

Diet of the european hake *Merluccius merluccius* (Pisces: Merluciidae) in the Western Mediterranean (Gulf of Lions)*

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SUMMARY: A total of 1526 hake stomach contents from specimens ranging between 8 and 65 cm in total length were studied in monthly samples taken in the Gulf of Lions in 1993. Key factors influencing the degree of stomach fullness were related to the size and season. The hake diet is comprised primarily of fish and crustaceans but there were size-related changes in the trophic spectrum. The youngest hake feed mainly on small crustaceans (such as euphausiids and mysids) and small benthic fishes (such as gobids). As the hake grows, the importance of fish in the diet increases. The larger specimens ≥ 25 cm TL feed increasingly on the larger decapods and, almost exclusively on active natatory fishes, such as the sardine.

Key words: hake, feeding, Western Mediterranean.

RESUMEN: LA DIETA DE LA MERLUZA *MERLUCCIVS MERLUCCIVS* (PISCES: MERLUCCIIDAE) EN EL MEDITERRÁNEO OCCIDENTAL (GOLFO DE LEÓN). – Se han analizado 1526 contenidos estomacales de merluza de tallas comprendidas entre los 8 y los 65 cm de longitud total, procedentes de muestreos mensuales realizados en 1993 en el golfo de León. Los principales factores que influyen en el grado de repleción estomacal han resultado ser la talla de la merluza y la estación del año en que se ha capturado. La dieta está compuesta principalmente por peces y crustáceos aunque se aprecian diferencias en la composición relacionadas con la talla. Las merluzas más jóvenes se alimentan básicamente de pequeños crustáceos (eufausiáceos y misidáceos) y pequeños peces bentónicos (góbidos). A medida que la merluza crece, la importancia de los peces en la dieta aumenta. Los ejemplares grandes ≥ 25 cm TL se alimentan más frecuentemente de grandes decápodos y casi exclusivamente de peces nadadores activos como la sardina.

Palabras clave: merluza, alimentación, Mediterráneo Occidental.

INTRODUCTION

The European hake (*Merluccius merluccius*, L., 1758) is one of the most important commercial fish in the Western Mediterranean and several studies have been conducted on biological aspects, such as larval distribution (Sabatés, 1990), growth (Aldebert and Carries, 1982; Aldebert and Morales-Nin, 1992), recruit distribution (Campillo *et al.*, 1991) and maturity (Bouhlal, 1975; Recasens, 1992), as well as on its population dynamics (Aldebert and Carries, 1989; Aldebert *et al.*, 1993).

Dietary studies would add to the knowledge of the role of the species in the ecosystem, and its impact on other species.

Information on hake feeding habits in the Mediterranean is incomplete, and deals mainly on little individuals (<40 cm) (Frogliia, 1973; Papaconstantinou and Caragitsou, 1987; Sartor, 1993), restricted depths: 30-40 m (Jukic, 1972), 200-400 m (Macpherson, 1977) or are general approaches without quantitative or semiquantitative details (Larrañeta, 1970). Furthermore, the high percentage of everted stomachs, mainly in the large individuals, a common characteristic in physoclistous fishes, particularly the gadiforms (Bowman, 1986), leads to scarcity of data on the diet of the adults of this species.

