Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina

Mariano Koen Alonso[a,b,c], Enrique Alberto Crespo[b,c], Néstor Aníbal García[b,c], Susana Noemí Pedraza[b,c], Pablo Ariel Mariotti[c] & Nancy Judith Mora[c]
[a]*Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada*
(e-mail: malonso@uoguelph.ca)
[b]*Centro Nacional Patagónico (CONICET), Boulevard Brown 3600, (9120) Puerto Madryn, Chubut, Argentina*
[c]*Universidad Nacional de la Patagonia, Boulevard Brown 3700, (9120) Puerto Madryn, Chubut, Argentina*

Synopsis

The diet of the spiny dogfish in northern and central Patagonian waters was studied from the by-catch of the bottom trawling fisheries directed to Argentine hake *Merluccius hubbsi* and Argentine red shrimp *Pleoticus muelleri* between 1996 and 1998. Food habits were analyzed in relation to sex and maturity of sharks. Also, the relationship between diet and abundance of the main prey was explored. Intraspecific diet comparisons were performed. Differences in diet were found between immature individuals, mature males, and mature females. The Argentine shortfin squid *Illex argentinus*, the Argentine hake and ctenophores *Pleurobrachia pileus* were the most important prey for the spiny dogfish. Immature and small individuals were pelagic predators. After sexual maturity, the spiny dogfish shifted its diet. Mature and large individuals tended to reduce the consumption of ctenophores, and increase the consumption of demersal and benthic species. Previous diet studies on the spiny dogfish in 1984–1985 and 1994 indicated that the Argentine hake was the most important prey. In the present study, carried out in 1998, squid was the most important prey, followed by the hake. This diet change was related to the major decrease of hake due to overfishing and the increase of squid abundance between 1994 and 1999.

Introduction

The spiny dogfish, *Squalus acanthias*, is distributed worldwide, including the Argentine continental shelf (Menni & López 1984). It is one of the most abundant and common elasmobranchs in these waters (Otero et al. 1982, Angelescu & Prenski 1987, Cousseau & Perrota 1998), especially in northern and central Patagonian waters (Menni & Gosztonyi 1982, Menni & López 1984, Menni 1985).

The spiny dogfish is a viviparous species, and forms schools segregated by size and sex. In Argentine waters offspring are born at 21–28 cm in total length (TL). Maximum TL values are 78 cm for males and 96 cm for females (Menni 1985, 1986). The minimum length

at maturity for males is around 62 cm TL, whereas for females it is around 70 cm (Menni 1985, 1986).

In the San Jorge Gulf (45–47°S) during 1984–1985 the diet of the spiny dogfish was dominated by Argentine hake, *Merluccius hubbsi*, throughout the year. Another important prey was the Argentine shortfin squid, *Illex argentinus*, whereas ctenophores were an important prey for those individuals smaller than 60 cm TL (Sánchez & Prenski 1996). In an extensive study performed during 1994, García de la Rosa & Sánchez (1997) found that the diet of the spiny dogfish consisted mainly of the same hake, squid, and ctenophore prey species. They also found differences in the diet between sexes, and detected a shift in the diet around 62 cm; a reduction in the consumption of

ctenophores and an increase in the consumption of fish and squid. It was suggested that this diet shift was related to sexual maturity (García de la Rosa & Sánchez 1997).

The Argentine hake and the Argentine shortfin squid have been the targets of the two main fisheries in Patagonian waters during the last decades. Currently, Argentine hake stocks have virtually collapsed due to overfishing (its estimated survey abundance dropped from 2.5 million tons in 1980 to 1 million tons in 1999), while the Argentine shortfin squid is exploited at its maximum sustainable level (Brunetti et al. 1998, Aubone et al. 1999).

In the present study we analyzed the food habits of the spiny dogfish in northern and central Patagonian waters to evaluate if there are differences in the diet between the sexes and if shifts in the diet occur with the onset of maturity. We also explored shifts in the occurrence of hake and squid in the diet of spiny dogfish to explore the effects of overfishing of Argentine hake.

Materials and methods

Sharks sampled

The samples analyzed were composed of 132 spiny dogfish collected in 1996 (n = 8), 1997 (n = 9), and 1998 (n = 115). Most of these animals (n = 121) were collected from the by-catch of commercial bottom trawls conducted for Argentine hake, while some of them (n = 11) were obtained from the by-catch of commercial trawls conducted for Argentine red shrimp, *Pleoticus muelleri*. The samples were taken between 41°S and 46°S, and most of the animals were captured in a range of 50–100 m depth (Figure 1). The animals collected in Argentine hake hauls were preserved on ice until the dissection, while those collected in Argentine red shrimp hauls were frozen on board at −20°C. After the dissections, the stomachs and intestines were stored frozen at −20°C until their analysis.

