

John Dory *Zeus faber* (Linnaeus, 1758) feeding off Galicia and in the Cantabrian Sea: Dietary shifts with size

F. Velasco and I. Olaso

Centro Oceanográfico de Santander. Instituto Español de Oceanografía. Apdo. 240. 39080 Santander (Cantabria), Spain

ABSTRACT

Between 1990 and 1997, stomach contents of 647 Atlantic John Dory *Zeus faber* (Linnaeus, 1758) measuring from 5-58 cm, were analysed volumetrically. The species was found to be almost entirely ichthyophagous: fishes constituted more than 99 % of its diet by volume, or 75 % in terms of number. Among these, there are some commercially and ecologically important gadoids and clupeoids. Using clustering and multi-dimensional scaling methods, four length ranges with a different diet composition were found: smaller fishes, measuring 5-9 cm, fed mainly on invertebrates (mysids and *Allotheutis* spp.) and small benthic fishes (e.g., gobiids and *Callionymus maculatus* Rafinesque-Schmaltz, 1810). In the transitional length range, 9-12 cm, *Gadiculus argenteus* Guichenot, 1850 replaced the invertebrates. From 12-30 cm, *Z. faber*'s diet basically comprised gadoids, such as *Micromesistius poutassou* (Risso, 1826), *G. argenteus* and *Merluccius merluccius* (Linnaeus, 1758), whereas specimens longer than 30 cm fed on larger fishes, including *M. poutassou*, clupeoids (mainly *Sardina pilchardus* Walbaum, 1792), and *Cepola rubescens* Linnaeus, 1766. Feeding was more intense in the smallest length range, and within each length range, a different diet composition by depth strata was also observed.

Key words: Dietary shifts, *Zeus faber*, John Dory, gadoids, clupeoids, northern Spain.

RESUMEN

Alimentación del pez de San Pedro *Zeus faber* (L., 1758) en las costas de Galicia y el mar Cantábrico: variación de la dieta con la talla.

Entre 1990 y 1997 se analizaron, con un método volumétrico, los contenidos estomacales de 647 ejemplares de pez de San Pedro *Zeus faber* (Linnaeus, 1758), abarcando un rango de tallas entre 5 y 58 cm. Se trata de una especie muy ictiófaga: su dieta está compuesta por peces en más del 99 % en volumen y del 75 % en número. Dentro de ella destacan gadiformes y clupeiformes de importancia, tanto ecológica como comercial. Utilizando análisis de clúster y MDS se identifican cuatro rangos de talla con composiciones de la dieta diferentes: los individuos menores, entre 5 y 9 cm, se alimentan principalmente de invertebrados (misidáceos y *Allotheutis* spp.) junto a pequeños peces bentónicos (Gobiidae y *Callionymus maculatus* Rafinesque-Schmaltz, 1810); a continuación, hay un rango de transición, de 9 a 12 cm, en el que el *Gadiculus argenteus* Guichenot, 1850 reemplaza a los invertebrados; entre 12 y 29 cm la dieta se compone fundamentalmente de gadiformes como *Micromesistius poutassou* (Risso, 1826), *G. argenteus* y *Merluccius merluccius* (Linnaeus, 1758); mientras, la alimentación entre los individuos mayores de 30 cm se basa en peces de mayor tamaño, entre los que destacan *M. poutassou*, clupeiformes (fundamentalmente *Sardina pilchardus* Walbaum, 1792) y *Cepola rubescens* Linnaeus, 1766, entre otros. También se observa mayor intensidad de alimentación en los peces del rango menor de tallas y diferentes composiciones de la dieta por estratos de profundidad dentro de cada rango de tallas.

Palabras clave: Cambios dietéticos, *Zeus faber*, pez de San Pedro, gadiformes, clupeiformes, norte de España.

INTRODUCTION

Although the Atlantic John Dory *Zeus faber* (Linnaeus, 1758) is a moderately abundant species in the demersal waters of the Cantabrian Sea and Galicia, its biology is almost unknown in the area and its abundance is little known apart from some data on its depth distribution (Sánchez, 1993, 1994; Sánchez, de la Gándara and Gancedo, 1995). A survey of the literature on its diet reveals only work by Silva (1992, in press) on the Portuguese coast, together with Stergiou and Fourtouni's (1991) study in Greece. According to these authors, *Z. faber* is highly ichthyophagous. Our preliminary observations in the area studied had indicated that its diet includes a high percentage of fish, some of them gadoids and clupeoids that are very important to this region, both in commercial terms and as prey of other predators.

