Food habits, selectivity, and foraging modes of the school shark *Galeorhinus galeus*

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ABSTRACT: The foraging ecology of the school shark *Galeorhinus galeus* was studied in Anegada Bay, Argentina, during the seasonal occurrence of this species in Argentinean waters (October to April) from 1998 to 2001. Of the 408 individuals examined, 168 (41.2%) had food remains in their stomachs. The proportion of individuals with food remains was negatively correlated with total length. In general, the diet was composed mainly of teleosts (98.5% IRI [index of relative importance]), with invertebrates and chondrichthyans as minor prey. The diet varied ontogenetically and seasonally. Juveniles and adults differed in their consumption of invertebrates, with juveniles preying more on benthic invertebrates, mainly the octopus *Octopus tehuelchus*, and adults on squid. From December to February, adults preyed mainly on benthic teleosts (almost exclusively the Atlantic midshipman *Porichthys porosissimus*), while from March to April the consumption of squid increased. A comparison of numbers of prey in stomachs with abundance of prey in the environment in March and April showed that, in these months, juveniles selected invertebrates and demersal teleosts and avoided pelagic teleosts and chondricthyan prey, and adults selected squid and avoided pelagic teleosts. This indicates that, during this period, *G. galeus* is not an opportunistic predator. The mean size of prey increased with increasing shark length, but even large sharks consumed small prey. All shark sizes consumed prey fragments that were significantly larger than other prey consumed whole. This indicates that *G. galeus* is able to overcome gape limitation by mutilating prey, and that the ontogenetic diet shift was not due to a change in the ability to seize prey.

KEY WORDS: *Galeorhinus galeus* · School shark · Predation · Piscivory · Diet · Gape limitation · Elasmobranch · Chondrichthyes

INTRODUCTION

Prey and predator characteristics such as size, morphology, activity levels and habitat use are key determinants of the outcome of the predator–prey relationship (Sih & Christensen 2001). Thus, while prey and predator characteristics may affect a predator's diet and its variation, environmental variation, such as seasonality, also adds new variables that ultimately affect the composition of a predator's diet. This complex interplay results in substantial variation in the diet and foraging patterns between seasons and during ontogeny (Heithaus 2004).

Ontogenetic and seasonal shifts in the diet of sharks are common, although the causes behind these shifts are not completely understood (Heithaus 2004). Ontogenetic shifts have been suggested to be the result of differences in habitat use by different life stages or, alternatively, to a change in predatory capability or efficiency (Lowe et al. 1996). For most piscivorous fishes, the mean and maximum size of prey increase with increasing predator size, while minimum prey size does

not change (Scharf et al. 2000). One of the main factors determining the maximum prey size that can be ingested is the predator's gape size (Juanes et al. 2002). As most piscivorous fishes ingest their prey whole, gape size imposes a limit on the size and type of prey consumed (i.e. a gape limitation) and sets up a size refuge for prey (Scharf et al. 1997). Some predators may evade gape limitation and increase the size of prey consumed by changing their foraging mode (i.e. the way they hunt and handle their prey). Eels can cut pieces off their prey by spinning once they bite them (Helfman & Clark 1986), and bluefish *Pomatomus saltatrix* may cut their fish prey into pieces and then swallow them (Scharf et al. 1997) instead of swallowing whole prey as usual. Among sharks, some large species (e.g. white *Carcharodon carcharias*, bull *Carcharhinus leucas*, and tiger sharks *Galeocerdo cuvier*) that feed on marine mammals, chondrichthyans or sea turtles may cut pieces off their prey mainly because they have large serrated teeth (Frazzetta 1988). However, it is not known if smaller piscivorous sharks, whose prey are not larger than themselves, have any strategy that evades gape limitation. In addition, foraging modes for evading gape limitation may not be equally possible for juveniles and adults, suggesting that ontogenetic changes in the anatomy of the feeding apparatus and feeding mechanisms may play an important role in determining the foraging mode of a predator through ontogeny, and thus produce ontogenetic diet shifts.

Prey availability may largely determine the opportunistic or selective nature of a predator. The foraging strategy of an opportunistic predator is to consume prey in the same proportions in which they are found in the environment, while a selective predator feeds on prey in different proportions to those in the environment (Chesson 1978, Jaksić 1989, Juanes et al. 2002). In this way, a comparison of prey consumption and prey availability (usually estimated by prey abundance) is crucial to evaluate the opportunism or selectivity of a predator (Jaksić 1989).

Sharks have often been considered opportunistic predators (e.g. Wetherbee et al. 1990, Motta & Wilga 2001). Nevertheless, only 2 studies on shark feeding have related diet composition with prey abundance: in the Bay of Biscay (northern Spain), the smallspotted catshark *Scyliorhinus canicula* is the most selective predator of 18 demersal crustacean-feeding fishes (Serrano et al. 2003); in contrast, in the Gulf of Carpentaria (northern Australia), 5 species of carcharhinid sharks appeared to feed opportunistically, and only 1 seemed to consume prey in a different proportion to that found in the environment (Salini et al. 1992).

The school shark *Galeorhinus galeus* (Carcharhiniformes: Triakidae), is a medium-sized shark that occurs in coastal and shelf temperate waters in the NE and SE Pacific, NE and South Atlantic, Mediterranean Sea, southern Australia and New Zealand (Compagno 1984, Last & Stevens 1994). The diet of *G. galeus* comprises mainly fishes and cephalopods, but the relative contribution of these prey varies among regions (Walker 1999). Similar proportions of fishes and cephalopods comprise the diet of *G. galeus* from Australia (47 and 37 % by weight, respectively) and South Africa (57 and 40 %, respectively) (see Walker 1999). In contrast, sharks from the Irish Sea have a mainly piscivorous diet (78 % of the diet were fishes, Ellis et al. 1996), as do those from the Azores (100 %, Morato et al. 2003). Some qualitative ontogenetic dietary differences have been reported, with juveniles consuming less fishes and cephalopods (Olsen 1954) or smaller and more coastal prey than adults (see Walker 1999).

Galeorhinus galeus has bladelike teeth with elevated crowns and basal cusplets (Compagno 1984). Although they are not usually considered as serrated teeth, we hypothesize that the basal cusplets may function as coarse serrations, allowing sharks to cut their prey into pieces and thus overcome gape limitation. Furthermore, the qualitative ontogenetic differences observed in the diet of *G. galeus* by other studies may be the result of differential ability to evade gape limitation dependent on individual size.