Stage of sexual maturity was determined by examination of the reproductive organs. The presence of mature oocytes and embryos within the uteri were considered to represent mature females, while the presence of sperm in epididymi and the degree of clasper calcification were used to determine maturity in males (Holden 1975, Pratt 1979, Tanaka et al. 1990, Peres & Vooren 1991). Nine immature males, 32 immature females, 49 mature males, and 43 mature females were examined.

Diet analysis

Stomachs of spiny dogfish were opened, the most conspicuous remains were separated and the rest of the remains were separated by flushing water, filtering with sieves and decantation trays (Koen Alonso et al. 1998, 2000).

The prey species were identified by their remains (e.g., otoliths, fish bones, squid beaks, crustacean exoskeletons) using the reference collection of the Marine Mammal Laboratory[1], and published catalogs (Clarke 1986, Menni et al. 1984, Roper et al. 1984, Boschi et al. 1992, Gosztonyi & Kuba[2], Boltovskoy 1999). The size and weight of prey at the time of ingestion were estimated from the remains using regression equations (Santos 1994, Koen Alonso et al. 1998, 1999, 2000). When no regression was available, the weight was assigned by comparison with undigested individuals of the same species and similar size or by weighing the fragments found in the stomach (Koen Alonso et al. 2000).

Data analysis

The importance of prey species was evaluated using the percent frequency of occurrence (%FO), the percent total number (%N), the percent total regression estimated wet weight (%W), and the Index of Relative Importance adjusted to 100% (%IRI) (Cortés 1997, Koen Alonso et al. 2000). Because the sample sizes were relatively small, cumulative trophic diversity curves using the pooled quadrat method were used to evaluate adequacy of the sample size for each group (Pielou 1966). Because the cumulative diversity curves are based on random orders of quadrats (digestive tracts in our analysis), 100 random orders of digestive tracts for each sample were evaluated to ensure that the curves really reached an asymptotic value. Each diversity curve was considered asymptotic if at least two previous values to the total sample trophic diversity (H_z) were in the range $H_z \pm 0.05 H_z$. The Brillouin index

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[1] Marine Mammal Laboratory, Centro Nacional Patagónico (CONICET), Boulevard Brown 3600, (9120) Puerto Madryn, Chubut, Argentina.

[2] Gosztonyi, A. & L. Kuba. 1996. Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica – Fundación Patagonia Natural (Puerto Madryn, Argentina) No. 4: 1–29.
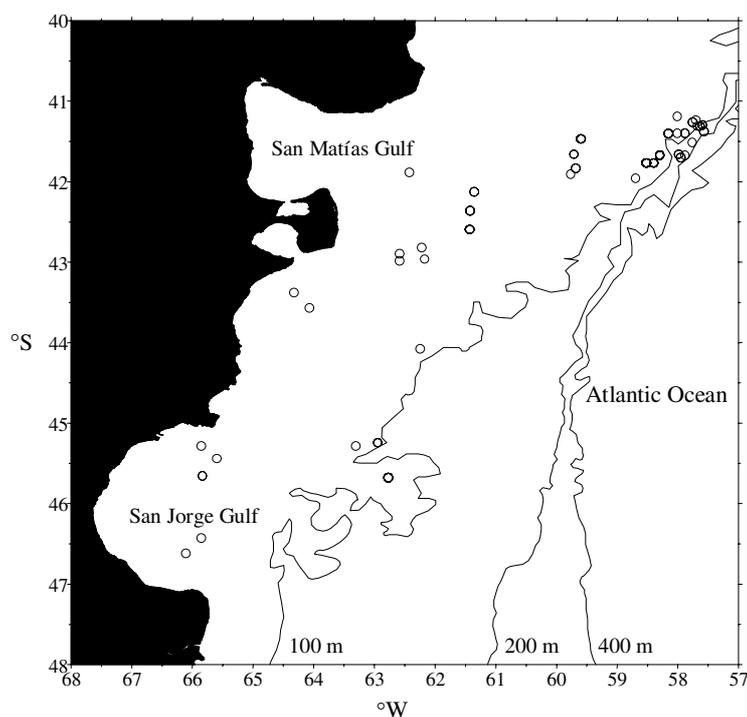
Figure 1. Study area. The open circles indicate sampling sites.

was employed to calculate trophic diversities (Pielou 1966, Magurran 1988).

