***J. Ocean Univ. China*** (Oceanic and Coastal Sea Research)
DOI 10.1007/s11802-014-2071-1
ISSN 1672-5182, 2014 13 (2): 278-282
*http://www.ouc.edu.cn/xbywb/*
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# Trophic Ecology of Sharks in the Mid-East Pacific Ocean Inferred from Stable Isotopes

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(Received June 18, 2012; revised July 28, 2012; accepted December 6, 2012)

**Abstract** As apex predators, sharks are of ecological and conservation importance in marine ecosystems. In this study, trophic positions of sharks were estimated using stable isotope ratios of carbon and nitrogen for five representative species caught by the Chinese longline fleet in the mid-east Pacific, *i.e.*, the blue shark (*Prionace glauca*), the bigeye thresher shark (*Alopias superciliosus*), the silky shark (*Carcharhinus falciformis*), the scalloped hammerhead (*Sphyrna lewini*), and the oceanic whitetip shark (*Carcharhinus longimanus*). Of these species, oceanic whitetip shark has the lowest trophic level and mean $\delta^{15}$N value (3.9 and 14.93‰ ± 0.84‰), whereas bigeye thresher shark has the highest level/values (4.5 and 17.02‰ ± 1.21‰, respectively). The bigeye thresher shark has significantly higher $\delta^{15}$N value than other shark species, indicating its higher trophic position. The blue shark and oceanic whitetip shark has significantly higher $\delta^{13}$C values than bigeye thresher shark, silky shark and scalloped hammerhead, possibly due to different diets and/or living habitats. The stable isotope data and stomach content data are highly consistent, suggesting that stable isotope analysis supplements traditional feeding ecology study of sharks, and thus contributes to understanding their trophic linkage.

**Key words** trophic level; stable isotope analysis; mid-east Pacific; shark

## 1 Introduction

Exploitation of sharks has intensified worldwide in recent decades, driven by an upsurge in demand for shark fins and meat as well as in by-catch in many fisheries (Myers *et al*., 2007). Understanding the role or trophic position (TP) of sharks as apex predators in terms of top-down control on community structure is of ecological and conservation importance (Myers *et al*., 2007; Baum and Worm, 2009; Hussey *et al*., 2012).

Stomach content analysis (SCA) is the traditional method for investigating trophic ecology of sharks (Cortés, 1999; Bowmen *et al*., 2000). Its application can be limited due to the snapshot sampling of stomach content data and the requirements for large amounts of individual samples (Hussey *et al*., 2010). Nitrogen and carbon stable isotope analyses allow minor invasive sampling of animals for studying endangered or difficult-to-study species (Hobson, 1999; Hussey *et al*., 2010), and thus have increasingly been used to address ecological questions over the last two decades (Cabana and Rasmussen, 1994; Fry, 2007; Wolf *et al*., 2009; Hussey *et al*., 2010). As stable carbon isotope ratio ($\delta^{13}$C) of animal tissues changes little during the upward movement of carbon in the food web, it can be used to evaluate the ultimate sources of energy for an organism. The stable nitrogen isotope ratio $\delta^{15}$N of an organism is typically estimated to be 3.4‰ (±1‰) of its diet, providing a means for TP quantification of the organism (Minagawa and Wada, 1984; Peterson and Fry, 1987; Cabana and Rasmussen, 1994; Post, 2002; Fry, 2007; Guzzo *et al*., 2011).

In this study, the TPs of sharks were calculated using stable isotope analysis (SIA) for five representative species caught by the Chinese tuna fishery in the mid-east Pacific. Results were compared with the estimates based on published diet data for better understanding of the feeding ecology of sharks in the mid-east Pacific.

## 2 Material and Methods

In November and December 2011, five representative shark species caught by the Chinese tuna fisheries were sampled in the mid-east Pacific (5°–8°N, 151°–170°W) (Fig.1). These included the Blue shark *Prionace glauca* (*n*=18, internal length 39−62 cm), the Bigeye thresher *Alopias superciliosus* (*n*=7, internal length 36−43 cm), the Silky shark *Carcharhinus falciformis* (*n*=19, internal length 24–49cm), the Scalloped hammerhead *Sphyrna lewini* (*n*=8, internal length 55−70cm), and the Oceanic

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whitetip shark *Carcharhinus longimanus* ($n$=5, internal length 34–53 cm).

