

Stable isotopic evidence for trophic groupings and bio-regionalization of predators and their prey in oceanic waters off eastern Australia

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Abstract Muscle tissue was collected for stable isotope analysis (SIA) from the main fish predators and their fish and cephalopod prey from oceanic waters off eastern Australia between 2004 and 2006. SIA of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ revealed that the species examined could be divided into three main trophic groups. A “top predator” group consisted mainly of large billfish (*Xiphias gladius* and *Tetrapturus audax*), yellowfin (*Thunnus albacares*), bigeye (*T. obesus*) and southern bluefin (*T. maccoyii*) tunas and sharks; with mako (*Isurus oxyrinchus*) the highest. Below this tier was a second group composed of mid-trophic level fishes including albacore tuna (*Thunnus alalunga*), lancet fish (*Alepisaurus ferox*), mahi mahi (*Coryphaena hippuris*) and ommastrephid squid. Underlying both groups was a grouping of small fishes including myctophids, small scombrids and nomeids as well as surface fishes including macrorhamphosids. These groupings were based largely on mean animal size which showed a positive linear relation to $\delta^{15}\text{N}$ ($r^2 = 0.58$). Some species showed significant ontogenetic variation in either $\delta^{15}\text{N}$ (swordfish, lancet fish, yellowfin and albacore tuna) or $\delta^{13}\text{C}$ (mako shark). We also noted a consistent latitudinal change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at $\sim 28^\circ\text{S}$ for the top predator species, particularly albacore and yellowfin tuna. The differences were consistent with a change from oligotrophic Coral Sea to nutrient rich Tasman Sea waters. These differences suggest that predatory

fishes may have extended residence time in distinct regions off eastern Australia.

Introduction

With the general requirement that oceanic fisheries be managed in an ecologically sustainable manner detailed information is needed on the way targeted species link with their prey and with other similar species (Worm and Duffy 2003). Central to this task is an understanding of the main food chain pathways. Stomach contents analysis (SCA) is the most common way for these interactions to be assessed. However, this is a time consuming and labour intensive process which is ultimately limited by the fact that SCA only recognises a single days’ feeding, and may be biased through differential digestion rates (e.g., MacDonald et al. 1982; James 1988). Biochemical techniques such as stable isotope analysis (SIA), which integrate feeding over an extended time period, have proven to be a valuable tool in determining trophic level for a range of predators and their prey (Peterson and Fry 1987). SIA can also provide a broader understanding of food chain links of top predators in pelagic ecosystems, temporally and spatially (Graham et al. 2007; Menard et al. 2007).

The stable isotopes of carbon and nitrogen have been used successfully in many lake and marine trophic studies to elucidate not only trophic positions, but also trophic shifts induced by disturbance and migration (e.g., Best and Schell 1996; Vander Zanden et al. 1999; Davenport and Bax 2002; Caraveo-Patino et al. 2007; Cherel and Hobson 2007; Sara and Sara 2007). The basic premise behind all these studies is that the carbon isotopic signature of predators is enriched relative to their food source by 1‰ or

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less (DeNiro and Epstein 1978; Fry and Sherr 1984) while nitrogen is enriched by -0.5 to 9‰ (mean ca. 3‰ ; DeNiro and Epstein 1981). Thus, with little trophic fractionation, carbon isotopic values are useful in establishing primary food sources while the potentially much larger fractionation observed with nitrogen isotopic composition means this isotope is more useful in establishing trophic position. However, results must be interpreted with caution as trophic enrichment is variable, even between individuals of the same species (DeNiro and Epstein 1981) which may well be due to ontogenetic shifts with age and/or size (Young et al. 2006; Sara and Sara 2007) and between tissue types of the same individual (Pinnegar and Polunin 1999; MacNeil et al. 2005, 2006). In addition, baseline signatures can vary both seasonally and spatially (Popp et al. 2007) and these variations will propagate up the food chain.

Davenport and Bax (2002) successfully used stable isotopes to investigate the trophic interactions on the continental shelf off south-eastern Australia and were able to clearly elucidate a trophic structure related to functional patterns in feeding. Studies by Young et al. (2006) and Sara and Sara (2007) utilised stable isotopes to investigate the trophic interactions of higher-order predators and demonstrated that trophic position appeared to be directly related to size for both swordfish and bluefin tuna, respectively. The results from these studies indicated that we may be able to investigate trophic interactions within the Australian Eastern Tuna and Billfish Fishery (ETBF) in a similar manner.

The ETBF is a longline fishery extending along the eastern seaboard of Australia to past the limits of the EEZ. There are now five species targeted by the fishery—swordfish (*Xiphias gladius*), albacore (*Thunnus alalunga*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*) and striped marlin (*Tetrapturus audax*)—as well as a suite of bycatch species. In all, ~ 200 species have been recorded from the longline catch (CSIRO Marine and Atmospheric Research, unpublished data). It is an Australian Commonwealth fishery and as such is required to be managed with regard to ecosystem sustainability. We, therefore, need to define the overall structure of the ETBF ecosystem, and whether we are dealing with one or a number of interrelated systems. For example, does the presence of the Tasman front effectively separate the fishery into two different regions requiring different management strategies?

The broad objective of this study therefore, was to determine the isotopic signatures of the main fish species and their prey within the ETBF. We aimed to identify the main trophic groups in relation to fish length and point of capture within the region. Second, we aimed to test whether the region could be separated based on the isotopic structure of the constituent species.

Methods

White muscle tissue of predator species were collected at sea on tuna longliners operating off eastern Australia between latitudes 25 and 35°S between 2004 and 2006 (Tables 1, 2; Fig. 1; Young et al. 2006). Details of fish length, and position and date of capture were included with each sample. Squid prey species were collected from predator stomach contents in the laboratory. Fish prey species were collected from mid-water tows taken on research voyages in the area (Young et al. 2009). All samples were frozen at sea and then transported to the laboratory where they were thawed for analysis.

Stable isotopes were determined for predators and their prey following Davenport and Bax (2002). Muscle tissue was usually collected from below the dorsal fin in fish and sections of mantle were collected from cephalopods. Although it is common to remove lipids from samples prior to SIA or to adjust data for lipids (e.g., McConnaughey and McRoy 1979), lipid removal for these samples was deemed to be unwarranted. We wanted our data to be comparable to that of Davenport and Bax (2002) who similarly did not remove lipids due to most Australian fish and crustaceans averaging only about 1% lipid (Nichols et al. 1998), reflecting the generally oligotrophic waters surrounding the continent and white muscle, in particular, is lipid poor (Pinnegar and Polunin 1999). In addition, we randomly selected a subset of samples from the major groups and found no difference in carbon isotope signature between samples prior to or post-lipid removal. Samples were dried at 55°C overnight, before being ground, homogenised and weighed into tin cups for analysis. Samples were analysed using a Carlo Erba NA1500 CNS analyser interfaced via a Conflo II to a Finnigan Mat Delta S isotope ratio mass spectrometer, operating in the continuous flow mode. Combustion and oxidation were achieved at $1,090^{\circ}\text{C}$ and reduction at 650°C . Samples were analysed at least in duplicate. Results are presented in standard δ notation:

$$\delta = \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. The standard for nitrogen is air and for carbon Vienna Pee Dee Belemnite (VPDB). The reproducibility of the stable isotope measurements was 0.2‰ for carbon and 0.3‰ for nitrogen.

