THE DIET OF THE BLUE SHARK (*PRIONACE GLAUCA* L.) IN AZOREAN WATERS

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Stomach contents of 195 *Prionace glauca* caught off the Azores from October 1993 to July 1994 were studied. Eighty three had empty stomachs. Only 23 contained whole or fleshy parts of animals (other than bait) and all belonged to the fish *Capros aper*, *Macrorhamphosus scolopax* and *Lepidopus caudatus* and the squids *Histioteuthis bonnellii* and *Taonius pavo*. Seventy five fish otoliths and 207 cephalopod lower beaks were identified to genus or species. Considering all fragments from the stomachs, including otoliths, cephalopod beaks and eye lenses, a minimum of 1411 fish, 4 crustaceans and 261 cephalopods were represented. Approximately 386 of the fish were represented by eye lenses alone. There was a mean of 2.4 species (1.8 cephalopods and 0.6 fish) and 15.2 animals represented in each stomach. Fish remains occurred in 83.0% of the stomachs and contributed 84.5% of animals to the diet. Cephalopod remains occurred in 75.7% and contributed 15.5% of animals. Estimates of the weights of fish and cephalopods suggest that cephalopods are probably the most important in the diet and these were almost entirely meso- or bathypelagic, neutrally buoyant cephalopods. Small epipelagic shoaling fish were present with a few much larger near-bottom fish. In all, there are at least 11 species of fish and at least 37 species of cephalopod in the diet. Size distributions of beaks and otoliths are presented. A number of rarely caught species of cephalopod are important in the diet. No difference was found in diet according to the size or between male and female *Prionace glauca*. Comparisons with swordfish and sperm whale diets from the same region clearly suggest selection in their predation.

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Analisaram-se os conteúdos estomacais de 195 *Prionace glauca*, capturadas nos Açores entre Outubro de 1993 e Julho de 1994. Oitenta e três indivíduos possuíam estômagos vazios. Apenas 23 estômagos continham animais inteiros ou semi-digeridos (excluindo o isco) pertencentes aos peixes *Capros aper*, *Macrorhamphosus scolopax* e *Lepidopus caudatus* e ás lulas *Histioteuthis bonnellii* e *Taonius pavo*. Setenta e cinco otólitos de peixe e 207 bicos inferiores de cefalópodes foram identificados até ao género ou espécie. Considerando todos os fragmentos encontrados nos estômagos, incluindo otólitos, bicos de cefalópodes e cristalinos, foram encontrados 1411 peixes, 4 crustáceos e 261 cefalópodes. Aproximadamente 386 peixes estavam representados apenas por cristalinos. Foi encontrada uma média de 2.4 espécies (1.8 cefalópodes e 0.6 peixes) e 15.2 indivíduos por estômago. Restos de peixes foram encontrados em 83% dos estômagos analisados contribuindo em 84.5% dos animais da dieta. Restos de cefalópodes, foram encontrados em 75.7% dos estômagos e compunham 15.5% dos animais da dieta. As estimações dos pesos de peixes e cefalópodes, sugerem que os cefalópodes são, provavelmente, o grupo mais importantes na dieta de tintureira e, que são quase exclusivamente cefalópodes de flutuabilidade neutra meso- ou batipelágicos. Ocorrem pequenos cardumes de peixes epipelágicos e alguns

peixes bentónicos maiores. No total, a dieta é composta por, pelo menos, 11 espécies de peixe e 37 de cefalópodes. É apresentada a distribuição de comprimentos de bicos e otólitos. Um número de espécies de cefalópodes raramente capturadas são, também, importantes para a dieta. Não foram encontradas diferenças na dieta relacionadas com o tamanho ou sexo de *Prionace glauca*. Comparações com a dieta de espadarte e de cachalote da mesma região, sugerem claramente a existência de selecção na predação.

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INTRODUCTION

The blue shark (*Prionace glauca)* is the most abundant of the pelagic sharks in the North Atlantic (McKenzie & Tibbo 1964; Draganik & Pelczarski 1984). Little detailed work has been done on their food in the region.

Previous work on blue shark diet was on fish caught in the South-west of England (Stevens 1973), Bay of Biscay (Clarke & Stevens 1974), Southwestern Equatorial Atlantic (Hazin et al. 1994), Gulf of Alaska (Le Brasseur 1964), Central Pacific (Strassburg 1958), California (Tricas 1979; Harvey 1989), Eastern Australia (Dunning et al. 1993) and in the Indian Ocean (Gubanov & Grigor´yev 1975). The present analysis contains a more detailed consideration of the cephalopod beaks than in most previous work.

This analysis of their stomach contents from the Azores is the sixth part of a continuing programme to analyse the diets of large predators in the food web of Azorean waters. Previously, the diet of sperm whales (*Physeter catodon* L.), (Clarke et al. 1993), one *Kogia breviceps* (Martins et al. 1985), swordfish, *Xiphias gladius* (Clarke et al. 1995), *Loligo forbesi* (Martins 1982) and, the shearwater, *Caleonectris diomedea borealis* (Cory, 1881) (Hartog et al. 1996) have been described from the Azores.

This work should have value for understanding the role of fish and cephalopods in the food-web of the Azores as well as for a greater understanding of the diet of blue shark.

The sharks included here also provided data for studies on other aspects of their biology (Silva 1996).

MATERIALS AND METHODS.

Stomachs were collected from 195 blue sharks, caught by drifting long-lines near the surface during research fishing off the islands of the central group of the Azores during the period 10.93-28.7.94. The sampling area for the research fishing, carried out by R.V. "Arquipélago" (of the Department of Oceanography and Fisheries, University of the Azores), was near the two islands of the central group of the Azores, Faial and São Jorge (193 samples), and from Princess Alice Bank to the South of Pico Island (2 samples). Most samples were from three long line sets, two close to the coasts at the West end of São Jorge and to the North of Faial respectively and one farther from the coast, to the Southwest of Faial.

Line setting began at about 1700-1800h and hauling started at about 0800h the following morning.

The monthly distribution of the collection of samples (189 had the date recorded) was March (77 with food remains and 67 without) April (12 and 6), May (3 with), July (3 with), October (4 with and 8 without) November (2 with and 1 without) and December (5 with and 1 without). These reflect the seasonal presence of blue sharks in the area.

