SCI. MAR., 54(4): 375-388 1990

The diet of *Sepia officinalis* (Linnaeus, 1758) and *Sepia elegans* (D'Orbigny, 1835) (Cephalopoda, Sepioidea) from the Ría de Vigo (NW Spain)*

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SUMMARY: The stomach contents of 1345 *Sepia officinalis* and 717 *Sepia elegans* caught in the Ría de Vigo have been examined. The feeding analysis of both species has been made employing an index of occurrence, as other indices gave similar results. The diet of both species is described and compared. Cuttlefish feed mostly on crustacea and fish. *S. officinalis* shows 40 different items of prey belonging to 4 groups (polychaeta, cephalopods, crustacea, bony fish) and *S. elegans* 18 different items of prey belonging to 3 groups (polychaeta, crustacea, bony fish). A significant change occurs in diet with growth in *S. officinalis*, but not in *S. elegans*, within the range studied. The variety of prey decreases with increase in size of *S. officinalis*, but not in *S. elegans*. Differences in feeding habits of male and female *S. officinalis* were not observed at any size, but were found in *S. elegans*. The feeding intensity of females increases with sexual maturity in *S. officinalis* but not in *S. elegans*. No seasonal changes in diet were found in absolute values and in order of importance of the prey clusters. *S. officinalis* fed on a wider variety of prey than *S. elegans*. The value and significance of some indices employed in feeding ecology is discussed.

Key words: Cephalopods, feeding, *Sepia officinalis*, *Sepia elegans*, Ría de Vigo.

RESUMEN: DIETA DE *SEPIA OFFICINALIS* Y *SEPIA ELEGANS* EN LA RÍA DE VIGO (NO DE ESPAÑA). — *Se estudia la alimentación de 1345 Sepia officinalis* y 717 *Sepia elegans*, capturadas en la Ría de Vigo, a partir de sus contenidos estomacales. Distintos índices alimentarios dieron informaciones similares por lo que se usa el Índice de Ocurrencia de presas en la descripción de la dieta de ambas especies. Los peces teleósteos y los crustáceos son las presas principales de las dos sepias. *S. officinalis* presenta 40 tipos de presas pertenecientes a 4 phyla (Anélidos: poliquetos; Moluscos: cefalópodos; Artrópodos: crustáceos; Cordados: teleósteos) y *S. elegans* 18 tipos de presas correspondientes a 3 phyla (Anélidos: poliquetos; Artrópodos: crustáceos; Cordados: teleósteos). Hay un cambio significativo de la dieta de *S. officinalis* con el tamaño, no ocurre esto en *S. elegans*. La variedad de presas disminuye con la talla de *S. officinalis*. En esta especie no hay diferencias en la dieta de machos y hembras, estas diferencias sí existen en *S. elegans*. En el caso de *S. officinalis* la intensidad de la alimentación aumenta en las hembras con la maduración. En esta misma especie no hay cambios estacionales de la dieta. La alimentación de *S. officinalis* presenta un espectro de presas más amplio que la de *S. elegans*. Se discute la utilización de algunos índices empleados en ecología de la alimentación.

Palabras clave: Cefalópodos, alimentación, *Sepia officinalis*, *Sepia elegans*, Ría de Vigo.

INTRODUCTION

Cephalopods are carnivores exhibiting rapid growth, high metabolic rates (O'DOR & WEBER, 1986) and, therefore, they have a great demand for energy. *Sepia officinalis* and *Sepia elegans* are two relatively abundant species in the Ría de Vigo (GUERRA *et al.*, 1986); as a result, its feeding must have a significant impact on prey species.

The only previous studies of the prey of *Sepia officinalis* Linnaeus 1758 in its natural habitat are those by NAJAI & KTARI (1979) in the Gulf of Tunis, SCALERA-LIACI & PISTICELLI (1982) in the Lesina Lagoon (Italy), GUERRA (1985) in the Ría de Vigo (NW Spain), and LE MAO (1985) in the Gulf of St. Malo (France). The first report on the natural diet of *Sepia elegans* Blainville 1827 is by GUERRA (1985) in the Ría de Vigo.

* Received October 27, 1989. Accepted November 29, 1990.

All these studies were carried out employing small numbers of stomachs, and for this reason they give useful but limited information. Moreover, the data of previous studies has not been analysed quantitatively to any significant extent. Apart from expanding, on the information of GUERRA (1985), and emphasizing quantitative aspects, present paper deals with the effect of sexual maturation on feeding and the possible existence of seasonal variations in diet.

MATERIAL AND METHODS

The stomach contents of 1345 *S. officinalis* and 717 *S. elegans* were examined. The animals were taken in 572 trawl hauls (of 20 minutes maximum duration) in the Ría de Vigo from April 1982 to February 1987. An otter trawl was used with a 6,3 m ground rope, and a cod-end of 35 mm mesh size. The sampling methods and gear used were described by ALONSO-ALLENDE & GUERRA (1984) and GUERRA *et al.* (1986). *S. officinalis* captured measured 14-237 mm dorsal mantle length (ML) and *S. elegans* 11-65 mm.

The material obtained was divided into two groups (A and B) which received different treatments; more quantitative information was recorded for group B.

Group A was made up of 525 *S. officinalis* and 379 *S. elegans* that were stored in labelled boxes on board with the total capture of each haul, then stored in the laboratory at 4 °C and frozen the following night a −20 °C, and analyzed following criteria similar to those used by GUERRA (1985).

Group B was composed of 820 *S. officinalis* and 338 *S. elegans* that were removed on board from the total capture, preserved in portable ice boxes and frozen in the laboratory at −20 °C, within 6 hours of capture. The dorsal mantle length (ML) in mm and the total weight (BW) in g were recorded, after removing excess fluid with blotting-paper. Animals were sexed and the stage of sexual maturity determined according to the maturity scale used by RICHARD (1971) and ALONSO-ALLENDE & GUERRA (1984). The digestive tract was removed and the fullness of the stomach recorded using a subjective scale of 0 to IV. Then the digestive tract was stored at −20 °C and later defrosted at room temperature. The stomach cuticle was removed and the contents weighed (mg) using a H 80 Mettler balance. Regurgitation was never observed.

For the study of the qualitative aspects of the diet and calculation of the occurrence index all specimens (groups A and B) were considered, but only group B was employed in the quantitative aspects of the diet.

Prey were identified to the lowest possible taxon. When it was not possible to identify a prey, and it was clearly different from others, it was placed in a different category and assigned to an arbitrary taxon. A Digestion Stage Index (DSI) was used to classify each prey within a four point scale (1, well digested — 4, recently digested) from our own observations and those of KARPOV & CAILLET (1978).

The following criteria were used in the identification of material in the stomach contents: a) remains of algae and marine phanerogams never showed breakdown or digestion and were not considered as prey; b) very small gastropods, ostracods, copepods and bivalve molluscs were not taken into account; c) cephalopods were frequently observed to bite each other in the net, the presence of cuttle-bones, beaks, lenses and/or statoliths was required before being considered as prey; d) crustacea were identified from eyes, mandibles or appendages after comparison with a reference collection of species known to inhabit the Ría de Vigo, together with descriptions and drawings of ZARIQUIEY-ÁLVAREZ (1968), INGLE (1980), MCLAUGHLIN (1980) and GONZÁLEZ-GURRIARÁN & MÉNDEZ (1985); e) bony fishes were usually identified from their otoliths after comparison with a reference collection of 53 species found in the Ría de Vigo, and with illustrations in CHAINE (1936), CHAINE & DUVERGIER (1934), SANZ-ECHEVARRÍA (1937), BAUZÁ-RULLÁN (1962), SCHMIDT (1968) and HÄRKÖNEN (1986), but scales, bones an other remains were also employed.

The number of individuals present in a single stomach was taken as the smallest from which all of the fragments could have originated.

Whole organisms were never encountered in the stomachs examined, as both species break up the prey during ingestion (GUERRA *et al.*, 1988). When more than one type of prey was present it was practically impossible to sort out the stomach contents, in which case the total stomach weight was divided by the total number of items: this occurred in 154 (24.7 %) of the stomachs containing food in *S. officinalis*, and 69 (18.9 %) stomachs in *S. elegans*.

The following indices were used:

Occurrence Index (OCI). — The quotient in percent between the number of stomachs with one type of prey present and the total number of stomachs examined which contained debris from one or several types of prey, each stomach being counted as many times as the number of different prey types it contained.

Numerical Importance Index (NII). — The relationship in percent between the number of individuals in each food category recorded for all stomachs and the total individuals in all food categories.