Intraspecific diet differences were evaluated using the Specific Overlap index (SO) (Petraitis 1979, Ludwig & Reynolds 1988). The SO evaluates the probability of obtaining the utilization curve of one group i from the utilization curve of another group k (SO_{ik}). The null hypothesis of $SO_{ik} = 1$ was tested using the U statistic (Ludwig & Reynolds 1988). The data employed for these analyses were the occurrences of those prey species which had a %IRI > 1% in the pooled sample (Koen Alonso et al. 2000). This analysis was also performed considering the ecological environment of prey; in which case all prey species were considered. The trophic groups compared were immature, mature male, and mature female spiny dogfish. Immature males and females were pooled because the sample size of immature males was small (n = 9).

Size of prey consumed among these groups were compared using the Kruskal–Wallis test. When significant differences were found, pairwise contrasts were made to locate the differences. The contrast method employed is based on a Z statistic (standard normal distribution) and was calculated according to Siegel & Castellan (1995). In order to keep a global α (α_{global}) of 0.05, the α for each contrast ($\alpha_{contrast}$) was set as 0.008 based on the following calculation: $\alpha_{contrast} = \alpha_{global}/[k(k-1)]$, where k = 3 (the number of groups compared with the original Kruskal–Wallis test) (Siegel & Castellan 1995).

Results

Characteristics of the sample

Sharks examined had a unimodal length frequency distribution with a mode of 65 cm of TL (Figure 2). However, the subgroups considered consisted of three different size ranges. The immature individuals presented a size range of 36.1–75.6 cm TL (the largest immature male and female were 63.7 and 75.6 cm TL respectively), mature males ranged from 57.5 to 76.8 cm TL, and mature females ranged from 66.5 to 94.7 cm TL.

For stomachs of all group combined, 90.9% had food remains. The food remains were at different stages of digestion. Whole and undigested prey items
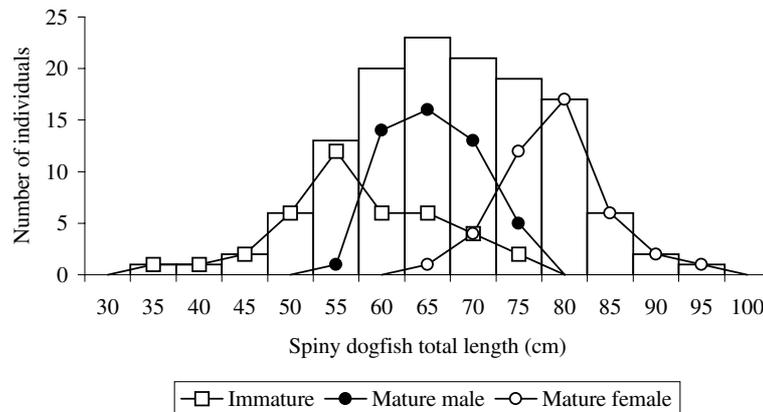
Figure 2. Length frequency distribution of the pooled sample of spiny dogfish analyzed in this study and the length frequency distribution by trophic groups (immature individuals, mature males, and mature females). Bars are pooled sample.

Table 1. Importance of prey of the spiny dogfish of northern and central Patagonian waters.

