Diet and trophic level of scalloped hammerhead shark (*Sphyrna lewini*) from the Gulf of California and Gulf of Tehuantepec, Mexico

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Abstract
We examined the diet and trophic level of *Sphyrna lewini* in the Gulf of California (GC) during 2001 and in the Gulf of Tehuantepec (GT) during 2005 using data from stomach content and stable isotope analysis of δ^{15}N and δ^{13}C. *S. lewini* diet was represented by pelagic and benthic prey species where the most important in weight was *Scomber japonicus* (27.70±4.54%) in GC, while in GT it was *Auxis* spp. (26.19±4.14%). There were differences for δ^{15}N and δ^{13}C between group sizes, showing a difference in the use of area and resources, while the differences for δ^{15}N and δ^{13}C between areas were related to changes in the isotopic signal from the base of the food web in each region. Based on δ^{13}C and δ^{15}N variability, diversity values (GC=3.69; GT=3.17) and diet breadth (GC=0.006; GT=0.002), we propose that *S. lewini* is an opportunistic predator. The trophic level of *S. lewini* was above four in all categories, which indicates that *S. lewini* is a tertiary consumer. We may conclude that *S. lewini* plays an important functional role as top predator within areas of Mexico.

Keywords: Shark, *Sphyrna lewini*, Gulf of Tehuantepec, Mexico, Stomach content analysis, Stable isotopes.

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Introduction

Knowledge of diet and trophic level of species have long been recognized as critical factors required for the successful conservation and management of shark species and their environment (Hussey *et al*., 2010). Different studies have applied stable isotopes and stomach content analysis on sharks to investigate the diet (Domi *et al*., 2005; Borrell *et al*., 2011) and trophic level (Fisk *et al*., 2002; Estrada *et al*., 2003), making possible the determination of prey consumed types, and possible variations in the trophic role at the intraspecific level in different areas, therefore establishing trophic interactions between species. This provides clues to the underlying ecosystem structure, making it an important basis for the management of fishery resources (Tripp-Valdez *et al*., 2010).

The scalloped hammerhead shark (*Sphyrna lewini*) is widely distributed along the Mexican Pacific coast and highly abundant in the Gulf of California (GC) and the Gulf of Tehuantepec (Castillo-Geniz et al., 1999). Some authors have identified *S. lewini* as a generalist predator that feeds on fish and cephalopods with changes in diet depending on sex and maturity stage (Klimley, 1983; Galván-Magaña *et al*., 1989), however, the trophic role of *S. lewini* along the Mexican coast is still unknown. Therefore, there is the need for studies in different locations to give insights and monitor more in detail the diet and trophic level of *S. lewini* and detect possible intraspecific variations.

The combination of stable isotopes (δ^{15}N and δ^{13}C) and stomach content analyses would help to understand the trophic role of *S. lewini* along the Mexican coast and will give insights for the fishery management of this species. Stomach-content analyses provide better taxonomic resolution, providing short-term dietary information (recently consumed elements) (Chipps and Garvey, 2007), while, δ^{15}N and δ^{13}C are used to elucidate the relative contribution of different potential food sources to the diet of a predator over a long time period (Hansson *et al*., 1997).

Although *S. lewini* is considered an important part of the elasmobranch fishery in Mexico (Castillo-Geniz *et al*., 1999) and was recently included in the red list of endangered species (IUCN; Estupiñán-Montaño *et al*., 2009), information on trophic ecology for this specie is scarce for the application of regulatory measures in the capture of sharks (Torres-Rojas *et al*., 2009). In this context, considering that sharks play an important role as top predators in the marine ecosystems of the world, the present study investigates the diet and trophic level of the scalloped hammerhead shark, *S. lewini,* from stable isotope (δ^{15}N and δ^{13}C) and stomach contents analyses to understand the ecological role that they develop and the possible intraspecific variation in two of the most important areas (GC and Gulf of Tehuantepec) in México.

Material and methods

Sampling was conducted in two different regions: 1) GC at La Paz Baja California Sur (24°08'32"N, 110°18'29"W) and 2) Gulf of Tehuantepec (GT) at a fishing camp called Chipehua in Oaxaca (16°02'3"N, 95°22'49"W) corresponding to the southern end of the North eastern

Tropical Pacific (Fig. 1). Both sampling locations are characterized by intense oceanographic physical dynamics, like

different water masses and potentially influenced by a shallow oxygen minimum zone (Lavin and Marinone, 2003).
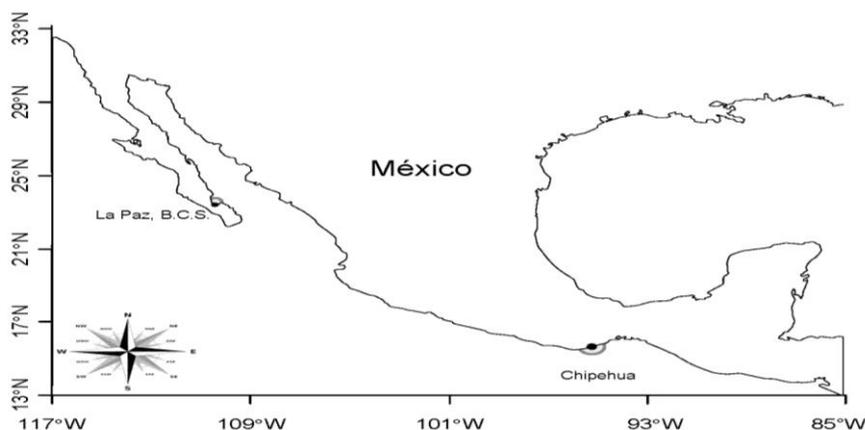
Figure 1: Studied area where *Sphyrna lewini* specimens were caught (Gulf of California and Gulf of Tehuantepec, Mexico). Gray circles= fishing area Black points= sampling area.

