau et al. 1982; Altabet et al. 1995; Gruber and Sarmiento 1997; Lourey et al. 2003). δ^{13}C values of phytoplankton decrease from low to high latitudes (Lourey et al. 2003) while δ^{15}N of particulate organic matter (POM) 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 isotope ecology “you are what you eat” (DeNiro and Epstein 1976). Consequently, the stable isotope ratios of animal tissues have the potential of characterizing the isotopically distinct regions crossed by migrating fish and investigating their feeding 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. 2007). A second objective was to document the feeding ecology of yellowfin tuna and swordfish, and potential ontogenetic effects on their trophic status. Ontogenetic shifts in tuna and swordfish feeding behaviour are also expected as larger fish usually expand their feeding 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 body length effects on the stable isotope values (δ^{15}N and δ^{13}C) of each species. According to the model predictions, the trophic positions of individuals of different body lengths 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. In this paper, we implement the isotope approach to gain insight into the feeding ecologies and movement patterns on the studied predators, the first initiative of this nature in the Indian Ocean.

Materials and methods

Sample collection

Fishes 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 (*T. albacares*) and 136 swordfish (*X. gladius*) from various body lengths were collected

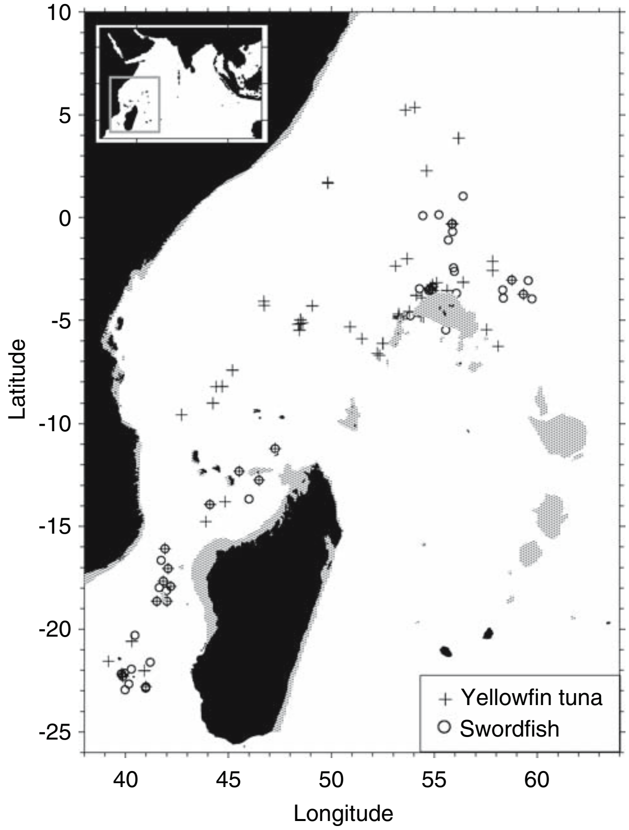


Fig. 1 Muscle sample collection sites of swordfish (*open circles*) and yellowfin tuna (*crosses*) in the western Indian Ocean

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 length that allows comparisons with tunas by reducing the bias due to the bill. Table 1 displays all the sample characteristics. White muscle tissues from the dorsal region before the first dorsal fin 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^2 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 δ^{13}C and δ^{15}N. Triplicate analyses performed on some samples confirmed that analytical reproducibility was very good (0.2‰ maximum variation). Isotopic ratios are expressed

Table 1 Sample characteristics of yellowfin tuna and swordfish

Cruise	Time period	Year	Group	Swordfish					Yellowfin tuna				
				N	Body length		Latitude		*N*	Body length		Latitude	
					Min	Max	Min	Max		Min	Max	Min	Max
AM1	August 13–24	2001	SW monsoon	0					18	108	156	–4	2
AM2	October 16–26	2001	SW monsoon	4	94	111	–4	0	5	122	140	0	0
AM6	July 13–30	2002	SW monsoon	13	100	203	–4	–3	1	136	136	–3	–3
AM9	July 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	September 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	October 6–November 7	2001	SW monsoon	0					66	39	149	–4	5
AM3	November 19–30	2001	NE monsoon	3	111	190	–5	–5	8	112	136	–5	–4
AM4	January 28–February 8	2002	NE monsoon	3	113	162	–4	–3	10	102	153	–4	–3
AM5	February 27–March 12	2002	NE monsoon	3	145	149	–1	1	0				
AM7	December 10–20	2002	NE monsoon	2	114	137	–5	–5	5	88	141	–6	4
AM8	January 29–February 9	2003	NE monsoon	7	76	162	–4	0	27	56	151	–5	0
ECO7	November 10–29	2004	NE monsoon	33	68	199	–23	–18	9	96	160	–23	–18
TAL	March 28–April 29	2002	NE monsoon	0					2	58	60	–15	–14
AVAD	February 2–10	2003	NE monsoon	0					21	61	164	–7	–5

in the conventional δ notation as parts per thousand (‰) deviation from the international standards: atmospheric nitrogen for δ^{15}N and VPDB Belemnite for δ^{13}C:

$$\delta X = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1{,}000,$$

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 (>50%, unpublished data; Estrada et al. 2005). As lipids are highly depleted in ^{13}C (Tieszen et al. 1983), C/N mass ratios were used to check the lipid extraction process. δ^{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 δ^{13}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 ± 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 length were not reduced for both species.

