

## Trophic size-structure of sailfish *Istiophorus platypterus* in eastern Taiwan estimated by stable isotope analysis

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(Received 5 March 2013, Accepted 26 October 2013)

To examine trophic dynamics over different size classes, an isotopic study of sailfish *Istiophorus platypterus* life-history stages was carried out. Samples were collected from eastern Taiwan and the South China Sea during April 2009 and February 2012. A total of 263 samples (111–245 cm, lower jaw fork length,  $L_{LJFL}$ ) were examined for changes in trophic structure in relation to  $L_{LJFL}$  by using stable isotope analysis of carbon ( $\delta^{13}C$ ) and nitrogen ( $\delta^{15}N$ ). The  $\delta^{15}N$  values for *I. platypterus* ranged from 7.51 to 14.19‰ (mean  $\pm$  s.d. =  $12.06 \pm 1.16$ ‰) and the  $\delta^{13}C$  values ranged from  $-22.04$  to  $-15.48$ ‰ (mean  $\pm$  s.d. =  $-17.62 \pm 1.10$ ‰). The  $\delta^{15}N$  values were positively dependent on  $L_{LJFL}$  ( $r^2 = 0.377$ ), whereas  $\delta^{13}C$  were negatively dependent on  $L_{LJFL}$  ( $r^2 = 0.063$ ). There were significantly different seasonal changes in nitrogen and carbon isotopic concentration, but no significant differences in concentrations between eastern Taiwan and the South China Sea were reported. The trophic level ( $T_L$ ) of each  $L_{LJFL}$  class was correlated, starting from 2.84  $T_L$  for size class I ( $L_{LJFL} < 140$  cm) and reaching 5.03  $T_L$  for size class VI ( $L_{LJFL} > 221$  cm). The mean  $\pm$  s.d.  $T_L$  was  $4.43 \pm 0.19$  for all samples. The results reveal that *I. platypterus* occupies a wide range of trophic levels and different size classes occupy different trophic positions in the pelagic ecosystem.

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Key words: apex predator; ecosystem structure; ontogenetic changes; pelagic food web.

### INTRODUCTION

It is estimated that commercial fisheries have removed >50 million t of tuna [albacore *Thunnus alalunga* (Bonnaterre 1788), Pacific bluefin tuna *Thunnus orientalis* (Temminck & Schlegel 1844), skipjack tuna *Katsuwonus pelamis* (Linnaeus 1758), yellowfin tuna *Thunnus albacores* (Bonnaterre 1788) and bigeye tuna *Thunnus obesus* (Lowe 1839)] from the Pacific Ocean since the mid-20th century (Sibert *et al.*, 2006), which has led to a debate on the effects of fisheries in altering marine ecosystems (Pauly *et al.*, 1998; Sibert *et al.*, 2006). Selective removal of large predators from food webs can impart significant changes to food web structures through trophic cascades (Carpenter *et al.*, 1985; Estes *et al.*, 1998; Pace *et al.*, 1999; Pauly *et al.*, 2001; Myers *et al.*, 2007). Marine food webs are complex, which makes them very

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difficult to understand and study. Recent concerns about the status of apex predators have caused researchers to take a closer look at their diets and migratory patterns in an effort to better understand trophic and ecosystem dynamics (Menard *et al.*, 2007; Revill *et al.*, 2009; Graham *et al.*, 2010).

Stable isotope analysis (SIA) can be used to estimate nutrient pathways and trophic relationships between organisms (Davenport & Bax, 2002; Bode *et al.*, 2004; Michener & Kaufman, 2007). Stomach content analysis provides a snapshot of the most recent foraging event whilst SIA of an organism's tissues can be used as an alternative and complementary tool to provide information on the time-integrated, assimilated diet (Harrigan *et al.*, 1989; Fry, 1998; Fantle *et al.*, 1999).

The isotopes of different elements move up trophic levels in a consistent manner, allowing researchers to naturally trace linkages in food webs. Changes in the ratios of stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) have been used to elucidate trophic relationships within marine food webs (Hobson *et al.*, 1997; Burns *et al.*, 1998; Lesage *et al.*, 2001; Revill *et al.*, 2009) and to investigate the relationship of contaminant uptakes with trophic position (Cabana & Rasmussen, 1994; Das *et al.*, 2000; Bearhop *et al.*, 2002; Nisbet *et al.*, 2002). Stable isotope ratios of a consumer are related to those of its prey (DeNiro & Epstein, 1978, 1981; Peterson & Fry, 1987; Peterson, 1999).  $\delta^{15}\text{N}$  measurements mainly serve as indicators of a consumer's trophic position (Hobson & Welch, 1992; Thompson *et al.*, 1995; Hobson *et al.*, 2002; Michener & Kaufman, 2007), whereas  $\delta^{13}\text{C}$  values are used to determine the sources of primary production, inshore *v.* offshore or pelagic *v.* benthic contribution to food intake (Hobson *et al.*, 1995; Smith *et al.*, 1996).

SIA provides a unique opportunity to better understand the role of pelagic fishes including sharks in pelagic ecosystems and may also provide insights into the origins and migratory behaviour of fishes. Reduction of these predator populations may impart significant effects on the upper trophic levels of the pelagic ecosystem (Myers & Worm, 2003) and lead to cascading effects on lower trophic levels.

The sailfish *Istiophorus platypterus* (Shaw 1792) is one of the several apex predators in pelagic food webs (Kitchell *et al.*, 2006) and is thought to adopt an opportunistic feeding strategy correlated with the abundance and distribution of their prey (Rosas-Alayola *et al.*, 2002). This epipelagic species is usually found above the thermocline, predominately distributed near coastlines and islands, segregates by size and undergoes spawning migrations in the Pacific Ocean (Nakamura, 1985). In eastern Taiwan, *I. platypterus* is seasonally abundant from April to October (peak abundance from May to July) and contributes substantially to the local economy where this species is targeted primarily by drift gillnets. They are also captured by set nets, harpoon fleets and as incidental by-catch in inshore longline fisheries (Chiang *et al.*, 2006).

*Istiophorus platypterus* off eastern Taiwan appear to be moderately exploited and have a relatively low risk of being overfished (Chiang *et al.*, 2009). The stock status of *I. platypterus* was listed as 'Least Concern' under International Union for the Conservation of Nature (IUCN) Red List criteria (Collette *et al.*, 2011). In order to monitor the long-term health of the ecosystem and stock status, there is an urgent need to establish fundamental ecological information to be used in ecosystem-based fishery management for this economically important species. The effects of fishing activities on the structure of the pelagic food web can be assessed by determining the trophic relationships of the top predators targeted by fisheries (Graham, 2008).

Information on trophic levels for different life-history stages for *I. platypterus* is lacking, and therefore no data are available to estimate the changes in trophic level through different size classes. To rectify this gap in knowledge, stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic analyses were conducted on muscle to investigate feeding patterns of different-sized *I. platypterus*. The main objectives of the study were to (1) calculate size-based trophic levels for *I. platypterus* and (2) to carry out the first isotopic background study of *I. platypterus* life stages in eastern Taiwan for ecosystem-based fishery management.

## MATERIALS AND METHODS

### DATA COLLECTION AND SAMPLING

*Istiophorus platypterus* samples were collected from eastern Taiwan and the South China Sea during April 2009 and February 2012 (Fig. 1). A total of 263 *I. platypterus* (141 males and 122 females) ranging from 111 to 245 cm lower jaw fork length ( $L_{\text{LJFL}}$ ) and from 4 to 64 kg in body mass (Table I) were examined for their carbon and nitrogen stable isotope compositions.