Fullness Index (FUI). — A subjective index of the fullness of the stomach. 0: empty. 1: up to 1/4 of its volume. 2: from 1/4 to 1/2 its volume. 3: from 1/2 to 3/4 its volume, and 4: full.

Importance in Weight Index (IWI). — The weight of one type of prey with respect to the total weight of all prey present in one group of specimens as a percentage.

Fullness Weight Index (FWI). — The relationship between the weight of the stomach contents (g) and the total body weight (g) multiplied by 10 000.

Emptiness Index (EMI). — The number of empty stomachs (FUI = 0) compared with the total number of stomachs as a percentage.

These indices have been discussed by HYNES (1950), BERG (1979), HANSSON (1980), HYSLOP (1980), STEVENSON & GREEN (1983) and JOBLING & BREIBY (1986). Combined indices have not been used in this study as their value has been criticized by STEVENSON & GREEN (1983).

To avoid the inconvenience of the IWI, another index was employed namely the "Importance of the Food Ratio" (IFR), defined as the sum of all the FWI of each specimen with a type of prey divided by the total all FWI of one specimen group. The IFR corrects for the effect of a few large prey in the stomach contents, and also corrects for predator weight.

To make a total comparison of the diets between different groups of the two species of cephalopod, the Chi-square test (CROW, 1982; LEGENDRE & LEGENDRE, 1979) was employed. The prey clusters formed for comparisons were as many as the requirements the Chi-square test allows. They are indicated in each case.

The term "Diet breadth" is used here to indicate the number of different prey fed upon by any group of animals. As the number of animals compared in each group can be different, in a direct comparison of the number of distinct prey types found it is expected that this number will increase as the size of the group increases. To avoid of this, 20 samples of each group were taken, each of them made up of 10 events (occurrence of one prey in one stomach). These samples were randomly selected from each predator group. The number of different prey types in each 10 events was recorded, and the mean and the standard deviation of each 20 samples calculated. These values were employed in the comparison between the groups considered. These comparisons were made using an Anova, after testing the data for normality and homogeneity of variance. If some of these statistic requirements were not fullfilled, then different data transformations were tested. Nonparametric procedures were used when those statistic requirements were not fulfilled even after these transformations.

In order to compare the diet of *S. officinalis* of various sizes, animals in group B were divided into three categories: a) the first comprised immature animals of ML < 65 mm, that is smaller or equal to the maximum ML of *S. elegans;* b) the second included maturing and mature (mainly males) specimens of $65 \leq$ ML < 120 mm; c) the last was made up of the largest animals, usually mature, of ML ≥ 120 mm (GUERRA & CASTRO, 1988). Specimens of *S. elegans* were divided into two categories, (a) those with a ML < 45 mm and (b) ML ≥ 45 mm were selected because they represent the mean value of the size frequency distribution; in the first size category 46 % of the females and 57 % of males with food in the stomach were mature, while in the second mature females and males with food in the stomach formed 80 to 95 % of the total, respectively (GUERRA & CASTRO, 1989).

The diet of the two species was compared in *S. officinalis* of ML < 65 mm and *S. elegans* of all sizes, when both species were captured in the same trawls. The *S. officinalis* ML means was 52.7 ± 8.5 mm and the *S. elegans* ML was 39.1 ± 8.6 mm, respectively; these means are significantly different ($p < 0.01$), but, nevertheless, comparisons were made because they were closest in size. Gear selectivity was probably not the cause of the differences in mean sizes between the two species since when *S. officinalis* was captured in areas where *S. elegans* does not appear, its size (40.5 ± 7.0 mm ML) was similar to that *S. elegans* ($p > 0.05$).

Comparison was made between the sexes of both species using groups A and B. Animals in which sex could not be determined were not considered.

To determine whether there was seasonal variation in the prey eaten, 178 *S. officinalis* were examined. The specimens were: captured in the same year, in the same area of the Ría de Vigo (central basin, where the bottom in mainly muddy), of similar size ($65 \leq$ ML< 120 mm), only captured within the normal fishing period (8.30 to 14.30 h), enough animals available for each season of the year, and males and females were grouped together as no differences in feeding habits were detected (see below). It was not possible to make a similar study of *S. elegans* as there was insufficient material.

RESULTS

Table 1 shows the values for the Indices of Occurrence (OCI) and Numerical Importance (NII). In order to compare them, a Chi-square was used, grouping the types of prey having the same values, but which separately did not fulfil the requirements of this test. The results were $X^2 = 34.85$ (f.d. = 35) for *S. officinalis* and $X^2 = 2.40$ (f.d. = 15) for *S. elegans*, and they show no significant differences between OCI and NII ($p > 0.05$). All the specimens of both species were employed to make this comparison.

OCI, IWI and IFR were also calculated for each species and size of specimens in group B. Prey were grouped in 11 and 8 clusters (Table 2-A and 2-B). The Concordance Coefficient of Kendall (SIEGEL & CASTELLAN, 1988) shows that the three indices give similar information ($p < 0.01$). For this reason and in order to simplify the presentation of the results and the comparisons, only the OCI Index was employed.

Description of the diet of both species

Table 1 shows the diet and the OCI values for all *S. officinalis* and the *S. elegans* specimens with respect to all the types of prey in their stomachs. The diet of *S. officinalis* was composed of 40 different prey items belonging to 4 groups (Polychaeta; Cephalopoda; Crustacea; bony fishes) and the diet of *S. elegans* of 18 different prey items of 3 groups (Polychaeta; Crustacea; bony fishes).

Considering only group B, the Emptiness Index (EMI) calculated of *S. officinalis* was 46.1 %. Of the remainder, one prey type was present in 40.6 % of the stomachs, 10.4 % contained two types of prey, 2.6 % three, and 0.4 % four. In *S. elegans* EMI was 27.8 %, while 58.6 % of the stomachs contained one type of prey, 12.1 % two types, and 1.5 % three types.

When two types of prey were present in one stomach they usually consisted of crustaceans and fish. A Chi-square test showed that the presence of both prey together was significantly larger than expected

TABLE 1. — Values fot the Indices of Occurrence (OCI) and Numerical Importance (NII) for each type of prey in the stomach contents of *Sepia officinalis* and *Sepia elegans*. No.: total number of specimens with food in te stomach.

	Sepia officinalis		*Sepia elegans*	
Taxon	OCI	NII	OCI	NII
POLYCHAETA	0.4	0.3	0.2	0.2
CEPHALOPODA	1.0	0.9	—	—
Sepia officinalis	0.4	0.3	—	—
Sepia elegans	0.1	0.1	—	—
Sepia sp	0.4	0.3	—	—
Sepiola sp	0.1	0.1	—	—
CRUSTACEA	57.8	57.1	82.0	83.0
AMPHIPODA	0.4	2.7	4.0	3.6
Caprellidea	0.1	0.1	0.2	0.2
Gammaridea	0.8	1.1	0.7	1.3
MYSIDACEA	—	—	0.2	0.2
DECAPODA CARIDEA	20.5	31.7	68.2	69.6
Palaemonidae	1.0	1.5	0.9	0.9
Palaemon sp	10.8	10.7	26.9	27.7
Palaemon serratus	4.4	6.2	—	—
Palaemon adspersus	0.1	0.1	1.9	1.7
Processa edulis	2.3	2.5	5.1	5.3
Crangonidae	0.1	0.2	—	—
Crangon crangon	1.7	1.6	17.1	16.4
Hippolytidae	—	—	1.9	3.2
DECAPODA ANOMURA	10.3	8.8	14.5	14.5
Paguridae	0.4	0.2	—	—
Porcellana platycheles	1.2	1.1	5.4	5.5
Pisidia longicornis	8.6	7.4	8.9	8.7
Galatheidae	0.1	0.1	—	—
Galathea intermedia	—	—	0.2	0.2
DECAPODA BRACHYURA	25.6	21.4	8.6	8.1
Portunidae	10.1	8.7	1.4	1.3
Polibius henslowii	3.2	2.1	—	—
Liocarcinus depurator	1.2	1.2	—	—
Liocarcinus holsatus	0.9	0.4	—	—
Liocarcinus marmoreus	0.9	0.8	—	—
Liocarcinus sp	4.5	3.6	6.5	6.2
Atelecyclus undecimdentatus	0.9	0.7	—	—
Pilumnus spinifer	0.3	0.2	—	—
Asthenognatus atlanticus	2.3	2.1	—	—
Carcinus maenas	0.3	0.3	—	—
Majidae	0.3	0.3	0.7	0.6
Inachus sp	0.9	1.0	—	—
TELEOSTEI	38.7	39.7	16.0	15.1
Gobiidae	7.0	5.9	0.2	0.4
Gobius sp	0.1	0.4	—	—
Gobius niger	1.6	1.6	—	—
Gobius paganellus	0.1	0.1	—	—
Lesuerigobius friesii	9.8	9.1	—	—
Pomatoschistus pictus	4.7	7.6	1.9	1.7
Pomatoschistus minutus	1.7	1.5	—	—
Pomatoschistus sp	1.3	1.1	—	—
Aphya minuta	3.5	5.3	13.3	12.6
Deltentosteus quadrimaculatus	0.3	0.2	—	—
Ammodytidae	0.8	0.7	—	—
Ammodytes tobianus	0.3	0.2	—	—
Callionymus lyra	2.8	2.4	0.2	0.2
Syngnathidae	1.5	1.3	—	—
Syngnathus sp	1.0	0.9	—	—
Syngnathus typhle	0.3	0.2	—	—
Trisopterus sp	0.1	0.1	—	—
Labridae	0.5	0.4	—	—
Symphodus sp	0.6	0.5	—	—
Trachinus vipera	0.1	0.1	—	—
Buglossidium luteum	0.1	0.1	—	—
Lepadogaster sp	0.1	0.1	—	—
Teleostean OD	0.1	0.2	—	—
Teleostean OE	0.1	0.1	—	—
Teleostean OP	—	—	0.2	0.2
Not identified	2.2	1.9	1.9	1.7
TOTAL 100 %	776	918	428	470
No.	623		366	

