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Abstract

The Yellowfin Tuna *Thunnus albacares* is one of the major fish species caught around subsurface fish aggregation devices (FADs) in the waters southwest of Taiwan. However, how it interacts with other organisms around FADs is poorly known. In this study, the diet and feeding habits of juvenile Yellowfin Tuna were estimated from the analysis of stomach contents from 1,477 specimens with FLs ranging from 24 to 108 cm and stable isotope analysis (202 specimens) collected around FADs in the waters southwest of Taiwan. The analysis of stomach contents indicated that juvenile Yellowfin Tuna with FL < 50 cm mainly feed on larval purpleback flying squid *Sthenoteuthis oualaniensis*, larval shrimps, and zooplanktonic organisms such as amphipods. Yellowfin Tuna with FL of ~50 cm switch their diet to teleost fishes such as Japanese Barracudina *Lestrolepis japonica*, Skinnycheek Lanternfish *Benthosema pterotum*, and fishes in the families Exocoetidae and Scombridae. Stable isotope analysis indicated that the δ^{15}N values ranged between 6.2‰ and 12.6‰, and the estimated trophic position varied from 3.18 ± 0.24 for tuna with FL < 30 cm, while it reached 4.59 ± 0.50 for those with FL > 50 cm and 4.75 ± 0.06 for those with FL > 90 cm. Based on the distinct diet shift of the juvenile Yellowfin Tuna, demonstrated by both stomach contents and stable isotope analyses, this study concluded that the tuna shift their diet at approximately 50 cm FL.

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The Yellowfin Tuna *Thunnus albacares* is distributed worldwide in tropical and subtropical waters (Collette and Nauen 1983) and is a common target species of commercial fisheries (Buckley et al. 1989). This Yellowfin Tuna in the western Pacific Ocean grow fast (von Bertalanffy $K = 0.392$ years^{-1}) and reach an asymptotic length of 175 cm FL and live for about 7.7 years (Su et al. 2003); at 50% maturity Wang (2005) measured sizes at 107.8 cm and 112.5 cm FL for females and males, respectively. The catch of Yellowfin Tuna has increased as a result of the use of fish aggregating devices (FADs) in subtropical waters, which attract the Yellowfin Tuna to linger around FADs.

Because juvenile Yellowfin Tuna found around subsurface FADs are a major target species of longline and trolling fisheries in the waters southwest of Taiwan, large amounts of fish are caught by these fisheries. In recent years, the impact of fishing on the Yellowfin Tuna stock was a cause of concern for the local government and environmental groups. Consequently, the government of Taiwan prohibited FAD deployment after 2006.

To understand the interaction between Yellowfin Tuna and other organisms, several attempts have been made to observe their feeding habits, including prey composition (Dragovich 1970; Dragovich and Potthoff 1972), feeding behavior (Bertrand et al. 2002; Potier et al. 2004), and feeding strategies (Rohit et al. 2010). In addition, several studies have documented the feeding habits of Yellowfin Tuna around FADs in different waters, including those around American Samoa (Buckley and Miller 1994) and of the Atlantic Ocean near the equator (Ménard et al. 2000b). Buckley and Miller (1994) indicated that food consumption in Yellowfin Tuna associated with FADs comprised a larger proportion of their body weight than it did in fish that were not FAD associated. However, all of the aforementioned studies focused on adult fish. As juvenile tuna are generally more prevalent around natural or artificial FADs (Ménard et al. 2000a), it is crucial to understand the predator–prey relationship between juvenile tuna and other organisms. Unfortunately, only a few studies have focused on the diet of juvenile Yellowfin Tuna (Brock 1985; Maldeniya 1996; Graham et al. 2007).

Analyzing stomach contents is the most common method of identifying prey items to assess interactions between predators and prey (MacDonald et al. 1982). However, because the metabolic rate of Yellowfin Tuna is fast (Olson and Boggs 1986), some of their quickly digested food is often missed using this approach (MacDonald et al. 1982). Stable isotope analysis can enhance the understanding of a fish's feeding habits as well as the food sources and trophic levels for a particular species (Peterson et al. 1985; Peterson and Fry 1987).

Stable isotope methods have been used in several studies that investigated the trophic interactions (Fry 1988; Hobson and Welch 1992), temporal and spatial variations in food web dynamics (Deegan and Garritt 1997; ÓReilly et al. 2002), migration (Fry et al. 2003), feeding and habitats (Harrigan et

al. 1989), and ontogenetic shifts (Renones et al. 2002) of aquatic organisms. Stable isotope analysis can provide further information to that obtained from the analyses of stomach contents (Pauly et al. 1998; Pinnegar et al. 2003) and can be used to determine diet or niche shifts (Grey 2001; Post 2003; Hammerschlag-Peyer et al. 2011) or to acquire accurate data regarding feeding habits (Harvey et al. 2002). Stable isotope analyses are based on measurements of the carbon and nitrogen isotope compositions of an organism's tissues, which contain information about the food or nutrient sources of the organisms consumed. During digestion and absorption, isotopic fractionation of $\delta^{15}N$ and $\delta^{13}C$ relative to prey items occurs at each trophic level (Minagawa and Wada 1984). For example, when trophic-related fractionation causes a mean value change of 3.4‰ (DeNiro and Epstein 1981) or 2.96‰ (Vanderklift and Ponsard 2003) on $\delta^{15}N$ and $-1.1‰$ (DeNiro and Epstein 1978) or $0.5 \pm 0.13‰$ (mean $\pm$ SE) (McCutchan et al. 2003) on $\delta^{13}C$, the trophic level of the predator increases by one level. Furthermore, metabolic activity affects the tissue turnover rate, which in turn affects the stable isotope values in different tissues (Fry and Arnold 1982). More metabolically active tissue will reflect more rapid changes in food habits than would less metabolically active tissues (Hobson and Clark 1992). In an organism, spatial and background information can be derived from various tissues. The muscle below the dorsal fin, which exhibits a smaller variance in $\delta^{15}N$ and $\delta^{13}C$ values in stable isotope analysis, has been widely used to evaluate food web structures (Pinnegar and Polunin 1999; Deudero et al. 2004).

Although studies have investigated the diet shifts of juvenile Yellowfin Tuna in Hawaiian waters (Graham et al. 2007) and food webs in the eastern Pacific Ocean (Olson et al. 2010) by using stable isotope analysis, no such study has been conducted on Yellowfin Tuna in Taiwanese waters. Hence, the objectives of this study were to investigate the feeding ecology and examine a possible ontogenetic shift in the diet and trophic level of juvenile Yellowfin Tuna around FADs in the waters southwest of Taiwan using stomach contents analysis and stable isotope analysis. The intent is that the results derived from this study can be used in ecosystem-based fishery management of this species in the future.

