Food habits of the Pacific angel shark *Squatina californica* in the southern Gulf of California, Mexico

by

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ABSTRACT. - The food habits of the Pacific angel shark, *Squatina californica*, was studied in analyzing the stomach contents of specimens monthly caught between September 2000 and March 2003 in the southern Gulf of California, Mexico. The data were analyzed according to length, season, years, and sex. A total of 414 stomachs were examined, of which 190 (46%) contained food and 224 (54%) were empty. The relative importance index (IRI) was calculated to measure the trophic preference. According to this index, the most important prey species are: the jack *Decapterus macrosoma* (47.5%), the daisy midshipman *Porichthys analis* (15.9%), the inotted lizardfish *Synodus evermanni* (8.0%), the soldierfish *Myripristis leiognathus* (7.2%), and the crustacean *Sicyonia penicillata* (8.0%). The Levin's standardized index (Bi) shows that the niche breadth is relatively narrow (Bi = 0.31), which means that the angel shark is a selective predator with a preference for demersal fishes. The Morisita-Horn index (C_λ) indicates niche trophic overlaps in diet between juveniles and adults (C_λ = 0.82) and between sexes (C_λ = 0.96).

RÉSUMÉ. - Régime alimentaire de l'ange de mer du Pacifique, *Squatina californica*, dans le golfe de Californie méridional, Mexique.

Le régime alimentaire de l'ange de mer du Pacifique, *Squatina californica*, a été étudié en analysant les contenus stomacaux de spécimens récoltés mensuellement entre septembre 2000 et mars 2003 dans le golfe de Californie méridional, Mexique. Les données ont été analysées en fonction de la taille, de la saison, de l'année et du sexe. Sur les 414 estomacs examinés, 190 (46%) contenaient de la nourriture et 224 (54%) étaient vides. L'indice d'importance relative (IRI) a été calculé pour mesurer la préférence trophique. Selon cet indice, les espèces-proies les plus importantes sont : le chinchard *Decapterus macrosoma* (47,5%), le poisson-crapaud *Porichthys analis* (15,9%), le poisson-lézard *Synodus evermanni* (8.0%), le poisson-soldat *Myripristis leiognathus* (7.2%), et le crustacé *Sicyonia penicillata* (8,0%). L'indice standardisé de Levin (Bi) montre que la largeur de niche est relativement étroite (Bi = 0,31), ce qui signifie que cet ange de mer est un prédateur sélectif avec une préférence pour les poissons démersaux. L'indice de Morisita-Horn (C_λ) indique un chevauchement des niches trophiques entre les juvéniles et les adultes (C_λ = 0,82), et entre les sexes (C_λ = 0,96).

Key words. - Squatinidae - *Squatina californica* - Angel shark - PSE - Gulf of California - Food habits.

The Pacific angel shark, *Squatina californica* (Ayres, 1859), is the only angel shark inhabiting the eastern Pacific Ocean (Compagno, 1999). This species has a mean size of 100 cm total length (TL) and specimens as large as 155 cm TL have been reported (Compagno *et al.*, 1995). This is a benthic shark with dorso-ventrally flattened body, whose distribution is from southern Alaska to the Gulf of California, and also possibly from Peru to southern Chile (Kato and Hernández-Carvallo, 1967; Compagno *et al.*, 1995; Natanson and Cailliet, 1986). In general, it inhabits muddy or sandy bottoms of temperate and tropical waters, and is common in the coastal and shallow waters of the continental shelf off the coast of California between 3 to 46 m depth, and in the Gulf of California to 183 m. It was observed at a depth of 205 m in the Central American Pacific (Compagno *et al.*, 1995; Gaida, 1997).

In the southern Gulf of California, the Pacific angel shark is caught seasonally and is one of the most abundant sharks. The landings vary between 13 and 26 tons mainly during winter (Villavicencio-Garayzar, 1996; Alonso-Castelán, 1998). The Pacific angel shark has a seasonal presence within the Gulf of California, indicating a migration during summer associated to reproduction (Galván-Magaña *et al.*, 1989). Although Pittenger (1984) and Fouts and Nelson (1999) studied the feeding habits of the angel Shark in Californian waters, few biological data exist for this species in the Gulf of California. Because of the importance of this species to ecology and fisheries, the present study was carried out to determine its food habits in the southern Gulf of California, including their variations by size, sex, years, and season.