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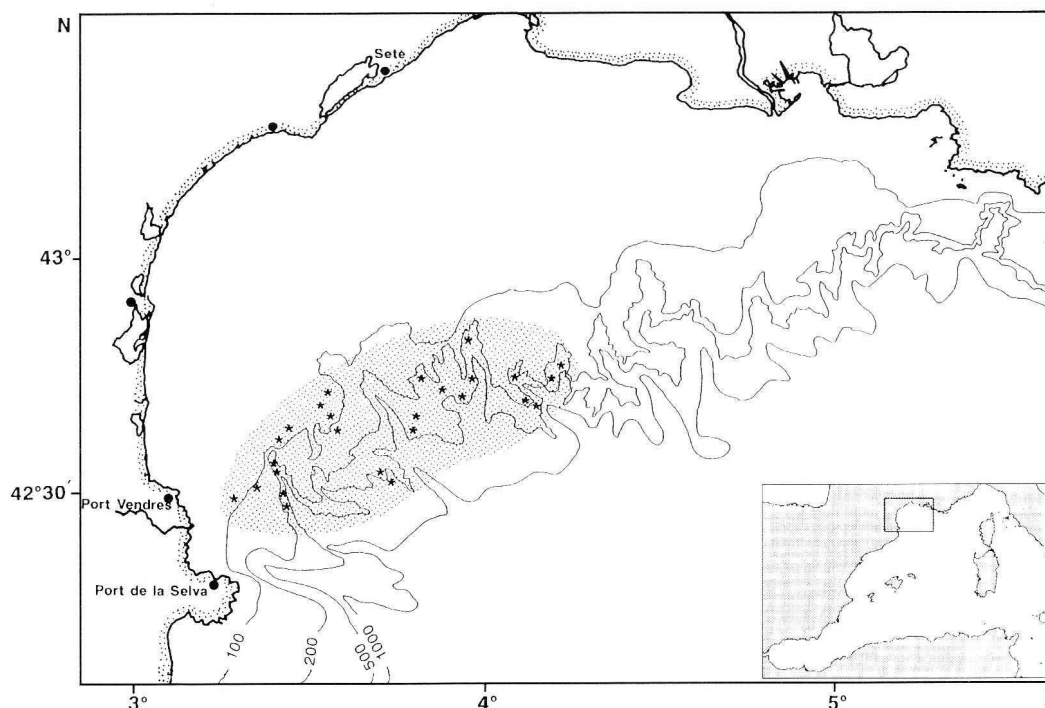


FIG. 1. – Study area with the *Merluccius merluccius* fishing grounds exploited by the Port de la Selva fleets on the grid.

At the present time there is not any work with a global information about the diet of hake in the Mediterranean. The aim of this study was to provide comprehensive information about the diet of the European hake, considering various aspects, such as a wide length range of hake (5-69 cm), sex and seasonality.

MATERIAL AND METHODS

Stomach samples were collected from monthly bottom trawl commercial landings in 1993 in the fishing port of Port de la Selva, Catalonia, Spain. These landings came from the western part of the Gulf of Lions, between 80-500 meters depth, where the Port de la Selva fleet normally works (Fig. 1). This fleet is on the fishing grounds from 8am to 4pm and daily returns to port. Most of the hauls were carried out between 80-200 m, that corresponds to the maximum abundance of hake in the community (Orsi Relini *et al.*, 1989).

A total of 3432 individuals ranging from 5 to 69 cm total length were analyzed. The characteristics of the samples are summarized in Table 1, and the length frequency distribution of the hake sample as a whole is showed in Fig. 2. Due to the difficulty to obtain diet information on hakes larger than 40 cm,

TABLE 1. – *Merluccius merluccius*. Characteristics of the stomachs sampled per size group, season and sex. FI = feeding index.

Size group (cm)	Num. of hakes	Contain food	Empty	Everted	% everted	FI
5.0 - 14.0	1042	534	400	108	10.3	0.57
14.5 - 24.5	1525	693	650	182	11.9	0.52
25.0 - 39.5	618	221	210	187	30.3	0.51
40.0 - 69.0	247	78	65	104	42.3	0.55
Season						
Winter	1146	518	478	150	13.1	0.52
Spring	832	408	306	118	14.6	0.57
Summer	757	296	317	144	19.0	0.48
Autumn	697	304	224	169	24.2	0.57
Sex						
Females	1283	533	518	232	18.1	0.52
Males	1633	727	676	230	14.1	0.51
Population	3432	1526	1325	581	16.9	0.53

a special effort was conducted in this way and a total of 247 individuals larger than this length were analysed. For each specimen, total length (TL, to the nearest half centimeter below), total weight (TW, in grams) and sex were recorded.