Precaudal lengths of the sharks were measured according to Compagno (1984). Stomachs were removed at sea immediately after capture and were deep frozen. After being thawed out in the laboratory, stomach contents were carefully sifted and sieved for all identifiable animal remains. General identification of flesh

and bone remains was followed by examination of otoliths and cephalopod beaks and the counting of the fish and cephalopod eye lenses. Methods used previously have been discussed elsewhere (CLARKE et al. 1995) and the same methods used for swordfish stomach contents have been applied here.

Estimates of the weights and lengths for the fish could only be very rough because otolith length to total wet weight relationships were only available for *Capros aper* and *Coelorhynchus coelorhynchus*. Rough estimates were obtained for some species by using relationships known for closely related species of the same genus (Table 1. given in SMALE et al 1995).

Estimates of the weights and mantle lengths (ML) of cephalopods were made from known relationships for the lower rostral length or, for octopods, the hood length (LRL, LHL) of each species or family found (CLARKE 1986). This could not be done for the octopods *Haliphron atlanticus* or *Japetella* because weights are not available. Standard lengths (from the longest arm tip to the apex of the mantle) were calculated from ratios obtained from drawings of the species in the literature (mainly reproduced by NESIS 1987).

Two *Trachurus* specimens, two *Illex* specimens and two *Illex* lower beaks were almost certain to have been from bait used in catching the sharks and were excluded from calculations.

RESULTS

GENERAL DESCRIPTION OF STOMACH CONTENTS

Eighty-three of the total samples (43.0%) were empty. The 112 *Stomachs* containing food remains averaged 152 cm in fork length (SD = 41.7 cm, range =105-280 cm). Sharks with no food remains averaged 173 cm. in fork length (SD = 41.3 cm, range = 107-296 cm).

Flesh remains occurred in 28.8% of stomachs with food (22.5% fish, 6.3% cephalopod). Otoliths occurred in 25.0% and cephalopod beaks occurred in 60.7%. 13.4% of the stomachs with food remains had only eye lenses.

Fish remains, including eye lenses, occurred in 83.0% of stomachs containing food and, excluding lenses, in only 34.8%. Cephalopod remains occurred in 70.5% and crustacean remains in only 3.6%. Two samples (1.6%) contained cephalopod but no fish remains at all but 51.7% contained cephalopod and no fish other than eye lenses. 20.5% contained both fish (excluding lenses) and cephalopod remains. The total number of fish represented by remains (including lenses) was 1411 and cephalopods was 256, a ratio of 5.5:1. The ratio of fish lenses to cephalopod lenses was 15.7:1. The number of fish otoliths was 75 and the number of cephalopod beaks was 422 giving a ratio of 1:5.6.

Fish (including lenses) comprised 84.5% and cephalopods 15.3% by number of all animals represented in the stomachs.

Fish averaged 0.8 species (SD = 0.6) and 15.2 individuals (SD = 23.0, 1-150) per stomach containing fish and 0.6 species and 12.6 individuals per stomach containing food.

Cephalopods averaged 2.4 species (SD = 2.1,1-11) and 3.2 individuals (SD = 3.15, range 1-16) per stomach containing cephalopods and 1.8 species and 2.3 individuals per sample with food.

SPECIES CONTRIBUTIONS

Flesh remains were all from the fish *Capros aper* (228 in 17 stomachs), *Macrorhamphosus scolopax* (160 in 6 stomachs) or *Lepidopus caudatus* (2 in 2 stomachs) and the cephalopods *Histioteuthis bonnellii* (3 in 3 stomachs) and *Taonius pavo* (1). Seventy-three of the 75 otoliths and 207 of the 225 cephalopod lower beaks were identified to genera or species.

Forty-four taxa comprising 11 fish, 31 cephalopods and two crustaceans were identified from otoliths, beaks, bones and flesh remains. The state of the crustaceans prevented specific identification but 2 shrimps and 2 isopods (which may have been parasites off fish) were present.

There was a mean of 2.4 species per stomach (SD = 2.2, range = 1-12) and a mean of 15.2 animals per stomach (SD = 22.3, range = 1-157).

FISH

Numerical composition of the fish are given in Table 1 including estimates of weight which are not accurate although of value for broad assertions. Most importantly, we have no data on *Lepidopus caudatus*, of which only pieces were present.

Capros aper contributed most (58.5%) of the fish represented by flesh remains (228 in 17 stomachs) as well as 57.3% of the otoliths. Only 31 fish were sufficiently complete to give accurate measurements and these had a peak of distribution at 50-60 mm (Fig. 1). Plots of eye lens diameters in two samples (Fig. 2) show that the great majority are from small fish, probably *Capros aper* or *Macrorhamphosus scolopax*. *Macrorhamphosus* comprised 41.0% (160 in 6 stomachs) of the fish represented by flesh but there were no free otoliths. One fish could be measured and this had a fork length of 73 mm. These percentages and occurrances suggest that *Capros aper* probably contributes more to the diet by weight than *Macrorhamphosus* but both are important. Both *Capros aper* and *Macrorhamphosus scolopax* occurred in sharks caught both near the coast and distant from it. *Coelorhynchus coelorhynchus* grows to 400-500 mm and estimates from otolith length show it to have probably contributed about one third of the weight of the *Capros aper* and *Macrorhamphosus scolopax* combined. *Lepidopus caudatus* only contributed 0.5% (2 in 2 stomachs) of the number of fish represented by flesh and no free otoliths.

Table 1

General information on samples, numbers and estimated sizes of fishes represented in stomach contents of blue shark.

