Journal of Experimental Marine Biology and Ecology 483 (2016) 97–103

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Trophic interactions among pelagic sharks and large predatory teleosts in the northeast central Pacific

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ARTICLE INFO

Article history:
Received 23 November 2015
Received in revised form 26 April 2016
Accepted 27 April 2016
Available online xxxx

Keywords:
Pelagic sharks
Stable isotope
Trophic roles
Trophic overlap
Central Pacific

ABSTRACT

Sharks are considered to play important roles in structuring marine ecosystems, consequently understanding their trophic ecology and interactions with other marine predators is required. In the central Pacific Ocean, whether the trophic roles of pelagic sharks are complementary or redundant to large teleost predators remains unclear. In this study, stable carbon and nitrogen isotope analysis were used to examine the isotopic niche overlap of eight pelagic shark species and six pelagic teleost predators, including tuna and billfish. Large intra-specific variation and minimal inter-specific variation in both δ^{15}N and δ^{13}C values were observed among sharks and teleosts. Moreover, there was a high degree of trophic overlap among pelagic shark and teleost species, with the exception of the blue shark, the δ^{13}C values of which indicated a much longer foraging time in the purely pelagic waters. Moreover, although the stable isotopic data suggested that the pelagic sharks in the study area share similar prey and habitats with other pelagic predators, such as tuna and billfish, blue sharks and shortfin mako sharks did not show isotopic overlap with these predators. These data highlight the diverse roles among pelagic sharks, supporting previous findings that this species complex is not trophically redundant; but further studies on the diet and fine-scale habitat used are required to verify this hypothesis.

1. Introduction

Pelagic sharks are primary bycatch species of longline fisheries operating in open ocean ecosystems and are prone to high fisheries mortality rates (Kitchell et al., 2002; Schindler et al., 2002). Their typically large pectoral fins render them attractive to the shark fin industry, to which they contribute a substantial percentage of total species traded (Clarke et al., 2006). But as k-selected species, pelagic sharks possess several biological attributes (low growth rate, late maturity, and low fecundity) that make them vulnerable to overfishing (White et al., 2012) and limit their recovery potential (Walker, 1998). The standardized catch rate of silky sharks (*Carcharhinus falciformis*) in the North Pacific Ocean, for example, was estimated to have decreased by 91.7% between 1950 and 1997 with the onset of commercial fishing (Baum and Myers, 2004). Pelagic sharks also range across poorly monitored regions (Gilman et al., 2008), therefore the annual global catch rate reported to the Food and Agriculture Organization of the United Nations (FAO) is likely largely underestimated (Clarke et al., 2006; Ferretti et al., 2010). More than 50% of pelagic species are currently considered threatened worldwide (Dulvy et al., 2008).

Conservation and management of pelagic sharks involves two key issues, consideration of their unique evolutionary characteristics in relation to biodiversity importance and global conservation priorities and mitigating over exploitation in fisheries to maintain the integrity of their ecological role in marine food webs (Kitchell et al., 2002). Most large shark species feed at or near the top of marine food webs; however, their trophic roles are thought to vary significantly among ecosystems, species and contexts (Heithaus et al., 2008; Kiszka et al., 2015). Declines in the abundance of large sharks have the potential to induce trophic cascades in coastal and demersal ecosystems (Ferretti et al., 2010), yet it remains unclear how their removal impacts the trophic structure of pelagic communities in open-ocean ecosystems (Ward and Myers, 2005; Kiszka et al., 2015).

To date, only one study has directly examined the effect of removing large pelagic sharks on ecosystem structure, finding conflicting results. Through an Ecopath with Ecosim model, Kitchell et al. (2002) identified limited effects of removing pelagic sharks on the overall fish community when assigning a standardized trophic level of approximately 4.5. Model results suggested compensatory effects of shark removal by other large teleost predators that have faster biomass turnover rates, such as tuna and billfish. When variable trophic roles among large and small sharks were considered within the model, however, non-linear effects were observed with negative consequences for ecosystem structure. Inter-specific variation in habitat use (Rabehagasoa et al., 2012), diet (Kiszka et al., 2014) and trophic complexity (Kiszka et al., 2015) is observed among pelagic sharks supporting the latter model predictions, but uncertainties over their ecological role/s remain. Specifically,

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http://dx.doi.org/10.1016/j.jembe.2016.04.013
0022-0981/

understanding the trophic dynamics of pelagic sharks, in the context of compensatory or divergent roles relative to other large teleost predators, is required.