Sample collection and processing
Samples were collected monthly from the artisanal shark fleet landings during 2001 and 2005. Once sharks were identified, total length (TL) in cm and sex of each specimen were recorded. Muscle tissue samples from the dorsal area and stomach contents of scalloped hammerhead sharks were collected. All samples were kept frozen (-20°C) until analysis in the Fish Ecology Laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR) at La Paz, Baja California Sur.

For stomach content analyses, we separated four levels of digestion according to Galván-Magaña (1989). The identification of fishes was based on descriptions given by Clothier (1950), Allen and Robertson (1994), Fischer *et al.* (1995), and Thomson *et al.* (2000). Cephalopods and cephalopod beaks were identified based on Clarke (1986) and

Wolff (1984). Crustaceans were identified using the keys by Fischer *et al.* (1995).

For isotopic analyses, (1) shark tissues were placed in vials fitted with Teflon lids and dried for 24 hours in a LABCONCO dry freezer at -45ºC, at a pressure of 24 to 27×10^{-3} mbar to eliminate moisture, (2) the samples were then ground in an agate mortar, and sub-samples (1mg) were weighed and stored in tin capsules (8 x 5mm), and (4) the C:N ratio and $\delta^{13}C$, $\delta^{15}N$ compositions were determined at the Stable Isotope Laboratory of the University of California at Davis, USA using an Isotope Ratio Mass Spectrometer (IRMS, 20-20 mass spectrometer, PDZEuropa, Scientific Sandbach, United Kingdom, UK) with a precision of 0.2% for $\delta^{13}C$ and 0.3% for $\delta^{15}N$.

Data analysis
For stomach contents analyses, we constructed cumulative prey curves

(Estimate S-program; Colwell, 2006) to determine whether the number of stomachs analyzed was adequate to represent the trophic spectrum of *S. lewini* in each area (Jiménez-Valverde and Hortal, 2003). Then, as an indicator of the degree of variability of the diet, the coefficient of variation was calculated. For this study, a coefficient of variation <0.05 was considered adequate for all stomachs for the representation of the trophic spectrum of *S. lewini* in each area (Steel and Torrie, 1992). Finally, we plotted the diversity vs. the number of stomachs analyzed.

The diet data from *S. lewini* were calculated as mean proportion by number (%MN), weight (%MW), and frequency of occurrence (%FO) for individual fish and then averaged for each prey type as described by Chipps and Garvey (2007). An analysis of similarities (ANOSIM) was used to evaluate diet differences between sexes, size groups (<100 and >100 cm TL, Bejarano-Alvarez *et al*., 2011), and areas (PRIMER 6 v. 6.1.6). When R is near zero, there is no separation between groups, while, when R is between 0.2 and 1.0, it shows that *S. lewini* doesn't have exactly the same diet (Clarke and Warwick, 2001).

The Shannon-Wiener diversity index, based on the abundance of all prey items, was used to calculate diversity (Pielou, 1975):

$$H' = -\sum_{i=1}^{s} (p_i) \ln(p_i)$$

where p_i is the numerical fraction of individuals belonging to the i-th species

The breadth of the *S. lewini* trophic niche was evaluated using Levin's standardized index, "*Bi*" (Krebs, 1999):

$$Bi = \frac{1}{n-1 \left\{ (1/\sum P^2_{ij}) - 1 \right\}}$$

where *Bi* is Levin's index for predator *i*, $\sum P^2_{ij}$ is the numerical proportion of the *j*th prey item in predator *i*'s diet; and *n* is the number of prey categories.

The trophic level based on stomach contents was calculated using the equation proposed by Christensen and Pauly (1992); the mean and standard deviation (SD) were calculated to determine the variability of individual values.

$$TP = 1 + (\sum_{i=1}^{n} DC_{ji})(TP_i)$$

where DC*ji* is the diet composition in weight, in terms of the prey proportion (*i*) in the predator´s diet (*j*); TP is the trophic position of prey species i; and n is the number of prey groups in the diet.

For isotopic analyses, the C:N ratios were used to determine whether samples had a low lipid content, assuming that C:N ratio values below 3.5 indicate a low lipid concentration in the tissue (Post *et al*., 2007). For any sample having values of C:N above 3.5, we used the following arithmetic correction proposed by Post *et al*. (2007):

$\delta^{13}C_{corrected} = \delta^{13}C_{untreated}$ -3:32 + 0:99 x C : N.

Stable isotope values (δ) were calculated using the formula proposed by Park and Epstein (1961):

$\delta^{15}N$ or $\delta^{13}C$ (‰) = [(R_{sample} / $R_{standard}$)-1] x 1000.

where, R_{sample} is the isotopic ratio of the heaviest stable isotope with relation to the lightest ($\delta^{13}C/\delta^{12}C$ or $\delta^{15}N/\delta^{14}N$), respectively in the sample and $R_{standard}$ is the value of the isotopic ratio for a known standard; in this case the composition of the carbon isotope is referred to as the standard Pee Dee Belemite formation and the nitrogen is reported with relation to the standard atmospheric air.

