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Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina

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The food habits of the beaked skate were studied utilising 274 individuals obtained from the incidental catches of the Argentine hake (*Merluccius hubbsi*) fishery. The most important prey were the Argentine hake, the southern cod (*Patagonotothen ramsayi*), the Argentine shortfin squid (*Illex argentinus*), the isopod (*Serolis schythei*), the "raneya" (*Raneya brasiliensis*, Pisces: Ophidiidae), and the Argentine anchovy (*Engraulis anchoita*). A total of 45 prey species was identified. No differences in the diet between sexes, but significant differences among size classes and between immature and mature individuals were found. Two size-related dietary shifts previously reported in this species, at around 35 cm and 85 cm total length were confirmed and related to changes in habitat utilisation. The first shift entails a major change from benthic prey (mostly crustaceans) to demersal-benthic prey (mostly fishes) and the second change from demersal-benthic to demersal-pelagic prey (increased consumption of Argentine hake and decreased consumption of southern cod). The second shift coincides with sexual maturation and may reflect a behavioural response to maturation.

Key words: Argentina, beaked skate, diet, *Dipturus chilensis*, food habits, intraspecific diet differences, Patagonia, *Raja flavirostris*, Southwestern Atlantic Ocean.

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Introduction

The beaked skate (*Dipturus chilensis*, also refered to as *Raja flavirostris*) is widely distributed over the Argentine continental shelf. Its highest abundances have been reported in northern and central Patagonian waters (Menni and Gosztonyi, 1982; Menni and López, 1984; García de la Rosa, 1998) where it is one of the most abundant members of the Family Rajidae. This species is usually caught as by-catch in the bottom trawling fishery for Argentine hake *Merluccius hubbsi* (Coscarella *et al.*, 1997). In recent years, the commercial importance of this species has been increasing (García de la Rosa, 1998), and it is now a valuable by-catch of the Argentine hake fishery, but its biology is poorly known.

The beaked skate is an oviparous species, with a size range of 15–250 cm total length (TL) (Norman, 1937; Bahamonde, 1950; this study). Crustaceans were reported as important prey in stomach contents of beaked skates collected in Chile (Bahamonde, 1950). Sánchez and Prenski (1996) found that stomatopods and *Munida* sp. were important prey species for small beaked skates (20–40 cm TL) but the Argentine hake was the main prey species for large individuals (TL>50 cm). Furthermore, two size-related diet shifts have been reported (García de la Rosa, 1998). The first takes place at around 35 cm TL, and involves the addition of fishes and molluscs to the diet, while the second, occuring around 85 cm TL, is evidenced by the almost complete disappearance of crustaceans from the diet (García de la Rosa, 1998).