Data analysis

Statistical analysis and visualisation of stable isotope data were carried out using the *Statistica* software package (Statsoft Inc.) in four steps. Predators and prey were initially grouped using cluster analysis of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each family (Ward's minimum variance method).

Table 1 Isotope values for $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) for 25 fish predators sampled off eastern Australia between 2004 and 2006

Species	N	Length (mm)				$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
		Mean	Min.	Max.	SE	Mean	Min.	Max.	SE	Mean	Min.	Max.	SE
<i>Thunnus alalunga</i>	34	918.2	760	1,050	13.7	12.2	10.7	14.9	0.1	−16.4	−18.5	−14.6	0.1
<i>Alepisaurus brevirostris</i>	3	666.7	590	730	41.0	10.1	9.5	10.6	0.3	−18.9	−19.3	−18.6	0.2
<i>Alepisaurus ferox</i>	19	921.7	600	1,520	58.1	11.6	10.1	13.5	0.2	−18.5	−19.3	−17.3	0.1
<i>Thunnus obesus</i>	10	1,063.0	700	1,180	47.4	13.8	13.1	15.0	0.2	−18.3	−19.5	−17.1	0.2
<i>Prionace glauca</i>	14	1,345.7	700	2,430	146.6	13.6	12.8	15.6	0.2	−17.2	−19.0	−14.9	0.3
<i>Coryphaena hippurus</i>	7	1,087.1	500	1,220	99.1	11.9	8.3	13.4	0.7	−17.4	−19.1	−15.3	0.5
<i>Carcharhinus obscurus</i>	1	2,160.0	2,160	2,160	NA	12.9	12.9	12.9	NA	−14.8	−14.8	−14.8	NA
<i>Carcharhinus falciformis</i>	1	790.0	790	790	NA	12.6	12.6	12.6	NA	−14.0	−14.0	−14.0	NA
<i>Rexea solandri</i>	1	350.0	350	350	NA	12.6	12.6	12.6	NA	−19.4	−19.4	−19.4	NA
<i>Gempylus serpens</i>	15	858.0	690	980	22.1	13.1	12.3	14.0	0.1	−18.8	−19.5	−17.6	0.1
<i>Lepidocybium flavobrunneum</i>	7	835.0	630	1,130	84.3	13.6	11.8	15.8	0.5	−20.5	−21.5	−19.3	0.3
<i>Isurus paucus</i>	1	2,450.0	2,450	2,450	NA	14.7	14.7	14.7	NA	−19.0	−19.0	−19.0	NA
<i>Tetrapturus audax</i>	8	1,779.1	1,190	2,150	98.5	13.2	9.2	15.2	0.7	−18.1	−23.4	−14.3	1.0
<i>Ruvettus pretiosus</i>	1	1,120.0	1,120	1,120	NA	15.0	15.0	15.0	NA	−21.2	−21.2	−21.2	NA
<i>Dasyatis violacea</i>	2	480.0	480	480	0.0	10.2	9.9	10.5	0.3	−18.9	−19.2	−18.7	0.2
<i>Psenes pellucidus</i>	1	690.0	690	690	NA	11.4	11.4	11.4	NA	−20.8	−20.8	−20.8	NA
<i>Manta birostris</i>	1	1,200.0	1,200	1,200	NA	11.8	11.8	11.8	NA	−18.2	−18.2	−18.2	NA
<i>Thunnus maccoyii</i>	17	1,530.0	1,160	1,690	28.3	14.3	13.0	15.7	0.2	−20.2	−23.2	−17.5	0.5
<i>Isurus oxyrinchus</i>	21	1,413.8	660	2,140	96.5	15.7	9.7	18.4	0.4	−16.7	−18.1	−14.4	0.2
<i>Sphyrna zygaena</i>	1	1,220.0	1,220	1,220	NA	13.5	13.5	13.5	NA	−15.4	−15.4	−15.4	NA
<i>Tetrapturus angustirostris</i>	2	1,505.0	1,450	1,560	55.0	13.6	13.5	13.7	0.1	−17.4	−17.4	−17.4	0.0
<i>Xiphias gladius</i>	30	1,167.8	255	2,100	77.1	13.2	9.1	15.7	0.2	−19.4	−23.9	−17.1	0.3
<i>Trachipterus spp</i>	1	2,240.0	2,240	2,240	NA	13.6	13.6	13.6	NA	−18.6	−18.6	−18.6	NA
<i>Thunnus albacares</i>	43	1,211.4	760	1,500	25.0	13.2	9.3	14.5	0.2	−18.5	−24.7	−16.0	0.2

Second, the relative importance of factors potentially influencing these groupings (season, latitude, longitude, animal length, sea surface temperature and chlorophyll *a*) were assessed further using a general linear model (GLM). Data were analysed using a non-stepwise approach in order to allow an assessment of the relative significance for each parameter (β). Third, the significance of the relationship between size and $\delta^{15}\text{N}$ was further investigated by using the method of Jennings et al. (2001). This method utilises a plot of $\delta^{15}\text{N}$ to \log_{10} (body length) to highlight any significant trends in isotopic signature with increasing body size. Fourth, latitudinal influence on predator isotopic signature was investigated by a moving mean and summed coefficient of variance analysis at each degree of latitude between 24 and 34°S. For the moving mean analysis, at each point of latitude the mean $\delta^{15}\text{N}$ value was calculated for two groups of predators; those north (all samples caught at a latitude \geq the target latitude) and those south (all samples caught at a latitude $<$ the target latitude) of that position. The summed coefficient of variance represents the

cumulative variance in the data as samples from each latitudinal band are added to the data pool.

Results

A total of 244 predator and 115 prey samples were analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Tables 1, 2; Fig. 1). Mean $\delta^{15}\text{N}$ values ranged from 10.1 (*Alepisaurus ferox*) to 15.1‰ (*Isurus oxyrinchus*); mean $\delta^{13}\text{C}$ ranged from −14.1 (*Carcharhinus falciformis*) to −21.2‰ (*Ruvettus pretiosus*) indicating wide differences in the isotopic signals across a range of pelagic fishes in the study area. Similar differences were noted across a wide range of potential prey species (Table 2).

Within species differences in isotope signature were also noted for both predators and prey. For example, mako shark (*I. oxyrinchus*) had $\delta^{15}\text{N}$ values ranging from 9.7 to 18.4‰ (diff. 8.7‰). Within species, differences were also noted for $\delta^{13}\text{C}$. For example, yellowfin tuna (*T. albacares*)