Here, we describe the diet of *Galeorhinus galeus*, evaluate ontogenetic and seasonal changes in their feeding habits, and compare diet composition with prey abundance in the environment in order to test the hypothesis that *G. galeus* is an opportunistic predator. We also assess the predator size–prey size relationship and test the hypothesis that *G. galeus* overcomes gape limitation by sectioning prey with their teeth. Finally, we evaluate the role of foraging mode in producing an ontogenetic diet shift.

MATERIALS AND METHODS

Study area. Anegada Bay (40° 30′ S, 62° 00′ W, Argentina) is a shallow and highly productive area with many small islands and sand/mud banks, shallower than 2 m during high tides, which are connected by channels to 24 m depth (usually 10 to 14 m depth). The bay is affected by discharge of continental waters by the Colorado and Negro rivers, which form a coastal front at their confluence with marine waters (Guerrero 1998). The water temperature is about 12°C in winter and 16 to 17°C in summer (Martos & Piccolo 1988).

Galeorhinus galeus is present in Anegada Bay every year between October and late April (i.e. spring to fall), when it is taken in a hook-and-line recreational shark fishery occurring in the outer part of the bay, mostly at depths between 5 and 20 m (Lucifora et al. 2004). Sam-

ples for the present study were taken from this fishery from October to April in the fishing seasons of 1998–1999, 1999–2000 and 2000–2001.

Food habits. The stomachs of *Galeorhinus galeus* were examined to determine their feeding habits. Total length (TL) was measured and sex and maturity were determined by examining the reproductive organs. Enlarged uteri and oviducal glands were considered to indicate mature females, while both the presence of convoluted epididymi and the degree of clasper calcification were used to determine maturity in males (Peres & Vooren 1991, Lucifora et al. 2004). The samples consisted of 241 adult females (>124 cm TL), 45 juvenile females (<124 cm TL), 108 adult males (>119 cm TL), and 14 juvenile males (<119 cm TL).

The stomach contents of each examined shark were sorted, identified to the lowest possible taxonomic level, weighed, and counted. Bait (almost exclusively mullet *Mugil* sp., rarely chub mackerel *Scomber japonicus*) was excluded from the analysis as it was identified before the boat departed for the fishing ground. Additionally, bait was easily recognized in the sharks' stomachs by the clear cuts made with knives and its undigested state. The abundances of the different prey in the diet of juveniles and adults are presented as numeric frequency (N_i: $100 \times$ number of individuals of Prey i recorded in the stomachs divided by the sum of all prey individuals); frequency of occurrence (F_i: percentage of stomachs which contained a particular Prey i); weight frequency (W_i: weight contribution of Prey i expressed as percentage of total stomach content weight); and the index of relative importance adjusted to 100 % (% IRI = $F_i \times (N_i + W_i)$) (Cortés 1997).

Prey were sorted into 7 ecological groups: benthic teleosts, demersal teleosts, pelagic teleosts, unidentified teleosts, chondrichthyans, squid and benthic invertebrates (including octopi), according to habitat descriptions for each prey species given by Menni (1983) and Cousseau & Perrotta (2000). Log-likelihood G tests (Zar 1984) were used to assess ontogenetic and seasonal differences in the diet. Ontogenetic dietary changes were assessed during fall (March to April). Seasonal changes in diet were assessed for adult *Galeorhinus galeus* among spring (October and November), summer (December, January, and February), and fall (March and April) samples. Pair-wise multiple comparisons were also performed with G-tests, using a sequential Bonferroni adjustment for the number of tests done (Rice 1989).

The order of stomachs sampled was randomized 100 times and the mean cumulative diversity of stomach contents (Shannon-Wiener diversity index) was plotted as a function of sample size to determine if a sufficient number of stomachs had been examined. This procedure was carried out for all juveniles and adults to determine sample size sufficiency in the general description of diet. Cumulative curves were separately built for spring, summer and fall adults to determine sample size sufficiency in seasonal comparisons and for fall juveniles to assess sample sufficiency in juvenile–adult comparisons, which were performed only in fall.

The graphical method of Amundsen et al. (1996) was employed to describe the individual contribution to trophic niche breadth and the degree of specialization of predators. This method plots the prey-specific index of every prey (P_i, which is defined as the number of individuals of Prey i divided by the total number of Prey individuals found within the stomachs containing Prey i) against F_i (Amundsen et al. 1996). Prey located in the upper-right of the plot are consumed by a high fraction of a specialized predator's population, while those located in the upper-left are consumed by a few individually specialized predators. In contrast, prey located in the lower half of the plot reflect a generalized foraging strategy (Amundsen et al. 1996). This method is analogous to calculating a niche breadth index, but gives additional information on individual contribution to a population niche (Amundsen et al. 1996).

To test prey selection patterns, we compared the number of prey groups consumed by juveniles and adults caught only in the fall with number of prey in the study area using G-tests (Jaksić 1989, Manly et al. 1993). Abundance data of prey in the study area were obtained from 24 trawls made with a bottom trawl net (footrope = 40.3 m, headrope = 35.3 m, codend mesh size = 103 mm, intranet mesh size = 22 mm, trawl speed = 4 knots, trawl duration = 15 min) in March 2002. The trawls used for the analysis were aimed to estimate abundances of benthic and demersal fishes for stock assessments, and they were carried out in the same area in which the shark fishery occurs. The catch of high numbers of *Galeorhinus galeus* during trawling (L. O. Lucifora pers. obs.) indicates that the area trawled is heavily used by the sharks. Most species caught in the trawls were medium- to small-sized teleosts and chondrichthyans. Some large species (e.g. *G. galeus* itself, spotback skates *Atlantoraja castelnaui*) were excluded from the analysis because they were judged to be too large to be preyed upon by *G. galeus*. Given the shallow depth of the area, the abundances of pelagic teleosts are not highly underestimated. We performed comparisons with prey groups (not individual prey species) in order to minimize possible annual variations in prey abundance, given that broad ecological groups are expected to show less interannual variation than individual species. Thus, the results are conservative estimates of the opportunistic or selective strategy of *G. galeus*.