Regarding different aspects of John Dory's biology, Righini and Voliani (1996) studied their distribution and growth parameters in the Tuscan archipelago, and found a considerable individual growth rate.

Even though available surveys indicate that *Z. faber* is not very abundant (Sánchez, 1993, 1994; Sánchez, de la Gándara and Gancedo, 1995), these data may be underestimates, because trawling, the method used, is probably not optimal, since this solitary species lives not only near the bottom, but also in mid-water (Wheeler, 1969; Whitehead *et al.*, 1986).

The present study was aimed at determining which gadoids, clupeoids and other fishes are preyed upon by *Z. faber*, and also to study the evolution of its diet with size, in order to determine its place in the trophic web of demersal fishes in the Cantabrian Sea and off Galicia, with the broader purpose of increasing the knowledge of the region's trophic ecology.

MATERIAL AND METHODS

During ten fishery research surveys carried out between 1990 and 1997 by the Insti-

tuto Español de Oceanografía off Galicia and in the Cantabrian Sea, stomach contents of 647 *Z. faber* were analysed. Surveys were carried out on the R/V *Cornide de Saavedra*, using random sampling stratified by depth and geographical areas, following the methodology explained in Sánchez (1994). All hauls used bottom-trawl gear, and lasted half an hour. Stomach content analysis was carried out volumetrically with a trophometer (Olaso, 1990) on board, according to the methodology described in Olaso, Velasco and Pérez (1998) and Velasco, Olaso and De la Gándara (1996). For each *Z. faber* specimen, the following was noted: total length, sex, maturity, stomach fullness (with food, empty or regurgitated) and total stomach volume in the case of non empty stomachs. Regarding the prey items, data were collected on: percentage of the total stomach volume, number, digestion stage, and, in the case of fishes, total length or otolith length. Total length was estimated from otolith length using the regression formulae from Pereda and Villamor (1991). Regurgitation was checked following Robb's (1992) criteria. Given that *Z. faber* is not a very abundant species, all the specimens from every haul were sampled.

To study possible dietary shifts and length ranges with a common feeding composition, the whole length distribution was divided into the ranges shown in table I. Frequency of occurrence and percentages in number and volume of each prey taxa were obtained. Following the methodology proposed by Field, Clark and Warwick (1982), data were transformed to $x^{1/4}$. Clustering and multidimensional scaling (MDS) methods were applied, with Statistica for Windows 4.3, to the resulting matrices, using the Bray-Curtis dissimilarity index, and UPGMA grouping algorithm for the cluster analysis. A 60 % dissimilarity level was chosen to split the groups. These methods were the ones used in previous work on *Z. faber*'s feeding habits (Stergiou and Fourtouni, 1991; Silva, in press), and therefore results could be compared easily.

The number of MDS dimensions was determined by plotting the stress versus the

Table I. Number of stomach contents sampled per length range (cm)

Range label	L5	L9	L12	L15	L18	L21	L24	L27	L30	L35	L40	L50	Total
Length range	5-8	9-12	13-15	16-18	19-21	22-24	25-27	28-30	31-35	36-40	41-50	51-58	
No.	39	90	122	66	47	40	38	37	46	38	57	27	647
Mean length	7.2	10.1	12.9	15.8	19.1	22.1	25.0	28.2	32.1	37.5	43.9	53.0	22.3

number of dimensions, following Kruskal and Wish's (1978) criteria. Three dimensions were used in both cases, and stress value was 0.03 in number and volume. Initial configuration for the MDS was obtained with a Principal Components Analysis. Possible explanations for the dimensions resulting from MDS analysis were tested using Spearman's rank order correlation coefficient between the co-ordinates of the objects and some characteristics of the objects. These were: mean predator length; mean stomach volume; mean prey volume; mean prey length; Total Fullness Index; diet breadth, using Levin's index; proportion of pelagic preys and pelagic fish preys versus benthic preys and benthic fish, respectively, in terms of number and volume, according to the classification used by Silva (1992), following the descriptions of Whitehead *et al.* (1986) for fish preys not included in that work (table II includes a column with pelagic-benthic definition of each prey used in the present paper).