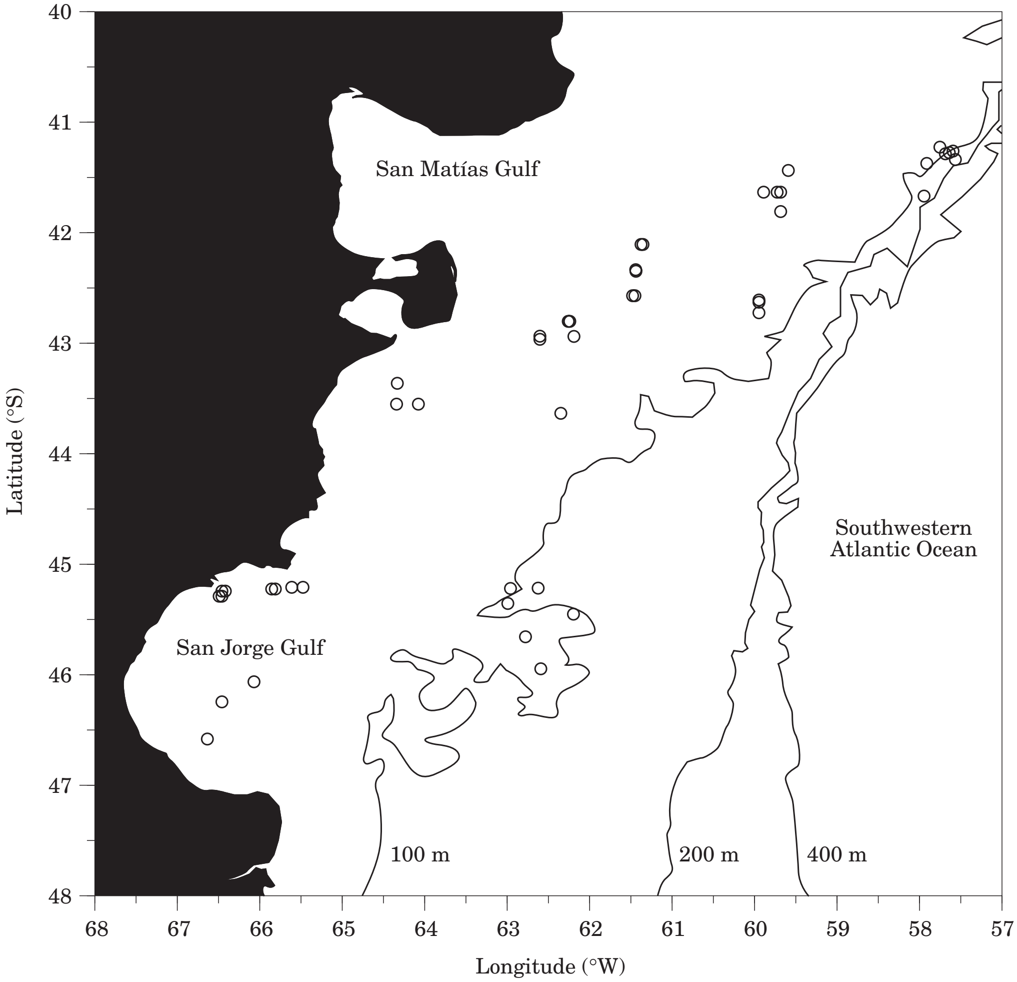

Figure 1. Study area. The empty circles indicate sampling sites.

Our objectives were to analyze the composition of the diet of the beaked skate of northern and central Patagonian waters, the prey sizes consumed, and to evaluate diet in relation to size, sex and maturity stage.

Materials and methods

Characteristics of the sample

The sample consisted of 274 beaked skates caught as a by-catch of the Argentine hake fishery in northern and central Patagonian waters between 1996 and 1998 (Figure 1).

Sex and total length were recorded. Maturity stage was assessed according to the presence of mature oocytes and eggs in the uteri of females, and the presence of sperm in epididimi and the degree of calcification of the claspers in males (Holden, 1975; Pratt, 1979; Tanaka *et al*., 1990; Peres and Vooren, 1991).

The food habits were studied by digestive tract contents analysis. Most of the beaked skates were preserved on ice on board until landing. Dissections were made at the laboratory between 1–4 days after landing. The digestive tracts were frozen at −20°C until their analysis. Digestive tract contents were separated using flushing water, a column of sieves and decantation trays (Koen Alonso *et al*., 1998, 2000).

Prey species were identified and quantified from their remains (complete prey items, otoliths, skull bones, squid beaks, exoskeletons of crustaceans, etc.) using the reference collection of the Marine Mammal Laboratory[1] and published catalogues (Clarke, 1986; Menni *et al*., 1984; Roper *et al*., 1984; Boschi *et al*., 1992; Gosztonyi

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and Kuba, 1996; Boltovskoy, 1999). Size (total length (TL) of fish and dorsal mantle length (DML) of squid, cm) and wet weight (W, g) of prey at the moment of ingestion were estimated from hard pieces found in the gut contents by using allometric regressions (Santos, 1994; Koen Alonso *et al.*, 1998, 1999, 2000).

Data analysis

The hypothesis that sex ratio was 1:1 was tested using the binomial test (Conover, 1999). The homogeneity in the composition of immature and mature individuals between sexes was evaluated using a Chi-squared test with Yates' continuity correction (Sokal and Rohlf, 1995).

The importance of prey was evaluated using the percentage frequency of occurrence (%FO), the percentage by number (%N), the percentage by regression estimated wet weight (%W) and the Index of Relative Importance relativized to 100% (%IRI) (Cortés, 1997; Koen Alonso *et al.*, 1998, 2000). These indices were calculated by species, major zoological groups (fish, crustaceans and molluscs) and ecological groups. The ecological groups considered were benthic (the prey species lives on the bottom), demersal (the prey species lives near the bottom but not linked to it) and pelagic (the prey species lives in the upper layers of the water column without relationship with the bottom). Demersal prey species were divided into demersal-pelagic (the prey has a diel vertical migration pattern, dispersing in the water column during the night and remaining close to the bottom during daylight hours) and demersal-benthic (the prey species does not migrate vertically).

Diet changes related to sex and size (TL) of the predators were evaluated using a loglinear analysis and considering the occurrences of the main prey species (Model: Size × Sex × Prey). The effect of sexual maturity on the diet was evaluated in a similar way. In this case, only those individuals within the 71.5–85 cm size range were considered. This range covered the sizes of the smallest mature individual and the largest immature individual. These beaked skates were classified into small (≤78.25 cm) and large size classes (>78.25 cm) and maturity stages (immature and mature). Also, only the occurrences of the main prey species in this size range were considered for the loglinear analysis (Model: Size × Maturity × Prey). These analyses were made using the likelihood ratio Chi-square statistic (G) and the significance of the interaction terms was assessed by an hierarchical backwards elimination procedure (Freeman, 1987).

The relationship between predator and prey sizes was evaluated using the Spearman rank correlation coefficient (r_s) (Conover, 1999). The variables considered in this analysis were the predator TL and the mean regression-estimated length of the prey. Also, the mean sizes of the main prey species of each beaked skate length class were calculated.