Foraging mode. The relationship between predator length and prey weight was assessed for undigested fish prey found within the stomachs. Regressions on

the 5, 50 and 95% quantiles were performed on these data to assess the relationship between minimum, median and maximum prey size consumed with predator TL, respectively (Scharf et al. 2000, Bethea et al. 2004).

Fish prey were classified as whole or sectioned (i.e. individual prey were cut into 2 or more pieces) and the total weight of the sectioned prey was determined by weighing all pieces of the same individual. Analysis of covariance (ANCOVA) was used to test for differences between whole and sectioned prey weight for a given predator length (Zar 1984). No difference between whole and sectioned prey weight is expected if prey sectioning is not related to overcoming gape limitation.

To determine if *Galeorhinus galeus* shifts at a certain length from swallowing their prey whole to sectioning them, we performed a logistic regression between the proportion of sectioned prey and shark TL (in 10 cm length intervals).

RESULTS

Food habits

All the sample sizes were sufficient for comparison, as the cumulative curves of diversity reached an asymptote (Fig. 1).
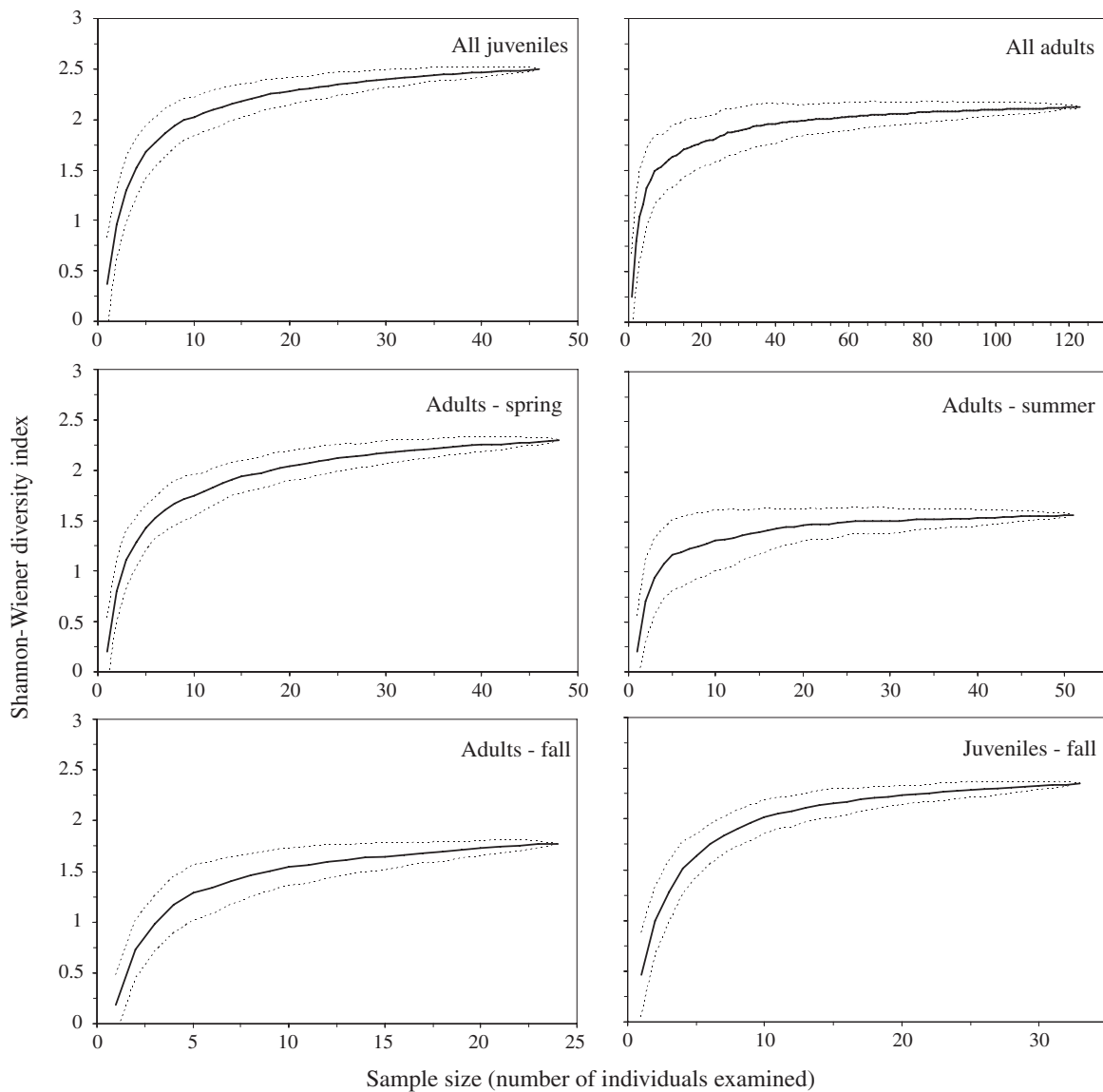

Fig. 1. *Galeorhinus galeus*. Cumulative mean diversity (continuous line) ±1 SD (dashed lines) within stomachs estimated by Shannon-Wiener diversity index, as a function of sample size in Anegada Bay, Argentina
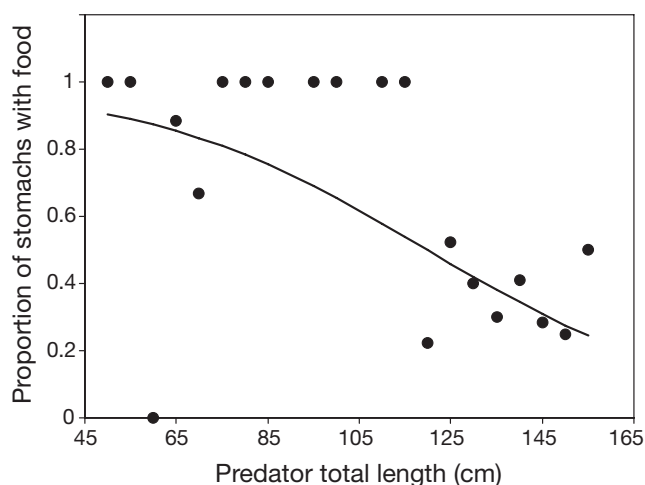
Fig. 2. *Galeorhinus galeus*. Logistic regression of proportion of stomachs with food and total length in Anegada Bay, Argentina

Of the 408 individuals examined, 168 (41.2%) had food remains in their stomachs. The proportion of individuals with food remains was negatively related to TL (logistic regression parameters = 3.854 and −0.032; n = 20; χ^2 = 35.654; p < 0.001; Fig. 2).