		No.			WW (g)			Estimated lengths (mm)			Based
	Occ	Total	%	Mean	Mean	Total	%	Mean	Min	Max	upon
Capros otoliths	17	43	9.3	2.5	5.0	215.0	4.0				relationship
Capros flesh	17	228	49.0	13.4	5.0	1140.0	21.0	63.0	40.3	90.1	specimens
Coelorhynchus coelorhynchus	1	2	0.4		399.2	798.4	14.7	448.0	444.1	451.8	*C. simorhynchus*
Diaphus effulgens	2	2	0.4	1.0	2.6	5.1	0.1	57.7	55.2	60.2	*D. hudsoni*
Diretmus argentius	8	17	3.7	2.1	11.6	197.4	3.6	52.7	23.5	97.0	
Electrona risso	3	4	0.9	1.3	3.0	12.1	0.2	43.4	19.0	60.6	
Lepidopus flesh	2	2	0.4	1.0	240.0	480.0	8.8				guess
Macrorhamphosus flesh	6	160	34.4	26.7	7.0	1120.0	20.6				guess
Muraena helena	2	2	0.4	1.0	700.0	1400.0	25.8	-	-	-	similar otoliths
Nezumia aequalis	1	1	0.2	1.0	5.0	5.0	0.1	19.6	19.6	19.6	*N. micronychodon*
Sphyraena sp.	1	2	0.4	2.0	29.3	58.6	1.1	167.6	161.9	173.4	*S. acutipinnis*
Type A	2	2	0.4	1.0							
Total Fishes		465				5431.5	100.0				
No. of otoliths	111	75	15.5	0.7							
Fish lenses	78	2204		28.3							
Shark teeth	4	4		1.0							
No. identified fish		465									
No. of fish	93	1411		15.2							
No. of cephs	79	256		3.2							
Animals represented	110	1669		15.2							

No- number; Occ- occurrence; WW- wet weight; ML- mantle length.

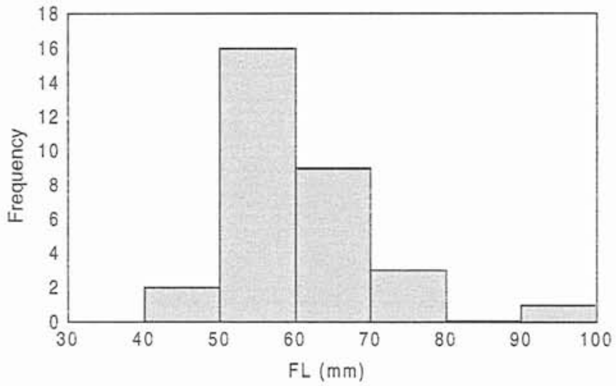

Fig. 1. *Capros aper* fork lengths.

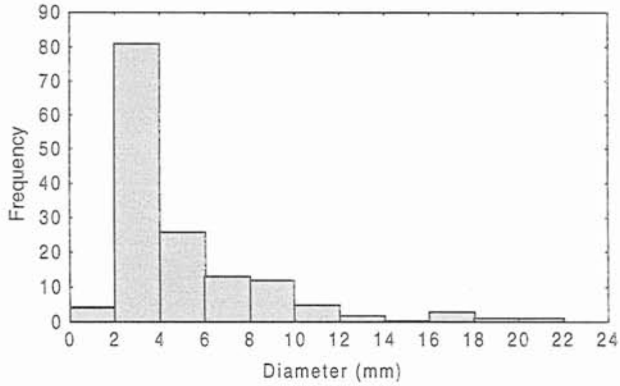

Fig. 2. Diameters of loose fish lenses randomly selected.

The pieces could not show the size of the fish but adults grow to over 2 m and in *Xiphias gladius* they averaged 239 g (CLARKE et al. 1995) which is used here in the absence of other data. Comparison with otoliths removed from fish show the otoliths of *Muraena helena* were from fish of about 700 g. *Nezumia aequalis*, *Diaphus effulgens* and *Electrona rissoi* otoliths are from small fish (estimated from SMALE et al. 1995).

Diretmus argentius has previously been regarded as rare in this area but was also found in swordfish stomachs (CLARKE et al. 1995). Its representation by 17 otoliths in 8 sharks suggests that it may be a popular and important minor constituent of the diet (SMALE et al. 1995).

CEPHALOPODA

Table 2 shows the numbers, occurrences and estimated weights (except for *Haliphron* and *Japetella*) contributed by the taxa identified in the collection of lower beaks from the stomachs of the blue shark. Over 37 different kinds of lower beak were recognised including 25 species which could be positively identified and several more which could be identified to genus. The beaks comprised 15 octopods in five families, one *Vampyroteuthis infernalis* and 209 teuthoids belonging to at least 12 families. 17 very small beaks left unnamed probably included *Brachioteuthis*, *Lycoteuthis*, *Abraliopsis* and *Helicocranchia* but these identifications were not positive and they were so small as to probably represent food of some larger species represented in the stomachs.

The collection is notable for the importance by number and occurrence of members of the Mastigoteuthidae (17.8% and 22.5% respectively), Chiroteuthidae (12.0% and 20.7%) and Grimalditeuthidae (6.2% and 9.0%), all families which are rarely caught in nets. The Histioteuthidae contribute the most of any family (31.1% by number, 39.6% occurrence). Species in families which are very rarely collected in nets are *Discoteuthis laciniosa* (Cycloteuthidae), *Valbyteuthis sp.*, *Grimalditeuthis richardi*, *Joubiniteuthis portieri*, *Octopoteuthis rugosa*, *Taningia danae* and *Haliphron atlanticus*. Estimates of weight do not include *Haliphron* and *Japetella*. While the latter is too small to make any difference to the overall conclusions, *Haliphron atlanticus* grows to considerable size and the beaks overlap in size the same species from sperm whale stomachs. As this species contributed ten large lower beaks and rough estimates from observations and one weighing of a buccal crown at sea by one of the authors (MRC) suggests that the individuals may each have weighed over 30 kg,

Table 2

Numbers, occurrences and estimated weights (except for *Haliphron* and *Japetella*) contributed by the cephalopods identified in the collection of lower beaks from the stomachs of the blue shark.