METHODS

Data collection.—Yellowfin Tuna were collected during the day near FADs in the waters southwest of Taiwan during January 2010–December 2011 using a 10-m trolling vessel (Figure 1). The specimens were stored on ice immediately after harvest and transported to the laboratory for analysis.

Stomach contents analysis.—Fork length (to 0.1 cm) and body weight (BW; to 0.01 kg) measurements were taken of all specimens. The stomach of each specimen was removed and the contents collected; prey species were identified to the lowest taxonomic level. Then, the prey species were counted and
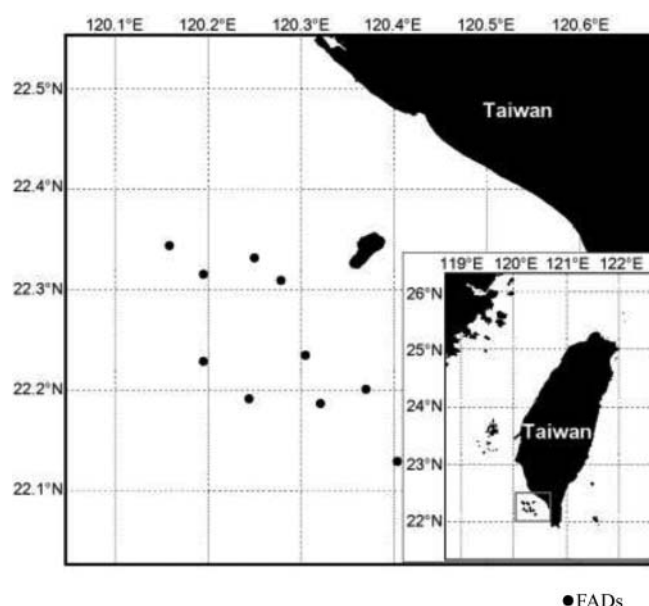
FIGURE 1. Sampling locations for Yellowfin Tuna around the subsurface FADs in southwestern waters of Taiwan.

weighed to within 0.01 g according to a previously described method (Hyslop 1980). The number of empty stomachs (<0.01 g prey/kg BW) was also counted. The feeding activity for size-classes was evaluated by the trend of the repletion index, which was expressed as grams of stomach contents per kilogram BW (Graham et al. 2007). These indices were calculated for each size-class of tuna and were used to discern differences in foraging success based on predator size. The Shapiro–Wilk test indicated that the repletion indices were not normally distributed; therefore, the Kruskal–Wallis test (Zar 2010) was used to examine the median of repletion indices among size-classes.

The importance of various prey species to the diet of the Yellowfin Tuna was assessed by calculating the following dietary indices:

$$\%N_i = \frac{N_i}{\sum_k N} \quad \text{and} \quad \%W_i = \frac{W_i}{\sum_k W},$$

where $\%N_i$ and $\%W_i$ are the percent abundance and percent weight of the ith prey species, respectively, k is the total number of species, N_i is number of individuals of the ith species, and W_i is the total weight of the ith species. These indices have been used extensively to analyze stomach contents data (Hyslop 1980). In addition, the mean percent abundance (%MN) and the mean percent weight (%MW) of the prey species were calculated following a previously described method (Graham et al. 2007).

To examine the feeding overlap in diet among different size-classes of Yellowfin Tuna, we applied the method

described by Graham et al. (2007) to divide the specimen sizes into five classes (classes I through V according to FL; i.e., I: <30 cm, II: 30–50 cm, III: 50–70 cm, IV: 70–90 cm, and V: 90–110 cm), and Morisita's original index (Horn 1966) was used to estimate the overlap by using the following equation:

$$C_{mh} = \frac{2\sum_{i=1}^{S} p_{A,i} \times p_{B,i}}{\sum_{i=1}^{S} p_{A,i}^2 + \sum_{i=1}^{S} p_{B,i}^2},$$

where C_{mh} is the Morisita–Horn index of overlap between Yellowfin Tuna size-classes A and B. The values $P_{A,i}$ and $P_{B,i}$ represent the contribution of the ith prey species to A and B in terms of the species dietary indices (i.e., %N, %W, %MN, and %MW), and S represents the total number of identified prey species in the feeding regime of the predator. A value for $C_{mh} \geq 0.6$ indicates a significant feeding overlap in diet for the fish between the two size-classes (Zaret and Rand 1971).

Stable isotope analysis.—The liver and white muscle tissues under the second dorsal fin of each specimen of the subsample randomly chosen from each size-class of Yellowfin Tuna as well as tissues of the prey fishes, the muscle of cephalopods, and the entire bodies of other prey were collected for stable isotope analysis. Theses tissues and prey were cleaned twice with distilled water immediately after dissection and stored at −40°C. They were then thawed and dried at 60°C for 27 h and homogenized to a fine powder. Aliquots of the homogenized samples (0.7–1.2 mg) were weighed using a Sartorius R200D digital analytical balance and packed into 8 × 5-mm tin cups to analyze the δ^{15}N and δ^{13}C values. The accuracy of the analysis was 0.2% for nitrogen and carbon, as estimated from standards analyzeds with the samples. The samples were combusted in an elemental analyzer (Flash EA-1112; Thermo Fisher Scientific, Bremen, Germany) to produce CO_2 and N_2, and the gas was analyzed using an isotope-ratio mass spectrometer (IMRS Delta V Advantage, Thermo Fisher Scientific) to determine its isotopic composition. The isotopic values were expressed as the difference in parts per thousand (‰) from the respective standards (Pee Dee belemnite limestone for δ^{13}C and N_2 in air for δ^{15}N):

$$\delta X = \left[\left(R_{sample}/R_{standard} \right) \right] \times 10^3,$$

where X represents ^{15}N or ^{13}C, and R represents the ratio of ^{15}N:^{14}N or ^{13}C:^{12}C of the sample or the standard material (Peterson and Fry 1987). The mean and SD of reference materials are as measured for USGS40 and L-glutamic acid. Nitrogen and carbon isotopic composition analyzed by the USGS40 was used to correct the basic sample. The USGS40 δ^{15}N = −4.52 ± 0.1‰ (air N_2) and δ^{13}C = −26.39 ± 0.1‰ (Vienna Pee Dee Belemnite).

