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Trophic niche of the Pacific Sierra (*Scomberomorus sierra*) in the southeastern Gulf of California: Assessing its importance as a predator and prey (Mesopredator) in the food web

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Abstract

The identification of interspecific links (trophic niche) is important to characterize resource use of a predator, and to know its trophic role (for example, mesopredator or top predator) in the food web. In this study, we examined: a) the trophic ecology of *Scomberomorus sierra* as a predator (niche breadth, trophic overlap, and trophic position) and b) its presence as a prey in the diets of the region´s top predators, to evaluate the critical link of *S. sierra* as a probable mesopredator in the food web of the southeastern Gulf of California (GC). Based on %PSIRI, the dominant diet of *S. sierra* were engraulids and cephalopods. The diet was similar between sexes and among size-classes. However, the isotopic niche breadth values and δ^{15}N variance (>1) reflect a broad niche for young adults likely related to a) changes in morphology (e.g., size of the mouth), b) development of the visual system, and c) changes in the energy requirements of the species reproductive stages. Seasonal changes in prey species' availability and abundance resulted in isotopic variations, indicating that *S. sierra* is an opportunistic predator. A wide range in trophic position value (from 3.8 to 4.2) indicated that it also is an intermediary carnivore, with a high degree of trophic plasticity. Although *S. sierra* has not a dominant role in top predators' diets, they share some prey species such as anchovies and other fish, depending on predator size. Therefore, *S. sierra* is a species with many prey-predator relationships in the southeastern GC food webs that may be considered a critical trophic link. This information is crucial for an ecosystem-based fisheries management in the Gulf of California.

KEYWORDS

Bayesian mixing models, *Coryphaena hippurus*, *Kajikia audax*, *Makaira nigricans*, MixSiar, stable isotopes, trophic ecology

1 | INTRODUCTION

The Gulf of California (GC) has many diverse ecosystems (marine and coastal) with high biodiversity and productivity that support complex benthic, benthopelagic and pelagic food webs (*e.g.* invertebrates, fish, cetaceans, and turtles), some of them with significantly high endemism (Brusca, 2010) and others with incalculable economic and ecological value (Torres-Rojas, Hernández-Herrera, Ortega-García, & Domeier, 2013; Torres-Rojas, Hernández-Herrera, Ortega-García, & Soto-Jiménez, 2014). For example, a well-developed tuna, shark, shrimp and sardine fisheries, as well as hundreds of skiffs dedicated to small scale fisheries; all exploit the resources of this region (Ramírez-Rodríguez, Amezcua, & Aguiar-Moreno, 2014; Rodriguez-Preciado et al., 2014; Torres-Rojas, Páez-Osuna, et al., 2014; Alatorre-Ramirez et al., 2017). However, there is still limited knowledge about the trophic interactions of the species subject to exploitation and of the food web structure at southeastern GC.

A prerequisite for the comprehension of the trophic interactions is identifying critical interspecific links that allows us to understand the connectivity between multiples components of the food web (Gelwick & McIntyre, 2017). Several authors indicated that scombrids are major components of the pelagic ecosystems (Collette & Nauen, 1983) and are considered tertiary to top predators in oceanic and coastal ecosystems (Margulies, 1997). In the case of *Scomberomorus sierra*, adults individuals (>60 cm Fork length "FL"; Aguirre-Villaseñor, Morales-Bojórquez, Morán-Angulo, Madrid-Vera, & Valdez-Pineda, 2006) have been reported as an opportunistic ichthyophagous top predators (Muro-Torres, Soto-Jiménez, Green, Quintero, & Amezcua, 2019), consuming mainly small fishes (Clupeidae and Engraulidae) and cephalopods (*e.g. Loligo* spp.) in the GC region (Moreno-Sánchez, Quiñonez-Velázquez, Abitia-Cárdenas, & Rodriguez-Romero, 2011). However, data related to the trophic niche of individuals <60 cm (FL) is scarce and knowledge regarding trophic interactions between *S. sierra* and their prey and predators, is necessary.

In food webs, mesopredators are often highly interlinked with their prey and predators, and their relatively small sizes and broad food options allow them to achieve higher population densities than larger predators (Prugh et al., 2009). Thus, changes in mesopredators population can ripple widely throughout an entire ecological community. The Pacific sierra (*S. sierra*) has been reported in the diets of pelagic and benthic predators in the southeastern GC (Torres-Rojas et al., 2013; Torres-Rojas, Hernández-Herrera, et al., 2014). Therefore, we explored the role of *S. sierra* (<60 cm "FL") as a critical link between trophic levels (possible mesopredator), which serve dual roles as both consumers of smaller animals and potential prey of larger carnivores in the structure of the southeastern GC food web.

The Pacific sierra (*S. sierra*) is widely distributed across the GC (Castillo-Yáñez, Pacheco-Aguilar, Márquez-Ríos, Lugo-Sánchez, & Lozano-Taylor, 2007; Thomson, Findley, & Kerstich, 2000). *Scomberomorus sierra* is particularly abundant along the coasts of Sinaloa, at southeastern GC. Its presence occurs from November to July, being more abundant between February and April (Castillo-Yáñez et al., 2007; Montemayor-López, Cisneros-Mata, Morga-López, Castro-Longoria, & Molina-Ocampo, 1999; Pérez-Ramos, 1994; Thomson et al., 2000). In 2014, the *S. sierra* catches in the GC region accounted for close to 15,000 ton/y and represented 19.2% of the national production (SAGARPA-CONAPESCA, 2017), highlighting the economic importance of this species (Juan-Jordá, Mosqueirad, Cooperf, Freirea, & Dulvyc, 2011; Majkowski, 2007; Del Moral-Simanek & Vaca-Rodríguez, 2009). From 2015, landings volume increased by over 20%, accounting for around 20,000 ton/y (SAGARPA-CONAPESCA 2017). Changes in the *S. sierra* catches could result in food web alterations (Top-down or Bottom-up events), but their associated effects are unknown. Therefore, this information is necessary for the ecosystem-based fisheries management of aquatic resources in the southeastern GC, through the estimation of trophic levels.

The use of carbon and nitrogen stable isotopes analysis (SIA) complemented by stomach content analyses (SCA) has proven to be the most useful tools to improve our knowledge of food-web structures, the feeding ecologies and functional roles of the species in natural ecosystems (Boecklen, Yarnes, Cook, & James, 2011). Based on SIA the temporally integrated information (weeks to months) on dietary habits was analyzed. SIA results indicate the diet assimilated by the consumer, ontogenetic shifts in consumer diet, and movement patterns between habitats, species migration, and connectivity; whereas SCA provides information relevant to the taxonomic and size composition of diets and clarifies predator-prey interactions in complex systems where species have diverse consumption patterns (Layman, Arrington, Montana, & Post, 2007; MacNeil, Skomal, & Fisk, 2005). The combined use of SIA and SCA help in defining the trophic interaction, in reconstructing species diets, estimating trophic positions (TP), elucidating resource acquisition and allocation patterns, characterizing niche properties, and constructing food webs (e.g. Amezcua, Muro-Torres, & Soto-Jiménez, 2015; Beaudoin, Tonn, Prepas, & Wassenaar, 1999; Dehn et al., 2007; Mantel, Salas, & Dudgeon, 2004; Muro-Torres et al., 2019; Torres-Rojas et al., 2013). All this information contributes to our understanding of fish population dynamics (Hansson et al., 1997).

In this context, incorporating SCA and SIA techniques, we analyzed 1) the trophic ecology of juvenile, preadults and young adult *S. sierra* in the southeastern GC to better understand the species' diet and TP and detect probable intraspecific (sex and/or size classes) differences in diet and TP over a fishing season under three climatic seasons (dry-cold, dry-warm, and humid-warm season), and 2) the importance of *S. sierra* in the diets of top predators (*e.g.* billfishes and common dolphinfish). The clarification of *S. sierra* interactions with prey species and predators based on both techniques, it is crucial to defining the trophic interactions and structure of the southeastern GC food web (Fleming, Nunez, & Sternberg, 1993; Miranda & Perissinotto, 2012), and one step toward optimizing multispecies fishery management in the GC region.

2 | MATERIAL AND METHODS

2.1 | Field sampling

Sampling was conducted at fishing grounds in Mazatlán (MZT), southeastern Gulf of California México (23°14'29'' N; 106°24'35''W; Figure 1) during one fishing period (August 2006 to May 2007). Mazatlán is the most representative of coastal communities that are highly reliant on industrial, artisanal and sport fishing off the southeastern GC. Samples of *S. sierra* were collected from the small-scale fishery, which operates year-round. The fishing gear consisted of 400, 600, and 800 m long gillnets, 150 and 200 meshes deep and 2.5–3 inches mesh size (INP, 2001; Aguirre-Villaseñor et al., 2006).