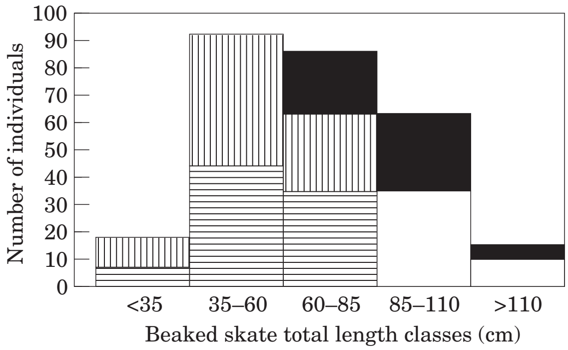

Figure 2. Length frequency distribution of the beaked skates analyzed, discriminated by sex and maturity stage. ▤, immature females; ▥, immature males; □, mature females; ■, mature males.

Results

Characteristics of the sample

The sample was composed of 143 males (87 immature and 56 mature) and 131 females (86 immature and 45 matures), with a range of 26–248 cm TL.

The sample had a unimodal length frequency distribution (Figure 2). Immature males ranged from 28.7–83.5 cm, whilst the size range of immature females was 26.0–85.0 cm. The TL varied between 71.5–222.0 cm for mature males, and between 88.4–248.0 cm for mature females.

Data analysis

The sex ratio was not significantly different from 1:1 both in the pooled sample (Binomial test; $p=0.507$), and in the samples discriminated by maturity condition (Immature: Binomial test; $p=1.000$; Mature: Binomial test; $p=0.320$). The homogeneity between sexes regarding the proportions of immature and mature individuals was not rejected ($\chi^2_{Yates}=0.49$; d.f.=1; $p=0.485$).

Diet

Only 17 digestive tracts (6.2%) were found to be empty. Frequently, intact prey items occurred together with highly digested remains.

Forty-five prey species were identified (21 fish, 15 crustacean, five mollusc, two annelid, one agnathan and one echinoderm species) (Table 1). The collection was composed of 1160 individual prey, and represented a total regression-estimated wet weight of 65 kg. However, only six prey species in the pooled sample had %IRI values greater than 1% (Table 1). These prey species

Table 1. Size and importance of prey of the beaked skate off Patagonia. EG: ecological group of the prey (B: benthic, DB: demersal-benthic, DP: demersal-pelagic, P: pelagic and NA: not assigned); Size of prey: whenever no indication, the mean corresponds to the average total length; s.d.: standard deviation; n: number of prey items (when the mean size was obtained using not all the individuals, the sample size employed for its calculation is indicated in parentheses); %N: percent number, %W: percent estimated wet weight; %FO: percent frequency of occurrence; %IRI: percent Index of Relative Importance.

		Size of prey (cm)						
Prey species	EG	Mean	s.d.	n	%N	%W	%FO	%IRI
Fish								
Merluccius hubbsi	DP	21.9	12.1	190 (187)	16.38	36.38	40.86	46.60
Patagonotothen ramsayi	DB	18.2	5.6	157	13.53	19.72	35.80	25.74
Raneya brasiliensis	DB	21.8	4.1	39	3.36	3.53	8.56	1.28
Engraulis anchoita	P	15.7	2.0	37	3.19	1.54	11.28	1.15
Genypterus blacodes	DB	34.0	12.9	6	0.52	1.83	2.33	0.12
Macruronus magellanicus	DP	68.2	10.3	3	0.26	5.89	0.78	0.10
Pseudoxenomystax albescens	DB	41.5	12.2	6	0.52	1.19	2.33	0.09
Unidentified fish	NA	—	—	8	0.69	0.38	3.11	0.07
Sympterygia sp.	B	23.1	14.9	4	0.34	2.09	1.17	0.06
Xystreuris rasile	B	20.9	5.0	6	0.52	0.79	1.95	0.05
Paralichthys isosceles	B	21.3	2.5	5	0.43	0.65	1.95	0.05
Congiopodus peruvianus	B	19.5	6.6	3	0.26	0.54	1.17	0.02
Unidentified skate	B	—	—	2	0.17	0.38	0.78	<0.01
Helicolenus lahillei	DB	25.0		1	0.09	0.77	0.39	<0.01
Psammobatis sp.	B	16.5	12.0	2	0.17	0.20	0.78	<0.01
Polipriion americanus	DB	—	—	1	0.09	0.62	0.39	<0.01
Stromateus brasiliensis	DP	28.3		1	0.09	0.48	0.39	<0.01
Seriolella punctata	DP	17.9		1	0.09	0.11	0.39	<0.01
Triathalassothia argentina	B	13.8		1	0.09	0.08	0.39	<0.01
Dipturus chilensis	B	17.0		1	0.09	0.05	0.39	<0.01
Iluocoetes fimbriatus	DB	10.0		1	0.09	0.03	0.39	<0.01
Agnathans								
Mixine sp.	B	26.0		1	0.09	0.04	0.39	<0.01
Molluscs								
Illex argentinus	DP	15.9[a]	4.8	112	9.66	18.00	26.46	15.82
Enteroctopus megalocyathus	B	—	—	19	1.64	2.30	3.89	0.33
Semirossia tenera	DB	—	—	3	0.26	0.02	1.17	<0.01
Eledone sp.	B	30.0		1	0.09	0.13	0.39	<0.01
Nudibranchs	B	11.0		1	0.09	0.08	0.39	<0.01
Crustaceans								
Serolis schythei	B	2.2	0.4	164	14.14	0.12	20.62	6.36
Munida spinosa	B	1.1[b]	0.2	182	15.69	0.31	1.56	0.54
Pterygosquilla armata armata	B	7.5	1.0	30	2.59	0.24	7.00	0.43
Unidentified amphipods	B	0.6	0.2	64	5.52	<0.01	3.11	0.37
Libinia spinosa	B	2.0[c]	0.7	20	1.72	0.07	7.39	0.29
non Serolidae isopods	B	2.0	0.4	22	1.90	0.02	5.45	0.23
Lithodes confundes	B	6.2[c]	2.0	7	0.60	1.23	2.72	0.11
Munida subrugosa	B	1.0[b]	0.9	30	2.59	0.04	1.17	0.07
Peltarion spinosulum	B	2.4[c]	0.7	9	0.78	0.06	2.33	0.04
Pleoticus muelleri	DB	6.4[b]	5.4	8	0.69	0.06	1.95	0.03
Unidentified crabs	B	—	—	4	0.34	0.01	1.17	<0.01
Unidentified crustaceans	NA	—	—	2	0.17	0.01	0.78	<0.01
Eurypodius latreillei	B	2.9[c]		1	0.09	<0.01	0.39	<0.01
Munida gregaria	B	2.5[b]		1	0.09	<0.01	0.39	<0.01
Peisos petrunkevitchi	DB	4.5[b]		1	0.09	<0.01	0.39	<0.01
Anelids								
Unidentified tube polychaetes	B	9.0		1	0.09	<0.01	0.39	<0.01
Eunice argentinensis	B	8.3		1	0.09	<0.01	0.39	<0.01
Echinoderms								
Arbacea dufresnei	B	2.0[d]		1	0.09	<0.01	0.39	<0.01