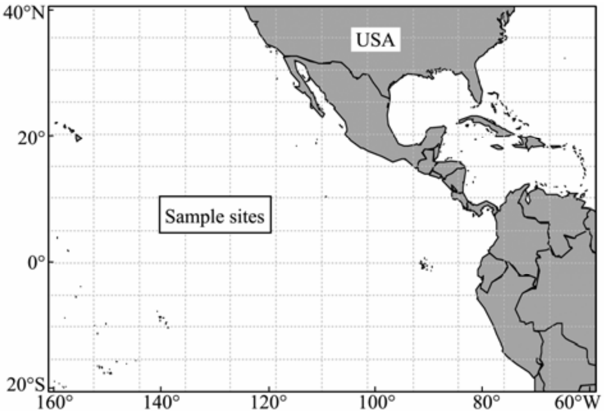

Fig.1 Sampling sites for the representative shark species caught by the Chinese longline fleet in the mid-east Pacific (Nov–Dec 2011).

Tissue samples were randomly collected from the sharks on the fishing vessels by removing from the vertebrae region. A small section of white muscle was excised from the region just below the skin and connective tissue, and then rinsed with distilled water three times to remove urea (Kim and Koch, 2011). All samples were frozen in cryovials at −20℃ prior to stable isotope analyses.

For stable isotope analyses, the tissue and muscle samples were dried at −55℃ for ≥24 h to constant weight, ground to fine homogeneous powders with an agate mortar and pestle, and then filtered through a 150-μm filter for homogenization. Approximately 1–2 mg of samples were weighed into 0.3 mg tin capsules and analyzed using an ISOPRIME 100 isotope ratio mass spectrometer (Isoprime Corporation, Cheadle, UK) and a vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). The isotope compositions of samples were expressed as $\delta^{13}C$ and $\delta^{15}N$ notation using the following equations:

$$\delta^{13}\mathrm{C}\ (‰)=\left(\frac{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{sample}}}{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{standard}}}-1\right)\times 1000,$$

$$\delta^{15}\mathrm{N}(‰)=\left(\frac{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{sample}}}{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{standard}}}-1\right)\times 1000,$$

where ‰ is parts per thousand; $^{13}C/^{12}C$ and $^{15}N/^{14}N$ are the atomic ratios of $^{13}C$ and $^{15}N$ in the sample or standard, respectively; and δ is the measure of heavy-to-light isotope in the sample. The standard reference materials for C and N were Pee Dee Belemnite carbonate and air, respectively. Reference standards USGS 24 (−16.049‰ vPDB) and USGS 26 (53.7‰ $vN_2$) were used for quantification of $^{13}C$ and $^{15}N$ stable isotope values, respectively. Every tenth sample was run in triplicate of a lab ref standard (Protein (−26.98‰ vPDB and 5.96‰ $vN_2$)) to assess the within-run precision, and a blank sample was run every ten samples to clear off residual gases. The analytical errors of $\delta^{13}C$ and $\delta^{15}N$ values were approximately 0.05‰ and 0.06‰, respectively.

Relative TP was estimated using the following equation:

$$\text{Trophic position}=\lambda+\frac{(\delta^{15}\mathrm{N}_{\mathrm{shark}}-\delta^{15}\mathrm{N}_{\mathrm{base}})}{\Delta n},$$

where λ is the TP of the organism used to estimate $\delta^{15}N_{\mathrm{base}}$, $\Delta_n$ is the enrichment in $^{15}N$ per trophic level, and $\delta^{15}N_{\mathrm{shark}}$ is the direct $\delta^{15}N$ measurement of the shark. Here, mesozooplankton was used as the baseline species (Popp *et al.*, 2007), which were estimated from the equation below:

$$\delta^{15}\mathrm{N}_{\mathrm{mesozoo}}=0.20(\pm 0.03)\times\mathrm{Latitude}+6.8(\pm 0.5).$$

Statistical analyses were performed using the R statistical package (Version 2.13.0; R Development Core Team, 2011). All stable isotope data were tested for normality using Shapiro-Wilk Test ($P>0.05$). Simple linear regression analyses were carried out on $\delta^{13}C$ and $\delta^{15}N$ values and the shark length. ANOVA was conducted separately for both isotope ratios, followed by multiple comparisons based on Tukey's HSD post hoc test.

