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International Council for the
Exploration of the Sea

CM 1998/M:26
On Impact of Cephalopods in the Food Chain
and Their Interaction with the Environment

THE ROLE OF CEPHALOPODS AS FORAGE FOR THE DEMERSAL FISH COMMUNITY IN THE SOUTHERN BAY OF BISCAY

by

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ABSTRACT

During annual autumn bottom-trawl surveys from 1988-1996, with the exception of 1989, 43.681 stomach contents of 27 demersal fish species were analysed. These species represent the trophic structure of demersal fish in the southern Bay of Biscay. A small part of their forage, 3% of the total prey volume and 0.66% of the total number of preys, comprises cephalopods, small (e.g. *Alloteuthis media, A. subulata, Rossia macrossoma* and some Sepiolidae), and large species (e.g. the squids *Illex coindetti, Todaropsis eblanae,* and *Loligo forbesi)*. In predator length ranges below 50 cm, the percentage of cephalopod prey did not reach 5 % of total volume. They are preyed on, in higher percentages, by *Lophius piscatorius, L. budegassa, S. canicula, Pagellus acarne, Raja montagui, Galeus melastomus* and *Aspitrigla cuculus*. Predators larger than 50 cm consume more cephalopods, 8 % of total volume, but only lophiids and elasmobranch fish feed on them, with consumption volume reaching 17% in large *L. piscatorius*. The different length-ranges of each cephalopod-consuming predator were noted, and the present paper uses data on abundance and distribution of predators and preys to obtain a general view of the energy transfer from cephalopods to demersal fish. This energy flow is represented by predator-prey relationships that vary from year to year.

Key words: predator-prey relationships, cephalopods, demersal fish, angler-fish, Cantabrian Sea

INTRODUCTION

Cephalopods are found as components of nekton in oceans all over the world, from the coast to the open sea, throughout the water column, especially on the continental shelf (Boyle, 1983). They are extremely voracious predators, and their carnivorous diet situates them at a relatively high trophic level (cf. Boyle 1983, compared with other molluscs). They are of great ecological and fishing importance, since they are the prey of marine mammals (Clarke, 1980), sea birds (Imber, 1975), and fish (Meyer and Smale 1991a,b); annual catch figures of some 2.5 million t (Caddy, 1995) reflect their impact on the fishery. However, the abundance and distribution of cephalopod species varies enormously from one place to another, and most of the literature on the role of this class as prey is either part of fishery assessments (Rosenberg *et al.*, 1990), or focuses on the diets of the classic cephalopod-eating predators, such as cetaceans (Clarke, 1980) and large epipelagic fish, e.g., sharks (Clarke and Stevens, 1974; Ebert *et al.*, 1992), tuna (Rancurel, 1976; Okutani and Tsukada, 1988), and swordfish (Toll and Hess, 1981). All of this research was carried out in certain cephalopod-rich areas.

In order to determine cephalopods' true importance in the marine food-chain, data must be collected on different areas regarding the class's trophic relationships with both its prey and its predators – not only with large predators that sample well, such as those cited in the previous paragraphs. Although publications on non-pelagic predators are scarce, Lipinsky *et al.* (1992) found that cephalopods make up an important percentage of the diet of groundfish around South Africa, and that this percentage is proportional to their abundance and availability as prey.

In ICES Division VIIIc, several projects have recently been conducted on the distribution (Olaso, 1990), taxonomy (Guerra, 1992), and biology of cephalopod species (González *et al.*, 1994). Little is known regarding their possible predators. The present paper addresses the importance of certain cephalopods in the diet of several demersal fish, and we relate their trophic consumption to data on their distribution and abundance.

MATERIAL AND METHODS

In order to determine the importance of cephalopods in the diet of demersal fish of the Cantabrian Sea and coasts off Galicia (Figure 1), stomach contents were analysed between 1988 and 1996, with the exception of 1989. The predator species were captured during the bottom trawl surveys conducted every autumn, and within the trophic structure demersal fish represented more than 90% of the biomass and 80% of the abundance in number of species. The methodology used in these surveys remained unchanged throughout this historical series. Trawling operations were carried out by day, at a speed of 3 knots. Hauls lasted 30 minutes, using a *baka* 44/60-type gear (ICES, 1996; Sánchez *et al.*, 1994) similar to those used by the Spanish fishing fleet in the region, but with a 20-mm mesh size in order to catch small specimens. In these surveys, a stratified random sampling design was applied to the entire area (ICES Divisions VIIIc and XIa, see Figure 1), covering depths of between 30 and 500 m (with special hauls as deep as 650 m) from the mouth of the River Miño (Spanish-Portuguese border) to the mouth of the River Bidasoa (Spanish-French border). The criteria for stratification of haul distribution were determined by selecting five biogeographical sectors and 100, 200 and 500 m isobaths, resulting in fifteen strata. The strategy used involved sampling the stratum in proportion to the surface area, as well as considering the number of ship-days available, which meant a mean of 110 hauls per survey. As an abundance index, the stratified mean catch in weight and number per 30-min. trawl was used, following the methodology described by Cochran (1971) and Grosslein and Laurec (1982).