[a]Dorsal mantle length.
[b]Length of the cephalothorax.
[c]Carapace length.
[d]Diameter of the sea urchin.

were the Argentine hake, the southern cod (*Patagonotothen ramsayi*), the Argentine shortfin squid (*Illex argentinus*), the isopod (*Serolis schythei*), the "raneya" (*Raneya brasiliensis*, Pisces: Ophidiidae), and the Argentine anchovy (*Engraulis anchoita*). In combination, these species represented 60.3% by number, 79.3% by regression-estimated wet weight, and an accumulated 96.9% of the %IRI.

The loglinear analysis of the occurrences of these six prey species, and the sex and size classes of the predator indicated significant interactions between prey species and size classes (G=20.55; d.f.=4; p=0.0004). However, the interaction between prey species and sex was non-significant (G=2.69; d.f.=5; p=0.7480). Thus, the diet changed with the size of the predator but not with its sex.

Size-related changes in the diet

The diet of the small beaked skates (<35 cm) was composed mostly of crustaceans, mainly the squat lobster *Munida spinosa* (Figure 3). Above this size, the incidence of fish and molluscs in the diet increased, and the southern cod, the Argentine hake and the Argentine shortfin squid became the main prey species (Figure 3). However, in the size range 35–60 cm, crustaceans (mainly the isopod *S. schythei*) were still frequent in the diet (Figure 3). Among fish, the southern cod was the main prey species of predators in the size range 35–85 cm, closely followed by the Argentine hake (Figure 3). Above 85 cm, the importance of the Argentine hake increased while the importance of the southern cod decreased (Figure 3).

In terms of ecological groups, these changes in diet implied a change in habitat utilisation by the beaked skate. The small individuals (<35 cm) were benthic feeders, the intermediate sized ones (35–85 cm) fed almost evenly on demersal-benthic and demersal-pelagic prey, while large individuals (>85 cm) were demersal-pelagic feeders (Figure 4). However, only the first change, at around 35 cm implied a major change in the diet composition, when crustaceans were replaced by fish and molluscs (Figure 5). After that, the main characteristic of the diet change was a gradual reduction in the importance of crustaceans. It should be highlighted that the %W of the major zoological groups in the diet remained almost constant for those individuals larger than 35 cm (Figure 5). This indicates that the quality of the diet, in terms of gross energy density, did not change with size above 35 cm.

Maturity-related changes in the diet

Two size-related diet shifts were previously reported in the beaked skate's diet (García de la Rosa, 1998). The first was observed at 35 cm, and corresponded to a major reduction of the importance of crustaceans in the diet. The second shift was detected at around 85 cm, when the beaked skate became a more demersal-pelagic predator (Figure 4). All individuals above this size were sexually mature (Figure 2). Taking into account that sex had no effect on the diet, the relationship between the second diet switch, predator size and maturity was explored, restricting the analysis to the occurrences of Argentine hake, southern cod, "raneya" and Argentine shortfin squid in the guts of the 43 individuals in the 71.5–85 cm size range (see Materials and methods).