A total of 43 (29 to species, 14 to class) different prey items were identified within the stomachs (Table 1). In general, teleost fishes were the most common prey (98.47% IRI, 80.31% N_i, 87.35% F_i, 95.59% W_i). Squid (0.66% IRI, 8.61% N_i, 11.31% F_i, 0.54% W_i), benthic invertebrates (0.56% IRI, 7.38% N_i, 10.71% F_i, 0.81% W_i), and chondrichthyans (0.31% IRI, 3.70% N_i, 7.14% F_i, 3.06% W_i) were minor components of the diet.

Juvenile *Galeorhinus galeus* mainly consumed demersal teleosts, the most important prey species being *Raneya brasiliensis* and the striped weakfish *Cynoscion guatucupa* (Table 1). Invertebrates, mainly the octopus *Octopus tehuelchus*, were frequent prey although their biomass contribution, and thus IRI values, was lower

Table 1. *Galeorhinus galeus*. Diet composition of juveniles (n = 45) and adults (n = 123) in Anegada Bay, Argentina. N_i: numeric frequency; W_i: weight frequency; F_i: frequency of occurrence; IRI: proportional index of relative importance

	Juveniles				Adults			
	% N_i	% W_i	% F_i	% IRI	% N_i	% W_i	% F_i	% IRI
Benthic teleosts	(11.12)	(18.7)	(15.22)	(5.96)	(32.26)	(41.19)	(36.59)	(48.06)
Batrachoididae								
Porichthys porosissimus	10.19	18.54	13.04	11.32	30.88	38.84	35.77	38.31
Paralichthyidae								
Paralichthys patagonicus					0.92	2.13	1.63	0.08
Cynoglossidae								
Symphurus sp.	0.93	0.16	2.17	0.07				
Unidentified flatfish					0.46	0.22	0.81	0.01
Demersal teleosts	(30.07)	(57.45)	(54.35)	(68.12)	(20.27)	(32.74)	(30.89)	(29.29)
Congridae								
Conger orbignyanus					0.46	1.18	0.81	0.02
Ophidiidae								
Raneya brasiliensis	14.81	6.63	23.91	15.49				
Serranidae								
Acanthistius brasilianus					0.46	0.15	0.81	0.01
Dules auriga	7.41	4.32	8.7	3.08				
Mullidae								
Mullus argentinus	0.93	0.54	2.17	0.10				
Sciaenidae								
Cynoscion guatucupa	6.48	35.48	13.04	16.54	16.13	28.12	25.2	17.30
Umbrina canosai	5.56	5.06	8.70	2.79				
Unidentified Sciaenidae	0.93	1.33	2.17	0.15				
Mugilidae								
Mugil sp.	0.93	4.09	2.17	0.33				
Percophidiidae								
Percophis brasiliensis					0.46	0.59	0.81	0.01
Pinguipedidae								
Pinguipes brasiliensis					2.3	2.48	3.25	0.24
Pseudopercis semifasciata					0.46	0.22	0.81	0.01
Pelagic teleosts	(5.56)	(2.71)	(8.70)	(0.94)	(7.83)	(6.91)	(10.57)	(2.79)
Clupeidae								
Brevoortia aurea					0.46	1.07	0.81	0.02
Engraulidae								
Engraulis anchoita	3.7	1.81	4.35	0.72	2.3	0.98	0.81	0.21
Atherinopsidae								
Odonthestes argentinensis					3.69	2.9	6.50	0.66

Table 1 (continued)

	Juveniles				Adults			
	% N_i	% W_i	% F_i	% IRI	% N_i	% W_i	% F_i	% IRI
Pomatomidae								
Pomatomus saltatrix					0.46	0.2	0.81	0.01
Carangidae								
Parona signata					0.46	1.41	0.81	0.02
Trachurus lathami	0.93	0.67	2.17	0.10				
Stromateidae								
Peprilus paru	0.93	0.23	2.17	0.08				
Stromateus brasiliensis					0.46	0.35	0.81	0.01
Unidentified teleosts	(23.15)	(14.82)	(34.78)	(39.90)	(20.74)	(13.82)	(25.20)	(13.38)
Chondrichthyans	(0.93)	(0.74)		(0.07)	(5.98)	(4.85)	(9.76)	(1.89)
Triakidae								
Mustelus schmitti	0.93	0.74	2.17	0.11	0.46	1.15	0.81	0.02
Rajidae								
Sympterygia acuta					0.46	1.37	0.81	0.02
Unidentified Rajidae					0.92	0.29	1.63	0.03
Myliobatidae								
Myliobatis spp.					0.46	0.56	0.81	0.01
Callorhynchidae								
Callorhinchus callorhynchus					0.46	0.23	0.81	0.01
Unidentified batoid					1.38	1.05	2.44	0.09
Unidentified chondrichthyan					1.84	0.2	3.25	0.10
Squid	(6.48)	(1.2)	(13.04)	(1.32)	(9.67)	(0.41)	(11.38)	(2.05)
Illex argentinus	1.85	0.01	4.35	0.24	5.99	0.03	6.50	0.60
Loligo sanpaulensis	3.7	1.18	6.52	0.96	2.3	0	3.25	0.12
Unidentified squid	0.93	0.01	2.17	0.06	1.38	0.38	2.44	0.07
Benthic invertebrates	(15.75)	(4.36)	(23.91)	(6.31)	(3.22)	(0.06)	(5.69)	(0.33)
Cnidaria								
Unidentified colonial cnidarian	1.85	0.96	4.35	0.24				
Mollusca								
Octopus tehuelchus	11.11	3.29	17.39	7.57	1.38	0.04	2.44	0.05
Unidentified octopus					0.46	0	0.81	0.01
Unidentified gastropod	0.93	0	2.17	0.06				
Crustacea								
Unidentified shrimp	0.93	0.06	2.17	0.18	0.46	0.01	0.81	0.01
Unidentified crab					0.46	0	0.81	0.01
Echinodermata								
Unidentified holothurian					0.46	0.01	0.81	0.01
Urochordata								
Unidentified ascidian	0.93	0.05	2.17	0.06				

(Table 1). The main dietary components of adult *G. galeus* were benthic teleosts; the Atlantic midshipman *Porichthys porosissimus* was the predominant prey species (Table 1). Demersal teleosts were the second most important prey category, with *C. guatucupa* being the main component (Table 1). The remaining prey had % IRI values lower than 1 (Table 1).