MATERIAL AND METHODS

From September 2000 to March 2003, monthly samples were taken in the following fishing camps: El Pardito, El Sauzoso, El Portugués and Ensenada de los Muertos, located

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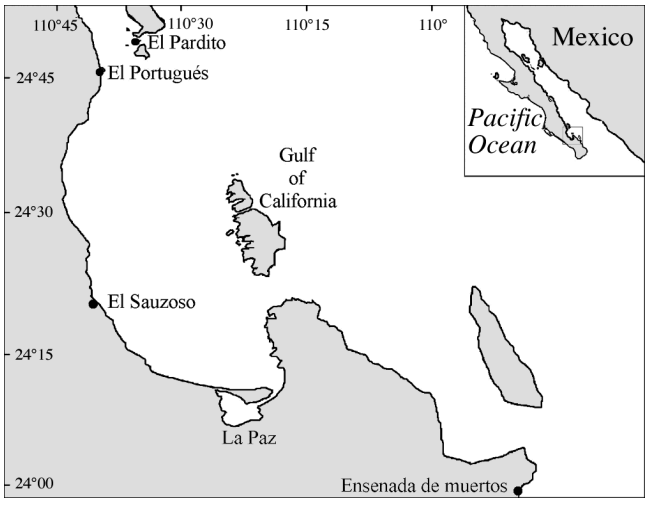

Figure 1. - Study area where the specimens of Pacific angel shark *Squatina californica* were caught. *[Zone d'étude où les spécimens d'anges de mer du Pacifique,* Squatina californica, *ont été cap - turés.]*

in southern Gulf of California (Fig. 1). Fishes were captured with multifilament gill net of mesh size between 10 and 30 cm. The nets were set at 1 to 10 km from the shoreline at sunset and inspected the following morning.

The total length (TL) with precision in centimetres and sex of each shark were recorded. The stomachs were extracted and their fullness was estimated as a percentage of stomach capacity. The food components were fixed in formalin solution.

Prey species were sorted by taxonomic groups for qualitative analysis. They were identified to the most specific level possible, depending on the degree of digestion. For the identification of the fishes, the following keys/works were used: Clothier (1950), Monod (1968), Miller and Lea (1972), Miller and Jorgensen (1973), Allen and Robertson (1994), Fischer *et al.* (1995), and Thomson *et al.* (2000). Cephalopods were identified by their beaks according to Clarke (1962, 1986), Iverson and Pinkas (1971) and Wolff (1982, 1984). Crustaceans were identified using the keys in Fischer *et al.* (1995).

The frequency of occurrence (% FO), numeric (% N) and gravimetric (% W) percentages were calculated. With these values, the relative importance index IRI was calculated (Pinkas *et al.*, 1971) using the following equation:

IRI =% FO (% W +% N)

The values of IRI were expressed in percentage to facilitate the comparison with others studies (Cortés *et al.*, 1996).

The total lengths were used to determine the size ranges; the number of class intervals was calculated using the Sturges equation (Daniel, 1997) and their amplitude was determined according to Daniel (1997). The juvenile and adult stages were defined according to Marqueda-Cava (2003) who determined that sharks greater than 80 cm TL were adults, and those with less than 80 cm TL are juveniles.

The trophic niche width (Bi) was calculated using the standardized Levin's Index (Hurlbert, 1978) that takes values from 0 to 1. A Bi of less than 0.6 indicates a specialist predator that uses few prey resources and prefers certain prey, while values over 0.6 indicate a generalist predator that uses all resources without preference.

The Morisita-Horn index C_λ (Smith and Zaret, 1982) was applied to evaluate diet overlaps between sizes and sexes. This index also ranges from 0, when the diet is completely different, to 1 when the diet of the sexes or sizes is the same. Values exceeding 0.6 are considered to overlap significantly.

RESULTS

A total of 414 stomachs were obtained, with 190 (46%) containing food and 224 (54%) being empty. The trophic spectrum included 23 prey species consisting of 18 fishes, 2 cephalopods and 3 crustaceans, and corresponding to 17 families and 17 genera (Tab. I).

The total weight of prey was 4827.6 g, of which fishes contributed 90%, crustaceans 1.7%, and cephalopods 0.005%. The fish *Decapterus macrosoma* and *Etrumeus teres* were the prey species with the highest total weights, with 42.1% and 13.3% respectively, followed by *Porichthys analis* (11.3%), *Synodus evermanni* (7.1%), *Myripristis leiognathus* (6.5%) and unidentified organic matter (UOM) with 8.3%.