Prey species	Ecological group	n	%N	%W	%FO	%IRI
Fishes						
Merluccius hubbsi	DP	40	14.39	18.22	23.33	16.00
Patagonotothen ramsayi	DB	26	9.35	9.69	15.00	6.00
Unidentified fish remains	NA	19	6.83	2.08	15.83	2.97
Engraulis anchoita	P	18	6.47	2.24	7.50	1.37
Raneya brasiliensis	DB	14	5.04	4.29	6.67	1.31
Stromateus brasiliensis	DP	2	0.72	4.39	1.67	0.18
Paralichthys isosceles	B	1	0.36	1.53	0.83	0.03
Unidentified skates	B	1	0.36	0.67	0.83	0.02
Austrolycus laticinctus	DB	1	0.36	0.07	0.83	0.01
Prionotus nudigula	B	1	0.36	0.33	0.83	0.01
Porichthys porosissimus	B	1	0.36	0.28	0.83	0.01
Mollusks						
Illex argentinus	DP	76	27.34	47.86	40.00	63.25
Enteroctopus megalocyathus	B	3	1.08	6.01	2.50	0.37
Loligo gahi	DP	3	1.08	0.60	2.50	0.09
Nudibranchs	B	1	0.36	0.06	0.83	0.01
Loligo sanpaulensis	DP	1	0.36	0.16	0.83	0.01
Semirossia tenera	DB	1	0.36	0.03	0.83	0.01
Crustaceans						
Themisto gaudichaudii	P	17	6.12	0.02	1.67	0.21
Unidentified crustaceans	NA	5	1.80	0.00	0.83	0.03
Crabs	B	2	0.72	0.25	1.67	0.03
Munida spinosa	B	3	1.08	0.05	2.50	0.06
Serolis schythei	B	4	1.44	0.00	0.83	0.03
Pleoticus muelleri	DB	2	0.72	0.02	1.67	0.03
Ctenophores						
?Pleurobrachia pileus	P	34	12.23	1.12	28.33	7.95
Cnidaria						
Hydrozoa	B	1	0.36	0.01	0.83	0.01
Anelids						
Aphrodita sp.	B	1	0.36	0.05	0.83	0.01

n = number of prey items, %N = percent number, %W = percent estimated wet weight, %FO = percent frequency of occurrence, %IRI = percent index of relative importance, P = pelagic, DP = demersal-pelagic, DB = demersal-benthic, B = benthic, and NA = not assigned.

were frequently found in the same stomachs as well digested prey.

Prey species

Stomachs of spiny dogfish examined contained 26 prey species: 11 fish, six mollusks, six crustaceans, one ctenophore, one hydrozoa, and one annelid species. A total of 278 individual prey were found in the stomachs, and the total regression estimated wet weight for all prey combined was 17.9 kg. The advanced state of digestion for ctenophores and hydrozoans prevented identification of these prey to the species level. On the basis of previous studies, the ctenophore species could be *Pleurobrachia pileus* (García de la Rosa & Sánchez 1997).

Only seven prey species had %IRI greater than 1% in the pooled sample (Table 1). These species were Argentine shortfin squid, Argentine hake, ctenophores, southern cod *Patagonotothen ramsayi*, unidentified fish remains, Argentine anchovy *Engraulis anchoita*, and 'raneya' *Raneya brasiliensis*.

The prey diversity curves were asymptotic for each of the three subgroups of spiny dogfish (Figure 3). Of the cumulative trophic diversity curves obtained, 92%, 98%, and 97% were asymptotic for immature individuals, mature males, and mature females, respectively. Therefore, we considered the sample sizes of these trophic groups large enough to evaluate differences among the diets.

For the seven prey species with %IRI greater than 1%, differences in the diet among immature, mature male, and mature female spiny dogfish were evaluated. There were significant differences in SO among these groups (Table 2), a high level of occurrence of ctenophores in the diet of immature dogfish and an elevated level of mollusks (squid) in mature females (Figure 4), and involved a shift from a more pelagic feeding in immature individuals to a demersal-pelagic feeding in mature individuals (Figure 5). Young sharks had significantly higher occurrences of pelagic prey than mature sharks, and no sex differences in the diet were found between mature individuals when the ecological environment of prey was considered.

Prey size

A significant difference was found in the dorsal mantle length (DML) of Argentine shortfin squid consumed by immature, mature male, and mature female spiny
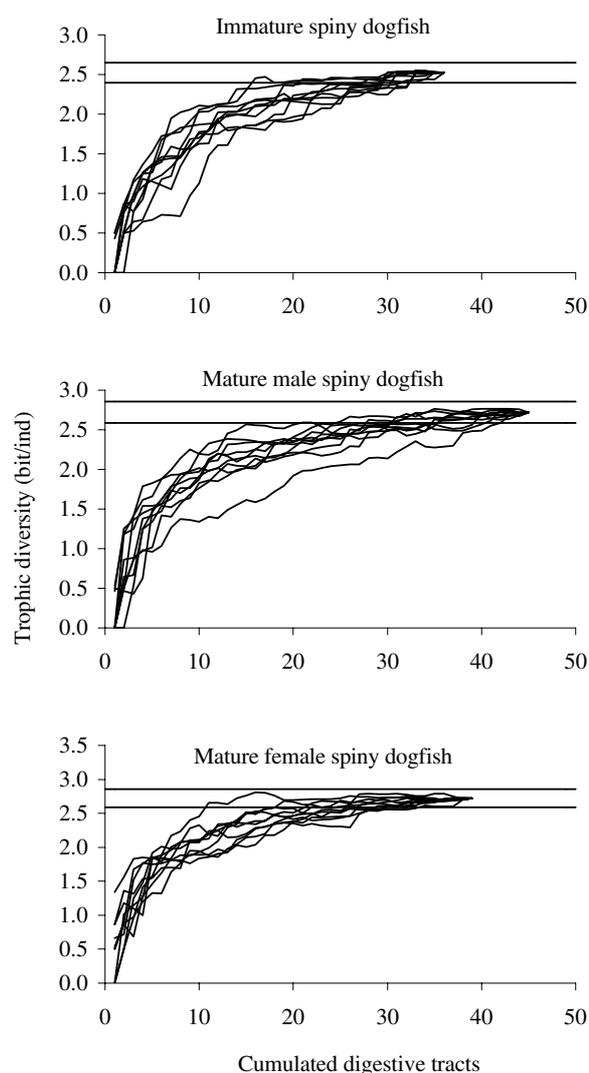