An ANOVA was used to examine the homogeneity of the mean values of δ^{13}C among size-classes. Then, Tukey's

multiple comparison method was used for pairwise comparison. As the Shapiro–Wilk test indicated that $\delta^{15}N$ values were not normally distributed, the Kruskal–Wallis test (Zar 2010) was used to examine the mean values of $\delta^{15}N$ among size-classes and Dunn's test was used for posterior comparison.

Because lipid content in fish tissue varies depending on species, it is usually estimated using an organic solvent extraction of lipids following Folch et al. (1957). Lipid extraction may result in the loss of some nonlipid compounds and thus alter $\delta^{15}N$ (Sotiropoulos et al. 2004; Sweeting et al. 2006; Logan et al. 2008; Elsdon et al. 2010; Varela et al. 2011). A mathematical lipid correction of $\delta^{13}C$ values provides a simple alternative to chemical lipid extraction. The normalization model of McConnaughey and McRoy (1979) is based on empirical equations describing the relationship between the two equations. The proportion of the lipid content (L) of the sample is calculated from the sample's C:N ratio:

$$L = 93/(0.246 \text{C:N} - 0.775) - 1.$$

Lipid-normalized $\delta^{13}C'$ is calculated from L and the measured $\delta^{13}C$ of the sample:

$$\delta^{13}C' = \delta^{13}C + D(I + 3.9) / (1 + 287L),$$

where D is the isotopic difference between lipids and proteins (D is assumed to be 6‰; McConnaughey and McRoy 1979) and I is a constant ($= -0.207$).

Food web studies generally explore the trophic structure and feeding relationships of aquatic organisms (Aberle and Malzahn 2007). Therefore, the following equation was used to estimate the trophic position (TP) of Yellowfin Tuna (Vander Zanden and Rasmussen 1999; Olson et al. 2010):

$$TP_{YFi} = \left(\frac{\delta^{15}N_{YFi} - \delta^{15}N_{baseline}}{TEF} \right) + 2,$$

where TP_{YFi} is the estimated trophic position for Yellowfin Tuna at the site of sample i, $\delta^{15}N_{YFi}$ is the $\delta^{15}N$ value of Yellowfin Tuna at the site of sample i, $\delta^{15}N_{baseline}$ is the corrected

isotope signature of the Yellowfin Tuna, and TEF is the trophic enrichment factor. The $\delta^{15}N$ value of consumers cannot be considered as an absolute measure of trophic position. Therefore, it is necessary to correct fish $\delta^{15}N$ signatures to account for variation in the $\delta^{15}N$ values of primary consumers (e.g., zooplankton, chironomids, and amphipods: Vander Zanden and Rasmussen 1999). The relationship can then be used to calculate baseline conditions ($\delta^{15}N_{baseline}$) that are used to correct $\delta^{15}N$ values for the secondary consumers (Vander Zanden and Rasmussen 1999). We used zooplankton as the isotopic baseline for the primary consumers when calculating the trophic position of the Yellowfin Tuna. The mean $\delta^{15}N$ value was 5.1 ± 0.3‰ ($n = 5$), and primary producers are at trophic level 1; primary consumers, such as herbivorous fishes and zooplankton, are at trophic level 2 or slightly higher (Post 2002). The TEF is a suitable indicator for estimating the isotopic relationships between Yellowfin Tuna and their prey. As no stable isotope analysis has been performed for other tuna species or sharks in Taiwanese waters, the average TEF value of marine fishes (2.4‰) has been used (Vanderklift and Ponsard 2003) when evaluating Yellowfin Tuna feeding habits (Olson et al. 2010).

RESULTS

Stomach Contents Analysis

In total, 1,477 Yellowfin Tuna (24–108 cm FL) were caught by means of trolling during the day. Of this total, 349 (23.6%) had empty stomachs.

The analysis of 1,128 Yellowfin Tuna stomachs indicated that the major contributors of %N were unidentified zooplankton (23.9%), amphipods (16.2%), crab larvae (8.0%), and purpleback flying squid (7.6%). The major %W contributors were Exocoetidae species (30.0%), unidentified fishes (17.8%), Bullet Tuna *Auxis rochei* (6.5%), purpleback flying squid (5.5%), and Japanese Barracudina (4.05%). The repletion indices of the Yellowfin Tuna ranged from 1.3 to 59.3 g/kg, and the Kruskal–Wallis test indicated that these values differed significantly by size ($H = 34.01$, $P < 0.01$; Table 1). Dunn's posterior test indicated that the repletion indices of Yellowfin

TABLE 1. Stomach contents of juvenile Yellowfin Tuna by size-class.

				Stomach contents			
					Repletion index (g/kg)		
Size-class (cm FL)		n	% with prey	Range	Mean	±SD	Median
I	<30	41	53.9	1.3–47.5	13.0	18.2	3.8
II	30–50	987	77.8	1.3–46.1	7.0	12.2	2.4
III	50–70	68	76.1	1.4–42.8	5.3	8.9	1.4
IV	70–90	19	76.3	1.3–29.5	5.0	7.6	5.7
V	90–110	13	92.9	1.5–59.3	23.1	15.1	23.7

Tuna in classes III and II were significantly different from those in classes I, IV, and V, but no significant difference was found for those between classes I and II.

The prey species were categorized into 17 groups to examine the major prey species of Yellowfin Tuna of different sizes. The major %MN contributors were mantis shrimp *Faughnia* spp. (49.5%) and purpleback flying squid (26.6%) for class I; unidentified zooplankton (25.7%), Amphipoda species (15.5%), and purpleback flying squid (9.4%) for class II; Scombridae species (25.1%), crab larvae (11.7%), and mantis shrimp (10.9%) for class III; Skinnycheek Lanternfish (74.2%), crab larvae (5.7%), and mantis shrimp (4.9%) for class IV; and Exocoetidae species (80.6%), and Scombridae species (11.1%) for class V (Table 2).

The major %MW contributors were purpleback flying squid (42.9%) and mantis shrimp (13.5%) for class I; unidentified fishes (30.1%), purpleback flying squid (11.4%), Scombridae species (10.0%), and Japanese Barracudina (6.3%) for classs II; Scombridae species (43.5%), Amphipoda species (6.1%), Carangidae species (5.6%), and purpleback flying squid (4.1%) for class III; Skinnycheek Lanternfish (39.1%), Carangidae species (29.6%), Scombridae species (10.1%) for class IV; and Exocoetidae species (70.4%) for class V (Table 2).