## 3 Results

ANOVA analysis showed that the $\delta^{13}C$ and $\delta^{15}N$ isotope values were significantly different among the five shark species ($F=43.97$, $P<0.00001$ and $F=4.48$, $P<0.01$, respectively) (Table 1). Multiple comparison *via* Tukey's test showed that the mean $\delta^{15}N$ values of *A. superciliosus* were significantly higher than those of other tested shark species except for *P. glauca*. The $\delta^{13}C$ values

Table 1 The stable isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) and trophic levels of sharks collected from the mid-east Pacific Ocean in Nov–Dec 2011

| Species | Sample size | $\delta^{13}C$ (‰) | | $\delta^{15}N$ (‰) | | C:N | | TP of Cortés (1999) | TP of this study | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | Mean | SD | Mean | SD | Mean | Mean | SD |
| PG | 18 | −18.31 | 0.54 | 15.77 | 1.07 | 2.81 | 0.13 | 4.1 | 4.17 | 0.32 |
| AS | 7 | −17.11 | 0.44 | 17.02 | 1.21 | 2.90 | 0.13 | 4.2 | 4.53 | 0.36 |
| CF | 19 | −17.08 | 0.35 | 15.45 | 0.99 | 2.82 | 0.08 | 4.2 | 4.07 | 0.29 |
| SL | 8 | −16.70 | 0.17 | 15.05 | 1.05 | 2.95 | 0.08 | 4.1 | 3.96 | 0.31 |
| CL | 5 | −18.79 | 0.17 | 14.93 | 0.84 | 3.14 | 0.10 | 4.2 | 3.92 | 0.25 |

Notes: PG, *Prionace glauca*; AS, *Alopias superciliosus*; CF, *Carcharhinus falciformis*; SL, *Sphyrna lewini*; CL, *Carcharhinus longimanus*; and SD, standard deviation.

Table 2 Tukey post-hoc comparisons of stable isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) for sharks collected from the mid-east Pacific Ocean in Nov–Dec 2011

| C_HSD | AS-PG | CF-PG | SL-PG | CL-PG | CF-AS | SL-AS | CL-AS | SL-CF | CL-CF | CL-SL |
|---|---|---|---|---|---|---|---|---|---|---|
| *P* value | $P<0.00001$ | $P<0.00001$ | $P<0.00001$ | $P<0.154$ | $P<0.999$ | $P<0.313$ | $P<0.00001$ | $P=0.188$ | $P<0.00001$ | $P<0.00001$ |
| Diff | 1.20 | 1.23 | 1.61 | −0.48 | 0.03 | 0.41 | −1.68 | 0.38 | −1.71 | −2.09 |
| N_HSD | AS-PG | CF-PG | SL-PG | CL-PG | CF-AS | SL-AS | CL-AS | SL-CF | CL-CF | CL-SL |
| *P* value | $P=0.0710$ | $P=0.885$ | $P=0.489$ | $P=0.514$ | $P<0.05$ | $P<0.01$ | $P<0.05$ | $P=0.890$ | $P=0.860$ | $P=0.999$ |
| Diff | 1.24 | −0.32 | −0.72 | −0.84 | −1.56 | −1.96 | −2.08 | −0.40 | −0.52 | −0.12 |

Notes: PG, *Prionace glauca*; AS, *Alopias superciliosus*; CF, *Carcharhinus falciformis*; SL, *Sphyrna lewini*; and CL, *Carcharhinus longimanus*.

of *P. glauca* and *C. longimanus* were significantly lower than those of *A. superciliosus*, *C. falciformis* and *S. lewini* (Table 2).

Due to limited sample size, ontogenetic changes in $\delta^{13}C$ and $\delta^{15}N$ were not examined for most shark species. *P. glauca* was the only species with total length data recorded and showing no significant relationships between the $\delta^{13}C$ or $\delta^{15}N$ values and the body sizes ($P=0.922$ and $P=0.415$, respectively). This was so despite the fact that the sampling of *P. glauca* did not cover their overall length range (Total length: 189.8–289.8 cm).