FIGURE 1 Fishing area of the artisanal fishing fleet off Mazatlán, Mexico, where the specimens of *Scomberomorus sierra* were caught

Since previous SCA studies reported that blue marlin (*Makaira nigricans*), striped marlin (*Kajikia audax*) (Torres-Rojas et al., 2013), and dolphinfish (*Coryphaena hippurus*) are *S. sierra* predators in the southeastern Gulf of California (Torres-Rojas, Hernández-Herrera, et al., 2014), we also collected specimens of these predators from sport fishing landings within a range of 30 nautical miles from the Mazatlán coastline. Based on previous SCA studies (Moreno-Sanchez et al., 2011), primary prey species of predators and *S. sierra* (*e.g.* Clupeidae and Engraulidae fishes) were also collected at the study area by using the following fishing gears: (a) shrimp trawl net, fitted with a 24-m footrope and a 50-mm liner at the codend; and (b) gill- net, 300 m long and fitted with a 75-mm liner (Amezcua, Madrid-Vera, & Aguirre-Villaseñor, 2006).

2.2 | Sample collection and processing

Once organisms were identified, their length in cm (fork length "FL" for *S. sierra*, *C. hippurus* and primary prey species, eye fork length "EFL" for *M. nigricans* and *K. audax*), and sex were recorded. Stomach contents and dorsal white muscle tissue (5 g) from each specimen were collected for the isotopic analysis and determine their recently consumed prey species to assimilated food, respectively. All samples were kept frozen (−20°C) until analysis in the Ichthyology Laboratory at the Instituto de Ciencias del Mar y Limnologia (ICMyL) in Mazatlán, Sinaloa.

For both techniques (SCA and SIA), prey items present in *S. sierra* and predators' diets were identified to the lowest possible taxonomic level. The following keys were used to identify fish: Clothier (1950), Monod (1968), Miller and Lea (1972), Miller and Jorgensen (1973), Cailliet, Love, and Ebeling (1986), Allen and Robertson (1994), Fischer et al. (1995), and Thomson et al. (2000). Cephalopods were identified by their beaks according to Clarke (1986). Iverson and Pinkas (1971), and Wolff (1982, 1984). Crustaceans were identified using Fischer et al. (1995).

To obtain isotopic data, white muscle of collected specimens were placed in vials with Teflon lids and dried for 24 hr in a dry freezer at a temperature and pressure of −45°C and 24 to 27 × 10^{-3} mbar. Samples were then ground in an agate mortar, and 1 mg sub-samples were weighed and stored in tin capsules (8 × 5 mm). The

TABLE 1 Isotopic values ($\delta^{13}C$ and $\delta^{15}N$, ‰) of A) *Scomberomorus sierra* prey species, and B) the main prey species of the three top predator collected off the south-eastern Gulf of California, used to calculate the mixing model (MixSiar) of *S. sierra* as prey specie (*SD* = standard deviation; *n* = number of samples; Superscript letter in species of commercial importance indicate the type of fishery: a artisanal, i industrial, a/i both, rf recreational fishery)

	Category	Code	*n*	$\delta^{15}N$ (‰)		$\delta^{13}C$ (‰)	
				Mean	*SD*	Mean	*SD*
A)							
[a/i]*Anchovia macrolepidota*	Fish	*Am*	3	14.17	1.79	−15.56	1.35
[a]*Haemulopsis nitidus*	Fish	*Hn*	3	18.61	0.12	−14.78	0.23
[a/i/cs]*Litopenaeus vannamei*	Crustacean	*Lv*	3	15.50	1.44	−16.32	0.89
[a/i]*Loligo* spp.	Squid	*Ls*	3	14.71	0.60	−16.60	0.05
[a]*Selene peruviana*	Fish	*Sp*	4	16.86	1.86	−16.92	0.91
[a]*Squilla mantoidea*	Crustacean	*Sm*	3	15.10	2.19	−17.34	0.24
B)							
[a]*Auxis thazard*	Fish	*Ath*	3	16.08	1.27	−17.11	0.27
[a]*Lagocephalus lagocephalus*	Fish	*Ll*	3	13.54	0.38	−16.36	0.36
[a]*Scomber japonicus*	Fish	*Sj*	3	17.41	0.89	−21.67	5.97
[a]*Selar crumenophthalmus*	Fish	*Sc*	3	15.60	0.32	−17.72	0.24
[a/i]*Dosidicus gigas*	Cephalopods	*Dg*	5	14.69	2.69	−17.25	1.03
[i]*Pleuroncodes planipes*	Crustaceans	*Pp*	3	11.00	1.69	−20.08	1.55

$\delta^{13}C$ and $\delta^{15}N$ compositions were determined by the Stable Isotope Laboratory at 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 0.2‰ precision. Stable isotope values (δ) were calculated using the formula proposed by Park and Epstein (1961).

2.3 | Data analysis

To detect intraspecific variation, the sampled organisms were grouped by sex, size classes (FL: <36 cm = juveniles, 36–45 cm = preadults and 45–60 cm = young adults; based on Aguirre-Villaseñor et al., 2006), and climatic season (dry-cold season “DCS”, from December 1 to March 31, dry-warm season “DWS”, from April 1 to June 30, and humid-warm season “HWS”, from July 1 to November 30; based on Amezcua, Ramírez, & Flores-Verdugo, 2019). For SCA, we constructed cumulative prey curves (EstimateS program; Colwell, 2006) for each category to determine whether the number of stomachs analyzed was representative of the trophic spectrum of *S. sierra* (Ferry & Cailliet, 1996). As an indicator of the degree of variability in the diet, the coefficient of variation (CV) of diversity values was calculated for all stomachs (for this study, a CV less than 0.05 was considered adequate) to represent the trophic spectrum of *S. sierra* (Steel & Torrie, 1992). For SIA, 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 arithmetic correction proposed by Logan et al. (2008). Also, data were tested for normality (Shapiro-Wilk test) and variance homogeneity (Levene's test). Statistical analyses were performed in Statistica v. 8.0 (Hill & Lewicki, 2007), with significance set at $p < .05$.

2.4 | Estimates of diet variation

Based on SCA, the prey-specific index of relative importance (%PSIRI) of each prey in the diet of *S. sierra* and top predators was calculated by using the formula: PSIRI = (%PNi + PWi) × %FO, where %FO is the percent frequency of occurrence (the number of stomachs containing prey i divided by the total number of stomachs, n), and %PNi and %PWi are the prey-specific abundances by number or weight, respectively (Brown, Bizzarro, Cailliet, & Ebert, 2012).

2.5 | Estimates of isotopic variability

Regarding SIA, stable isotope-derived data failed the normality and variance homogeneity assumptions; therefore, a Kruskal-Wallis (nonparametric ANOVA) test was used to detect intraspecific variations in $\delta^{13}C$ and $\delta^{15}N$ among size classes and climatic season, when differences were found, a post-hoc, one-way nonparametric Dunn´s test for multiple comparisons was used. A Mann Whitney U test was used to compare isotope values between sexes (Zar, 1999).

TABLE 2 Prey-specific index of relative importance (%PSIRI) for the diets (>90%) of *Makaira nigricans*, *Kajikia audax*, *Coryphaena hippurus*, and *Scomberomorus sierra* captured off Mazatlan, Mexico: x = not present in the diet; highest contributions in bold; *SWC* = stomachs with contents