Diet composition in each length range defined by clustering and MDS analysis was studied with Partial Fullness Index (PFI), and feeding intensity was compared using the percentage at empty stomachs and the Total Fullness Index (TFI). PFI and TFI were proposed by Bowering and Lilly (1992), and in the present paper the original formulae were modified and calculated as follows:

$$PFI_i = \frac{\sum_{Haul=1}^H \left[\frac{F+R}{F \times (F+R+E)} \times \sum_{j=1}^k \frac{V_{ij}}{L_j^3} \right] 10^4}{H}$$

$$TFI = \sum_{i=1}^x PFI_i$$

where F is the number of full stomachs; R is the number of regurgitated stomachs; E is the number of empty stomachs; V_{ij} is the volume of prey i in the stomach j , k being the number of stomachs in the haul; L_j the length of the predator j and H the number of hauls in which the predator appears, and x the total number of different prey categories consumed by the predator throughout the study. An explanation of these modifications can be found in Velasco and Olaso (1998).

To study differences in emptiness percentages among depth strata and length ranges, the χ^2 test was used, and linear regression techniques were used to determine predator-prey size relationships.

RESULTS

A total of 647 *Z. faber* stomach contents were sampled; their length-range distribution is shown in table I. Diet composition is summarised in table II. Thirty-four different prey taxa were identified: 23 fishes, 7 crustaceans, 2 cephalopods, salpae and algae; since identification was sometimes impossible, unidentified groups of fishes, crustaceans and molluscs were created, as well as a group for unidentified remains. Regurgitation was found in a mere 3 % of the sampled stomachs, and seems to be rare in this species.

Length variation

Cluster analysis (figure 1a,b) shows three differentiated groups with a dissimi-

Table II. Diet composition of *Z. faber* in frequency of occurrence (% F) and percentage in number (% N), volume (% V) and in PFI units, and prey classification regarding their benthic or pelagic habits

	Pel/Ben	% F	% N	% V	PFI
Crustaceans		8.26	21.90	0.34	0.0887
Amphipoda: Hyperiidae	B	0.28	0.61	0.00	0.0003
Decapoda	B	2.75	3.22	0.12	0.0246
Macrura: <i>Scyllarus</i> spp.	B	0.28	0.15	0.01	0.0008
Unidentified Natantia	B	2.20	2.14	0.11	0.0204
Unidentified Decapoda	B	0.28	0.92	0.01	0.0035
Euphausiacea	-	0.83	0.92	0.01	0.0233
Isopoda	B	2.75	1.53	0.14	0.0031
Mysidacea	-	1.65	15.31	0.05	0.0331
Unidentified crustaceans	B	0.55	0.31	0.01	0.0043
Molluscs Cephalopoda		3.03	2.14	0.44	0.3203
Decabrachia		1.93	1.23	0.40	0.3120
<i>Alloteuthis</i> spp.	P	1.38	0.92	0.34	0.2966
<i>Sepiola</i> spp.	B	0.55	0.31	0.05	0.0153
Unidentified Cephalopoda	-	1.10	0.92	0.04	0.0084
Fishes		93.39	75.50	99.20	3.1137
Anacanthini: (Gadoidei)		27.27	21.44	29.39	1.3812
Gadidae		25.90	20.37	28.47	1.3482
<i>Gadiculus argenteus</i> Guichenot, 1850	P	15.70	12.56	4.37	0.8911
<i>Micromesistius poutassou</i> (Risso, 126)	P	9.64	7.20	22.53	0.4412
<i>Trisopterus minutus</i> (Linnaeus, 1758)	P	1.10	0.61	1.56	0.0160
Merlucciidae: <i>Merluccius merluccius</i> (Linnaeus, 1758)	P	1.38	1.07	0.92	0.0330
Apodes: Congridae: <i>Conger conger</i> (Linnaeus, 1758)	B	0.28	0.15	0.07	0.0017
Callionymoidei: Callionymidae: <i>C. maculatus</i>	B	12.40	8.58	1.53	0.4082
Gobioidei: undetermined Gobiidae	B	7.71	10.11	0.88	0.2637
Isospondyli: (Clupeoidei)		6.61	4.44	32.53	0.2485
Argentiniidae: <i>Argentina sphyraena</i> Linnaeus, 1758	P	1.93	1.23	0.85	0.0446
Clupeidae: <i>Sardina pilchardus</i> (Walbaum, 1792)	P	3.58	2.30	28.70	0.1731
Engraulidae: <i>Engraulis encrasicolus</i> (L., 1758)	P	0.55	0.31	0.45	0.0056
Sternoptychidae: <i>Maurollicus muelleri</i> (Gmelin, 1788)	P	0.28	0.31	0.03	0.0175
Unidentified Clupeoidei	P	0.28	0.31	2.50	0.0077
Percoidae		10.19	7.81	22.03	0.2817
Ammodytidae: <i>Ammodytes tobianus</i> Linnaeus, 1758	P	0.28	1.07	0.40	0.0120
Carangidae: <i>Trachurus trachurus</i> (Linnaeus, 1758)	P	1.65	0.92	2.39	0.0382
Cepolidae: <i>Cepola rubescens</i> Linnaeus, 1766	B	7.99	5.67	19.08	0.2241
Sparidae: <i>Boops boops</i> (Linnaeus, 1758)	B	0.28	0.15	0.16	0.0074
Pleuronectoidei		1.93	1.53	1.36	0.0384
Bothidae: <i>Arnoglossus</i> spp.	B	1.10	1.07	1.09	0.0221
Unidentified Pleuronectoidei	B	0.83	0.46	0.27	0.0163
Scombroidei: Scombridae: <i>Scomber scombrus</i> L., 1758	P	0.28	0.15	2.93	0.0114
Scorpaenoidei: unidentified Triglidae	B	0.28	0.15	0.75	0.0030
Zeomorphi: Caproidae: <i>Capros aper</i> (Linnaeus, 1758)	P	1.65	1.84	0.33	0.0166
Unidentified fishes		33.33	19.30	7.40	0.4594
Fish larvae	P	0.28	0.15	0.01	0.0005
Unidentified Gobioidei and Callionymoidei	B	0.28	0.15	0.01	0.0136
Unidentified fishes	-	32.78	18.99	7.39	0.4453
Algae	B	0.28	0.15	0.01	0.0005
Tunicata: Salpidae	P	0.28	0.15	0.01	0.0001
Unidentified		0.28	0.15	0.01	0.0024
TFI					3.5258
No. Stomach contents analysed					647
No. Empty stomachs					264
No. Regurgitated stomachs					20
No. Hauls with <i>Z. faber</i>					188