The  $L_{\text{LJFL}}$  is a reliable measure of *I. platypterus* body length that allows comparisons with tunas by reducing the bias due to the length of the bill. On the basis of the information on comparable feeding studies in *I. platypterus* and tuna (Arizmendi-Rodríguez *et al.*, 2006; Menard *et al.*, 2006), size classes for *I. platypterus* were segregated by 20 cm intervals of <140, 141–160, 161–180, 181–200, 201–220 and 221+ cm  $L_{\text{LJFL}}$  (Table I). The sex of each specimen was determined based on the appearance of the gonads (Chiang *et al.*, 2006). White muscle was collected from the posterior, epaxial region and stored frozen at  $-80^\circ\text{C}$  until processing. Dissected tissues were acidified (10% HCl) to remove residual carbonates, rinsed with distilled water and fully freeze-dried for *c.* 48 h.

### STABLE ISOTOPE ANALYSIS

After freeze-drying, samples were ground to a homogeneous powder and 1–2 mg of this powder was weighed in ultra-clean tin capsules for stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic analyses (Davenport & Bax, 2002). Analytical precision (s.d.,  $n = 5$ ) was 0.2‰ for both nitrogen and carbon, as estimated from standards analysed together with the samples. Samples were combusted in an elemental analyser (Flash EA-1100 NC, Thermo-Finnigan; www.thermoscientific.com) to produce  $\text{CO}_2$  and  $\text{N}_2$ , which flowed through a Gas Chromatography (GC) column for separation and into a mass spectrometer (Thermo Finnigan Delta<sup>plus</sup> Advantage) for separately determining isotopic compositions. Isotopic values were expressed in parts per thousand (‰) as deviations from standards (Peedee belemnite limestone for  $\delta^{13}\text{C}$  and nitrogen in air for  $\delta^{15}\text{N}$ ):  $\delta X = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 10^3$ , where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding  $^{13}\text{C}:^{12}\text{C}$  or  $^{15}\text{N}:^{14}\text{N}$  ratio (Peterson & Fry, 1987).

The trophic level ( $T_L$ ) of *I. platypterus* sampled was estimated using the equation:  $T_L = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) \text{TEF}^{-1} + 2$ .  $\delta^{15}\text{N}$  values provide an indication of the trophic level of a consumer (Post, 2002). Primary producers are trophic level 1, primary consumers are trophic level 2 and so on.

Trophic enrichment factor (TEF) represents a best estimate of isotopic enrichment between *I. platypterus* and its diet. An TEF of 2.4‰ was adopted: the mean TEF for marine fishes was based on the Vanderklift & Ponsard (2003) review of literature that reported consumer diet  $^{15}\text{N}$  enrichment (Caut *et al.*, 2009).

Spatial heterogeneity or seasonal cycles in nitrogen dynamics can drive significant and rapid fluctuations in  $\delta^{15}\text{N}$  values (*e.g.* zooplankton or copepods) at the base of the food web (Rolff, 2000; Syvaranta *et al.*, 2006). To determine trophic position accurately, the food web must be standardized relative to a baseline indicator. Long-lived primary consumers, such

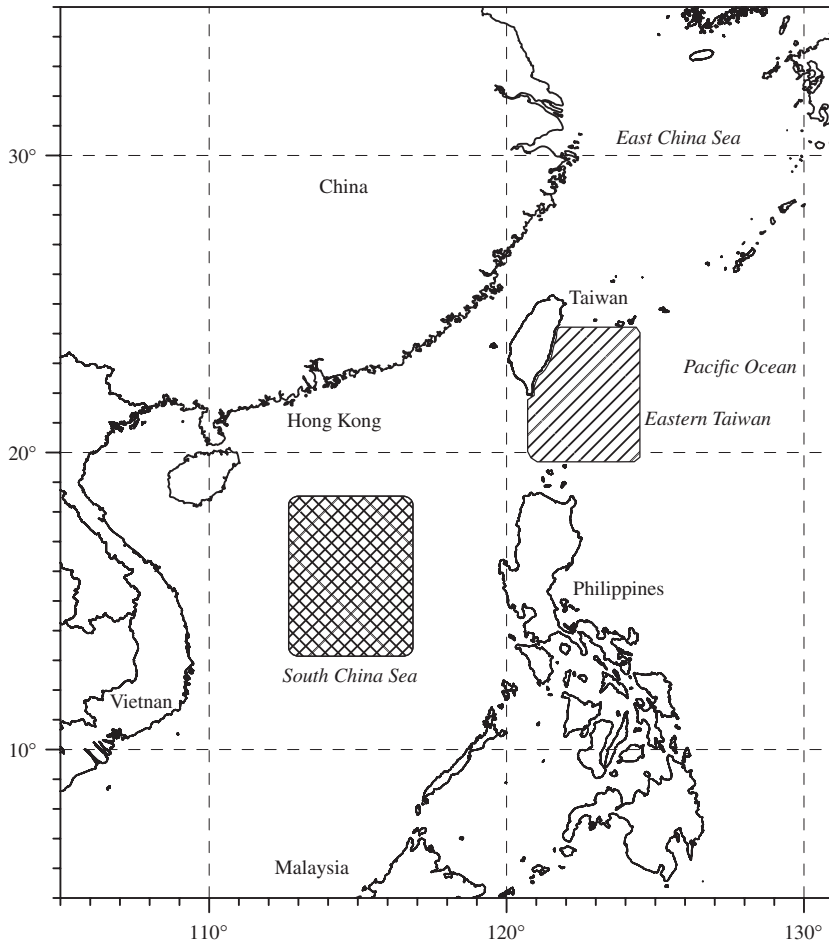


FIG. 1. Map of study area showing locations of *Istiophorus platypterus* samples taken for stable isotope analysis from eastern Taiwan (▨,  $n = 30$ ) and from the South China Sea (▩,  $n = 233$ ) during April 2009 and February 2012.

as snails and mussels, in aquatic food webs can provide an appropriate baseline to quantify the trophic position of secondary consumers (Post, 2002). Therefore, the mean  $\pm$  s.d. values for the herbivorous marine snail *Chlorostoma argyrostoma argyrostoma* of  $6.24 \pm 0.29\text{‰}$  ( $n = 5$ ) from the east coast of Taiwan were chosen as a trophic baseline (this study), which corresponded to the mean isotopic values of primary consumers. Stable isotopes of carbon and nitrogen were calculated for each size class and then used to reveal differences in trophic levels based on the predator size.

## DATA ANALYSIS

Linear regression was used to fit the relationships between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with  $L_{\text{LJFL}}$  for all samples ( $n = 263$ ). The effects of  $L_{\text{LJFL}}$ , year, season and differences between sampling areas were investigated by performing multivariate analysis of variance (MANOVA) on the carbon and nitrogen stable isotope data. One-way ANOVA was used to test the difference among size class in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .  $P < 0.05$  was considered to indicate statistical significance. For

TABLE I. Isotopic values and estimated trophic level ( $T_L$ ) by size classes of *Istiophorus platypterus* (estimated age at lower jaw fork length,  $L_{LJFL}$ , from Chiang *et al.*, 2004)

Size class	$L_{LJFL}$ (cm)	Age (years)	$n$	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			$T_L$ Mean $\pm$ s.d.
				Mean $\pm$ s.d.	Maximum	Minimum	Mean $\pm$ s.d.	Maximum	Minimum	
I	< 140	<2	7	-16.90 $\pm$ 0.44	-16.01	-18.32	8.11 $\pm$ 0.45	8.84	7.51	2.84 $\pm$ 0.07
II	141–160	3–4	10	-16.78 $\pm$ 0.48	-15.48	-18.80	10.68 $\pm$ 0.83	12.84	9.41	3.98 $\pm$ 0.13
III	161–180	5–6	69	-17.30 $\pm$ 0.98	-15.95	-20.69	11.88 $\pm$ 0.88	13.67	8.85	4.32 $\pm$ 0.14
IV	181–200	7–8	130	-17.79 $\pm$ 1.18	-15.96	-21.66	12.27 $\pm$ 0.90	14.19	9.93	4.51 $\pm$ 0.14
V	201–220	8–10	40	-17.85 $\pm$ 0.93	-16.03	-19.76	12.52 $\pm$ 0.89	13.98	10.66	4.60 $\pm$ 0.14
VI	> 221	>11	7	-18.18 $\pm$ 1.46	-17.06	-22.04	13.51 $\pm$ 0.67	14.15	12.56	5.03 $\pm$ 0.11
	Total		263	-17.62 $\pm$ 1.10	-15.48	-22.04	12.06 $\pm$ 1.16	14.19	7.51	4.43 $\pm$ 0.19

$n$  = sample size.

seasonal analysis, the monthly samples were divided into spring (February to April), summer (May to July), autumn (August to October) and winter (November to January) seasons. Tukey's honestly significant difference (HSD) test was used for posterior multiple comparisons of means when significant main effects were detected. All statistical analyses were performed using the programme 'R' ([www.r-project.org](http://www.r-project.org)).