			No per shark when	Occ.		WW (g)			ML (mm)			Std l	N, E
	No	% No	cephs pres.	No	%	Total	%	Mean	Min	Max	Mean	Mean	
Histioteuthidae	70	31.1	8.1	44	39.6	5341.1	19.6	76.3					
Histioteuthis bonnellii	28	12.4	1.3	21	18.9	3056.6	11.2	109.2	25.2	107.9	45.6	146.0	N
H.celetaria	13	5.8	1.9	7	6.3	1147.3	4.2	88.3	19.1	81.0	57.9	185.1	N
Histioteuthis A	2	0.9	1.0	2	1.8	248.7	0.9	124.4	31.5	107.8	69.6	222.8	N
Histioteuthis B	17	7.6	1.9	9	8.1	411.2	1.5	24.2	8.6	61.9	31.9	102.2	N
H. reversa	10	4.4	2.0	5	4.5	477.3	1.7	47.7	35.3	59.7	51.4	164.4	N
Mastigoteuthidae	40	17.8	6.1	25	22.5	3936.5	14.4	98.4					
Mastigoteuthis sp.	14	6.2	1.8	8	7.2	1363.0	5.0	97.4	88.4	181.4	138.3	290.5	N
M. flammea	12	5.3	2.0	6	5.4	511.6	1.9	42.6	18.6	140.7	92.5	194.2	N
M. magna ?	1	0.4	1.0	1	0.9	340.0	1.2	340.0	204.7	204.7	204.7	429.8	N
M. hjorti	13	5.8	1.3	10	9.0	1721.9	6.3	132.5	18.6	164.0	120.3	252.7	N
Chiroteuthidae	27	12.0	5.3	23	20.7	1817.4	6.7	67.3					
C. imperator	5	2.2	1.0	5	4.5	395.6	1.4	79.1	131.3	145.9	137.4	508.3	N
Chiroteuthis A	1	0.4	1.0	1	0.9	54.3	0.2	54.3	128.8	128.8	128.8	476.6	N
Chiroteuthis B	3	1.3	1.0	1	0.9	63.3	0.2	21.1	87.2	101.9	93.8	346.9	N
C. veranyi	8	3.6	1.1	7	6.3	1239.5	4.5	154.9	123.9	192.4	163.5	604.9	N
Valbyteuthis	10	4.4	1.1	9	8.1	64.7	0.2	6.5	50.5	79.9	63.7	153.0	N
Grimalditeuthidae	14	6.2	1.4	10	9.0	180.1	0.7	12.9	70.1	89.7	79.5	139.2	N
Cranchiidae	12	5.3	6.3	18	16.2	1179.5	4.3	98.3					
Megalocranchia	1	0.4	1.0	1	0.9	196.6	0.7	196.6	419.6	419.6	419.6	587.5	N
Taonius pavo	8	3.6	1.1	7	6.3	612.7	2.2	76.6	233.4	350.1	315.9	410.7	N
Teuthowenia megalops	2	0.9	2.0	1	0.9	324.8	1.2	162.4	273.2	277.3	275.2	357.8	N
Liocranchia	1	0.4	1.0	1	0.9	45.5	0.2	45.5					N

this would suggest that this deep sea, near bottom species might provide most of the mass of the cephalopods. However, these octopods are extremely fragile and watery in consistency (the factor accounting for its very rare capture) and probably provides less nourishment than its size would suggest. In addition, The blue shark can dismember prey and morsels, including the beaks and may have bitten these off large prey. Excluding *Haliphron atlanticus* from the calculations, the Histioteuthidae contribute 19.7% by estimated wet weight. Of greater importance by weight are the Octopoteuthidae (30.7%). A histogram of estimated mean weights of all the cephalopod species (Fig. 3a) shows that most are less than 100 g in weight but *Taningia* is much larger with an estimated weight of over 3400 g.

Histograms of the lower rostral lengths of the commoner species show unimodal distributions (Figs 4 and 5).

Most of the cephalopod species are represented by only one lower beak per stomach. Up to 2 lower beaks occur in 5 species comprising *Grimalditeuthis*, *Teuthowenia*, *Taonius*, *Ancistrocheirus* and

Table 2 *continued*

Numbers, occurrences and estimated weights (except for *Haliphron* and *Japetella*) contributed by the cephalopods identified in the collection of lower beaks from the stomachs of the blue shark.

			No per shark when	Occ.		WW (g)			ML (mm)			Std l	N, E
	No	% No	cephs pres.	No	%	Total	%	Mean	Min	Max	Mean	Mean	
Ancistrocheiridae	9	4.0	1.1	8	7.2	4834.9	17.8	537.2	158.4	239.9	199.1	438.1	N
Octopoteuthidae	7	3.1	4.0	13	11.7	8303.8	30.5	.1186.3					N
Octopoteuthis rugosa	5	2.2	1.0	5	4.5	1067.4	3.9	213.5	69.0	195.9	155.6	326.7	N
Taningia danae	2	0.9	1.0	2	1.8	6821.9	25.1	3410.9	443.5	533.8	488.7	781.9	N
Onychoteuthidae	6	2.7	2.0	6	5.4	414.5	1.5	69.1					
Onychoteuthis banksi	5	2.2	1.0	5	4.5	344.1	1.3	68.8	129.7	141.9	134.6	201.9	
Onychoteuthis B	1	0.4	1.0	1	0.9	70.5	0.3	70.5	135.8	135.8	135.8	203.7	
Joubiniteuthidae	3	1.3	1.0	3	2.7	12.7	0.1	4.2	45.6	70.1	54.6	109.2	N
Cycloteuthidae. *Discoteuthis lacinosa*	2	0.9	1.0	2	1.8	311.4	1.1	155.7	155.0	158.1	156.6	360.1	N
Gonatidae	1	0.4	1.0	1	0.9	300.3	1.1	300.3	248.1	248.1	248.1	397.0	N. oil
Ctenopterygidae	1	0.4	1.0	1	0.9	57.7	0.2	57.7	89.5	89.5	89.5	143.2	
v. sm. squid spp.	17	7.6	1.6	11	9.9	20.0	0.1	1.2					
Vampyroteuthidae	1	0.4	0.5	2	1.8	370.0	1.4	370.0	90.7	90.7	90.7	254.0	N.Cl
Alloposidae	10	4.4	1.0	10	9.0			0.0			625.0	2000.0	N.Cl
Argonautidae	1	0.8	1.0	1	0.0	46.0	0.1	46.0	10.0	10.0	10.0	22.0	N.Cl.E.
Ocythoidae	2	1.6	1.0	2	0.0	130.0	0.4	65.0	20.0	20.0	20.0	58.0	N.Cl.E.
Bolitaenidae	2	0.9	1.0	2	1.8		0.0	0.0			55.5	94.4	N.Cl
TOTAL LOWER.	225	100.0	25.4	96	82.0	27.236.0	100.0	121.1					
with Haliphron						57.236.0							

No- number; Occ- occurrence; WW- wet weight; ML- mantle length; Std l- standard length; N-neutrally buoyant; E- epipelagic; Cl - chloride; v.sm.- very small.

Valbyteuthis. Up to 3 beaks occur in *Mastigoteuthis* and *Chiroteuthis* and up to 4 in *Histioteuthis.*

This probably reflects the shoaling habits of the species; possibly those which swim closer together are more susceptible to capture in groups.