Using the four metrics (%MN, %N, %MW, and %W) Morisita's original index indicated there was a significant overlap of the diets of fish in size-classes II and III (Table 3).

No significant overlap existed between size-classes III and IV or between size-classes IV and V. These results suggested that between size-classes II and III, at an FL of approximately 50 cm, Yellowfin Tuna shifted their diets. Both classes II and III overlapped at FLs of approximately 50 cm; thus, their feeding habits were similar and exhibited significant overlap. Tuna in other size-classes ate different prey and had very low values for the Morisita index.

Stable Isotope Analysis

A total of 154 samples of Yellowfin Tuna white muscle and liver tissues plus 48 prey species were examined. Averaged $\delta^{13}C$ and $\delta^{13}C'$ values were $-17.1 \pm 0.50‰$ (mean $\pm$ SD) and $-17.0 \pm 0.50‰$ for the white muscle tissue and $-18.6 \pm 0.6‰$ and $-18.5 \pm 0.6‰$ for liver tissue, respectively. A significant difference in $\delta^{13}C'$ values was found between the white muscle and liver tissues (paired t-test: $P < 0.01$). The $\delta^{15}N$ values were estimated to range from 6.2‰ to 12.6‰ for the white muscle tissue and from 7.1‰ to 12.2‰ for the liver tissue. The $\delta^{15}N$ values of the white muscle and liver tissues of the juvenile Yellowfin Tuna differed significantly among the size classes (Kruskal–Wallis test: $P < 0.01$). The mean $\pm$ SD $\delta^{15}N$ of the white muscle tissue was $7.6 \pm 0.7‰$ for size-class I. The difference in $\delta^{15}N$ values between class I and class III was 3.7‰ (Table 4). The $\delta^{15}N$ values of the muscle and

TABLE 2. Comparision of the 17 prey groups in the diets of juvenile Yellowfin Tuna measured as (%MN) and (%MW), by size-class (cm FL).

Prey item	<30 cm %MN	<30 cm %MW	30–50 cm %MN	30–50 cm %MW	50–70 cm %MN	50–70 cm %MW	70–90 cm %MN	70–90 cm %MW	90–110 cm %MN	90–110 cm %MW
Japanese Barracudina *Lestrolepis japonica*			1.6	6.3	0.3	0.3				
Skinnycheek Lanternfish *Benthosema pterotum*			0.5	0.3	0.4	0.1	74.2	39.1		
Moonfish *Mene maculata*			0.4	0.2	0.3	0.5				
Flying fishes (Exocoetidae)			0.1	6.5	0.3	0.8			80.6	70.4
Butterfly fishes (Chaetodontidae)	0.9	0.3	2.7	1.3	0.4	0.1				
Bullet Tuna *Auxis rochei*			1.6	10.0	25.1	43.5	1.4	10.1	11.1	28.4
Puffers (Tetraodontidae)			0.5	0.4	0.3	1.9				
Blue Jack Mackerel *Trachurus picturatus* and scads (Carangidae)			0.2	0.9	0.3	5.6	0.8	29.6		
Unidentified fishes	3.7	9.5	5.8	30.1	5.2	21.8	0.8	9.2	8.3	1.2
Mantis shrimp *Faughnia* spp.	49.5	13.5	7.4	5.2	10.9	1.9	4.9	0.1		
Other shrimps	0.9	0.1	6.2	2.8	4.0	0.5				
Crab larvae	4.6	0.8	7.0	1.0	11.7	0.5	5.7	0.1		
Purpleback flying squid *Sthenoteuthis oualaniens*	26.6	42.9	9.3	11.5	0.3	4.1	2.2	2.5		
Unidentified squids	3.7	28.3	10.2	9.1	2.2	6.5	0.7	0.4		
Amphipods			15.5	4.2	10.1	6.1				
Unidentified zooplankton	4.6	1.7	25.7	6.5	16.3	2.2	1.6	0.5		
Other prey	5.5	2.9	5.3	3.8	11.9	3.6	7.7	8.4		

TABLE 3. Moriseta's original index of the dietary overlap of juvenile Yellowfin Tuna by size-class. An asterisk indicates significant overlap ($C_{mh} \geq 0.6$). Values in bold italics below the diagonal are %MN and %MW.

Size-class	Size-class and FL (cm)				
	I	II	III	IV	V
Size-class	<30	30–50	50–70	70–90	90–110
Overlap of prey taxa in terms of *%N* and *%MN*					
I		0.32	0.40	0.08	0.01
II	*0.38*		0.85*	0.06	0.09
III	*0.33*	*0.67**		0.09	0.07
IV	*0.08*	*0.06*	*0.08*		0.005
V	*0.006*	*0.08*	*0.08*	*0.002*	
Overlap of prey taxa in terms of *%W* and *%MW*					
I		0.47	0.18	0.08	0.001
II	*0.52*		0.76*	0.23	0.016
III	*0.22*	*0.65**		0.39	0.13
IV	*0.08*	*0.24*	*0.33*		0.03
V	*0.002*	*0.22*	*0.32*	*0.07*	

liver tissues showed a distinct positive shift at a FL of 50 cm (Figure 2). The δ^{15}N values of the white muscle (8.8 ± 1.3‰) and liver tissues (8.9 ± 1.3‰) of the tuna with FL < 50 cm (classes I and II) were significantly lower than those of the muscle (11.5 ± 0.9‰) and liver tissues (10.8 ± 0.9‰) of the tuna with FL > 50 cm (classes III, IV, and V) (Dunn's test: $P < 0.01$). Yellowfin Tuna > 50 cm FL exhibited a wider range of δ^{15}N values than those < 50 cm FL (Figure 2). The δ^{15}N values of the white muscle and liver tissues increased with the weight of the fish, reaching an asymptote for weights > 5.5 kg. This relationship can be expressed as: δ^{15}N = 7.03 + 3.97[1 − exp(−0.63W)] ($r^2 = 0.62$, $P < 0.01$) for white muscle and δ^{15}N = 6.77 + 4.98[1 − exp(−0.48W)] ($r^2 = 0.72$, $P < 0.01$) for liver (Figure 2). The δ^{15}N values of the white muscle and liver tissues increased 3.3‰ and 1.9‰ for the size-classes of <50 cm FL and >50 cm FL, respectively.