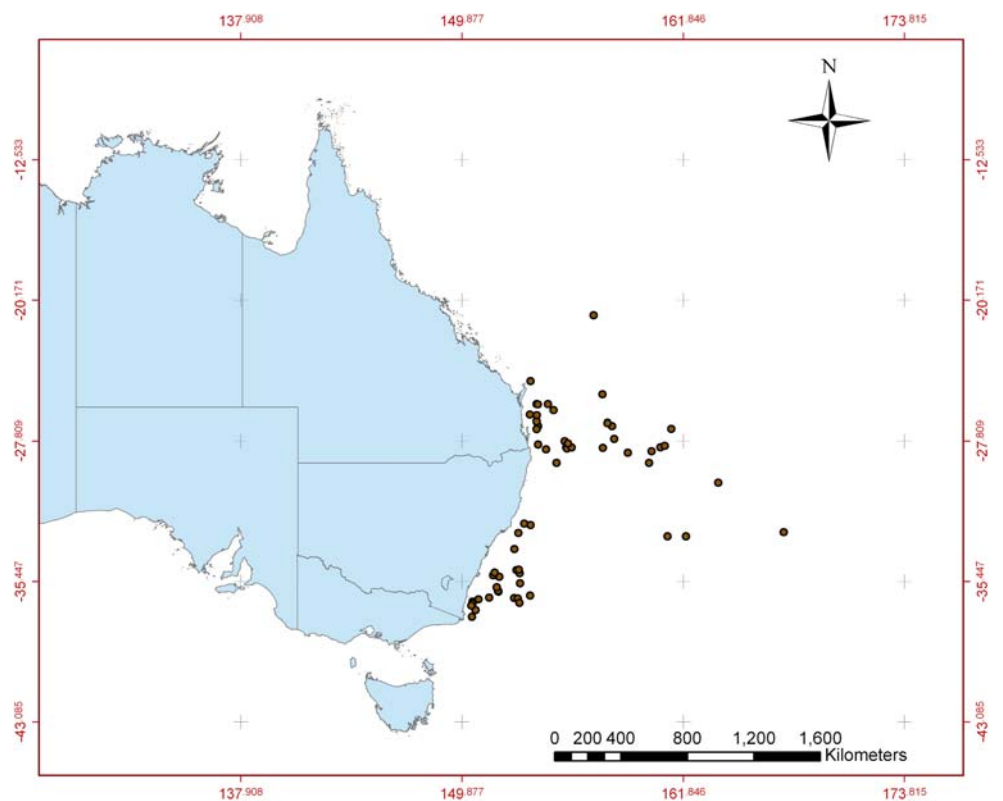
Table 2 Isotope values for $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) for 32 “prey” species sampled off eastern Australia between 2004 and 2006

Prey	N	Length (mm)				$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
		Mean	Min.	Max.	SE	Mean	Min.	Max.	SE	Mean	Min.	Max.	SE
Fish	80	163.1	30	650	16.0	10.5	6.5	14.0	0.1	-18.9	-21.6	-14.1	0.1
Alepisauridae													
<i>Alepisaurus brevirostris</i>	4	439.5	285	650	79.9	10.7	10.1	11.1	0.2	-18.5	-18.7	-18.1	0.1
<i>Alepisaurus</i> spp.	3	288.3	73	496	122.2	10.4	9.8	11.4	0.5	-18.7	-19.0	-18.2	0.2
	7	374.7	73	650	69.9	10.6	9.8	11.4	0.2	-18.6	-19.0	-18.1	0.1
Scombridae													
<i>Auxis rochei rochei</i>	6	248.6	222	283	10.0	10.1	9.1	10.9	0.3	-17.2	-17.6	-16.7	0.1
<i>Katsuwonus pelamis</i>	2	347.5	275	420	72.5	9.4	8.3	10.4	1.0	-17.2	-17.6	-16.9	0.3
	8	276.9	222	420	25.1	9.9	8.3	10.9	0.3	-17.2	-17.6	-16.7	0.1
Bramidae													
<i>Brama brama</i>	2	442.5	425	460	17.5	13.4	13.2	13.7	0.3	-18.1	-18.5	-17.8	0.3
<i>B. orcini</i>	2	229.0	96	362	133.0	13.4	12.8	14.0	0.6	-18.2	-18.2	-18.1	0.0
<i>Brama</i> spp.	1	NA	525	525	NA	NA	12.3	12.3	NA	NA	-18.1	-18.1	NA
<i>I. brasiliensis</i>	1	NA	385	385	NA	NA	11.8	11.8	NA	NA	-14.1	-14.1	NA
	6	375.5	96	525	74.2	12.9	12.3	14.0	0.3	-17.5	-18.5	-14.1	0.1
Nomeidae													
<i>Cubiceps pauciradiatus</i>	1	NA	240	240	NA	NA	11.5	11.5	NA	NA	-17.7	-17.7	NA
<i>C. ceruleus</i>	1	NA	385	385	NA	NA	11.8	11.8	NA	NA	-14.1	-14.1	NA
<i>Cubiceps</i> spp.	1	NA	220	220	NA	NA	9.7	9.7	NA	NA	-18.4	-18.4	NA
	3	281.7	220	385	42.0	11.0	9.7	11.8	0.5	-16.7	-18.4	-14.1	1.1
Myctophidae													
<i>Ceratoscopelus warmingii</i>	15	80.0	80	80	0.0	9.6	8.4	10.5	0.2	-19.5	-20.4	-18.5	0.1
<i>Diaphus brachycephalus</i>	4	75.0	75	75	0.0	11.2	11.0	11.4	0.1	-18.8	-18.9	-18.7	0.0
<i>D. perspicillatus</i>	4	75.0	75	75	0.0	11.0	10.6	11.5	0.2	-19.5	-20.7	-18.9	0.4
<i>Diaphus</i> spp.	4	75.0	75	75	0.0	10.8	10.4	11.1	0.2	-20.0	-20.9	-19.1	0.4
<i>D. termophilus</i>	4	75.0	75	75	0.0	12.0	11.6	12.3	0.1	-19.0	-19.6	-18.0	0.4
	31	77.4	75	80	0.5	10.4	8.4	12.3	0.2	-19.4	-20.9	-18.0	0.1
Exocoetidae													
<i>Paraexocoetus</i> spp.	1	NA	96	96	NA	NA	6.5	6.5	NA	NA	-18.2	-18.2	NA
<i>Exocoetidae</i>	2	227.5	210	245	17.5	10.4	10.1	10.8	0.3	-17.6	-17.8	-17.5	0.1
	3	183.7	96	245	45.0	9.1	6.5	10.8	1.3	-17.8	-18.2	-17.5	0.2
Gempylidae													
<i>Gempylus serpens</i>	1	NA	354	354	NA	NA	9.4	9.4	NA	NA	-19.0	-19.0	NA
<i>Gempylidae</i>	3	145	145	145	0.0	11.5	10.9	12.6	0.6	-18.8	-19.6	-17.8	0.5
	4	197.3	145	354	52.3	11.0	9.4	12.6	0.7	-18.9	-19.6	-17.8	0.4
Macrorhamphosidae													
<i>Macrorhamphosus scolopax</i>	8	40.0	40	40	0.0	9.3	8.1	10.3	0.4	-20.6	-21.6	-19.9	0.3
	8	40.0	40	40	0.0	9.3	8.1	10.3	0.4	-20.6	-21.6	-19.9	0.3
Paralepididae													
<i>Sudis atrox</i>	1	NA	60	60	NA	NA	9.7	9.7	NA	NA	-19.3	-19.3	NA
<i>Paralepididae</i>	2	90	90	90	0.0	10.0	9.7	10.2	0.3	-19.6	-19.7	-19.6	0.1
	3	80.0	60	90	10.0	9.9	9.7	10.2	0.2	-19.5	-19.7	-19.3	0.1
Scomberesocidae													
<i>S. saurus scomberoides</i>	3	320.0	320	320	0.0	10.1	9.9	10.3	0.1	-17.9	-18.1	-17.8	0.1
	3	320.0	320	320	0.0	10.1	9.9	10.3	0.1	-17.9	-18.1	-17.8	0.1
Tetraodontidae													
	1	NA	31	31	NA	NA	9.1	9.1	NA	NA	-18.1	-18.1	NA

