



Trophic ecology of *Mustelus schmitti* (Springer, 1939) in a nursery area of northern Patagonia

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ARTICLE INFO

Article history:

Received 10 September 2010
Received in revised form 2 March 2011
Accepted 3 March 2011
Available online 16 March 2011

Keywords:

Trophic ecology
Diet
Mustelus schmitti
Shark
Nursery area

ABSTRACT

Mustelus schmitti is an endangered endemic shark of the southwest Atlantic, and an important economical resource in Argentina, Brazil and Uruguay. The objective of this study was to describe the trophic ecology of *M. schmitti* in Anegada Bay, its feeding strategy and diet composition, along with the possible dietary shifts, due to season, sex, ontogeny and the different geographical features of the bay. Our results show that *M. schmitti* is a carnivorous opportunistic predator, feeding on a variety of benthic invertebrates. The diet presented seasonal and ontogenetic variations, while no differences in diet composition were observed between sexes or the different sampling sites. This species behave as a generalize feeder, with a wide trophic spectrum and a diverse diet.

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1. Introduction

The smoothhound, *Mustelus schmitti* (Springer, 1939) is a small shark of the Triakidae family, with a maximum total length of 110 cm. This species is endemic to the Southwest Atlantic, from the south of Brazil to Argentine's Patagonia (22° S to 47°45' S), and is known to migrate seasonally in large numbers between wintering grounds in south Brazil and summer grounds in Argentina (Figueiredo, 1977; Vooren, 1997). The species occurs from coastal waters to 120 m depth, at bottom temperatures of 5.5 to 11.0 °C and surfaces temperatures of 8 to 11.7 °C (Menni, 1985). In Argentina, it is more abundant in littoral waters of Buenos Aires province and northern Patagonia, where salinity is higher than 22.44 psu (Massa et al., 2004).

This species is an important economical resource in Argentina, Brazil and Uruguay, and is also exported to England and China (Massa and Lasta, 2000). The smoothhound is fished by both industrial and artisanal fishing fleets. From 1994 to 2002 the reported captures were around 6.000 t per year for the coastal area of Buenos Aires province. Since 2006, the reported captures have increased, reaching 9.000 t in 2008 (Fernández Aráoz et al., 2009; Massa et al., 2010).

The exploitation of this species throughout its distribution range, has lead to recent declines in its populations, despite Maximum Permitted Catch regulations established by the Secretaria de Agricultura, Ganaderia, Pesca y Alimentacion (SAGPyA) in Argentina and

the Dirección Nacional de Recursos Acuáticos (DINARA) in Uruguay (Massa et al., 2004). *M. schmitti* is currently considered vulnerable in these two countries by the International Union for Conservation of Nature (IUCN). The species is categorized as critically endangered in Brazil, given observed declines of 85% of the winter migrating population, due to boundless fishing rates, probable extirpation of a local breeding population and continuing intense fishing. The IUCN has assigned an overall global assessment of endangered; that summarizes the situation throughout the species' range. This is of great cause for concern, given that market demand is increasing and fisheries are still exploiting the resource (Massa et al., 2010).

Most shark species have geographically discrete nurseries, which are usually located in highly productive, shallow waters (e.g. coastal marshes and estuaries), where the young can find abundant food (Castro, 1987). These areas are often the shallower parts of the population's range (Springer, 1967). In Argentine waters, nursery areas for *M. schmitti* were reported in Samborombón Bay (Cousseau, 1982, 1986), Bahía Blanca estuary (Lopez Cazorla, 1987) and Anegada Bay (Colautti et al., 2010), which are located in Buenos Aires province, and in Engaño Bay (Van der Molen et al., 1998) on north Patagonia. However, additional definition and criteria used to identify nursery areas have been suggested by Heupel et al. (2007) and Knip et al. (2010). Regardless of the definition, protection of these nursery areas, and of the breeding females, juveniles and neonates within, is vital for the species conservation (Heupel et al., 2007; Knip et al., 2010; Massa et al., 2010; Simpfendorfer and Milward, 1993).

While sharks are susceptible to overfishing (Hall, 1999), small coastal sharks have a greater recovery potential (Stevens et al., 2000) than their larger counterparts. Therefore it is theoretically possible to

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achieve sustainable fisheries of *M. schmitti*, if adequate management strategies, based on the species' biology, are provided; as suggested by Andrade et al. (2008) for *Rhizoprionodon lalandii*.

Several studies describe the reproduction and other biological processes of *M. schmitti* (Chiaramonte and Pettovello, 2000; Colautti et al., 2010; Cortés and Massa, 2006; Cousseau et al., 1998; Menni, 1985; Menni et al., 1986; Segura and Milessi, 2009; Sidders et al., 2005). However few studies have dealt exclusively with its diet, a key biological aspect for the management of fish resources (Stevens et al., 2000), and none were conducted in Anegada Bay. Lopez Cazorla (1987) in Bahía Blanca estuary, and Menni et al. (1986) and Olivier et al. (1968) in Mar del Plata coast, report that the main prey items of the diet of *M. schmitti* are crabs and polychaetes. Chiaramonte and Pettovello (2000) found crabs to be the only main item in the diet of *M. schmitti* in the southern portion of Patagonia (38° 44' S). Studies conducted on other *Mustelus* species in South America show similar results, as those reported by Navia et al. (2007) and Rojas (2006).

Based on the bibliographic information, it is hypothesized that the population of *M. schmitti* from Anegada Bay feeds mainly on benthic crustaceans, and that its trophic ecology varies with seasons, sex, maturity and the different geographical features of the Bay. In order to test these hypotheses the objectives of this study were to describe the diet composition of the population of *M. schmitti* from Anegada Bay, its ontogenetic shifts and its relations (if any) with seasons, sex, and the different geographical features of the Bay, determined by the sampling sites.

2. Materials and methods

2.1. Study area

Anegada Bay, located in the south of Buenos Aires province, Argentina (from 39.96°S to 40.60°S and from 62.10°W to 62.46°W), is an integral natural reserve under the multiple usage category. It has

an important ecological value due to great biodiversity and high environmental complexity, composed of diverse aquatic environments, with wide muddy intertidal areas, sandy bottom beds, islands, and sand and gravel beaches. Commercial and sport fishing, and tourism are the principal human activities in the Bay.