Stomach contents were sampled on all the trawls from Cape Finisterre to Fuenterrabía, that is, excluding those from ICES Division IXa (see Figure 1). Once the fish had been sorted by species, weighed and measured, a certain number of specimens per size-range and species were set aside randomly, trying to cover a minimum sampling number of the priority species within the limits of available time and personnel (Bowman, 1982; Olaso, 1990). For these selected specimens, data were collected on their length to the nearest cm, gender, and stage of sexual maturity.

All stomachs of the samples were examined, and the number of empty stomachs was recorded. Up to 1993, stomachs that were empty and presented external signs of regurgitation (elongated, soft stomach, or traces of food in the mouth), or those that contained prey whose state of digestion indicated that they had been captured during the trawl, were omitted. From 1993, it was decided that the state of the gallbladder of all hake taken during the hauls should be examined, following Robb's criteria (Robb, 1992), in order to determine whether stomachs that were apparently empty had regurgitated their contents shortly before capture, or were truly empty; stomachs that contained prey captured during the haul (gallbladder not having been used) were considered empty. If the stomach contained food, the volume of its contents was measured in cm^3 with a trophometer (Olaso, 1990). Taxonomic identification of prey was as precise as possible, preferably to the species level, above all in fish, decapod crustaceans and cephalopod molluscs. However, given the common problems involved in clearly determining stomach content remains, preys often have to be classified in larger taxa groups. In cephalopods, superorders Decabrachia and Octobrachia as stated in Guerra (1992, after Fioroni, 1981) were used, since these two groups were much easier to identify than the classical identification among three different orders (Sepioidea, Teuthoidea and Octopoda). For each prey, percentage of total stomach volume was determined, noting state of digestion, number of specimens and size-ranges (minimum, maximum and median); where this was not possible, the size of hard parts of fish and decapod crustaceans were measured (e.g., otoliths). Methods used to assess the diet composition of each predator species (Hyslop, 1980) were frequency of occurrence, F; numerical percentage, N; and volume percentage, V. As is stated in Bowen (1983), N and F represent better the influence of predation on cephalopod preys, while V works better when assessing the importance of the prey within predator diet.

RESULTS

Between 1988 and 1996, with the exception of 1989, 43907 stomach contents of the 27 most abundant demersal fish species along the Galician and Cantabrian coasts were analysed. Their distribution by species, length and fullness state are summarized in Table I.

Table II illustrates the importance of cephalopod molluscs in the trophic web in the Cantabrian Sea and off Galicia between 1988 and 1996, and also in the ecosystem as abundance indices using data from the 1996 survey. Comparing the importance of cephalopods within the stomach contents with other taxa, it is observed that cephalopods are in third place in terms of volume after fish and crustaceans, but they only make up 3 % of total volume consumed, a small figure when compared with the 70% made up by fish or the 25% of crustaceans. In terms of number, cephalopods are even less important, being the sixth group with only 0.66 % of the total number of preys, after crustaceans (81%), fish (11%), echinoderms, polychaets and gastropod mollusks, all of which have percentages smaller than 2.5%. Regarding frequency, cephalopods appear in 2.3 % of the stomachs, while crustaceans appear in 69%, fish in 36% and polychaets in 4%, (the total is larger than 100% because many stomachs have more than one kind of prey). If we compare these results with those shown by abundance indices in the 1996 survey, we see that the importance of cephalopods as a class, particularly in terms of number (10.8%), is much larger in the ecosystem than in the demersal trophic web, while in volume/weight terms (4.7%) the difference is not so remarkable. But this is above all due to *Alloteuthis* being less accessible to predators than to the trawl gear, since their distribution of abundance is large at depths of less than 100 m. It must be taken into account that the strong pressure exerted by the fishery in the area has reduced the mean length of large predators, which are usually target species of the fleet.

Studying the results in greater detail within the cephalopod groups in the trophic web, we see that in volume the most important cephalopods are the Decabrachia (1.73%), with ommastrephidae and loliginidae standing out among them, and also the octopods, *Octopus* spp. and *Eledone cirrhosa*, (0.71%). Nevertheless, in terms of number, smaller cephalopods, such as *Alloteuthis* spp. and sepiolids are the most abundant. No single species stands out clearly, given that identification of stomach contents does not usually make it possible to reach the taxonomic level of species, and the remains usually have to be assigned to a larger taxa, this being the reason for the higher percentages of the undetermined decabrachia and undetermined cephalopods. These results are not so different to those from the 1996 survey catches, in which *Alloteuthis* spp. is the most abundant genus in number, while Ommastrephids and the white-spotted octopus are the most abundant in volume.