Prey Item			*Makaira nigricans* SWC = 32	*Kajikia audax* SWC = 24	*Coryphaena hippurus* SCW = 359	*Scomberomorus sierra* SWC = 112
Cephalopoda	Ommastrephidae	*Dosidicus gigas*	6.6	**24.2**	4.1	x
	Rest of cephalopod	Cephalopods	0.1	x	0.6	**18.7**
Crustacea	Squillidae	*Squilla biformis*	x	x	x	0.4
		Squilla mantoidea	x	x	x	2.5
		Squilla panamensis	x	x	x	0.2
	Peneidae	Peneids	x	x	0.1	**15.9**
	Galatheidae	*Pleuroncodes planipes*	x	x	**53.4**	x
	Rest of crustacean	Crustaceans	0.1	x	0.1	3.8
Teleostei	Congridae	Congrids	x	x	x	0.9
	Muraenesocidae	Muraenesocids	x	x	x	0.1
	Clupeidae	Clupeids	x	x	x	2.6
		Sardinops caeruleus	x	**21.7**	0.3	x
	Engraulidae	Engraulids	x	x	x	**44.9**
		Anchoa spp.	x	x	x	0.1
	Hemirhamphidae	*Hemiramphus saltator*	0.1	x	**19.3**	x
	Carangidae	Carangids	0.2	0.1	0.1	0.1
		Decapterus spp.	0.1	6.7	0.2	x
		Selar crumenophthalmus	5.0	6.4	3.0	x
		Selene peruviana	x	0.1	0.1	0.1
	Gerreidae	Gerreids	x	x	x	0.1
	Haemulidae	Haemulids	x	x	0.1	0.1
	Scianidae	Scianids	x	x	0.2	0.1
	Polynemidae	*Polydactylus approximans*	x	x	x	0.1
	Scombridae	*Auxis* spp.	**82.1**	3.20	0.3	x
		Scomber japonicus	0.1	**29.0**	3.0	x
	Balistidae	*Balistes polylepis*	0.1	0.1	3.4	x
	Unidentified teleosts	Fish	0.1	0.1	0.1	0.1

2.6 | Explanatory variables (CCA) of the Scomberomorus sierra diet

Based on SCA, the diet of *S. sierra* was analyzed using canonical correspondence analysis (CCA; ter Braak, 1986) to identify the presence of explanatory variables (the relationships between biological assemblages of species and their environment; ter Braak & Verdonschot, 1995) that may influence the dietary proportions, therefore, in the isotopic mixing model (Parnell & Inger, 2019). In the present study, CCA assessed the multivariate diet response of *S. sierra* to a number of explanatory variables (sexes, sizes classes, climatic season). The data set and explanatory variables were analyzed following the methodology described by Jaworski and Ragnarsson (2006), and CCA test was carried out in Canoco v.5 (ter Braak & Šmilauer 2012). The results of CCA were presented in the form of ordination diagrams containing the continuous explanatory variables plotted as arrows along with points for prey categories. Only CCA diagrams and selected univariate plots (to aid interpretation of the CCA results) are shown here.

2.7 | Contribution of prey species to *Scomberomorus sierra* diet and Top Predators diet based on isotopic composition

Based on SIA, the isotopic contributions of various prey to *S. sierra* and Pacific sierra´s contribution to predators were evaluated with MixSIAR, a Bayesian isotope-mixing model (Jackson, Inger, Parnell, &

Bearhop, 2011; Parnell, Inger, Bearhop, & Jackson, 2008). This model estimates the probability distribution of the contribution of n prey to a mixture and evaluates the uncertainty associated with the isotopic values of the prey and predator (Parnell, Inger, Bearhop, & Jackson, 2010). The results of this analysis are reported as percentage distributions ranging from 0% to 99%, where the minimum and maximum values are used to determine the importance prey in a diet (Madigan et al., 2012).

To increase the discriminatory power of the mixing model, Phillip et al. (2014) recommend the use of six clearly discriminated sources for a C and N isotopes system. Therefore, we analyzed the isotope values for Pacific sierras' six primarily prey species, which composed 95% of the *S. sierra* diet (enrichment factor of 3.4‰; based on Post, 2002). When estimating Pacific sierra´s contribution to the nutrition of the three pelagic predator (*M. nigricans*, *K. audax* and *C. hippurus*) captured in the study area (enrichment factor of 1.9‰; based on Madigan et al., 2012), we also generated mixing models with the isotope values of six prey species, including *S. sierra* (Table 1).

2.8 | Estimates of trophic niche width and trophic overlap

Based on SCA, the *S. sierra* trophic niche width was evaluated using Levin´s standardized index, "*Bi*" (Krebs, 1999), which ranges from 0 to 1, with low values (<0.6) indicating a specialist predator and high values (>0.6) indicating a generalist predator (Labropoulou & Eleftheriou, 1997). Data were pooled and separated by sex, size classes, and climatic season. The Equation (1) for Levin's standardized index for predator *j* is as follows:

$$\mathrm{Bi} = \frac{1}{n - l\left\{(1/\sum P_{ji}^{2}) - 1\right\}} \qquad (1)$$

where $\sum P_{ji}^{2}$ is the numerical proportion of the *j*th prey item in predator *i*'s diet and.

n is the number of prey categories.

Based on SCA, the diet similarity between sexes, among size-classes, and climatic season was analyzed using permutation randomization methods in a Bray–Curtis dissimilarity matrix (analysis of similarity [ANOSIM] in PRIMER 6 version 6.1.6). The technique is based upon permutation-randomization methods in the similarity matrix. If R is close to zero, the H_o cannot be rejected (*e.g.* there is no separation between groups).

Based on SIA, the isotopic niche widths and overlap were estimated using the standard ellipses method of the SIBER (Stable Isotope Bayesian Ellipses in R) package, version 2.1.3 proposed by Jackson et al. (2011) in R 3.4.2 (R Development Core Team 2017, Vienna, Austria). SIBER uses measurements of isotopic ration based on ellipses (SEAc) calculated by a covariance matrix that defines their shape and area within a 95% confidence interval (Jackson et al., 2011; Trasviña-Carrillo et al., 2018). For isotopic trophic overlap, we use the scale proposed by Langton (1982) in which values of 0–0.29 indicate low overlap, values from 0.30–0.59 correspond to a medium overlap and values >0.60 are related to a high overlap between groups. Whereas isotopic niche breadth values (SEAc) and δ^{15}N variance >1 reflects a broad niche (Jaeger, Blanchard, Richard, & Cherel, 2009; Newsome, del Rio, Bearhop, & Phillips, 2007).

2.9 | Estimates of trophic position

Based on SCA, the trophic position (TP) of *S. sierra* was calculated using the Equation (2) proposed by Christensen and Pauly (1992):

$$\mathrm{TP} = 1 + \left(\sum_{i=1}^{n} \mathrm{DC}_{ji}\right)(\mathrm{TP}_{i}) \qquad (2)$$

TABLE 3 Isotopic composition (δ^{13}C and δ^{15}N presented in ‰) of *Scomberomorus sierra*, *Kajikia audax*, *Makaira nigricans*, and *Coryphaena hippurus* in the south-eastern Gulf of California

				δ^{15}N (‰)		δ^{13}C (‰)	
Species	Category	Code	*n*	Mean	*SD*	Mean	*SD*
$^{a/i}$*S. sierra*	Males	M	32	17.98	0.89	−17.51	1.12
	Females	F	15	18.25	1.13	−17.48	1.01
	Juveniles	*J*	3	18.00	0.75	−17.92	0.82
	Preadults	*PA*	30	18.12	0.93	−17.43	1.14
	Young Adults	*YA*	14	17.95	1.13	−17.57	1.02
	Humid-warm season	HWS	17	18.71	0.83	−17.13	0.99
	Dry-cold season	DCS	20	17.96	0.82	−17.66	1.14
	Dry-warm season	DWS	10	17.16	0.66	−17.81	1.00
^{rf}*K. audax*	Top predator	*Ka*	13	16.41	1.17	−16.86	0.82
^{rf}*M. nigricans*	Top predator	*Mn*	6	16.60	0.51	−17.12	0.72
$^{a/rf}$*C. hippurus*	Top predator	*Ch*	48	14.77	1.80	−17.24	0.59

Note: Superscript letter in species of commercial importance indicate the type of fishery: a artisanal, i industrial, a/i both, rf recreational fishery.

Abbreviations: DCS, dry-cold season; DWS, dry-warm season; HWS, humid-warm season; J, Juveniles; *n*, number of samples; PA, Preadults; *SD*, standard deviation; YA, Young Adults.