The primary objective of this study was to quantify trophic interactions and niche overlap of pelagic sharks and large predatory teleosts in the northeast central Pacific Ocean using long term integrated measures of carbon and nitrogen stable isotopes in muscle tissue. Specifically, the study investigated (1) inter- and intra-specific variations in trophic roles and niche overlap among eight commonly caught pelagic shark species; (2) niche overlap between pelagic sharks and commonly occurring pelagic teleost predators and; (3) relationships between individual species body size and body size of all species combined relative to trophic position.

2. Materials and methods

2.1. Study species and sampling area

A total of 130 individuals from 8 species of pelagic sharks and 6 large predatory teleosts, including silky (*C. falciformis*), blue (*Prionace glauca*), smooth hammerhead (*Sphyrna zygaena*), scalloped hammerhead (*Sphyrna lewini*), oceanic whitetip (*Carcharhinus longimanus*), shortfin mako (*Isurus oxyrinchus*), pelagic thresher (*Alopias pelagicus*), and bigeye thresher (*Alopias superciliosus*) sharks and, bigeye tuna (*Thunnus obesus*), skipjack tuna (*Katsuwonus pelamis*), mahi-mahi (*Coryphaena hippurus*), escolar (*Lepidocybium flavobrunneum*), swordfish (*Xiphias gladius*), and black marlin (*Makaira indica*) were randomly sampled from the bycatch of tuna longline fishing vessels working in the northeast central Pacific (FAO major fishing area 77: 8°–10°N, 115°–125°W). All sampling took place between June and November 2014 (Fig. 1). The precaudal length (PCL) of each shark, fork length (FL) of the tuna and tuna-like species and lower jaw to fork-in-tail length (LF) of the billfish were recorded to the nearest cm (Table 1). Fish samples were immediately stored frozen following sampling and then archived in an ultra-low temperature freezer (−40 °C) prior to analysis.

2.2. Stable isotope analysis

For sharks and predatory teleosts, white muscle tissue was excised from the vertebrae region and the base of the dorsal fin, respectively. All samples were immediately freeze-dried at −55 °C for ≥48 h and then ground to a fine powder using a Retsch mixer mill MM 400 (Haan, Germany). For sharks, powered muscle tissue was divided into two subsamples and both treated with a deionized water rinse to remove ^{15}N depleted urea that is considered to bias nitrogen isotope values in elasmobranchs (Li et al., 2016). One of these samples was then lipid extracted following the standard chloroform and methanol (2:1) approach of Bligh and Dyer (1959) to remove potential lipid effects on δ^{13}C values (Hussey et al., 2012). For teleost predators, two subsamples were also taken; one untreated bulk sample to determine δ^{15}N values, and the second lipid extracted to determine δ^{13}C values. Water rinsing to remove urea from shark muscle tissue samples involved soaking them in 4.0 ml of deionized water, vortexing them for 1 min, and then leaving them undisturbed for 24 h at room temperature. The samples were then centrifuged for 5 min, water rinse removed and the procedure repeated a further two times.

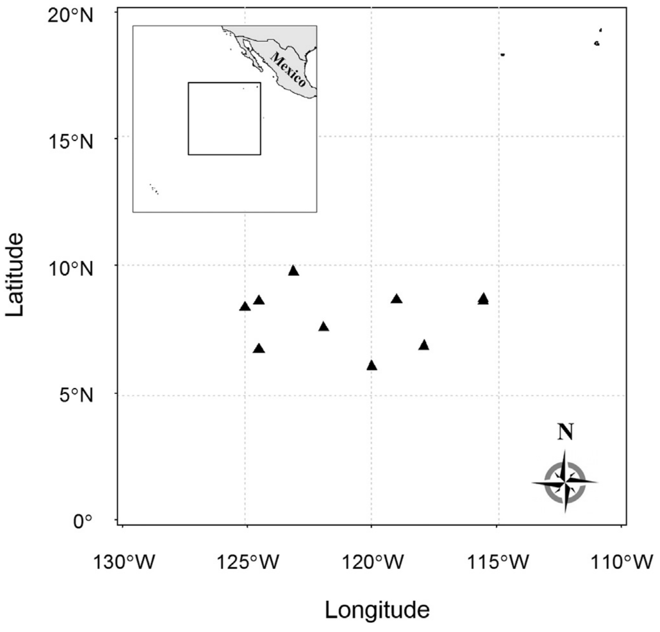

Fig. 1. Sampling locations in the northeast central Pacific Ocean.

Following drying, the samples were weighed (1.0–1.5 mg) into 0.3 mg tin capsules and analyzed using an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation; Cheadle, UK) and vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH; Hanau, Germany). The reference standards for carbon and nitrogen were VPDB and AIR, respectively. The intra-lab standards used to normalize δ^{13}C and δ^{15}N values were USGS 24 (−16.1‰) and USGS 26 (53.7‰), respectively. The analytical error of δ^{13}C and δ^{15}N values were <0.1‰.