Statistical analysis

Linear regressions were used on the δ^{15}N and δ^{13}C data for each species to test the covariates of interest, i.e. latitude and body length. 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–March), and is characterized by winds blowing from the Asian continent to the equatorial zone. 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. Therefore, each observation can be classified according to the season on which it was made (NE or SW monsoon, Table 1). The five 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 four seasons (including the two additional inter-monsoon seasons) was also tested but not retained as the various models fit to the δ^{15}N and δ^{13}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 length 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 length 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 δ^{15}N and δ^{13}C values for yellowfin tuna and swordfish plotted versus body length, latitude and season (NE and SW monsoons) are shown in Figs. 2 and 3. The δ^{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 δ^{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 δ^{13}C values is therefore more reduced than the δ^{15}N range ($\approx$2‰ vs. 5‰).

δ^{15}N values were significantly different between seasons for both species (Kruskal–Wallis $\chi^2 = 13.18$, $P < 0.001$ for yellowfin tuna; Kruskal–Wallis $\chi^2 = 14.27$, $P < 0.001$ for swordfish). For δ^{13}C, the difference between seasons was significant for swordfish (Kruskal–Wallis $\chi^2 = 4.81$, $P = 0.03$), but not for yellowfin tuna (Kruskal–Wallis $\chi^2 = 0.26$, $P = 0.61$). Linear regression models with latitude and body length added sequentially were significant ($P = 0.026$ for δ^{15}N and $P < 0.001$ for δ^{13}C for yellowfin tuna; $P < 0.001$ for δ^{15}N and δ^{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 δ^{15}N may differ between seasons.

Linear mixed-effects models (lme models) were fitted to the muscle δ^{15}N values grouped by season. The most parsimonious model for swordfish was obtained with both latitude and body length as fixed-effect covariates ($P < 0.0001$). For yellowfin tuna, compared with a lme model containing latitude only, the fit was only marginally improved when body length was added ($P = 0.092$). This P-value evidences a lack of significance of body length for yellowfin tuna δ^{15}N values at a significance level of 5%, a result already exhibited in Fig. 2. According to the likelihood ratio test, lme models for both species provided a

Fig. 2 Muscle δ^{15}N values from yellowfin tuna (**a**) and swordfish (**b**) plotted versus body length or latitude according to the considered season: SW monsoon (*full symbols*) and NE monsoon (*open symbols*). Simple linear regression for δ^{15}N versus body length was not significant for yellowfin tuna ($F_{[1,243]} = 0.48$, $P = 0.49$ and $r^2 = 0.002$) and significant for swordfish ($F_{[1,134]} = 58.47$, $P < 0.0001$ and $r^2 = 0.30$). Both regressions were significant for δ^{15}N versus latitude ($F_{[1,243]} = 81.11$, $P < 0.0001$ and $r^2 = 0.25$ for yellowfin tuna; $F_{[1,134]} = 12.06$, $P < 0.001$ and $r^2 = 0.082$ for swordfish)