Table 2 continued

Prey	N	Length (mm)				$\delta^{15}\text{N}$ (‰)				$\delta^{13}\text{C}$ (‰)			
		Mean	Min.	Max.	SE	Mean	Min.	Max.	SE	Mean	Min.	Max.	SE
Trichiuridae	2	130.0	130	130	0.0	11.0	11.0	11.1	0.0	-19.2	-19.3	-19.0	0.2
Trachichthyidae	2	30.0	30	30	0.0	10.4	10.4	10.4	0.0	-19.3	-19.7	-19.0	0.4
Squid	35	289.2	60	588	25.1	12.4	6.8	14.6	0.3	-17.0	-18.2	-14.8	0.2
Architeuthidae													
<i>Architeuthis</i> spp.	3	564.0	540	588	24.0	11.8	10.4	13.0	0.8	-16.3	-17.5	-15.3	0.7
	3	564.0	540	588	24.0	11.8	10.4	13.0	0.8	-16.3	-17.5	-15.3	0.7
Chiroteuthidae													
<i>Chiroteuthis</i> spp.	2	232.5	130	335	102.5	12.5	11.5	13.5	1.0	-16.5	-18.0	-15.1	1.4
	2	232.5	130	335	102.5	12.5	11.5	13.5	1.0	-16.5	-18.0	-15.1	1.4
Cranchiidae													
<i>Leachia</i> spp.	1	NA	60	60	NA	NA	11.2	11.2	NA	NA	-17.6	-17.6	NA
	1	NA	60	60	NA	NA	11.2	11.2	NA	NA	-17.6	-17.6	NA
Ommastrephidae													
<i>E. luminosa</i>	1	136.0	87	185	49.0	11.8	10.2	13.3	1.5	-16.2	-17.6	-14.8	1.4
<i>Notodarus gouldi</i>	3	410.0	370	450	23.1	13.0	12.3	13.4	0.4	-17.2	-17.4	-17.0	0.1
<i>Ommastrephes. bartramii</i>	16	338.1	145	475	22.2	12.6	6.8	14.6	0.5	-16.9	-17.9	-15.0	0.2
<i>O. volatilis</i>	3	75.0	70	83	4.0	12.5	12.2	12.9	0.2	-17.7	-18.2	-16.9	0.4
<i>Stenoteuthis oualaniensis</i>	1	NA	215	215	NA	NA	13.4	13.4	NA	NA	-17.1	-17.1	NA
<i>T. eblanae</i>	4	179.7	150	203	15.6	11.5	6.9	13.5	1.6	-17.3	-17.9	-16.6	0.3
	29	281.8	70	475	24.0	12.4	6.8	14.6	0.3	-17.0	-18.2	-14.8	0.2

Fig. 1 Map of study area showing position of capture of samples taken for isotope analysis off eastern Australia between 2004 and 2006



exhibited a $\delta^{13}\text{C}$ range from -24.7 to -16.0‰ (diff. 8.7‰). Of the smaller “prey” species that we sampled $\delta^{15}\text{N}$ of myctophid fishes ranged from 8.4 to 12.3‰ (diff. 3.9‰) and had a $\delta^{13}\text{C}$ range of -20.9 to -18.0‰ (diff. 2.9‰) (Table 2). Isotope values of the dominant squid group, family Ommastrephidae, had a $\delta^{15}\text{N}$ signal ranging from 6.8 to 14.6‰ (diff. 7.8‰) but with a lower degree of variation in carbon, with a $\delta^{13}\text{C}$ range of -18.2 to -17.0‰ (diff. 1.2‰).

Broad scale food web groupings

A dual isotope plot for all predators, selected fish and squid families (where $n \geq 5$) is shown in Fig. 2. Three distinct groupings were apparent and these could be assigned as mid-level prey, mid-level predators and generalist top predators. Mako sharks (*I. oxyrinchus*) occupied the highest trophic position slightly above the generalist predators. In addition to the bi-plot, we also performed a cluster analysis on the same data (Fig. 3). The resulting dendrogram showed the same three groupings and also that the mid-level predators and mid-level prey were not as distinct from each other as these two groups were from the top-level predators. In particular, *Alepisaurus* spp. spanned these two groups as both mid-level prey when juvenile and a mid-level predator as adults.

Size relationships

There was a significant relationship between mean length and mean $\delta^{15}\text{N}$ across all taxa analysed ($r^2 = 0.7$; $\beta = 0.760$; $\text{SE} = 0.162$, $P < 0.0005$; Fig. 4) indicating that the above pattern may be partly explained by the mean

size of the particular species. However, there was no similar relationship with $\delta^{13}\text{C}$ indicating that other factors were important in the observed differences. Multiple linear regression of spatial, temporal and biotic variables confirmed that size was just one of a number of factors influencing isotope concentration.

Grouping variables

Multiple regression analysis found that for $\delta^{15}\text{N}$ the variables species, length, and longitude were significant in explaining 68% of the variability ($r^2 = 0.69$, $F = 8.9$, $P < 0.0001$). For $\delta^{13}\text{C}$, 60% of the total variability could be explained using the variables species, year, latitude, longitude and length ($r^2 = 0.59$, $F = 6.0$, $P < 0.0001$). We further examined the response of “species” to environmental factors using a GLM. No consistent environmental effects were found across the range of species tested, although length was a significant factor for the ‘top predator’, swordfish and albacore species in relation to $\delta^{15}\text{N}$ (Table 3). Similarly, no overall patterns were detected for $\delta^{13}\text{C}$, although area of capture and ‘year’ were important for some of the species (Table 4).

Even though the GLM showed no consistent relationship between length and the stable isotope values, an analysis of $\delta^{15}\text{N}$ versus \log_{10} (length) showed significant size-related effects indicating a trend towards more enriched $\delta^{15}\text{N}$ values (higher trophic level) with increasing size (Fig. 5). This effect appears to be weak for individual species such as mako sharks and *Alepisaurus* spp. (Fig. 5), but there was still a significant overall difference between mean $\delta^{15}\text{N}$ values for small and large fish. Swordfish and albacore tuna showed the most significant differences

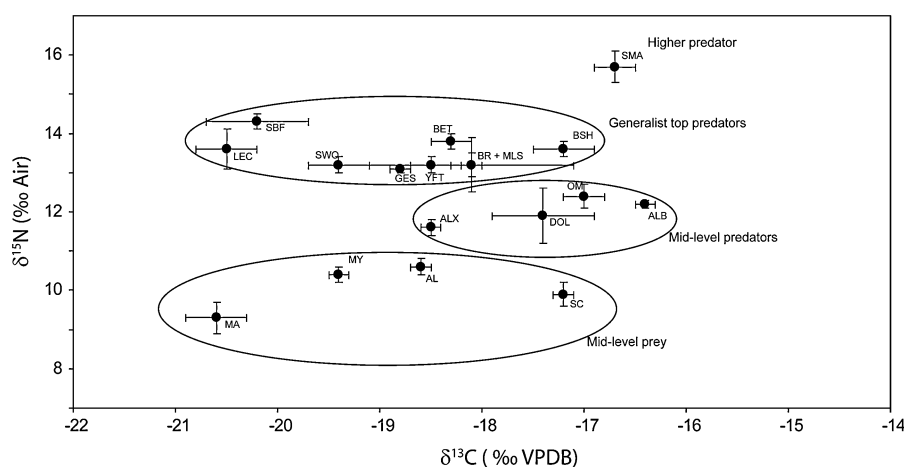


Fig. 2 Biplot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the main predators and prey off eastern Australia showing three broad trophic levels but also showing a wide variation in carbon across the species. (AL juv. *Alepisaurus* sp., ALB *T. alalunga*, ALX adult *A. ferox*, BET *T. obesus*, BR *Bramidae*, BSH *P. glauca*, DOL *C. hippurus*, GES *G. serpens*, LEC *L.*

flavobrunneum, MA *M. scolopax*, MLS *T. audax*, MY *Myctophidae*, OM *Ommastrephidae*, SBF *T. maccoyii*, SC *Scombridae*, SMA *I. oxyrinchus*, SWO *X. gladius*, YFT *T. albacares*). BR and MLS are superimposed