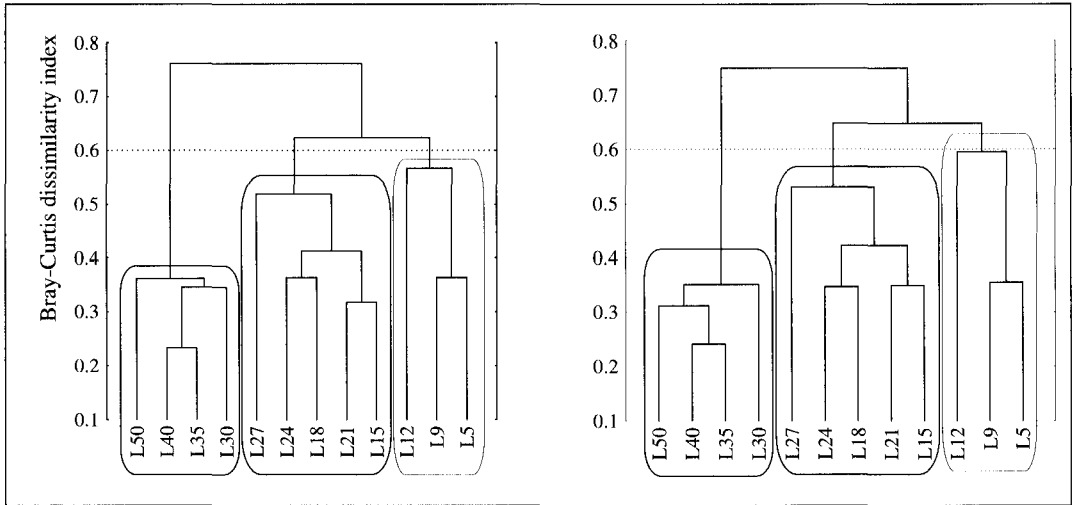


Figure 1. *Z. faber* length-range clusters grouped by (a) number and (b) volumen of the preys

larity level of 60 %; but especially in the case of volume, the group of smallest length ranges is close to that level of dissimilarity. Therefore, we have at least two groups: specimens measuring 30 cm or more, and those smaller than that; it appears that the latter group can be split into specimens measuring less than 15 cm, and those measuring 15-30 cm.