In number, the trophic spectrum was composed of 185 prey organisms with 86.0% of fishes, 11.0% of crustaceans and 1.6% of cephalopods. The most important components were: *M. leiognathus* (21.1%), *P. analis* (18.9%), *D. macro - soma* (12.4%), *S. evermanni* (11.9%) and *Sicyonia penicilla - ta* (10.3%).

The fishes were the most frequent prey found in the stomachs, representing 80% of stomachs, followed by the crustaceans (10%), the cephalopods (1.6%), and UOM (26.3%). The most frequent prey species was *P. analis* (15.3%), followed by *D. macrosoma* (11.1%), *M. leiognathus* (11.1%), *S. evermanni* (9.5%), *S. penicillata* (8.9%) and UOM (26.8%).

According to the index of relative importance, *D. macro - soma* (29.7%) was the most important prey, followed by *P. analis* (22.7%), *M. leiognathus* (15.0%), UOM (10.9%), *S. evermanni* (8.9%), the crustacean *S. penicillata* (5.2%), and *E. teres* (4.2%) (Fig. 2).

The stomachs of females had food in 115 cases, while 75 male stomachs had food. According the values of IRI, females feed on *D. macrosoma* (29.6%), *P. analis* (28.9%), *M. leiognathus* (9.6%), *S. evermanni* (8.2%) and *E. teres* (5.7%), whereas males feed on *D. macrosoma* as the most important prey, followed by *M. leiognathus* (25%), *P. analis*

Table I. - Trophic spectrum of the Pacific angel shark *Squatina californica* prey in the southern Gulf of California, expressed in numeric (N), gravimetric (W), frequency of occurrence (FO) and index of relative importance (IRI) absolues values and percentages. *[Spectre trophique des proies de l'ange de mer du Pacifique,* Squatina californica, *dans le sud du golfe de Californie. Résultats exprimés en valeurs absolues et en pourcentages, en nombre (N), en poids (W), en fréquence de présence (FO) et en indice d'abondance relative (IRI).]*

Prey species	FO	%FO	N	%N	W	%W	IRI	%IRI
MOLLUSCA								
Enoploteuthidae								
Abraliopsis affinis	2	1.05	2	1.08	0.21	0.00	1.14	0.06
Mastigoteuthidae								
Mastigoteuthis dentata	1	0.53	1	0.54	0.02	0.00	0.28	0.01
Subtotal			3	1.62	0.23	0.00	1.42	0.07
ARTHROPODA								
Crustacea	1	0.53	1	0.54	3.96	0.08	0.33	0.02
Isopoda	1	0.53	2	1.08	0.91	0.02	0.58	0.03
Sicyonidae								
Sicyonia penicillata	17	8.95	19	10.27	77.93	1.61	106.29	5.24
Subtotal			22	11.89	82.80	1.71	107.20	5.29
TELEOSTEI								
Clupeidae								
Etrumeus teres	9	4.74	9	4.86	641.00	13.28	85.93	4.23
Sardinops caeruleus	1	0.53	1	0.54	36.01	0.75	0.68	0.03
Batracoididae								
Porichthys analis	29	15.26	35	18.92	544.52	11.28	460.95	22.71
Holocentridae								
Myripristis leiognathus	21	11.05	39	21.08	313.58	6.50	304.83	15.02
Labridae	1	0.53	1	0.54	8.92	0.18	0.38	0.02
Serranidae								
Diplectrum pacificum	6	3.16	8	4.32	205.71	4.26	27.09	1.33
Paralabrax maculatofasciatus	1	0.53	1	0.54	26.06	0.54	0.57	0.03
Synodontidae								
Synodus evermanni	18	9.47	22	11.89	341.28	7.07	179.62	8.85
Synodus scituliceps	2	1.05	2	1.08	28.79	0.60	1.77	0.09
Carangidae								
Decapterus macrosoma	21	11.05	23	12.43	2031.68	42.08	602.48	29.69
Mugilidae								
Mugil spp.	1	0.53	1	0.54	11.38	0.24	0.41	0.02
Scombridae								
Scomber japonicus	1	0.53	1	0.54	1.70	0.04	0.31	0.02
Stromateidae								
Peprilus snyderi	1	0.53	1	0.54	13.61	0.28	0.43	0.02
Ophichthidae								
Ophidion iris	9	4.74	9	4.86	36.65	0.76	26.62	1.31
Triglidae								
Bellator gymnostethus	1	0.53	1	0.54	10.22	0.21	0.39	0.02
Muraenidae	3	1.58	3	1.62	51.28	1.06	4.23	0.21
Pleuronectiformes	1	0.53	1	0.54	12.25	0.25	0.42	0.02
Pomacentridae								
Chromis spp.	2	1.05	2	1.08	30.85	0.64	1.81	0.09
Subtotal			160	86.46	4345.49	90.02	1698.92	83.71
Unidentified organic matter	51	26.84	0	0.00	399.12	8.27	221.91	10.93
Total	190		185	100.00	4827.64	100.00	2029.45	100.00

(12.1%), *S. evermanni* (9.6%) and *S. penicillata* (8.1%).