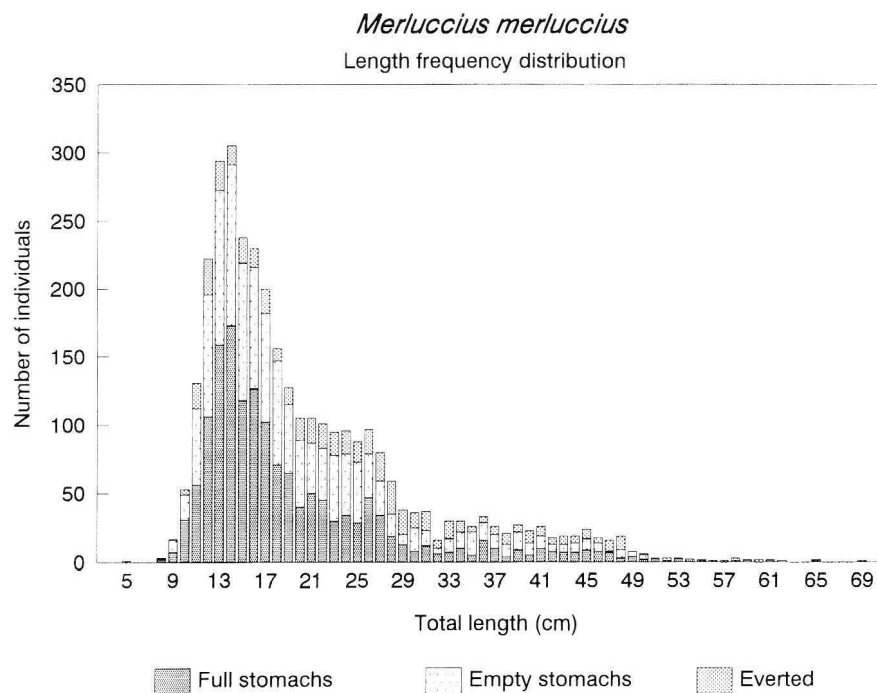


FIG. 2. – Length frequency distribution of the *Merluccius merluccius* specimens analysed.

Prey items were found in the stomach of 1526 individuals ranging from 8 to 65 cm. The stomach contents were removed and then fixed in 5% buffered formalin. Each prey item was identified to the lowest taxonomic level possible, counted and weighed to the nearest 0.01 g. Feeding intensity was studied using Feeding Index (FI) (Hureau, 1970), defined as follows:

$$FI = fs / (fs + es)$$

where

fs = stomachs containing prey
es = empty stomachs

(everted stomachs were not considered in this index). Moreover, for each specimen containing prey was calculated a Total Fullness Index (TFI) (Bowering and Lilly, 1992), modified as follows:

$$TFI = (Ws * 104) / TW$$

where

Ws = stomach content weight
TW = specimen total weight

This index, was previously employed with Atlantic species to assess stomach fullness from a quantitati-

ve standpoint (Bowering and Lilly, 1992; Pedersen and Riget, 1993). In the present study, the individual weight (TW) was utilized as the denominator of the index instead of L3, in order to evaluate TFI with more exactness. On the other hand, it is known that digestion rate could affect TFI values, but in this case the problem is reduced due to all samples have been collected at the end of fishing day so, digestion rate has affected all samples in the same way.

The contribution of each prey item to the diet was described in terms of the percentage of occurrence frequency (F), the percentage of abundance composition (N), and the percentage of biomass composition (W) (Hyslop, 1980). To complete this information, a modified version of the Index of Relative Importance (Iri, Pinkas *et al.*, 1971) was used:

$$IRI = F (N + W)$$

For each prey item, this index was expressed as:

$$\%IRI = (IRI / \sum_{a=1}^n IRI) * 100$$

where

n = number of different prey items

IRI is an useful index to determine main preys (Olaso and Rodríguez-Marín, 1995) as it combines occurrence, quantity and weight.

F and %IRI results are discussed more extensively comparing two different ways of quantify the diet that improves the results obtained (Hyslop, 1980; Rosecchi and Nouaze, 1987).