Regarding the importance of cephalopods within the diet of each predator, shown in volume and number in Table III and Table IV respectively, we can see that no predator can be considered specialised in cephalopod predation, not even in a particular length range. In volume, the species that consume more cephalopods are both species of angler-fish and lesser-spotted dogfish (*S. canicula*), but none of them reaches 10% of their total volume of consumption. By length ranges, some predators show a high percentage of cephalopods, but in some cases sample size is not enough to be sure of this result (e.g. John Dory smaller than 10 cm or redfish larger than 30 cm). Beside these anecdotal cases, white angler-fish larger than 50 cm feeds on cephalopods in 17.6% of the volume and *Raja montagui* in 11.4% between 30 and 50 cm. In numbers, percentages are even smaller. Lesser-spotted dogfish is the species which consumes the largest number of cephalopods (4% for the whole length distribution and 6% in fish larger than 50 cm), almost 3% of white angler-fish diet in number are cephalopods, 9% in the larger ones. For all other predators, cephalopod consumption is even less important, with values that do not reach 2.5% for all distributions and 5% within particular length ranges, except in some cases in which the sample size is too small for results to be considered significant. In general, predators prey more on cephalopods in larger length ranges than on the smaller ones. Cephalopods can also be considered more important in their diets, as deduced from the percentages in volume and number for the whole predator set, shown in the same tables.

Table V shows each cephalopod prey species as a percentage of the total number consumed by each predator species. Prey taxa have been grouped in larger taxa to reduce the bias produced by undetermined items and the small number of some prey species. This table attempts to summarise the importance of each predator consumption for each prey group and, as stated previously, results are therefore shown only in terms of number. As is clear from the results, lesser-spotted dogfish is the most important predator for several cephalopod groups, such as ommastrephids, sepiolids, and the group comprising *Octopus* spp. and white-spotted octopus, beside the two undetermined groups of Decabrachia and Octobrachia and the total cephalopod class. Megrim (*L. whiffiagonnis*) is the second predator in importance for the total cephalopod class, as well as for the total Decabrachia group and ommastrephids; it is also the main predator of Sepiids with 50% of the total sepiids number. Hake is the main predator of *Alloteuthis* spp. and the second of *Loligo* spp. Nevertheless, white angler-fish, the predator with the highest volume percentage of cephalopods in its diet, is not so important as a predator of cephalopods, given that it mainly preys on large species such as ommastrephids, octopus or white spotted octopus, which make up a remarkable volume percentage but are not so important in number.

Figure 2 and Figure 3 represent the correlation between cephalopod yearly abundances within stomach contents and surveys in terms of number and volume-weight respectively. There is no clear relationship between the two abundances in number terms, as is shown in the plots and Pearson's coefficients. Volume-weight abundances seem to be more correlated, at least for *Alloteuthis* spp., *Loligo* spp. and Ommastrephids.

DISCUSSION

According to the results of our work, cephalopods do not play an important role as forage of demersal fish in the Cantabrian Sea and off Galicia, and no predator is specialised in this group.

Their scarce presence, in both number and volume in stomach contents, as well as the comparison of these results with the abundance from surveys, indicate that their importance in the demersal fish food web is lesser than it is in the ecosystem. This difference is likely to be even greater considering Clarke's (1983) assertion on the poor results of nets in the open ocean for cephalopod sampling. These results agree with those from similar studies carried out with demersal fish in other areas (Armstrong, 1982; Du Buit, 1968; Gibson and Ezzi, 1987; Gotshall, 1969; Meyer and Smale, 1991b) and only differ with the results of Lipinski et al. (1992), who found an important predation of cephalopods in a set of demersal fish predators including *Merluccius capensis*, some ray species or angler fish. Our results also contrast with the role of cephalopods for many large epipelagic fishes (swordfish, tuna, istiophorids), sharks and cetaceans, or even marine birds (see introduction references). This fact is surprising considering the abundance of this class in the demersal ecosystem and its nutritional energy, reasons which may be explained by cephalopods' defensive adaptations and habits (ink-ejection, cryptic colouring together with the wait and capture behaviour of many sepiids, sepiolids or octopods, schooling behaviour in ommastrephids and loliginids (Clarke, 1966), and their own aggressive and predatory habits).

The large size of many cephalopods, compared with the size of most of the predators, could be another reason for the low presence of cephalopods in demersal fish diet, given that large predators are the ones that prey more on cephalopods. In all likelihood many predators of small or medium size cannot capture large cephalopods, and are constrained to prey only on the smaller ones. It must also be taken into account that the predators analysed beolng to soft bottoms. Pereda & Olaso (1990) find that the diets of hake and monk in hard bottoms are more diverse and present larger sized preys, and that monkfish consume more cephalopods than in soft bottoms. As a matter of fact, the small *Allotheutis* spp. is the prey that appears in