Figure 3. Cummulative trophic diversity curves for each trophic group considered. The straight lines indicate the range $H_z \pm 0.05 H_z$. Each graph shows ten randomly selected curves from the 100 curves obtained for each trophic group.

dogfish ($H = 7.873$, $n = 75$, $p = 0.019$). Pairwise contrasts indicated a significant difference between DML of Argentine shortfin squids consumed by immature and mature female spiny dogfish ($Z = 2.505$, $n_{immature} = 14$, $n_{mature\ female} = 38$, $p = 0.006$); whereas the other two comparisons were not significant (immature vs. mature male: $Z = 0.755$, $n_{immature} = 14$, $n_{mature\ male} = 23$, $p = 0.225$; mature male vs. mature female: $Z = 1.996$, $n_{mature\ male} = 23$, $n_{mature\ female} = 38$, $p = 0.023$) (Figure 6). This is a reflection of consumption of larvae and juveniles (DML < 16 cm) Argentine

Table 2. Diet overlap analysis among immature, mature male, and mature female spiny dogfish considering: (a) prey species and (b) ecological environment of prey.

Source of variation	i	k	SO_{ik}	U	df	p
(a) Specific overlap index considering prey species						
Sex & maturity stage	Immature (48)	Mature males (52)	0.622	45.623	6	<0.001
	Immature (48)	Mature females (64)	0.522	62.327	6	<0.001
	Mature females (64)	Immature (48)	0.061	357.1	6	<0.001
	Mature females (64)	Mature males (52)	0.012	560.940	6	<0.001
	Mature males (52)	Immature (48)	0.797	23.638	6	<0.001
	Mature males (52)	Mature females (64)	0.652	44.549	6	<0.001
(b) Specific overlap index considering the ecological environment of prey						
Sex & maturity stage	Immature (42)	Mature males (52)	0.775	21.363	3	<0.001
	Immature (42)	Mature females (62)	0.841	14.548	3	0.002
	Mature females (62)	Immature (42)	0.841	21.429	3	<0.001
	Mature females (64)	Mature males (52)	0.963	4.703	3	0.195
	Mature males (52)	Immature (42)	0.722	33.856	3	<0.001
	Mature males (52)	Mature females (62)	0.955	4.831	3	0.185

SO_{ik} = specific overlap of group i onto group k, U = statistic to test the null hypothesis that SO_{ik} = 1, p = probability of the statistic. The number of species or ecological environment of prey occurrences in each trophic group is indicated in parentheses.

shortfin squid in the pelagic environment (Brunetti et al. 1998) by immature spiny dogfish.

No differences were found between the TL of Argentine hake (H = 4.023, n = 35, p = 0.134) or of southern cod (H = 1.008, n = 26, p = 0.604) consumed by immature, mature male, and mature female spiny dogfish (Figure 6). However, only immature spiny dogfish consumed primary juveniles of Argentine hake (4–13 cm TL). This stage exhibits pelagic schooling behavior and does not follow the typical daily vertical migration pattern of Argentine hake (Angelescu & Prenski 1987).

Discussion

The results confirm the characterization of the spiny dogfish as a fairly non selective predator. The most important prey items, the Argentine shortfin squid and the Argentine hake, are abundant species in the northern and central Patagonian waters, and are considered key species in the dynamics of this marine community (Otero et al. 1982, Angelescu & Prenski 1987, Prenski & Angelescu 1993, Brunetti et al. 1998).