The studies were conducted in the southern part of the Bay, characterized by San Blas tidal channel, where three sampling stations were placed. This channel is 2.5 km wide and 12 km long and has a maximum depth of 28 m. San Blas station (40.5307° S, 62.2249° W) was close to island Omega, on the northern flank of the channel, where the sampling depth ranged from 3 to 4.5 m. Punta Ramirez station (40.5211° S, 62.3182° W) was placed at the mouth of the Jabalí stream, where the sampling depth ranged from 0.8 to 3 m. Los Pocitos station (40.466° S, 62.366° W) was placed on the southern flank, near the fisher village with the same name, on the inner part of the Bay, where the sampling depth ranged between 2.8 and 6.4 m. Bottom sediments at San Blas are comprised of unconsolidated sand, while at Los Pocitos, they are consolidated fine-sand sediment. Bottom sediments at Punta Ramirez share characteristics with the other two sites (Fig. 1) (Cuadrado and Gomez, 2010). Distances between sites were as follow: San Blas–Punta Ramirez: approximately 8 km; Punta Ramirez–Los Pocitos: approximately 8 km; and San Blas–Los Pocitos: approximately 14 km.

Surface water temperature was measured during the sampling surveys, using the on-board echo sounder.

2.2. Sampling methods and data collection

Specimens of *M. schmitti* were collected with seasonal frequency, from February (summer) to November (spring) of 2008. The fishing gear consisted of two batteries of seven gill nets. Each net was 25 m long and 2 m height with different mesh size (64, 70, 80, 105, 135, 150 and 170 mm stretched). Nets were placed parallel to the coast at the

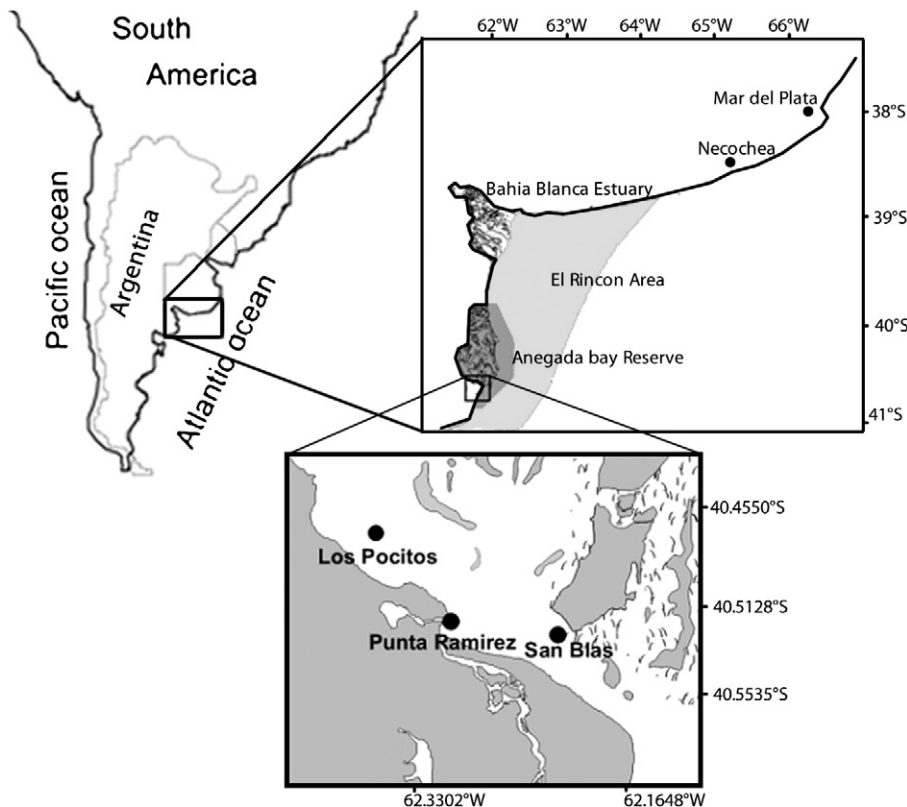


Fig. 1. Sampling sites on Anegada Bay, Argentina.

bottom of each of the sample stations described in Section 2.1, at dusk, and collected twelve hours later, at dawn.

All fish were measured *in situ* to the nearest cm total length (Lt) and subsequently grouped into 1-cm size-classes. A subsample composed of ten randomly selected specimens of each size-class was used for further analysis. Each specimen was measured (Lt, in mm), weighed (total weight, W, in g) and sexed and the maturity stage was determined macroscopically using a maturity key with five stages for females, namely I1, I2, I3, M1, M2 and four stages for males, namely I1, I2, I3, M, (Sidders *et al.*, 2005). I1 for both sexes were considered neonates, while I2 and I3 were considered juveniles. Accordingly, females were classified as adults if they, at least, exhibited ovaries containing yellow follicles (M1 and M2) and males were considered as adults if they showed totally calcified claspers (M). Stomachs were taken from these fish, kept in plastic bags and frozen at -15°C for transportation and storing. Evidence of regurgitation was not observed in any of the fishes sampled.

In the laboratory, the samples of the day were defrosted to be analyzed. Each stomach content was sorted, counted, weighed and identified to the lowest possible taxon. The unidentifiable material was weighed and labeled “Remains”.

2.3. Data analysis

Mean total length and standard deviation for each season, sample site, sex and maturity stages were calculated for the entire sample and for the subsample.

Cumulative prey curves were used to determine whether an adequate number of stomachs had been examined to describe the diet precisely. The order in which stomachs were analyzed was randomized 100 times to minimize bias resulting from sampling order. The mean number of new prey categories found in the stomachs (with standard deviation) was plotted against the total number of stomachs analyzed. The asymptote of the curve indicated the minimum sample size required to adequately describe the diet (Ferry and Caillet, 1996).