most predators, 16, whereas large cephalopods, such as ommastrephids or *Loligo* spp. appear in only 4 and 7 predators respectively, all of them large or medium-large. There are seasonal abundance variations of some cephalopods, such as ommastrephids, but according to González et *al.* (1994) autumn is the moment when they enter the fishery, and therefore this factor should not be important to the results of this study. Beside that, Velasco and Olaso (in press) in a study of the seasonal diet of hake, the third cephalopod consumer and one of the main predators in the ecosystem, did not find any seasonal change in the consumption of cephalopods throughout the year, which remains very small in all seasons.
Lesser-spotted dogfish's important role as cephalopod predator in terms of number may also be related to its scavenging behaviour (Olaso *et al*, in press; Kaiser and Spencer, 1995), and probably many of the cephalopods preyed on by dogfish are individuals damaged or killed by bottom-trawling, which have been left on the bottom or discarded from fishing vessels. This fact is supported by the high percentage of the total of undetermined, and therefore highly digested, cephalopods found in dogfish stomachs (51.7%). This explanation probably also works for some other fishes that are not fast swimmers and consume an important part of some normally fast-swimming cephalopods which are already dead or injured on the seabed, as is the case of rays' consumption of ommastrephids and undetermined dechabrachia.

Clarke's idea of estimating cephalopod abundance from predation (Clarke, 1983) does not look suitable in most demersal ecosystems. (Lipinski *et al.* (1992) found that demersal predators from South African waters prey on cephalopods depending on their abundance and availability). This is especially true in the case of the area studied; the poor correlations between number percentages in the stomachs and survey number abundances suggest that demersal predators are quite poor samplers of cephalopods, especially compared with cetaceans, such as sperm whales. The high correlations between volume percentages in stomach contents and weight abundances in surveys are difficult to explain, since those relationships would be logical if weight survey abundances were due to the catch of larger cephalopods rather than to a larger catch in terms of number. Nevertheless, Pearson coefficients between the survey's weight and number abundances are high (0.93 for *Alloteuthis* spp., 0.95 for *Loligo* spp. and 0.89 for ommastrephids), and therefore no causal relationship between stomach volume percentages and survey abundances can be deduced.

Therefore, with the results of this study and comparing them with the works on cephalopod feeding habits within the area (Gonzalez et al., 1994; Guerra and Rocha 1994), we can conclude that cephalopods, especially the larger ones, are more important as predators than as forage prey for demersal fish in the demersal trophic web of the Cantabrian Sea and off Galicia. Also, demersal fish do not seem to be important predators of cephalopods, but rather an important part of their consumption due to scavenging. Only smaller cephalopods, such as *Alloteuthis* spp or sepiolids, are preyed on by an important number of the fish studied, while larger ones, such as ommastrephids or *Loligo* spp. are preyed on by large fishes, such as angler fish or hake.

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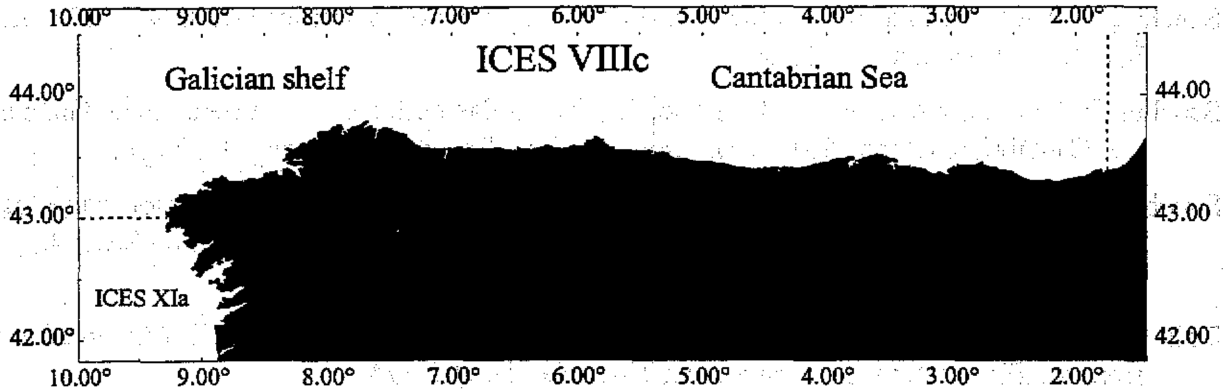

Figure 1.- Area covered in the study, only ICES Division VIIIc was covered in stomach sampling.

Table I.- Number of empty, full and regurgitated stomachs analysed, and the length range per predator species.