Fig. 3 Cluster analysis of predator and prey species from eastern Australian waters showing three main clusters consisting of top predator, mid-level predators and prey

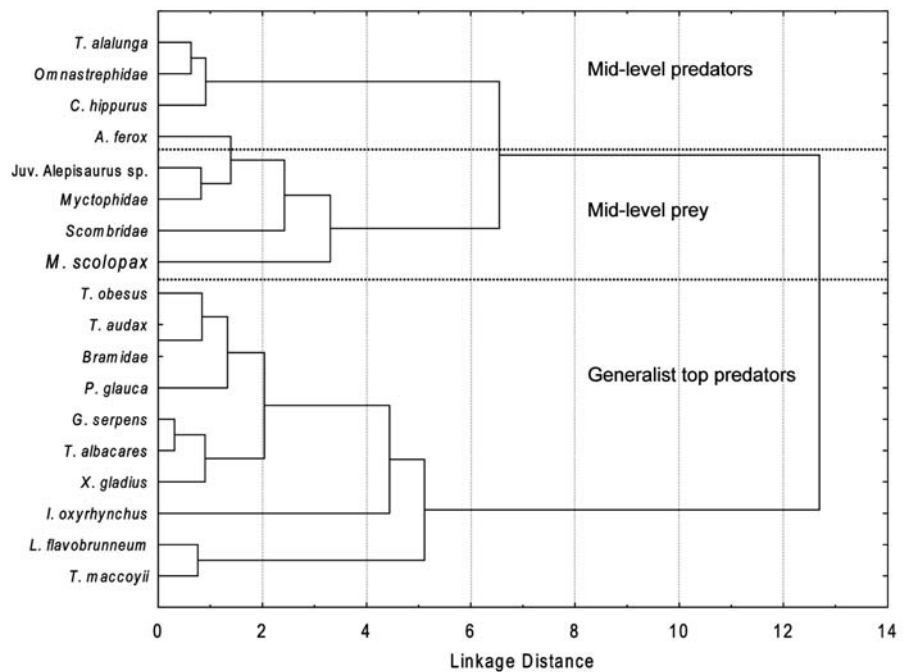
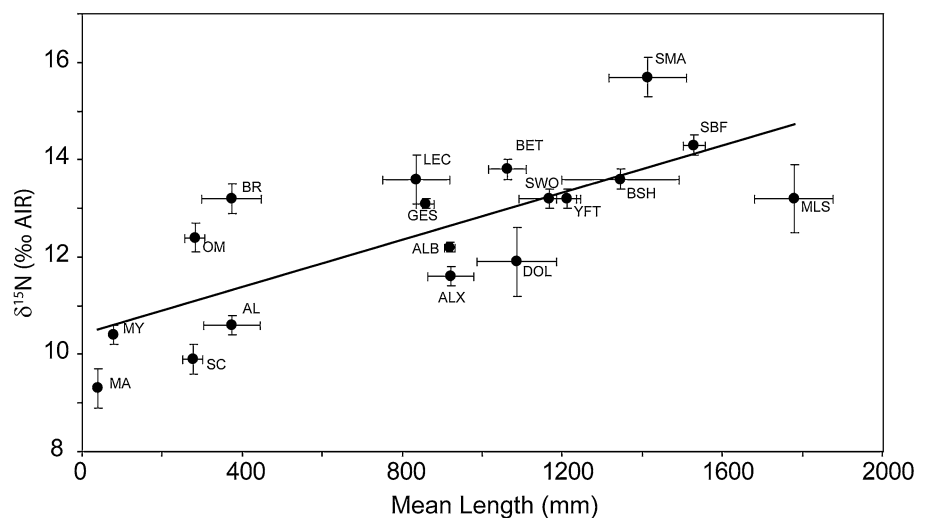


Fig. 4 Mean $\delta^{15}\text{N}$ for individual species plotted against mean species length (mm) for main predator and prey groupings. (AL juv. *Alepisaurus* sp., ALB *T. alalunga*, ALX adult *A. ferox*, BET *T. obesus*, BR *Bramidae*, BSH *P. glauca*, DOL *C. hippurus*, GES *G. serpens*, LEC *L. flavobrunneum*, MA *M. scolopax*, MLS *T. audax*, MY *Myctophidae*, OM *Omnastrephidae*, SBF *T. maccoyii*, SC *Scombridae*, SMA *I. oxyrinchus*, SWO *X. gladius*, YFT *T. albacares*)



between large and small fish, but albacore display a trend opposite to that observed for the dataset as a whole (Fig. 5), becoming less enriched with increasing size. There was no significant difference in $\delta^{15}\text{N}$ with size for the yellowfin tuna sampled.

Samples of predators were collected over a wide geographical range, covering 17° of latitude and 13° of longitude (Table 1; Fig. 1). Results from the GLM (Tables 3, 4) showed significant spatial variability in both carbon and nitrogen isotope concentration for some predator and prey groupings. Adequate spatial coverage was limited for an in-depth analysis. However, plots of moving means and summed coefficients of variance of isotope concentration for the groups “All predators”, swordfish,

yellowfin and albacore tuna had a strong latitudinal component with breaks noticeable at 28 and 34°S for both $\delta^{15}\text{N}$ (Fig. 6) and $\delta^{13}\text{C}$ (Fig. 7).

Discussion

Trophic groupings

Three trophic groups were distinguished in pelagic waters off eastern Australia based on their mean $\delta^{15}\text{N}$ signature, generally considered to be an indicator of trophic position (although see Popp et al. 2007). The first group was characterised by a general grouping of top predators

Table 3 Standardised parameter estimates (β) with standard errors from GLM analysis for latitude, longitude, length, SST, Chl a and Year versus $\delta^{15}\text{N}$

Predator	Latitude		Longitude		Length		SST		Chl a		Year	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
All top	0.093	0.136	-0.073	0.106	0.368	0.074	-0.102	0.113	0.054	0.087	0.255	0.089
All mid	0.199	0.160	-0.174	0.134	-0.112	0.150	-0.321	0.110	-0.072	0.183	-0.133	0.141
All prey	-0.234	0.246	-0.466	0.178	-0.040	0.177	0.168	0.211	-0.528	0.187	-0.156	0.160
<i>X. gladius</i>	-0.196	0.218	0.044	0.186	0.577	0.137	0.032	0.203	0.143	0.158	0.289	0.199
<i>Alepisaurus</i> spp.	0.903	0.930	-0.488	0.532	0.560	0.312	-0.227	0.576	-0.104	0.461	0.614	1.048
<i>I. oxyrinus</i>	0.362	0.277	0.238	-1.014	0.218	-0.148	0.344	-1.28	0.259	-0.293	0.178	0.343
<i>T. alalunga</i>	0.380	0.412	0.155	0.226	-0.549	0.242	0.008	0.398	0.503	0.553	-0.075	0.224
<i>T. albacares</i>	-0.559	0.162	-0.430	0.118	0.135	0.082	-0.085	0.073	-0.069	0.082	-0.053	0.136