TABLE 2. — Occurrence Index (OCI), Importance in Weight Index (IWI), Importance of the Food Ratio (IFI) and Kendall Concordance Coefficient (W) values for each size group of *Sepia officinalis* (A) and *Sepia elegans* (B). ML: Mantle length in mm.

A

Prey cluster	*ML < 65*			*65 ≤ ML < 120*			*ML ≥ 120*		
	OCI	*IWI*	*IFI*	*OCI*	*IWI*	*IFI*	*OCI*	*IWI*	*IFI*
POLYCHAETA	1.8	0.3	0.3	—	—	—	—	—	—
CEPHALOPODA	0.6	0.1	0.1	0.7	0.6	0.5	1.7	1.9	1.7
CRUSTACEA	72.5	64.8	75.4	53.3	53.5	55.6	36.8	55.9	46.7
Palaemonidae	22.2	22.7	26.4	24.7	18.8	21.3	5.1	2.8	4.3
Other Caridea	16.8	8.9	16.1	3.0	1.4	1.6	—	—	—
Anomura	9.0	7.0	4.7	1.7	1.3	1.3	—	—	—
Portunidae	10.2	17.9	15.0	18.7	25.8	27.6	29.9	50.8	40.7
Other Brachyura	9.0	6.7	7.7	5.3	6.2	3.9	1.7	0.4	1.8
Other Crustacea	5.4	1.7	5.6	—	—	—	—	—	—
TELEOSTEI	24.6	34.8	24.2	46.0	45.9	43.9	61.5	44.1	51.6
Gobiidae	19.2	31.9	19.8	38.0	38.2	35.5	51.3	39.8	46.0
Other Teleostei	5.4	2.8	4.4	8.0	7.8	8.4	10.3	4.3	5.6
Not identified	0.6	0.1	0.1	—	—	—	—	—	—
TOTAL 100 %	167	16.3	7215	300	86.6	9273	117	134.3	3136
W		0.9761			0.9894			0.9228	

B

Prey cluster	*ML < 45*			*ML ≥ 45*		
	OCI	*IWI*	*IFI*	*OCI*	*IWI*	*IFI*
Polychaeta	0.5	0.1	0.1	—	—	—
Crustacea	82.7	95.1	94.9	81.0	85.8	86.6
Other Crustacea	3.7	1.3	1.5	2.9	0.7	0.5
Palaemonidae	22.5	39.4	39.9	28.6	55.1	43.5
Other Caridea	31.9	36.0	37.0	23.8	8.9	22.9
Anomura	17.8	14.5	12.3	14.3	11.3	10.9
Brachyura	6.8	4.0	4.3	11.4	9.9	8.8
Toleostei	16.8	4.9	5.1	19.1	14.2	13.4
Aphya minuta	13.6	2.8	3.1	10.5	2.7	3.0
Other Teleostei	3.1	2.1	2.0	8.6	11.5	10.3
TOTAL 100 %	191	5.8	7362	105	4.8	3446
W		0.9683			0.8175	

in both *Sepia* species ($p < 0.01$), taking into account the frequencies of both prey groups in all the specimens with food present in the stomach.

Feeding in relation to size in *S. officinalis*

The OCI values for each prey type and size group are given in table 3, in which all specimens were used.

Table 4-A gives the OCI values for the different prey clusters for each size group, including all the specimens of *S. officinalis*. The significance of the values obtained by a test of difference between two percentages (SOKAL & ROHLF, 1981) is given in the same table. The test was applied to each prey cluster between two consecutive size groups. Table 4-A also gives the results of the comparison of total diet between consecutive size categories using a Chi-square test.

S. officinalis changes its diet, the intake of crustaceans decreasing ($p < 0.01$) and of fish increasing ($p < 0.01$) with growth. There is a significant increase in Portunidae eaten ($p < 0.01$ and $p < 0.05$), and they are most frequently taken by the largest cuttlefish. "Other crustaceans" were eaten less often as cuttlefish grew larger ($p < 0.05$ and $p < 0.01$), but the intake of "Other Brachyura" did not alter; the intake of Palaemonidae dropped only in cuttlefish with ML ≥ 120 mm. Of teleosts there was a significant increase in Gobiidae ($p < 0.01$), but no significant change ($p > 0.05$) in other fish eaten. Polychaetes were taken only by *Sepia* of ML < 65 mm. Cannibalism was infrequent but did occur in all sizes.

The maximum values of Fullness in Weight Index (FWI) *S. officinalis* group B were 446.5 (4.5 % of the BW), 235.5 (2.5 %) and 147.6 (1.5 %) for ML < 65, 65 ≤ ML < 120 and ML ≥ 120 mm, respectively,

TABLE 3. — Occurrence Index (OCI) values for each prey item, species and size groups. No.: total number of specimens with food in the stomach. In: number of different item prey. ML: mantle length in mm.

Taxon	*Sepia officinalis*			*Sepia elegans*	
	ML < 65	*65 ≤ ML < 120*	*ML ≥ 120*	*ML < 45*	*ML ≥ 45*
POLYCHAETA	1.3	—	—	0.4	—
CEPHALOPODA					
Sepia officinalis	—	0.5	0.6	—	—
Sepia elegans	—	—	0.6	—	—
Sepia sp	0.5	0.3	0.6	—	—
Sepiola sp	—	—	0.6	—	—
CRUSTACEA					
AMPHIPODA	1.3	0.3	—	2.6	5.5
Caprellidea	0.5	—	—	0.8	—
Gammaridea	2.7	—	—	1.1	—
MYSIDACEA	—	—	—	0.4	—
DECAPODA CARIDEA					
Palaemonidae	3.1	0.8	—	0.7	1.2
Palaemon sp	18.3	13.0	1.1	25.1	29.0
Palaemon serratus	0.9	6.9	2.9	—	—
Palaemon adspersus	—	0.3	—	1.5	2.5
Processa edulis	5.4	2.4	—	4.5	6.8
Crangonidae	0.9	—	—	—	—
Crangon crangon	5.8	0.3	—	20.2	11.7
Hippolytidae	—	—	—	1.5	2.5
DECAPODA ANOMURA					
Paguridae	0.5	—	0.6	—	—
Porcellana platycheles	3.6	0.3	—	7.1	2.5
Pisidia longicornis	10.3	9.0	0.6	8.2	9.9
Galatheidae	0.4	—	—	—	—
Galathea intermedia	—	—	—	0.4	—
DECAPODA BRACHYURA					
Portunidae	4.9	11.4	12.1	1.1	1.9
Polibius henslowii	—	1.3	8.1	—	—
Liocarcinus depurator	—	1.9	0.6	—	—
Liocarcinus holsatus	—	0.5	1.7	—	—
Liocarcinus marmoreus	—	2.1	—	—	—
Liocarcinus sp	4.9	3.5	6.3	4.9	9.3
Atelecyclus undecimdentatus	—	0.8	1.7	—	—
Pilumnus spinifer	—	—	1.2	—	—
Asthenognatus atlanticus	4.9	2.1	1.2	—	—
Carcinus maenas	—	0.8	—	—	—
Majidae	—	0.8	—	1.1	—
Inachus sp	2.7	0.5	—	—	—
TELEOSTEI					
Gobiidae	4.5	6.4	10.9	1.1	—
Gobius sp	—	1.3	4.0	—	—
Gobius niger	—	—	0.6	—	—
Gobius paganellus	—	—	0.6	—	—
Lesuerigobius friesii	0.4	8.8	25.9	—	—
Pomatoschistus pictus	2.7	8.2	—	0.4	4.3
Pomatoschistus minutus	—	1.6	3.5	—	—
Pomatoschistus sp	3.1	0.5	0.6	—	—
Aphya minuta	4.9	3.5	1.7	14.2	11.1
Deltentosteus quadrimaculatus	—	0.5	—	—	—
Ammodytidae	1.8	0.5	—	—	—
Ammodytes tobianus	—	0.5	—	—	—
Callionymus lyra	3.6	0.8	5.2	0.4	—
Syngnathidae	2.2	—	—	—	—
Syngnathus sp	—	1.9	1.7	—	—
Singnathus typhle	—	1.3	1.2	—	—
Trisopterus sp	—	—	0.6	—	—
Labridae	—	0.5	1.2	—	—
Symphodus sp	—	0.5	1.7	—	—
Trachinus vipera	—	0.3	—	—	—
Buglossidium luteum	—	0.3	—	—	—
Lepadogaster sp	0.4	—	—	—	—
Teleostean OD	—	—	0.6	—	—
Teleostean OE	—	0.3	—	—	—
Teleostean OP	—	—	—	—	0.6
Not identified	3.6	2.4	—	2.3	1.2
Total 100 %	224	376	174	267	162
No.	194	306	123	233	133
In	21	28	22	17	11