*T* test analysis on the other four species showed no statistical differences between the observed TP inferred from stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses and the expected TP calculated from diet data by Cortés (1999): *P. glauca* $df=17$, $P>0.05$; *C. falciformis* $df=18$, $P>0.05$; *S. lewini* $df=7$, $P>0.05$ and *C. longimanus* $df=4$, $P>0.05$. However, the TP of *A. superciliosus* was significantly higher than the estimation of Cortés (1999) ($df=6$, $P=0.049$).

## 4 Discussion

As apex predators, sharks play a critical role in marine food webs. In this study, the trophic levels were examined *via* stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses for five representative species commonly caught by the Chinese longline fleet in the mid-east Pacific Ocean. Results indicate that these sharks have high position in marine food webs. The $\delta^{15}N$ values of trophic level range from 3.35 to 5.26 (average 4.13), suggesting that the sharks utilize similar food resources to those of other high-level marine consumers (Cortés, 1999).

The SIA-based TP estimates of *P. glauca*, *C. falciformis*, *S. lewini* and *C. longimanus* (Table 1) do not differ significantly from the SCA-based values determined by Cortés (1999). Although the TP of *A. superciliosus* was found highest in our study area and significantly higher than that reported by Cortés (1999) ($P=0.049$), it has no significant difference from the SCA-based value in Fishbase (Bowman *et al.*, 2000) (TP=4.5). Cortés (1999) found that *A. superciliosus* consume more cephalopods than the other shark species, and McNail *et al.* (2005) reported that the thresher shark has higher muscle $\delta^{15}N$ values than blue sharks, implying its higher trophic level of diet than that of other species. This was likely the reason that *A. superciliosus* has the highest TP among all the studied shark species, as squid has higher $\delta^{15}N$ and $\delta^{13}C$ values than fish prey (Estrada *et al.*, 2003).

In marine environments, $\delta^{13}C$ value indicates the lower versus higher latitude plankton, and inshore versus offshore, or pelagic versus benthic contribution to food intake (Hobson *et al.*, 1994; Cherel *et al.*, 2000). In the present study, the five tested shark species are oceanic and inhabit proximate latitudes. Compared with the other shark species, *A. superciliosus* and *C. falciformis* has significantly higher $\delta^{13}C$ values (−17.11‰ and −17.08‰, respectively), suggesting that their habitats are most likely similar. *P. glauca* (−18.31‰ $\delta^{13}C$ values) and *C. longimanus* (−18.79‰ $\delta^{13}C$ values) seem to share similar food sources. We suggest that these four species benefit more from pelagic food chain than *S. lewini* does. Our results indicated that the five shark species have segregated TPs and different $\delta^{13}C$ values. This is supported by their trophic niche overlap relationship as described by the 'niche space' plot (Fig.2), which is based on the $\delta^{13}C$-$\delta^{15}N$ metrics plotted with the mean stable isotope signatures of the studied shark species. The relative positions of shark species in such plot space have been used to infer characteristics of the food web structure (Layman *et al.*, 2007).

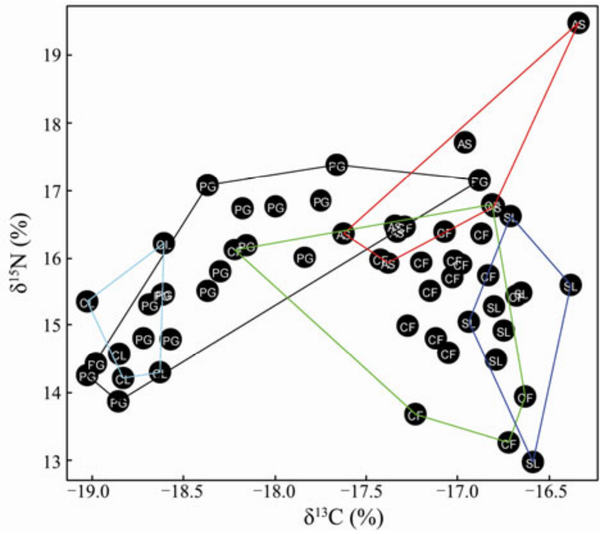

Fig.2 'Niche space' plot of five representative shark species commonly caught by the Chinese longline fleet in the mid-east Pacific. PG, *Prionace glauca*; AS, *Alopias superciliosus*; CF, *Carcharhinus falciformis*; SL, *Sphyrna lewini*; and CL, *Carcharhinus longimanus.*