2.3. Inter-species comparisons, relative values, isotope niche and niche overlap

To examine inter species differences among sharks and predatory teleosts, analysis of variance (ANOVA) was performed on species δ^{15}N and δ^{13}C values followed by Tukey's HSD (Honestly Significant Difference) paired comparisons.

To determine the isotopic niche width and niche overlap among species and guilds, the SIBER package (Stable Isotope Bayesian Ellipses) in R (Version 3.1.2) was used. Briefly, this method permits the use of a multivariate ellipse-based Bayesian metric for robust statistical comparisons between data sets with different sample sizes (Jackson et al., 2011).

2.4. Trophic position (TP)

The trophic position of individual sharks and predatory teleosts was estimated based on nitrogen stable isotopes following the scaled $\Delta\delta^{15}$N framework approach based on a dietary δ^{15}N value-dependent $\Delta\delta^{15}$N model (Hussey et al., 2014).

Relative TP was calculated as follows:

$$\mathrm{TP} = \frac{\log\left(\delta^{15}\mathrm{N}_{\mathrm{lim}} - \delta^{15}\mathrm{N}_{\mathrm{base}}\right) - \log\left(\delta^{15}\mathrm{N}_{\mathrm{lim}} - \delta^{15}\mathrm{N}_{\mathrm{TP}}\right)}{\mathrm{k}} + \mathrm{TP}_{\mathrm{base}}$$

where $\mathrm{TP}_{\mathrm{base}}$ is the TP of the baseline species, $\delta^{15}\mathrm{N}_{\mathrm{lim}}$ the saturating isotope value, k represents the rate at which $\delta^{15}\mathrm{N}_{\mathrm{TP}}$ approaches $\delta^{15}\mathrm{N}_{\mathrm{lim}}$ and $\delta^{15}\mathrm{N}_{\mathrm{TP}}$ is the δ^{15}N value of the shark or predatory teleost. Omnivorous copepods (mean $\delta^{15}\mathrm{N} = 8.7‰$, $n = 66$) sampled in the study area were used as the baseline species (Olson et al., 2010). The $\delta^{15}\mathrm{N}_{\mathrm{lim}}$ and k values of 21.93 and 0.14, respectively, were derived from a meta-analysis of experimental isotope data (Hussey et al., 2014).

2.5. Size-based isotope relationships

Linear regression was used to investigate the relationship between δ^{15}N and δ^{13}C values and shark length (PCL) for three species (silky, blue and smooth hammerhead shark) with sufficient sample numbers.

Table 1
Characteristics of sharks and other fish sampled in the northeast Pacific Ocean. Stable isotopic values are displayed as the mean (standard deviation) (range).

Species	Common name	*n*	Length (cm) Mean (range) (type)	δ^{15}N (‰) Mean (SD) (range)	δ^{13}C (‰) Mean (SD) (range)	CD (SD)	TP^{15}N Mean (SD)
Carcharhinus falciformis	Silky shark	46	106 (57–167) (PCL)	16.0 (0.8) (13.6–17.5)	−16.4 (0.3) (−17.0 to −15.4)	0.7 (0.5)	4.6 (0.4)
Prionace glauca	Blue shark	28	153 (130–205) (PCL)	16.1 (1.3) (11.8–17.8)	−17.8 (0.7) (−18.8 to −16.4)	1.1 (0.9)	4.7 (0.6)
Sphyrna zygaena	Smooth hammerhead shark	20	152 (103–218) (PCL)	16.1 (1.3) (14.2–19.1)	−15.9 (0.23) (−16.5 to −15.5)	1.1 (0.7)	4.7 (0.8)
Sphyrna lewini	Scalloped hammerhead shark	6	161 (106–131) (PCL)	17.3 (0.6) (16.3–18.1)	−16.3 (0.3) (−16.6 to −15.8)	0.6 (0.3)	5.4 (0.4)
Carcharhinus longimanus	Oceanic whitetip shark	7	110 (97–122) (PCL)	16.4 (0.5) (15.8–17.3)	−16.2 (0.1) (−16.4 to −16.0)	0.5 (0.3)	4.8 (0.3)
Isurus oxyrinchus	Shortfin mako shark	5	148 (109–195) (PCL)	15.5 (1.0) (14.5–17.2)	−15.5 (0.5) (−16.0 to −14.6)	0.8 (0.7)	4.3 (0.6)
Alopias pelagicus	Pelagic thresher shark	13	151 (95–184) (PCL)	16.3 (0.8) (14.3–17.2)	−16.6 (0.3) (−17.1 to −16.1)	0.7 (0.5)	4.7 (0.4)
Alopias superciliosus	Bigeye thresher shark	5	148 (121–173) (PCL)	17.0 (0.9) (15.7–18.1)	−16.6 (0.5) (−17.4 to −16.3)	0.8 (0.4)	5.2 (0.6)
Thunnus obesus	Bigeye tuna	5	122 (106–158) (FL)	14.9 (1.7) (12.8–16.7)	−16.6 (0.1) (−16.8 to −16.5)	–	4.1 (0.8)
Makaira indica	Black marlin	5	132 (127–147) (LF)	15.5 (0.6) (14.9–16.5)	−16.5 (0.5) (−16.8 to −15.6)	–	4.3 (0.3)
Katsuwonus pelamis	Skipjack tuna	5	51 (43–68) (FL)	15.8 (0.7) (14.6–16.5)	−16.9 (0.1) (−17.0 to −16.8)	–	4.5 (0.4)
Coryphaena hippurus	Mahi-mahi	4	92 (86–104) (FL)	13.9 (2.7) (9.9–15.7)	−16.5 (0.3) (−16.7 to −16.2)	–	3.7 (1.0)
Xiphias gladius	Swordfish	4	124 (116–140) (LF)	16.6 (0.3) (16.3–17.0)	−16.4 (0.3) (−16.7 to −16.2)	–	4.9 (0.2)
Lepidocybium flavobrunneum	Escolar	3	112 (95–132) (FL)	15.6 (0.9) (14.6–16.3)	−16.6 (0.2) (−16.7 to −16.4)	–	4.4 (0.4)