TABLE 4. — Prey clusters used for total comparison of the diet between size groups, OCI values, significance levels of the differences and results of the Chi-square test. No.: total specimens number with food in the stomach; ML: mantle length in mm; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$.

A

Sepia officinalis					
Prey clusters	ML < 65		65≤ML<120		ML ≥ 120
POLYCHAETA	1.3	—	—	—	—
CEPHALOPODA	0.5	n.s.	0.8	n.s.	2.3
CRUSTACEA	71.0	**	59.0	**	37.9
Palaemonidae	22.3	n.s.	21.0	**	4.0
Other Caridea	12.1	**	2.7	**	—
Anomura	14.7	*	9.3	**	1.2
Portunidae	9.8	**	20.7	*	28.7
Other Brachyura	7.6	n.s.	5.1	n.s.	4.0
Other Crustacea	4.5	**	0.3	n.s.	—
TELEOSTEI	23.7	**	37.8	**	59.8
Gobiidae	15.6	**	31.0	**	47.7
Other Teleostei	8.0	n.s.	6.9	n.s.	12.1
Not identified	3.6	—	2.4	—	—
TOTAL 100 %	224		376		174
No.	194		306		123
x^2		63.4		55.6	
f.d.		8		7	
p		**		**	

B

Sepia elegans			
Prey clusters	ML < 45		ML ≥ 45
POLYCHAETA	0.4	n.s.	—
CRUSTACEA	81.3	n.s.	82.7
Palaemonidae	27.3	n.s.	32.7
Other Caridea	26.2	n.s.	21.0
Anomura	15.7	n.s.	12.4
Brachyura	7.1	n.s.	11.1
Other Crustacea	4.9	n.s.	5.6
TELEOSTEI	16.1	n.s.	16.1
Aphya minuta	14.2	n.s.	11.1
Other Teleostei	1.9	n.s.	4.9
Not identified	2.3	—	1.2
TOTAL 100 %	267		162
No.	233		133
x^2		8.7	
f.d.		6	
p		n.s.	

with newly ingested prey, and the EMI were 56.0 %, 41.6 % and 34.7 %, respectively for these groups. The EMI value for the smallest animals was significantly higher than in the other groups ($p < 0.01$). The percentages with stomachs whose Fullness Index (FUI) was 3 or 4 (FUI 3 + 4) were 14.87, 19.04 and 29.22 for the same three groups. Only the percentage of the last group (ML ≥ 120 mm) was significantly higher than the others. The number of different prey items ingested alters slightly with size: 21 for ML < 65 mm, 28 for 65 ≤ ML < 120 mm and 14 for ML ≥ 120 mm. However, the Diet breadth of *S. officinalis* (Table 5-A) does not show significant changes ($p > 0.05$) between the size categories considered, although it was higher for the smallest animals than for the largest ones.

Feeding in relation to size in *S. elegans*

The OCI values for each prey type and each size group of all *S. elegans* is given in table 3.

Table 4-B gives the OCI values for different prey clusters considered for each size category of all specimens, the significance of the differences between percentages and the results of the total diet comparison between consecutive size categories using a Chi-square test. The results suggest that *S. elegans* does not change its diet with growth in the sizes examined.

The maximum FWI values were 531.9 (5.3 % of BW) and 360.9 (3.6 % of BW) for ML < 45 and ML ≥ 45 mm, respectively from group B, and the values of the EMI were 23.9 % and 34.1 %, respectively. A significant rise of EMI ($p < 0.05$) was observed. The FWI 3 + 4 were 32.5 % and 27.9 % for each size group; these values showed no significant difference ($p > 0.05$).

Table 5-B shows the Diet breadth, and indicated that it is not significantly different for the size groups ($p > 0.05$).

Feeding, sex and sexual maturation in *S. officinalis*

The OCI values obtained for the different prey clusters by sex and size groups are given in table 6. In this, the number of specimens with food from the whole sample and the percentage of specimens of group B with empty stomachs are recorded. Animals whose sex could not be determined were not included.

TABLE 5. — Mean ($\bar{X}$) and standard deviation (S) of the Diet Breath (see text) for each group and species: A) *Sepia officinalis*. B) *Sepia elegans*. C) *S. officinalis* (ML < 65 mm) and all *S. elegans* captured in the same hauls. The significance of a comparison test (see text) between adjacent size group is shown. The number of samples was 20.

	Size group (mm ML)	$\bar{X}$	*S*	*p*
A	ML < 65	5.0	0.97	
				> 0.05
	65 ≤ ML < 120	4.8	1.33	
				> 0.05
	ML ≥ 120	4.3	1.17	
B	ML < 45	4.0	1.03	> 0.05
	ML ≥ 45	4.3	1.16	
C	*S. officinalis*	4.7	0.81	< 0.05
	S. elegans	3.9	1.16	

TABLE 6. — Occurrence Index values, number of specimens with food in the stomach (No.), and percentage of empty stomachs (EMI) for each size groups of *Sepia officinalis*. ML: mantle length in mm.

Taxon	*ML < 65*		*65 ≤ ML < 120*		*ML ≥ 120*	
	Males	*Females*	*Males*	*Females*	*Males*	*Females*
POLYCHAETA	1.0	1 1.8	—	—	—	—
CEPHALOPODA	1.0	—	1.7	—	4.9	1.5
CRUSTACEA						
Palaemonidae	20.0	23.9	21.9	20.2	4.9	3.8
Other Caridea	14.3	11.0	2.8	2.5	—	—
Anomura	13.3	15.6	9.6	9.1	2.4	0.8
Brachyura	17.1	18.4	24.7	26.8	26.8	34.6
Other Crustacea	1.9	4.6	—	0.5	—	—
TELEOSTEI						
Gobiidae	20.0	15.6	29.8	31.8	51.2	46.6
Other Teleostei	8.6	4.6	5.6	8.1	9.8	12.8
Not identified	2.9	4.6	3.9	1.0	—	—
TOTAL 100 %	105	109	178	198	41	133
No.	89	97	141	165	32	91
EMI	58.7	53.6	42.9	41.0	31.0	37.8

The percentage of *S. officinalis* males and females, with food present in the stomach, was similar to that of the whole population (GUERRA & CASTRO, 1988), females of ML ≥ 120 mm being more abundant than males ($p < 0.01$).

Results of the Chi-square test and the prey clusters employed are indicated in table 7. These results show no significant differences in the types of prey taken by males and females of any size groups.

S. officinalis males and females of group B of each size group with Fullness Index (FUI 3 + 4 and FUI = 0 (EMI)) were compared using percentages (Fig. 1a). No significant difference was obtained in any case ($p > 0.05$), suggesting that feeding intensity of this species is similar for both sexes at each size.

Within each sex, the percentage with empty stomachs (EMI) was significantly higher in males ($p < 0.01$) and females ($p < 0.05$) of ML < 65 mm. When a similar comparison was made taking into account only males whose FUI was 3 + 4, there were no significant differences between size groups ($p > 0.05$). In females a significant increase of the specimens whose FUI was 3 + 4 was only found in the largest size group ($p < 0.01$).