The mean δ^{13}C′ values of the white muscle and liver tissues were −17.4 ± 0.4‰ and −18.2 ± 0.8‰, respectively, for size-class I. These mean δ^{13}C′values were −16.7 ± 0.4‰ and
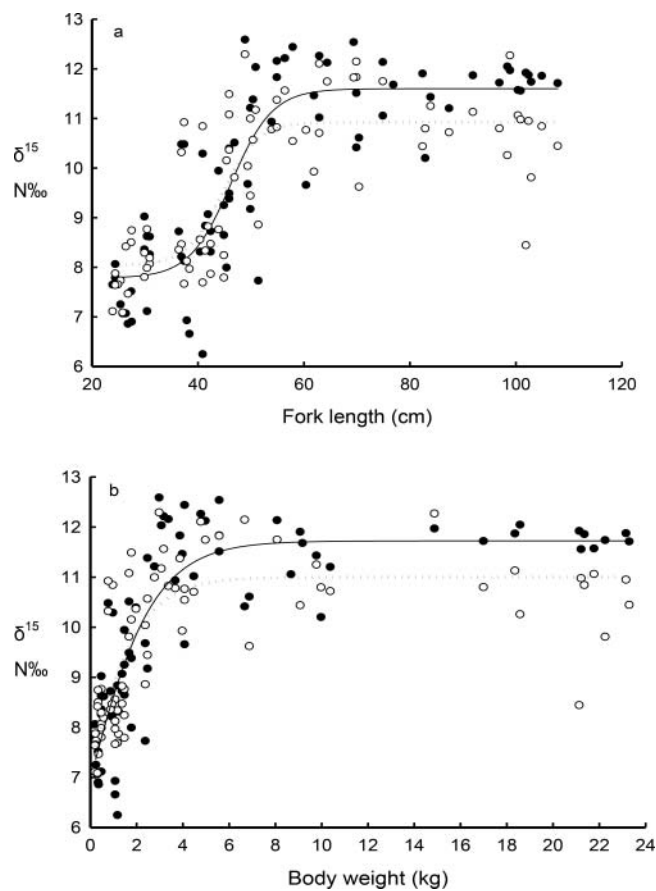

FIGURE 2. Relationships between δ^{15}N values and both (**a**) fork length and (**b**) body weight of Yellowfin Tuna. White muscle is represented by a solid line and filled circles, and liver is represented by a dashed line and open circles. In panel (a) the four-parameter, sigmoid models were estimated as: δ^{15}N = 7.78 + 3.818/{1 + exp[−(FL − 46.2)/3.91]} ($r^2 = 0.856$) for white muscle and δ^{15}N = 8.03 + 2.887/{1 + exp[−(FL − 44.5)/3.34]} ($r^2 = 0.797$) for livers. In panel (b) the three-parameter exponential growth models were estimated as: δ^{15}N = 7.03 + 3.97[1 − exp(−0.63BW)] ($r^2 = 0.62$) for white muscle and δ^{15}N = 6.77 + 4.98[1 − exp(−0.48BW)] ($r^2 = 0.723$) for livers.

−18.2 ± 0.4‰ for size-class III, and the differences in δ^{13}C′ values from class I to class III were 0.7‰ and 0‰ in white muscle and liver tissues, respectively (Table 4). The δ^{13}C′ values of the white muscle and liver tissues of Yellowfin Tuna < 50 cm FL (−17.3 ± 0.4‰ and −18.5 ± 0.6‰, respectively) were not significantly different from those of tuna > 50 cm FL (−16.8 ± 0.5‰ and −18.3 ± 0.4‰). The δ^{13}C′ values of the white muscle tissue were negatively related to FL and BW ($P < 0.05$), but these relationships were not significant for the liver tissue ($P > 0.05$; Figure 3a, b). Carbon isotopic concentration was negatively correlated with FL and BW (Figure 3a, b), but this relationship was very weak. The δ^{13}C′ values of the white muscle and liver tissues did not have a significant relationship with FL or BW.

The δ^{15}N values ranged from 4.2‰ to 11.3‰ for the 48 prey specimens (Table 5). The trophic niche of the juvenile

TABLE 4. Mean δ^{15}N (‰) and δ^{13}C′ (‰) (±SD) of juvenile Yellowfin Tuna by size-class.

Size-class (n)	δ^{15}N (±SD)		δ^{13}C′ (±SD)	
	Muscle	Liver	Muscle	Liver
I (12)	7.6 (0.6)	7.9 (0.5)	−17.5 (1.3)	−18.3 (0.8)
II (29)	9.0 (1.4)	9.2 (1.3)	−17.2 (0.41)	−18.5 (0.5)
III (20)	11.3 (1.3)	10.8 (1.3)	−16.7 (0.4)	−18.2 (0.4)
IV (9)	11.3 (1.0)	10.6(1.3)	−17.0 (0.8)	−18.4 (0.4)
V (7)	11.7 (0.1)	10.4 (0.9)	−16.9 (0.2)	−18.5 (0.3)

TABLE 5. Mean δ^{15}N (‰) and δ^{13}C′ (‰) (±SD) of juvenile Yellowfin Tuna by prey items.