TABLE 4 Summary of food categories in stomachs of *Scomberomorus sierra* captured off Mazatlan, Mexico, expressed as prey-specific by number (%PNi), prey-specific abundances by weight (%PWi), frequency of occurrence (%FO), and percentage of the Prey-Specific Index of Relative Importance (%PSIRI)

HWS **Prey item**			**Habitat**	***Juveniles*** ***SWC = 3***			
				%PNi	**%PWi**	**%FO**	**%PSIRI**
Cephalopoda	Rest of cephalopod	Cephalopods	x	**50.0**	**97.9**	**33.3**	**24.6**
Crustacea	Squillidae	*Squilla biformis*	C/D	x	x	x	x
		Squilla mantoidea	C/D	x	x	x	x
		Squilla panamensis	C/D	x	x	x	x
	Peneidae	Peneids	C/D	x	x	x	x
	Rest of crustacean	Crustaceans	x	x	x	x	x
Teleostei	Congridae	Congrids	C/D	x	x	x	x
	Muraenesocidae	Muraenesocids	C/D	x	x	x	x
	Clupeidae	Clupeids	C/P:N	x	x	x	x
	Engraulidae	Engraulids	C/P:N	**83.3**	**67.3**	**100**	**75.4**
		Anchoa spp.	C/P:N	x	x	x	x
	Carangidae	Carangids	C/B:P	x	x	x	x
		Selene peruviana	C/B:P	x	x	x	x
	Gerreidae	Gerreids	C/D	x	x	x	x
	Haemulidae	Haemulids	C/B:P	x	x	x	x
	Sciaenidae	Sciaenids	C/D	x	x	x	x
	Polynemidae	*Polydactylus approximans*	C/D	x	x	x	x
	Unidentified teleosts	Fish	x	x	x	x	x

DWS **Prey item**			**Habitat**	***Juveniles*** ***SWC = 0***			
				%PNi	**%PWi**	**%FO**	**%PSIRI**
Cephalopoda	Rest of cephalopod	Cephalopods	x	x	x	x	x
Crustacea	Squillidae	*Squilla biformis*	C/D	x	x	x	x
		Squilla mantoidea	C/D	x	x	x	x
		Squilla panamensis	C/D	x	x	x	x
	Peneidae	Peneids	C/D	x	x	x	x
	Rest of crustacean	Crustaceans	x	x	x	x	x
Teleostei	Congridae	Congrids	C/D	x	x	x	x
	Muraenesocidae	Muraenesocids	C/D	x	x	x	x
	Clupeidae	Clupeids	C/P:N	x	x	x	x
	Engraulidae	Engraulids	C/P:N	x	x	x	x
		Anchoa spp.	C/P:N	x	x	x	x
	Carangidae	Carangids	C/B:P	x	x	x	x
		Selene peruviana	C/B:P	x	x	x	x
	Gerreidae	Gerreids	C/D	x	x	x	x
	Haemulidae	Haemulids	C/B:P	x	x	x	x
	Sciaenidae	Sciaenids	C/D	x	x	x	x
	Polynemidae	*Polydactylus approximans*	C/D	x	x	x	x
	Unidentified teleosts	Fish	x	x	x	x	x

Preadults *SWC = 16*				*Young Adults* *SWC = 21*			
%PNi	**%PWi**	**%FO**	**%PSIRI**	**%PNi**	**%PWi**	**%FO**	**%PSIRI**
75.0	**76.1**	**18.7**	**14.1**	**66.6**	**53.0**	**23.8**	**14.2**
x	x	x	x	x	x	x	x
25.0	19.8	6.2	1.4	50.0	50.0	4.7	2.3
25.0	19.8	6.2	1.4	50.0	50.0	4.7	2.3
51.3	**57.4**	**37.5**	**20.4**	**69.0**	**71.0**	**33.3**	**23.3**
x	x	x	x	x	x	x	x
100	100	6.2	6.2	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	100.0	100.0	9.5	9.5
80.0	**81.4**	**62.5**	**50.4**	**84.8**	**88.2**	**52.3**	**45.3**
x	x	x	x	x	x	x	x
41.6	34.4	12.5	4.7	x	x	x	x
x	x	x	x	50.0	66.2	4.7	2.7
33.3	4.4	6.25	1.1	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x

Preadults *SWC = 8*				*Young Adults* *SWC = 18*			
%PNi	**%PWi**	**%FO**	**%PSIRI**	**%PNi**	**%PWi**	**%FO**	**%PSIRI**
66.6	**75.7**	**62.5**	**44.5**	**75.0**	**73.7**	**22.2**	**16.5**
x	x	x	x	x	x	x	x
33.3	7.3	12.5	2.5	x	x	x	x
33.3	7.3	12.5	2.5	x	x	x	x
66.6	**68.8**	**37.5**	**25.4**	**58.3**	**51.8**	**22.2**	**12.2**
x	x	x	x	50.0	11.2	5.5	1.7
x	x	x	x	x	x	x	x
x	x	x	x	100.0	100.0	5.5	5.5
x	x	x	x	100.0	100.0	5.5	5.5
100.0	**100.0**	**25.0**	**25.0**	**81.2**	**87.1**	**44.4**	**37.4**
x	x	x	x	100.0	100.0	11.1	11.1
x	x	x	x	33.3	20.3	5.5	1.4
x	x	x	x	x	x	x	x
x	x	x	x	33.3	68.5	5.5	2.8
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	100.0	100.0	5.5	5.5
x	x	x	x	x	x	x	x

DCS				*Juveniles* *SWC = 7*			
Prey item			**Habitat**	**%PNi**	**%PWi**	**%FO**	**%PSIRI**
Cephalopoda	Rest of cephalopod	Cephalopods	x	x	x	x	x
Crustacea	Squillidae	*Squilla biformis*	C/D	x	x	x	x
		Squilla mantoidea	C/D	x	x	x	x
		Squilla panamensis	C/D	x	x	x	x
	Peneidae	Peneids	C/D	x	x	x	x
	Rest of crustacean	Crustaceans	x	50.0	15.3	14.2	4.6
Teleostei	Congridae	Congrids	C/D	x	x	x	x
	Muraenesocidae	Muraenesocids	C/D	x	x	x	x
	Clupeidae	Clupeids	C/P:N	x	x	x	x
	Engraulidae	Engraulids	C/P:N	**92.8**	**97.8**	**100.0**	**95.3**
		Anchoa spp.	C/P:N	x	x	x	x
	Carangidae	Carangids	C/B:P	x	x	x	x
		Selene peruviana	C/B:P	x	x	x	x
	Gerreidae	Gerreids	C/D	x	x	x	x
	Haemulidae	Haemulids	C/B:P	x	x	x	x
	Sciaenidae	Sciaenids	C/D	x	x	x	x
	Polynemidae	*Polydactylus approximans*	C/D	x	x	x	x
	Unidentified teleosts	Fish	x	x	x	x	x

Note: x = not present in the diet; most significant contributors in bold; SWC = stomachs with content; Juveniles, Preadults, and Young Adults (based on Aguirre-Villaseñor et al., 2006); DCS = dry-cold season, DWS = dry-warm season, and HWS = humid-warm season (based on Amezcua et al., 2019), Habitat = Prey species habitats (C, Coastal; O, Oceanic; P, Pelagic; B, Benthic; D, Dermersal; N, Neritic; based on Robertson & Allen, 2015)

DC_{ji} is the diet composition by weight, in terms of prey proportions (*i*) in the predator´s diet (*j*). TP_i is the trophic position of prey species *i*, and *n* represents the number of prey groups in the diet. Fish TP values species were obtained from Fishbase (Froese & Pauly, 2003), while cephalopods and crustaceans TP values were obtained from Cortés (1999). TP means and standard deviation (*SD*) were calculated to ascertain the variability of individual values.

Based on SIA, TP of *S. sierra*, predators, and prey species was calculated using the Equation (3) proposed by Post (2002):

$$\mathrm{TP} = \lambda + \frac{\left(\delta^{15}\mathrm{N}_{\mathrm{Predator}} - \delta^{15}\mathrm{N}_{\mathrm{Base}}\right)}{\Delta^{15}\mathrm{N}} \tag{3}$$

λ represents the TP of food web base, $\delta^{15}N_{predator}$ is the nitrogen signature of the fish of interest, and $\Delta^{15}N$ is the trophic discrimination factor. We considered *Anchovia macrolepidota* (Engraulidae) to be base of the food web (λ = 2.6, Froese & Pauly, 2003; $\delta^{15}N_{base}$ = 14.17 ± 1.79‰), and we assumed a theoretical ^{15}N enrichment values of 3.4‰ for *S. sierra* (Post, 2002); whereas for top pelagic predators we considered zooplankton to be base of the food web (λ = 2; $\delta^{15}N_{base}$ = 10.63 ± 0.71‰), and we assumed a theoretical ^{15}N enrichment values of 1.9‰ based on Madigan et al. (2012).

3 | RESULTS

A total of 129 specimens of *S. sierra* were sampled, ranging from 25.0 to 55.5 cm FL with a mean size of 42.6 cm [±0.5 *SD*], no adult organisms (>60 cm FL) were sampled. Of the total, 112 individuals contained food (87%) and 17 were empty (13%); 40 were females and 72 were males; 10 were juveniles, 45 were preadults and 57 were young adults; 40 individuals were obtained in HWS, 46 in DCS, and 26 in DWS.