In order to try to understand the reason for this difference, an analysis of the feeding following sexual maturation of both sexes was made. Figure 1b shows the number of animals and the FUI for both sexes of mature and immature individuals of group B while omitting animals in which sex could not be determined. No significant difference was found between immature and mature males for EMI or FUI 3 + 4 ($p > 0.05$), but a significant increase of mature females with FUI 3 + 4 was found ($p < 0.01$). No significant difference between immature males and immature females was observed with respect to EMI

TABLE 7. — Results of Chi-square test and prey clusters used in the total diet comparison between sexes for each species size group. ML: mantle length in mm.

	Sepia officinalis			*Sepia elegans*	
	ML < 65	65 ≤ ML < 120	ML ≥ 120	ML < 45	ML ≥ 45
X^2	4.00	1.12	2.55	11.28	20.18
f.d.	6	4	3	5	6
p	> 0.05	> 0.05	> 0.05	< 0.05	< 0.01
Prey clusters	Palaemonidae Other Caridea Anomura Brachyura Other Crustacea Gobiidae Other Teleostei	Caridea Anomura Brachyura Gobiidae Other Teleostei	(Cephalopoda + Anomura + Palaemonidae) Brachyura Gobiidae Other Teleostei	Other Crustacea Palaemonidae Other Caridea Anomura Brachyura Teleostei	Other Crustacea Palaemonidae Other Caridea Anomura Brachyura *Aphia minuta* Other Teleostei

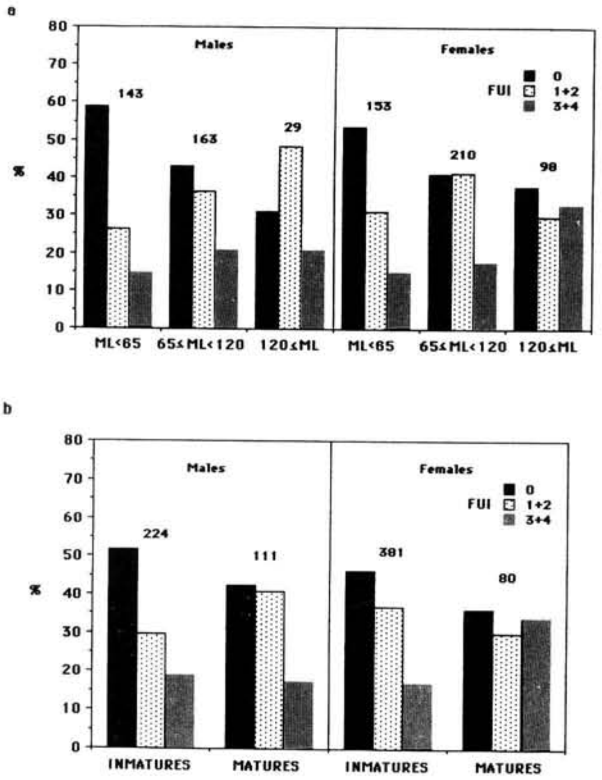

FIG. 1. — Percentage of stomachs with different Fullness Index (FUI) for each sex and size group (a) and sex and maturity state (b) of *Sepia officinalis*. Number of specimens is given above histograms. ML: mantle length in mm.

and FUI 3 + 4 ($p > 0.05$). The number of mature females with FUI 3 + 4 was significantly higher than in mature males ($p < 0.01$).

These results indicated an increase in feeding intensity with sexual maturity of female *S. officinalis*.

Feeding, sex and sexual maturation in *S. elegans*

The results of the Chi-square test used in the total diet comparison between sexes of each species size group and the prey clusters employed are shown in table 7.

Table 8 gives the OCI values obtained for the distinct prey clusters and the significance of their differences for sex and size groups. The number of specimens with food in the whole sample and the percentage of specimens of the group with empty stomachs is included. Animals whose sex could not be determined were excluded.

These results show the existence of significant differences in feeding for both size groups between males and females and a significant increase in Brachyura eaten by females ($p < 0.05$ and $p < 0.01$). In the specimens of ML ≥ 45 mm the frequency of Palaemonidae eaten increased, while "Other Caridea" taken was significantly lower in females than males. No significant differences were observed when males of both size categories were compared, and the same occured for females.

The EMI showed significant difference between males and females of ML ≥ 45 mm ($p < 0.01$), more males being found with empty stomachs than females.

The FUI for *S. elegans* group B, excluding animals whose sex could not be determined, is shown in Fig. 2a. Both sexes with FUI 3 + 4 of each size group were compared using a percentage test, but no significant differences were found ($p > 0.05$). This indicates a similar feeding intensity in males and females at all sizes. No significant differences were found when males or females of each size group were compared.

The FUI for both sexes, immature and mature groups is shown in Fig. 2b. The comparison was made employing a percentage test and no significant differences ($p > 0.05$) for FUI 3 + 4 and EMI were found between immature and mature animals of either sex. Thus, there is no significant increase in feeding intensity with sexual maturity in *S. elegans*.

Feeding of *S. officinalis* in relation to the seasons

The prey clusters, the OCI corresponding to each cluster, the number of specimens with food and the percentage of empty stomachs were used to compare

TABLE 8. — Occurrence Index values, number of specimens with food in the stomach (No.) and empty stomach percentages (EMI) for each sex and each *Sepia officinalis* size groups. ML: mantle length in mm; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$.

Prey clusters	*ML < 45*			*ML ≥ 45*		
	Males		*Females*	*Males*		*Females*
POLYCHAETA	0.7	n.s.	—	—	—	—
CRUSTACEA	80.8		82.8	74.0		86.6
Palaemonidae	30.5	n.s.	24.3	22.0	*	37.5
Other Caridea	21.9	n.s.	30.8	32.0	*	16.1
Anomura	20.5	n.s.	13.1	8.0	n.s.	14.3
Brachyura	3.3	*	11.2	2.0	**	15.2
Other Crustacea	4.6	n.s.	2.8	10.0	n.s.	3.6
TELEOSTEI	15.2		16.8	24.0		12.5
Aphya minuta	13.9	n.s.	14.0	14.0	n.s.	9.8
Other Teleostei	1.3	n.s.	2.8	10.0	n.s.	2.7
Not identified	3.3	—	0.9	2.0	—	0.9
TOTAL 100 %	151		107	50		112
No.	132		93	47		86
EMI	21.2		26.9	50.0		24.7

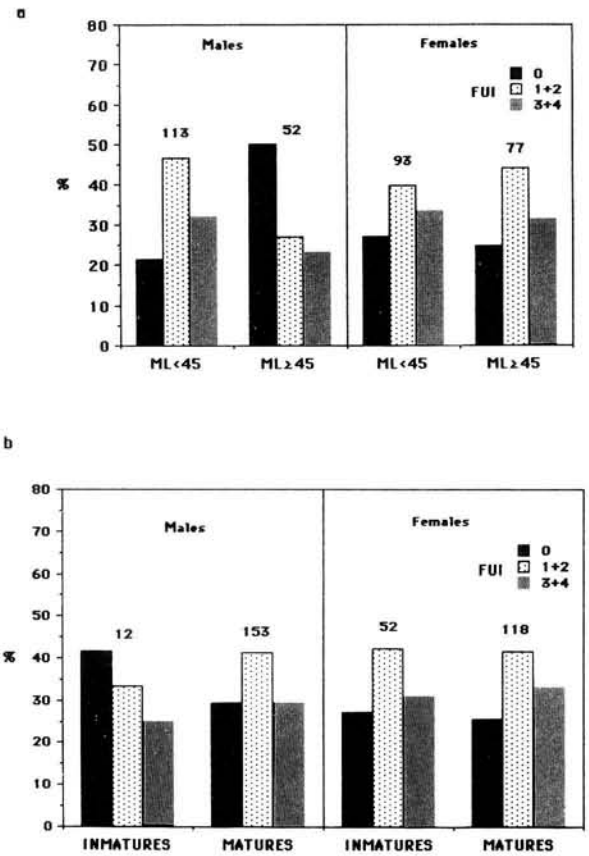

FIG. 2. — Percentage of stomachs with different Fullness Index (FUI) for each sex and size group (a) and sex and maturity state (b) of *Sepia elegans*. Number of specimens is given above histograms. ML: mantle length in mm.

feeding of *S. officinalis* through the seasons of the year (Table 9).

The prey clusters were Caridea, Brachyura and Teleostei, which are permitted by the Chi-square test employed. No significant differences in feeding patterns were shown throughout the year ($p > 0.05$).

The EMI showed a significant difference taking into account the whole year ($p < 0.05$), as the speciments caught in winter had an elevated EMI.