MDS analysis (figure 2 for numbers and figure 3 for volume) splits the sample into only two groups: specimens measuring more than 30 cm, and those smaller than 24 cm, while ranges L24 and L27 are placed between those groups. Range L5 is clearly

different from all the others, being this difference most probably due to the absence of gadoids in the diet of this length range.

The best correlation of each length range's features with the resulting MDS scores (Table III) was between mean predator length and dimension 1 of both number and volume. This result indicates that size is the main factor determining *Z. faber's* diet. Significant correlations were also found between dimension 1 and those variables highly correlated with predator length for *Z. faber*, such as mean prey length, mean prey volume, mean stomach volume and pelagic fish prey proportion in both num-

Table III. Spearman correlation index between some *Z. faber* characteristics within the length ranges studied, and the dimensions of the MDS analysis with number and volume (*): $p < 0.05$; (**): $p < 0.01$

	DIMNUM1	DIMNUM2	DIMNUM3	DIMVOL1	DIMVOL2	DIMVOL3
Mean predator length	** 0.9437	0.0586	0.1474	** 0.9168	-0.1300	0.0885
Mean prey length	** 0.9183	0.1359	-0.0209	** 0.9024	-0.2953	-0.0114
Mean prey volume	** 0.9130	0.3198	0.0850	** 0.8446	-0.4171	0.1418
Mean stomach volume	** 0.9100	0.3178	0.0930	** 0.8358	-0.4119	0.1601
Pelagic fish prey prop. (no.)	** 0.8849	-0.0373	-0.0310	** 0.8912	-0.1118	-0.1342
Pelagic fish prey prop. (vol.)	** 0.8840	-0.0596	-0.0267	** 0.8622	-0.2380	-0.1404
Pelagic prey prop. (no.)	** 0.8748	-0.0134	0.2108	** 0.8464	-0.1621	-0.2770
Pelagic prey prop. (vol.)	** 0.8674	-0.0178	-0.2224	** 0.8401	-0.1601	-0.3057
TFI	* -0.6578	0.4492	0.1874	* -0.7025	-0.3559	0.3424
Mean predator prey number	* -0.6262	0.3466	0.2916	* -0.6701	-0.1842	0.3626
Levin's diet breadth		0.1150	-0.4674		0.2521	-0.1901

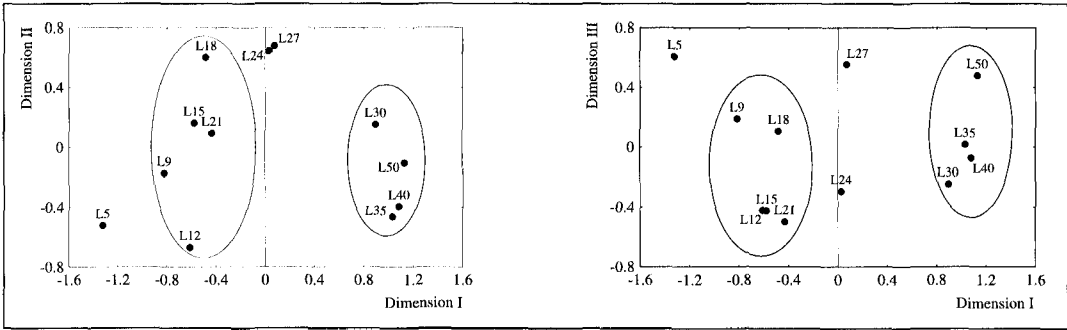


Figure 2. Bidimensional plots of MDS final configuration for prey numbers analysis.