Dietary composition differences among maturity stages, seasons and locations, were assessed with a nonparametric multivariate analysis of variance (NPMANOVA), using item frequency and weight data (Anderson, 2001; McArdle and Anderson, 2001). The Gower distance matrix was constructed using a fourth root transformation of the original variables, with 5000 permutations of the data matrix. In the cases where a significant difference was found, pairwise comparisons were performed; where no significant differences were found, data were grouped for further analysis. All tests used a significance level of $p = 0.05$.

Diet composition was examined using the Index of Relative Importance (IRI) (Pinkas *et al.*, 1971) which summarizes the information obtained by three different quantification methods:

$$IRI = \%O(\%N + \%W)$$

Where %O is the frequency of occurrence of each item, expressed as a percentage, %N is the percentage of the total number of food items, and %W is the percentage of the total weight of the stomach contents (wet weight) calculated for each food category. IRIs were standardized to 100% by calculating the percentage of the total IRI contributed by each prey type (%IRI), and ranged from 0 (absent from diet) to 100 (the only prey consumed; Cortés, 1997). These indices were calculated for the lowest possible taxon identified. Since only 4 adult sharks were captured during the cold seasons, the results presented in Table 3 for that category might be biased.

The feeding behavior of *M. schmitti* was evaluated according to a modification of the Costello graphic method, in which the prey specific abundance (P_i) (which is defined as the percentage a prey i comprises of all prey items in only those predators in which prey i occurs), is plotted against the frequency of occurrence, allowing interpretations about the feeding strategy of the predator (Amundsen *et al.*, 1996; Costello, 1990). Prey wet weight was used to calculate P_i .

To evaluate the presence of groups and validate the decisions regarding maturity stage and season grouping, a series of cluster analyses were performed, using a Euclidean distance matrix with a Ward linkage method. Clusters were built using frequency of the prey items, with ungrouped seasons.

Prey diversity was assessed using Shannon–Wiener's diversity index (Wilson and Bossert, 1971) to estimate the dietary breadth. The uniformity index was also calculated and used to statistically analyze the differences between seasons and maturity stages with a NPMANOVA (Anderson, 2001; McArdle and Anderson, 2001).

The trophic level (TL) of *M. schmitti* was calculated according to Cortés (1999). Data from other studies on the diet of *M. schmitti* were used to calculate TL in order to compare with our results.

Statistical analyses and calculations were performed using R statistical software (R Development Core Team, 2009).

3. Results

A total of 1577 individuals of *M. schmitti* were captured. The size of these fish ranged from 19 to 84 cm Lt (mean \pm SD; mode: 46 cm \pm 9 cm; 39 cm). The subsample was composed of 519 sharks, and their size ranged from 25 to 81 cm Lt, (mean \pm SD; mode: 49 cm \pm 9 cm; 40 cm) (Fig. 2). Individuals captured in summer and spring had a larger maximum, mode and mean Lt than those captured in autumn and winter, while minimum Lt was smaller in summer and spring compared to autumn and winter (Table 1). No individuals of *M. schmitti* were captured in Punta Ramirez station.

Surface water temperature values ranged from 7 to 21.7 $^{\circ}\text{C}$, registering the lower values in winter, while the higher were reported in the summer months.

Table 2 presents the number of stomachs analyzed for each season, location and maturity stage, as well as the number of empty stomachs

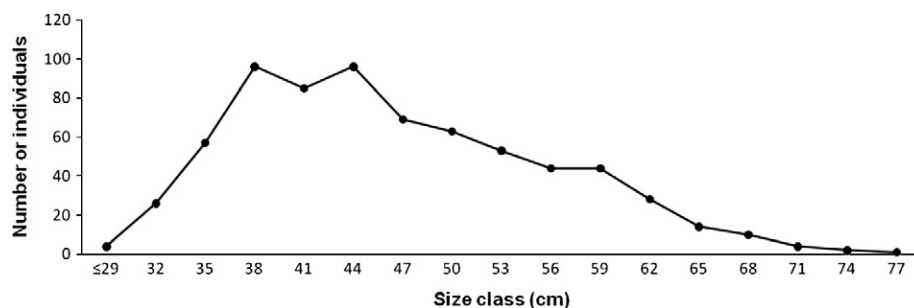


Fig. 2. Size class (total length, cm) frequency curve of *Mustelus schmitti*.

Table 1

Mode, mean, standard deviation (SD), maximum (Max) and minimum (Min) total length (cm) of *Mustelus schmitti* in Anegada bay.

Season	Total length (cm)				
	Mode	Mean	SD	Max	Min
Spring	45	51.63	9.93	81.40	25.40
Summer	55	51.99	9.45	79.10	31.80
Autumn	40	43.07	6.10	59.40	32.30
Winter	39	41.16	4.10	51.10	33.20

Table 2

Number of *Mustelus schmitti* stomachs analyzed by season, location and maturity stages. n_c : number of stomach with contents; n_e : number of empty stomachs; n_{c+e} : total number of stomachs.

Seasons	Summer		Autumn		Winter		Spring		Totals
	Los Pocitos	San Blas	Los Pocitos	San Blas	Los Pocitos	San Blas	Los Pocitos	San Blas	
Neonates	13	11	9	10	0	20	11	14	88
Juveniles	26	28	12	32	0	31	52	40	221
Adults	45	33	0	4	0	0	61	20	163
n_c	84	72	21	46	0	51	124	74	472
n_e	10	8	3	1	0	3	12	10	47
n_{c+e}	94	80	24	47	0	54	136	84	519

found. Of the 472 stomach examined 47 (10%) were empty, most of them from average size animals.

The cumulative prey curves reached an asymptote, in most cases, after ten individuals (Fig. 3); hence sample size was large enough to properly describe the diet of this species in Anegada Bay.