TABLE 9. — Seasonal feeding of *Sepia officinalis*. Occurrence Index values for each prey cluster. No.: number of specimens with food in the stomach. EMI: empty stomach percentages. The prey events not considered are indicated.

Prey clusters	*Spring*	*Summer*	*Autumn*	*Winter*
Caridea	10.8	40.0	37.0	36.2
Brachyura	32.4	22.4	25.9	17.2
Teleostei	56.8	37.7	37.0	46.6
No.	34	22	21	11
EMI	47.7	38.9	47.5	70.2
Not considered	1 Anomura	—	1 Anomura	1 no identified 2 *Sepia* sp

The FWI of all the *S. officinalis* was used to compare feeding throughout the year. A Kruskal-Wallis test was applied between seasons, and the result of this was $H=5.7840$ ($p< 0.05$). These figures indicate that no significant changes occur in FWI throughout the year. A similar result was obtained in the case of stomachs with FUI 3 + 4.

TABLE 10. — A) Occurrence Index values for each prey type, number of different prey item (In) and total number of specimens (No.) with food in the stomachs of the *Sepia officinalis* (ML < 65 mm) and all *Sepia elegans* captured in the same hauls. B) Total diet comparison between both groups, results of Chi-square test used and significance of the differences between each prey cluster of both species. ML: mantle length; n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

A

Taxon	*S. officinalis*	*S. elegans*
Polychaeta	0.8	—
Crustacea		
Amphipoda	0.8	2.9
Gammaridea	—	0.6
Palaemonidae	32.8	42.9
Processa sp	4.2	12.4
Crangon crangon	3.4	11.2
Hippolytidae	—	0.6
P. plathycheles	0.8	2.4
P. longicornis	16.0	6.5
Galatheidae	0.8	—
Brachyura		
Portunidae	9.3	—
Liocarcinus sp	5.9	4.1
Majidae	3.4	—
Teleostei		
Pomatoschistus sp	5.0	1.8
Other Gobiidae	1.7	1.2
Aphia minuta	3.4	12.4
Callionymus lyra	6.7	—
Syngnathidae	1.7	—
Ammodytidae	3.4	—
Not identified	—	1.2
Total 100 %	119	170
In	16	12
No.	66	90

B

Prey clusters	*S. officinalis*		*S. elegans*
Polychaeta	0.8	n.s.	—
Crustacea	77.3	n.s.	83.5
Palaemonidae	32.8	n.s.	42.9
Other Caridea	7.6	**	24.1
Anomura	17.7	*	8.8
Portunidae	15.1	**	4.1
Other Brachyura	3.4	**	—
Other Crustacea	0.8	n.s.	3.5
Teleostei	21.8	n.s.	15.3
Gobiidae	10.1	n.s.	15.3
Other Teleostei	11.8	**	—
Not identified	—	—	1.2
X^2		48.64	
f.d		6	
p		***	

Comparison of the diets of *S. officinalis* and *S. elegans*

The OCI for each prey type is given in table 10A. The OCI for each prey cluster and the significance of this difference between the two species is given in table 10B. This table also shows the results of the total comparison of their diets using these prey clusters, with the exception of polychaetes (in only one specimen of *S. officinalis*), which were not considered, and "Other Brachyura", which were placed with "Other Caridea". Both prey cluster changes were imposed by the requirements of the Chi-square test employed.

From this data it is concluded that the clusters "Other Caridea", Anomura, Portunidae, "Other Brachyura" and "Other Teleostei" had significantly different frequencies ($p < 0.01$ and $p < 0.05$) between the two species, but the remaining clusters did not.

Considering only group B, the EMI was 52.2 % for *S. officinalis* and 24.5 % for *S. elegans*, giving a significant difference ($p < 0.01$). A significantly higher proportion of stomachs with FUI 3 + 4 was found in *S. elegans* than in *S. officinalis* ($p < 0.01$).

The Diet breadth and the significant levels of differences between the means test are given in table 5C. These results suggest that the feeding of *S. officinalis* has a Diet breadth (16 different prey types) significantly greater ($p < 0.05$) than *S. elegans* (12 different prey types).

DISCUSSION

Crustacea and bony fishes are the main groups in the diet of *S. officinalis* and *S. elegans* (NAJAI & KTARI, 1979; SCALERA-LIACI & PISTICELLI, 1982; GUERRA, 1985 and LE MAO, 1985). The presence of decapod cephalopods and polychaetes was also observed by NAJAI & KTARI (1979) and GUERRA (1985). NAJAI & KTARI (1979) also found isopods, copepods, ostracods, octopod cephalopods, lamellibranchs, gastropods, pteropods and nemerteam worms in the diet of *S. officinalis*. PALMEGIANO & SEQUI (1984) also found bryozoans, foraminiferans and insects. Foraminiferans, small gastropods, small lamellibranchs, ostracods, copepods and remains of algae and *Zostera* were also present in our samples, but we consider these items to have been ingested by chance with real prey.

S. officinalis is cannibalistc, capturing and eating smaller animals (NAJAI & KTARI, 1979; LE MAO, 1985; GUERRA, 1985), but cannibalism seems to be only incidental. The life style of this species (MANGOLD-WIRZ, 1963; BOLETZKY, 1983; GUERRA & CASTRO, 1988), and its relatively low metabolic rates could be an explanation. O'DOR & WELLS (1987) have found cannibalism to be common in late seasons for squids, as they are otherwise unable to mantain daily food intake.

The range of crustacea eaten by *S. officinalis* in this study is very similar to that observed by LE MAO (1985) and GUERRA (1985), any differences being due to the habitat and the fact that ours was a larger sample. In contrast to PALMEGIANO & SEQUI (1984) and LE MAO'S (1985) observations, neither isopods nor mysids have been found in the present study, probably due to the scarcity of small specimens. LE MAO (1985) found a great abundance of mysids in specimens smaller than 20 mm ML.

LE MAO (1985) found demersal and pelagic species (*Dicentrarchus labrax, Spondilyosoma cantharus, Atherina presbyter, Belone belone* and Clupeidae) in the diet of large specimens of *S. officinalis*. Although these species are relatively common in the Ría de Vigo (GUERRA *et al.*, 1986) they were not present in the stomach contents examined here. A comparison between zones is rather difficult because of differences in habitat and size of the cuttlefish (larger in the Gulf of Saint Malo). These factors can lead to this disparity.

It is of note that the proportion of flatfish in the stomach contents of *S. officinalis* is low, especially as various species of all sizes of pleuronectiforms are very abundant in the Ría, and frequently were caught together in the same trawl haul as the cuttlefish (GUERRA *et al.*, 1986). Similar results were obtained by GUERRA (1985) and LE MAO (1985), and agree with the observations of RICHARD (1971), and with our experiences in experimental tanks.

RICHARD (1975) observed in the aquarium the need for diet changes between crustacea and fish, as we have found in the wild. This could be due to nutritional requirements or perhaps a need for copper as was found in *Octopus vulgaris* (GHIRETTI & VIOLANTE, 1964), but this requires confirmation.

For the size groups employed, there are changes in the diet of *S. officinalis* with the substitution with growth of crustaceans by fishes, and species of both prey groups with small maximum size for others with greater maximum size. Thus, for crustaceans there is, in this study, a fall of the proportion of Caridea and Anomura, and an increase in Portunidae, although BOUCHER-RODONI *et al.* (1987) found the opposite for Caridea.

Many Theutoidea alter their diet as they grow from crustacea to fish and cephalopods (MANGOLD, 1983; SUMMERS, 1983; BOUCAUD-CAMOU, 1987; NIXON, 1987) and a similar change was found in *S. officinalis* (GUERRA, 1985). There may be several reasons for this change: 1) Energetic ones, which can explain why prey size increases within the same zoological group, as the group change, bearing in mind that here we are comparing maximum size of the prey, not actual sizes of the prey captured, which were not measured. As a result, *S. officinalis* could behave as an energy maximizer forager (SCHOENER, 1971). The finding that the larger part of the stomachs with food had only one prey item supports this assumption. 2) It may have special nutritional requirements for sexual maturation; or 3) Availability of prey. This last reason presupposes environmental heterogeneity where prey were captured, which seems improbable because only 4 % of the *S. officinalis* specimens appeared isolated from other size groups.

No diversity indices were applied because they are not suitable for a sampling process which does not allow access to all species (FREISINGER *et al.*, 1981). This is the case of a subsampling process employing the stomachs of that predator. Furthermore, even good sampling does not correct the problem of the availability of prey for the predators (GRIFFITHS, 1975; HYATT, 1979). For this reason the use of Diet breadth has been prefered. Although this does not have a direct ecological meaning, it may provide an indication of the variety of resources employed by a predator.