## RESULTS

The  $\delta^{13}\text{C}$  values for *I. platypterus* ranged from  $-22.04$  to  $-15.48\text{‰}$  (mean  $\pm$  s.d. =  $-17.62 \pm 1.10\text{‰}$ ) and the  $\delta^{15}\text{N}$  values ranged from  $7.51$  to  $14.19\text{‰}$  (mean  $\pm$  s.d. =  $12.06 \pm 1.16\text{‰}$ ) (Table I). There were no significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between males ( $\delta^{13}\text{C}$  mean  $\pm$  s.d. =  $-17.47 \pm 1.03\text{‰}$ ;  $\delta^{15}\text{N}$  mean  $\pm$  s.d. =  $12.03 \pm 1.20\text{‰}$ ) and females ( $\delta^{13}\text{C}$  mean  $\pm$  s.d. =  $-17.86 \pm 1.20\text{‰}$ ;  $\delta^{15}\text{N}$  mean  $\pm$  s.d. =  $12.10 \pm 1.11\text{‰}$ ) and samples were pooled for further analyses.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values plotted with  $L_{\text{LJFL}}$  are shown in Fig. 2. Carbon isotopic concentration was negatively dependent on  $L_{\text{LJFL}}$  [Fig. 2(a)] but the low  $r^2$  indicates that this relationship is very weak although significant ( $r^2 = 0.063$ ,  $P < 0.001$ ). Nitrogen isotopic concentration was positively dependent on  $L_{\text{LJFL}}$  ( $r^2 = 0.377$ ,  $P < 0.001$ ) [Fig. 2(b)].

Results of seasonal analysis indicated that there were significant differences in  $\delta^{13}\text{C}$  (MANOVA,  $F_{3,256} = 12.560$ ,  $P < 0.001$ ) and  $\delta^{15}\text{N}$  isotopic concentrations ( $F_{3,256} = 5.592$ ,  $P < 0.001$ ). The results examining geographic location and isotopic composition showed that there were no significant differences in  $\delta^{13}\text{C}$  (MANOVA,  $F_{1,256} = 1.078$ ,  $P > 0.05$ ) and  $\delta^{15}\text{N}$  ( $F_{1,256} = 0.022$ ,  $P > 0.05$ ) between the two sampling areas. Seasonal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  s.d.) for *I. platypterus* from 2009 to 2011 is plotted in Fig. 3. The  $\delta^{13}\text{C}$  values in autumn and winter were higher than in spring and summer [Fig. 3(a)] and the  $\delta^{15}\text{N}$  values show decreasing trends from spring to summer [Fig. 3(b)].

In this study, *I. platypterus* belong to six size classes (Table I) ranging from juveniles (not older than 2 years, class I) to at least 11 years old (class VI) (Chiang *et al.*, 2004). Values of  $\delta^{13}\text{C}$  showed significant differences among size classes (ANOVA,  $F_{5,257} = 4.68$ ,  $P < 0.001$ ). In terms of nitrogen isotopic concentrations, there were also significant differences between size classes (ANOVA,  $F_{5,257} = 40.48$ ,  $P < 0.001$ ). Mean carbon isotopic concentration for each size class increased from I to II, but decreased from III to VI [Fig. 4(a)]. They exhibited size-specific changes in nitrogen isotopic concentration and mean  $\delta^{15}\text{N}$  values increased significantly from size classes I to VI [Fig. 4(b)]. Smaller *I. platypterus* displayed nitrogen-depleted values (mean  $\pm$  s.d. =  $8.11 \pm 0.45\text{‰}$ ), whereas values in larger *I. platypterus* were more enriched ( $13.51 \pm 0.67\text{‰}$ ).

The outcome of Tukey's HSD test for  $\delta^{13}\text{C}$  values by size class was  $\text{I} = \text{II} = \text{III} > \text{IV} = \text{V} = \text{VI}$ , and for  $\delta^{15}\text{N}$  values was  $\text{I} < \text{II} < \text{III} < \text{IV} = \text{V} = \text{VI}$ . As determined from Tukey's HSD tests, size classes III and IV showed significant differences in regard to carbon. Size classes I and II, II and III and III and IV showed significant differences in regard to nitrogen. Furthermore, Tukey's HSD tests indicated positive shifts in  $\delta^{15}\text{N}$  between  $L_{\text{LJFL}}$  of  $<140$  and  $141\text{--}160$  cm,  $141\text{--}160$  and  $161\text{--}180$  cm and also between  $L_{\text{LJFL}}$  of  $161\text{--}180$  and  $181\text{--}200$  cm. Negative shifts in  $\delta^{13}\text{C}$   $L_{\text{LJFL}}$ , however, were observed at  $161\text{--}180$  and  $181\text{--}200$  cm.

The trophic structure of *I. platypterus* by size class is shown in Fig. 5 and Table I. Trophic levels are correlated with  $L_{\text{LJFL}}$  (Fig. 6) ( $r^2 = 0.901$ ,  $P < 0.001$ ). The  $T_{\text{L}}$  of *I.*

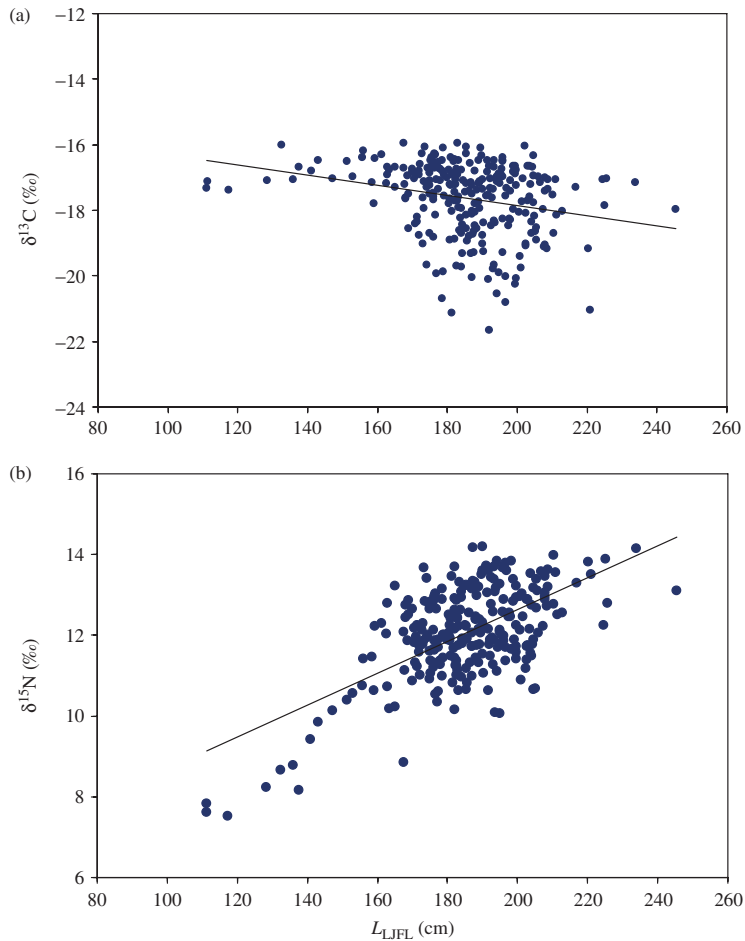


FIG. 2. Length of lower jaw to fork length ( $L_{LJFL}$ ) of *Istiophorus platypterus* and (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values. The curves were fitted by (a)  $y = -0.0153x - 14.777$  and (b)  $y = 0.0393x + 4.768$ .