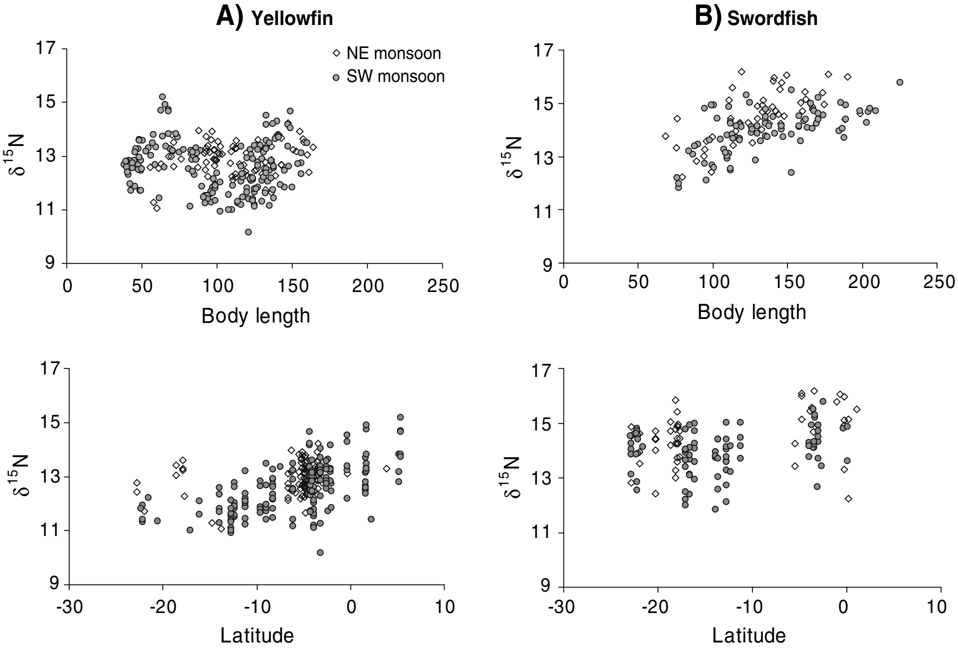
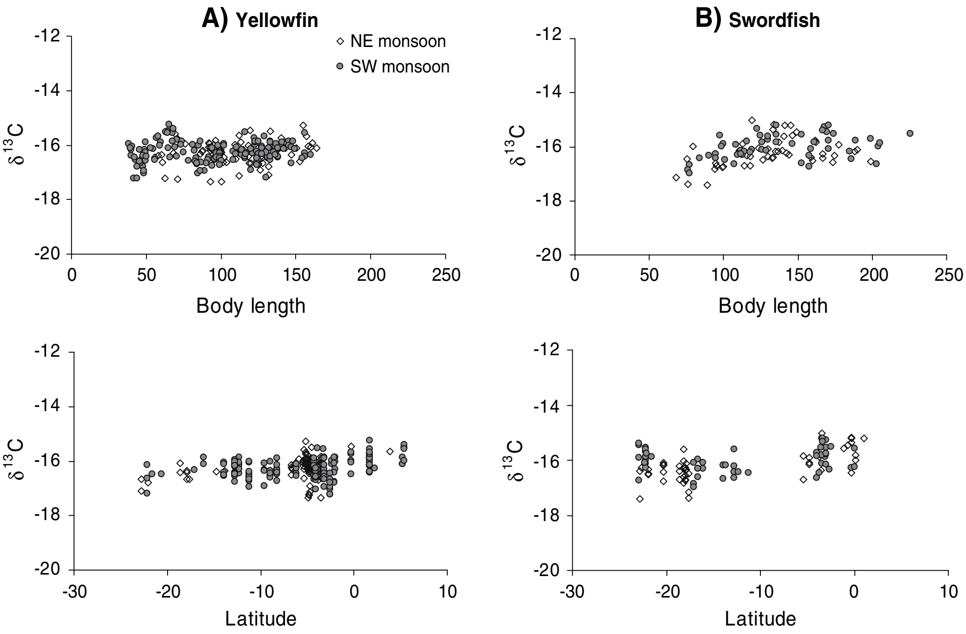


Fig. 3 Muscle δ^{13}C values from yellowfin tuna (**a**) and swordfish (**b**) plotted versus body length or latitude according to the considered season: SW monsoon (*full symbols*) and NE monsoon (*open symbols*). Simple linear regressions were significant for δ^{13}C versus body length ($F_{[1,228]} = 4.32$, $P = 0.039$ and $r^2 = 0.02$ for yellowfin tuna; $F_{[1,101]} = 17.59$, $P < 0.0001$ and $r^2 = 0.15$ for swordfish), and for δ^{13}C versus latitude ($F_{[1,228]} = 25.87$, $P = 0.0001$ and $r^2 = 0.10$ for yellowfin tuna; $F_{[1,101]} = 24.38$, $P < 0.0001$ and $r^2 = 0.19$ for swordfish)



much better description of the δ^{15}N data than the linear regression models did ($P < 0.0007$ and 0.0001 for yellowfin tuna and swordfish, respectively). Figure 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 δ^{15}N values for each season, and confirm that latitude was the strongest linear fixed-effect for yellowfin tuna, while body length 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 δ^{15}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 model fits to the fish muscle δ^{13}C values