Diet composition differed significantly between juveniles and adults ($G = 18.15$, df = 2, p < 0.05). Juveniles consumed more benthic invertebrates than adults ($G = 7.70$, df = 1, p < 0.05), and adults preyed more on squid than did juveniles ($G = 13.07$, df = 1, p < 0.05). There was no difference in the consumption of pelagic, demersal, benthic or unidentified teleosts ($G = 0.02$, 4.33, 4.60 and 0.27, respectively, p > 0.05) between juveniles and adults (see Table 2).

Diet composition of adult *Galeorhinus galeus* differed significantly among seasons ($G = 62.78$, df = 12, p < 0.05, Fig. 3). These differences were due to a higher consumption of benthic teleosts during summer ($G = 25.67$, df = 2, p < 0.05) and squid during fall ($G = 25.67$, df = 2, p < 0.05). Of the benthic teleosts, 96% were *Porichthys porosissimus*, and of the squid, 62% were the Argentine shortfin squid *Illex argentinus*.

The 24 trawl samples used to estimate prey abundance caught 51 757 individuals of 48 different species of fish and invertebrates, including all but 1 (i.e. *Illex argentinus*) of the species consumed by *Galeorhinus galeus*. This indicates that the samples were representative of the prey assemblage present in the study area. Both juveniles and adults consumed prey in pro-

portions significantly different from those in the environment during fall (G = 50.03 and 70.73, respectively, df = 5, p < 0.05). Juveniles preyed on demersal teleosts, squid, and octopi more than expected, benthic teleosts were consumed in the same proportion as in the environment, and chondrichthyans and pelagic teleosts were avoided (Table 2). Adult *G. galeus* preyed on squid more than expected, pelagic teleosts were consumed less than expected, and the

Table 2. *Galeorhinus galeus.* Patterns of feeding selectivity for juveniles (n = 33) and adults (n = 24) based on number of prey (%N_i) consumed and number of prey available in the habitat during fall (March and April). 0: prey consumed in accordance with their availability; +, −: prey consumed significantly more or less than expected, respectively (p < 0.05). G = log-likelihood ratio test-statistic

Prey group	Habitat %N_i expected	Juveniles %N_i observed	G		Adults %N_i observed	G	
Benthic teleosts	<0.01	7.25	2.80	0	25	3.69	0
Demersal teleosts	37.8	55.07	10.19	+	28.13	0.89	0
Pelagic teleosts	61.89	5.80	88.99	−	6.25	40.06	−
Chondrichthyans	4.57	0	6.12	−	0	2.68	0
Squids	0.12	7.25	10.72	+	37.50	19.81	+
Benthic invertebrates	0.18	24.64	62.96	+	3.13	0.99	0

remaining prey groups were consumed in the same proportion as in the environment (Table 2).

P_i – F_i plots showed that, during spring, adult *Galeorhinus galeus* were not specialized on any particular prey; they had high individual variability in the consumption of different prey. In contrast, during summer, the strategy shifted substantially with a clear specialization on benthic teleosts (almost exclusively *Porichthys porosissimus*) and a lower importance of other prey (Fig. 4). In fall, adult *G. galeus* did not predominantly consume any particular prey over the others, while juveniles were more specialized in consuming demersal teleosts (Fig. 4).

Foraging patterns

Minimum, median and maximum prey size increased significantly with increasing TL of the sharks (slope and intercepts of 5; 50; 95% quantile regressions = 0.257 and −14,318; 1.071 and −44.616; 5.511 and −278.304, respectively; p < 0.05). The relationship was asymmetric and the increase in maximum prey size consumed was much faster than that of minimum prey size. Thus, even large *Galeorhinus galeus* continued to consume small prey (Fig. 5).

The weight of consumed fish prey increased significantly with increasing TL of the sharks, for both whole (r = 0.668, n = 42, Student's t = 5.68, p < 0.001) and sectioned prey (r = 0.474, n = 46, t = 3.57, p < 0.001). Sectioned prey were frequently found in the stomachs, in a similar proportion to whole prey (53.3 and 46.7%, $n_{sectioned}$ = 48, n_{whole} = 42, χ^2 = 0.099, df = 1, p = 0.754). For any given shark length, sectioned prey consumed were significantly heavier (i.e. larger) than prey consumed whole (ANCOVA, $F_{2,85}$ = 34.56, p < 0.001, Fig. 6).

Sharks of all lengths examined were able to section prey. There was no significant relationship between the proportion of sectioned prey and shark TL (logistic regression parameters = −0.646 and 0.006; n = 8; χ^2 =
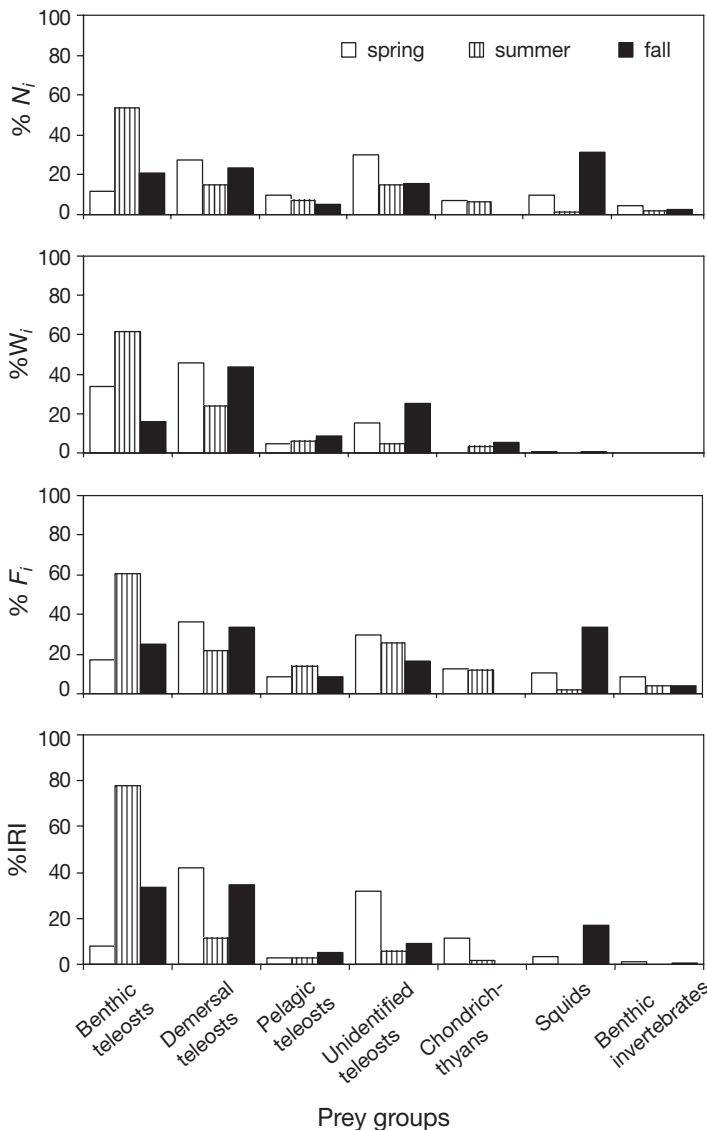