Moreover, these results indicate differences in the diet among the three trophic groups of spiny dogfish: immature, mature male, and mature female. These trophic groups can be viewed in several ways. The differences represent differences in the diet among sexes and size classes, and may be associated with the formation of schools segregated by sex and size

(Menni 1985). These conclusions agree with previously published food habits studies for several populations of spiny dogfish species (Jones & Geen 1977, Hanchet 1991, García de la Rosa & Sánchez 1997).

In a less explored path, differences among trophic groups indicate differences in the diet between immature and mature spiny dogfish. By canonical correlation analysis of the %FO of prey items, García de la Rosa & Sánchez (1997) found a size-related shift in the diet for sharks when they reach approximately 62 cm TL. They suggested that this shift could be associated with sexual maturation. However, García de la Rosa & Sánchez (1997) did not evaluate differences in the diet among sharks of different maturity levels, and they pooled sexes. In our study, we found differences in the diet between immature and mature sharks, and the minimum TL at maturity were 57.5 and 66.5 cm for males and females respectively. Averaging sexes, the minimum TL at maturity was exactly 62 cm; the same size at García de la Rosa & Sánchez (1997) found the shift in the diet using a purely size-based analysis. So it appears the shift is associated with onset maturity and shift from pelagic to more demersal habitat utilization.

In short, our results indicate that considering the most important prey species, there are differences in the diet among immature, mature male, and mature female spiny dogfish (Table 2), and at this level the differences may be associated with schools segregated by size and sex. However, the analysis considering the ecological environment of prey, only showed significant differences between immature and mature individuals.
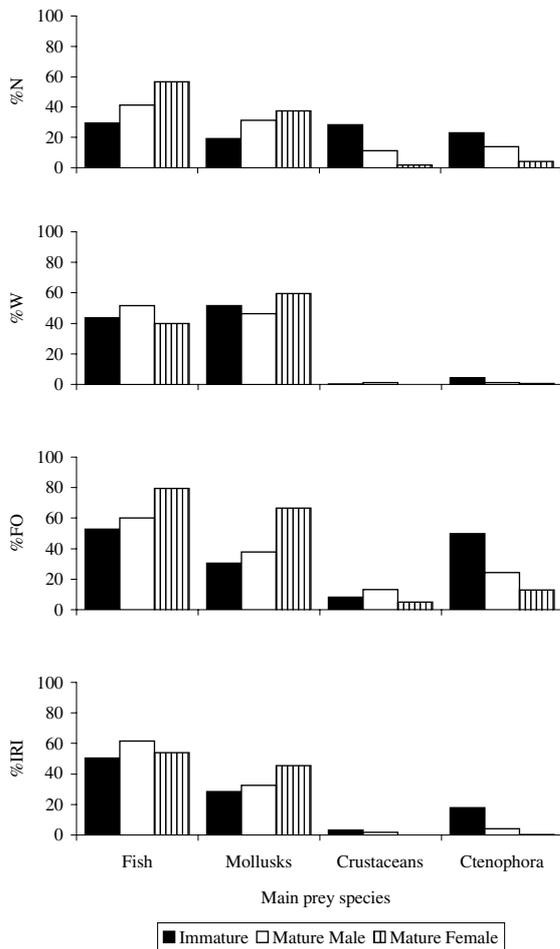
Figure 4. Diet composition for spiny dogfish trophic groups based on the animal groups of prey. %N = percentage by number, %W = percentage by regression-estimated wet weight, %FO = percent frequency of occurrence, and %IRI = percent index of relative importance.

Figure 5. Diet composition for spiny dogfish trophic groups based on the ecological environment of prey. %N = percentage by number, %W = percentage by regression-estimated wet weight, %FO = percent frequency of occurrence, and %IRI = percent index of relative importance.