To make a total diet comparison of any two groups, that is, to compare the interaction consumer-environment (LAWLOR, 1980) the most widely used procedures in feeding studies are the Contingence Tables, the Spearman Rank Correlation Coefficient (FRITZ, 1974) and the α Schoener Coefficient (HURLBERT, 1978; ABRAMS, 1980; LINTON *et al.*, 1981). Different conclusions about the diet similarity can be obtained with each procedure. The former two have statistical validity and the third involves the use of a subjective decision on placing the limit to consider if diet overlap exists. The Spearman method does not account for frequency differences between groups, but uses only their rank order. The Contingency Tables, based on a Chi-square test, take into account the magnitude of differences, and set some restrictions on the minimum size of the groups to be compared, which sometimes imposes the formation of clusters not always totally comparable. In spite of this shortcoming, if we consider the advantages indicated, this method has been selected to make total diet comparisons.

The FWI decrease with size agrees with a fall in the basal metabolism with respect to weight with growth, and also with a possible allometric growth of the stomach (O'DOR & WELLS, 1987).

If the maximum FWI values in percentage of the total *S. officinalis* body weight found are considered as the daily ration, they are low in relation to those found under aquarium conditions (PASCUAL, 1978), and from oxygen consumption in quiescent conditions (JOHANSEN *et al.*, 1982). However, although more than one meal per day may be taken, CASTRO & GUERRA (1989) have suggested only one meal is taken each day, and this is supported by the physiology of digestion and the time taken to digest one meal, of 15-20 hours, by this species (BIDDER, 1966; BOUCAUD-CAMOU & BOUCHER-RODONI, 1983). Another explanation may be that the initial stages of digestion are rapid. A meal of *Carcinus maenas* eaten by one of 100 mm ML, in an experimental tank, lost 38 % of its initial weight after 82 minutes (18 °C), and two cuttlefish (90 and 95 mm ML) ate *Palaemon serratus*, and lost 59 and 66 %, respectively, after 30 minutes at 18 °C (CASTRO, unpublished data). This effect could be more pronounced in small specimens with faster digestion processes (BOUCAUD-CAMOU *et al.*, 1985). It may account for the larger number of empty stomachs in animals of ML < 65 mm and nocturnal feeding in those captured between 8.30 and 14.30 hours (CASTRO & GUERRA, 1989).

The significant increase of the feeding intensity observed in large sexually mature females is perhaps related to sexual maturation: females of this species would need greater food ingestion for egg production. This contradicts reduction of feeding at the end of the sexual maturation and during the spawning as found in other cephalopods (MANGOLD, 1987), but is supported by several observations which indicate that the feeding continues while spawning (BOLEZTKY, 1987, 1988) and may even increase during this period in *Sepia* (PALMEGIANO & SEQUI, 1984).

The *S. elegans* diet we found was similar to that wich had been found earlier (GUERRA, 1985).

The absence of important changes in the diet, the amount of food ingested and the Diet breadth with growth may be due to the size range (11-63 mm ML) examined. It is probable that feeding changes could have been detected if smaller individuals had been present in the samples, as it is known that feeding and digestive processes do undergo changes during the life cycle of cephalopods (BOUCHER-RODONI *et al.*, 1987).

The significant rise of the EMI observed in *S. elegans* could be related to a decrease of the metabolic activity at great sizes. This effect could also explain the maximum values of the Fullness in Weight Index (5.3 and 3.6 % of the BW) found, which are probably low, being a daily ration, as was found also in *S. officinalis*.

The significant differences found in the diet between males and females of *S. elegans* may be due to the small size of the sample.

A high level of empty stomachs found in males of ML $\geqslant$ 45 mm with respect to females of both size categories and smaller males was found. This may be due to higher metabolism in the smallest specimens, and an increase in feeding by females for egg production.

Both *S. elegans* and to *S. officinalis* seem to fed upon the same resources, but they catch prey in different proportions.

The percentage of empty stomachs was significantly higher in *S. officinalis* than in *S. elegans* ($p < 0.001$), and the percentage of stomachs with FUI 3 + 4 was significantly larger in *S. elegans* than in *S. officinalis* ($p < 0.01$). Without information on digestion rate and feeding periodicity in *S. elegans* we cannot be sure whether there is a variation in intensity between them or whether the results simply reflect scaling of feeding with growth.

Diets with similar prey types, although in different proportions, and different distribution area for similar sizes, suggest trophic competition between the small specimens of *S. officinalis* and *S. elegans*, as indicated by GUERRA (1985). However, none of these phenomena are either sufficient or necessary to prove trophic competition. Furthermore, a qualitatively or quantitatively equal diet does not necessarily involve trophic competition, unless there are insufficient turnover rates, low abundance and prey availability with respect to the potential competitor populations (LAWLOR, 1980; ABRAMS, 1980). However, trophic competition could exist in unfavourable cases. For these reasons, only well controlled experiments are able to prove trophic competition and its consequences (HASTINGS, 1987).

ACKNOWLEDGEMENTS

Our gratitude is expressed to the crew of San Juan. Many thanks to M.ª Teresa Fernández for technical assistance. We would like also to thanks Dr. M. Nixon for advice and suggestions. This work has been carried out with the financial support of CICYT and CSIC (Projet number PR84-0069).

REFERENCES

ABRAMS, P. — 1980. Some comments on measuring niche overlap. *Ecology*, 61: 44-49.

ALONSO-ALLENDE, J. M. & A. GUERRA. — 1984. Crustáceos Decápodos y Moluscos Cefalópodos de la ría de Vigo. Diputación de Pontevedra. Premio investigación, Vigo. *Inst. Inv. Pesq.* (mimeo): 152 pp.

BAUZÁ-RULLÁN, J. — 1962. Contribución al estudio de los otolitos de los peces. *Bol. R. Soc. Esp. Hist. Nat. (Biol.)*, 60: 5-26.

BERG, J. — 1979. Discussion of methods of investigating the food of fishes with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae), *Mar. Biol.*, 50: 263-273.

BIDDER, A. — 1966. Feeding and digestion in cephalopods. In: K. M. Wilburg y C. M. Yonge (eds.): *Physiology of Mollusca*. Vol. 2, pp. 97-124. Academic Press, New York.

BOLETZKY, S. V. — 1983. *Sepia officinalis*. In: P. R. Boyle (ed.): *Cephalopod Life Cycles*, pp. 31-52. Academic Press, New York.

— 1987. Fecundity variation in relation to intermittent or chronic spawning in the cuttlefish *Sepia officinalis* L. (Mollusca, Cephalopoda). *Bull. Mar. Sci.*, 40 (2): 382-388.

— 1988. A new record of long-continued spawing in *Sepia officinalis* (Mollusca, Cephalopoda). **Rapp.** *Comm. int. Mer Médit.*, 31, 2: 257.

BOUCAUD-CAMOU, E. 1987. Ecophysiologie de la nutrition chez les mollusques céphalopodes. *Haliotis*, 16: 267-282.

BOUCAUD-CAMOU, E. & R. BOUCHER-RODONI. — 1983. Feeding and digestion in cephalopods. In: A. S. M. Saleuddin y K. M. Wilbur (eds.): *The Mollusca*, pp. 149-188. Academic Press, London.

BOUCAUD-CAMOU, E., M. YIM M. & A. TRESGOT. — 1985. Feeding and digestion of young *Sepia officinalis* L. (Mollusca: Cephalopoda) during post-hatching development. *Vie Milieu* 35 (3/4): 263-266.

BOUCHER-RODONI, R., E. BOUCAUD-CAMOU, & K. MANGOLD. — 1987. Feeding and digestion. In: P. R. Boyle (ed.): *Cephalopods life cycles*. Vol. 2, pp 85-108. Academic Press, London.

CASTRO, B. G. & A. GUERRA. — 1989. Feeding pattern of *Sepia officinalis* (Cephalopoda: Sepioidea) in the Ría de Vigo (NW Spain). *J. Mar. Biol. Ass. U.K.*, 69: 545-553.

CHAINE, J. — 1936. Recherches sur les otolithes des poissons. Étude descriptive et comparative de la Sagitta des Téléostéens (3eme partie). *Extrait Actes Société Linnéenne Bordeaux*. E. Drouillard (Ed.), LXXXVIII, 994 pp.

CHAINE, J. & J. DUVERGIER. — 1934. Recherches sur les otolithes des poissons. Etude descriptive et comparative de la Sagitta des Teléostéens. *Extrait Actes Societé Linnéenne Bordeaux*. E. Drouillard (Ed.) LXXXVI, 242 pp.