Both the degree of fullness and the diet of the hake were studied considering the following factors: the season, sex, and four size groups: <14.5, 14.5-24.5, 25-39.5, ≥40 cm TL. Size groups were chosen using the following criteria: 14.5 cm is the estimated mean length at one year of age for hake in this zone (Aldebert and Morales-Nin, 1992), the second group is assumed to comprise the rest of immature specimens, the third group comprises mature males and maturing females, and the last group represents adult males and females (Recasens, 1992).

The variations in FI and TFI with these factors were investigated using the G-test of heterogeneity and the ANOVA, respectively (Sokal and Rohlf, 1981). A log transformation was necessary to normalize the TFI data. Season, size class and sex effects were tested using a multifactorial ANOVA: to obtain a balanced matrix, a set of 400 random data was chosen. Moreover, for this analysis, size classes were divided into two groups, <25 cm and ≥25 cm TL, which represent, approximately, the immature fish and the adults respectively.

RESULTS

The overall feeding index was slightly over 0.50. The index remained near this value for the different size groups (Table 1) and for the other factors considered. In all cases, application of the G-test revealed no significant differences between size, sex or season. In addition, Table 1 shows that the percentage of everted stomachs increases notably with size, reaching a value of 42.3 in the largest hakes.

TABLE 2. – *Merluccius merluccius*. Results of ANOVA on TFI data (after log transformation). Effects of season, size class and sex.

	Sum of squares	df	Mean squares	F	Sign level	r≤
Model	839.60	399	2.104	1.068	ns	0.53
Season	47.52	3	15.841	8.037	**	
Size class	20.92	1	20.916	10.612	**	
Sex	2.56	1	2.557	1.298	ns	
Season-size class	4.73	3	1.577	0.800	ns	
Season-sex	2.17	3	0.723	0.367	ns	
Size class-sex	2.61	1	2.609	1.324	ns	
Season-size class-sex	2.27	3	0.755	0.383	ns	
Error	756.83	384	1.971			

**p<0.001

The mean weight of the stomach contents was about 0.7 g. These weight values varied from 0.26 in spring to 2.80 in summer.

The results of the multifactorial analysis on log (TFI) data showed highly significant effects of season and size class, while the sex and the combination of the factors did not represent a significant effect (Table 2). Table 3 can be utilized for interpreting the ANOVA results; the TFI values related to the immature fish are higher than those of the mature ones. As for seasonality the higher values of TFI are in summer.

In the analysis of 1526 stomach contents from individuals ranging between 8 and 65 cm TL, 57 prey items were identified (Table 4). The diet comprised mainly of bony fishes, followed by crustacean decapods, mysids and euphausiids. Other taxa found were amphipods, cephalopods, isopods, crinoids and thaliaceans.

Among the fishes, which represented 79.2% of the IRI and 50.1% of F, the most important preys were sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), gobiids (mainly *Lesueurigobius friesii*, *Deltentosteus quadrimaculatus*), poor-cod (*Trisopterus minutus capelanus*) and red band-fish (*Cepola rubescens*). Furthermore, a major proportion of the fishes found in the stomachs was comprised of unidentified specimens, often found in an advanced state of digestion.

TABLE 3. – *Merluccius merluccius*. Values of TFI index, calculated for each factor studied.

Factors	TFI		
	Mean	St.error	n (full stomachs)
Size			
8.0-14.0	280.2	21.709	534
14.5-24.5	321.3	16.380	693
25.0-39.5	237.4	27.240	221
40.0-65.0	200.0	44.998	78
Season			
Winter	200.0	18.381	518
Spring	217.0	22.357	408
Summer	407.5	28.562	296
Autumn	266.4	23.422	304
Sex			
Females	269.5	17.600	533
Males	307.4	15.059	727
Total population	288.4	14.622	1526