Prey composition showed significant differences between seasons ($F = 7.8900$; $P < 0.01$) and maturity stages ($F = 5.9083$; $P < 0.01$), but there were no differences regarding sampling locations ($F = 1.5142$; $P > 0.1$). Sexes were pooled for these analyses since a NPMANOVA did not detect any significant difference in diet composition between them ($F_{1,147} = 0.852$; $P = 0.390$). Interactions between factors presented no differences as well ($F = 2.0236$; $P = 0.0778$). The pairwise comparison revealed that neither summer and spring nor winter and

autumn were statistically different. However, each group of seasons was different from the other ($P < 0.01$). Hence, our analysis considers seasons grouped as “Warm” (spring and summer) and “Cold” (autumn and winter).

The diet of *M. schmitti* was composed by 26 items of which 8 were identified to species level, 6 to genera level and 3 to family level. The remaining items were identified to higher taxonomic categories (Table 3).

The values of IRI%, O%, N% and W% are shown in Table 3, for the season groups, the maturity stages and the total data of *M. schmitti*. In warm seasons, decapods (particularly *Neohelice granulata*) were the most important prey item (<85% IRI) for all maturity stages. The highest importance was registered in neonates (<95% IRI), being less important in adults and juveniles. Other preys presented less than 10% of the IRI.

Decapods were also the most frequent item in the stomach contents for this season group (found in 100% of the stomach analyzed). Polychaetes and bivalves were more frequent in juveniles and adults than in neonates, while isopods remained fairly constant. Amphipods were more frequent in juveniles than in the other maturity stages. Antozoa frequency decreases from neonates to adults. *Artemisa longinaris*, *Lucipa* spp. and Cephalopods were only preyed by adult.

During the cold seasons, decapods' importance decreased; however, they remained the most important prey for all maturity stages. Polychaete worms became more important, reaching almost a 25% IRI for neonates and around 40% IRI for juveniles and adults. Polychaetes and decapods were found in every stomach analyzed. Bivalves were only present in juveniles at low frequency. Amphipods, Cephalopods and Stomatopods were absent from the diet during this season group.

The feeding strategy of *M. schmitti* is depicted in Fig. 4. During the warm seasons, neonates showed a weak specialization for *N. granulata*, and a generalized behavior for the rest of the items, presenting a diverse diet (Fig. 4a), which also matches the diversity index calculated (Table 4). Juveniles showed a more generalized and diverse diet than neonates. *Cryptograpsus angulatus* and *Corystoides abbreviatus* were consumed more frequently by this maturity stage, and represented approximately 30% of the stomach total content and

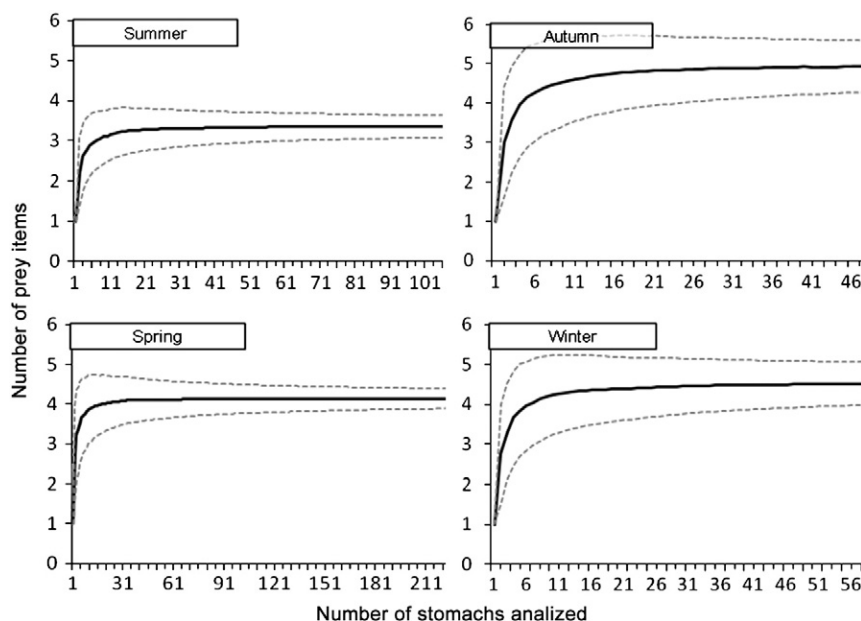


Fig. 3. Cumulative prey curves for the smoothhound stomachs during summer ($n = 106$), autumn ($n = 48$), winter ($n = 60$) and spring ($n = 237$). The black line is the mean number of new prey items, calculated for each sample size, after a 500-time randomization order of stomach contents. The gray dotted lines are standard deviations.

Table 3
Relative importance index (IRI%), frequency of occurrence (O%), number (N%) and weigh (W%) for each prey item, season group, maturity stage and total sample of *Mustelus schmitti*. Entries in bold are the superior taxonomic levels values of the parameters, calculated as groups: Isopoda, Decapoda, etc., instead of by species.