Onset of sexual maturity and the related change in the energetic needs due to reproduction could trigger shift in the feeding habits, which involved a change in habitat utilization. Nevertheless, the overall energetic quality of the diet, coarsely inferred from the %W data by animal groups, does not change so dramatically (Figure 4), but the %W contains no information about the cost of feeding at the individual level. If in the demersal habitat the cost of feeding is reduced (e.g., higher encounter rates for fish and squid), even keeping the same diet composition will produce an increase in the net energy intake rate and, therefore, it will improve the quality of the diet. Of course, this kind of explanation
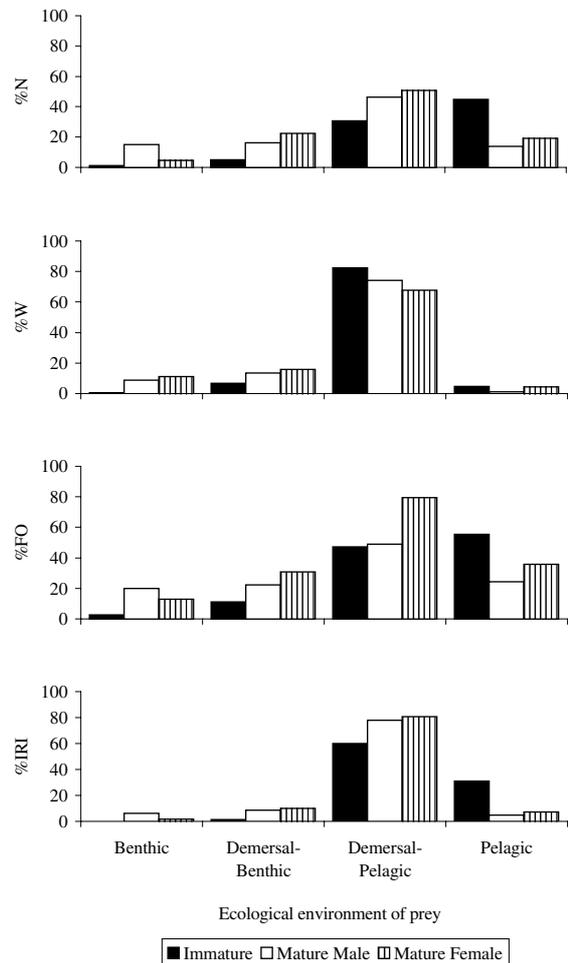
assumes that the acquisition of energy is the bottleneck of the process. However, there is no information that allows us to discard the idea that this shift in habitat utilization is led by other non diet-related factors (e.g., increased probability of finding mates, safer places for reproduction, etc).

In previous studies (Sánchez & Prenski 1996, García de la Rosa & Sánchez 1997) the Argentine hake was the most important prey for the spiny dogfish in northern and central Patagonian waters. However, our results indicate that the relative importance of Argentine shortfin squid is highest, followed by Argentine hake.
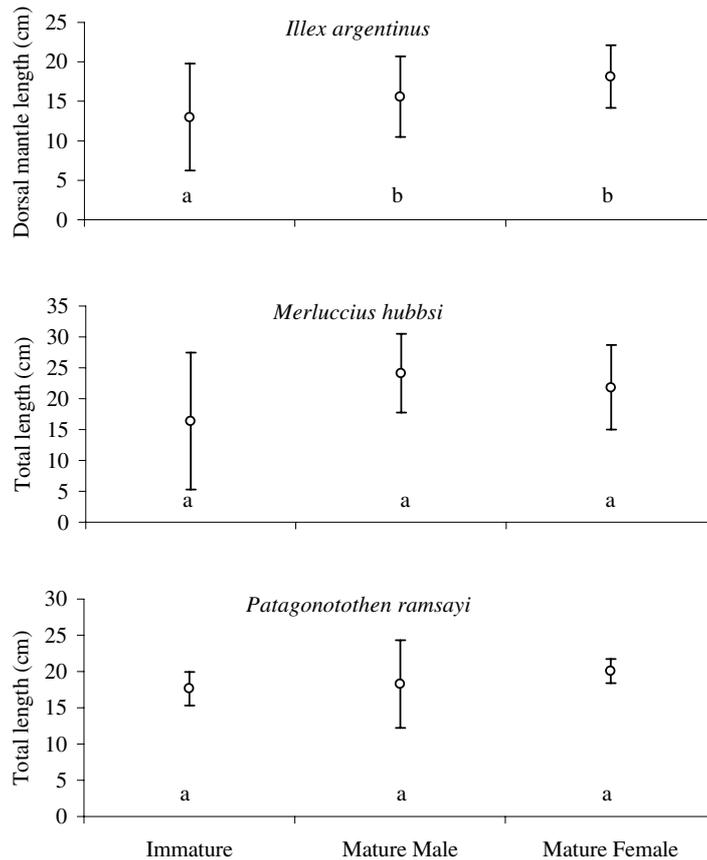
Figure 6. Mean length of Argentine shortfin squid *Illex argentinus*, Argentine hake *Merluccius hubbsi*, and southern cod *Patagonotothen ramsayi* consumed by each spiny dogfish trophic group. The bars indicate ±1 standard deviation. Different letters below the bars indicate statistically significant differences in the sizes consumed by the corresponding spiny dogfish trophic groups.
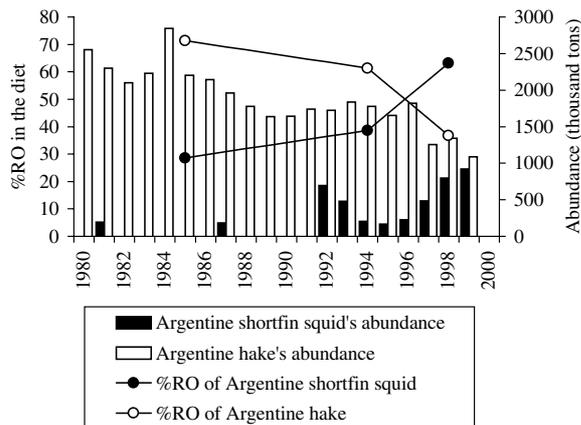