3.1 | Diet variation of S. sierra and pelagic predators

The prey species accumulation curve showed that the number of stomachs we analyzed was sufficient for characterizing the *S. sierra* diet (General CV = 0.005), also for sexes (Male CV = 0.01;

Preadults ***SWC = 21***				***Young Adults*** ***SWC = 18***			
%PNi	**%PWi**	**%FO**	**%PSIRI**	**%PNi**	**%PWi**	**%FO**	**%PSIRI**
51.2	**47.7**	**57.1**	**28.2**	**75.0**	**94.1**	**16.6**	**14.1**
26.6	27.5	9.5	2.5	50.0	50.0	5.5	2.7
28.3	26.0	33.3	7.7	50.0	50.0	5.5	2.7
28.3	26.8	33.3	9.0	x	x	x	x
48.3	**55.7**	**28.5**	**14.8**	56.2	62.6	22.2	13.2
x	x	x	x	**75.0**	**69.8**	**27.7**	**20.1**
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
71.1	**80.5**	**47.6**	**36.1**	**86.1**	**79.7**	**50.0**	**41.4**
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x
16.6	13.1	4.7	0.7	x	x	x	x
16.6	9.5	4.7	0.6	x	x	x	x
x	x	x	x	x	x	x	x
x	x	x	x	100.0	100.0	5.5	5.5

Females CV = 0.009), climatic season (HWS CV = 0.01; DCS CV = 0.01; DWS CV = 0.02) and size-classes (preadults CV = 0.01; young adults CV = 0.01), except for juveniles (CV = 0.17), therefore, the results of this category can only infer ecological trends. Based on SCA, the trophic spectrum consisted of 1 cephalopod species, 6 crustacean species from 3 families, and 12 fish species from 10 families. According to the prey-specific index of relative importance (%PSIRI), for *S. sierra*, fish from the family Engraulidae (44.9%) were the diet´s most important components, for *M. nigricans* was *Auxis* spp. (82.1%), for *K. audax* was *Scomber japonicus* (29.0%), and for *C. hippurus* was *Pleuroncodes planipes* (53.4%, Table 2), and according to ANOSIM low similarity was found among predators ($R = .45$).

3.2 | Isotopic variability of S. sierra and pelagic predators

Subsamples for δ^{13}C and δ^{15}N analysis were collected from muscles tissue ($n = 47$), this subsample included 15 males and 32 females; 3 were juveniles, 30 were preadults and 14 were young adults. Separated by climatic season, this subsample included 17 individuals from HWS, 20 from DCS, 10 from DWS. The C:N ratios for muscle were between 3.0 and 3.5 and averaged 3.2, thus, an arithmetic correction based on the C:N ratio was not required. Based on SIA, the average δ^{15}N value (±*SD*) for dorsal muscle of *S. sierra* was 18.06 ± 0.97‰, 16.60 ± 0.51‰ for *M. nigricans*, 16.41 ± 1.17‰ for *K. audax* and 14.77 ± 1.80‰ for *C. hippurus* (Table 3). Regarding δ^{13}C, the average values (±*SD*) were − 17.50 ± 1.07‰, −17.12 ± 0.72‰, −16.86 ± 0.82‰, and − 17.24 ± 0.59‰ respectively (Table 3).

3.3 | Diet variation of S. sierra by sexes and size classes

Based on SCA, the ANOSIM showed a high similarity in the diets between sexes ($R < .01$), and among the three size classes ($R < .01$). Based on SIA, no significant differences in isotopic values were observed between the sexes [δ^{15}N (U = 206.00, $p = .43$); δ^{13}C (U = 236.00, $p = .92$)], or size classes (for δ^{15}N, $H_{(2, 47)} = 1.14$, $p = .94$; for δ^{13}C, $H_{(2, 47)} = 1.11$, $p = .57$) (Table 3 and 4).

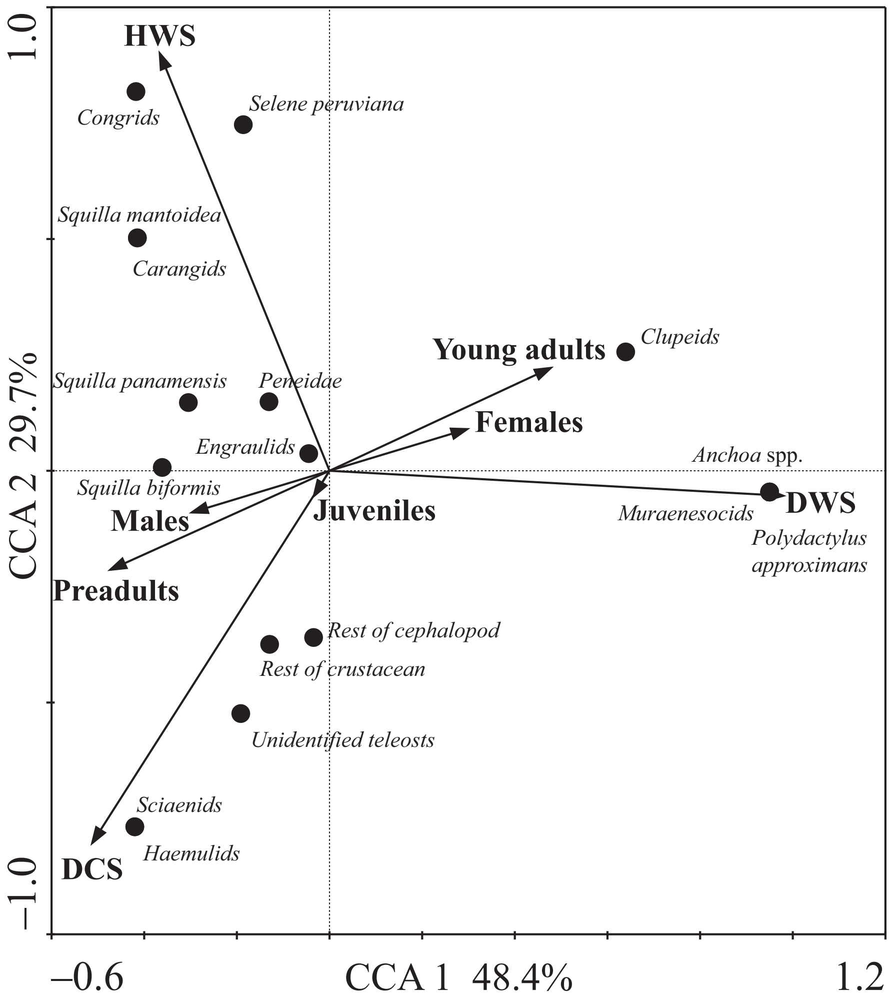

FIGURE 2 CCA ordination diagrams for *Scomberomorus sierra* in Mazatlan, Mexico. The arrows indicate explanatory variables, with the arrowheads indicating the increase in gradient

3.4 | Diet variation of Scomberomorus sierra among climatic season

Based on SCA, the ANOSIM showed a high similarity in the diets among climatic season (R = .02). However, based on SIA, significant differences in δ^{15}N values were observed among climatic season (for δ^{15}N, $H_{(2,\,47)} = 16.8$, $p < .01$). Post-hoc tests identified differences in δ^{15}N values between HWS and DWS (Dunn´s test, $p < .05$) (Table 3 and 4).

3.5 | Explanatory variables (CCA) of the *Scomberomorus sierra* diet

Based on SCA, pelagic species were the main contributors to *S. sierra* diet (%PSIRI values from 41 to 95), followed by demersal (%PSIRI values from 14 to 25) and bentopelagic species (%PSIRI values from 1 to 12.5) (Table 4). The CCA explained 10% of the total variation in the diet data. The first two canonical axes accounted for 78% of the constrained (explainable) variation. The climatic season was the main explanatory variable. Congrids were mainly eaten by *S. sierra* in HWS and their importance decreased with the change of climatic season. Sciaenids and Haemulids were eaten by *S. sierra* in DCS. *Polydactylus approximans* and *Anchoa* spp. increased their dietary contribution during DWS (Figure 2).