We compared the $\delta^{13}C$ and $\delta^{15}N$ values among sexes, size groups, and areas. Data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test). Stable isotope derived data failed these assumptions; therefore, a non-parametric (Mann-Whitney) test was used to detect intraspecific variations. We used Spearman's rank correlation analyses to test whether the size (TL) had significant effects on $\delta^{15}N$ values in *S. lewini* tissues (Zar, 1999). Statistical analyses were performed in Statistica v. 8.0 (Hill and Lewicki, 2007), with significance set at $p < 0.05$.

Trophic level was calculated using isotope values with the equation proposed by Post (2002). The trophic level value used as $\delta^{15}N$ at the base of the food web for GC was particulate organic material (POM) based on Altabet *et al.* (1999) ($\delta^{15}N = 9.3‰$) and for GT was POM based on Thunell and Kepple (2004) ($\delta^{15}N = 6.2‰$), and was assigned a trophic level of 1 (White *et al.*, 2007) with an enrichment factor of 3.4‰ (Post, 2002). We then calculated the mean and standard deviation (SD) to represent variability.

$$TP = \lambda + \frac{\left(\delta^{15}N_{Predator} - \delta^{15}N_{Base}\right)}{\Delta_n}$$

Where λ is the trophic position for POM, Δ_n is the theoretical value of ^{15}N enrichment per trophic level, $\delta^{15}N_{Predator}$ is the $\delta^{15}N$ value of each individual *S. lewini*, $\delta^{15}N_{Base}$ is the $\delta^{15}N$ value of POM.

Results

The total length (TL) of *S. lewini* in GC ranged from 83 to 162 cm, with an average length of 98.6 cm (SD=18.92), whereas *S. lewini* in GT ranged from 51 to 270 cm (TL), with an average of 187.53 cm (SD= 53.81). Of the total 21 *S. lewini* specimens sampled in GC, 14 stomachs (66%) contained food (4 males and 10 females), and 7 (34%) were empty. All samples were obtained during 2001. Of the total *S. lewini* samples in GT ($n=100$), 100 stomachs (100%) contained food; 86 were males, 14 were females (Table 1).

Table 1: Stomach content analyzed and C:N ratio for *Sphyrna lewini* in the Gulf of California and Gulf of Tehuantepec by sex, size class and year (S.D.=Standard deviation; *n*=total of *S. lewini* sampled; x= no samples).

| Species | Category | *n* | Total of stomach with content analyzed | Isotopes samples | C:N | | | |
					Min	Max	Mean	SD
Gulf of California		21	14	21				
	Males	8	4	8	2.92	3.19	3.09	0.09
	Females	13	10	13	2.97	3.19	3.07	0.07
	<100cm	14	9	14	2.97	3.19	3.08	0.06
	>100cm	7	5	7	2.92	3.19	3.06	0.10
	2001	21	14	21	2.92	3.19	3.08	0.08
	2005	x	x	x	x	x	x	x
Gulf of Tehuantepec		100	100	79				
	Males	86	86	41	2.42	3.66	3.18	0.24
	Females	38	14	38	2.82	3.44	3.20	0.14
	<100cm	9	9	6	3.12	3.38	3.24	0.10
	>100cm	91	91	73	2.42	3.63	3.18	0.20
	2001	x	x	x	x	x	x	x
	2005	100	100	79	2.42	3.66	3.19	0.19

The C:N values for *S. lewini* muscle in GC range from 2.92 to 3.20, with an average of 3.08±0.08. The *S. lewini* C:N values in GT range from 2.42 to 3.66, with an average of 3.19±0.19 (Table 1). Prey species accumulation curves showed that a sufficient number of stomachs were analyzed to characterize the diet of *S. lewini* in GC (cumulative number of stomachs to reach a C.V. ≤0.05=12) and *S. lewini* in GT (cumulative number of stomachs to reach a C.V. ≤0.05=76) (Fig. 2).

Diet for S. lewini

For *S. lewini* in GC, 16 different taxa, including 15 families were identified as prey items. According to the digestion level, 12% of prey items were at level 1,

38% were at level 2, 35% were at level 3, and 15% were at level 4. Based on %MW, the most important prey items were *Scomber japonicus* (27.70%±4.54), *Synodus evermanni* (18.85%±3.67) and *Porichthys analis* (12.58%±3.32). The ANOSIM showed no diet separation between the sexes (R=0.03) and size groups (R=0.12). The diversity index value was 3.69 and diet breadth value was 0.006.