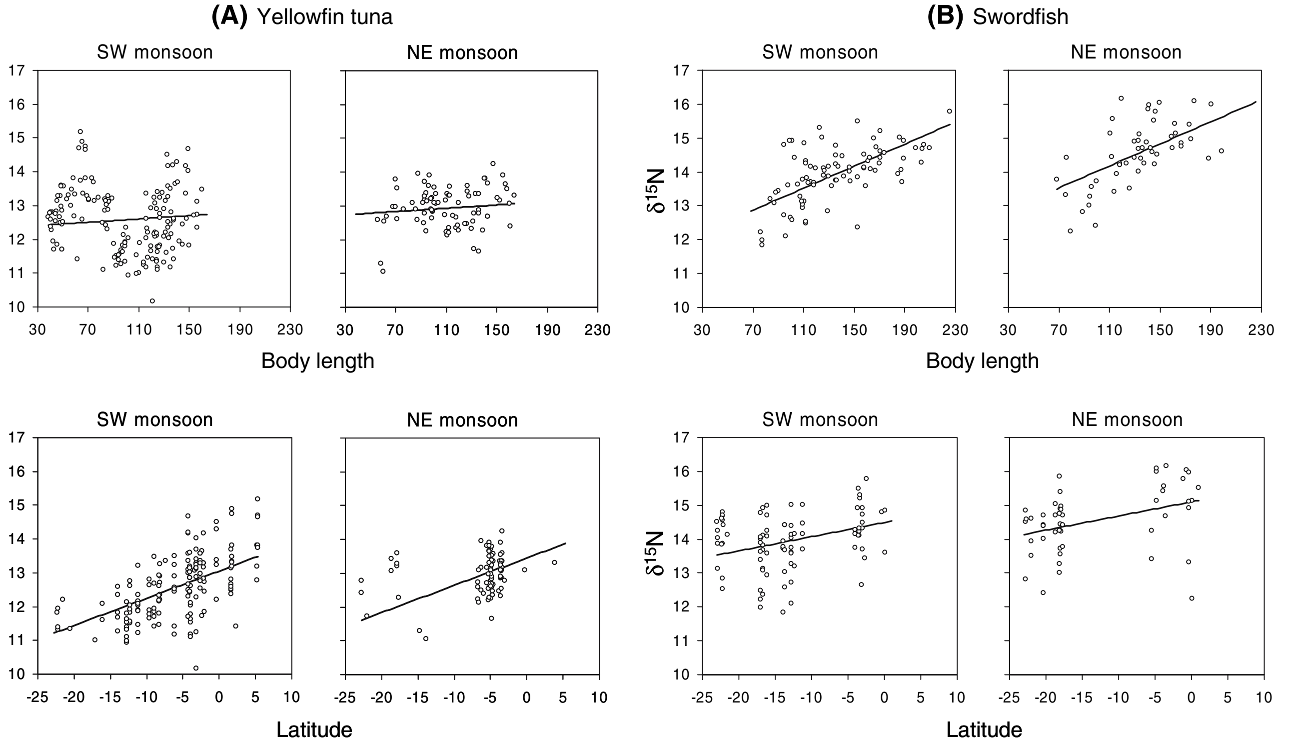


Fig. 4 Within-season predicted muscle δ^{15}N values (*solid lines*) from the linear mixed-effects models for yellowfin tuna (**a**) and swordfish (**b**) plotted versus body length or latitude. The original data (*open circles*) were superimposed on the predicted lines within each season, SW monsoon (*left side*) and NE monsoon (*right side*)

were not significantly better than the linear regression models ($P > 0.50$ for yellowfin tuna and $P = 0.33$ for swordfish).

Body length data was well balanced along latitude for swordfish, while the distribution for yellowfin tuna displayed a surplus of small individuals in the high latitudes and a deficit of small individuals in the low latitudes (figures not shown). However, linear mixed-effects models provide a flexible and powerful tool for analysing unbalanced grouped data. In addition, the effect of body length on stable isotope ratios was weak for yellowfin tuna. Table 2 lists the coefficients and standard errors estimated by the most parsimonious models fit to the δ^{15}N and δ^{13}C data.

Discussion

Our results provide evidence for a relationship between latitude and body length with δ^{15}N and δ^{13}C values of yellowfin tuna and swordfish. The use of body mass instead of body length may partly explain the observed variability

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 δ^{15}N values of yellowfin tuna and swordfish, and estimated intercepts and slopes (with standard errors) for linear regression models fit to the δ^{13}C values of yellowfin tuna and swordfish

Coefficients		δ^{15}N	δ^{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)
Body length	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	–

(Fig. 4). Indeed, two fish of the same length can have different masses, due to different overall nutritional states, with possible consequences on the δ^{13}C and δ^{15}N values. However, due to the sampling conditions, we were only able to record body lengths. Linear mixed-effects models were used for δ^{15}N data and provided identical slopes with different intercepts between the two seasons for both latitude and body length. Simple linear models with no seasonal effect were selected for δ^{13}C data. Both body length and latitude influence δ^{15}N values of the two species more strongly than δ^{13}C values. Model predictions at the population level allow us to analyse these effects separately. Figure 5a illustrates δ^{15}N and δ^{13}C predicted values of yellowfin tuna and swordfish as a function of varying body lengths for fish caught at different latitudes (–10° and 0°). In the same way, Fig. 5b represents δ^{15}N and δ^{13}C predicted values for fish of different lengths (80 and 160 cm) as a function of a latitudinal gradient. We now examine the 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 δ^{15}N and δ^{13}C in marine food webs.