Predator species	Empty	Full	Regurgitated	Total	Length range
Antonogadus macrophtalmus	140	461	5	606	7-19
Aspitrigla cuculus	343	879	31	1253	9-39
Aspitrigla obscura	180	252	3	435	11-33
Callionymus lyra	197	427	1	625	11-32
Conger conger	596	1213	40	1849	16-192
Eutrigla gurnardus	356	641	15	1012	9-36
Galeus melastomus	59	331	0	390	14-76
Helicolenus dactylopterus	77	154	4	235	9-41
Lepidorhombus boscii	2649	5502	39	8190	5-44
Lepidorhombus whiffiagonis	2034	3063	16	5113	7-54
Lophius budegassa	378	286	78	742	5-80
Lophius piscatorius	852	546	89	1487	6-114
Merluccius merluccius	3237	3285	1279	7801	7-78
Micromesistius poutassou	3653	2954	16	6623	10-38
Mullus surmuletus	38	251	0	289	9-42
Pagellus acarne	169	429	9	607	15-37
Phycis blennoides	152	393	84	629	9-55
Raja clavata	37	402	0	439	13-99
Raja montagui	25	191	0	216	21-91
Raja naevus	92	78	0	170	19-84
Scomber scombrus	71	150	1	222	15-44
Scyliorhinus canicula	392	2475	6	2873	12-75
Trigla lucerna	70	149	11	230	15-72
Trigla lyra	52	184	11	247	9-46
Trisopterus luscus	114	619	7	740	10-54
Trisopterus minutus	121	383	13	517	8-32
Zeus faber	159	196	12	367	6-58
Total	16243	25894	1770	43907	

Table II.- Prey composition for the whole predator set between 1988 and 1996 (with the exception of 1989). F, N, V Indices. Abundance indices from 1996 survey in number and biomass.

	Stomachs			Surveys	
	F	N	V	% No./haul	% Kg/haul
CEPHALOPOD MOLLUSCS	2.34	0.66	3.06	10.78	4.74
Decabrachia	1.19	0.34	1.73	10.54	3.63
Histioteuthidae: *Histioteuthis* spp.	0.01	0.00	0.03	-.--	-.--
Loliginidae	0.41	0.13	0.44	8.59	0.78
Alloteuthis media	0.10	0.03	0.04	8.36	0.38
Alloteuthis subulata	0.03	0.01	0.02	0.08	0.01
Alloteuthis spp.	0.25	0.08	0.13	-.--	-.--
Loligo spp.	0.04	0.01	0.25	0.15	0.39
Ommastrephidae	0.07	0.02	0.62	1.57	2.63
Illex coindetii	0.02	0.00	0.25	0.15	0.43
Todarodes sagittatus	-.--	-.--	-.--	0.02	0.05
Todaropsis eblanae	0.02	0.00	0.15	1.41	2.15
Ommastrephidae indeterminados	0.03	0.01	0.22	-.--	-.--
Sepiidae	0.13	0.04	0.06	0.10	0.14
Sepia elegans	0.02	0.00	0.00	0.06	0.01
Sepia officinalis	0.00	0.00	0.00	0.03	0.12
Sepia orbignyana	0.03	0.01	0.02	0.01	0.01
Sepiidae indeterminados	0.08	0.02	0.03	-.--	-.--
Sepiolidae	0.36	0.10	0.18	0.26	0.09
Rossia macrosoma	0.03	0.01	0.07	0.03	0.06
Sepiola spp.	0.03	0.01	0.01	0.23	0.03
Sepiolidae indeterminados	0.30	0.08	0.10	-.--	-.--
Decabrachia indeterminados	0.22	0.06	0.41	-.--	-.--
Octobrachia	0.25	0.07	0.94	0.24	1.11
Bathypolypodinae: *Bathypolipus* spp.	0.01	0.00	0.00	0.00	0.00
Eledoninae: *Eledone cirrhosa*	0.01	0.00	0.02	0.23	1.00
Octopodinae	0.02	0.00	0.50	0.01	0.10
Octopus defilippi	0.01	0.00	0.10	0.00	0.02
Octopus vulgaris	0.01	0.00	0.40	0.01	0.08
Octopus spp. & *E. cirrhosa* undeterminated	0.22	0.06	0.19	-.--	-.--
Opisthoteuthidae: *Opistotheuthis agassizi*	0.00	0.00	0.22	-.--	-.--
Cephalopoda indeterminados	0.92	0.25	0.39	-.--	-.--
CRUSTACEANS	69.24	81.42	24.51	17.97	10.35
FISH	35.86	11.16	70.36	69.26	83.81
ECHINODERMS	1.09	2.26	0.27	1.63	0.49
ALGAE	0.05	0.01	0.02	-.--	-.--
POLYCHAETA	4.10	1.74	1.02	0.05	0.01
BIVALVE MOLLUSCS	0.34	0.18	0.04	0.00	0.01
CNIDARIA	0.05	0.01	0.03	0.17	0.13
GASTROPOD MOLLUSCS	0.95	1.12	0.13	0.06	0.09
PORIFERA	0.00	0.00	0.00	0.00	0.00
SIPUNCULIDS	0.21	0.06	0.12	-.--	-.--
TUNICATA	0.29	0.39	0.18	0.00	0.00
OTHERS (Mud, stones, plastics..)	0.91	0.96	0.25	0.08	0.38

Table III.- Cephalopod volume percentage in each predator. Arranged in total percentage order. (in brackets the number of predators with food sampled where less than 30)