The Mann–Whitney U test showed significant differences in $\delta^{15}N$ $\delta^{15}N$ (U=13.0, *p*<0.05) and $\delta^{13}C$ (U=7.5, *p*<0.05) between size groups. However, no differences were found between sexes ($\delta^{15}N$ [U=44.0, *p*=0.56]; $\delta^{13}C$ [U=46.5, *p*=0.69]). Significant relationships were observed (R=-0.49, *p*<0.05) between size and $\delta^{15}N$ (Fig. 3).
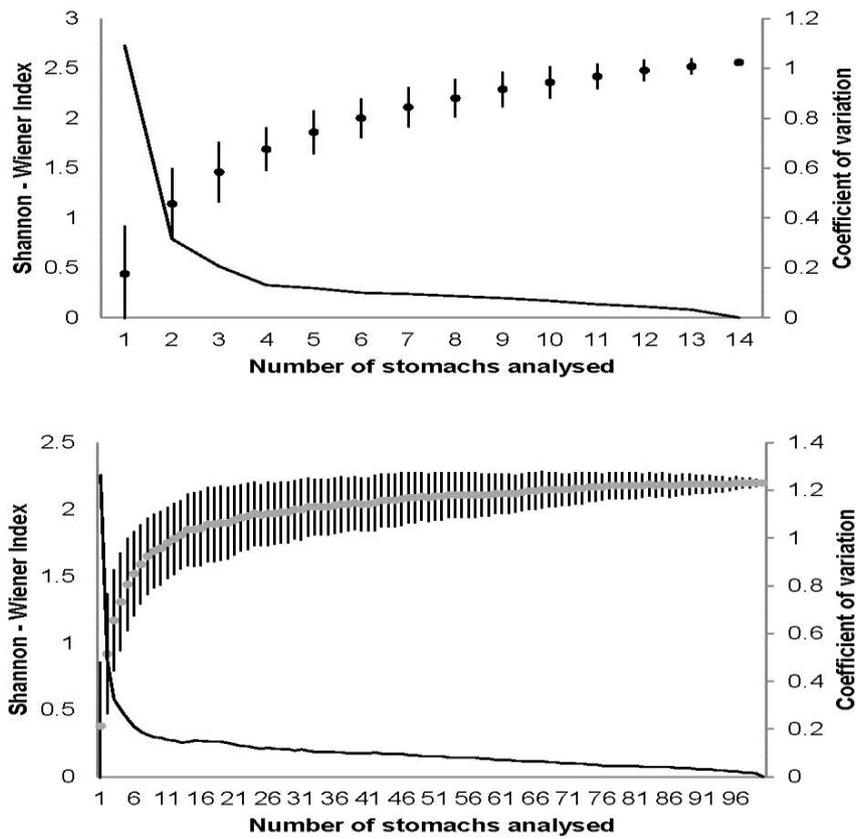
Figure 2: Randomized cumulative prey curves generated for *Sphyrna lewini*. Shannon-Wiener diversity index=black circles for Gulf of California and gray circles for Gulf of Tehuantepec, S.D.= vertical lines and black line=Coefficient of variation.
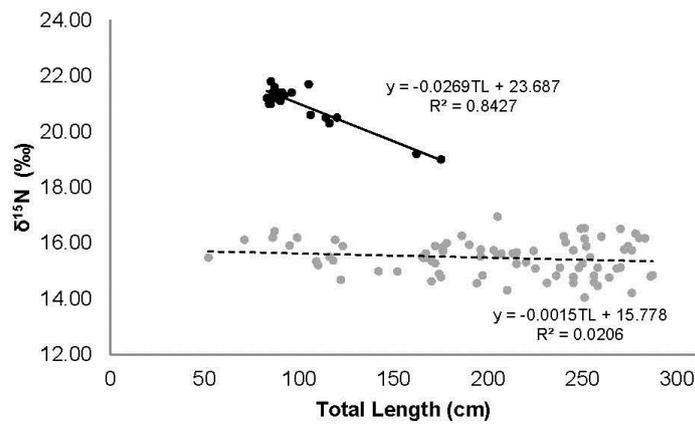
Figure 3: Relationships between δ¹⁵N and total length for *Sphyrna lewini* in the Gulf of California (black circles) and in the Gulf of Tehuantepec (gray circles). Fine continuous line for the Gulf of California and broken for the Gulf of Tehuantepec.

For *S. lewini* in GT, 23 different taxa, including 16 families were identified as prey items. According to the digestion level, 2% of prey items were at level 1, 20% were at level 2, 46% were at level 3, and 32% were at level 4. Based on %MW, the most important prey items were *Auxis* spp. (26.19%±4.14), *Mastigoteuthis dentata* (20.48%±19.20) and *Euthynnus lineatus* (14.75%±3.53) (Table 2). The ANOSIM showed no diet separation between the sexes (R=0.03) and size groups (R=0.09). The diversity index value was 3.17 and diet breadth value was 0.002. The Mann–Whitney U test showed significant differences in $\delta^{15}N$ (U=82.50, *p*<0.05) and $\delta^{13}C$ (U=103.50, *p*<0.05) between size groups. However, no differences were found between sexes ($\delta^{15}N$ [U=752.50, *p*=0.79]; $\delta^{13}C$ [U= 649.00, *p*=0.20]). No linear relationship was observed (R=-0.09, *p*=0.42) between size and $\delta^{15}N$ (Fig. 3).

Table 2: Summary of food categories in stomachs of *Sphyrna lewini* from the Gulf of California "GC" and from the Gulf of Tehuantepec "GT", Mexico expressed as percentages of the Mean proportion by number (%MN), Mean proportion by weight (%MW) and frequency of occurrance (% FO) (x=not present in the diet; *n*=stomachs with contents; SD=Standard deviation).