PCL, precaudal length; FL, fork length; LF, lower jaw to fork-in-tail length; CD, mean centroid distance; TP$_{15N}$, trophic position based on Hussey et al. (2014).

2.6. Statistics

The statistical analyses were performed using R (Version 3.1.2; R Development Core Team, 2014). All stable isotope data were tested for normality using the Shapiro-Wilk test ($p > 0.05$).

3. Results

The tissue samples from 130 sharks representing 8 species were collected (Table 1). In addition, 26 from other pelagic predators of 6 species were sampled for stable isotope analysis (Table 1). No significant linear relationship was observed between the δ^{13}C and the corresponding δ^{15}N isotopic values for all sampled individuals ($F_{1,\ 154} = 0.14$, $p = 0.71$), neither for those of shark species ($F_{1,\ 128} = 0.54$, $p = 0.47$). The shark individuals exhibited a relatively wider isotopic range of δ^{13}C (−18.8 to −14.6‰) and δ^{15}N (11.9–19.1‰) than other pelagic predators (Table 1). One-way ANOVA results indicated that both the δ^{13}C and δ^{15}N values are significantly different among species in the pelagic community (δ^{13}C, $F_{13,\ 142} = 27.83$, $p < 0.05$; δ^{15}N, $F_{13,\ 142} = 3.10$, $p < 0.05$) (Fig. 2), and significant differences of isotopic signatures were also observed among all shark species (one-way ANOVA; δ^{13}C: $F_{7,\ 122} = 47.01$, $p < 0.05$; δ^{15}N: $F_{7,\ 122} = 2.25$, $p < 0.05$). The Tukey's HSD tests indicated that blue shark had significantly lower δ^{13}C values than other shark and other pelagic predator species (Table 2; Fig. 2). Shortfin mako shark had significantly higher δ^{13}C values than other species, except for smooth hammerhead and oceanic whitetip shark. Only mahi-mahi had significantly lower δ^{15}N values than all other species.

Stable isotope values suggested a considerable niche overlap of corrected standard δ^{15}N-δ^{13}C ellipses areas (SEAc) among the shark species except for blue sharks and shortfin mako sharks (Fig. 3a, Table 3a), which did not exhibit isotopic overlap with most of the other shark species. For blue sharks, limited isotopic niche overlap occurred with bigeye thresher sharks. Approximately 28% of the smooth hammerhead shark SEAc was contained within the SEAc of shortfin mako sharks. Blue shark had the largest isotopic niche space (2.26), followed by bigeye thresher shark (1.48) and shortfin mako shark (1.46). Similar SEA areas were found among silky sharks (0.66), smooth hammerhead sharks (0.73), scalloped hammerhead sharks (0.67), and pelagic thresher sharks (0.75). Compared with other guilds, a remarkable niche overlap was observed (Fig. 3b, Table 4). Nearly 100% of the billfish SEAc was within the SEAc of pelagic sharks, and 61.37% and 24.18% of tuna niche space was represented by overlapped SEAc with pelagic sharks and billfish, respectively. When blue and shortfin mako sharks were treated as separate guilds, a considerable change in the structure of SEAc overlap was detected (Fig. 3c, Table 5). The SEAc of both blue and shortfin mako sharks did not overlap with other species guilds.