GENERAL

A general appraisal of the information in Tables 1 and 2 suggests that the cephalopods contribute considerably more weight than the fish to the diet since, even without *Haliphron atlanticus*, the cephalopods exceed 27000 kg while, with some reasoned guesses, the fish are estimated to probably contribute less than 6000 g.

SIZE AND HABITS OF PREY TARGETED

Estimates of the mean standard lengths of the cephalopod species (Table 2) range between 22 mm and 781 mm and the estimated mean wet weights range from 1 to 3410 g (excluding *Haliphron atlanticus* at 2000 mm and 30000 g). Histograms of their size distributions (Fig. 3b)

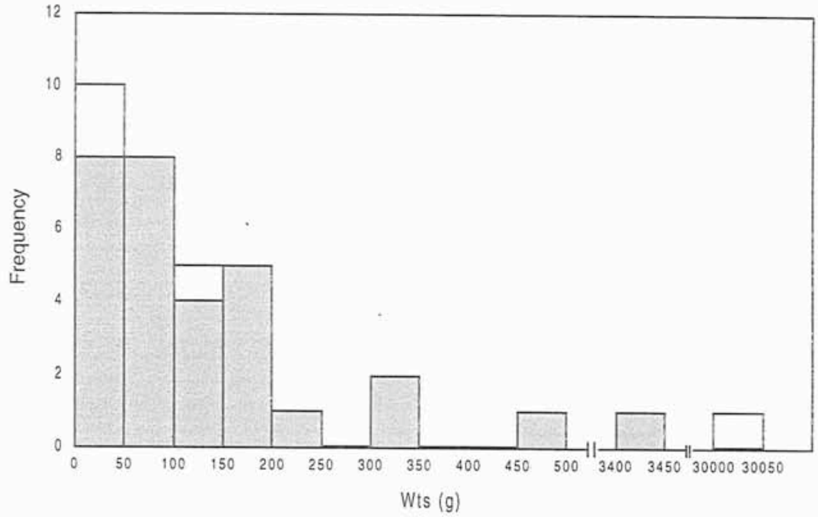

Fig. 3a. Distribution of the estimated mean weights of all cephalopods species (squids filled, octopods not filled).

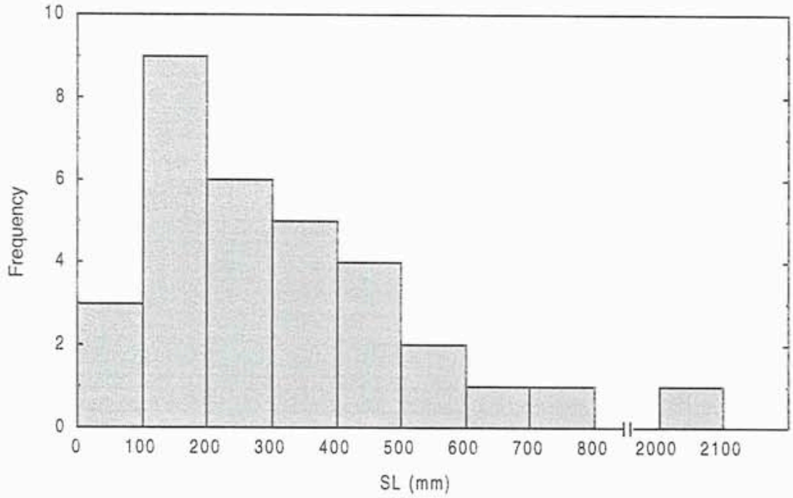

Fig 3b. Histogram showing the estimated mean standard lengths of cephalopods from stomachs of *Prionace glauca*.

show peaks at 100-200 mm and 1-100 g dropping to 700 mm and 250 g respectively and then just 2 and 4 species respectively at greater size. This may indicate a marked preference for small, although having the capacity to eat much larger, cephalopods. Only the *Onychoteuthis* and *Ctenopteryx* are not neutrally buoyant and slow swimming. This is achieved by Ocythoidae with an air bladder, *Gonatus* by an oily digestive gland, *Vampyroteuthis* and the octopods by sulphate replacement with chloride and the rest, "ammoniacal squids", by metallic ion replacement with ammonium ions.

Thus, these sharks seem to select slow-swimming cephalopods which hang fairly motionless in the water and require little speed or effort in their capture. While the odd shoal of small fish may be taken, the larger fish are rarer in the diet and some of these may be taken close to the bottom where mobility is restricted.

Sex of the Blue Shark and Diet

Thirty-two male and 56 female blue sharks containing food were sexed. The males averaged 152 cm (SD = 41.7, range 110-280 cm) in precaudal length and the females 153 cm (SD = 29.0, range 105-221 cm). Stomachs with contents weighed an average of 488 g (SD = 451.3, range 94-2424) in the males and 476 g (SD = 340.5, range 28-1705 g) in the females. Males had a mean of 15.4 animals (SD = 21.6) and 2.6 species (SD = 2.4) while females had 11.9 animals (SD = 12.8) and 2.7 species (SD = 2.2) represented in the stomachs having food. No significant differences between the food species of the two sexes could be detected.