The results indicated that the interaction between size and prey was not significant (G=3.41 d.f.=3 p=0.3332), but the interaction between maturity stage and prey was significant (G=8.17; d.f.=3; p=0.0426). Thus, the second dietary shift detected at around 85 cm by García de la Rosa (1998) appeared to be more related to sexual maturity than to growth in size.

Relationship between predator and prey sizes

A positive significant correlation was found between the mean regression-estimated length of prey in the digestive tracts and the total lengths of the beaked skate in the pooled sample (r_s=0.686; n=253; p<0.001). This general pattern was also observed for each of the main prey species (Figure 6), although the mean lengths of some prey showed a tendency to reach an "asymptotic" value in the larger predator size classes (Figure 6).

Discussion

The results indicate that the beaked skate is a broad-spectrum predator that exhibits demersal and benthic feeding habits. Also, its active predatory capabilities are illustrated by the consumption of demersal-pelagic prey like Argentine hake and Argentine shortfin squid.

Early studies suggested that crustaceans were the main component in the diet of the beaked skate (Bahamonde, 1950). However, this conclusion could be related to the size range of the beaked skates analyzed in that study. Bahamonde's sample was composed of 26 animals in the size range 27–65 cm collected in southern Chile (41°30′S–42°S). These sizes correspond to small and immature individuals. *Munida gregaria* represented 83.8% of the diet, by number, while *Serolis* sp. and stomatopods were also found (Bahamonde, 1950). Even though our results indicate that the southern cod and the Argentine hake were the most important preys of beaked skates between 35–60 cm, crustaceans also had a high importance. In fact, the squat lobster was the most important prey in the diet of those individuals <35 cm.

More recent and detailed studies carried out in Argentine waters indicated that crustaceans were important prey for small beaked skates, whereas fishes