Latitudinal effect

The range of variation for the δ^{15}N values is 2.4‰ for swordfish and 1.1‰ for yellowfin tuna along a latitudinal gradient of about 30° (Fig. 5b), whereas those variations are <1‰ for δ^{13}C (0.8 and 0.7‰ for yellowfin tuna and swordfish, respectively). Three hypotheses can be put forward to explain the δ^{15}N and δ^{13}C increase from the Mozambique Channel to the Somali basin: (1) dietary changes, (2) starvation and (3) a shift in δ^{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 δ^{15}N and δ^{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 δ^{15}N values of POM might occur. In particular, the Somali region should have higher δ^{15}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 δ^{15}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

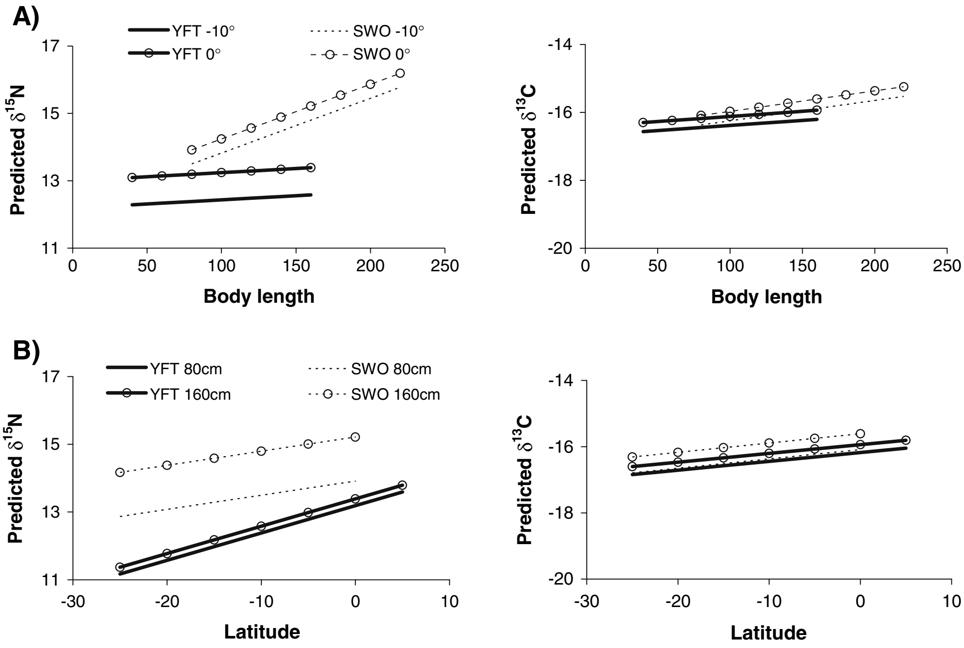


Fig. 5 Population predicted muscle δ^{15}N and δ^{13}C values from the linear models (linear mixed-effects models for δ^{15}N and simple linear models for δ^{13}C) for swordfish (*SWO*, *dashed line*) and yellowfin tuna (*YFT*, *full line*) plotted versus body length **a** considering two different fixed latitudes (0°N or 10°S); and plotted versus latitude **b** for two different body lengths (80 or 160 cm)

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 δ^{15}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 feeding locations of marine predators of the southern Ocean, δ^{13}C displayed strong variations with latitude, whereas δ^{15}N values responded mainly to trophic enrichment (Quillfeldt et al. 2005; Cherel and Hobson 2005, 2007). Indeed, in the southern hemisphere, the geographical δ^{13}C gradient in POM of surface waters is well defined, and ranges from high δ^{13}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 (annual mean surface temperatures vary from 25.5 to 28.5°C; see Fig. 2.5 in Tomczak and Godfrey 1994), which could explain the weak δ^{13}C variations in the western tropical Indian Ocean revealed by our study. Broad δ^{15}N gradients, as observed in this study, have been found in other open ocean regions. Comparing leatherback turtle δ^{15}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 δ^{15}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 regions (the Arabian Sea versus the subtropical gyre), we are probably observing a diluted effect of this general intra-basin difference. Furthermore, isotope values of muscle tissues of these species might never reflect the isotope values of their recent diet plus the corresponding trophic enrichment, because of their continuous movement, their opportunistic feeding behaviour and their muscle tissue isotopic turnover (half-life around 50 days, B. S. 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 δ^{15}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. 3 months for yellowfin tuna (B. S. 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 δ^{15}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: (1) yellowfin tuna are more resident than swordfish, (2) swordfish have a slower turnover rate or tissue growth than yellowfin tuna, (3) 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 δ^{15}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 δ^{15}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 δ^{15}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 δ^{13}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 δ^{13}C ranges we observed in our data were low compared to the intra-individual variability. Our results suggest that muscle δ^{13}C values of fish in these open sea ecosystems of the western Indian Ocean might not be useful to document seasonal changes, to delineate feeding locations or to track fish movement. This is in contrast to studies conducted in the southern Indian Ocean where δ^{13}C has been shown to be a useful tool (Cherel and Hobson 2005, 2007).