Figure 7. Abundance estimates of Argentine hake *Merluccius hubbsi*, and Argentine shortfin squid *Illex argentinus*, and the relative occurrence (%RO) of these species in the diet of the spiny dogfish in 1985, 1994, and 1998.

Our sample was mostly obtained from the by-catch of commercial hauls targeting Argentine hake, whereas the samples analyzed in previous studies were obtained from research hauls (Sánchez & Prenski 1996, García de la Rosa & Sánchez 1997). If our results were biased, the importance of Argentine hake in our sample should have been higher than in previous studies. However, the opposite situation was observed. The methodology of the present and previous studies was similar enough to avoid methodological bias. Regarding the geographical coverage, the study by Sánchez & Prenski (1996) was conducted within a more restricted area (San Jorge Gulf), whereas the present study and that of García de la Rosa & Sánchez (1997) covered almost the same area.

The main difference among these studies was the years surveyed. The Sánchez & Prenski (1996) study was performed mostly during 1985, the García de la Rosa & Sánchez (1997) study was

performed during 1994, whereas the samples analyzed in the present study were mostly obtained in 1998. The major change in the Patagonian marine community in the period 1985–1999 was a decrease of the Argentine hake stocks as a consequence of overfishing (Aubone et al. 1999).

There are survey abundance estimates of Argentine hake between 1985–1999, but the estimations for the Argentine shortfin squid do not cover the entire period. There are no abundance estimates for the Argentine shortfin squid in 1985, when the Sanchez & Prenski (1996) sample was taken, but there are data for 1981 and 1987. There are also abundance estimates for both prey species in the period 1992–1999 (Otero et al. 1982, Brunetti & Pérez Comas 1989, Prenski & Angelescu 1993, Bezzi et al. 1994, Bambill et al. 1996, Brunetti personal communication, Pérez personal communication, Prenski personal communication). These abundance estimates correspond to the Patagonian management stock of Argentine hake, and to the summer and south Patagonian spawning stocks of Argentine shortfin squid (Brunetti et al. 1998, Aubone et al. 1999).

Because García de la Rosa & Sánchez (1997) did not estimate %W, the relative occurrence (%RO) of Argentine hake and Argentine shortfin squid for previous studies and for ours were compared ($\%RO_i = [O_i/(O_h + O_s)]100$ where O_i is the occurrence of one or the other prey species, and O_h and O_s are the occurrences of Argentine hake or Argentine shortfin squid respectively). Based on the %RO and the abundance information for hake and squid, it appears that changes in the diet of spiny dogfish over time can be attributed to changes in prey availability (Figure 7). Also, the more similar diet composition observed in 1985 and 1994 could be related to similar abundance of hake and squid during these years and prior to the marked decrease in the abundance of the Argentine hake that occurred after 1996.

Fishery dependent dietary shifts should be studied to a greater extent in a range of top predators. The Argentine hake and the Argentine shortfin squid are important prey species for several marine mammals and fishes in the northern and central Patagonia marine community (Sánchez & Prenski 1996, García de la Rosa & Sánchez 1997, Koen Alonso et al. 1998, 1999, 2000). Hake and squid support two major fisheries in Argentine waters (Brunetti et al. 1998, Aubone et al. 1999). Therefore changes in predator–prey interactions may have important rammifications for population dynamics of hake and squid, and could be important considerations to include for sustainable and integrated management of these Argentine fisheries.

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