Size of angel sharks ranged from 33 to 95.5 cm TL (mean TL = 76.2 cm ± 10.6 SD), and eight class intervals were obtained. The most frequent stomachs with food were found for the sharks of the interval 76-89 cm TL. The main food components in the average size using IRI were: *M. leiognathus*, *S. penicillata*, *S. evermanni*, *D. macrosoma* and *P. analis* (Tab. II).

Juveniles (less than 80 cm TL) feed mainly on *D. macro - soma* (IRI 47.5%), *P. analis* (15.9%), *S. penicillata* (8.0%),

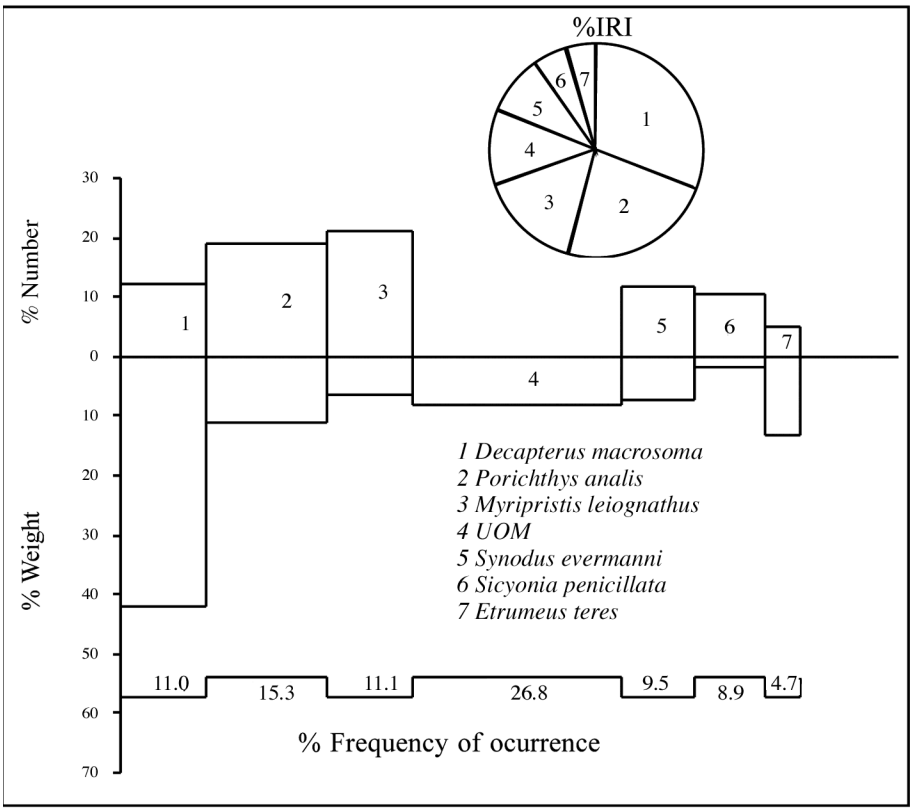

Figure 2. - Trophic spectrum of the Pacific angel shark *Squatina californi - ca*, presented as percentage of number and weight, in frequency of occurrence and IRI. *[Spectre trophique de l'ange de mer du Pacifique,* Squatina californica, *présenté en pourcentages numé - riques et pondéraux, en fréquence de présence et en IRI.]*

S. evermanni (8.0%), and *M. leiognathus* (7.2%). Adults (greater than 80 cm TL) feed on *P. analis* (IRI 27.5%), *M. leiognathus* (23.0%), *D. macrosoma* (11.0%) and *S. ever - manni* (8.5%).