Figures in bold represent P values <0.05

Table 4 Standardised parameter estimates (β) with standard errors from GLM analysis for latitude, longitude, length, SST, Chl a and year versus $\delta^{13}\text{C}$

Predator	Latitude		Longitude		Length		SST		Chl a		Year	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
All top	0.093	0.137	0.081	0.106	-0.095	0.074	0.413	0.113	0.050	0.087	0.191	0.090
All mid	0.349	0.101	0.399	0.084	-0.115	0.094	-0.044	0.069	-0.081	0.115	0.439	0.089
All prey	-0.341	0.183	0.303	0.132	0.384	0.132	0.677	0.157	0.291	0.139	-0.055	0.119
<i>X. gladius</i>	-0.274	0.333	0.353	0.283	-0.266	0.209	0.452	0.309	0.376	0.241	0.177	0.303
<i>Alepisaurus</i> spp.	2.699	1.041	0.378	0.596	0.508	0.350	0.644	0.646	0.903	0.516	2.741	1.174
<i>I. oxyrinus</i>	-0.823	0.278	0.404	0.183	-0.172	0.168	1.104	0.264	-0.259	0.199	-0.457	0.136
<i>T. alalunga</i>	-0.030	0.367	0.119	0.201	-0.087	0.216	0.490	0.355	-0.158	0.494	0.249	0.200
<i>T. albacares</i>	0.418	0.349	-0.026	0.254	-0.155	0.176	0.169	0.158	0.080	0.178	0.019	0.292

Figures in bold represent P values <0.05

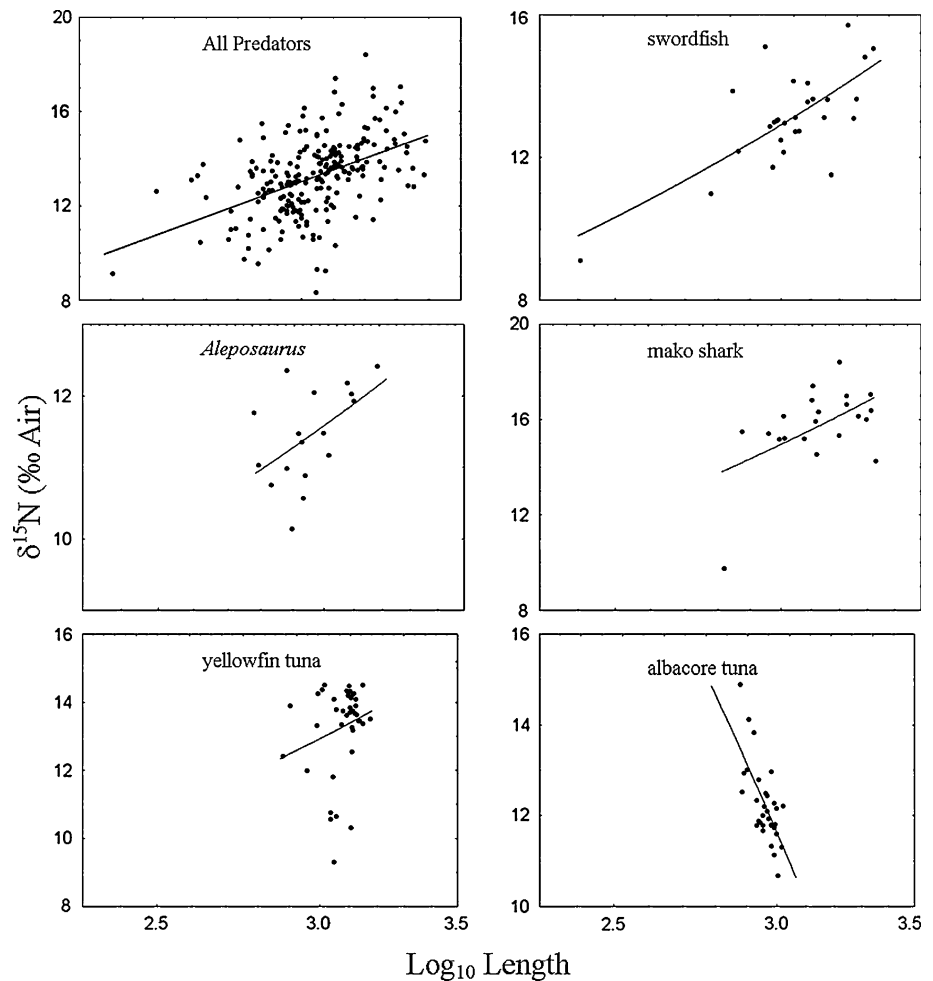
composed of shark, tuna and billfish (Fig. 2). Of the top order grouping, only mako shark could be distinguished as a potentially higher predator. This agrees with results in the Northwest Atlantic which showed mako sharks sitting above a range of pelagic shark species including blue sharks (Estrada et al. 2003; MacNeil et al. 2005). The main group, however, which also included the tunas and billfish, could not be separated by $\delta^{15}\text{N}$. In contrast, swordfish that overlapped in length and area with yellowfin tuna in the Indian Ocean had a $\delta^{15}\text{N}$ 0.7–2.8‰ higher than the latter (Menard et al. 2007). They reasoned this was due to differences in trophic ecology and behaviour of the two species in the region, particularly diving capability. One possibility for the lack of difference between the two species off eastern Australia was the samples were collected from similar areas so potentially they would be feeding on the same prey species. Lansdell and Young (2007) identified 11 prey species that were common to yellowfin tuna and swordfish from eastern Australian waters, including dominant prey such as *Ommastrephes*

bartramii, which contributed significantly to the diet of both predators.

Below the top order group was a broad grouping of species with a smaller mean size composed of ommastrephids, albacore, adult *Alepisaurus* spp. and dolphin fish. This group consisted of species regarded primarily as piscivores and agrees with a similar grouping from the study off southeast Australia by Davenport and Bax (2002). That study reported a group of tertiary consumers, dominated by primary piscivores, with a mean $\delta^{15}\text{N}$ signature of ca. 12.5‰ (this study 12.1‰). Below this group lay a base of mid-level prey species including myctophids, juvenile *Alepisaurus* spp., small scombrids and macrorhamphosids, which are generally zooplanktivorous.