*platypterus* by size class, starting from mean  $\pm$  s.d. of  $2.84 \pm 0.07$  (class I), represents a probable baseline level for this species at an age of  $<2$  years (disregarding larval stages), and reaching a  $T_L$  of  $5.03 \pm 0.11$  at ages of  $>11$  years (class VI), which probably represents the top level. The mean  $\pm$  s.d.  $T_L$  of *I. platypterus* for all samples was  $4.43 \pm 0.19$ .

## DISCUSSION

### BODY LENGTH EFFECT ON $\delta^{15}\text{N}$

The present results provide evidence for a clear relationship between body length and  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of *I. platypterus*. The  $L_{LJFL}$  significantly influences  $\delta^{15}\text{N}$  values [Fig. 2(b)] more strongly than  $\delta^{13}\text{C}$  values [Fig. 2(a)], which indicates a shift in

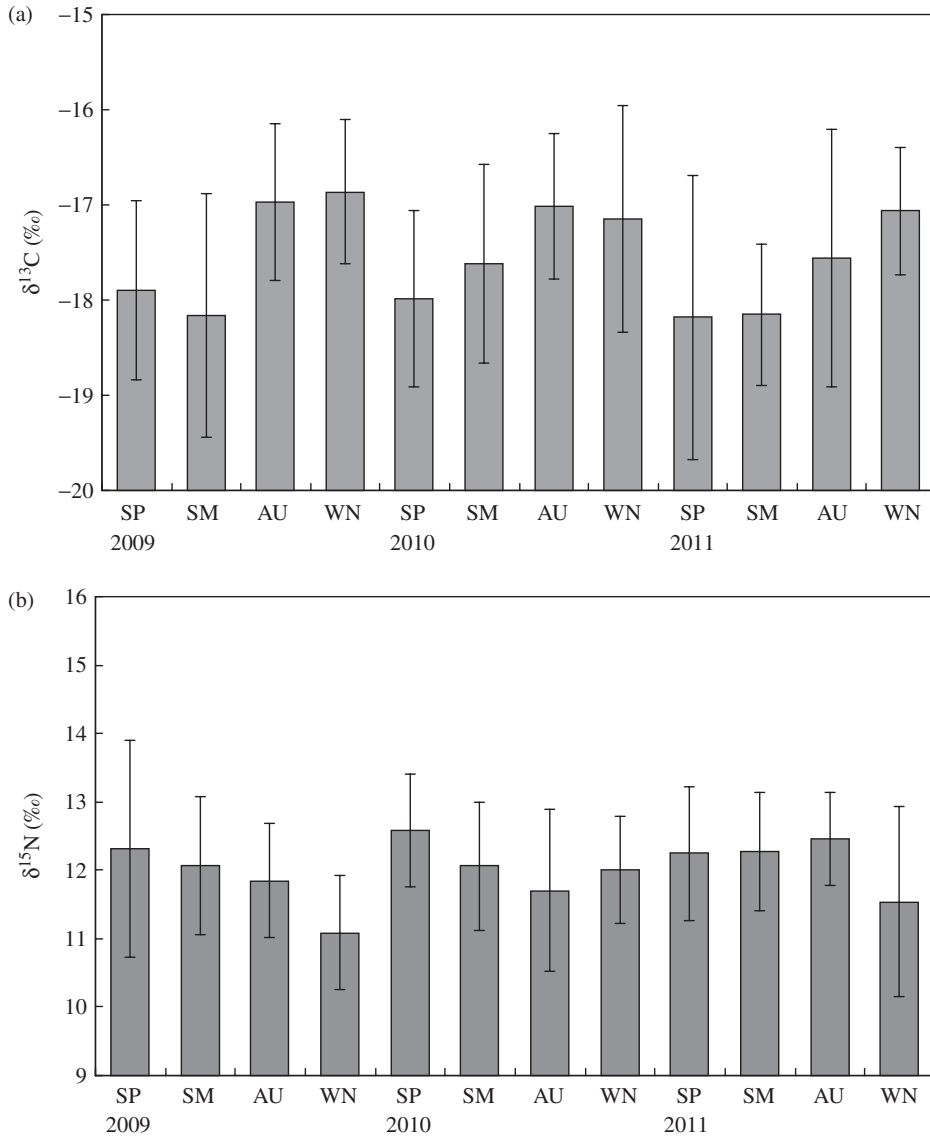


FIG. 3. Seasonal variation in (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values (mean  $\pm$  s.d.) for *Istiophorus platypterus* from 2009 to 2011 (SP, spring; SM, summer; AU, autumn; WN, winter).

diet and trophic position through the different size classes [Figs 4(b) and 5]. The diet of many species changes throughout their life cycle, particularly as their increasing size facilitates adaptation to other prey (Graham *et al.*, 2007). Stable carbon and nitrogen isotope ratios have been used to trace the dietary changes of a species according to its life cycle and the variability of the ecosystem (Loch & Hily, 2005).

The present results indicate that a distinct positive shift in  $\delta^{15}\text{N}$  occurs in the white muscle of *I. platypterus* between  $L_{\text{LJFL}}$  of <140 and 141–160 cm, between 141–160



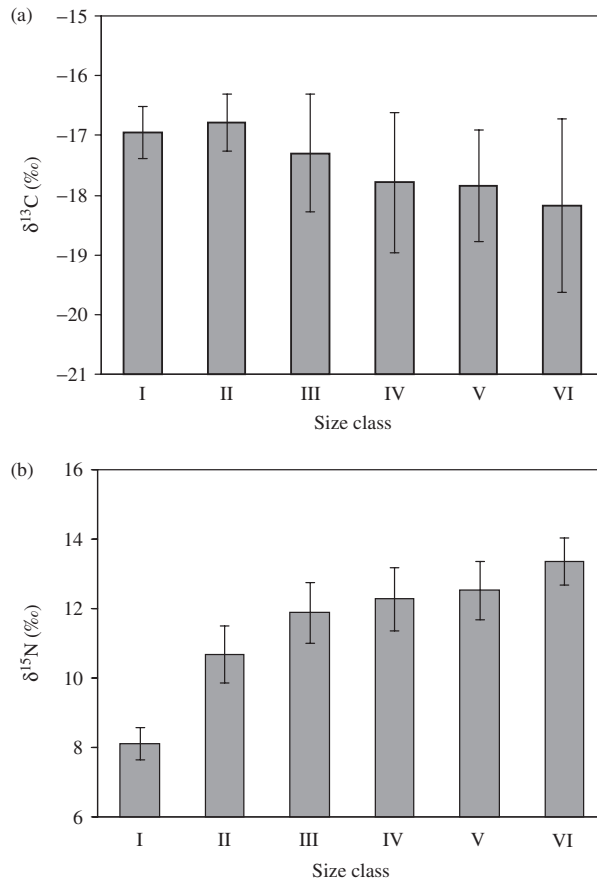


FIG. 4. Isotopic composition of (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values (mean  $\pm$  S.D.) for each size class of *Istiophorus platypterus* analysed in the study (see Table I for size class limits). The outcome of Tukey's HSD test for mean  $\delta^{13}\text{C}$  values was I = II = III > IV = V = VI and for mean  $\delta^{15}\text{N}$  values was I < II < III < IV = V = VI.