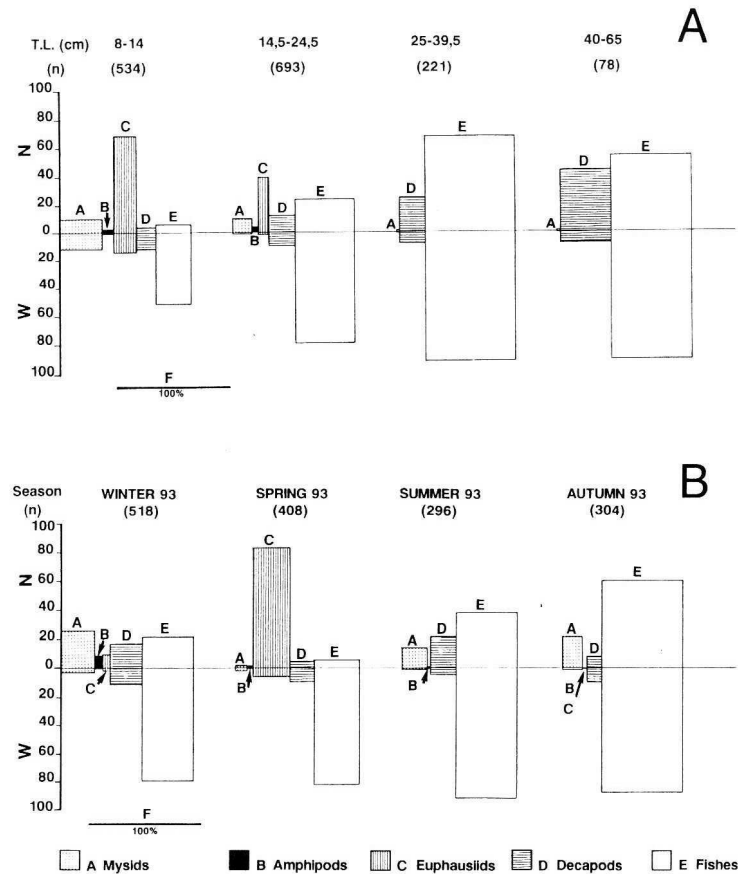


FIG. 3. – *Merluccius merluccius*. Percentages of frequency of occurrence (F), by number (N) and by weight (W) of higher taxonomic groups of prey, calculated by predator length (A) and by season (B).

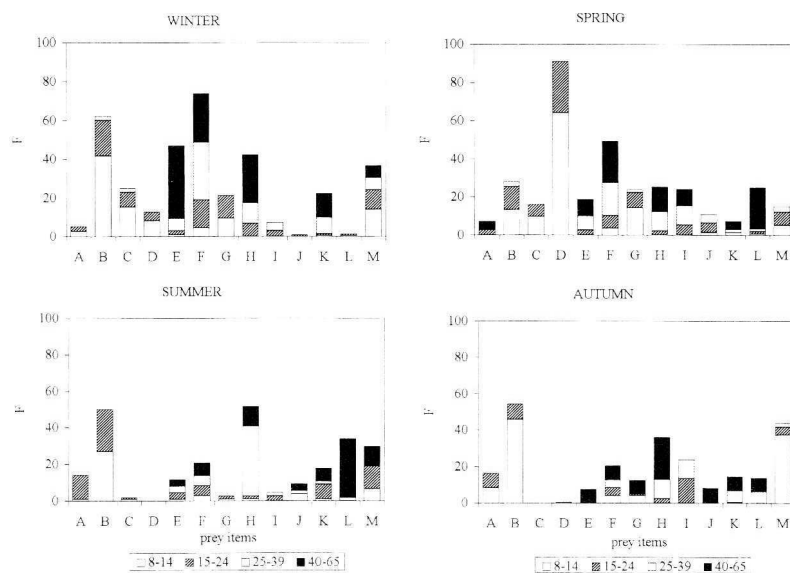


FIG. 4. – *Merluccius merluccius*. Main prey items for length group and season. Prey items: A, Cephalopoda; B, *Lophogaster typicus*; C, Lysianassidae; D, Euphausiacea; E, *Solenocera membranacea*; F, *Processa* sp.; G, Crangonidae; H, *Sardina pilchardus*; I, *Engraulis encrasicolus*; J, *Merluccius merluccius*; K, *Trisopterus m. capellanus*; L, *Cepola rubescens*; M, Gobiidae. Length groups are expressed in centimeters and data are expressed in F (frequency of occurrence).