3.6 | Contribution of prey species to *Scomberomorus sierra* and Top Predators diet based on isotopic composition

Based on SIA, regarding to MixSIAR, *Anchovia macrolepidota* and *Squilla mantoidea* significantly contributed to the *S. sierra* diet, without sex distinction (Table 5a). Differences in the *S. sierra* diet were significant among size classes. The prey species *S. mantoidea* and *Selene peruviana* contributed most to the isotopic composition of juveniles (0.22 and 0.19, respectively), while preadults and young adults preyed mainly on *S. mantoidea* and *A. macrolepidota* (0.40 and 0.25, 0.31 and 0.22, respectively) (Table 5b). The relative isotopic contributions of prey to isotopic composition of *S. sierra* also varied among climatic season. For example, *S. mantoidea* and *S. peruviana* were the main contributors during HWS (0.21 and 0.22, respectively), while *L. vannamei* and *S. mantoidea* were the predominant prey during DCS (0.24 and 0.24, respectively). In DWS, *S. mantoidea* was the predominant prey (0.32) (Table 5c). According to MixSIAR, *S. sierra*´s isotopic contribution to predators' isotopic

TABLE 5 Estimated proportional prey inputs (as determined from MixSIAR) to the diets of A) male and female, B) size classes, and C) climatic season of *Scomberomorus sierra* in the waters south of the Baja California peninsula, Mexico (CI = confidence interval; Superscript letter in species of commercial importance indicate the type of fishery: a artisanal, i industrial, a/i both, rf recreational fishery; highest contributions in bold)

A)	Males		Females	
Prey species	Mean	97.5% CI	Mean	97.5% CI
$^{a/i}$*Anchovia macrolepidota*	**0.47**	**0.13–0.85**	**0.21**	**0.10–0.71**
^{a}*Haemulopsis nitidus*	0.03	0.10–0.11	0.03	0.10–0.13
$^{a/i}$*Litopenaeus vannamei*	0.07	0.12–0.26	0.23	0.10–0.67
$^{a/i}$*Loligo* spp.	0.05	0.11–0.25	0.15	0.10–0.47
^{a}*Selene peruviana*	0.04	0.10–0.13	0.11	0.10–0.48
^{a}*Squilla mantoidea*	**0.30**	**0.14–0.89**	**0.24**	**0.10–0.65**

B)	Juveniles		Preadults		Young adults	
Prey species	Mean	97.5% CI	Mean	97.5% CI	Mean	97.5% CI
$^{a/i}$*A. macrolepidota*	0.19	0.13–0.47	**0.25**	**0.10–0.79**	**0.22**	**0.01–0.63**
^{a}*H. nitidus*	0.08	0.10 –0.26	0.01	0.01–0.05	0.03	0.01–0.10
$^{a/i}$*L. vannamei*	0.13	0.11–0.51	0.11	0.01–0.45	0.14	0.01–0.53
$^{a/i}$*Loligo* spp.	0.16	0.12–0.44	0.09	0.01–0.23	0.10	0.01–0.40
^{a}*S. peruviana*	**0.19**	**0.11–0.59**	0.10	0.02–0.30	0.17	0.02–0.55
^{a}*S. mantoidea*	**0.22**	**0.11–0.68**	**0.40**	**0.01–0.82**	**0.31**	**0.02–0.74**

C)	*HWS*		*DCS*		*DWS*	
Prey species	Mean	97.5% CI	Mean	97.5% CI	Mean	97.5% CI
$^{a/i}$*A. macrolepidota*	0.16	0.01–0.59	0.15	0.01–0.62	0.14	0.01–0.50
^{a}*H. nitidus*	0.02	0.01–0.09	0.01	0.01–0.07	0.03	0.01–0.13
$^{a/i}$*L. vannamei*	0.15	0.02–0.45	**0.24**	**0.01–0.77**	**0.28**	**0.01–0.77**
$^{a/i}$*Loligo* spp.	0.21	0.01–0.65	0.12	0.01–0.40	0.09	0.01–0.32
^{a}*S. peruviana*	**0.22**	**0.01–0.66**	0.21	0.01–0.76	0.12	0.01–0.48
^{a}*S. mantoidea*	0.21	0.01–0.64	**0.24**	**0.01–0.76**	**0.32**	**0.01–0.71**

TABLE 6 Estimated proportional inputs of *Scomberomorus sierra* and 6 prey species (as determined from MixSIAR) to the diets of three top predators in the waters south of the Baja California peninsula, Mexico (CI = confidence interval; Juveniles, Preadults, and Young Adults; based on Aguirre-Villaseñor et al., 2006).

		Makaira nigricans		Kajikia audax		Coryphaena hippurus	
Prey species	Category	Mean	97.5% CI	Mean	97.5% CI	Mean	97.5% CI
Auxis thazard	Fish	0.05	0.04–0.19	0.04	0.01–0.14	0.02	0.02–0.03
Lagocephalus lagocephalus	Fish	0.21	0.03–0.41	0.26	0.05–0.45	0.18	0.14–0.19
Scomber japonicus	Fish	0.02	0.02–0.08	0.01	0.01–0.05	0.03	0.01–0.04
Selar crumenophthalmus	Fish	0.06	0.04–0.21	0.03	0.02–0.13	0.03	0.01–0.03
Dosidicus gigas	Cephalopods	0.07	0.07–0.27	0.12	0.07–0.40	0.04	0.03–0.19
Pleuroncodes planipes	Crustaceans	0.37	0.26–0.49	0.38	0.26–0.49	0.71	0.64–0.71
Juveniles sierras	Fish	0.03	0.02–0.11	0.01	0.01–0.07	0.06	0.01–0.08
Preadults sierra	Fish	0.03	0.02–0.12	0.02	0.02–0.08	0.04	0.01–0.09
Young adults sierra	Fish	0.03	0.02–0.11	0.02	0.02–0.09	0.02	0.01–0.05

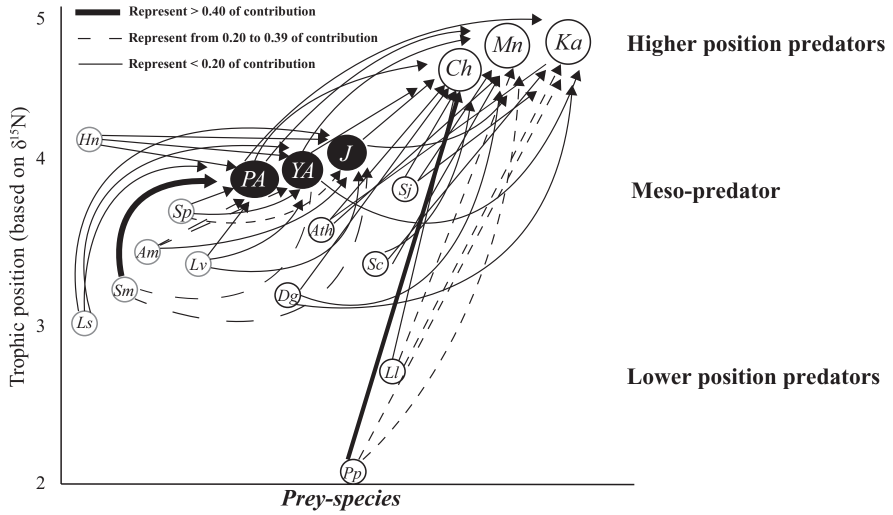

FIGURE 3 Schematic showing isotope mixing model estimates of food flow through the south-easter Gulf of California. Arrows indicate inputs of a trophic group to another; arrows size is proportional to median mixing model estimates of prey inputs of trophic group to others. Species abbreviated as in Table 1 and 3. Trophic position of *Coryphaena hippurus*, *Makaira nigricans*, *Kajikia audax*, *Scomberomorus sierra* and prey´s were calculated in the present study. Black circles = top predators prey´s; gray circles = *S. sierra* prey´s

composition relative to other prey species was approximately 3% (Table 6; Figure 3).

3.7 | Niche width, Trophic overlap and Trophic Position

Based on SCA, the niche width (Levin index) ranges estimated were < 0.6 between sexes, among size classes, and climatic season (Table 7). Based on SIA, according to SIBER, isotopic niche width values (SEAc) were above 1 for all categories, whereas, δ^{15}N variance were above 1 for all categories, except for females and young adults (Table 7). The overlap was high between sexes (Figure 4a), medium overlap among size classes (Figure 4b) and climatic season (Figure 4c), except between HWS and DWS (low overlap = 0.26).

Trophic position estimates calculated from SCA ranged from 3.5 to 4.3 (TP = 4.0 ± 0.28), while estimates using SIA ranged from 3.2 to 4.4 (TP = 3.9 ± 0.28). SCA indicated no significant TP differences according to sexes ($U = 1{,}399.50$, $p = .80$), size classes ($H_{(2, 112)} = 2.91$, $p = .23$) or climatic season ($H_{(2, 109)} = 3.16$, $p = .20$). TP´s estimated with δ^{15}N did not differ between sexes ($U = 206.00$, $p = .43$) or size classes ($H_{(2, 47)} = 0.11$, $p = .94$). However, according to the SIA, TP values of *S. sierra* captured in HWS were significantly higher than those of DWS ($H_{(2, 47)} = 16.88$, $p < .05$) (Table 7). For top predators, trophic positions were 5.0 for *K. audax*, 5.1 for *M. nigricans*, and 4.1 for *C. hippurus*.