and 161–180 cm and also between 161–180 and 181–200 cm. Larger fishes, within and between species, generally have a higher  $\delta^{15}\text{N}$  signal than smaller fishes (Revill *et al.*, 2009). Larger size provides more opportunity for feeding on larger prey organisms and selecting from a greater variety of prey species (Davenport & Bax, 2002). Fishes with a high  $\delta^{15}\text{N}$  signal generally have a high proportion of fishes in their diet or they eat other species with a high  $\delta^{15}\text{N}$  signal (Bulman *et al.*, 2001). This pattern indicates a considerable accumulation of  $^{15}\text{N}$ , which can be explained either by (1) physiological changes or (2) a result of the changing allocation of isotopes or from changes in tissue turnover rates during different size classes (Hesslein *et al.*, 1993; Overman & Parrish, 2001). The marked retention of the heavier isotope ( $^{15}\text{N}$ ) in *I. platypterus*, scaled to size, was probably due to shifts in diet and habitat (Cocheret de la Morinière *et al.*, 2003; Graham *et al.*, 2007).

The size effect in resource allocation has been well documented in fishes (Pinnegar & Polunin, 2000; Renones *et al.*, 2002; Bode *et al.*, 2004), and it is thought to be

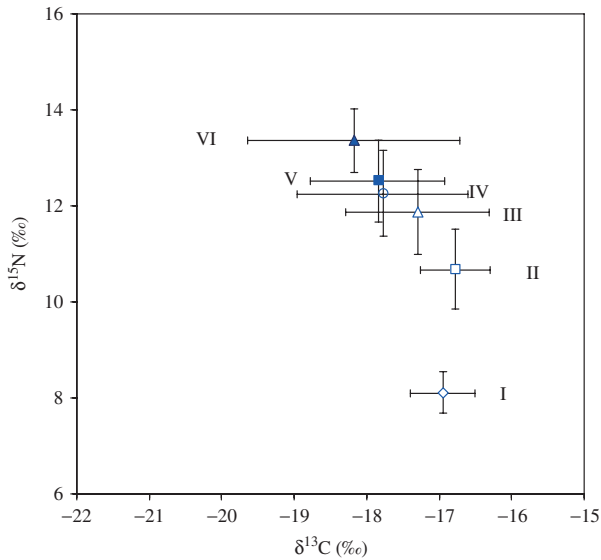


FIG. 5. Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  s.d.) from each size class of *Istiophorus platypterus* ( $\blacktriangle$ ,  $>221$  cm;  $\bullet$ , 201–220 cm;  $\circ$ , 181–200 cm;  $\triangle$ , 161–180 cm;  $\square$ , 141–160 cm;  $\diamond$ ,  $<140$  cm).

associated with changes in habitat (Werner & Gilliam, 1984). Menard *et al.* (2007) found low variability in the  $\delta^{15}\text{N}$  values of yellowfin tuna *Thunnus albacares* (Bonaterre 1788) at fork lengths ( $L_F$ ) of 39–164 cm in the western Indian Ocean. Sara & Sara (2007), however, found increasingly higher  $\delta^{15}\text{N}$  values for older *T. thynnus* up to 13 years old and weighing 225 kg. *Thunnus thynnus* live longer and reach larger maximum sizes than *T. albacares*. On the basis of  $\delta^{15}\text{N}$  values and stomach contents, Graham *et al.* (2007) described trophic changes through ontogeny in 40 cm *T. albacares* in nearshore waters around Oahu, Hawaii. Except for very small individuals (Maldeniya, 1996), however, marked trophic ontogeny is not characteristic of *T. albacares* (Olson & Boggs, 1986; Buckley & Miller, 1994; Menard *et al.*, 2006).

In eastern Taiwan, stomach contents sampled in this study revealed that *I. platypterus* were also generalist predators feeding mainly on epipelagic fishes [especially frigate mackerel *Auxis rochei rochei* (Risso 1810)]. Arizmendi-Rodríguez *et al.* (2006) noted that *I. platypterus* in Mexico fed on epipelagic prey (*Auxis* spp. and juveniles of finescale triggerfish *Balistes polylepis* Steindachner 1876) as well as on neritic and benthic prey. This study found the feeding composition of *I. platypterus* diet to be similar to tunas and swordfish *Xiphias gladius* L. 1758 diets which have been characterized as opportunistic feeders (Menard *et al.*, 2007). *Istiophorus platypterus* spend most of their time, day and night, in the upper uniform mixed layer above 50 m (Chiang *et al.*, 2011), but *X. gladius* spend most of their time deeper than 400 m during the day and must periodically return to the mixed layer to warm muscles and to repay oxygen debts. *Xiphias gladius* overlap with many species at night when they stay in the mixed layer around 100 m, presumably feeding on many of the same prey species (Abascal *et al.*, 2010). *Xiphias gladius* make deeper daytime diving excursions than *I. platypterus* to pursue mesopelagic prey. Similar to tuna and *X. gladius*, diets of *I. platypterus* change as they grow

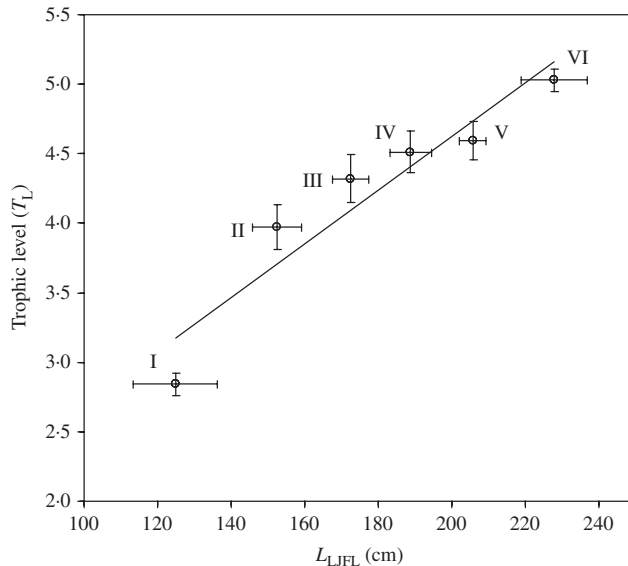


FIG. 6. Relationship between length of lower jaw to fork length ( $L_{LJFL}$ ) and trophic level ( $T_L$ ) using  $\delta^{15}\text{N}$  concentrations of the herbivorous marine snail *Chlorostoma argyrostoma argyrostoma* (mean  $\pm$  S.D. =  $6.24 \pm 0.29\text{‰}$ ) as a trophic baseline. Also shown overlaid are the midpoints of the six size classes of *Istiophorus platypterus* in the study. The curve was fitted by  $y = 0.0193 (\pm 0.003)x + 0.762 (\pm 0.583)$  ( $r^2 = 0.901$ ).

which enables them to exploit a great variety of resources. Foraging ecology theory confirms that the trophic levels of an organism, because of diet, can vary according to ontogeny, resulting in a shift of position within the food web (Werner & Gilliam, 1984).

#### BODY LENGTH EFFECT ON $\delta^{13}\text{C}$

Given that  $\delta^{15}\text{N}$  increases at higher trophic levels than  $\delta^{13}\text{C}$  (DeNiro & Epstein, 1981), the lower differences for mean  $\delta^{13}\text{C}$  between size classes of *I. platypterus* [Fig. 4(a)] were not unexpected. The range of  $\delta^{13}\text{C}$  values for *I. platypterus* was highly variable [Figs 2(a) and 4(a)], which suggests that this variable might be useful to delineate feeding locations or to track fish movements.