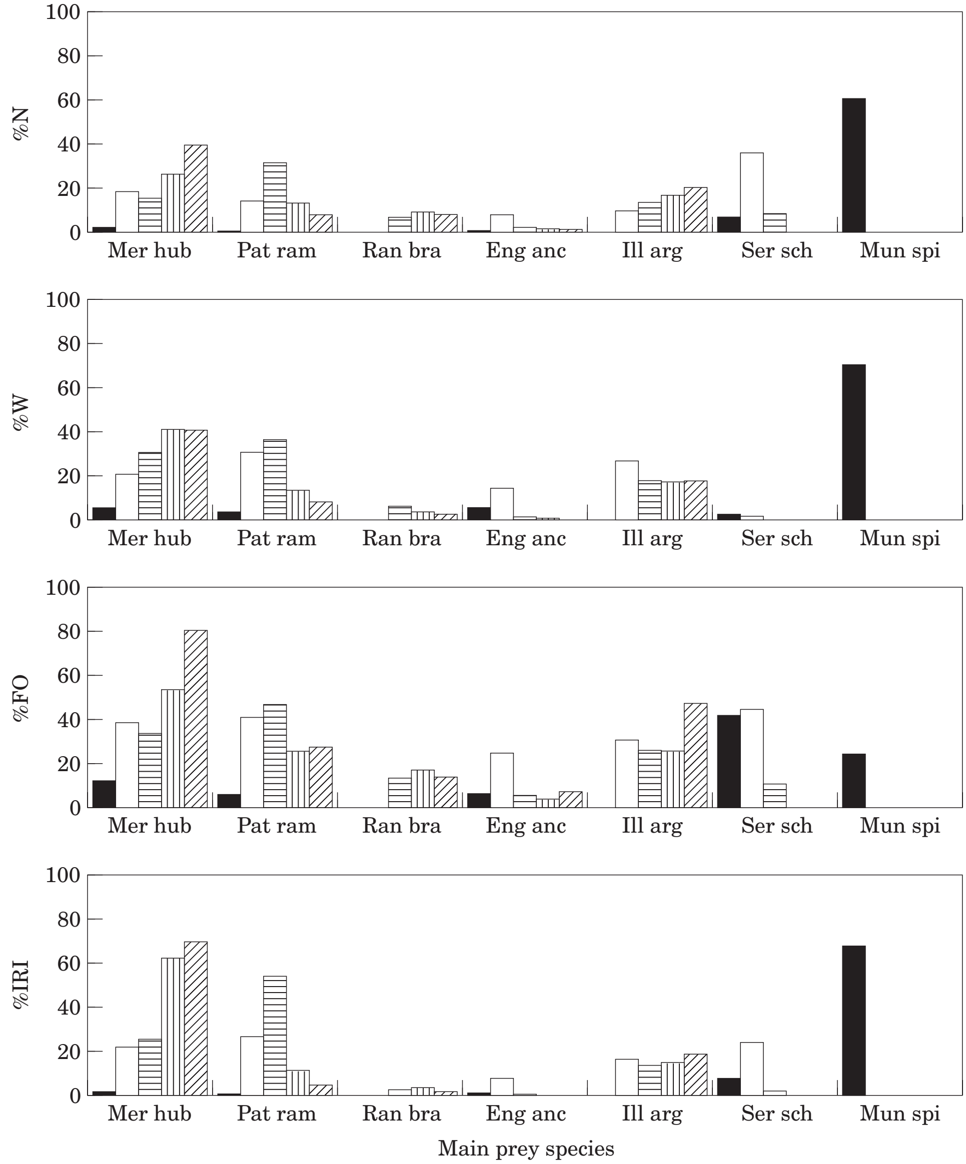

Figure 3. Size-related variations in the importance of the main prey species of the beaked skate, based on the five length classes considered. %N = percentage by number, %W = percentage by regression estimated wet weight, %FO = percent frequency of occurrence and %IRI = percent Index of Relative Importance. Mer hub: Argentine hake (*Merluccius hubbsi*), Pat ram: southern cod (*Patagonotothen ramsayi*), Ran bra: "raneya" (*Raneya brasiliensis*), Eng anc: Argentine anchovy (*Engraulis anchoita*), Ill arg: Argentine shortfin squid (*Illex argentinus*), Ser Sch: isopod (*Serolis schythei*) and Mun spi: squat lobster (*Munida spinosa*). ■, <35 cm; □, 35–60 cm; ▤, 60–85 cm; ▥, 85–110 cm; ▨, >110 cm.

and molluscs were important in the larger ones (Sánchez and Prenski, 1996; García de la Rosa, 1998). In the San Jorge gulf (45°S–47°S), the squat lobster and stomatopods were the most important prey of beaked skates measuring 20–40 cm (Sánchez and Prenski, 1996). For those between 40–50 cm, the importance of crustaceans decreased and the importance of fishes and squid increased. For individuals >50 cm, the diet was dominated by fishes, mainly Argentine hake (Sánchez and Prenski, 1996).

The other recent work was carried out in almost the same geographical area as our study, found the same general pattern, and detected two size-related shifts in the diet of the beaked skate (García de la Rosa, 1998). These shifts, detected by canonical correlation analysis of the %FO of prey, were located around 35 cm and