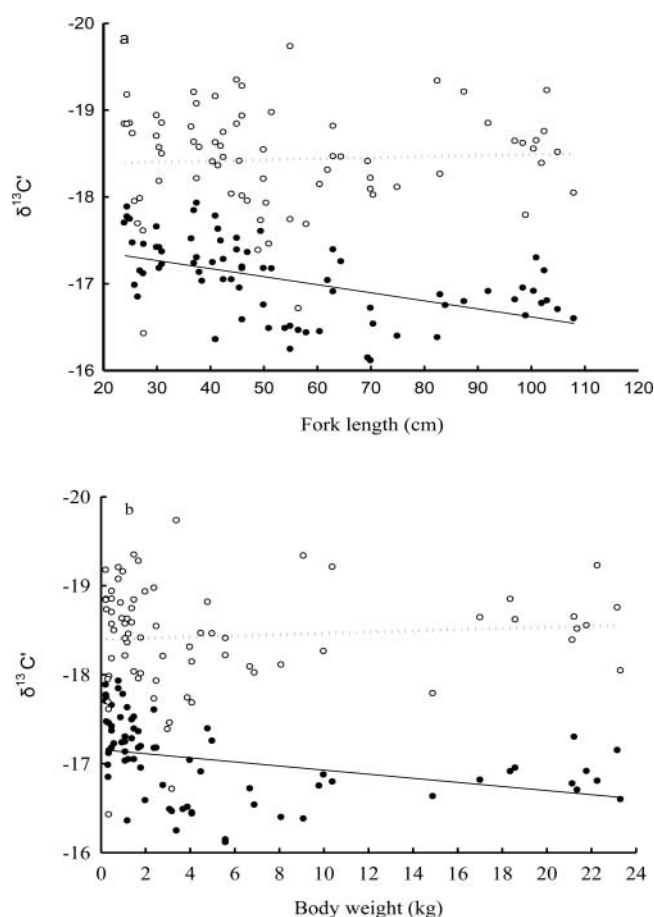| Prey item (n)	δ^{15}N (±SD)	δ^{13}C′ (±SD)
Mackerel *Rastrelliger* spp. (2)	8.6 (0.2)	−17.8 (0.6)
Bullet Tuna *Auxis rochei* (4)	10.8 (1.1)	−16.9 (0. 6)
Japanese Barracudina *Lestrolepis japonica* (3)	11.3 (0.9)	−17.7 (0.3)
Skinnycheek Lanternfish *Benthosema pterotum* (3)	11.0 (0.8)	−17.0 (0.7)
Mackerel Scad *Decapterus macaerllus* (2)	9.2 (0.2)	−17.1 (0.1)
Whitetip Scad *Decapterus maruadsi* (2)	9.2 (0. 5)	−19.0 (0.2)
Moonfish *Mene maculata* (2)	9.3 (0.21)	−18.6 (0.2)
Flying fishes (Exocoetidae) (5)	10.4 (0.1)	−17.7 (0.2)
Butterfly fishes (larval Chaetodontidae) (2)	10.4 (1.1)	−20.2 (0.1)
Pacific Pomfret *Brama japonica* (1)	9.3	−19.6
Purpleback flying squid *Stenoteuthis oualaniensis* (4)	8.4 (2.4)	−18.27 (0.5)
Octopus *Octopus* sp. (1)	8.4	−17.74
Mantis shrimp *Faughnia* spp. (5)	4.8 (1.5)	−17.87 (1.1)
Shrimp postlarva (4)	4.2 (1.0)	−17.87 (1.1)
Amphipoda (5)	7.4 (2.1)	−19.7 (1.6)
Crab megalopa (3)	5.1 (0.3)	−19.7 (1.2)

FIGURE 3. Relationship between δ^{13}C′ values and both (**a**) fork length and (**b**) body weight of Yellowfin Tuna. White muscle is represented by the a solid line and filled circles, and liver is represented by a dashed line and open circles. In panel (a) δ^{13}C′ $= -17.546 - 0.0093$FL for white muscle and δ^{13}C′ $= -18.367 + 0.0012$FL for liver. In panel (b) δ^{13}C′ $= -17.158 + 0.023$BW for white muscle and δ^{13}C′ $= -18.397 + 0.0069$BW for liver.

Yellowfin Tuna from the different size-classes and of the prey species are shown in Figure 4a, b. The postlarval shrimp, larval crabs, and mantis shrimp, the major components of size-class I, showed an average δ^{15}N value that was 3.4‰ less than that of the prey tissue. The δ^{13}C′ values of the prey varied from −16.9‰ to −20.2‰, but this information could not be used to identify the diet inputs because there was almost no difference in the δ^{13}C′ values of the white muscle between the size-classes < 50 cm FL (−17.3 ± 0.4‰) and >50 cm FL (−16.8 ± 0.5‰).

Trophic Position

The trophic structure of the Yellowfin Tuna by size-class is shown in Figure 4a and Table 6. The TP of the Yellowfin Tuna ranged from 3.2 to 4.8 depending on size, with a mean ± SD of 4.5 ± 0.6 ($r^2 = 0.75$, $P < 0.01$) (Figure 5). The TP of Yellowfin Tuna with FL < 30 cm (class I) was 3.2 ± 0.2,

which represents a probable baseline level for this species at an age < 4 months (Hampton and Fournier 2001). The TP of the tuna with FL > 50 cm (class III) was 4.6 ± 0.50, and the TP reached a peak level of 4.8 ± 0.1 at FL > 90 cm.

DISCUSSION

Stomach Contents

The juvenile Yellowfin Tuna associated with FADs in the waters southwest of Taiwan feed on different prey. The stomach contents analysis showed that a diet shift occurs around the size of 50 cm FL when they are still young of the year (age 0) according to Su et al. (2003). Yellowfin Tuna < 50 cm FL mainly feed on crustaceans and squid larvae; the tuna then switch at > 50 cm FL to a more varied diet from higher trophic levels, including teleost fishes. Maldeniya (1996) documented similar results showing that Yellowfin Tuna < 40 cm FL fed on zooplankton, crustaceans, and cephalopods, whereas those with FL ≥ 50 cm shifted their diet to feed on fish. The ontogenetic stages of a fish involve physical, structural, and physiological changes that result in behavioral changes (Noakes and Godin 1988). The time when fish shift to piscivory varies among individuals for the same cohort (Post 2003). Early hatched individuals with higher growth rates can make an
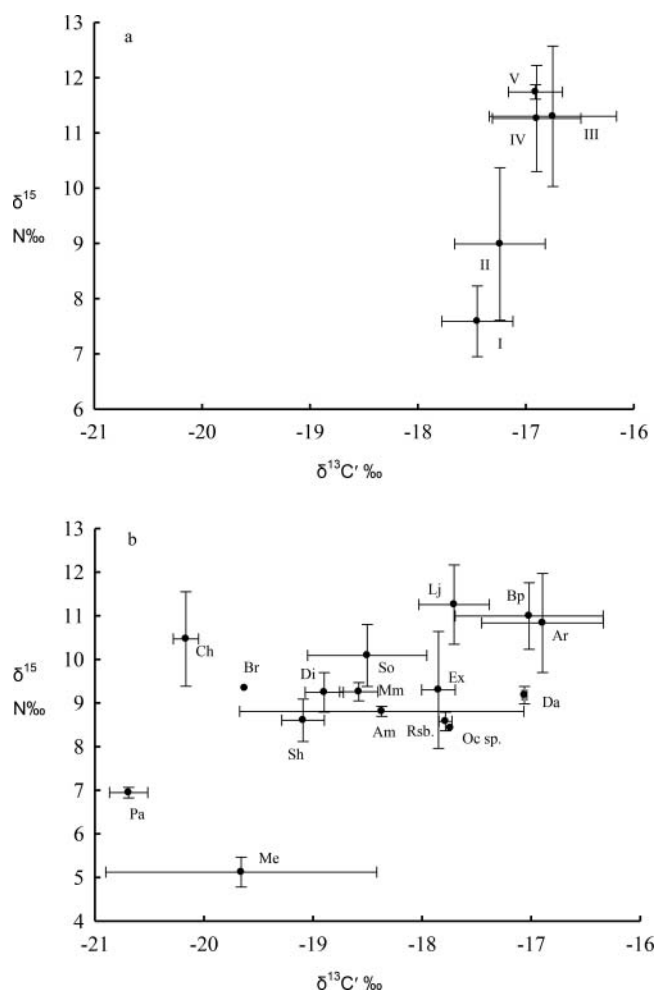
FIGURE 4. Mean $\delta^{13}C'$ and $\delta^{15}N$ values of (**a**) the white muscle of Yellowfin Tuna size-classes I–V and (**b**) prey species. R sp. = *Rastrelliger* sp.; Ar = *Auxis rochei*; Lj = *Lestrolepis japonica*; Oc sp. = *Octopus* sp.; Ex = Exocoetidae; Am = Amphipoda; Ch = larval Chaetodontidae; Sh = postlarval shrimps; Bp = *Benthosema pterotum*; So = *Sthenoteuthis oualaniensis*; Pa = *Faughina* spp.; Me = larval crabs; Br = *Brama* sp. Vertical and horizontal bars represent SD values.