Fig. 3. *Galeorhinus galeus*. Seasonal dietary composition of adult school sharks in Anegada Bay, Argentina. N_i: numeric frequency; W_i: weight frequency; F_i: frequency of occurrence; IRI: proportional index of relative importance
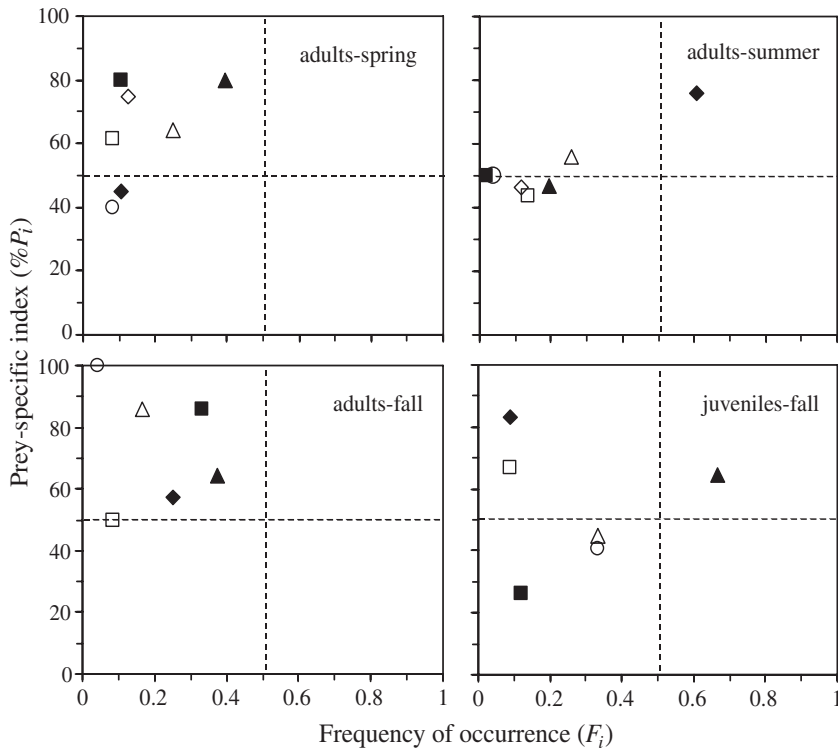
Fig. 4. *Galeorhinus galeus*. Prey-specific index (P_i) vs. frequency of occurrence (F_i) for school sharks. High values on *y*-axis indicate high individual specialization; high values on *x*-axis indicate high consumption of a prey by predator population. (◆) Benthic teleosts, (◇) chondrichthyans, (○) benthic invertebrates, (■) squid, (□) pelagic teleosts, (▲) demersal teleosts, (△) unidentified teleosts

0.679; p = 0.410; Fig. 7). This indicates that ontogenetic diet shift was not related to a change in foraging mode.

DISCUSSION

Despite *Galeorhinus galeus* being a commercially important species worldwide (Walker 1999), this is the first study to analyze aspects of its trophic ecology other than diet composition. Our results indicate that *G. galeus* in Anegada Bay is a piscivorous predator that shifts its diet ontogenetically and seasonally. It also changes its foraging strategy seasonally, feeds selectively, and alters its foraging mode depending on prey size, even at small lengths.

Food habits and foraging strategy

Since specific (i.e. mass-standardized) metabolic rate decreases with increasing body size (Schmidt-Nielsen 1984), it is unlikely that a small individual digests its meals more slowly than a large individual. Thus, a higher proportion of stomachs containing prey in small sharks may be the result of a higher consumption rate of small individuals compared to large individuals. This pattern has been found in the broadnose sevengill shark *Notorynchus cepedianus* (Lucifora et al. 2005), a species in which higher consumption rates in small individuals relative to large individuals have been experimentally observed (Van Dykhuizen & Mollet
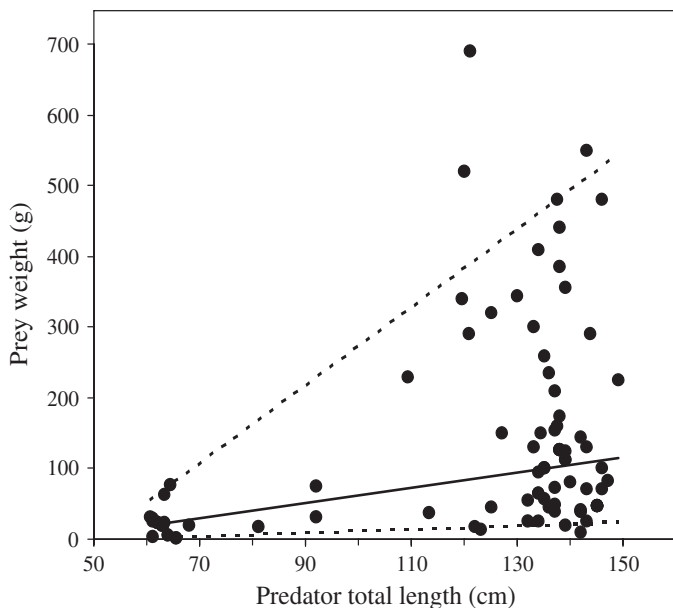