The mean trophic level of shark species was 4.7, and high intraspecific variations of TP were found in most shark species, with blue sharks and scalloped hammerhead sharks presenting the largest and smallest range, respectively.

The relationships between stable isotope values for body size for all of the species and sample size >20 were examined (Fig. 4). The results showed that a significant relationship did not occur between PCL and δ^{15}N (silky sharks, $F_{1,\ 44} = 3.97$, $p = 0.052$, $R^2 = 0.04$; blue sharks,

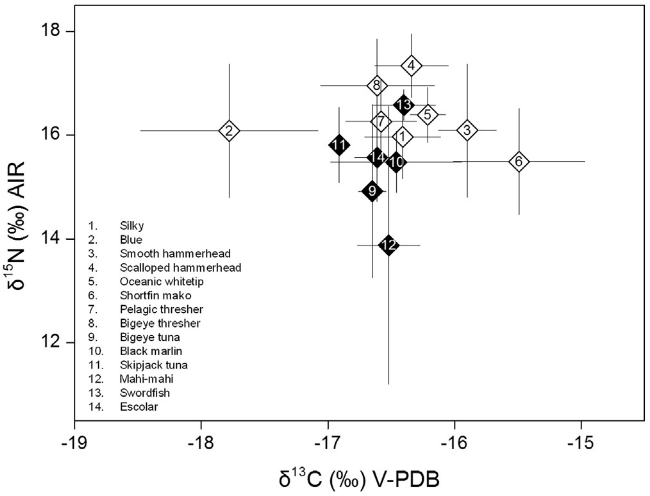

Fig. 2. A biplot of δ^{13}C and δ^{15}N values (mean ± SD) for pelagic sharks (open diamonds) the large predatory teleosts (black diamonds) of the northeast central Pacific pelagic community.

Table 2
p-Values based on Tukey's HSD test for $\delta^{15}N$ and $\delta^{13}C$ values. Significant values are indicated by an * with different degrees.

	Silky	Blue	Smooth	Scalloped	Oceanic whitetip	Shortfin mako	Pelagic thresher	Bigeye thresher	Bigeye tuna	Black marlin	Skipjack tuna	Mahi-mahi	Swordfish
$\delta^{13}C$													
Blue	****												
Smooth	***	****											
Scalloped	1.000	****	0.524										
Oceanic white	0.992	****	0.891	1.000									
Shortfin mako	***	****	0.775	*	0.146								
Pelagic thresher	0.987	****	***	0.994	0.775	****							
Bigeye thresher	0.999	****	*	0.998	0.915	**	1.000						
Bigeye tuna	0.994	*****	*	0.992	0.847	**	1.000	1.000					
Black marlin	1.000	****	0.250	1.000	0.999	*	1.000	1.000	1.000				
Skipjack tuna	0.358	**	***	0.539	0.169	***	0.962	0.996	0.999	0.889			
Mahi-mahi	1.000	*****	0.226	1.000	0.994	*	1.000	1.000	1.000	1.000	0.978		
Swordfish	1.000	****	0.562	1.000	1.000	0.060	1.000	1.000	1.000	1.000	0.847	1.000	
Escolar	1.000	*****	0.218	1.000	0.977	*	1.000	1.000	1.000	1.000	0.999	1.000	1.000
$\delta^{15}N$													
Blue	1.000												
Smooth	1.000	1.000											
Scalloped	0.170	0.334	0.404										
Oceanic white	1.000	1.000	1.000	0.934									
Shortfin mako	1.000	0.997	0.998	0.211	0.981								
Pelagic thresher	1.000	1.000	1.000	0.733	1.000	0.985							
Bigeye thresher	0.793	0.916	0.938	1.000	1.000	0.658	0.994						
Bigeye tuna	0.704	0.604	0.637	0.018	0.543	1.000	0.496	0.146					
Black marlin	0.999	0.997	0.997	0.205	0.979	1.000	0.983	0.648	1.000				
Skipjack tuna	1.000	1.000	1.000	0.513	1.000	1.000	1.000	0.916	0.988	1.000			
Mahi-mahi	*	*	*	**	*	0.595	*	**	0.975	0.604	0.294		
Swordfish	0.998	1.000	1.000	0.998	1.000	0.963	1.000	1.000	0.545	0.960	0.998	*	
Escolar	1.000	1.000	1.000	0.529	0.998	1.000	0.999	0.885	1.000	1.000	1.000	0.719	0.994

**** Represents $p < 0.0001$.
*** Represents $p < 0.001$.
** Represents $p < 0.01$.
* Represents $p < 0.05$.

$F_{1,\,26} = 0.007$, $p = 0.94$, $R^2 = 0.0003$; and smooth hammerhead sharks, $F_{1,\,44} = 3.97$, $p = 0.052$, $R^2 = 0.06$), with only the blue shark exhibiting a markedly positive relationship between $\delta^{13}C$ and PCL ($F_{1,\,26} = 6.53$, $p < 0.05$, $R^2 = 0.20$).