observed for juvenile Yellowfin Tuna in this study. For the same age-0 cohort, some fast-growing individuals switched to piscivory, but the remainder continued to feed on crustaceans and squid larvae.

Grubbs (2010) documented that larger fish consume a wider range of prey than do smaller ones. On the other hand, McCormick (1998) concluded that juveniles of various fish species typically consume a wider variety of prey than adults do because of the differences in their size (Herrel and Gibb 2006). We found that juvenile Yellowfin Tuna in classes II and III consumed a wider variety of prey species than those in classes IV and V. This is likely because some individuals in classes II and III had not yet shifted to piscivory, but all Yellowfin Tuna in classes IV and V fed mainly fish. The ontogenetic diet shifts can reduce the intraspecific competition and increase the survival rate of juvenile Yellowfin Tuna.

The relationship between the sizes of predators and prey is perhaps the most crucial factor that influences the predator–prey relationships (Miller et al. 1988; Fuiman and Magurran 1994). Stronger predators have a greater ability to chase prey. In feeding strategies of fish, mouth size and gape size limit feeding on prey larger than the fish's own mouth (Renones et al. 2002; Arim et al. 2007). To match increased energy requirements, a quantitative or qualitative change in diet is expected (Cooper et al. 2007). Olson and Boggs (1986) mentioned that the daily ration of Yellowfin Tuna is 3.9–6.7% of their body mass and their energy requirement is a function of swimming speed. As the fish grow larger and have faster swimming speeds, the need for more energy can be achieved by switching to a prey species with high lipid and energy content (Olson and Boggs 1986). The mortality in the age-0 stage is very high and those individuals that shift to pisicivory can grow faster by gaining more energy from their prey and thus have a better chance to survive (Olson 1996). Similar findings observed in this study suggest that Yellowfin Tuna acquire more energy by shifting their diet to fish when their FLs > 50 cm.

Sheldon et al. (1977) and Smetacek (1999) concluded that the size of a fish is a crucial factor that affects the trophic interactions between various marine organisms because most predators are larger than their prey. Therefore, predators can feed on the largest prey possible to maximize energy intake (Schoener 1971; Charnov 1976). In this study, many of the stomachs of the Yellowfin Tuna in the smallest size-class contained prey

early transition to piscivory, which may result in an increase in growth and a decrease in mortality (Post 2003). Such phenomena can have critical implications for population dynamics, community structure, and ecosystem function (Olson 1996; Hammerschlag-Peyer et al. 2011). Similar behavior was

TABLE 6. Statistics of isotopic $\delta^{15}N$ and $\delta^{13}C'$ values in the muscle tissue of juvenile Yellowfin Tuna by size-class and estimated trophic position.

Size-class	Mean FL (cm) $\pm$ SD	BW range (kg)	$\delta^{15}N$ range (‰)	$\delta^{13}C'$ range (‰)	Mean TP $\pm$ SD
I (<30 cm)	26.2 ± 2.6	0.2 to 0.6	6.9 to 9.0	-16.8 to -17.9	3.2 ± 0.2
II (30–50 cm)	41.2 ± 5.9	0.6 to 2.8	6.2 to 12.6	-16.6 to -17.8	3.6 ± 0.6
III (50–70 cm)	61.8 ± 8.1	2.8 to 8.7	7.7 to 12.5	-16.1 to -17.4	4.6 ± 0.5
IV (70–90 cm)	88.9 ± 8.0	9.1 to 14.6	11.1 to 12.0	-16.4 to -18.5	4.7 ± 0.2
V (90–110 cm)	103.1 ± 2.6	14.6 to 23.4	11.5 to 11.9	-16.6 to -17.3	4.8 ± 0.1

species that were relatively large. For example, the Yellowfin Tuna with a FL of 40 cm preyed on Japanese Barracudina with a FL of 20 cm. These results are similar to those reported in the aforementioned studies, in which fishes shifted their diet to consume prey that would provide maximum energy.

Yellowfin Tuna in size-classes II and III (*%MN*) exhibited feeding overlap at a FL of approximately 50 cm (Table 3); this result was consistent with the diet shift and findings reported by Graham et al. (2007) regarding Yellowfin Tuna with FLs ranging from 45 to 50 cm. Yellowfin Tuna of size-classes IV and V (2 years old and older: Su et al. 2003) primarily fed on Skinnycheek Lanternfish and flying fish and exhibited no feeding overlap with those of other size-classes. The samples from classes IV and V used in this study were all collected in April. During the period of April–July, exocoetid fishes are prevalent in Taiwanese waters and these fishes are also the main prey of tunas (Oxenford and Hunte 1999) and Dolphinfish *Coryphaena hippurus* (Wu et al. 2006). Therefore, the stomachs of Yellowfin Tuna ≥ 100 cm FL mainly contained these prey (Table 2).