Body length effect

Figure 5a indicates changes in the δ^{15}N and δ^{13}C model predictions along a gradient of body length, for fish caught at two different latitudes. In each case, the δ^{15}N values exhibited a stronger body length effect for swordfish than for yellowfin tuna. The isotopic difference between large (220 cm) and small (80 cm) swordfish was about 2.3‰, whereas it was <0.5‰ for yellowfin tuna of 40–160 cm. The same pattern is supported by δ^{13}C values, but isotopic differences are much more reduced (0.8 and 0.4‰ for swordfish and yellowfin tuna, respectively). The lower differences for δ^{13}C are not surprising given that δ^{15}N is known to increase much more with trophic levels than δ^{13}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; Estrada et al. 2006). 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) who studied yellowfin tunas collected from nearshore Fish Aggregating Devices around Hawaii. Tunas ranged from 23.5 to 154.0 cm FL and the ontogenetic change concerned small yellowfin tunas between 45 and 50 cm FL. Therefore, we conclude that the body length of yellowfin tuna does not have a strong impact on its δ^{15}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 δ^{15}N values because mesopelagic fish such as myctophids and paralepidids have shown lower mean δ^{15}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 length influences the δ^{15}N values of swordfish, as already shown by Young et al. (2006) with much fewer data. This influence is much more pronounced in swordfish than for yellowfin tuna (although diet shifts for small juvenile yellowfin tuna can occur, as shown by Graham et al. 2007), due to the change in the feeding ecology of swordfish through its ontogeny.

Trophic level differences

Over the body lengths and latitudes common to both species, and for a similar length or latitude, the δ^{15}N values of swordfish were about 0.7–2.8‰ higher than those of yellowfin tuna (Fig. 5a). The greatest δ^{15}N differences between both species were found in large fishes (160 cm) sampled in the south (25°S), while the smallest differences occurred in small fishes (80 cm) sampled in the north (5°N). In a recent study conducted in the same area, Potier et al. (2007) established that (1) 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, (2) 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 (Potier et al. 2007). 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 δ^{15}N values of swordfish and yellowfin tuna, once the body length and latitudinal effects are removed, illustrate different trophic levels between both species due to distinct feeding strategies. Graham et al. (2007) hypothesized that mesopelagic prey might have δ^{15}N values higher than epipelagic species. This assumption could strengthen the δ^{15}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 fish length and latitudinal effects on δ^{15}N and δ^{13}C values of two migratory highly opportunistic predators: yellowfin tuna (*T. albacares*) and swordfish (*X. gladius*). However, in these open sea ecosystems of the western Indian Ocean, δ^{15}N was much more useful than δ^{13}C to delineate trophic relationships and to track fish movements. Linear mixed-effects models developed here will allow us to make predictions of δ^{15}N values and to correct for any body length or latitude differences in future food web studies. This study also confirmed that baseline δ^{15}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 fish length effects according to species illustrated the potential of stable isotopes to investigate complex trophic ecology and feeding 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 δ^{15}N values of yellowfin tuna and swordfish, isotopic analyses of mesopelagic species together with POM from these regions are needed. Spatial and size-based variation in the δ^{15}N of marine pelagic fish should be considered when using δ^{15}N to detect trophic-level variation in natural communities.

Acknowledgements The authors gratefully thank the Seychelles Fishing Authority (SFA), the crew of the longliner “Amitié”, the crew of the longliner “Cap Morgane” and the observers onboard the purse seiners for helping us to collect the samples. We also thank B. S. Graham for providing the unpublished data on tuna isotopic turnover and for many helpful discussions, and Y. Cherel, D. P. Gillikin and E. Bradbury for very thoughtful comments on the manuscript. This work, a part of the THETIS programme of the IRD (Institut de Recherche pour le Développement), is also supported by the REMIGE project funded by Agence Nationale de la Recherche (ANR 2005 Biodiv-11).