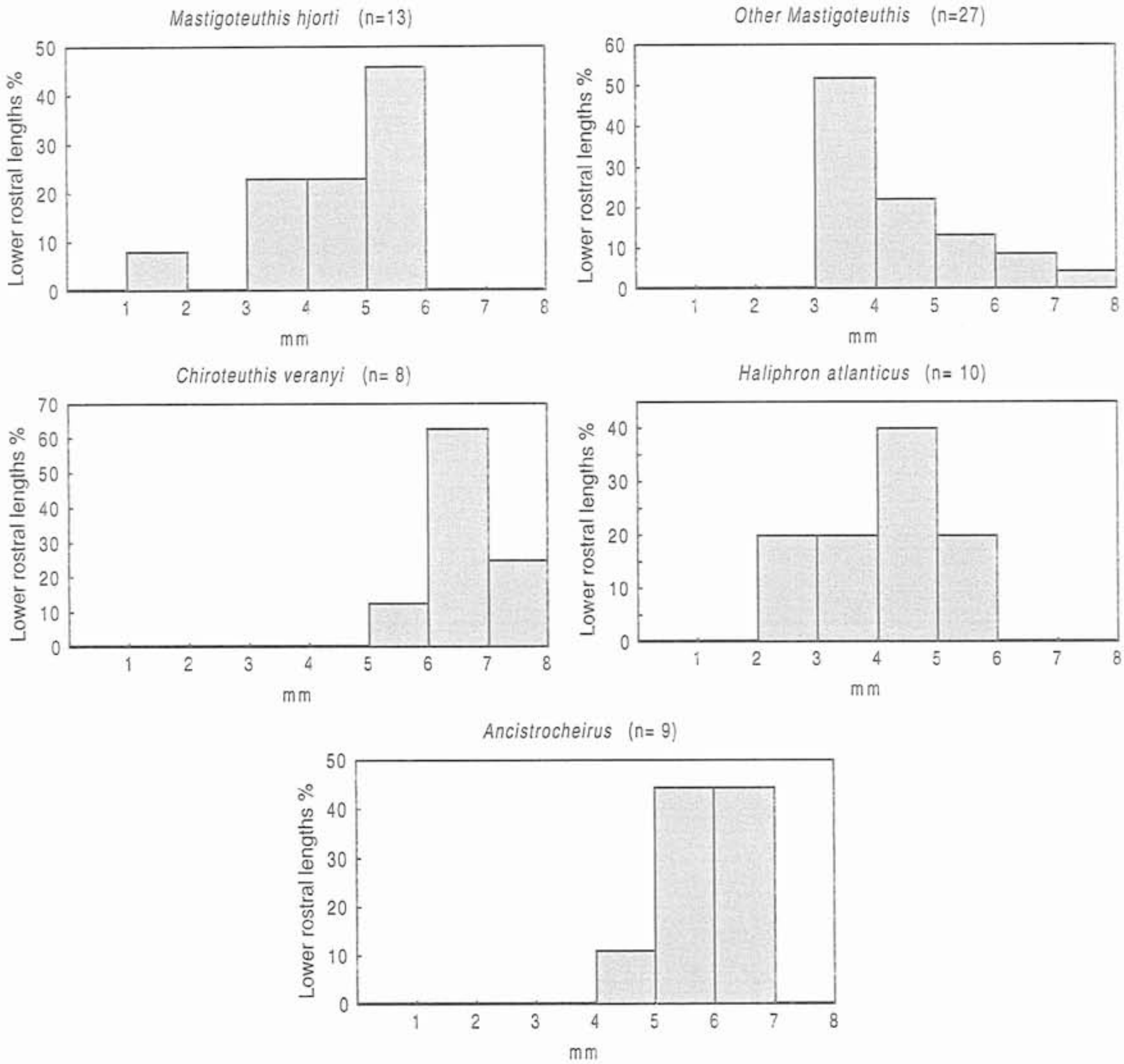

Fig. 4. Lower rostral lengths of the commoner beaks of cephalopods present in the stomachs of *Prionace glauca*.

SIZE OF THE BLUE SHARK AND DIET

To examine differences in diet attributable to the sizes of blue shark we compared the samples from 56 fish of 94-154 cm (mean 133.8 cm, SD = 14.8 cm) with those from 53 fish with fork lengths of 155-280 cm (mean = 186.6 cm, SD = 30.9 cm). Weight of stomach contents averaged 345 g (SD = 345.4 g) and 650 g (SD = 518.1 g) respectively. No significant differences between the small and large blue sharks were found in the species eaten, the number of fish, the number of cephalopods or the number of species.

DISCUSSION

METHODOLOGY

As with swordfish (CLARKE et al. 1995), there are considerable sources of error when comparing the ratios of fish to cephalopods in the diet. Thus,