Prey item			*S. lewini* "GC" (*n* = 14)			*S. lewini* "GT" (*n* = 100)		
			%MN (SD)	%MW (SD)	%FO	%MN (SD)	%MW (SD)	%FO
Cephalopoda	Loliginidae	*Lolliguncula (Loliolopsis) diomedeae*	3.57 (1.33)	0.10 (0.05)	7.14	0.16 (1.67)	0.10 (0.16)	1.00
	Gonatidae	*Gonatus* spp.	7.14 (2.67)	7.14 (2.63)	7.14	x	x	x
	Enoploteuthidae	*Abraliopsis affinis*	0.79 (0.29)	0.01 (0.01)	7.14	x	x	x
	Ancistrocheiridae	*Ancistrocheirus lesueurii*	x	x	x	0.22 (0.22)	0.01 (0.01)	1.00
	Ommastrephidae	*Dosidicus gigas*	3.96 (1.48)	0.05 (0.02)	7.14	1.00 (1.00)	1.00 (1.00)	1.00
		Sthenoteuthis oualaniensis	x	x	x	0.11 (0.11)	0.01 (0.01)	1.00
	Mastigoteuthidae	*Mastigoteuthis dentata*	x	x	x	30.36 (29.38)	20.48 (19.20)	47.00
	Argonautidae	*Argonauta nouryi*	x	x	x	1.79 (1.38)	1.87 (1.46)	3.00
Crustacea	Squillidae	*Squilla biformis*	x	x	x	3.80 (1.84)	0.83 (0.06)	9.00
	Penaeidae	*Farfantepenaeus californiensis*	4.76 (1.21)	2.08 (0.57)	14.29	1.90 (1.43)	1.98 (1.63)	4.00
	Galatheidae	*Pleuroncodes planipes*	2.38 (0.89)	0.64 (0.24)	7.14	x	x	x
Teleostei	Muraenidae	*Gymnothorax* spp.	0.79 (0.27)	0.35 (0.13)	7.14	1.26 (1.19)	1.06 (1.01)	3.00
	Clupeidae	*Sardinops caeruleus*	3.57 (1.36)	0.80 (0.29)	7.14	x	x	x
	Synodontidae	*Synodus evermanni*	13.69 (2.80)	18.85 (3.67)	28.57	x	x	x
	Batrachoididae	*Porichthys analis*	7.93 (2.66)	12.58 (3.32)	14.29	x	x	x
	Belonidae	*Strongylura exilis*	x	x	x	3.00 (1.14)	3.00 (1.14)	3.00
	Hemirhamphidae	*Oxyporhamphus micropterus*	x	x	x	3.44 (1.39)	4.27 (1.42)	9.00
	Exocoetidae	*Exocoetus volitans*	x	x	x	1.33 (1.21)	1.00 (1.00)	2.00
	Serranidae	Serranids	7.14 (1.81)	7.19 (2.66)	14.29	x	x	x
		Paralabrax maculatofasciatus	7.14 (2.67)	7.14 (2.73)	7.14	x	x	x
	Echeneidae	*Remora remora*	x	x	x	0.33 (0.33)	0.95 (0.95)	1.00
	Carangidae	*Caranx caballus*	x	x	x	2.64 (1.54)	3.49 (1.98)	5.00
		Chloroscombrus orqueta	x	x	x	2.50 (1.54)	2.10 (1.04)	5.00
		Decapterus spp.	x	x	x	0.17 (0.16)	0.29 (0.28)	1.00

Table 2 continued:

	Selar crumenophthalmus	x	x	x	0.58 (0.15)	1.02 (0.39)	2.00
Coryphaenidae	*Coryphaena* spp.	x	x	x	7.71 (2.33)	12.29 (13.33)	15.00
Labridae	*Oxyjulis californica*	0.79 (0.27)	1.28 (4.81)	7.14	x	x	x
Acanthuridae	*Prionurus punctatus*	7.14 (2.73)	7.14 (6.73)	7.14	x	x	x
Scombridae	*Auxis* spp.	x	x	x	22.40 (7.39)	26.19 (4.14)	33.00
	Euthynnus lineatus	x	x	x	12.06 (3.39)	14.75 (3.53)	17.00
	Katsuwonus pelamis	x	x	x	1.00 (1.00)	1.00 (1.00)	1.00
	Scomber japonicus	21.42 (3.80)	27.70 (4.54)	28.57	x	x	x
	Thunnus albacares	x	x	x	1.00 (0.00)	1.00 (1.00)	1.00
Paralichthyidae	*Paralichthys woolmani*	7.73 (2.30)	6.97 (1.10)	14.29	x	x	x
Balistidae	*Canthidermis maculatus*	x	x	x	1.16 (1.12)	1.32 (1.47)	2.00

Diet comparison between areas for S. lewini

According to ANOSIM, *S. lewini* showed changes in diet composition between areas (R=0.36; Table 2). Significant differences were found between small *S. lewini* (δ^{15}N [U=0.00, $p<0.05$]; δ^{13}C [U=16.00, $p<0.05$]) and large *S. lewini* (δ^{15}N [U=0.00, $p<0.05$]; δ^{13}C [U=41.00, $p<0.05$]) of both areas. Also, between large *S. lewini* from GC and small *S. lewini* from GT (δ^{15}N [U=0.00, $p<0.05$]; δ^{13}C [U=1.00, $p<0.05$]) and between small *S. lewini* from GC and large *S. lewini* from GT for δ^{15}N (U=0.00, $p<0.05$) but not for δ^{13}C (U=511.00, $p=1.00$) (Fig. 4).

Trophic level for S. lewini

The trophic level of *S. lewini* determined from δ^{15}N was 4.42±0.21 for GC and 3.72±0.18 for GT. While the trophic level obtained from stomach contents was 4.56±0.69 for GC and 4.79±0.55 for GT. The mean trophic level value estimated from the stomach contents of *S. lewini* in all size groups was 4.5 and 4.8 for GC and GT, respectively. While the mean trophic level value estimated from stable isotope was 3.7 and 4.5 for GC and GT, respectively in all size groups (Table 3).

Table 3: Isotopic composition (δ^{13}C and δ^{15}N presented in ‰) and trophic level (TL) of *Sphyrna lewini* sampled in the Gulf of California and Gulf of Tehuantepec México (*n*=number of samples, sd=Standard deviation).