An intra-specific variation in isotopic values was found for several species, with blue sharks showing the largest range for both isotopic values (Table 1). The mean centroid distance (CD) of each individual from the mean of all individuals were calculated, which represents the trophic diversity of a population, for all shark species. The CD significantly differed among all shark species (one-way ANOVA: $F_{7,\,122} = 2.36$, $p < 0.05$). However, significant differences were not observed between any two shark species based on Tukey's HSD test.

4. Discussion

Using stable isotope analysis, this study demonstrates the trophic interactions among shark species, as well as the relative isotopic niche overlap between sharks and other top predator guilds in the northeast central Pacific pelagic community. Moreover, the trophic levels of these pelagic predators have also been calculated.

The results suggested that pelagic sharks from the study area generally occupy similar trophic positions, whereas considerable intra-specific variations occur in isotopic values among shark species. The $\delta^{15}N$ and $\delta^{13}C$ values of all sampled shark species exhibited a relatively wide range, indicating that each species might feed upon more than one trophic level and forage in distinct habitats.

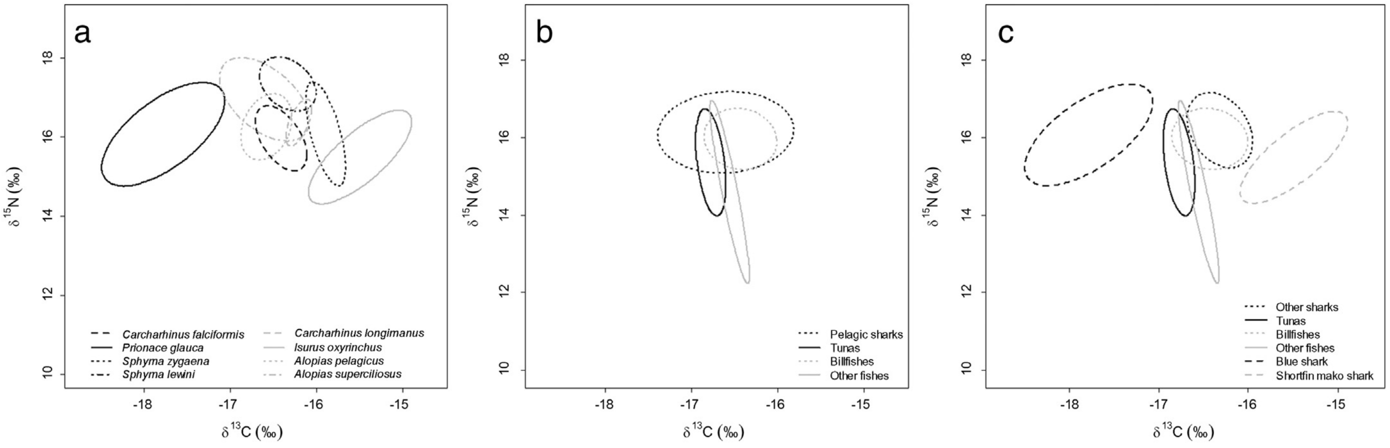

Fig. 3. Stand ellipse areas corrected for sample size (SEAc) of pelagic sharks (a), pelagic guilds (b), and pelagic guilds with blue sharks and shortfin mako sharks separated from the pelagic shark guild (c).

Table 3
Percentage of overlap of the corrected standard ellipses (SEAc) among all of the shark species.

Code	Silky	Blue	Smooth	Scalloped	Oceanic whitetip	Shortfin mako	Pelagic thresher	Bigeye thresher
Silky	–	0	0	0	13	0	57	50
Blue	0	–	0	0	0	0	0	0.
Smooth	0	0	–	8	4	28	0	1
Scalloped	0	0	9	–	6	0	9	53
Oceanic whitetip	0	0	14	17	–	0	9	81
Shortfin mako	0	0	14	0	0	–	0	0
Pelagic thresher	50	0	0	8	3	0	–	63
Bigeye thresher	22	0	14	24	12	0	32	–