References

Altabet MA, François R, Murray DW, Prell WL (1995) Climate-related variations in denitrification in the Arabian Sea from sediment ^{15}N/^{14}N ratios. Nature 373:506–509

Bertrand A, Bard F-X, Josse E (2002) Tuna food habits related to the micronekton distribution in French Polynesia. Mar Biol 140:1023–1037

Block BA, Teo SLH, Boustany AB, Stokesbury MJW, Farwell CA, Weng KC, Dewar H, Williams TD (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Brill RW, Block BA, Boggs CH, Bigelow KA, Freund EV, Marcinek DJ (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Mar Biol 133:395–408

Brill RW, Bigelow KA, Musyl MK, Fritches KA, Warrant EJ (2005) Bigeye tuna (*Thunnus obesus*) behavior and physiology and their relevance to stock assessments and fishery biology. Col Vol Sci Pap ICCAT 57:142–161

Capone DG, Carpenter EJ (1982) Nitrogen fixation in the marine environment. Science 217:1140–1142

Carey FG, Robinson BH (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish Bull 79:277–292

Carpenter EJ (1983) Nitrogen fixation by marine Oscillatoria (*Trichodesmium*) in the world’s oceans. In: Carpenter EJ, Capone DG (eds) Nitrogen in the marine environment. Academic, New York, pp 65–103

Cherel Y, Hobson KA, Weimerskirch H (2005) Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. Oecologia 145:533–540

Cherel Y, Hobson KA (2005) Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proc R Soc Lond B 272:1601–1607

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cury P, Shannon LJ, Shin Y-J (2003) The functioning of marine ecosystems: a fisheries perspective. In: Sinclair M, Valdimarsson G (eds) Responsible fisheries in the marine ecosystem. FAO and CABI publishing, Rome, Wallingford, UK, pp 103–123

Dagorn L, Holland K, Hallier JPTM, Moreno G, Sancho G, Itano DG, Aumeeruddy R, Girard C, Million J, Fonteneau A (2006) Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). Aquat Liv Res 19:85–88

Davis R (2005) Intermediate-depth circulation of the Indian and South Pacific oceans measured by autonomous floats. J Phys Oceanogr 35:683–707

DeNiro MJ, Epstein S (1976) You are what you eat (plus a few ‰): the carbon isotope cycle in food chains. Geol Soc Am Conf Abstr 8:834–835

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Essington TE, Schindler DE, Olson RJ, Kitchell JF, Boggs C, Hilborn R (2002) Alternative fisheries and the predation rate of yellowfin tuna in the eastern Pacific Ocean. Ecol Appl 12:724–734

Estrada JA, Lutcavage ME, Thorrold SR (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. Mar Biol 147:37–45

Estrada JA, Rice AN, Natanson LJ, Skomal GB (2006) Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology 87:829–834

FAO (2003) Fisheries management 2. The ecosystem approach to fisheries. FAO, Rome

FAO (2006) FAO yearbook of fishery statistics capture production 2004, vol 98. FAO, Rome

Fonteneau A (1997) Atlas of tropical tuna fisheries world catches and environment. ORSTOM Editions, Paris

François R, Altabet MA, Goericke R (1993) Changes in the δ^{13}C of surface water particulate organic matter across the subtropical convergence in the SW Indian Ocean. Global Biogeochem Cycles 7:627–644

Frank KT, Petrie B, Shackell NL, Choi JS (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecol Lett 9:1–10

Frederiksen M, Edwards M, Richarson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Fry B (1988) Food web structure on Georges Bank from stable C, N and S isotopic compositions. Limnol Oceanogr 33:1182–1190

Fry B (2006) Stable isotope ecology. Springer, Berlin, 308pp

Gaye-Haake B, Lahajnar N, Emeis K-C, Unger D, Rixen T, Suthhof A, Ramaswamy V, Schulz H, Paropkari AL, Guptha MVS, Ittekkot V (2005) Stable nitrogen isotopic ratios of sinking particles and sediments from the northern Indian Ocean. Mar Chem 96:243–255

Graham BS, Popp B, Olson R, Allain V, Galvan F, Fry B (2006) Employing chemical tags to determine trophic dynamics and movement patterns of migratory predators in the equatorial Pacific Ocean. In: Proceedings of the 5th international conference on applications of stable isotope techniques to ecological studies, Belfast-Northern Ireland, 13–18 August

Graham BS, Grubbs D, Holland K, Popp BN (2007) A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. Mar Biol 150:647–658

Gruber N, Sarmiento JL (1997) Global patterns of marine nitrogen fixation and denitrification. Global Biogeochem Cycles 11:235–266

Hernandez-Garcia V (1995) The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic, with emphasis on the role of cephalopods. Fish Bull 93:403–411

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment. Chapman and Hall, New York

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326

Insightful (2005) S-Plus 7. Insightful Corporation, Seattle, WA

Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar Ecol Prog Ser 240:11–20

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1–27

Kornilova GN (1981) Feeding of yelllowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesu*s, in the Equatorial Zone of the Indian Ocean. J Ichthyol 20:111–119