Predator /Length range	<10	10-14	15-19	20-29	30-49	>50	Total
L. piscatorius	(6) *0.00	0.00	0.32	[illegible] 5.32	2.15	[illegible]	8.04
S. canicula	--	(7) *12.20	7.09	3.29	2.91	5.09	6.01
L. budegassa	0.00	1.75	7.23	0.00	5.29	7.20	5.41
P. acarne	--	--	(16) *0.00	6.47	2.75	--	4.29
R. montagui	--	--	--	(30) *1.76	11.49	1.93	4.24
A. obscura	--	(16) *0.00	(23) *0.00	3.84	--	--	3.45
G. melastomus	--	--	3.73	6.41	0.95	(25) *3.25	3.19
H. dactylopterus	--	3.48	0.00	0.49	[illegible]	--	1.91
M. poutassou	--	1.17	0.74	2.31	(16) *0.30	--	1.84
L. whiffiagonis	(7) *0.00	0.00	3.05	1.05	2.51	--	1.82
R. clavata	--	--	(5) *0.00	1.14	2.38	1.56	1.67
A. cuculus	--	0.63	0.92	1.79	0.27	--	1.42
E. gurnardus	--	0.15	0.38	2.11	(8) *0.00	--	1.35
C. conger	--	--	(1) *0.00	(9) *0.00	0.66	1.79	1.29
M. merluccius	3.01	2.95	2.01	0.06	0.10	9.01	1.05
T. luscus	--	(17) *0.00	0.00	1.40	0.00	--	0.88
R. naevus	--	--	--	(6) *0.00	0.00	1.13	0.85
M. surmuletus	--	0.62	0.00	0.59	(24) *0.70	--	0.58
A. macrophtalmus	(16) *0.00	0.00	1.86	--	--	--	0.54
C. lyra	--	(4) *0.00	0.00	0.61	--	--	0.43
T. lyra	--	0.59	(4) *0.00	(26) *0.00	(23) *0.00	--	0.24
T. minutus	--	0.27	0.00	0.54	--	--	0.21
Z. faber	[illegible]	0.00	(25) *5.13	0.14	0.00	(10) *0.00	0.20
L. boscii	0.00	0.17	0.22	0.19	0.07	--	0.18
P. blennoides	--	0.00	0.00	0.00	0.00	--	0.00
S. scombrus	--	--	0.00	0.00	0.00	--	0.00
T. lucerna	--	0.00	0.00	0.00	0.00	0.00	0.00
Total (all predators)	3.65	1.76	1.31	1.09	1.35	7.99	3.06

Table IV.- Cephalopod number percentage in each predator. Arranged in total percentage order. (in brackets the number of predators with food sampled whereless than 30).

Predator/length range	5-9	10-14	15- 19	20 -29	30 -49	50-192	TOTAL
S. canicula	--	(7) *5.88	2.70	2.63	2.96	5.99	4.01
L. piscatorius	(6) *0.00	0.00	1.16	1.57	4.23	8.79	2.93
H. dactilopterus	--	3.81	0.00	1.32	(4) *20.00	--	2.41
L. budegassa	0.00	2.13	2.38	0.00	2.34	4.44	2.17
Z. faber	(3) *33.33	0.00	(25) *10.53	1.16	0.00	(10) *0.00	2.03
G. melastomus	--	--	2.76	1.67	1.54	(25) *1.43	1.75
R. montagui	--	--	--	0.71	2.03	1.88	1.72
C. conger	--	--	(1) *0.00	(9) *0.00	1.18	1.91	1.43
R. naevus	--	--	--	(6) *0.00	0.00	3.41	1.33
M. merluccius	0.91	1.09	2.10	0.38	0.42	(31) *2.27	1.06
R. clavata	--	--	(5) *0.00	0.50	1.48	0.81	0.91
L. whiffiagonis	(7) *0.00	0.00	0.82	0.56	2.20	--	0.83
A. cuculus	--	0.45	0.18	0.62	0.47	--	0.48
P. acarne	--	--	(16) *0.00	0.44	0.41	--	0.42
M. surmuletus	--	0.50	0.00	0.32	(24) *0.71	--	0.33
A. obscura	--	(16) *0.00	(23) *0.00	0.39	--	--	0.30
M. poutassou	--	0.06	0.06	0.39	(16) *1.18	--	0.21
T. luscus	--	(17) *0.00	0.00	0.38	0.00	--	0.21
T. lyra	--	0.23	(4) *0.00	(26) *0.00	(23)* 0.00	--	0.18
E. gurnardus	--	0.07	0.11	0.30	(8) *0.00	--	0.15
C. lyra	--	(4) *0.00	0.00	0.20	--	--	0.12
L. boscii	0.00	0.04	0.11	0.13	0.24	--	0.11
T. minutus	--	0.42	0.00	0.27	--	--	0.11
A. macrophtalmus	(16) *0.00	0.00	0.28	--	--	--	0.07
P. blennoides	--	0.00	0.00	0.00	0.00	--	0.00
S. scombrus	--	--	0.00	0.00	0.00	--	0.00
T. lucerna	--	0.00	0.00	0.00	0.00	0.00	0.00
Total (all predators)	0.51	0.43	0.26	0.44	1.30	3.66	0.66

Table V.- Each cephalopod prey species as a percentage of total number consumed by each predator species of the set studied.