Area	Category	*n*	δ^{15}N (‰)			δ^{13}C (‰)			TL Diet (sd)	TL δ^{15}N (sd)
			Min	Max	Mean (sd)	Min	Max	Mean (sd)		
Gulf of California		21								
			20.30	21.60	21.02 (0.43)	-16.70	-16.10	-16.37 (0.23)	4.37 (1.05)	4.44 (0.12)
	Males	8	19.00	21.80	20.91 (0.88)	-17.50	-15.50	-16.46 (0.61)	4.70 (0.55)	4.41 (0.26)
	Females	13	21.00	21.80	21.30 (0.22)	-16.80	-15.50	-16.20 (0.35)	4.52 (0.76)	4.53 (0.06)
	<100cm	14	19.00	21.70	20.26 (0.91)	-17.50	-16.40	-16.90 (0.43)	4.63 (0.62)	4.22 (0.26)
	>100cm	7								

Table 3 continued:

	n								
Gulf of Tehuantepec	79								
		14.05	16.95	15.45	-16.79	-15.06		4.80	3.78 (0.16)
Males	41			(0.57)			-16.08 (0.43)	(0.55)	
		14.21	16.53	15.48	-16.75	-15.20		4.72	3.79 (0.20)
Females	38			(0.68)			-16.19 (0.41)	(0.59)	
		15.48	16.42	16.06	-16.55	-15.06		4.87	3.95 (0.09)
<100cm	6			(0.32)			-15.63 (0.58)	(0.36)	
		14.05	16.95	15.42	-16.79	-15.15		4.78	3.77 (0.18)
>100cm	73			(0.62)			-16.18 (0.38)	(0.57)	

Discussion

Diet comparison

In the current study, the mean length of the captured *S. lewini* in GC (98.6 cm) was less than the typical maturity length (170 to 288cm TL; Bejarano-Alvarez *et al*., 2011) in the study area, suggesting that fishing activities take place at least partially in nursery habitats. Similar findings have been documented off Mazatlan waters (Torres-Rojas *et al*., 2009). These data reinforce the conclusion that juveniles of this species are being fished in the GC. Unlike the Gulf of Tehuantepec, where the mean length was 187.53 cm, indicating the presence of adult organisms.

Adult *S. lewini* specimens at the southern of Mexico have been previously reported by Anislado-Tolentino and Robison-Mendoza (2001) who found sizes above 200cm. Borrell *et al*. (2011) mention that the gears used may have influenced the (in the interpretation of which species were) species composition of the caught. However, in the current study all samples proceed of the artisanal shark fleet (7 m long boats with 75-hp engine) use a deep long-line as fishing gear, so we can assume that the fishing effort was similar. Therefore, we can infer that there is segregation between areas by *S. lewini*, where juveniles are most abundant in the GC while adults will be present in the GT.

In general, the diet of *S. lewini* includes a large variety of species (Galván-Magaña *et al*., 1989; Torres-Rojas *et al*., 2009). In the present study, the diet of *S. lewini* includes a total of 16 species in GC and 23 in GT. However, this trophic spectrum is low compared with other studies of *S. lewini* in Mexico, where the food spectrum can attain 87 species (Torres-Rojas *et al*., 2006). The observed differences may be a response to bio-geographical distributions of the prey species and can be used as indicator of local preferences. Support for this assumption lies in the fact that the diversity values (3.69 for GC and 3.17 for GT) in this study were similar to those obtained by Torres-Rojas *et al*. (2006) in the coast of Mazatlan (3.42). Another indication of the above is the fact that Torres-Rojas *et al*. (2006) analyzed 556 stomachs while this study did not pass the 100 stomachs by area. However, despite the low number of stomachs analyzed for each area, according to the coefficient of variation and cumulative curves of prey species (Fig. 2), these were sufficient to characterize the *S. lewini* diet generally in the GC and in the Gulf of Tehuantepec.

Due to the variance in the digestion level observed at the stomach content of *S. lewini* at both sites, we can assume that they constantly feed. Torres-Rojas *et al.* (2009) report similar behavior in Mazatlan. However, we observed the presence of prey digestion states 3 and 4. According to gastric evacuation rates measured in *S. lewini*, the fish digest food within 5–22 h (Bush and Holland, 2002) and sharks caught are collected at dusk (18:30 h), reflecting that most feeding activity occurs at night. This coincides with reports by Klimley *et al.* (1988), who mention that *S. lewini* is more active at night.

In the present study, the main dietary items of *S. lewini* in GC were teleostei, mollusca (essentially cephalopods) and crustacea distributed along the water column (epipelagic, mesopelagic and benthic; Table 2). The mesopelagic fish *S. japonicus* belonged to the Scombridae family, which was the dominant prey items in the diet of this species in number, occurrence, and weight, indicating the ability of *S. lewini* to forage in pelagic habitats. Effectively, this species has been described as a mesopelagic feeder (Klimley, 1983; Galván-Magaña *et al.*, 1989). The presence of benthic fish such as *S. evermanni* and *P. analis* in the stomach contents of *S. lewini* is also evidence of this species as a benthic predator. These and other benthic fish species have also been reported to be an important part of the diet of *S. lewini* captured off the GC (Klimley, 1983; Galván-Magaña *et al.*, 1989; Torres-Rojas *et al.*, 2009).