CROW, M. E. — 1982. Some statistical techniques for analyzing the stomach contents of fish. In: G. M. Caillet y C. A. Simenstad (eds.). *Fish food habits studies*. Proceedings of the Third Pacific Workshop, Washington Sea Grant Publ., Univ. Washington: 8-15.

FREINSINGER, P., R. POOLE & E. SPEARS. — 1981. A simple measure of niche breadth. *Ecology*, 62 (1): 27-32.

FRITZ, E. S. — 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. *Copeia*, 1: 210-14.

GHIRETTI, F. & U. VIOLANTE. — 1964. Richerche sul metabolismo del rame in *Octopus vulgaris*. *Boll. Zool. (Torino)*, 31: 1081-1092.

GONZÁLEZ-GURRIARÁN, E. & M. MÉNDEZ. — 1985. *Crustáceos decápodos de las costas de Galicia, I. Brachyura*. Cuadernos da Area de Ciencias Bioloxicas, Seminario de Estudos Galegos, Ed. do Castro. O Castro-Sada, A Coruña, vol. 2, 242 pp.

GRIFFITHS, D. — 1975. Prey availability and the food of predators. *Ecology*, 56: 1209-1214.

GUERRA, A. — 1985. Food of the cuttlefish *Sepia officinalis* and *Sepia elegans* in the Ría de Vigo (NW Spain). *J. Zool. Lond.* (A), 207: 511-519.

GUERRA, A., J. M. ALONSO-ALLENDE, G. PÉREZ-GÁNDARAS, M. J. FERREIRO, A. J. FIGUERAS, & U. LABARTA. — 1986. Especies bentónicas y demersales de la Ría de Vigo. Pescas de arrastre de fondo (1982-84). *Datos Informativos Inst. Inv. Pesq.*, 15: 1-188.

GUERRA, A. & B. G. CASTRO. — 1988. On the life cycle of *Sepia officinalis* (Cephalopoda, Sepioidea) in the Ría de Vigo (NW Spain). *Cah. Biol. Mar.*, 29: 395-405.

— 1989. Some aspects of the biology of *Sepia elegans* (Cephalopoda, Sepioidea) from the Ría de Vigo (NW Spain). *Vie Milieu*, 39 (3/4): 213-218.

GUERRA, A., M. NIXON & B. G. CASTRO. — 1988. Initial stages of food ingestion by *Sepia officinalis* (Mollusca, Cephalopoda). *J. Zool. Lond.*, 214: 189-197.

HANSSON, S. — 1980. An evaluation of different methods for determination of food composition of fish. *ICES C.M./F:* 28: 1-14.

HÄRKÖNEN, T. — 1986. *Guide to the otoliths of the bony fishes of the Northeast Atlantic.* Daubin ApS. Sweden, 256 pp.

HASTINGS, A. — 1987. Can competition be detected using species co-occurence data? *Ecology*, 68 (1): 117-123.

HURLBERT, S. M. — 1978. The measurement of niche overlap and some relatives. *Ecology*, 59: 67-77.

HYATT, K. D. — 1979. Feeding strategy. In: W. S. Hoar, D. J. Randall y J. R. Brett (eds.): *Fish. Phisiology*. Vol. 8, pp. 71-119. Academic Press, New York.

HYNES, M. G. N. — 1950. The food of the freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Ani. Ecol.*, 19 (1): 36-58.

HYSLOP, E. J. — 1980. Stomach contents analysis - A review of methods and their application. *J. Fish. Biol.*, 17: 411-429.

INGLE, R. W. — 1980. *British crabs.* British Museum (Natural History). Oxford University Press Inc., New York, 222 pp.

JOBLING, M. & A. BREIBY. — 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia*, 71: 265-274.

JOHANSEN, K., O. BRIX, S. KORNERUP, & G. LYKKEBOE. — 1982. Factors affecting 0_2-uptake in the cuttlefish *Sepia officinalis, J. Mar. Biol. Ass. U.K.*, 62: 187-191.

KARPOV, K. A. & G. M. CAILLET. — 1978. Feeding dynamics of *Loligo opalescens. Fish. Bull.*, 169: 45-65.

LAWLOR, L. R. — 1980. Overlap, similarity and competition coefficients. *Ecology*, 61 (2): 245-251.

LEGENDRE, L. & P. LEGENDRE. — 1979. *Ecologie Numérique.* Tome I. Masson Ed. Paris, 197 spp.

LE MAO, P. — 1985. Place de la seiche *Sepia officinalis* (Mollusque, Céphalopode) dans les chaines alimentaires du golfe Normano-Breton. *Cah. Biol. Mar.*, 26: 331-340.

LINTON, L. R., R. W. DAVES & F. J. WRONA. — 1981. Resource utilization indices: An assessment. *J. Anim. Ecol.*, 50: 283-292.

MANGOLD-WIRZ, K. — 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mar Catalane. *Vie et Milieu*, supp., 13: 1-285.

MANGOLD, K. — 1983. Food, feeding and growth in Cephalopods. *Mem. Nat. Mus. Victoria*, No. 44: 81-93.

— 1987. Reproduction. In: P. R. Boyle (ed.): *Cephalopod life cycles.* Vol. 2, pp. 157-200. Academic Press, London.

MCLAUGHLIN, P. A. — 1980. *Comparative morphology of recent Crustacea.* W. H. Freeman y Company, San Francisco, 177 pp.

NAJAI, S., & M. H. KTARI. — 1979. Étude du régime alimentaire de la seiche commune *Sepia officinalis* L., 1758 (Mollusque, Céphalopode) du Golde de Tunnis. *Bull. Inst. Natn. Scient. Techn. Océanogra. Pêche Salammbô*, 6: 53-61.

NIXON, M. — 1987. The diet of cephalopods. In: P. R. Boyle (ed.): *Cephalopod life cycles.* Vol. 2, pp. 215-231. Academic Press, London.

O'DOR, R. K. & D. N. WEBER. — 1986. The constrains of cephalopods: why squid aren't fish? *Can. J. Zool.*, 64: 1591-1605.

O'DOR, R. K. & M. J. WELLS. — 1987. Energy and nutrient flow in cephalopods. In: P. R. Boyle (ed.): *Cephalopod life cycles.* Vol. 2 pp. 109-133. Academic Press, London.

PALMEGIANO, G. B. & R. SEQUI. — 1984. Seppia, una novità per la maricoltura. *Informatore Zootecnico*, 19: 30-36.

PASCUAL, E. — 1978. Crecimiento y alimentación de tres generaciones de *Sepia officinalis* en cultivo. *Inv. Pesq.*, 42 (2): 421-443.

RICHARD, A. — 1971. *Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de* Sepia officinalis *L. (Mollusque, Céphalopode).* Thèse Doct. Sci. nat. No. 243. Univ. Lille, France, 264 pp.

— 1975. L'élevage de la seiche *(Sepia officinalis L.*, Mollusque Céphalopode). *10th Europ. Symp. Mar. Biol.*, Ostend (Bélgica), 1: 359-380.

SANZ-ECHEVERRÍA, J. — 1937. Los otolitos de los Lábridos de España (primera parte). *Bol. Soc. Ibér. Cienc. nat.*, 37: 29-45.

SCALERA-LIACI, L. & G. PISCITELLI. — 1982. Alimentazione di *Sepia officinalis L.* nelle laguna di Lesina. *Boll. Mus. Ist. Biol. Univ. Genova*, 50: 398.

SCHMIDT, W. — 1968. Verleichend morphologische studie über die otolithen mariner knochenfische. *Anch. Fisch. Wiss.*, 19 (1): 1-96.

SCHOENER, T. W. — 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, 2: 309-404.

SIEGEL, S. & N. J. CASTELLAN. — 1988. *Nonparametric statistics for behavioral sciences.* McGraw-Hill, New York, 399 pp.

SOKAL, R. & F. ROHLF. — 1981. *Biometry*. W. H. Freeman and Co., San Francisco, 859 pp.

STEVENSON, M. J. & R. H. GREEN. — 1983. Redundancy of variables used to describe importance of prey species in fish diets. *Can. J. Fish. Aquat. Sci.*, 40 (5): 635-37.

SUMMERS, W. C. — 1983. Physiological and trophic ecology of cephalopods. In: W. D. Russell-Hunter (ed.): *The Mollusca.* Vol. 6, pp. 261-279 Academic Press, New York.

ZARIQUIEY ÁLVAREZ, R. — 1968. Crustáceos decápodos ibéricos. *Inv. Pesq.*, 32, 510 pp.

Scient. ed. E. Macpherson.