Values of  $\delta^{13}\text{C}$  indicate the original source of primary producers and the isotopes can also help to determine shifts in diet over temporal and spatial scales. These shifts may correlate with seasonal changes reflecting phytoplankton abundance (Michener & Kaufman, 2007). The relatively depleted  $\delta^{13}\text{C}$  values of large *I. platypterus* observed in this study could be for two reasons: (1) larger *I. platypterus* may feed on prey items with lower  $\delta^{13}\text{C}$  values or (2) larger *I. platypterus* could migrate from lower  $\delta^{13}\text{C}$  value habitats. As there is an extended residency period of perhaps months for muscle to register differences in diet (Graham *et al.*, 2007), the difference in isotopic signature is evidence of extended residence time in particular regions.

*Istiophorus platypterus* <160 cm  $L_{LJFL}$  displayed a narrow range in  $\delta^{13}\text{C}$  values [Figs 2(a) and 4(a)], and from this it is inferred that smaller *I. platypterus* may

not move as long distances as larger *I. platypterus*. Those >160 cm  $L_{LJFL}$  showed wide variation in  $\delta^{13}C$  values, which presumably indicates movement into different habitats. Hobson (1999) illustrated this approach by using the maxim 'you are what you swim in' that complements the well-known dogma of stable isotope ecology 'you are what you eat' (DeNiro & Epstein, 1976). There is a wide body of evidence which suggests that stable isotope ratios of animal tissues have the potential of characterizing isotopically distinct regions inhabited by migrating fishes (Menard *et al.*, 2007; Graham *et al.*, 2010).

## GEOGRAPHIC AND SEASONAL EFFECTS

There were no significant differences in  $\delta^{13}C$  and  $\delta^{15}N$  concentrations between eastern Taiwan and the South China Sea. Hwang *et al.* (2007) studied indicator species of copepod that characterize the Kuroshio Current and the northern South China Sea and revealed that water masses from the northern South China Sea were the same as those of the Kuroshio Current. From the characteristics of water masses and stable isotopic signatures of *I. platypterus*, samples from the South China Sea and eastern Taiwan could be inferred as coming from the same stock. In other words, using these data, the null hypothesis of different stock compositions could be refuted.

The present results suggest that muscle  $\delta^{13}C$  values of adult *I. platypterus* (>161 cm  $L_{LJFL}$ ) in pelagic ecosystems of eastern Taiwan might be useful to document seasonal changes, to delineate feeding locations and to track fish movement. The  $\delta^{13}C$  values of primary producers can vary predictably among ocean basins. High-latitude pelagic ecosystems typically have much lower  $\delta^{13}C$  values than pelagic ecosystems at lower latitudes (Graham *et al.*, 2010). On the basis of the electronic tag data, adult *I. platypterus* with lower  $\delta^{13}C$  values probably migrate from the north Pacific Ocean near Japan, whereas *I. platypterus* with higher  $\delta^{13}C$  values may migrate from the central Pacific Ocean near the equator along the Kuroshio Current to eastern Taiwan (Chiang *et al.*, 2011).

There were significant differences in seasonal variation of stable isotopes over time, which are interpreted here as reflecting *I. platypterus* feeding on different prey species. This behaviour was inferred from the analysis of *I. platypterus* stomach contents (Evans & Wares, 1972; Arizmendi-Rodríguez *et al.*, 2006). It is suggested that future studies combine SIA with stomach contents and pop-up satellite archival tags to provide the requisite data to interpret the feeding ecology and movement patterns of this important species.

## TROPIC LEVELS OF *I. PLATYPTERUS*

*Istiophorus platypterus* displayed a wide range of trophic levels (Fig. 6 and Table I), shifting from  $T_L$  of  $2.84 \pm 0.07$  for smaller fish (<140 cm,  $L_{LJFL}$ , age <2 years) to  $T_L$  of  $5.03 \pm 0.11$  for larger adults (>221 cm,  $L_{LJFL}$ , age >11 years). The mean  $\pm$  s.d.  $T_L$  of *I. platypterus* estimated in this study was  $4.43 \pm 0.19$  from nitrogen isotopes, and was similar to  $4.5 \pm 0.8$  estimated from diet composition data (Froese & Pauly, 2013). The overall increase in trophic position by size is generally considered to be the result of intraspecific accumulation of heavy isotopes with somatic growth in body mass (Lindsay *et al.*, 1998; Jennings *et al.*, 2002), *e.g.* trophic position and  $\delta^{15}N$  increase with mean size.

TABLE II. Comparison of isotopic values for  $\delta^{15}\text{N}$  (‰) and  $\delta^{13}\text{C}$  (‰) for *Istiophorus platypterus* and other top predators in pelagic ecosystems

Species	<i>n</i>	Size range	$\delta^{15}\text{N}$ (‰)			$\delta^{13}\text{C}$ (‰)			Study area	Reference
			Mean	Minimum	Maximum	Mean	Minimum	Maximum		
<i>Xiphias gladius</i>	30	22.5–210 (cm)	13.2	9.1	15.7	-19.4	-23.9	-17.1	Eastern Australia	Revill <i>et al.</i> (2009)
<i>Kajikia audax</i>	8	119–215 (cm)	13.2	9.2	15.2	-18.1	-23.4	-14.3	Eastern Australia	Revill <i>et al.</i> (2009)
<i>Thunnus maccoyii</i>	17	116–169 (cm)	14.3	13.0	15.7	-20.2	-23.2	-17.5	Eastern Australia	Revill <i>et al.</i> (2009)
<i>Thunnus thynnus</i>	35	0.7–225 (kg)	9.7	7.2	13.1	-18.1	-18.9	-17.2	Mediterranean Sea	Sara & Sara (2007)
<i>Thunnus albacares</i>	245	40–160 ( $L_F$ , cm)	-	10.2	15.2	-	-17.4	-15.2	Western Indian Ocean	Menard <i>et al.</i> (2007)
<i>Xiphias gladius</i>	136	68–225 ( $L_{LJFL}$ , cm)	-	11.8	16.2	-	-17.4	-15.0	Western Indian Ocean	Menard <i>et al.</i> (2007)
<i>Istiophorus platypterus</i>	263	111–245 ( $L_{LJFL}$ , cm)	12.1	7.5	14.2	-17.7	-22.0	-15.5	Eastern Taiwan	This study

*n*, sample size;  $L_F$ , fork length;  $L_{LJFL}$ , lower jaw fork length.

The isotope values for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for *I. platypterus* and other top predators in the pelagic ecosystem were compared from different areas (Table II). Most top predators (tuna and billfishes) in the pelagic ecosystem have a wide variation of  $\delta^{15}\text{N}$  values. In this study, values for *I. platypterus* were calculated at 7.5–14.2‰ and are comparable to other apex predators such as *X. gladius* (9.1–15.7‰) and striped marlin *Kajikia audax* (Philippi 1887) (9.2–15.2‰) in eastern Australia (Revill *et al.*, 2009); *T. thynnus* (7.2–13.1‰) in the Mediterranean Sea (Sara & Sara, 2007) and *T. albacares* (10.2–15.2‰) and *X. gladius* (11.8–16.2‰) in the western Indian Ocean (Menard *et al.*, 2007).

Nitrogen stable isotope data have proven useful in elucidating size- and age-related changes in trophic level of many fish species (Lindsay *et al.*, 1998; Vander Zanden *et al.*, 2000; Overman & Parrish, 2001; Jennings *et al.*, 2002). Studies of  $\delta^{15}\text{N}$  enrichment across different size classes of fishes demonstrated that trophic positions within a community were largely determined by the size of organisms (Jennings *et al.*, 2001, 2002). Thus, the wide differences in nitrogen isotope values observed between the smallest and largest size classes probably represent differences in the trophic status of the prey consumed.