Dietary studies of *S. lewini* in the Gulf of Tehuantepec are scarce. Cabrera-Chavez and Castillo-Geniz (2000)

classified *S. lewini* as a generalist feeder, where smaller animals fed primarily on shrimps, the mid-size animals mainly on crabs, and the largest ones primarily on teleosts. In the present study, the major prey groups of *S. lewini* in GT were teleostei (Scombridae) mollusca (mostly cephalopoda) and crustacea (mainly Squillidae and Penaeidae family). The presences of the epipelagic fish *Auxis* spp. denote the ability of *S. lewini* to forage near the surface. However, we can see the presence of mesopelagic (*M. dentata*) and benthic species (*Squilla biformis*) too, similar to the reported in the GC.

The C:N values show that the white-muscle tissue of *S. lewini* (is free of lipids) has a low lipid content, as it is below the 3.5 value reported by Post *et al.* (2007) as critical to influence in the $\delta^{13}C$. On the other hand the $\delta^{15}N$ in elasmobranchs can be affected due to the presence of urea in their tissues (Hussey *et al.*, 2010) by enriching N^{14} which result in a decrease in $\delta^{15}N$ values (Gannes *et al.*, 1998) skewing ecological interpretations (Kim and Koch, 2011), However, it has been observed that the urea concentration is related to the location where the tissue is taken. The dorsal area presents lower concentration of urea as a consequence of lower distribution of red muscle fibers. Therefore, the dorsal muscle use in this work seems to be the ideal study of diet and trophic level of *S. lewini*, since that would present a lower isotopic variation as a result of the low concentrations of urea.

In the present study stomach content analysis and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) determinations allowed us to demonstrate the diversity and wide trophic spectrum of

S. lewini. In agreement to previous studies (Clarke, 1971; Duncan and Holland, 2006; Torres-Rojas *et al*., 2009) the stable isotopic composition of *S. lewini* reflected the exploitation of benthic realm fee although other pelagic species (*S. japonicus* and *Auxis* spp.) had a major presence in the stomach content, therefore, $\delta^{15}N$ we would reflect in an integrated manner the preferences of *S. lewini* in the water column (Hussey *et al*., 2012).

Some inferences can be drawn based on *S. lewini* $\delta^{13}C$ values and POM $\delta^{13}C$ values previously reported. In the GC $\delta^{13}C$ from -15‰ to -10‰ has been reported for coastal species (Niño-Torres *et al*., 2006). While, in GT Aurioles Gamboa *et al*. (2009) mentioned a uniform $\delta^{13}C$ values in POM close to -20‰ (Goericke and Fry, 1994) between 0° and 30° in both hemispheres, Based on $\delta^{13}C$ values of muscle we can assume that *S. lewini* reflect a preference for coastal areas (near to -15‰) and only rarely in oceanic areas in both areas (Table 3).

Some authors mention that *S. lewini* fed on coastal and oceanic prey species related the preferences to ontogenetic changes; where small sharks have a preference to mesopelagic small cephalopods in coastal waters and larges sharks feed mostly of epipelagic fishes in oceanic areas (Klimley, 1983; Galván-Magaña *et al*., 1989). In this study, these changes were not detected from SCA indicating similar diets between sizes groups, but, they were detected with SIA, possibly due to the fact that *S. lewini* feed on ecologically equivalent prey items but feed in different areas, similar to the findings described by Aurioles-Gamboa *et al*. (2006) for sea lions. For example *Auxis* spp. which is reported in coastal and oceanic areas, due to its wide distribution can be consumed by small and large sharks, which causes similar ANOSIM values. However since the prey species comes from different areas, the isotopic values are different. The $\delta^{13}C$ values supports the results reported by Klimley *et al*. (1993) and Galván-Magaña *et al*. (1989) where large *S. lewini* showed more negative values (indicating preferences for oceanic waters) and small *S. lewini* had less negative values (indicating preferences for coastal waters; Fig. 4). This was also observed for *S. lewini* caught off Gujarat, India (Borrell *et al*., 2011).
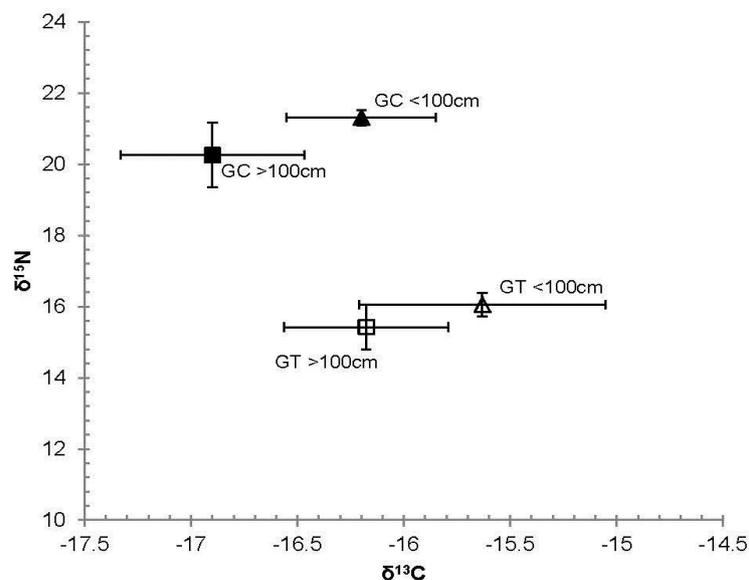
Figure 4: Mean±SD δ¹³C and δ¹⁵N values of *Sphyrna lewini* sizes groups in the Gulf of California (GC) and in the Gulf of Tehuantepec (GT). GC<100 cm (n=14), GC>100cm (n=7), GT<100cm (n=6), GT>100cm (n=73).