Large sharks are capable of large-scale movements and rapid home range expansion (Bonfil *et al*., 2005; Hussey *et al*., 2011). The large variation in $\delta^{15}$N of *A. superciliosus* could be related to its large-scale migration, which has been found in coastal waters over continental shelves, inshore shallow waters and distant high seas (Fishbase, 2012). The food chain length of food webs inshore is much longer than that offshore, resulting in additional $\delta^{15}$N fractionations and higher $\delta^{15}$N values of top predators (Link, 2002; Estrada *et al*., 2003), consistent with the $\delta^{13}$C data. The $\delta^{13}$C values from offshore food webs tend to be more $\delta^{13}$C-depleted than those from inshore habitats (France, 1995; Estrada *et al*., 2003). In the present study, *A. superciliosus* has the highest $\delta^{15}$N (19.47‰) and $\delta^{13}$C values (−16.34‰), whereas it has the lowest $\delta^{15}$N value (15.92‰) and the second lowest $\delta^{13}$C value (−17.38‰). Future study needs to examine the the spatial variation in inshore and offshore shark isotopic signatures in order to evaluate this hypothesis.

Lipids are depleted in $^{13}$C relative to proteins. Thus, the variation in lipid content among organisms or tissue types can potentially introduce considerable bias into stable $^{13}$C isotope analyses (Post *et al*., 2007). The C:N ratio is considered to be a good predictor of lipid content. In the present study, the C:N values of tested samples are significantly lower than the values (3.4 and 3.5) reported by Post *et al*. (2007) and Reum (2011). Researches indicate that the low C:N in elasmobranch might result from the high concentration of nitrogenous waste compounds in elasmobranch tissues (Hussey *et al*., 2010). Therefore, we removed the urea before the stable isotope analysis and considered that the obtained SIA data are correct with minimal effects of the lipid effects. Despite the fact that the 3.4‰ fractionation in $\delta^{15}$N might be inaccurate for calculation of shark TPs, our results are correlated well with the SCA data. Considering the variability of discrimination factors between taxon and species, tissue and diet with environment and feeding rate, further work needs to investigate the specific discrimination factors of these five shark species.

Oceanic sharks are generally large in size and highly migratory, and thus are difficult to be studied in natural environments or under laboratory conditions. Our results provided evidence regarding the preliminary trophic roles of these five shark species in the mid-east Pacific. However, the deficiency of this study should be noted as well. The metabolic turnover rate of shark muscle has been considered to be approximately 488 d (MacNeil *et al*., 2005). Hence, our TP estimates represent their feeding habits in the past year only. Stomach content analysis and stable isotope analysis from multiple tissues with different metabolic turnover rates should be carried out on these shark species to investigate their diet shift before being captured.

Researches on the feeding ecology of mid-east Pacific sharks are scarce till date, probably because of the difficult sampling. In addition, collecting stomach contents of elasmobranchs is particularly difficult due to the requirements of extended time period or field area for field sampling (Borrell *et al*., 2011). By comparison, the SIA requires less intrusive sampling and can provide direct, long-term feeding information. The muscle isotopic signature reported in this study only provides a yearly average TP of sharks. Continual sampling and relative stable isotope analysis may be useful for monitoring relative TP of shark species in the Mid-Pacific over time. To perform large-scale sampling and collect accurate baseline species isotopic signatures will improve the data quality and help investigate the trophic implication and impact of removal of these large pelagic fishes in oceanic ecosystems.

## Acknowledgements

The authors thank Mrs. Zheng Xiaochun and Teng Yunlu for shark tissues sampling and stable isotope analysis. Li Yunkai was supported by the National Natural Science Foundation of China (No. 41206124), Ph.D. Programs Foundation of Ministry of Education of China (No.201 23104120001), the ‘Chen Guang’ Project of Shanghai Municipal Education Commission (No. D-8004-10-0206), and the Shanghai Education Development Foundation (No. B-8102-10-0084). Zhu Jiangfeng and Dai Xiaojie were supported by the National Natural Science Foundation of China (No. 41106118) and the Scientific Observing and Experimental Station of Oceanic Fishery Resources, Ministry of Agriculture, China. We thank the reviewers for insightful and constructive comments.

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**(Edited by Qiu Yantao)**