The difference in the mean $\delta^{15}\text{N}$ value of the top predators and mid-level predators (ca. 1.5‰) was less than the often quoted $\delta^{15}\text{N}$ trophic fractionation of 3.4‰ (Post 2002) indicating overlap in the prey eaten by both groups. This is not surprising, particularly given that of the species examined, only lancet fish were analysed separately as

Fig. 5 Relationship between $\delta^{15}\text{N}$ and \log_{10} of body length for all predators and key species



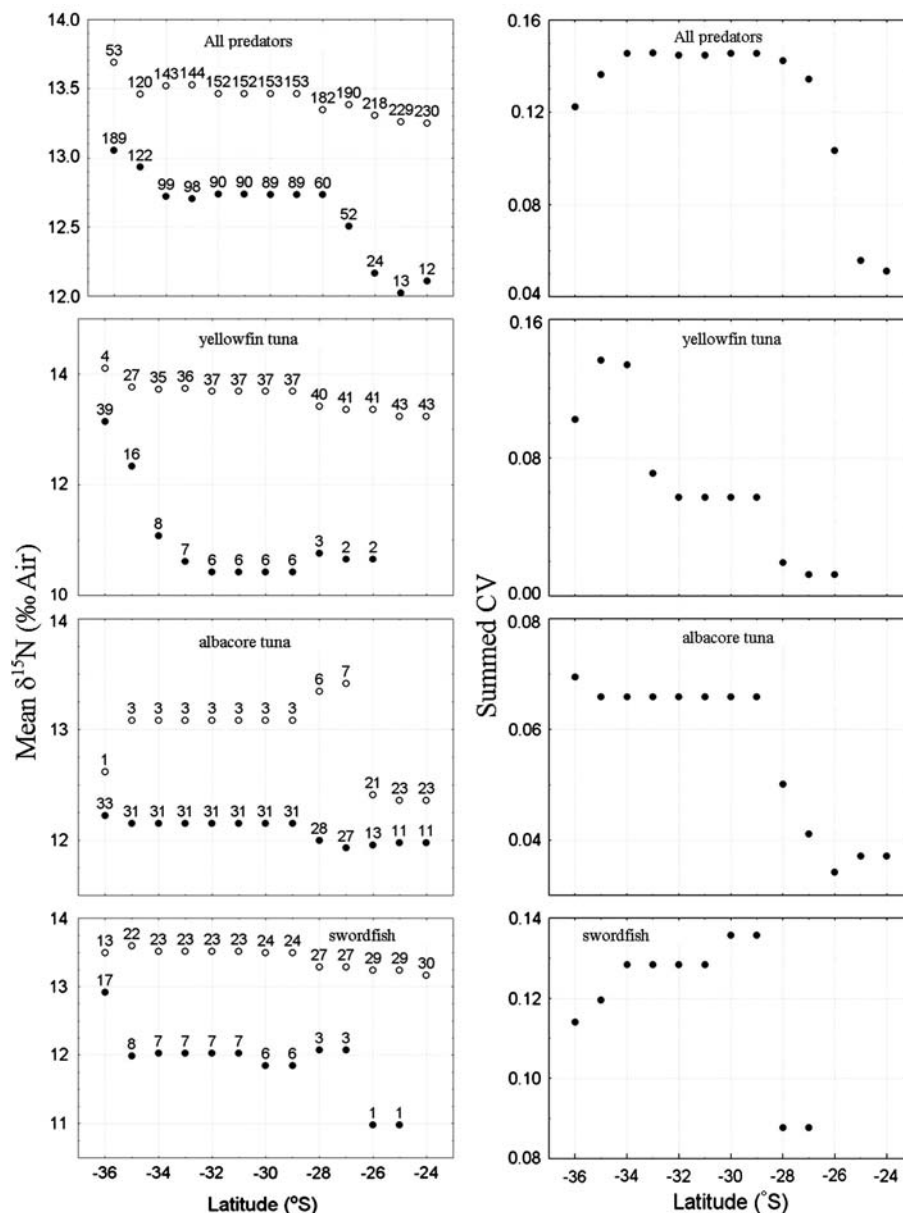
larger (adults) and smaller (juveniles) fish. The effect of fish size on $\delta^{15}\text{N}$ has been reported consistently (e.g., Jennings et al. 2001). Off eastern Australia, as swordfish length increased, diet changed from small fish such as myctophids with a low $\delta^{15}\text{N}$ signature to squid with a higher $\delta^{15}\text{N}$ (Young et al. 2006). The difference between the top predator and prey groupings, however, was very close to the difference of 3.4‰ suggested by Post (2002) and others, indicating that in broad terms the ‘top predator’ and ‘prey’ groups were the main trophic categories off eastern Australia. There is some evidence for this from recently completed multi-species diet comparisons in the region which showed significant dietary overlap between a range of fish top- and middle-order predators (Young et al. 2009).

Variability with size

Previous studies of pelagic food webs have shown that a large fraction of total variance in the natural abundance of stable isotopes in organisms, ranking from plankton to fishes, was due to individual organism size (Montoya et al.

1990; Fry and Quinones 1994). Also, studies of $\delta^{15}\text{N}$ enrichment across size classes of fishes demonstrated that trophic positions within a community were largely determined by the size of the organisms while inter-specific relationships between maximum body mass and $\delta^{15}\text{N}$ were of low relative importance (Jennings et al. 2001, 2002). The overall increase in trophic position was generally caused by the intra-specific accumulation of heavy isotopes with the growth in body mass (Rau et al. 1989; Lindsay et al. 1998; Jennings et al. 2002). Our study largely supports this perspective, with trophic position and $\delta^{15}\text{N}$ mainly increasing with the mean size of the fish, both within and between species (Fig. 4). However, there were exceptions, we think related to the specific behavioural and physiological differences between top predator fishes. For example, the $\delta^{15}\text{N}$ of albacore decreased with increasing size, apparently due to a shift in feeding from higher to lower trophic prey species. In a companion study we found that crab megalopa, which have a $\delta^{15}\text{N}$ of 7.9 (Davenport and Bax 2002), made up over half of the diet of albacore caught north of 28°S (Young et al. 2009). South of this divide fish and squid were the major prey species which

Fig. 6 Mean $\delta^{15}\text{N}$ for sample populations north (filled circle) and south (open circle) and the summed coefficient of variance at each degree of latitude in the study area. Numbers refer to number of valid samples in each group



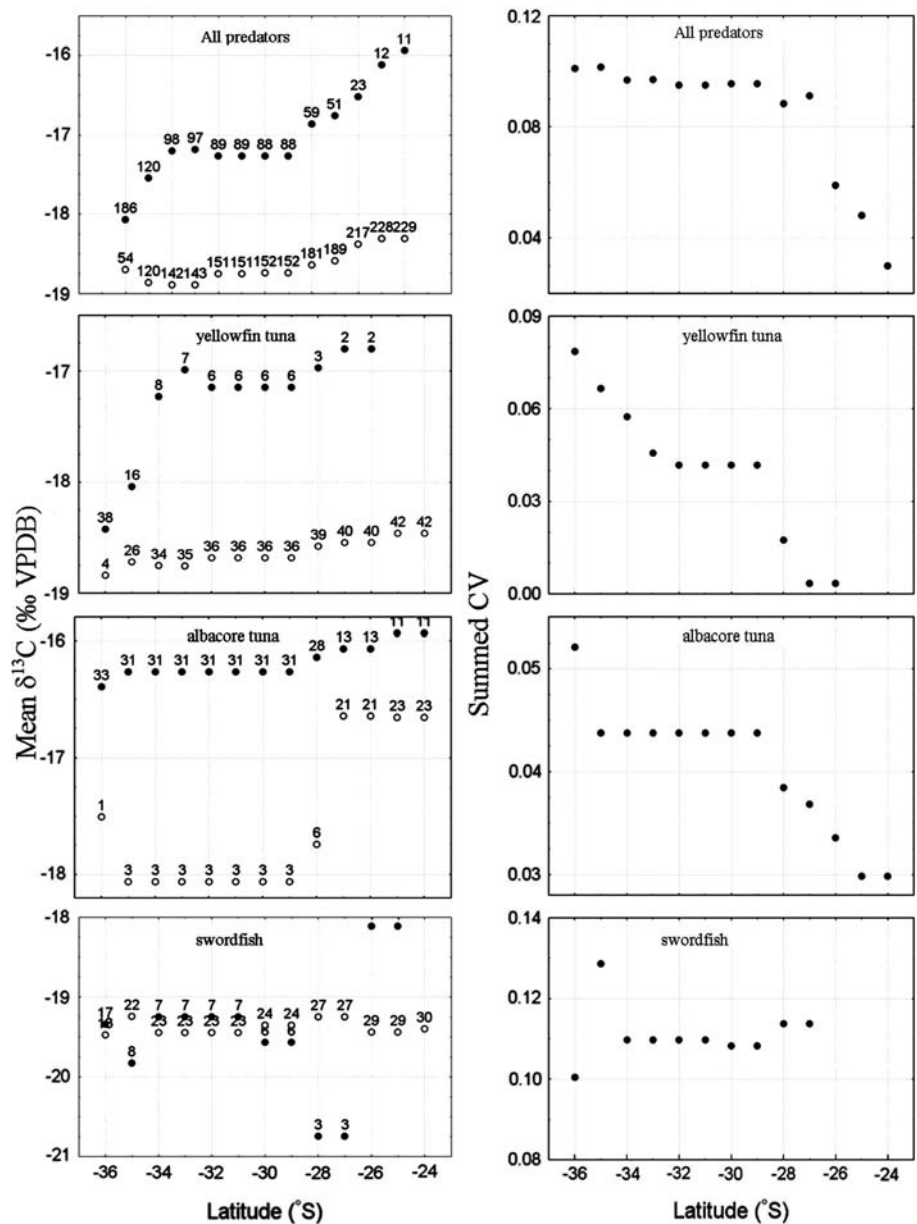
this and other studies in the area have shown to have higher $\delta^{15}\text{N}$ values (Davenport and Bax 2002; Young et al. 2006).