The positive relationship of onthogenic variation and $\delta^{15}N$ has been previously reported (Borrell *et al*., 2011), however in this study we observed a negative relationship, which is related to the use of habitat by *S. lewini* because benthic coastal food webs have more trophic levels (Link, 2002), and in consequence, more enriched $\delta^{15}N$ values, while in epipelagic oceanic area it is the opposite (Estrada *et al*., 2003). The $\delta^{15}N$ from *S. lewini* muscle is in concordance to those reported by Galván-Magaña *et al*. (1989), despite being small the isotopic differences in these were significant and reflect that large sharks consumed epipelagic prey (low $\delta^{15}N$ values; White *et al*., 2007) species and small sharks consumed benthic prey as reflected by high $\delta^{15}N$ values reported by Altabet *et al*. (1999) for sediment organic matter. Moreover, the relationship between $\delta^{15}N$ and total length for *S. lewini* was

negative (clearly in GC). Therefore, *S. lewini* feeds in different areas (coastal vs. oceanic) depending on the size and use of resources will depend on their distribution. These differences could not be detected with stomach contents, but they could be observed from stable isotopes if the distribution was in the water column (epipelagic vs. benthic), showing some of the advantages in the use of stable isotopes.

Researchers have typically categorized *S. lewini* as being an opportunistic feeding strategy predator (Klimley, 1983; Galván-Magaña *et al*., 1989; Torres-Rojas *et al*., 2009), meaning that individuals simply prey on the resources available in a given place and time (Torres- Rojas *et al*., 2006). In this study, the estimates for the degree of specialization (Levin's Index) for *S. lewini* in both areas showed a specific type of diet (low *Bi* values). However, the

diversity values showed the use of a larger array of species and the high variability in $\delta^{15}N$ and $\delta^{13}C$ suggests a variation in the type of food being consumed and use of different foraging areas (Jennings *et al*., 1997).

The dominant prey species in the diet in each area (*S. japonicus* for GC and *Auxis* spp. for GT) presents characteristics of the formation of large schools and a wide distribution. The high consumption of scombrids by *S. lewini* on the Mexican coast has been previously observed (Torres-Rojas *et al*., 2009) which makes us suppose that it is commonly available in different areas. Our comparison of the diets of *S. lewini* between the GC and Gulf of Tehuantepec shows that these populations forage on different prey (*Scomber japonicus* in GC and *Auxis* spp. in GT), although in both areas the preys inhabit the same ambience (epi end mesopelagic). Therefore, based on these finding, *S. lewini* could be considered as an opportunistic predator in both areas.

Trophic level comparison

Our comparison between the stomach content analysis and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) indicate that that small differences in $\delta^{13}C$ values and large differences in $\delta^{15}N$ values between predators from two regions (GC and Gulf of Tehuantepec) in the Mexican coasts are primarily due to differences generated at the base of the food web in their respective ecosystems (Altabet *et al*., 1999; Thunell and Kepple, 2004), and to a less degree to their trophic or foraging ecology. Importantly, both the GC and the Gulf of Tehuantepec are immersed in a region of

high microbial nitrogen removal processes, favored by a low oxygen concentration in the water column, which increase the $\delta^{15}N$ by selectively removing ^{14}N from the dissolved nitrogen (NO_3^-), and transferring this enrichment signal to the base of the food web.

Altabet *et al*. (1999) report POM $\delta^{15}N$ for GC around 9‰, while Thunell and Kepple (2004) report POM $\delta^{15}N$ for GT around 6‰ which are significantly different to the average open ocean $\delta^{15}N$ (4‰, Sigman *et al*., 2009). The influence of the $\delta^{15}N$ at the base of the food web and its transference through the $\delta^{15}N$ of higher predators has been documented in top predators (Aurioles *et al*., 2006).

In the present study, trophic levels calculated from SCA were above 4 in both areas, similar to those obtained by Borrell *et al*. (2011) which report TL values around 4.45 cm for *S. lewini*. However when we compare the trophic level obtained from $\delta^{15}N$, theses TL values were similar to those obtained with SCA only in GC, but not for the GT (Table 3). We believe the most likely explanation for the TL difference is the underestimation of the $\delta^{15}N$ differences at the base of the food chain between the sites. Casey and Post (2011) highlighted the importance of using and adequate $\delta^{15}N$ base line and the disagreement between raw $\delta^{15}N$ data and the calculation of trophic positions while Martínez del Rio *et al*. (2009) suggested the use of $\delta^{15}N$ from the base of the food web at the same time and locations for trophic level studies.

Besides the differences found between techniques in GT, similar patterns within them are observed in the TL values

between sex, sizes groups and areas show similar trophic roles. Most sharks are apex predators that occupy tertiary trophic levels (Cortes, 1999; Duncan *et al.*, 2006). Therefore, in the present study based on SCA and SIA, *S. lewini* could be considered as a top predator in Mexican coasts and the high variability (SD) in $\delta^{15}N$ could indicate that *S. lewini* can occupy different trophic levels.

In conclusion, our data support previous findings on relation to the distribution *of S. lewini* size groups and confirm the exploitation of a lower maturity size at the GC. The diet of *S. lewini* in Mexican coasts is constant and composed of epipelagic and benthic species. Therefore the use of different resources results in the presence of higher trophic levels and diversity values. Furthermore, although the trophic levels were similar between categories showing similar functional roles, it is displayed in different areas, small sharks in coastal areas and large sharks in oceanic areas. Therefore, we may conclude that *S. lewini* plays an important functional role as a top predator within areas of Mexico.

Acknowledgements

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