With respect to capture location of the sharks, the main preys at El Pardito were *M. leiognathus* (IRI 55.2%), *P. analis* (19.6%), *S. evermanni* (13.2%), *S. penicillata* (4.3%), and *Ophidion iris* (4.1%), while at Ensenada de los Muertos, *P. analis* was the most important prey (53.5%,) followed by *M. leiognathus* (3.5%) and *E. teres* (3.5%). The locations in the Bay of La Paz (El Portugués and El Sauzoso) were grouped because they are close together; the prey species *D. macrosoma* (75.8%) was the most important, followed by *S. evermanni* (6.4%) and *E. teres* (3.6%).

The monthly data were grouped into warm (April, June, September and October) and cold seasons (January, February, March, November and December) for analysis of seasonal variation in diet. In the warm season, *P. analis* (52.5%) was the most important prey species, followed by *M. leiognathus* (10.3%) and *S. penicillata* (5.6%). During the cold season, the main food components were *D. macrosoma* (57.5%), *M. leiognathus* (12.0%), *S. evermanni* (10.8%) and *P. analis* (5.2%) (Fig. 3). In the analysis by years, some prey species were always present (*M. leiognathus*, *S. evermanni*), but the relative importance in the diet changed by year, like *D. macrosoma* in 2003 (Fig. 4).

The Levin's index indicated that the trophic niche width was narrow (Bi = 0.31). Therefore the angel shark is considered as a predator with a marked preference for certain prey.

According to the Morisita-Horn index, there was significant overlaps between sexes (C_λ = 0.96), seasons (C_λ = 0.70), and between juveniles and adults (C_λ = 0.82).

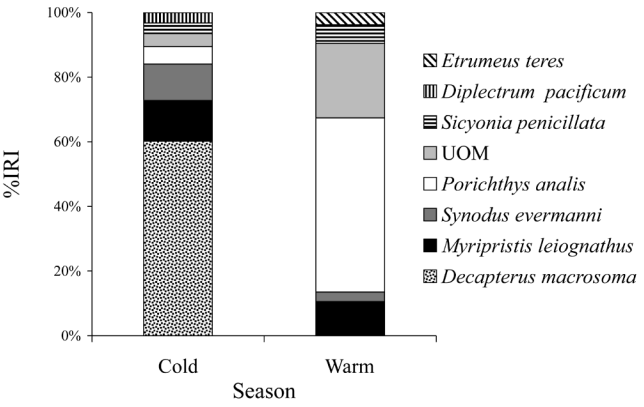

Figure 3. - Trophic analysis by season of the diet of the Pacific angel shark *Squatina californica* represented as percentages of index of relative importance (% IRI). *[Analyse trophique par sai - son du régime alimentaire de l'ange de mer du Pacifique,* Squatina californica, *exprimée en pourcentages de l'indice d'abondance rel - ative (% IRI).]*

Size class	I	II	III	IV	V	VI	VII	VIII
Total length (cm)	41-47	48-54	55-61	62-68	69-75	76-82	83-89	90-96
Number of stomachs	2	10	10	17	30	63	47	11
Abraliopsis affinis					1	1		
Bellator gymnostethus						1		
Chromis spp.								2
Crustacea						1		
Decapterus macrosoma	1			2	2	16	2	
Diplectrum pacificum		1	4		1	2		
Etrumeus teres					1	3	5	
Isopoda				2				
Labridae			1					
Mastigoteuthis dentata					1			
Mugil spp.				1				
Muraenidae		1				1		1
Myripristis leiognathus		4	2	2	2	4	20	5
Ophidion iris		2	2	2			3	
Paralabrax maculatofasciatus						1		
Pleuronectiformes						1		
Peprilus snyderi					1			
Porichthys analis				3	5	14	9	4
Sardinops caeruleus							1	
Scomber japonicus					1			
Sicyonia penicillata	1	1	2	3	4	4	4	
Synodus evermanni		2	1	4	2	9	4	
Synodus scituliceps							2	
Total	2	11	12	19	21	58	50	12

Table II. - Trophic spectrum in the diet of the Pacific angel shark *Squatina californica* in the southern Gulf of California by size class, in absolute values, from stomachs with food. [*Spectre trophique du régime alimentaire de l'ange de mer du Pacifique,* Squatina californica, *dans le sud du golfe de Californie, en fonction de la classe de taille, en valeurs absolues, établi à partir des estomacs contenant de la nourriture.]*

DISCUSSION

The high proportion of empty stomachs found during the sampling period could be attributed to the method of fishing, as the gill nets are checked by the fishermen the next morning or afternoon, and sometimes even two days after setting them. Therefore, food ingested by the sharks was in an advanced state of digestion or gone. However, Simpfendorfer (1998) suggested that gill nets contributed to fewer empty stomachs than other more selective methods. Because the Pacific angel shark eats during the night (Fouts and Nelson, 1999), the state of prey digestion was advanced or complete in many stomachs.