Fig. 5. *Galeorhinus galeus*. Relationship between fish prey weight and predator total length. Continuous line: median prey weight (50% quantile), dashed lines: minimum (5% quantile) and maximum (95% quantile) prey weight
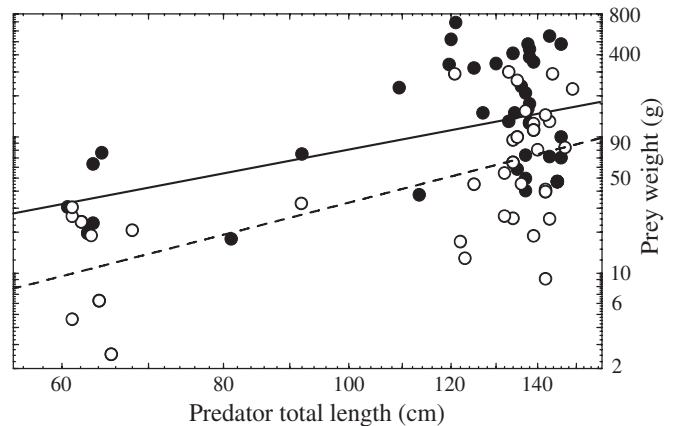

Fig. 6. *Galeorhinus galeus*. Relationship between prey weight and predator total length for fish prey consumed whole (○, dashed line) and sectioned (●, continuous line)
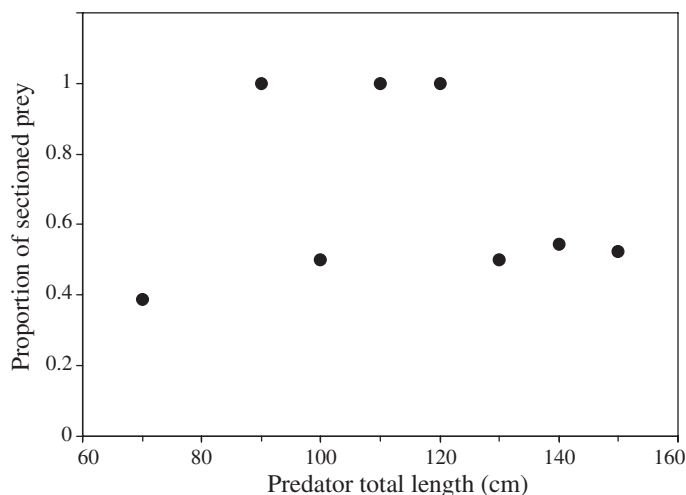
Fig. 7. *Galeorhinus galeus*. Proportion of fish prey consumed sectioned by school sharks of various sizes (10 cm total length intervals)

1992). This behaviour is thought to be adaptive — a higher consumption rate may be selected in juveniles because they invest much energy in growth (Lucifora et al. 2005).

Teleost fishes were the main prey of *Galeorhinus galeus*. This is consistent with observations in other SW Atlantic localities (Menni 1985, Menni et al. 1986), the Irish Sea (Ellis et al. 1996) and the Azores (Morato et al. 2003). However, it contrasts with the diet of *G. galeus* in Australia and South Africa, where teleosts and cephalopods are equally important (Walker 1999).

Juveniles consumed significantly more benthic invertebrates (mainly the octopus *Octopus tehuelchus*) than adults. This may reflect a difference in habitat use because, in addition to *O. tehuelchus*, other common prey of juveniles (like *Dules auriga*) are more common in rocky habitats and are not an important prey of the adults. The other difference between juveniles and adults was the high consumption of squid by adults, mainly *Illex argentinus*. Remarkably, *I. argentinus* is uncommon in the study area during fall, when it is concentrated in north Patagonian shelf waters south of Anegada Bay (Brunetti et al. 1998). In fall, most adult *Galeorhinus galeus* in the study area are males (Lucifora et al. 2004), which are concentrated in the north Patagonian gulfs during the summer (42 to 44° S, Elías et al. 2004). This suggests that male *G. galeus* are sympatric with *I. argentinus* and may prey on it in the north Patagonian shelf. The highly digested state of squid remains found in the stomachs (often only beaks and a few soft tissues) indicates that they were consumed some days before the sharks were caught. This agrees with the hypothesized northwards migration of male *G. galeus* from Patagonian waters in fall (Lucifora et al. 2004).

The diet of adult *Galeorhinus galeus* showed seasonal differences due to a higher consumption of benthic teleosts in summer. Almost all benthic teleosts were *Porichthys porosissimus*. During the winter, *P. porosissimus* remains buried in soft bottom habitats throughout the day and feeds during the night. In spring and summer (breeding season), males migrate to rocky habitats where they establish and maintain a territory. There, they emit low frequency sounds in order to attract females (Lane 1967, Brantley & Bass 1994) and, during courtship, produce bioluminescent displays (Crane 1965). We hypothesize that these behavioural changes may increase the vulnerability and/or availability of this prey, causing *G. galeus* to shift to consume *P. porosissimus* during summer. The lemon shark *Negaprion brevirostris* exhibits a similar pattern, shifting to prey heavily on the Gulf toadfish *Opsanus beta* (a relative of *P. porosissimus* with a similar reproductive behaviour) during the reproductive season of this prey (Wetherbee et al. 1990). Recent evidence indicates that the scarecrow toadfish *O. phobetron* is preyed upon by *N. brevirostris* during the toadfish's breeding season and at the time of the day when the toadfish produces sounds (Newman et al. 2004), suggesting that sound production for courting increases the vulnerability of sound-emitting fishes to predation by sharks, supporting our hypothesis.

The importance of *Porichthys porosissimus* in the diet of *Galeorhinus galeus* is also evident by analyzing the foraging strategy of adult *G. galeus* by season. In summer, the foraging strategy changed from a generalized to a specialized one. This indicates that *G. galeus* has a sufficiently plastic foraging behaviour to change from one strategy to another. There is also an ontogenetic shift in the foraging behaviour because juveniles have a foraging strategy specialized in demersal teleosts while adults (in seasons other than summer) have a generalist strategy. This variation is to be expected for a predator that spends part of the year in shallow coastal waters and part in outer continental shelf waters (Menni 1985, Menni et al. 1986, Peres & Vooren 1991, Vooren 1997, West & Stevens 2001, Lucifora et al. 2004) where foraging opportunities are different.