In this study, the wide variation of  $\delta^{13}\text{C}$  values for *I. platypterus* (–22.0 to 15.5‰) was comparable with the ranges for *X. gladius* (–23.9 to 17.1‰) and *K. audax* (–23.4 to 14.3‰) in eastern Australia (Revill *et al.*, 2009). These values, however, were higher than in *T. thynnus* (–18.9 to 17.2‰) in the Mediterranean Sea (Sara & Sara, 2007), and *T. albacares* (–17.4 to 15.2‰) and *X. gladius* (–17.4 to 15.0‰) in the western Indian Ocean (Menard *et al.*, 2007). Large differences in  $\delta^{13}\text{C}$  values within and between species probably indicate that they utilize different food sources or that their food webs are based on different primary producers.

The present results indicate that SIA could be used to estimate trophic levels for *I. platypterus*. Long-term monitoring of trophic dynamics will be necessary to understand ecosystem changes to a top predator's population dynamics in relation to human exploitation and climate change (Logan *et al.*, 2011). The results of this study also provide a basis for ecosystem structure variables and further study using isotopes can possibly determine habitat and movement patterns over temporal and spatial scales. This study was mainly concerned with sampling *I. platypterus* exploited by the commercial fishery and it is suggested that more effort should be made to obtain additional information on the ecology of juvenile *I. platypterus* (<110 cm,  $L_{\text{LJFL}}$ ) which are not usually caught by the traditional fishing gears (*e.g.* harpoon, longline and gillnet). Lastly, further investigations need to focus on other components of the pelagic ecosystem, including tuna, billfish, sharks and their prey items, which form the important base of the pelagic food web.

We thank two anonymous reviewers for providing valuable comments on previous drafts of this manuscript. This study was in part supported financially by the National Science Council of Taiwan through the grant NSC 99-2611-M-056-002 to W.-C.C. Thanks to M. K. Musyl for the language editing of the manuscript.

## References

- Abascal, F. J., Mejuto, J., Quintans, M. & Ramos-Cartelle, A. (2010). Horizontal and vertical movements of swordfish in the southeast Pacific. *ICES Journal of Marine Science* **67**, 466–474.

- Arizmendi-Rodríguez, D. I., Abitia-Cárdenas, L. A., Galván-Magaña, F. & Trejo-Escamilla, I. (2006). Food habits of sailfish *Istiophorus platypterus* off Mazatlan, Sinaloa, Mexico. *Bulletin of Marine Science* **79**, 777–791.
- Bearhop, S., Waldron, S., Votier, S. C. & Furness, R. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable in avian blood and feathers. *Physiological and Biochemical Zoology* **75**, 451–458.
- Bode, A., Alvarez-Ossorio, M. T., Carrera, P. & Lorenzo, J. (2004). Reconstruction of trophic pathways between plankton and the North Iberian sardine *Sardina pilchardus* using stable isotopes. *Scientia Marina* **68**, 165–178.
- Buckley, T. W. & Miller, B. S. (1994). Feeding habits of yellowfin tuna associated with fish aggregation devices in American Samoa. *Bulletin of Marine Science* **55**, 445–459.
- Bulman, C., Althaus, F., He, X., Bax, N. J. & Williams, A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**, 537–548.
- Burns, J. M., Trumble, S. J., Castellini, M. A. & Testa, J. W. (1998). The diet of Weddel Seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotopes analysis. *Polar Biology* **19**, 272–282.
- Cabana, G. & Rasmussen, J. B. (1994). Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* **372**, 255–257.
- Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. (1985). Cascading trophic interaction and lake productivity. *BioScience* **35**, 634–639.
- Caut, S., Angulo, E. & Courchamp, F. (2009). Variation in discrimination factors ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology* **46**, 443–453.
- Chiang, W. C., Sun, C. L., Yeh, S. Z. & Su, W. C. (2004). Age and growth of the sailfish *Istiophorus platypterus* in the eastern Taiwan waters. *Fishery Bulletin* **102**, 251–263.
- Chiang, W. C., Sun, C. L., Yeh, S. Z., Su, W. C. & Liu, D. C. (2006). Spawning frequency and batch fecundity of the sailfish *Istiophorus platypterus* in waters off eastern Taiwan. *Zoological Studies* **45**, 483–491.
- Chiang, W. C., Sun, C. L., Wang, S. P., Yeh, S. Z., Chen, Y., Su, W. C., Liu, D. C. & Chen, W. Y. (2009). Analysis of sex-specific spawning biomass per recruit of the sailfish, *Istiophorus platypterus*, in the waters off eastern Taiwan. *Fishery Bulletin* **107**, 265–277.
- Chiang, W. C., Musyl, M. K., Sun, C. L., Chen, S. Y., Chen, W. Y., Liu, D. C., Su, W. C., Yeh, S. Z., Fu, S. C. & Huang, T. L. (2011). Vertical and horizontal movements of sailfish *Istiophorus platypterus* near Taiwan determined using pop-up satellite tags. *Journal of Experimental Marine Biology and Ecology* **397**, 129–135.
- Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., Hemminga, M. A., Huiskes, A. H. L. & der Velde, G. (2003). Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Marine Ecology Progress Series* **246**, 279–289.
- Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., Elfes, C., Fox, W., Graves, J., Harrison, L. R., McManus, R., Minte-Vera, C. V., Nelson, R., Restrepo, V., Schratwieser, J., Sun, C. L., Amorim, A., Brick Peres, M., Canales, C., Cardenas, G., Chang, S. K., Chiang, W. C., de Oliveira Leite, N. Jr., Harwell, H., Lessa, R., Fredou, F. L., Oxenford, H. A., Serra, R., Shao, K. T., Sumaila, R., Wang, S. P., Watson, R. & Yáñez, E. (2011). High value and long life—double jeopardy for tunas and billfishes. *Science* **333**, 291–292.
- Das, K., Lepoint, G., Loizeau, V., Debacker, V., Dauby, P. & Bouqueneau, J. M. (2000). Tuna and dolphin associations in the North-east Atlantic: evidence of different ecological niches from stable isotope and heavy metal measurements. *Marine Pollution Bulletin* **40**, 102–109.
- Davenport, S. & Bax, N. J. (2002). A trophic study of a marine ecosystem off south eastern Australia using stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 514–530.
- DeNiro, M. J. & Epstein, S. (1976). You are what you eat (plus a few per mil): the carbon isotope cycle in food chains. *Geological Society of America Abstracts with Programs* **8**, 834–835.