Squatina californica is a carnivorous predator, which feeds mostly on demersal fish (e.g. *P. analis*, *M. leiognathus*, *S. evermanni*, *Diplectrum pacificum*, *O. iris*) and few pelagic species (*D. macrosoma* and *E. teres*), although it sometimes feeds on prey of mesopelagic waters that make daily vertical migrations, such as the cephalopods *Abraliopsis affinis* and *Mastigoteuthis dentata*. These species were low in importance in the trophic spectrum, but reveal the opportunism of this predator.

Certain characteristics of the food components indicate that this shark uses ambush as a principal mode of capture, since prey, like *D. macrosoma*, *P. analis*, *M. leiognathus*, *O. iris*, and *E. teres*, often presented the scare of a bite in the ventral part of the body. The Pacific angel shark apparently remains buried and immobile in the sand, and allows the prey to roam close by. Its mimetic colour pattern makes it invisible for the prey. When the prey is close enough to its mouth, the shark jumps to grasp and engulf it (Fouts and Nelson, 1999).

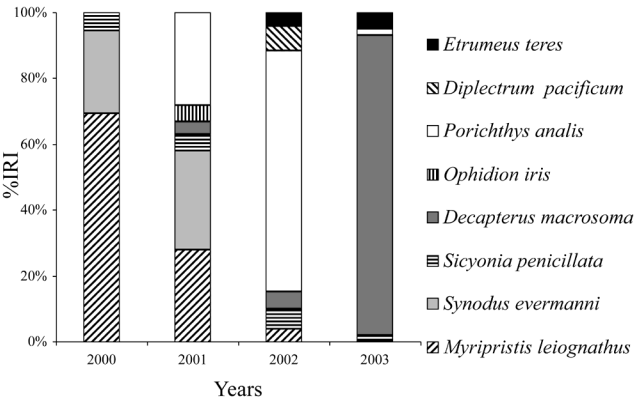

Figure 4. - Trophic analysis by year for the Pacific angel shark *Squatina californica* represented as percentages of index of relative importance (% IRI). *[Analyse trophique par année du régime alimentaire de l'ange de mer du Pacifique,* Squatina californica, *exprimée en pourcentages de l'indice d'abondance relative (% IRI).]*

The prey of the Pacific angel shark (*M. leiognathus*, *P. analis*, *O. iris*, *S. evermanni*) were species that shelter in caves, crevices, and under ledges during the day, and emerge during the night to feed on crustaceans and other organisms. The principal prey *D. macrosoma* is a pelagic fish that inhabits mainly coastal zones close to the bottom (Allen and Robertson, 1994). According to Pittenger (1984), *S. californica* often locates itself adjacent to rock-sand interfaces or patch reefs to increase encounter rates with potential prey, because rocky reefs serve as refuge for a wide variety of fish.

The dominance of *D. macrosoma*, *P. analis*, and *M. leiognathus* indicates that the Pacific angel shark is selective in choosing prey according to its ambush strategy and food requirements. This predator is considered a specialist conditional on food availability. When prey is abundant, the shark can select a particular food to maximize consumption and energy utilization. However, when the food is limited, it cannot afford this selectivity, and then feeds on the available prey (Wetherbee *et al.*, 1990).

Squatina californica was found to be highly piscivorous. The fishes *D. macrosoma*, *P. analis*, *M. leiognathus*, and the crustacean *S. penicillata* were present in every size class of shark. The prey showed different orders of importance in the diet, reflecting the abundance of food species. This can be explained because the availability of food resources depends on water temperature, since the abundance of some prey species varies both in number and biomass over the year (Sierra *et al.*, 1994).

There was a high overlap by sex ($C_\lambda = 0.96$), because 8 preys were found in the diet of both sexes. *P. analis*, *M. leiognathus* and *D. macrosoma* were the most important prey for females and males alike. Segregation by sex can reduce competition for food, according to Zayas-Álvarez (1998), but there is less segregation during the reproductive season (March to May), when several common food resources and an overlap in trophic niche were found. When males and females use the same feeding site, this is compensated with the existence of abundant food resources (Colwell and Futuyma, 1971). The feeding areas of the Pacific angel shark have abundant and diversified prey, what probably reduces the competition for food within the angel shark population.

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