A small amount of cannibalism was recorded, representing a 0.14 of %IRI and 1.5 of F. In the autumn and largest hakes (>40 cm), this phenomenon reached its highest value: a frequency of 7.7%.

Decapods, representing 5.9% of the total IRI and 21.8% of F, were mainly constituted by Processidae, *Solenocera membranacea* and Crangonidae.

Prominent among the mysids was *Lophogaster typicus*, which was found in 18.7% of the stomachs.

The euphausiids, represented almost entirely by the specimens unidentified, were most significant in the percentage of abundance in number, constituting more or less 50% of prey items.

Variations in the diet related to length changes were appreciable (Fig. 3A and Fig. 4). The diet of the specimens smaller than 25 cm TL was more diverse in comparison with larger individuals, which fed almost exclusively on fish and decapods. Both types of prey gradually increased in importance with the size of the predator. Mysids and euphausiids were notable only in the specimens of the first two size groups. Also, changes in the specific composition of fishes and decapods were related to variation in size: in the smallest hakes, mainly gobiids and small Crangonidae (0.17 g average weight) were found. The prey size increased with the predator size: in the hakes larger than 40 cm TL, the decapods *S. membranacea* and Processidae and the fishes *S. pilchardus*, *T. m. capelanus* and *C. rubescens* were important. Fish-prey of remarkable size were often found, particularly in the fourth size group.

The diet showed some differences throughout the seasons (Fig. 3B, Fig. 4): fishes constituted the main prey items all year round and specially in autumn, giving an IRI of 92.8%. However, the mean weight of fish-prey per season was greatest in summer, with a value of 6.7 g. Spring is the most distinctive period; only during this season euphausiids were found in large quantities in the hake stomachs (N=83.6%, %IRI=42.4).

Related both size and season (Fig. 4), hakes smaller than 14 cm feed mainly on mysids all year round except in spring when they eat euphausiids. Main preys of hakes between 14.5 and 39.5 cm are fishes: gobiids for hakes between 14.5 and 24.5 cm and small pelagic fishes for hakes between 25 and 39.5 cm. Largest hakes feed in winter on *S. membranacea* and sardine, in spring and summer on *C. rubescens* and in autumn on sardine.

TABLE 4. – *Merluccius merluccius*. Trophic spectrum. For each prey item: F = percentage of occurrence frequency; N = percentage of abundance composition; W = percentage of biomass composition; %IRI = (IRI/(IRI)*100 where IRI = F (N+W); * < 0.1.