Prey item	Summer and Spring												Autumn and Winter												Total			
	Neonates (n:29)				Juveniles (n:140)				Adults (n:141)				Neonates (n:31)				Juveniles (n:67)				Adults (n:4)							
	%O	%N	%W	IRI%	%O	%N	%W	IRI%	%O	%N	%W	IRI%	%O	%N	%W	IRI%	%O	%N	%W	IRI%	%O	%N	%W	IRI%	%O	%N	%W	IRI%
CRUSTACEA																												
Amphipoda	3.4	8.6	1.0	0.2	12.1	20.9	1.5	1.7	0.7	0.2	0.1	0.0													4.7	8.2	0.5	0.2
Gammaridae					0.7	0.1	0.2	0.0	0.7	0.2	0.1	0.0													0.5	0.1	0.1	0.0
Caprellidae	3.4	8.6	1.0	0.2	11.4	20.8	1.3	2.3	0.0																4.2	8.1	0.4	0.3
Isopoda	20.7	2.9	2.9	0.6	19.3	2.1	1.4	0.4	22.0	2.3	1.0	0.4	12.9	2.9	2.9	0.4	34.3	3.9	2.4	1.1					22.7	2.4	1.1	0.5
<i>Cirolana</i> sp.	13.8	2.0	1.5	0.3	11.4	1.3	0.7	0.2	11.3	1.2	0.3	0.1	9.7	2.5	2.8	0.3	20.9	2.6	1.4	0.4					13.2	1.5	0.5	0.2
<i>Serolis marplatensis</i>	6.9	1.1	1.4	0.1	7.9	0.8	0.9	0.1	10.6	1.1	0.7	0.1	3.2	0.7	1.8	0.0	13.4	1.4	1.4	0.2					9.5	1.0	0.7	0.1
Stomatopoda	3.4	0.6	3.4	0.1					0.7	0.1	0.1	0.0													0.5	0.1	0.2	0.0
<i>Heterosquilla</i> sp.	3.4	0.6	3.4	0.1					0.7	0.1	0.1	0.0													0.5	0.1	0.2	0.0
Decapoda	100	82.4	86.5	96.4	100	67.1	74.8	89.4	100	88.2	76.3	93.0	100	85.1	73.0	77.0	100	77.8	60.1	62.2	100	64.1	71.9	59.3	100	77.9	72.9	89.4
<i>Peisos petrunkevitchi</i>	3.4	0.6	0.8	0.0									3.2	1.8	1.8	0.1	1.5	0.4	0.5	0.0					0.7	0.1	0.1	0.0
<i>Artemisa longinaris</i>									0.7	0.1	0.1	0.0													0.2	0.0	0.1	0.0
<i>Leucipa</i> sp.									0.7	0.1	0.1	0.0													0.2	0.0	0.1	0.0
<i>Neohelice granulata</i>	93.1	76.3	64.4	93.5	82.1	57.6	47.0	77.3	87.2	74.1	50.1	82.0	100	80.1	63.8	76.0	97.0	70.9	50.3	61.5	75.0	47.6	10.3	19.2	90.8	67.8	49.5	81.3
<i>Corystoides abbreviatus</i>	13.8	1.7	6.5	0.8	31.4	5.2	13.6	5.3	41.8	6.9	9.5	5.2					4.5	0.5	1.1	0.0	25.0	4.8	3.3	0.9	27.7	4.7	9.1	2.9
<i>Cryptograpsus angulatus</i>	13.8	2.9	8.2	1.1	25.0	2.8	8.0	2.4	33.3	4.7	10.1	3.7	6.5	1.1	2.7	0.1	20.9	4.0	6.2	1.1	25.0	7.1	3.9	1.2	25.7	3.6	8.4	2.4
<i>Loxopagurus</i> sp.	3.4	0.6	1.6	0.1	10.0	0.9	2.4	0.3	2.8	0.2	0.2	0.0					3.0	0.4	1.1	0.0					5.2	0.4	0.9	0.1
<i>Libinia spinosa</i>	6.9	0.9	5.9	0.3	2.1	0.2	1.9	0.0	7.1	0.8	4.0	0.3									25.0	4.8	54.8	6.6	4.0	0.4	3.8	0.1
<i>Pilumnoides</i> sp.					2.9	0.2	0.5	0.0	7.1	1.0	1.6	0.1													3.5	0.4	0.9	0.0
<i>Platyanthus</i> sp.									0.7	0.1	0.4	0.0					3.2	0.7	1.8	0.0	3.0	0.4	1.0	0.0	1.0	0.1	0.2	0.0
Talasinidea					4.3	0.4	1.3	0.1	1.4	0.2	0.2	0.0	9.7	1.4	3.0	0.2	11.9	1.2	1.0	0.1					4.7	0.4	0.5	0.0
ANELIDA																												
Oligochaeta					2.1	0.2	0.3	0.0	0.7	0.1	0.1	0.0	9.7	1.4	2.6	0.2	14.9	1.7	1.7	0.3					4.2	0.3	0.3	0.0
Polychaeta	20.7	2.0	3.3	0.8	55.7	5.0	10.8	8.0	48.9	4.0	8.3	4.6	93.5	12.0	34.3	22.4	100	15.6	37.0	36.1	100	40.5	38.9	38.7	69.3	6.4	12.8	10.2
MOLLUSCA																												
Gasteropoda					2.1	0.2	1.0	0.0	2.1	0.2	0.6	0.0					3.0	0.4	1.3	0.0	25.0	7.1	3.1	1.1	2.2	0.2	0.6	0.0
Cephalopoda									3.5	0.4	1.0	0.0													1.2	0.1	0.5	0.0
<i>Loligo gahi</i>									0.7	0.1	0.3	0.0													0.2	0.0	0.2	0.0
Octopodidae									2.8	0.3	0.8	0.0													1.0	0.1	0.4	0.0
Bivalvia	20.7	2.0	5.8	0.9	24.3	2.2	7.1	1.4	30.5	2.6	6.7	1.6					3.0	0.4	1.2	0.0					21.2	1.9	5.7	1.0
Solenidae	20.7	2.0	5.8	1.2	22.1	2.0	6.9	1.8	28.4	2.5	6.7	2.0					3.0	0.4	1.2	0.0					19.7	1.8	5.7	1.1
Veneridae					2.1	0.2	0.2	0.0	2.1	0.2	0.1	0.0													1.5	0.1	0.1	0.0
Misc																												
SIPUNCULIDAE					0.7	0.1	0.2	0.0																	0.2	0.0	0.1	0.0
ANTOZOA	13.8	1.4	1.4	0.3	7.9	0.6	0.3	0.1	5.7	0.4	0.2	0.0	9.7	1.4	2.0	0.2	9.0	0.9	0.7	0.1	25.0	4.8	2.9	0.9	8.2	0.6	0.2	0.1
VERTEBRATA																												
Unid. Fish	0.3	0.2	0.2	0.5	0.3	0.1	0.0	0.0	1.3	0.3	3.0	0.1					0.3	0.1	0.0	0.0					2.5	0.3	1.4	0.0