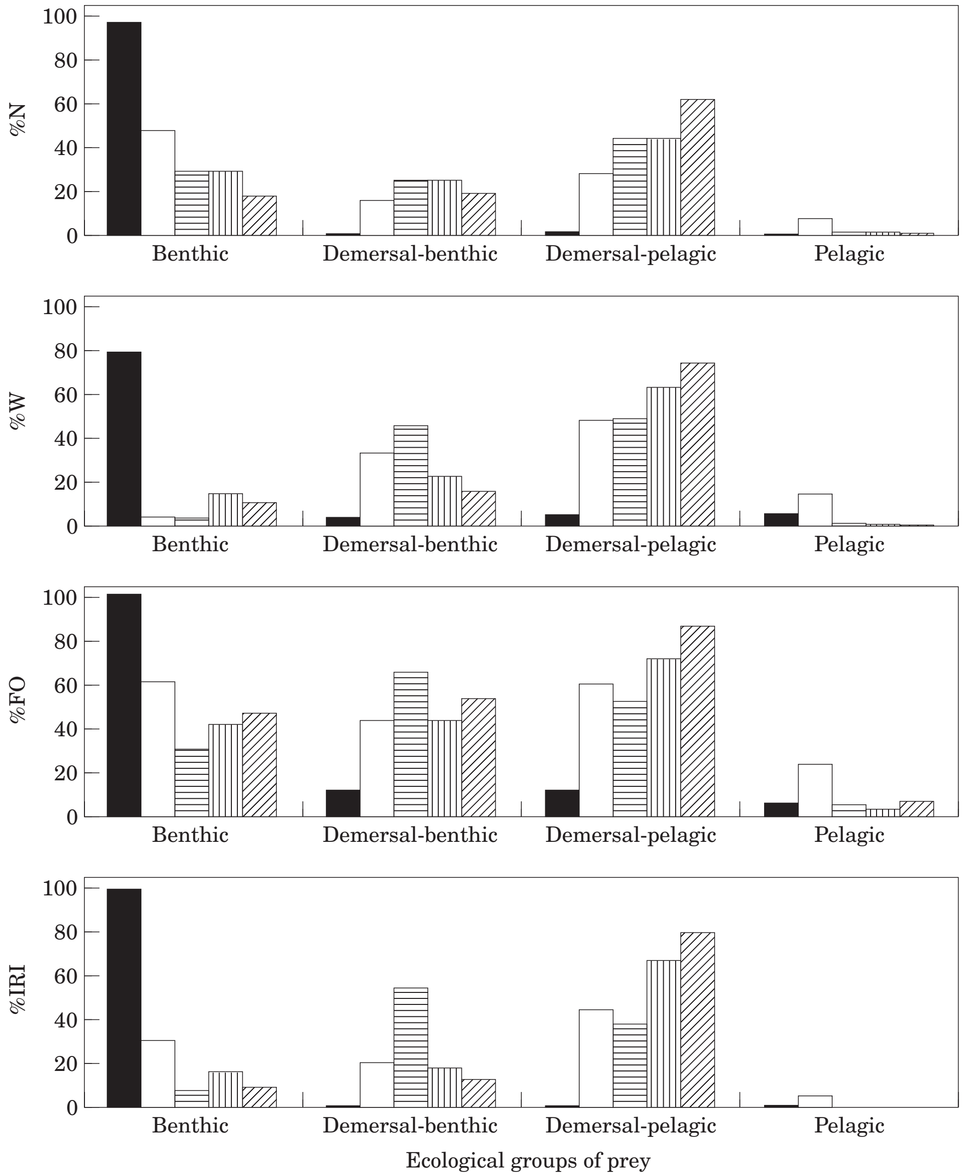

Figure 4. Size-related variations in the importance of the ecological groups of prey of the beaked skate, based on the five length classes considered. %N=percentage by number, %W=percentage by regression estimated wet weight, %FO=percent frequency of occurrence and %IRI=percent Index of Relative Importance. See Figure 3 for key.

85 cm TL (García de la Rosa, 1998). The first shifts implied a change from an almost exclusively carcinophagous diet to a mixed diet that included fishes and molluscs. The second shift implied a change to a more fish based diet (García de la Rosa, 1998).

Diet switching is a phenomenon widely observed in fishes but there are no unique explanations for it (Gerking, 1994). In general terms, these changes are usually related to modifications in the environmental conditions or to the energetic requirements of the animals. In the latter case, diet switching is often associated with optimization of the energy gained from one or another type of diet (Stephens and Krebs, 1986).

An increase in the importance of fish in the diet related to growth, changing from a mostly carcinophagous diet to an ichthyophagous one, has been described for several skate species (Tyler, 1972; Holden and Tucker, 1974; Ajayi, 1982; Templeman, 1982; Pedersen, 1995).

In the case of the beaked skate, the two dietary shifts reported by García de la Rosa (1998) appear to be associated with two different biological processes,

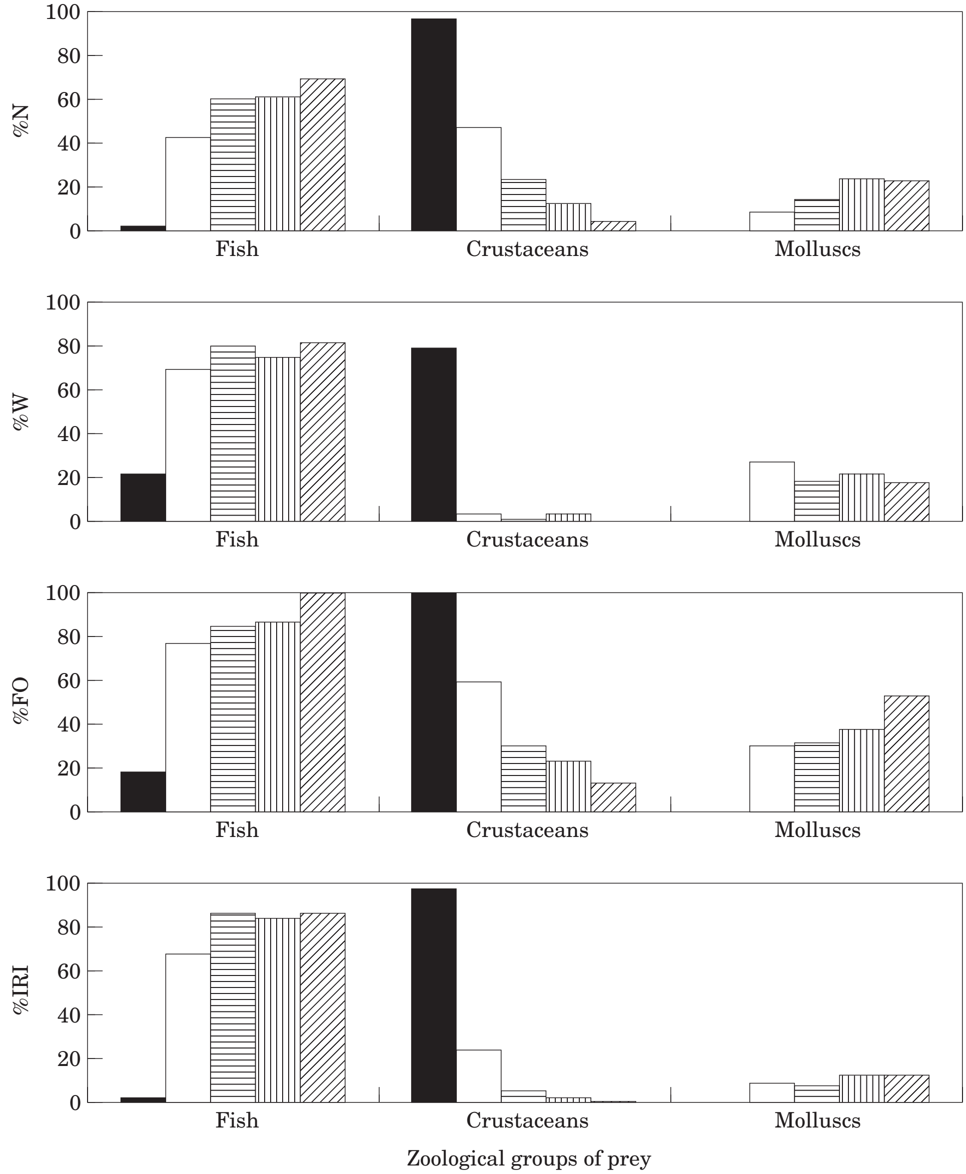

Figure 5. Size-related variations in the importance of the main zoological groups of prey of the beaked skate, based on the five length classes considered. %N = percentage by number, %W = percentage by regression estimated wet weight, %FO = percent frequency of occurrence and %IRI = percent Index of Relative Importance. See Figure 3 for key.