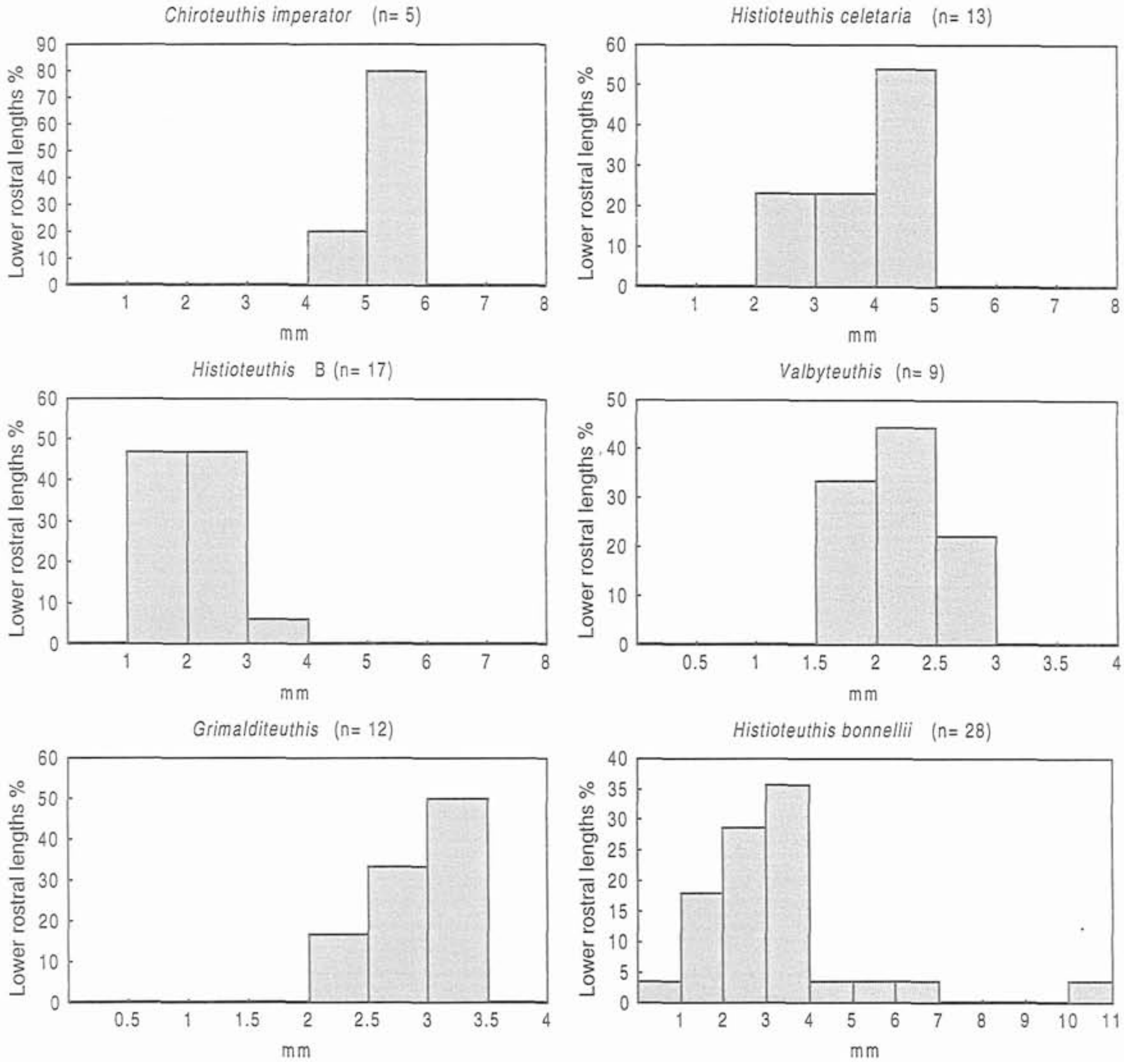

Fig. 5. Lower rostral lengths of the commoner beaks of cephalopods present in the stomachs of *Prionace glauca*.

while cephalopod beaks outnumbered otoliths by 5.6 to one, fish lenses often occurred in large numbers (up to 224) without being accompanied by, or with only very few, otoliths. Although it was previously pointed out that the ratios of fish to cephalopod lenses were of little value as evidence for the ratio of the groups in the food because cephalopod lenses broke up much more quickly in the stomach, it is useful to take the number of fish lenses into account as their presence may be the last remaining evidence of the presence of fish in the diet. Also they may suggest that elasmobranchs, which do not have otoliths, are important in diets although no other evidence was found here.

As shown before (CLARKE 1996) although otoliths and beaks in diet studies must be used with care, we believe the additional information they give well justifies their use. If only identifiable flesh were used for identification, only five instead of 11 species of fish and two instead of 27 species of cephalopod would have

been recognised. Computations from beak size can only give rough estimates but provide some guide to the relative importance by weight of the cephalopods. For the species occurring here, most relationships are reasonably accurate except for *Ocythoe*, *Haliphron*, *Discoteuthis*, *Valbyteuthis* and *Grimalditeuthis*, together only comprising 9.6% of the number of beaks and of these, only *Haliphron*, forms a substantial part of the diet by weight.

In determining the relative importance of fish and cephalopods from flesh, or beaks and otoliths, various problems arise. The flesh of many neutrally buoyant cephalopod species is digested much more rapidly than firm fish flesh; also, cephalopods have no bones, which take longer to digest than flesh. Equally, the much quicker disappearance of cephalopod eye lenses also biases their comparison towards fish. On the other hand, because some otoliths take only a few hours to digest (JOBLING & BREIRY 1986; HERNANDEZ-GARCIA 1995) and beaks show no signs of being digested and probably pass through the sharks' guts intact, their comparison tends to bias numbers towards cephalopods. In the blue shark the partially digested state of some of the otoliths and the large number of small fish eye lenses compared to the number of otoliths support the view that some otoliths have disappeared from the stomachs before examination. However, the effect on the otolith to beak ratio was probably not extremely large because of the close values of the ratios otoliths to beaks 1:5.6 (biased towards cephalopods), fish to cephalopod lenses 15.7:1 (biased towards fish) and fish to cephalopod flesh of 5.5:1 (biased towards fish). Perhaps we should ignore the lens data since cephalopod lenses certainly break up very much more quickly than fish lenses, and accept that the evidence from flesh and hardparts are biased in opposite directions by about the same amount. Halfway between the two may be near the truth although much more information comes from the hard parts.

PROXIMITY TO LAND AND REGIONAL COMPARISONS

The results of previous work on the diet of the blue shark show distinct differences depending on the region studied (Table 3) and the types of analysis employed.

The specific composition of fish and cephalopods in the samples varies greatly between areas, particularly for the fish. The closest similarity in the cephalopods to the Azores region is the Bay of Biscay (CLARKE & STEVENS 1974) where 92.6% of the species were neutrally buoyant and 5 species are the same as in the Azores. In Monterey Bay, California, five genera of deep, neutrally buoyant squids were the same as in the Azores. However, because the sharks were caught in coastal waters, they were also eating muscular *Loligo* and *Octopus*. Similarly, off Cornwall, U.K. remains of the muscular, neritic Sepiidae, Sepiolidae and Octopodidae constituted the diet (CLARKE & STEVENS 1974).

Oceanic samples showed a numerical dominance of cephalopods in the diet and samples near or on the Continental shelves showed a dominance of fish (STEVENS 1973) or even crustaceans (HARVEY 1989). Crustaceans are barely included in the diet off the Azores although they were very important in four years off California and no bird remains were found in stomachs here as sometimes found elsewhere (HAZIN et al. 1994). *Macrorhamphosus scolopax* and *Capros aper* were in both inshore and offshore localities.

PREDATOR COMPARISONS

Eighteen of the 40 species of cephalopods from stomachs of sperm whales caught off the Azores (CLARKE et al. 1993) also occurred in the blue shark diet of the area which comprised 27 identified species. Genera eaten by blue shark and swordfish but not found in stomachs of sperm whales in the region are *Argonauta*, *Ocythoe*, *Ctenopteryx*, *Valbyteuthis* and *Grimalditeuthis*. Squids of the last three genera are all too small to be likely targets of the whales and the first two may live rather too near the surface to be taken by the whales, all the food of which, is thought to live at considerable depths. Considering the importance of octopoteuthids to sperm whales (5.9% by number) it is interesting that they were

Table 3

Prionace glauca. Comparison of general results with the literature (No.-number. Occ.-occurrence; Vol.-volume; Wt.-weight; s.-same; f-family;.g-genera).