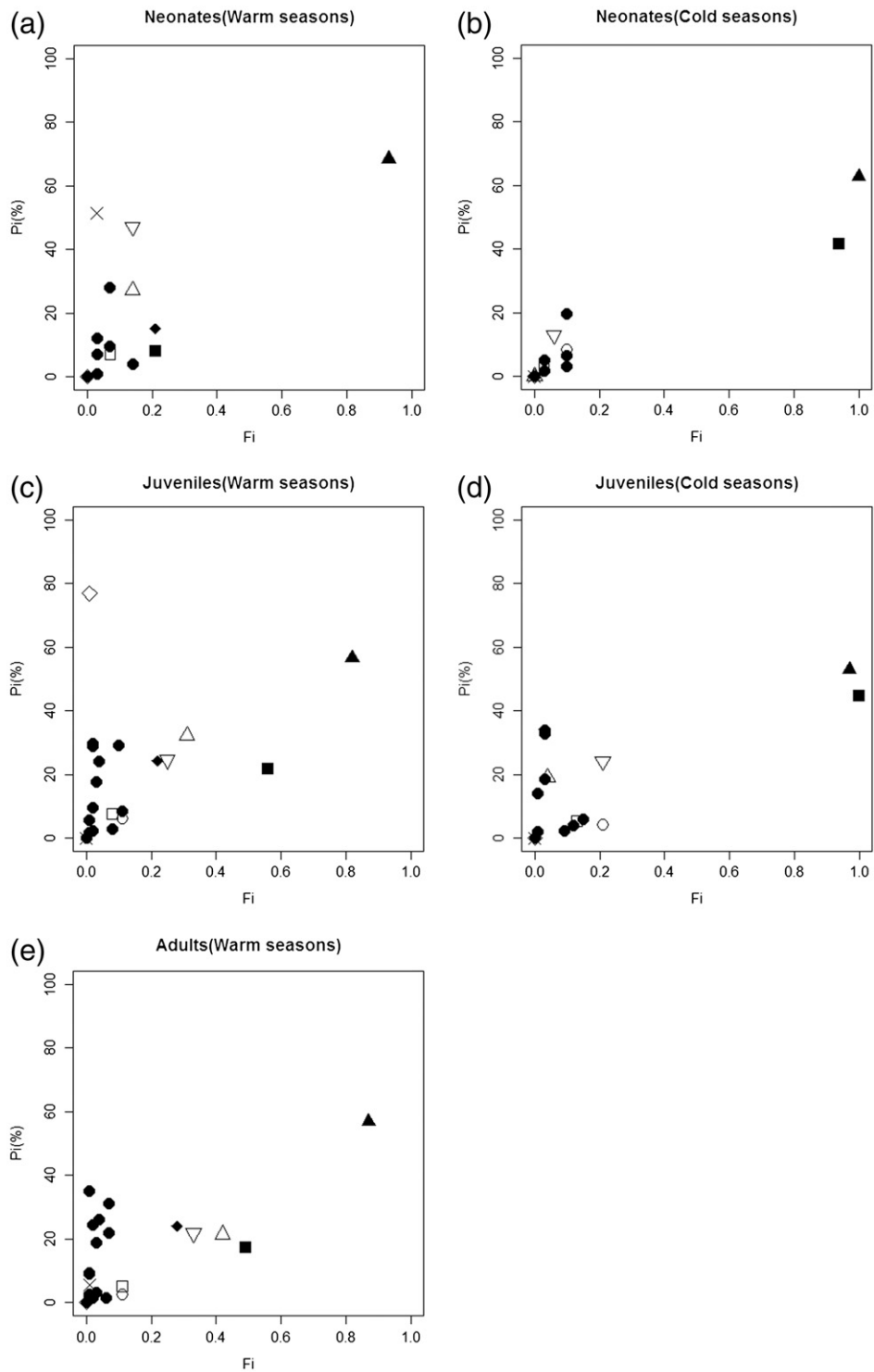


Fig. 4. Specific abundance in percentage (Pi) plotted against frequency of occurrence (Fi) of prey items for *Mustelus schmitti* diet. (a) Neonates during the warm seasons, (b) neonates during the cold seasons, (c) juveniles during the warm seasons, (d) juveniles during the cold seasons and (e) adults during the warm seasons. Prey items: *Neohelice granulata* (▲), polychaete worms (■), *Corystoides abbreviatus* (△), *Cryptograpsus angulatus* (▽), *Serolis marplatensis* (□), *Cirolana* sp. (○), Solenoid bivalves (◆), *Heterosquilla* sp. (X), Sipunculids (◇), and other items (●).

Table 4
Prey richness (number of species), diversity (H') and uniformity (U) for each season group and maturity stage of *Mustelus schmitti*. WS: Warm seasons; CS: Cold seasons.

Maturity stage	Richness		Diversity		Uniformity	
	WS	CS	WS	CS	WS	CS
Neonates	14	10	2.45	1.98	0.63	0.57
Juveniles	19	15	2.74	2.12	0.63	0.53
Adults	23	7	2.69	1.93	0.58	0.69

polychaetes presented a stronger population component to the diet. Adult smoothhounds also presented a generalist feeding behavior, with less frequency of polychaetes and more frequency of crabs.

Neonates, during the cold seasons, presented a narrow dietary breath, a more clear specialization in *N. granulata*, and a weak specialization for polychaetes (Fig. 4b). Juveniles presented a weak specialization for both *N. granulata* and polychaete worms (Fig. 4d). The number of adults captured during this season group was not