though both are accompanied by changes in habitat utilisation. The first shift, from benthic to demersal-benthic predation, facilitates growth through an increase in the quality of the diet (replacing crustaceans with more energetically profitable fishes and molluscs). It seems likely this shift is triggered by attainment of a size large enough to permit consumption of the new class of prey items. The second shift, from demersal-benthic to demersal-pelagic predation, changes the most important prey items without changing the quality of the diet (at least in the simple measure of %W of major zoological groups consumed). The second shift coincides with sexual maturation and our loglinear analysis suggests it is triggered by maturation rather than by size. Possibly the dietary shift is only part of a larger behavioural response to maturation.

Finally, considering the diversity of the diet, the prey size consumed and the most important prey species, the beaked skate can be considered a generalist predator. Some of its main prey species (Argentine hake, Argentine shortfin squid, ''raneya'' and Argentine anchovy) were also found to be main prey species of the

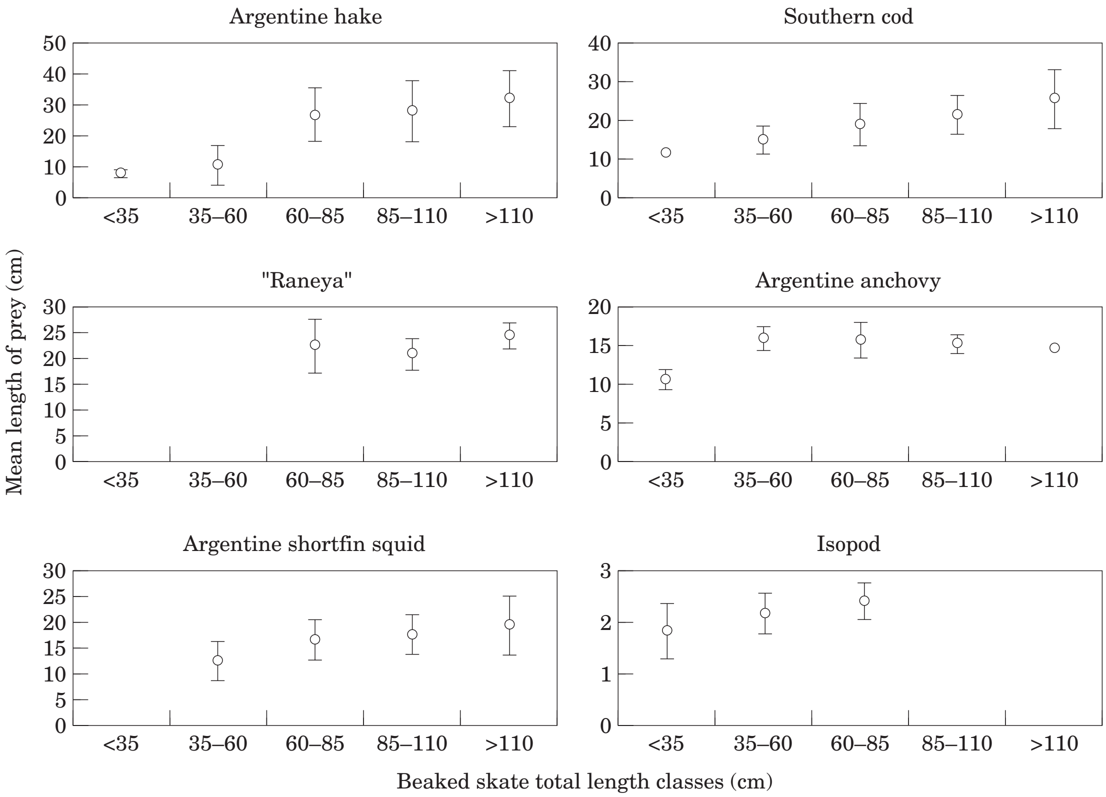

Figure 6. Size-related variations in the mean length of the main prey species in the diet of the beaked skate, based on the five length classes considered. The bars indicate the standard deviation. All lengths are total lengths with the exception of the Argentine shortfin squid where the length corresponds to the dorsal mantle length.

southern sea lion (*Otaria flavescens*) in the same geographical area (Koen Alonso *et al.*, 2000). Also, the sizes of these prey consumed by large beaked skates were similar to the sizes consumed by the southern sea lion, and both top predators appear to consume them in those sizes most frequent and available in the environment (Koen Alonso *et al.*, 2000).

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