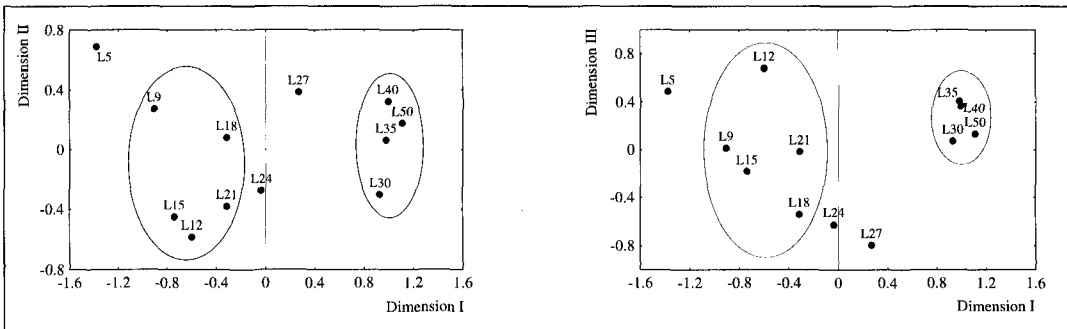


Figure 3. Bidimensional plots of MDS final configuration for prey volume analysis

ber and volume. No correlation was found for the other two dimensions. Regarding this correlation between predator length and pelagic fish prey proportion, shown in figure 4, it appears that there are four different levels, which coincide with those ranges into which we divided *Z. faber's* length distribution.

Given the results of the clustering and MDS analyses, total length distribution was divided into four length ranges: 5-8 cm and 9-11 cm were separated, because of the results of both analyses; 12-14 cm was placed within a 15-29 cm group, after observing their diet composition; the 30-58 cm range clearly stands on its own in analyses. Table IV summarises *Z. faber's* diet composition in those length ranges using PFI. In the smallest length range, there are no gadoids at all; dragonet *Callionymus maculatus* Rafinesque-Schmaltz, 1810, gobiids and cephalopods (mainly *Allotheutis* spp.) stand out, accounting for more than 60 % of the diet, according to PFI; crustaceans, mainly mysids, made

up 13 % of the diet. In the 9-11 cm length range, gobiids and dragonets were even more important, with 42 % of the TFI, but silvery pout *Gadiculus argenteus* Guichenot, 1850 and red bandfish *Cepola rubescens* Linnaeus 1766 also appeared, with 25 %, taking the place of cephalopods and crustaceans, which drop to 9 % and 3 %, respectively. In the next length range, 12-29 cm, gadoids—silvery pout, blue whiting *Micromesistius poutassou* (Risso, 1826) and hake *Merluccius merluccius* (Linnaeus, 1758)—make up 55 % of the diet, and gobiids and dragonets decline to 17 %. In the largest length group, gadoids, mainly blue whiting, account for 37 % of the total; clupeoids, mainly sardine *Sardina pilchardus* Walbaum, 1792, for 23 %; and red bandfish for 21 %.

Regarding feeding intensity, also summarised in Table IV, the smaller *Z. faber* feed more intensely, having a larger TFI and a smaller emptiness percentage. The latter was significantly higher only in the 30-58 cm length range ($\chi^2_3 = 14.63$; $p < 0.01$).