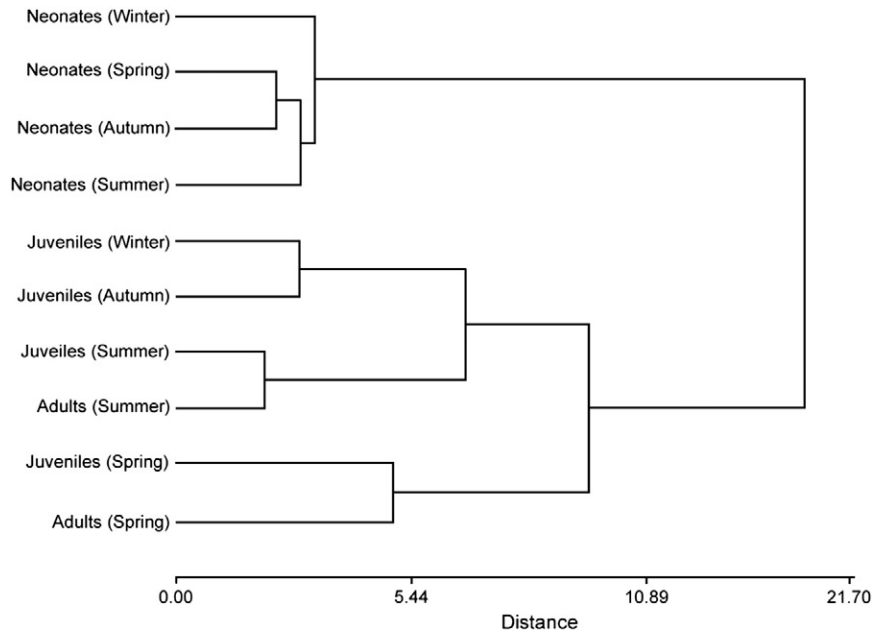


Fig. 5. Cluster dendrogram using frequency of the prey items of *Mustelus schmitti*, with a Ward linkage method and a Euclidean distance.

enough to build Amundsen graphics without incorporating important biases, thus it was omitted.

The cluster analysis performed (Fig. 5) shows three clusters. The first, groups neonates from all seasons together. The second, groups cold seasons' juveniles first, and then summer juveniles and adults. The third groups spring adults and juveniles.

Prey diversity was higher in warm seasons and lower in cold seasons, whereas the differences in H' values for the different maturity stages were small (Table 4). Differences between season groups ($P=0.016$) but not between maturity stages ($P=0.3$) were found.

Trophic level for *M. schmitti* for all maturity stages, all along the year was 3.51. Those studies that provided sufficient information to calculate the TL are shown on Table 5.

4. Discussion

The maximum Lt recorded was smaller than that reported by Chiamonte and Pettovello (2000), Cortés and Massa (2006), Pereyra et al. (2008), Sidders et al. (2005) and by Segura and Milessi (2009) (Table 6). Chiamonte and Pettovello (2000) took their samples in summer months using hook and line from the coast and from artisanal fishermen disembark. Pereyra et al. (2008) sampled seasonally from large trawling ships, which operate on coast and on deep waters. Sidders et al. (2005) performed a seasonal sampling and took their samples from a fish processing plant that receives fish from both hook and line fishermen and commercial trawl fisheries, both fishing in the coastal area of Necochea city; Segura and Milessi (2009) sampled monthly from July 2005 to October 2006, on the Atlantic coast of Uruguay, getting their samples from artisanal fishermen using gillnets. Cortés and Massa (2006) performed their sampling from

monthly commercial fisheries disembarks. There are several possible explanations for the differences observed. From Table 6, it can be observed that sampling methods and years were fairly similar (Excepting Chiamonte and Pettovello study), with sampling years ranging from 2004 to 2006. This information suggest that maximum Lt decreases as sampling year increases, from 1000 mm Lt in 2004 to 880 mm Lt in 2006 (Table 6). Colautti et al. (2010), working with *M. schmitti* from Anegada Bay suggest that overexploitation of this species in the southern Atlantic might deplete larger individuals, which is reflected on smaller maximum Lt captured. Fernández Aráoz et al. (2009) concluded that the officially declared annual captures of the Argentine commercial fisheries, have increased from 6000 t to 9000 t since 2002 to 2008. In the area around Anegada Bay, total captures increased from 2800 t in 2004, to 3500 t in 2008. The increasing exploitation of this species, might explain the chronological reduction in maximum Lt observed in the literature. The increasing captures in front of the protected area of Anegada likely explain the small maximum Lt registered in the present study, as explained by Colautti et al. (2010).

The number of empty stomachs found was relatively low compared with the findings of Chiamonte and Pettovello (2000; 15%) and closely matches the reported value by Menni et al. (1986; 10%). Sharks generally feed during the night hours (Randall, 1967),

Table 5
Trophic level of *Mustelus schmitti* calculated from diet information.

Authors	Trophic level	Study area
Present study	3.55	Anegada bay
Chiamonte and Pettovello (2000)	3.62	Ría Deseado
Lopez Cazorla (1987)	3.53	Bahía Blanca Estuary
Menni et al. (1986)	3.50	Mar del Plata
Olivier et al. (1968)	3.54	Mar del Plata

Table 6
Maximum total length (Max Lt; mm) registered for *Mustelus schmitti* in different year, areas and from different sample sources.

Study	Max Lt (mm)	Sampling year	Area	Sample sources
Present study	840	2008	Anegada Bay	Gillnets
Segura and Milessi (2009)	880	2006	Punta del Diablo, Uruguay	Gillnets
Cortés and Massa (2006)	950	2005	Mar del Plata	Commercial disembarks
Sidders et al. (2005)	970	2004	Quequen port, Buenos Aires	Hook and line, trawling nets
Pereyra et al. (2008)	1000	2004	Oceanic coast of Uruguay	Trawling nets
Chiamonte and Pettovello (2000)	913	1998	Ría Deseado	Hook and line

hence individuals fished with hook and line during day time probably had digested a large proportion of their stomach content at the moment they were caught, while individuals fished with gillnets during the night, as suggested by Kamura and Hashimoto (2004), might have reduced that bias in our study. This might explain the higher empty stomach proportion and the lower number of prey species identified by Chiaramonte and Pettovello (2000).