Lesage V, Hammill MO, Kovacs KM (2001) Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. Mar Ecol Prog Ser 210:203–221

Longhurst AR (1998) Ecological geography of the sea. Academic, New York

Lourey MJ, Trull TW, Sigman DM (2003) Sensitivity of δ^{15}N of nitrate, surface suspended and deep sinking particulate nitrogen to seasonal nitrate depletion in the Southern Ocean. Global Biogeochem Cycles 17:1081. doi:10101029/2002GB001973

Maldeniya R (1996) Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. Environ Biol Fish 47:101–107

Markaida U, Hochberg FG (2005) Cephalopods in the diet of swordfish (*Xiphias gladius*) caught off the west coast of Baja California. Pac Sci 59:25–41

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

Moteki M, Arai M, Tsuchiya K, Okamoto H (2001) Composition of piscine prey in the diet of large pelagic fish in the eastern tropical Pacific Ocean. Fish Sci 67:1063–1074

Naqvi SWA, Naik H, Pratihary A, D'Souza W, Narvekar PV, Jayakumar DA, Devol AH, Yoshinari T, Saino T (2006) Coastal versus open-ocean denitrification in the Arabian Sea. Biogeosciences 3:621–633

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott M, López-Ibarra G, Galván-Magaña G, Fry B (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable isotopes as indicators of ecological change. Elsevier/Academic, Terrestrial Ecology Series, Amsterdam, pp 168–184

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Potier M, Marsac F, Lucas V, Sabatié R, Hallier J-P, Ménard F (2004) Feeding partitioning among tuna taken in surface and mid-water layers: the case of yellowfin (*Thunnus albacares*) and bigeye (*T obesus*) in the western tropical Indian Ocean. West Indian Ocean J Mar Sci 3:51–62

Potier M, Marsac F, Cherel Y, Lucas V, Sabatié R, Maury O, Ménard F (2007) Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. Fish Res 83:60–72

Quillfeldt P, McGill RAA, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. Mar Ecol Prog Ser 295:295–304

Rau GH, Sweeney RE, Kaplan IR (1982) Plankton ^{13}C:^{12}C ratio changes with latitude: differences between northern and southern oceans. Deep-Sea Res I 29:1035–1039

Rau GH, Mearns AJ, Young DR, Olson RJ, Schafer HA, Kaplan IR (1983) Animal ^{13}C/^{12}C correlates with trophic level in pelagic food webs. Ecology 64:1314–1318

Roger C (1994) Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. Fish Oceanogr 3:133–141

Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol Evol 19:256–263

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248

Sheldon RW, Sutcliffe WH, Paranjape MA (1977) Structure of pelagic food chain and relationship between plankton and fish production. J Fish Res Board Can 34:2344–2353

Schell DM, Saupe SM, Haubenstock N (1989) Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by δ^{13}C techniques. Mar Biol 103:433–443

Schott FA, McCreary JP (2001) The monsoon circulation of the Indian Ocean. Prog Oceanogr 51:1–123

Sinclair M, Valdimarsson G (2003) Responsible fisheries in the marine ecosystem. FAO & CABI Publishing, Rome, Wallingford, UK

Takai N, Onaka S, Ikeda Y, Yatsu A, Kidokoro H, Sakamoto W (2000) Geographical variations in carbon and nitrogen stable isotope ratios in squid. J Mar Biol Assoc UK 80:675–684

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable isotopes in animal tissues: implications for δ^{13}C analyses of diet. Oecologia 57:32–37

Tomczak M, Godfrey JS (1994) Regional oceanography: an introduction. Pergamon, Oxford

Trull TW, Armand L (2001) Insights into Southern Ocean carbon export from the δ^{13}C of particles and dissolved inorganic carbon during the SOIREE iron release experiment. Deep-Sea Res II 48:2655–2680

Wada E, Hattory A (1991) Nitrogen in the sea: forms, abundances, and rate processes. CRC, FL, USA

Wallace B, Seminoff J, Kilham S, Spotila J, Dutton P (2006) Leatherback turtles as oceanographic indicators: stable isotope analyses reveal a trophic dichotomy between ocean basins. Mar Biol 149:953–960

Walters CJ (2003) Folly and fantasy in the analysis of spatial catch rate data. Can J Fish Aquat Sci 60:1433–1436

Watanabe H (1960) Regional differences in food composition of the tunas and marlins from several oceanic areas. Rep Nankai Reg Fish Res Lab 12:75–84

Young J, Lansdell M, Riddoch S, Revill A (2006) Feeding ecology of broadbill swordfish, *Xiphias gladius*, off eastern Australia in relation to physical and environmental variables. Bull Mar Sci 79:793–809