REGION	Group	No.%	Occ.%	Vol-wt%	Main food	S. taxa as here	No. spp.	No.	L. (cm)	% empty	Author
Azores	fish	84.5	15.7		*Capros*		9+	194	105-296	42.8	this paper
	cephalopods	15.3	3.24		*Alloposus/Taningia*		37+				
Bay of Biscay	fish				?			151	144-266	32 & 43	CLARKE & STEVENS 1974
	cephalopods		58		Cranchiidae	5 spp.	11				
English Channel	fish							12	81-180	100	CLARKE & STEVENS 1974
	cephalopods		22		Sepiidae	0	3				
SW Equatorial	fish	19	56		*Alepisaurus*			90	162-227	72	HAZIN et al. 1994
Atlantic	cephalopods	26	36								
California	fish	4	75-85	62.7 Vol	*Engraulis*	0	16	150	96-204	18	HARVEY 1989
	cephalopods	1.8	50-60	20.4 Vol	*Loligo*	6 gen	9				
					Euphausids (most of all)						
California	fish		75		*Engraulis*	0	8	81		6	TRICAS 1979
	cephalopods		76		*Histioteuthis/Loligo*	7 gen	13				
Gulf of Alaska	fish				Salmon	0	5	29	76-137	17	LE BRASSEUR 1964
	cephalopods										
Eastern Australia	fish				?						
	cephalopods				*Anchistrocheirus/Taningia*	8 gen	13	18			DUNNING et al. 1993

important in blue sharks (3.1% by number, 30.7% by weight (excluding *Haliphron*) although they were not found in the diet of swordfish. The great importance in the diet of mesopelagic and bathypelagic cephalopods, for example in the Histioteuthidae, Mastigoteuthidae, Chiroteuthidae and Alloposidae (over 94% by number), show that blue sharks forages for food much deeper than swordfish and it probably collects most of its food deeper than 500 m.

Although some of these have diel vertical migrations bringing them into the top 200 m at night (CLARKE & LU 1974, 1975; LU & CLARKE 1975a, 1975b) many of them, particularly those in the size range taken by the sharks, are not normally found shallower than 400 m. The cephalopod diet is in marked contrast to *Xiphias gladius* from the same area (CLARKE et al. 1995) in which only 26% of the lower beaks belong to species rarely, if ever, coming shallower than 400 m. CAREY & SCHAROLD (1990), by attaching transmitters to blue sharks, showed that they regularly swam to 400 m and one swam to 600 m and the large excursions were in daylight hours.

The fish remains from blue shark provide evidence which contrasts with that provided by the cephalopod beaks in that they include a high percentage (92.7%) of the epipelagic shoaling species *Capros aper* and *Macrorhamphosus scolopax* although the latter are also found near the bottom. These contribute 83% by number to the swordfish diet. Other species in the blue shark diet such as *Muraena helena*, *Coelorhynchus coelorhynchus* and *Lepidopus caudatus* were probably taken on or near the bottom. Although, numerically, the shallow living fish in the diets of both blue shark and blue shark are dominant (CLARKE et al. 1995), very rough estimates of weight suggest that the deeper fish species are at least as important for food.

In summary, the blue shark offshore probably collects the bulk of its food from depths greater than 500 m and even close to the bottom (*Haliphron atlanticus* has been filmed on the bottom. pers. commn R. Young). It also eats small shoaling fish at shallow depths and large bottom fish. *Xiphias gladius*, on the other hand, eats fewer deep cephalopods although it also goes deep for larger fish and also eats both shallow cephalopods and fish. This difference may be a reflection of the preference of swordfsih for muscular prey since 71.6% by number and 93.8 % by estimated weight of cephalopods are muscular contrasting with 3.6% and 2.9% respectively for blue shark Clearly the latter can deal easily with ammoniacal species of cephalopods in its diet.

The mean weight of the cephalopods in the diet of blue shark is 120 g, for swordfish is 224 g and for sperm whale is 923 g. The fish eaten by blue shark (mean 11.7 g) and swordfish (mean = 13.3 g) are certainly much smaller than in the sperm whale (R. CLARKE 1956). Comparison of the lower rostral lengths show that the shared species *Histioteuthis bonnellii*, *H. celetaria*, *H. reversa*, *Ancistrocheirus lesueuri*, *Chiroteuthis veranyi*, and *Haliphron atlanticus* are all smaller in blue shark than in the sperm whale. Other species common to the three predators are too few to show valid differences.

Differences between the cephalopods from these three predators, all caught around Faial and Pico, are so great (in species, size, and depth where they live) that we consider these comparison valid in spite of the sampling not being simultaneous.

Competition for food between these three predators off the Azores is reduced by the sperm whale targetting larger and probably deeper cephalopods than blue shark and the latter targetting more ammoniacal and fewer muscular cephalopods than swordfish

Concerning the question of whether these sharks can be considered oportunistic, sampling what they encounter, or selective (WETHERBEE et al. 1990) can be resolved by these comparisons with the other two predators. Totally different diets of the three species reflects their diving habits but also their acceptance or preference for ammoniacal cephalopods.

FOOD CONSUMPTION

If it is like other sharks studied, the blue shark probably feeds intermittently during the day or night (WETHERBEE et al. 1990). These samples, which were all from sharks caught at night, contain beaks, otoliths and eye lenses which had been in the stomach for some time and were, presumably, from a previous feeding period, as well as fairly recently consumed fish and cephalopods. This is consistent with the conclusion that the sharks ate the flesh remains on the night of capture (as they would have been more digested otherwise) and the other remains were from a period previous to capture, possibly the previous night, if they generally feed during a nocturnal activity cycle (WETHERBEE et al. 1990). The length of time between feeding periods would probably be sufficient to dissolve many of the smallest otoliths such as *Capros aper* but not those of the larger fish which would account for there being more identifiable flesh remains of *Capros* than of otoliths (228:43).

Estimates of the annual consumption of various other species of sharks (WETHERBEE et al. 1990) gives a range of estimate from 1.5-11.3 times the body weight per year. Perhaps consumption of the large and active the blue shark could be expected to be closer to the highest value and 10x seems reasonable. Landings of the shark in the Azores has averaged about 100t over the last few years although, because it was not deemed of commercial value, catches were probably far more than that. As a minimum estimate of weight of food consumed by a migrant population off the Azores (they may only spend 3 months in the region and they average 3yrs (SILVA 1996)) we might take 100x3x10/4 = 750 t as the annual consumption of the blue shark which is only a tenth of the estimate for swordfish of over 7280-8680t and one five hundredth of the estimate for sperm whales of over 373000 t (CLARKE 1995).

FUTURE

While several papers now show the considerable regional variation in the species eaten by the blue shark, there is no evidence for annual changes in any one place and in Monterey Bay the major components varied little over four years. This gives hope in the value of stomach content analysis for monitoring major, long-term changes in ecological balance within an area.

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