N. granulata was identified as the most important item in the diet of all maturity stages and all seasons; while polychaete worms turned important during autumn–winter. Smale and Compagno (1997) pointed out that as sharks grow they develop the strength and size needed to capture bigger prey. This was reported for several other sharks by Bethea et al. (2004), Chiaramonte and Pettovello (2000), Lucifora et al. (2006) and Lucifora et al. (2009). Pyke et al. (1977) and Scharf et al. (2000) suggest that the low cost of capture and the high encounter probability are likely to explain this continuous inclusion of the small preys in the diet of large individuals. As Smale (1991) and Lucifora et al. (2009) report for other sharks, *M. schmitti* might take mouthfuls of prey without further handling, which could explain the relatively large %N of *N. granulata* in all seasons. Other studies in which trophic aspects of *M. schmitti* are mentioned (Chiaramonte and Pettovello, 2000; Lopez Cazorla, 1987; Menni et al., 1986; Olivier et al., 1968) also pointed out that the main preys of this shark are benthic crabs, although they do not attempt to analyze the seasonal variations that were found to occur in Anegada Bay, nor the feeding strategy used by *M. schmitti*. This prevents us from assessing differences between studies regarding those biological features of the smoothhounds. The relative proportion of crabs was similar in those studies; however Chiaramonte and Pettovello (2000) found small amounts of polychaete worms in their study of Ría Deseado, while other authors, as Lopez Cazorla (1987) in Bahía Blanca estuary and Menni et al. (1986) and Olivier et al. (1968) in Mar del Plata, found proportions (30–35%) similar to ours. These authors also reported an important proportion of shrimps, not present in the study of Chiaramonte and Pettovello (2000) or in the present.

The TL calculated for *M. schmitti* closely matches the standardized TL estimated for this species by Cortés (1999). This characteristic categorizes it as a secondary consumer. TL values calculated from other studies are similar to our finding (Table 5). Other *Mustelus* species that consume benthic crustaceans have similar standardized TL: *M. asterias*, *M. canis*, *M. lenticulatus* and *M. manazo* have TL that range from 3.5 to 3.7 (Cortés, 1999), while species that consume fishes and cephalopods, like *M. punctulatus*, *M. mustelus*, *M. lunatus* and *M. fasciatus* have higher TL that range from 3.8 to 4.2 (Cortés, 1999).

M. schmitti behaves as a generalist feeder in Anegada Bay, where crabs and polychaetes were the most important items. Prey diversity also supports this assumption. *M. schmitti* in Anegada Bay feeds mainly on *N. granulata*, which Bortolus et al. (2003) and Iribarne (2001) characterize as the dominant crab in the salt marshes of the southwest Atlantic. However, Menni et al. (1986) and Olivier et al. (1968) reports *A. longinaris* and *Corystoides chilensis* as the main preys of *M. schmitti* captured in Mar del Plata, while Chiaramonte and Pettovello (2000) found *C. angulatus* to be the dominant prey item in Ría Deseado. Despite specific differences, all these preys are benthic decapods.

Elasmobranchs are often considered opportunistic predators, usually with an electivity index around zero, and with wide trophic spectrums, as Scenna et al. (2006) and Vögler et al. (2003) reports. The differences in the feeding habits reported for *M. schmitti* between Chiaramonte and Pettovello (2000), Lopez Cazorla (1987), Menni et al. (1986) and Olivier et al. (1968), and our study, could be correlated then, with differences in prey assemblages and abundances between the areas where the different studies were performed, rather than active selection by the predator, as suggested by Barry et al. (2008) for other species of shark. Similarly, differences in diet composition between “warm” and “cold” seasons and between maturity stages may represent changes in the seasonal patterns of distribution of the benthic organisms that *M. schmitti* preys upon.

Sex segregation appears common among sharks (Klimley, 1987; Wearmouth and Sims, 2008), where adult males and females of the same species use different habitats. Said differences can arise from several causes, like differences in body size between sexes, habitat preference and differential nutritional requirements. Pereyra et al. (2008) mentions that *M. schmitti* exhibits sexual differences in body size and sexual segregation. However, in the present study, sexual differences seemed not to influence the diet of *M. schmitti*. It might be theorized that, as a generalist feeder, this species' diet is likely determined by the prey assemblages of its feeding areas. The lack of geographic specific differences in the diet may arise from the fact that sample sites were not far away enough to exhibit differences in the benthic assemblages, despite each site's different geomorphologic characteristics. Detailed quantitative information on the distribution and availability of potential benthic prey in Anegada Bay would improve the assessment of the feeding habits of *M. schmitti* in this area.

Ontogenetic shifts in the diet composition of *M. schmitti* were observed. Richness and diversity increases as the individuals grow from neonates to adults. The same behavior was observed in *Mustelus mustelus*, which shows an increase in prey diversity as the individuals grow to larger sizes (Saïdi et al., 2009). Fanelli et al. (2009) report a similar pattern for other two species of sharks, *Galeus melastomus* and *Etmopterus spinax*. In contrast, Yamaguchi and Taniuchi (2000) found ontogenetic shifts in the diet of *Mustelus manazo*, in which diversity of prey decreases as individuals grow in size.

There are several lines of evidence that suggest that Anegada Bay may represent a nursery area for *M. schmitti*. Adult smoothhounds remain in this Bay for extended periods of time during the breeding season (from spring to the end of summer) and then leave the area to return again next year (Colautti et al., 2010). Neonates and juveniles stay in the Bay along the year, whereas adults are only present during the warm seasons (Fig. 2 and Table 1). Low number of empty stomachs in neonates and juveniles, and the differences in the diet of neonates and adults suggests that the young smoothhounds find enough food in this area. Heupel et al. (2007) and Knip et al. (2010) point out that these kinds of evidences are accurate for identifying nursery areas.

5. Conclusions

Our results show that: (1) *M. schmitti* is a carnivorous opportunistic predator, feeding on a variety of benthic invertebrates; (2) the species use a generalized feeding strategy, (3) whose diet seemed to be influenced by seasonality and individuals' maturity stage; (4) *N. granulata* and polychaete worms were the principal component of the smoothhound's diet; and (5) Anegada Bay might represent a nursery area for *M. schmitti*.

Acknowledgments

Financial support from the PAE No. 22666/04 – ANPCyT is gratefully acknowledged. The authors are also thankful to Dr. D. Colautti, Dr. C. Baigún, B.Sc. F. Llomprat, B.Sc. S. Calvo, B.Sc. H. Oñatibia, B.Sc. M. Patiño Ruiz, Mr. Matias Lopez and Mr. Juan Marino for their technical assistance in the data collection and field operations. The helpful comments on the manuscript by anonymous reviewers are also greatly acknowledged.

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