- DeNiro, M. J. & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochemica et Cosmochimica Acta* **42**, 495–506.
- DeNiro, M. J. & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochemica et Cosmochimica Acta* **45**, 341–351.
- Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476.
- Evans, D. H. & Wares, P. G. (1972). Foods habits of striped marlin and sailfish off Mexico and southern California. *U.S. Fish and Wildlife Service Research Report* **76**, 1–10.
- Fantle, M. S., Dittel, A. I., Schwakm, S. M., Epifanio, C. E. & Fogel, M. L. (1999). A food web analysis of the juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. *Oecologia* **120**, 416–426.
- Fry, B. (1998). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* **33**, 1182–1190.
- Graham, B. S. (2008). Trophic dynamics and movements of tuna in the tropical Pacific Ocean inferred from stable isotope analyses. PhD Thesis, University of Hawaii, Manoa, HI, U.S.A.
- Graham, B. S., Grubbs, D., Holland, K. & Popp, B. N. (2007). A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology* **150**, 647–658.
- Graham, B. S., Koch, P. L., Newsome, S. D., McMahon, K. W. & Aurioules, D. (2010). Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In *Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping* (West, J. B., Bowen, G., Dawson, T. & Tu, K., eds), pp. 299–318. New York, NY: Springer-Verlag.
- Harrigan, P., Zieman, J. & Macko, S. (1989). The base of nutrimental support for the gray snapper *Lutjanus griseus*: an evaluation base on a combined stomach content and stable isotope analysis. *Bulletin of Marine Science* **44**, 65–77.
- Hesslein, R. H., Hallard, K. A. & Ramal, P. (1993). Replacement of sulphur, carbon, and nitrogen of growing broad whitefish *Coregonus nasus* in response to a change in diet traced by  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$ . *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2071–2076.
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**, 314–326.
- Hobson, K. A. & Welch, H. E. (1992). Determination of trophic relationships within a high Arctic marine food web using stable-isotope analysis. *Marine Ecology Progress Series* **84**, 9–18.
- Hobson, K. A., Ambrose, W. G. Jr. & Renaud, P. E. (1995). Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Marine Ecology Progress Series* **128**, 1–10.
- Hobson, K. A., Hughes, K. D. & Ewins, P. J. (1997). Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. *Auk* **114**, 467–478.
- Hobson, K. A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J. M. & Fortier, M. (2002). A stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep Sea Research II* **49**, 5131–5150.
- Hwang, J. S., Dahms, H. U., Tseng, L. C. & Chen, Q. C. (2007). Intrusions of the Kuroshio Current in the northern South China Sea affect copepod assemblages of the Luzon Strait. *Journal of Experimental Marine Biology and Ecology* **352**, 12–27.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Boon, T. (2001). Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology* **70**, 934–944.
- Jennings, S., Warr, K. J. & 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. *Marine Ecology Progress Series* **240**, 11–20.
- Kitchell, J. F., Martell, S. J. D., Walters, C. J., Jensen, O. P., Kaplan, I. C., Watters, J. R., Essington, T. E. & Boggs, C. H. (2006). Billfishes in an ecosystem context. *Bulletin of Marine Science* **79**, 669–682.



- Lesage, V., Hammil, M. O. & Kovacs, K. M. (2001). Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. *Marine Ecology Progress Series* **210**, 203–221.
- Lindsay, D. J., Minagawa, M., Mitani, I. & Kawaguchi, K. (1998). Trophic shift in the Japanese anchovy *Engraulis japonicus* in its early life history stages as detected by stable isotope ratios in Sagami Bay, Central Japan. *Fisheries Science* **64**, 403–410.
- Loch, F. L. & Hily, C. (2005). Stable carbon and nitrogen isotope analysis of *Nephrops norvegicus*/*Merluccius merluccius* fishing grounds in the Bay of Biscay (Northeast Atlantic). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 123–132.
- Logan, J. M., Rodríguez-Marín, E., Goni, N., Barreiro, S., Arrizabalaga, H., Golet, W. & Lutcavage, M. (2011). Diet of young Atlantic bluefin tuna *Thunnus thynnus* in eastern and western Atlantic foraging grounds. *Marine Biology* **158**, 73–85.
- Maldeniya, R. (1996). Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environmental Biology of Fishes* **47**, 101–107.
- Menard, F., Labrune, C., Shin, Y. J., Asine, A. S. & Bard, F. X. (2006). Opportunistic predation in tuna: a size-based approach. *Marine Ecology Progress Series* **323**, 223–231.
- Menard, F., Lorrain, A., Potier, M. & Marsac, F. (2007). Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. *Marine Biology* **153**, 141–152.
- Michener, R. H. & Kaufman, L. (2007). Chapter 9: stable isotope ratios as tracers in marine food webs: an update. In *Stable Isotopes in Ecology and Environmental Science* (Lajtha, K. & Michener, R. H., eds), pp. 238–282. Boston, MA: Blackwell Scientific.
- Myers, R. A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283.
- Myers, R. A., Baum, J. K., Shepard, T. D., Powers, S. P. & Peterson, C. H. (2007). Cascading effects of the loss of apex predator sharks from a coastal ocean. *Science* **315**, 1846–1850.
- Nakamura, I. (1985). FAO Species Catalogue. Vol. 5. *Billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date*. FAO Fisheries Synopsis **125**(5).
- Nisbet, I. C. T., Montoya, J. P., Burger, J. & Hatch, J. J. (2002). Use of stable isotopes to investigate individual differences in diets and mercury exposures among common terns *Sterna hirundo* in breeding and wintering grounds. *Marine Ecology Progress Series* **242**, 267–274.
- Olson, R. J. & Boggs, C. H. (1986). Apex predation by yellowfin tuna *Thunnus albacares*: independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1760–1775.
- Overman, N. C. & Parrish, D. L. (2001). Stable isotope composition of walleye:  $^{15}\text{N}$  accumulation with age and area-specific differences in  $^{13}\text{C}$ . *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1253–1260.
- Pace, M. L., Cole, J. J., Carpenter, S. R. & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**, 483–488.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing down marine food webs. *Science* **279**, 860–863.
- Pauly, D., Palomares, M. L., Froese, R., Sa-a, P., Vakily, M., Preikshot, D. & Wallace, S. (2001). Fishing down marine Canadian aquatic food webs. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 51–62.
- Peterson, B. J. (1999). Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. *Acta Oecologica* **20**, 479–487.
- Peterson, B. & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**, 293–320.
- Pinnegar, J. K. & Polunin, N. V. C. (2000). Contributions of stable isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia* **122**, 399–409.
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718.

- Renones, O., Polunin, N. V. C. & Goni, R. (2002). Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. *Journal of Fish Biology* **61**, 122–137.
- Revell, A. T., Young, J. W. & Lansdell, M. (2009). Stable isotopic evidence for trophic groupings and bio-regionalization of predators and their prey in oceanic waters off eastern Australia. *Marine Biology* **156**, 1241–1253.
- Rolff, C. (2000). Seasonal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of size-fractionated plankton at a coastal station in the northern Baltic proper. *Marine Ecology Progress Series* **203**, 47–65.
- Rosas-Alayola, J., Hernández-Herrera, A., Galvan-Magaña, F., Abitia-Cárdenasa, L. A. & Muhlia-Melob, A. F. (2002). Diet composition of sailfish *Istiophorus platypterus* from the southern Gulf of California, Mexico. *Fisheries Research* **57**, 185–195.
- Sara, G. & Sara, R. (2007). Feeding habits and trophic levels of bluefin tuna *Thunnus thynnus* of different size classes in the Mediterranean Sea. *Journal of Applied Ichthyology* **23**, 122–127.
- Sibert, J., Hampton, J., Kleiber, P. & Maunder, M. (2006). Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* **314**, 1773–1776.
- Smith, R. J., Hobson, K. E., Koopman, H. N. & Lavigne, D. M. (1996). Distinguishing between populations of fresh- and salt-water harbour seals *Phoca vitulina* using stable-isotope ratios and fatty acid profiles. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 272–279.
- Syvaranta, J., Hamalainen, H. & Jones, R. I. (2006). Within-lake variability in carbon and nitrogen stable isotope signatures. *Freshwater Biology* **51**, 1090–1102.
- Thompson, D. R., Furness, R. W. & Lewis, S. A. (1995). Diets and long-term changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Northern Fulmars *Fulmarus glacialis* from two northeast Atlantic colonies. *Marine Ecology Progress Series* **125**, 3–11.
- Vander Zanden, M. J., Shuter, B. J., Lester, N. P. & Rasmussen, J. B. (2000). Within- and among population variation in the trophic position of the aquatic top predator, lake trout. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 725–731.
- Vanderklift, M. A. & Ponsard, S. (2003). Sources of variation in consumer-diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia* **136**, 169–182.
- Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**, 393–425.

### Electronic Reference

- Froese, R. & Pauly, D. (2013). *FishBase*, Version (10/2013). Available at [www.fishbase.org](http://www.fishbase.org) (accessed October 2013).