	Histioteuthis spp.	*Alloteuthis* spp.	*Loligo* spp.	Ommastrephid.	Sepiidae	Sepiolidae	Decabrachia undet.	Total Decabrach.	*Bathypolipus* spp.	*Octopus* spp. + *E. cirrhosa*	*Opistoteuthis* sp.	Total Octobrachia	Cephalopods undet.	TOTAL
S. canicula	33.33	7.83	0.00	41.18	13.89	35.92	34.48	22.90	50.00	47.76	0.00	47.14	51.57	36.92
L. whiffiagonis	0.00	17.39	0.00	17.65	50.00	8.74	8.62	15.94	50.00	0.00	0.00	1.43	7.87	11.36
M. merluccius	0.00	24.35	30.77	5.88	8.33	7.77	3.45	13.33	0.00	4.48	0.00	4.29	6.30	9.72
M. poutassou	33.33	12.17	0.00	5.88	0.00	11.65	8.62	9.57	0.00	4.48	0.00	4.29	5.12	7.32
P. acarne	0.00	6.09	7.69	0.00	2.78	0.00	3.45	3.19	0.00	8.96	0.00	8.57	4.33	4.19
C. conger	0.00	4.35	0.00	0.00	0.00	0.97	3.45	2.32	0.00	5.97	0.00	5.71	5.91	4.04
A. cuculus	0.00	0.87	0.00	0.00	2.78	10.68	1.72	4.06	0.00	5.97	0.00	5.71	2.76	3.74
R. montagui	0.00	9.57	38.46	5.88	0.00	0.97	0.00	5.80	0.00	1.49	0.00	1.43	1.18	3.59
R. clavata	0.00	7.83	7.69	0.00	0.00	0.00	13.79	5.22	0.00	1.49	0.00	1.43	1.57	3.44
L. piscatorius	33.33	0.87	0.00	5.88	2.78	2.91	8.62	3.48	0.00	7.46	100.00	8.57	1.18	3.14
G. melastomus	0.00	0.00	0.00	0.00	5.56	0.97	5.17	1.74	0.00	5.97	0.00	5.71	3.15	2.69
L. boscii	0.00	0.87	0.00	0.00	5.56	6.80	1.72	3.19	0.00	1.49	0.00	1.43	1.57	2.39
L. budegassa	0.00	1.74	0.00	17.65	2.78	0.00	1.72	2.03	0.00	0.00	0.00	0.00	0.39	1.20
E. gurnardus	0.00	0.00	0.00	0.00	0.00	4.85	1.72	1.74	0.00	0.00	0.00	0.00	0.39	1.05
A. obscura	0.00	0.00	0.00	0.00	2.78	4.85	0.00	1.74	0.00	0.00	0.00	0.00	0.00	0.90
H. dactylopterus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.36	0.90
M. surmuletus	0.00	0.00	0.00	0.00	0.00	1.94	0.00	0.58	0.00	4.48	0.00	4.29	0.39	0.90
T. luscus	0.00	0.87	0.00	0.00	2.78	0.97	0.00	0.87	0.00	0.00	0.00	0.00	1.18	0.90
Z. faber	0.00	2.61	0.00	0.00	0.00	0.00	0.00	0.87	0.00	0.00	0.00	0.00	1.18	0.90
R. naevus	0.00	1.74	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.39	0.45
C. lyra	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.58	0.00	0.00	0.00	0.00	0.00	0.30
T. minutus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.30
A. macrophtalmus	0.00	0.87	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.15
T. lyra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.15
TOTAL NUMBER	3	115	13	17	36	103	58	345	2	67	1	70	254	669