Evidence for bio-regionalization from SIA

$\delta^{13}\text{C}$ —we found a generally negative shift in $\delta^{13}\text{C}$ of muscle tissue with increasing latitude, likely due to water temperature which is known to affect the solubility of CO_2 and subsequently the $\delta^{13}\text{C}$ of plankton (Rau et al. 1989). In this study, there was a $\sim 9^\circ\text{C}$ difference between northern (25°C) and southern (16°C) waters. Using the equation from Rau et al. (1989), this could equate to a difference of ca. 2‰ in the $\delta^{13}\text{C}$ of phytoplankton irrespective of other factors. This is the same as the mean difference measured

in this study between the samples collected in the northern area (-17‰) and those caught in the southern area (-19‰). Analysis of the stable isotope data using moving means and summed coefficients of variance (Fig. 6) clearly showed that for all predators combined and individual target species, latitude is an important correlate of carbon isotopic signature. Changes were observed at 28 and 34°S . The former is the approximate position of the Tasman front which separates warm oligotrophic waters of the Coral Sea from colder Tasman Sea waters of sub Antarctic origin. The northern region is also the site of a chain of seamounts frequently targeted by ETBF. The more southerly position at $\sim 34^\circ\text{S}$ has a highly variable oceanography that includes warm-core eddies and intrusions of rich Tasman Sea waters

Fig. 7 Mean $\delta^{13}\text{C}$ for samples north (filled circle) and south (open circle) and the summed coefficient of variance at various latitudes. Numbers refer to number of valid samples in each group



of more southerly origin. Also, the eddies in this region are generally associated with the shelf break and act to produce upwelling along the shelf edge (Young et al. 2001). The resulting productivity in the area attracts aggregations of yellowfin tuna, and was also the site for many years of a fishery for juvenile southern bluefin tuna (Hynd 1974, Shingu 1978).

As there is a period of months for muscle tissue to register differences in diet (Graham et al. 2007), the difference in isotopic signature is evidence of extended residence time in particular regions. Frequent migrations between north and south would cause a “blurring” of the isotopic signature of samples collected in the two regions. The difference in $\delta^{13}\text{C}$ values for swordfish samples appear

to shift in the opposite direction to that expected, becoming more enriched in the southern area. However, the difference may be length-related as the fish sampled north of 28°S were dominated by two large individuals with high $\delta^{13}\text{C}$ values. A similar pattern was noted by Baird et al. (2008) for particulate organic matter who suggested this may have been the result of higher productivity in the Tasman Sea leading to draw-down of aqueous CO_2 and thus enriched values of $\delta^{13}\text{C}$.

$\delta^{15}\text{N}$ —individuals caught in the northern area were, on average, more depleted in their $\delta^{15}\text{N}$ value compared with those in the south, a result also found by Baird et al. (2008). They found $\delta^{15}\text{N}$ values for particulate organic matter ranging from ~6‰ north of the Tasman front to 10‰ in the

south. Of the key species of interest, this effect was most significant in yellowfin tuna. The nitrogen isotopic signature of a predator is set not only by trophic position, but also by the signature at the base of the food chain. Thus, the differences observed could be due to factors affecting either or both of these parameters. The primary factor influencing the nitrogen isotopic signature of phytoplankton is the concentration and source of nutrients being utilised and this is particularly important in oligotrophic waters, such as those to the north of the Tasman front. We were not able to obtain direct measured values for particulate nitrogen in the study area. However, Davenport and Bax (2002) reported $\delta^{15}\text{N}$ values for primary producers in south-eastern Australia (south of the Tasman front) of 6‰, consistent with oceanic NO_3^- , which resulted in tertiary consumers having $\delta^{15}\text{N}$ values of around 13‰, similar to those determined for the top predators caught in the southern region in this study. More recently, Baird et al. (2008) reported the same value from north of the Tasman front but with a much higher value (10‰) to the south.

The relatively depleted $\delta^{15}\text{N}$ values of predators we observed in the northern area could potentially be due to several reasons. First, predators could be feeding at a lower trophic position, which is possible given that myctophids were more prevalent in the diet of many of the species from this region (Young et al. 2009). Second, predator isotope values could be directly influenced by regional variations in the $\delta^{15}\text{N}$ of the primary producers on which the food web is based. Oligotrophic waters such as those north of the front largely rely on regenerated nutrients for primary production, which in turn can lead to a depleted $\delta^{15}\text{N}$ value. In addition, nitrogen fixation can also be an important process in nutrient poor waters, which will also cause a trend to more depleted $\delta^{15}\text{N}$ values (Mahaffey et al. 2005). At times, northern Australian waters are known to exhibit high rates of nitrogen fixation due to the common presence of *Trichodesmium* sp. (Revelante et al. 1982) and unicellular diazotrophs (Montoya et al. 2004). Thus, it would seem likely that the most probable cause of the slightly depleted $\delta^{15}\text{N}$ values in samples from the northern area can be directly attributed to variation in phytoplankton isotope values.

Future research

While good stomach content data will continue to be necessary, this study has shown that stable isotopes can add to our understanding of trophic interactions, and also provide valuable information on spatial patterns and residence times for top predators in the region. In future, multiple-tissue sampling may utilise differences in tissue metabolism to discern trophic dynamics with a minimum of sampling effort (Kurle and Worthy 2002) and over

different time scales. There is clearly a need in this study to identify the $\delta^{15}\text{N}$ signature at the base of area-specific food chains and while this is difficult utilising conventional filtering techniques, especially in oligotrophic waters, techniques such as compound-specific isotope analysis of compounds such as amino acids have the potential to provide this information from the target species themselves (McClelland and Montoya 2002).

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