Prey selection

Both juvenile and adult *Galeorhinus galeus* have a selective diet in Anegada Bay during the fall. Ecosystem characteristics and the interplay between foraging and predation avoidance may play an important role in producing the prey selection pattern found in both the juveniles and adults.

Pelagic teleosts are the most abundant prey group in the environment (despite a possible underestimation by the bottom trawl net); however, they are significantly under-represented in the juvenile and adult diet. This contrasts with the pattern in the Azores, where pelagic fishes were reported to be a main component of the diet by Morato et al. (2003). This geographic difference in diet may be explained by the environmental differences between Anegada Bay and the Azores. The Azorean shelf is narrow and waters deeper than 600 m are found near the coast; consequently, the pelagic community dominates even at shallow depths (Morato et al. 2003). In contrast, Anegada Bay and the adjacent shelf ecosystem have a gentle slope (the 200 m isobath is located about 300 km eastward from the shoreline), which makes the demersal and benthic community more accessible for *Galeorhinus galeus*. The shallow characteristics of Anegada Bay and the adjacent shelf suggest that the entire water column is easily available to adult *G. galeus*, which are capable of vertical migrations of up to 600 m (West & Stevens 2001). We therefore believe that its avoidance of pelagic teleosts in Anegada Bay may be due to a preference for demersal prey that could be more profitable or easier to catch. Alternatively, *G. galeus* may avoid using the open, and often turbid, water column to diminish predation risk from *Notorynchus cepedianus*, which is able to catch large prey in turbid waters (Ebert 1991), and effectively preys on large *G. galeus* in Anegada Bay (Lucifora et al. 2005).

The avoidance of chondrichthyans by juveniles may be related to a size disadvantage of the predator relative to the prey, since even the smallest chondrichthyans may be too large for juvenile *Galeorhinus galeus*. This is supported by neither a shift to selection nor avoidance of chondrichthyans by adult *G. galeus*.

Methodological issues may have affected results in 2 out of the 6 prey groups analyzed. The sampling gear employed may have underestimated the abundance of benthic invertebrates, causing an overestimation of selectivity for these prey by juveniles. In addition, squid consumed outside the study area (see above) account for a large fraction of squid consumed by adults, which overestimates the selection by adults.

While some sharks may be opportunistic predators (Salini et al. 1992), our results show that *Galeorhinus galeus* may be selective. This is also suggested for other sharks by other studies. In Maranhão (northern Brazil), sharks as a whole consume only 22 out of 117 bony fish species present in the area (Lessa & Menni 1994), and the diet of the bonnethead shark *Sphyrna tiburo* is based on 2 *Callinectes* crab species uncommon in that area (Lessa & Almeida 1998). In addition, the abundance of tiger sharks *Galeocerdo cuvier* in Shark Bay (Australia) is positively correlated with the presence of the energetically most profitable prey, dugongs *Dugong dugon* and sea snakes, suggesting that these prey are selected (Heithaus 2001). White *Carcharodon carcharias* and blue *Prionace glauca* sharks feed selectively on the blubber of dead whales, possibly maximizing their energy intake (Long & Jones 1996). These findings suggest that, at least on some occasions, sharks may be more selective than previously thought.

Changes in foraging mode

Galeorhinus galeus is able to consume larger prey as it grows, but large sharks do not abandon the consumption of small prey. Although this pattern is contrary to the predictions of optimal diet theory, it is the most common predator–prey size pattern found in piscivorous fishes (Scharf et al. 2000, Juanes et al. 2002). This is hypothesized to be a result of the higher vulnerability of small prey compared to large prey due to higher encounter rates and the higher probability of capture once detected. This makes them profitable even for large predators (Scharf et al. 2000). The same pattern is present in other sharks (the spiny dogfish *Squalus acanthias* and the dusky smoothhound *Mustelus canis*: Scharf et al. 2000). However, it is not apparent in other species such as the Atlantic sharpnose shark *Rhizoprionodon terraenovae* and juvenile spinner sharks *Carcharhinus limbatus* (Bethea et al. 2004), or even in a batoid, the yellownose skate *Dipturus chilensis* (Lucifora et al. 2000), in which minimum prey size increases faster (relative to maximum prey size) than in *G. galeus*, *S. acanthias* and *M. canis*. Differences in prey availability may explain the different patterns found in these species. In environments with a greater choice of prey, elasmobranchs may be more selective, feeding only on larger prey and thus matching the predictions of optimal diet theory. This may produce the pattern found in *R. terraenovae*, *C. limbatus*, and *D. chilensis*. More work on other species is needed to detect a general pattern amongst elasmobranchs.

Our results show that *Galeorhinus galeus* of all sizes are able to cut prey with their teeth, despite having only coarse basal serrations (cusplets). This lack of variability in foraging mode among the different size classes of a predator also occurs in the swellshark *Cephaloscyllium ventriosum* (Ferry-Graham 1998) and the nurse shark *Ginglymostoma cirratum* (Robinson & Motta 2002), and is presumably due to isometric growth of the different parts of the feeding apparatus (Ferry-Graham 1998, Robinson & Motta 2002). The consistency of foraging mode through ontogeny suggests that isometry is also characteristic of the growth

pattern of the feeding apparatus in *Galeorhinus galeus*. The ontogenetic diet shift may be due to a change in habitat use rather than in foraging mode and morphology.

Galeorhinus galeus makes extensive use of its cutting ability, with half of all its prey being consumed in pieces. This behaviour may allow *G. galeus* to reduce gape limitation, since the total size of sectioned prey consumed is significantly larger (and presumably more profitable) than the size of prey consumed whole. Although it has not previously been studied, we hypothesize that this behaviour is common among piscivorous sharks, especially within the order Carcharhiniformes, which contains many species with serrated dentitions.

In conclusion, our results indicate that the ontogenetic diet shift in *Galeorhinus galeus* is not due to an ontogenetic change in foraging mode. The shift is more likely due to a change in habitat use, presumably arising from a decrease in predation risk as *G. galeus* grows. *G. galeus* cannot be described as an opportunistic predator. Its ability to change its foraging strategy and foraging modes, depending on prey size, allows it to use resources from different habitats and situations.

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