Stable Isotope Analysis

Sarà and Sarà (2007) and Varela et al. (2013) indicated that larger predators often exhibit higher $\delta^{15}N$ values than smaller predators do. Bearhop et al. (2004) reported significant variations in $\delta^{15}N$ values and increased diversification of prey among tuna at FL > 45 cm. Graham et al. (2007) and Olson et al. (2010) reported that the stable isotope values of Yellowfin Tuna tend to increase with an increase in body size. In this study, $\delta^{15}N$ and $\delta^{13}C'$ values of the muscle tissues of Yellowfin Tuna < 30 cm FL were 7.6 ± 0.6‰ and −17.5 ± 1.3‰,
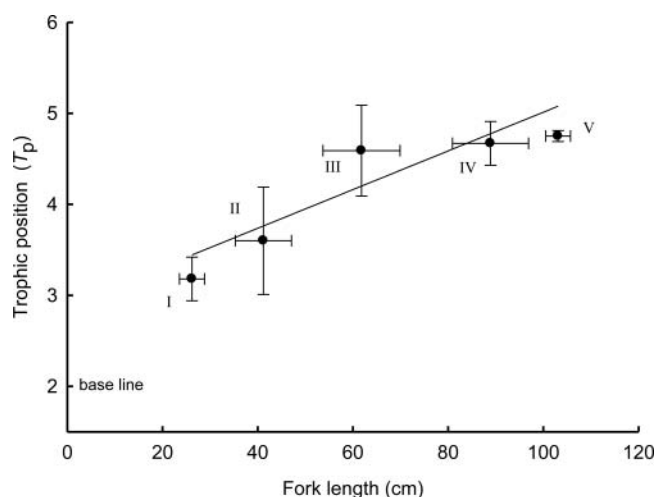

FIGURE 5. Relationship between trophic position (TP) and fork length of Yellowfin Tuna using $\delta^{15}N$ concentration of the zooplankton (5.13 ± 0.26‰) as a baseline. The TP–FL relationship of size-classes I–V was fitted by TP = 4.4827 + 0.0043FL (r^2 = 0.75). Vertical and horizontal bars represent SD values.

while for those > 50 cm FL, the $\delta^{15}N$ and $\delta^{13}C'$ values were 11.5 ± 0.9‰ and −16.8 ± 0.5‰, respectively (Table 4). A significant difference in $\delta^{15}N$ values was observed between Yellowfin Tuna < 30 cm FL and those > 50 cm (*t*-test: $P < 0.01$); these results are consistent with those of the aforementioned studies (Graham et al. 2007; Olson et al. 2010).

The $\delta^{13}C$ is derived from organic carbon in the ecosystem, and it has been used to track the movement of animals between areas with different food sources (Kurle and Worthy 2001). In this study, very few differences in $\delta^{13}C$ values were found among the size-classes (Tables 4, 5), suggesting that the prey and predators were likely from the same ecosystem. The stable isotope $\delta^{13}C'$ value of the muscle tissue of the juvenile Yellowfin Tuna varied with size ($P < 0.05$), but such variation could not be found for the liver tissue ($P > 0.05$) (Figure 3a, b). Graham (2008) estimated the half-life turnover rate of the liver to be shorter than that of muscle tissue (12 versus 63 d), because the metabolic rate of the liver is higher than that of muscle tissue (Suzuki et al. 2005; Guelinckx et al. 2007). Weng et al. (2013) reported that juvenile Yellowfin Tuna that lingered around a single FAD in the waters southwest of Taiwan for >31 d fed on various types of prey during this period and their muscle tissue exhibited varied stable isotope N and C values. The movement of juvenile Yellowfin Tuna from other waters to Taiwanese waters may alter their food intake and increase their nutrient supply. Future archival tag studies may facilitate clarification of this phenomenon.

Although the stable isotope analysis did not provide information regarding prey diversity, variability in the $\delta^{15}N$ values of predators can provide information that can be used in trophic level assessment (Bearhop et al. 2004). A trophic level change of 3.4‰ in $\delta^{15}N$ and −1.1‰ in $\delta^{13}C$ values indicates the existence of a predator–prey relationship (DeNiro and Epstein 1978, 1981). Thus, the difference of 4.1‰ in $\delta^{15}N$ values between the Yellowfin Tuna of size-class II and the postlarval shrimp, larval crabs, and mantis shrimp implies a predator–prey relationship (Tables 4, 5). However, nutrient sources affect the N values of food webs due to spatial and temporal variations (O'Reilly et al. 2002). Even identical prey collected in different waters may exhibit different stable isotope values (Graham et al. 2007; Sarà and Sarà 2007; Varela et al. 2013). According to a survey conducted by Dore et al. (2002), surface mixed waters are primarily affected by N_2 fixation, which changes with the seasons, potentially causing the aforementioned differences in the stable isotope values of the prey.

Epply and Peterson (1979) indicated that in the open sea ecosystem, the nutrients of surface waters are limited between the flux and the mixed layer. Therefore, the nitrogen content below the mixed layer that varies among seasons will be higher than that of the surface waters. Significant seasonal changes have been observed in the waters southwest of Taiwan. During autumn and winter, the Kuroshio Current branches northward (high temperature and salinity) and the China coastal currents (low temperature and salinity) flow

southward into west Taiwan, whereas during spring and summer, the South China Sea surface current (high temperature and low salinity) flows northward into west Taiwan waters (Jan et al. 2002, 2010). The China coastal currents and Kuroshio Current system bring rich nutrients to this important fishing ground, and juvenile Yellowfin Tuna feed on several juvenile fishes, Parasquillidae species, Amphipoda species, and postlarval shrimp. Prey at this stage float on surface waters, and the stable isotope $\delta^{15}N$ values of these prey are lower than those of mesopelagic prey (Rau et al. 1989). For the Yellowfin Tuna with an average ($\pm$SD) FL of 53.9 cm ($\pm$2.1), the $\delta^{15}N$ value was 11.3‰ ($\pm$1.5) and the TP was 4.6 ($\pm$0.6); the fish shifted their diet to scombroid fishes and Japanese Barracudina.

Because the size range of the specimens did not cover all of the age-classes, the results obtained in this study can only be applied to juvenile Yellowfin Tuna. To provide more information on the food web in the waters southwest of Taiwan future studies should focus on collecting large-sized specimens and investigating the carbon and nitrogen composition of environmental nutrients.

Conclusions

Taken together, the results of the stomach contents and stable isotope analyses provide important evidence regarding ontogenetic shifts in the diet, feeding strategies, and stable isotope variations of juvenile Yellowfin Tuna. The stomach contents and stable isotope values differed significantly among tuna at different trophic positions. This ontogenetic shift in the diet of juvenile Yellowfin Tuna occurs at a FL of 50 cm.

ACKNOWLEDGMENTS

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