4 | DISCUSSION

As a predator, the trophic spectrum of juveniles, preadults and young adults of *S. sierra* in the Gulf of California indicated a wide

TABLE 7 Trophic position (TP), Diet breadth values (*Bi*), isotopic niche width (INW; >1 reflect a broad niche; based on Jaeger et al., 2009), δ^{15}N variance (>1 reflect a broad niche; based on Newsome et al., 2007) and isotopic overlap (IO: *low overlap, **medium overlap, ***high overlap; based on Langton, 1982), by sex, size classes and climatic season of *Scomberomorus sierra* in the south-eastern Gulf of California

		Diet TP		δ^{15}N TP		*Bi*		INW	δ^{15}N variance	
Category	Code	Average	SD	Average	SD	Average	SD	Average	Average	IO
Males	M	4.04	0.30	3.89	0.33	0.3	0.1	3.24	0.79	0.61*** M vs F
Females	F	4.05	0.27	3.81	0.26	0.2	0.1	3.72	1.29	
Juveniles	J	4.21	0.03	4.06	0.22	0.4	0.1	1.93	0.57	0.32** J vs. PA 0.31** J vs. YA 0.57** PA vs YA
Preadults	PA	4.02	0.27	3.85	0.27	0.4	0.1	3.32	0.86	
Young Adults	YA	4.05	0.30	3.87	0.33	0.2	0.7	3.82	1.29	
Humid-warm season	HWS	4.03	0.30	4.03	0.24	0.3	0.2	2.69	0.68	0.50** HWS vs DCS
Dry-cold season	DCS	4.09	0.25	3.81	0.24	0.4	0.1	3.11	0.69	0.26* HWS vs DWS
Dry-warm season	DWS	3.97	0.30	3.57	0.19	0.4	0.1	2.09	0.44	0.41** DCS vs DWS

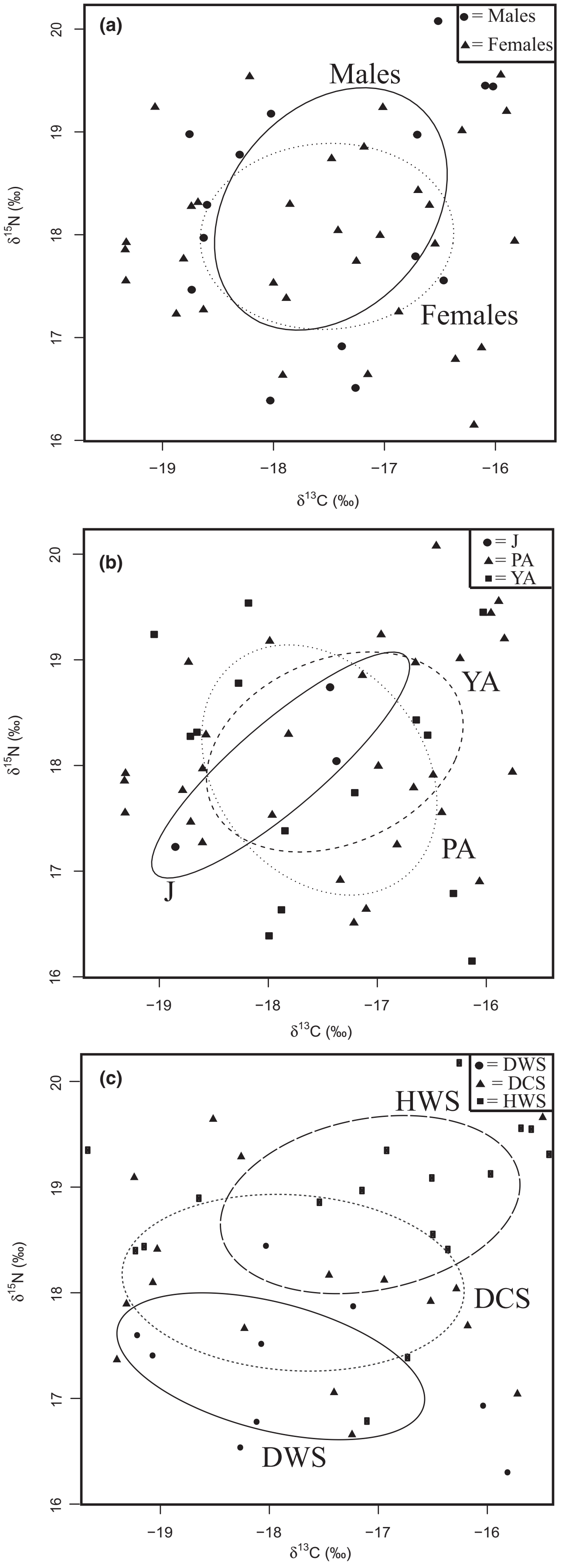

FIGURE 4 Standard ellipses for muscle of *Scomberomorus sierra* between sex (a), among sizes classes (b) and climatic season (c) in Mazatlan, Mexico. In "a", black triangles and dotted line ellipse = females, black circles and straight line ellipse = males; In "b", black circles and straight line ellipse = Juveniles "J", black triangles and dotted line ellipse = Preadults "PA", black square and dashed line ellipse = Young Adults "YA"; In "c", black circles and straight line ellipse = DWS, black triangles and dotted line ellipse = DCS, black square and dashed line ellipse = HWS

consumption range, dominated by 18 species and composed primarily of pelagic-neritic prey species. However, the presence of benthopelagic species (*e.g. Selene peruviana*, Lopez-Peralta and Arcila, 2002) and demersal species (*e.g. Polydactylus approximans*; Motomura, Kimura, & Iwatsuki, 2002) in the SCA, as well as significant contribution from *Squilla mantoidea* (demersal species) indicate that *S. sierra* has vertical movements in the water column.

Scombrid species make sharp descents and ascents around dawn and dusk called spike dives (Fenton, Ellis, Falterman, & Kerstetter, 2015; Willis, Phillips, Muheim, Diego-Rasilla, & Hobday, 2009), probably associated with the diel vertical movements of their prey species such as cephalopods (Galvan-Magaña et al., 2013). In the present study, the isotopic composition (δ^{13}C and δ^{15}N; Table 3) of *S. sierra* captured in the southeastern Gulf of California was comparable to that of other predators consuming coastal pelagic species (Torres-Rojas et al., 2013). Pelagic species such as the blue marlin (*Makaira nigricans*) usually present δ^{15}N (15.28 to 16.60‰) and δ^{13}C (−17.33 to −16.05‰) values lower than benthic species such as juvenile scalloped hammerhead shark, *Sphyrna lewini* (δ^{15}N values from 18.67 to 19.72‰, δ^{13}C values from −15.06 to −14.79‰) (Torres-Rojas et al., 2013; Torres-Rojas, Páez-Osuna, et al., 2014). Therefore, SCA and SIA confirm that *S. sierra* is primarily a coastal pelagic predator that possesses the ability to migrate into the water column. The advanced structural development in the visual system makes *S. sierra* morphologically equipped to feed in reduced light conditions (Blaxter, 1986), thereby increasing the amount of habitat available for foraging.

Engraulids fish were the main diet constituent for *S. sierra*. Moreno-Sanchez et al. (2011) mention that in three areas of Northwest Mexico, this predator fed mainly on fish prey from the families Clupeidae and Engraulidae, followed by a lower proportion of cephalopods (squid). Also, *S. sierra* exhibits considerable similarity in its food spectrum with other species from the genus *Scomberomorus*. Previous studies have reported that fish of the family engraulidae and crustaceans primarily comprise the diets of *S. lineolatus* (Devaraj, 1998) and *S. commerson* (Bakhoum, 2007). Rapid addition of large prey items, especially fish, into the diet characterizes the early life history of scombrids (Hunter, 1981).