n=1526				
Prey items	F	N	W	%IRI
CEPHALOPODA (total)	3.3	1.0	2.8	-
<i>Sepia orbignyana</i>	0.1	*	0.1	*
<i>Sepietta oweniana</i>	0.9	0.3	0.9	0.1
Unid. Sepiolidae	0.8	0.2	0.5	*
<i>Alloteuthis</i> sp.	0.8	0.2	0.9	*
<i>Todarodes sagittatus</i>	0.1	*	0.2	*
Unid. Ommastrephidae	0.1	*	0.1	*
Unid. Cephalopoda	0.5	0.1	0.1	*
MYSIDACEA (total)	20.8	9.9	1.1	-
<i>Lophogaster typicus</i>	18.7	9.0	1.0	9.4
<i>Siriella</i> sp.	2.2	0.8	*	0.1
Unid. Mysidacea	0.5	0.2	*	*
ISOPODA (total)	0.7	0.2	*	-
Unid. Cymothoidea	0.7	0.2	*	*
AMPHIPODA (total)	5.9	3.3	0.1	-
<i>Phronima sedentaria</i>	0.1	*	*	*
<i>Vibilia armata</i>	0.5	0.2	*	*
Unid. Lysianassidae	5.2	3.0	0.1	0.8
Unid. Gammaridae	0.2	0.1	*	*
EUPHAUSIACEA (total)	10.9	53.7	1.2	-
<i>Meganyctiphanes norvegica</i>	0.2	0.1	*	*
Unid. Euphausiacea	10.8	53.6	1.1	29.8
DECAPODA (total)	21.8	9.2	8.3	-
<i>Aristeus antennatus</i>	0.3	0.1	1.3	*
<i>Solenocera membranacea</i>	2.6	0.9	2.2	0.4
<i>Sergestes arcticus</i>	0.4	0.6	0.3	*
<i>Alpheus glaber</i>	1.5	0.5	0.5	0.1
<i>Chlorotocus crassicornis</i>	1.1	0.3	0.5	*
<i>Plesionika</i> sp.	0.2	0.1	0.1	*
<i>Pontocaris lacazei</i>	0.4	0.1	*	*
<i>Pontocaris cataphracta</i>	0.1	*	*	*
<i>Pontocaris</i> sp.	0.1	*	*	*
<i>Pontophilus spinosus</i>	1.4	0.5	0.1	*
Unid. Crangonidae	4.1	2.2	0.3	0.5
<i>Pasiphaea sivado</i>	0.4	0.1	0.1	*
<i>Processa canaliculata</i>	2.8	1.1	1.2	0.3
<i>Processa</i> sp.	5.2	1.6	1.1	0.7
<i>Callinassa</i> sp.	0.1	*	*	*
<i>Upogebia</i> sp.	0.3	0.1	*	*
Unid. Decapoda	3.2	1.0	0.5	0.2
Unid. Crustacea	15.1	6.1	0.7	5.2
CRINOIDEA (total)	0.9	0.3	0.1	-
<i>Leptometra phalangium</i>	0.9	0.3	0.1	*
THALIACEA (total)	0.1	*	*	-
Unid. Thaliacea	0.1	*	*	*
PISCES (total)	50.1	16.4	85.8	-
<i>Antonogadus megalokynodon</i>	0.3	0.1	0.2	*
<i>Gadiculus a. argenteus</i>	0.1	*	0.1	*
<i>Phycis blennoides</i>	0.1	*	1.6	0.1
<i>Trisopterus m. capelanus</i>	1.9	0.6	4.3	0.5
<i>Micromesistius poutassou</i>	0.1	*	0.1	*
<i>Mora moro</i>	0.1	*	0.2	*
<i>Merluccius merluccius</i>	1.5	0.4	1.5	0.1
<i>Lesueurigobius friesii</i>	3.8	1.2	0.9	0.4
<i>Deltentosteus quadrimaculatus</i>	2.2	0.7	1.5	0.2
<i>Cristallogobius linearis</i>	0.1	*	*	*
Unid. Gobiidae	3.3	1.0	1.3	0.4
Unid. Myctophidae	0.2	0.1	0.2	*
<i>Callionymus maculatus</i>	0.3	0.1	0.3	*
<i>Cepola rubescens</i>	1.5	0.6	12.9	1.0
<i>Echiodon dentatus</i>	1.3	0.4	0.7	0.1
Unid. Congridae	0.3	0.1	1.5	*
<i>Engraulis encrasicolus</i>	3.8	1.1	7.6	1.7
<i>Sardina pilchardus</i>	4.1	1.2	27.7	6.0
<i>Scomber</i> sp.	0.1	*	1.5	*
Unid. Osteichthyes	27.4	8.5	21.7	41.8

DISCUSSION

The European hake is a demersal active predator throughout its entire life cycle. Furthermore, due to its wide bathymetric distribution and its abundance, it plays an important role in the communities of continental shelf and upper slope (Papaconstantinou and Caragitsou, 1987). The distribution and abundance of this species may be a function of fish trophic morphology and feeding behaviour. Furthermore feeding strategies are factors that play an important role in the relationship between species and in the energy transference between trophic levels.