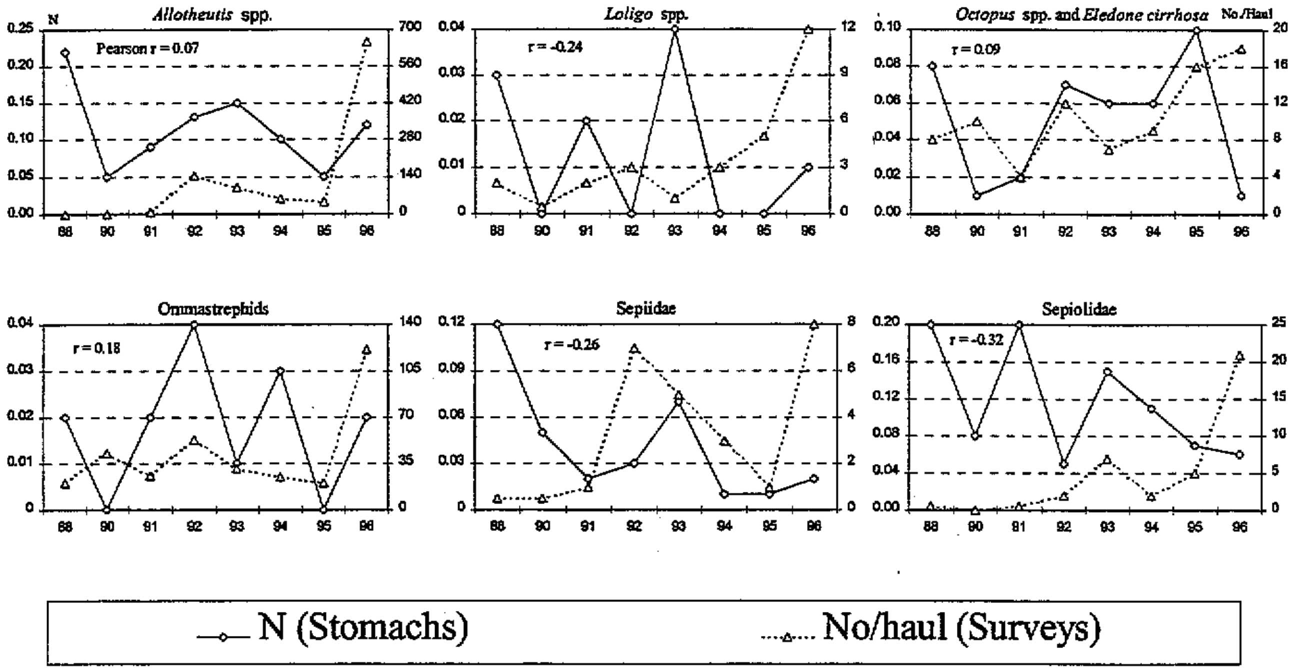

Figure 2.- Plots of main cephalopod prey group number percentage in stomach sampling and survey number abundance in number per 30-min. haul.

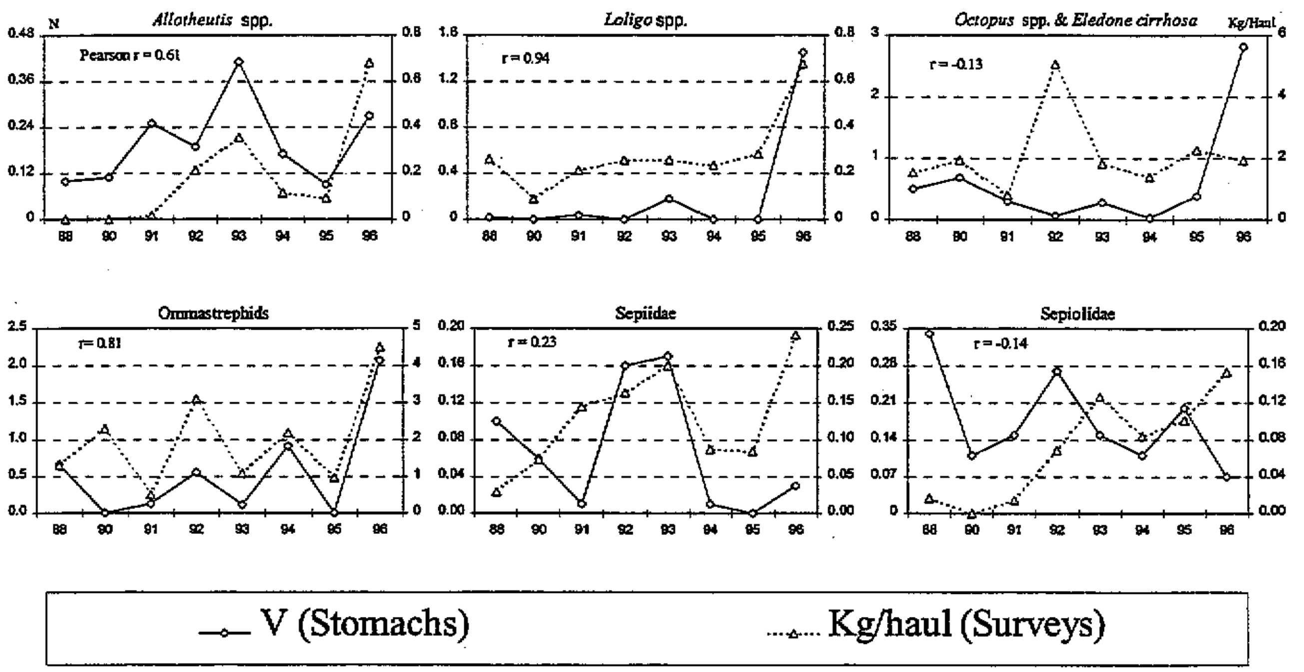

Figure 3.- Plots of main cephalopod prey group volume percentage in stomach sampling and survey weight abundance in kg per 30-min. haul.

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