Blue sharks and shortfin mako sharks exhibited substantial isotopic differences from other shark species. Although the δ^{15}N values indicated that all of the sharks foraged at a similar trophic level, the δ^{13}C values of blue sharks were much lower than that of the other shark species, whereas the δ^{13}C values of shortfin mako sharks were much greater. In marine environments, decreased δ^{13}C values were observed from the productive inshore coastal waters to the offshore pelagic areas, or from pelagic to demersal zones (Cherel et al., 2008). The lower δ^{13}C values of blue sharks indicated that this species might spend a longer time in the offshore pelagic food web or forage for more δ^{13}C-depleted prey. The gut content analysis (GCA) of blue sharks indicated that this species foraged upon a greater amount of small pelagic fish compared with other shark species which prefer squid (Cortés, 1999; Estrada et al., 2003), although the lower δ^{13}C values could have been caused by its foraging strategy, which included searching for preys in the δ^{13}C-depleted deep sea area (Kubodera et al., 2007). Similar patterns were observed in the southwestern Indian Ocean, where different foraging habitats of blue sharks and silky sharks were identified (Rabehagasoa et al., 2012). Because shortfin mako sharks are considered a formidable predator occupying the top of the marine food web, the intermediate and highly variable δ^{15}N values observed in our study for this species were unexpected, although they may be explained by considerable changes in the diet of shortfin mako sharks between coastal and pelagic waters. Stillwell and Kohler (1982) documented that bluefish were the predominant prey for inshore young shortfin mako sharks (85% total prey volume), whereas cephalopods appeared more frequently in the stomachs of offshore sharks in the Atlantic. This pattern might have occurred in our study as well because the sampled shortfin mako sharks were considered immature, which indicates that they may prefer fish rather than squid or other elasmobranchs which would increase (Semba et al., 2009). In addition, this explanation is supported by the δ^{13}C data in our study, which shortfin mako sharks are known as a highly migratory species that have the ability to migrate between inshore and offshore environments (Stillwell and Kohler, 1982). As the turnover rate of isotopic data in shark muscles was estimated at over a year (MacNeil et al., 2005), the δ^{13}C values obtained here might indicate the relative inshore activity of shortfin mako sharks from 1 year ago. Shortfin mako sharks with the most enriched δ^{15}N values (17.21‰) also had the most enriched δ^{13}C values (−14.64‰) because inshore food webs were more productive and had additional δ^{15}N fractionations (Estrada et al., 2003). Thus, a larger number of shortfin mako shark samples should be collected in the future to test this theory.

Table 4
Percentage overlap of the corrected standard ellipses (SEAc) among the different guilds.

	Pelagic sharks	Tunas	Billfish	Other fish
Pelagic sharks	–	16	40	10
Tunas	61	–	24	23
Billfish	100	16	–	18
Other fish	37	24	27	–

As noted, significant differences were not observed in the isotopic values between the two hammerhead shark species. Although these shark species had a similar trophic niche width according to the SEAc (smooth hammerhead, 0.73; scalloped hammerhead, 0.67), they showed low niche overlap (Table 3), which was consistent with the results found by Loor-Andrade et al. (2015), who concluded that this difference was linked to alternative individual foraging strategies. These two hammerhead shark species consumed prey with different isotopic compositions in different foraging areas (Loor-Andrade et al., 2015). Compared with the hammerhead sharks, higher niche overlaps were found between the two thresher sharks. The δ^{15}N data showed that the bigeye thresher shark may forage at a higher trophic level than the pelagic thresher despite their coexistence in a similar habitat (inferred from δ^{13}C). The bigeye thresher shark was known to feed on large pelagic teleost fish and elasmobranchs (Gruber and Compagno, 1981), whereas the diet of the pelagic thresher shark was presumably small schooling fish and squid (Smith et al., 2008). The SEAc of the silky shark indicated that this species occupied an intermediate trophic level between the hammerhead and bigeye.

In marine ecosystems, segregation in feeding habits has been largely described as a common mechanism to permit the coexistence of several competing marine predators (Albo-Puigserver et al., 2015). However, when treating pelagic sharks as an entire guild, high overlap in SEAc was detected among the guilds of pelagic sharks, tuna, and billfish at the apex of the northeast central Pacific pelagic food web (Fig. 3b). Overall, pelagic sharks shared a similar trophic level with tuna and billfish, and the overall isotopic values of the pelagic community exhibited a narrower range in δ^{13}C. This similarity indicates that other pelagic predators might compensate for reductions in shark abundance, which may have been why Kitchell et al. (2002) concluded that the trophic structure was not significantly impacted after the removal of pelagic sharks. However, when blue sharks and shortfin mako sharks were separated from the pelagic shark guild, overlap was not detected between these two species with either tuna or billfish (Fig. 3c), which indicates the extraordinary trophic role of blue sharks and shortfin mako sharks in the northeast central Pacific ecosystem.