The information provided by the TFI results can be related to the energy requirement per unit of weight. The highest values of the index are found in the medium-sized specimens, from one year of age to the onset of maturity. The TFI fluctuations found throughout the year appear to be associated with a qualitative change in the diet. The low TFI value found in spring can be related with the euphausiids. In this season this group plays a major role among the resources available to the hake (Razouls and Kouwenberg, 1993) even if its importance in biomass is low. In addition, the high value of TFI in summer can be chiefly related to the greater contribution in weight of the fishes.

The results of this study show that the hake diet consists of prey items which inhabit the water column, as well as bottom-dwelling prey. The typically benthic species play a secondary role in the hake diet. All this implies that feeding may occur at different levels of the water column, given that many of the prey items move vertically, following a nyctemeral rhythm (Franqueville, 1971; Mauchline, 1984).

The hake diet consists primarily of fish and crustaceans. During ontogenic development, this species occupies different trophic levels, with the diet of the recruits (<14.5 cm) more diversified, in order to zoological groups, than the diet of the adults and based chiefly on small crustaceans (euphausiids, mysids and amphipods) and small benthonic fishes (gobids). As the hake increases in size (14.5-39.5 cm), the diet becomes dominated by larger fish and secondarily by decapods. Hake larger than 40 cm TL are piscivorous, preying mainly on active natatory fishes, such as sardine, red-band fish and also some species of large decapods like *S. membranacea*. These results agree with those of Yannopoulos (1977), who found that starting with the 30 cm TL, a change occurred in the trophic niche of this species. These modifications in feeding behaviour, as the hake grows, could be related, among other fac-

tors, to changes in the sensory organs that enhance capability of fish to detect and locate prey, as was related by Lombarte and Popper (1994) studying the hair cell proliferation in the inner ear, specially in the sacculus, an endorgan specialised in sound reception. Furthermore an increase of visual acuity and scotopic sensitivity of hake retina (Mas-Riera, 1991) has associated with changes in diet. Juvenile hakes feed almost exclusively on relatively low mobile preys, whilst prey items of adult specimens have a good capability of swim.

The specific composition of the hake diet is more different in Mediterranean than in the Atlantic waters (Olaso, 1990; Guichet, 1995). Variations found in the present study, are primarily due to the different communities considered. In the Atlantic waters, the main role in the hake's diet is played by the blue whiting *Micromesistius poutassou*, anchovy (*E. encrasicolus*) and, in the largest individuals, by *Trachurus trachurus*. In our case, the main fish species in the adults diet are *S. pilchardus*, much more abundant in western Mediterranean than anchovy (Abad *et al.*, 1992), and *C. rubescens*, that has its maximum of abundance on muddy bottoms between 50-150 m (Martín and Sabatés, 1991). The seasonal variations found in this study concur with the studies of Sartor (1993) and Olaso (1990), particularly regarding the greatest presence of fish on stomachs in autumn.

Both factors, size and seasonality, determine the main characteristics of the diet. In summary, Euphausiids have importance in spring and in hakes smaller than 25 cm, while the rest of the year this role is played by Mysids (*L. typicus*). Decapods are abundant in hakes larger than 25 cm; specially *Processa* sp. and *S. membranacea* play an important role for largest hakes in winter. Fishes are the main prey items for hakes larger than 14 cm: gobids for little and medium hakes, anchovy for hakes between 14.5 and 39.5 and for hakes larger than 40 cm, main preys are sardine in autumn and winter and red-band fish in spring and summer.

As for cannibalism, which is a very important aspect for other species of the genus, such as *M. capensis* (Leonart *et al.*, 1985), we have confirmed that this phenomenon is of slight importance in *M. merluccius*, as other authors in the Mediterranean (Macpherson, 1977) and in the Atlantic (Guichet, 1995) had already pointed out. In the present study, the frequency of cannibalism was very low specially in winter. Cannibalism may be a population survival mechanism when resources are scarce in the environment, and also serves as an important recruitment control factor (Sale, 1982).

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