The relative abundances of anchovies in the *S. sierra* diet relates to their availability in different regions (Fischer et al., 1995). For example, *Anchovia macrolepidota* is found inside estuarine systems (Amezcua & Amezcua-Linares, 2014; Amezcua et al., 2019), and inshore along sandy beaches and in tide streams and forms large schools (Whitehead et al. 1988). Mendoza, Castillo-Rivera, Zarate-Hernández, and Ortiz-Burgos (2009) found that *A. macrolepidota* is highly abundant in the Mexican coast between February and October, the fishing season of *S. sierra* in our study's region. Therefore, the high proportions of anchovies (%PSIRI and MixSIAR) in the diet of *S. sierra* likely relates to spatial and temporal circumstances, as has been observed for other species (*e.g. Selene peruviana*) in the southern Gulf of California (Tripp-Valdez, Arreguin-Sanchez, & Zetina-Rejon, 2012). The relative contributions of engraulid fish to the diets of *S. sierra*, as well as to those of *Scomberomorus* spp. are relevant to future anchovy's management plans, thus, the possible bottom-up effects of *Scomberomorus* spp. diets must be considered.

Although engraulid fish were the most important in the *S. sierra* diet based on SCA, two species had the highest isotopic contribution to the muscle of *S. sierra* (*A. macrolepidota* and *S. mantoidea*). Tripp-Valdez, Galván-Magaña, and Ortega-García (2010) mention that crustaceans such as *Hemisquilla californiensis* juveniles (megalops) are more abundant during the warm season in the southeastern Gulf of California. Therefore, both techniques confirmed the presence of *S. sierra* prey items previously reported to be abundant in the area.

In this study, no difference in male and female *S. sierra* diets was observed with either technique, coinciding with previous reports on other *Scomberomorus* species (Devaraj, 1998; Bakhoum, 2007). ANOSIM based on SCA revealed no differences in *S. sierra* diet based on size classes. However, medium overlap related to size, particularly between juveniles and young adult individuals, were observed using SIBER based on SIA. The fact that the two techniques yielded different results may relate to: (a) their relative time portrayals, and (b) the low SIA sample size for juveniles. For example, isotopic muscle turnover represents integrated diet information (*e.g.* months; Hobson & Clark, 1992; Hobson, Schell, Renouf, & Noseworthy, 1996), while SCA is a snapshot of what the organism consumes before it is captured. Further, SCA data are biased towards larger prey (*e.g.* rapid digestion of smaller prey), while SIA reveals an integrated signal of the entire diet. Therefore, the lack of differences in ANOSIM values among size classes may relate to high consumption of a particular prey species (engraulid fish) that dominates the stomach content composition. The use of SIBER allow us to detect changes in the trophic role based on the isotopic composition of the predator (Vinagre, Maguas, Cabral, & Costa, 2011), however, the sample size of juveniles is low to make valid comparisons, allowing to infer only ecological trends. Despite this, the present study highlights the importance of combining techniques to portray both short- and long-term diet information.

Most predators alter their feeding habits based on their abilities to catch larger prey species, which relates to growth of the predators themselves (Graham, Grubbs, Holland, & Popp, 2007). In the case of *S. sierra*, regarding δ^{15}N variance, the differences among size classes are due to the inclusion of other prey species in the diet (*e.g.* cephalopods and crustaceans) as the individual grows. Devaraj (1998) mentions that *S. lineolatus* undergoes diet alterations depending on size. In the case of *S. sierra*, the inclusion of an increased number of prey species in preadults (organisms > 36 cm) may relate to development of the visual system, as well as changes in the energy requirements of the species reproductive stages. *S. sierra* has a first maturity characterized by a total length of 37.5 cm (Aguirre-Villaseñor et al., 2006; Lucano-Ramirez et al., 2011) and increasing resource consumption may indicate preparation for a reproductive stage.

Scombrids have an advanced visual system ontogeny, which likely contributes to their well-developed foraging abilities. Margulies (1997) mentions that adult scombrids are highly visual, active predators (Tamura & Wisby, 1963), but early juvenile function with a more limited visual system. In the case of *S. sierra*, the juvenile visual system is characterized by a simplex (pure cone) retina with little accommodative function and no dark-light adaptive ability, suggesting that first-feeding juveniles are restricted to daylight feeding. Thus, the feeding habits changes of *S. sierra* observed in this study relate to morphological, reproductive and visual changes (Blaxter, 1986).

According to the ANOSIM, *S. sierra* diet composition has not seasonal differences, which may be attributed to the relatively high abundance of anchovy in the southeastern GC around year, the preferred prey item (Moreno-Sanchez et al. 2011; present study). However, seasonal variation in *S. sierra* feeding activity was detected using SIA and CCA, which indicated diet changes during the fishing season. According to MixSIAR, *S. sierra* has two distinct well season-defined diets - *S. mantoidea* prevails in DCS and DWS, and *S. peruviana* prevails in HWS. Sakamoto (1982) mentions that *S. sierra* feeding activity changes temporally due to variations in the abundance of fish, water temperature and prey availability. This seasonal variation was observed with the CCA in the present study and has been previously reported for other *Scomberomorus* species (Devaraj, 1998; Bakhoum, 2007).

Scombrid fish have an opportunistic feeding strategy, in which they consume an area´s most abundant prey species. Conversely, in this study, the Levin index (Bi < 0.6) and δ^{15}N variance indicated that *S. sierra* have a specialist feeding strategy in nearly all categories (δ^{15}N variance < 1), except for females and young adults when they are generalists (δ^{15}N variance > 1). The specialist strategy could be related to the high abundance of anchovies in the diet, however, according to CCA the *S. sierra* diet varies with the climatic season, and the species displays an opportunistic feeding strategy like other species of its genus. This pattern may be associated with the metabolism of species of this genus (Olson & Scholey, 1990; Wexler, 1993).

Trophic positions are important for defining the position of different species within the food web (Bakhoum, 2007). In the present study, trophic positions based on SIA were similar than those estimated using stomach contents, where both reveal a high degree of trophic plasticity in *S. sierra* of the southeastern Gulf of California.

The Pacific sierra TP value calculates by SCA (~4) did not differ significantly from that of *S. sierra* in the southern continental shelf of Colombia (4.21) (López-Peralta & Arcila, 2002), and the one estimated in the north-central part of the Gulf of California (4.5 SCA and 4.8 SIA; Muro-Torres et al., 2019). Conversely, according to Collette and Nauen (1983), the TP of *S. sierra* was 2.8 and higher. These findings, which indicate that *S. sierra* is a secondary to tertiary carnivore, comply with this study´s values calculated with SIA (~3.7). These results suggest that *S. sierra* has different functional roles in the food web related to the ontogenetic stage and should be considered an important predator in the southeastern Gulf of California (Abitia-Cardenas et al. 2010; Tripp-Valdez et al., 2010).

As a prey, previous studies have reported the presence of juveniles and preadults of *S. sierra* in the diets of pelagic and benthic predators in the study area (Torres-Rojas et al., 2013; Torres-Rojas, Hernández-Herrera, et al., 2014; Torres-Rojas, Páez-Osuna, et al., 2014). In the present study, *S. sierra* was not a dominant prey item for the three top predators, but further studies must confirm this presumption (collection of more samples at different scales of space and time). Despite the simplicity of this study´s mixing model, some authors mention a renewed emphasis on understanding that pathways of biomass and energy flow in exploited ecosystems (Olson et al., 2014; Watters et al., 2003). Thus, this study´s results provide useful information on mid-trophic level communities in pelagic habitats, a prerequisite for gaining insight into the role of predators.

In conclusion, the complementary use of SCA and SIA enables detection of *S. sierra* trophic ecology variation, which was previously undetermined in this region. Variation in diet among size classes indicated ontogenetic changes associate with reproductive stages and the visual system development. Finally, seasonal diet variations indicated an opportunistic feeding strategy, as well as the ability to fulfill different roles in the food web. Thus, *S. sierra* may be a key mesopredator in the southeastern Gulf of California.

This knowledge could aid in fisheries management and in the development of adaptive plans for *S. sierra* and other fisheries on the Mexican coasts. Non-fishery management plans currently exist for *S. sierra*, an in general for most fin fish species captured in Mexico. Although Mexican regulations for anchovies, billfish and dolphinfish fisheries exist, the inadequate or lack of management of one or more of these interrelated species could affect the ecological and economical sustainability of this multi-species fishery. More studies focused on trophic ecology of other commercial and ecologically important species allow us to understand their functional role in ecosystems.

Since *S. sierra* is a species with many prey-predator relationships, including several commercially important species in the southeastern GC food webs, we assumed that *S. sierra* could constitute a critical trophic link transferring energy from low-trophic levels up to large apex species (a potential mesopredator). The knowledge of its trophic niche contributes to understand the species' trophic roles in the southeastern GC food web (e.g., transferring energy from low-trophic levels up to large apex species). Because of the connectance of *S. sierra* with multiples species that sustains industrial, artisanal, and sport fisheries, the knowledge obtained in this research could also be useful to formulate an ecosystem-based fisheries management for the region.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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