Ontogenetic variations in the foraging ecology and habitat use of three pelagic sharks with sample sizes >20 were examined, and significant relationships were not observed between shark body size and δ^{15}N values for silky, blue and smooth hammerhead sharks, respectively though an ontogenetic diet shift was common in shark species (Lowe et al., 1996; Borrell et al., 2011). This ontogenetic shift may have been caused by the distinct δ^{15}N values of the baseline species, for which large variations have recently been detected in the Pacific Ocean (Olson et al., 2010), and isotopic values of highly migratory predators, which reflect a long period of time-integrated foraging both inside and outside the study area (Heithaus et al., 2013). The significantly positive relationship between the δ^{13}C value and body length of blue shark might indicate an increasing proportion of squid in their diet because squid have less-depleted δ^{13}C values compared with fish prey (Estrada et al., 2003; Markaida and Sosa-Nishizaki, 2010). However, these results must be confirmed with a much larger sample size for the SIA and GCA.

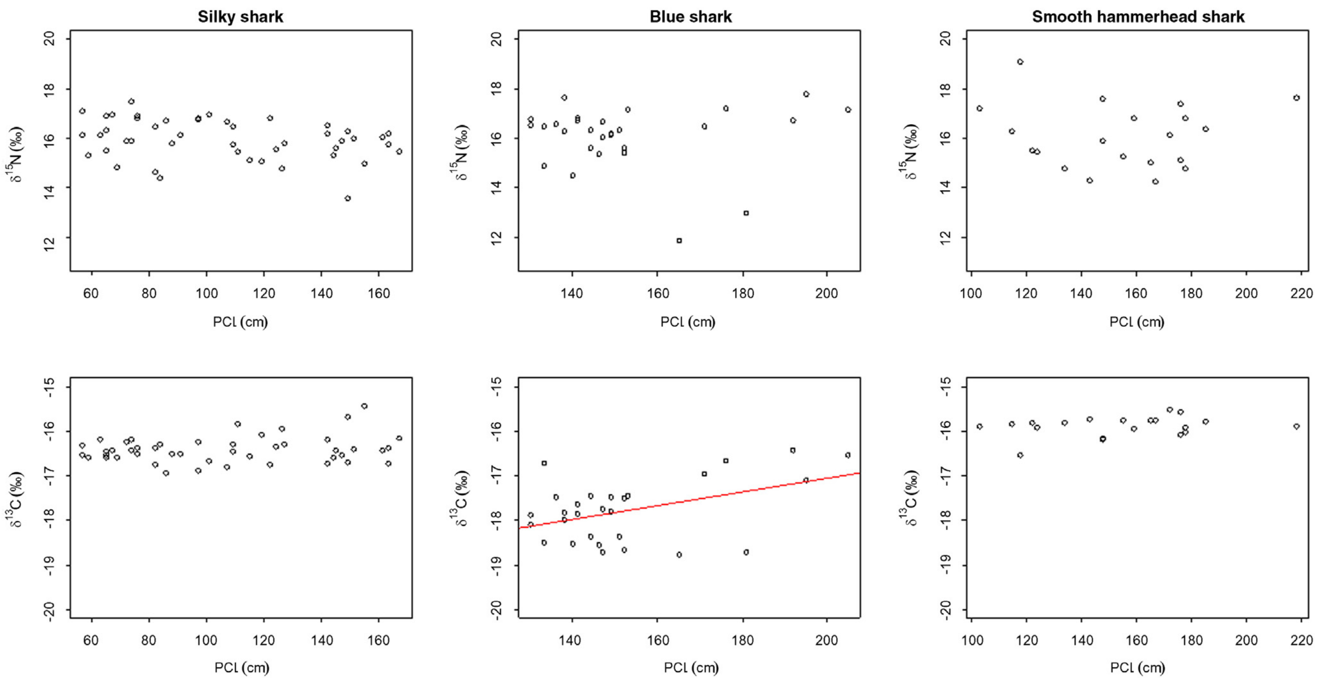

Fig. 4. Influence of size on $\delta^{15}N$ (upper) and $\delta^{13}C$ values (lower) in silky shark (*C. falciformis*), blue shark (*P. glauca*), and smooth hammerhead shark (*S. zygaena*).

5. Conclusions

In this study, large intra-specific variations in $\delta^{15}N$ and $\delta^{13}C$ values and a high degree of isotopic overlap were found among all pelagic shark species in the northeast central Pacific Ocean. Moreover, stable isotopic data suggested that pelagic sharks in the study area also shared similar prey and habitats with other pelagic predators, such as tuna and billfish. The exceptions to this pattern were blue sharks and shortfin mako sharks, which did not show isotopic overlap with tuna and billfish. These results highlight the divergent role of the pelagic sharks instead of being trophically redundant.

Acknowledgment

We thank observers who helped us with the collection and processing of isotopic samples. Li, Y. was supported by National Natural Science Foundation of China (#41206124; #41541042) and Ph.D. Programs Foundation of Ministry of Education of China (#20123104120001). **[SS]**

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.04.013.

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