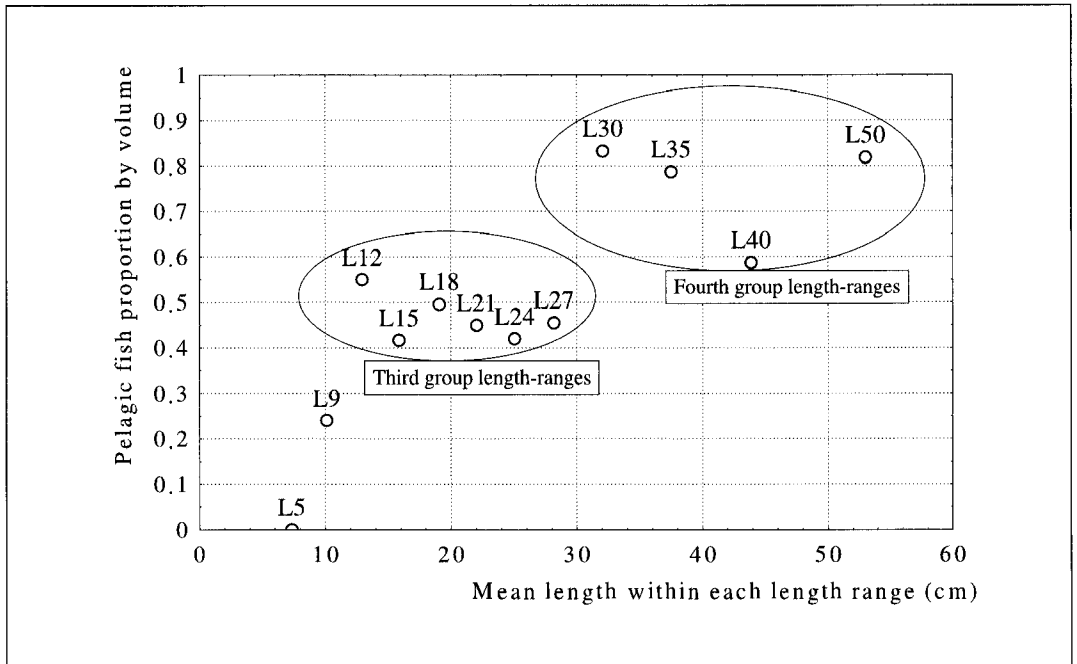


Figure 4. Pelagic fish prey proportion against mean length within each range

Depth variation

Concerning depth distribution, *Z. faber* was found from 44-225 m, and three depth strata were studied, according to Table V, where we can see that emptiness percentage is significantly smaller in the deeper strata ($\chi^2_2 = 8.614$; $p = 0.013$), and TFI shows no marked changes.

In figure 5 *Z. faber's* diet composition is summarised by length range and depth strata as PFI percentages. The smallest length range is well represented only in stratum B, where gobiids and dragonets are the main prey, but it appears that crustaceans are noteworthy only in stratum A. In the 9-12 cm length range, gobiids and dragonets are the main prey found in strata A and B, while *G. argenteus* is more important in stratum C. The 12-29 cm length range shows the major changes within the depth distribution: in stratum A, it shows a broad feeding range, with gobiids and dragonets, *C. rubescens*, *M. merluccius*, *G. argenteus* and *M. poutassou* as important preys; in stratum B, gadoids (*G. argenteus*, *M. poutas-*

sou and *M. merluccius*) are the main preys; whereas *G. argenteus*, dragonets and gobiids are most important in the deepest stratum. The largest length range also shows some variability with depth: clupeoids, mainly *S. pilchardus*, together with *C. rubescens*, are the main preys in stratum A; at 100-150 m, *S. pilchardus* and *M. poutassou* constitute the most important part of the diet; and in stratum C, *M. poutassou* makes up more than the 75 % of *Z. faber's* feeding.

Predator-prey size relationships

Figure 6 presents the regression of fish-prey length versus predator length, also indicating specific prey lengths (red band-fish were excluded, because of their elongate body morphology). These results show that there is a positive relationship between both factors, and we can also see that there is a shift in predator-prey length distributions; for predators larger than 30 cm, there are almost no preys smaller than 140 mm. This shift splits *Z. faber's* diet into two groups: on one hand, we have *Z. faber*

Table IV. TFI, percentage of empty stomachs and diet composition in PFI of *Z. faber* by length range

Length range (cm)	5-8	9-11	12-29	30-58	TOTAL
Crustaceans	1.2116	0.1553	0.0256	0.0082	0.0887
Molluscs Cephalopoda	2.5112	0.4483	0.0354	0.0000	0.3203
<i>Alloteuthis</i> spp.	2.2616	0.4199	0.0155	0.0000	0.2966
Salpids, algae and unidentified	0.0905	0.0000	0.0025	0.0000	0.0030
Fishes	5.5654	4.3624	3.0423	2.6382	3.1137
<i>Gadiculus argenteus</i>	0.0000	0.7467	1.0977	0.0158	0.8911
<i>Micromesistius poutassou</i>	0.0000	0.0000	0.5081	0.9648	0.4412
<i>Merluccius merluccius</i>	0.0000	0.0000	0.1060	0.0000	0.0330
Total gadoids	0.0000	0.7467	1.7118	0.9806	1.3653
<i>Argentina sphyraena</i>	0.0000	0.0000	0.0879	0.0212	0.0446
<i>Sardina pilchardus</i>	0.0000	0.0000	0.0000	0.5346	0.1731
<i>Engraulis encrasicolus</i>	0.0000	0.0000	0.0000	0.0237	0.0056
Clupeoids undetermined	0.0000	0.0000	0.0000	0.0256	0.0077
Total clupeoids	0.0000	0.0000	0.0879	0.6051	0.2310
Gobiids and <i>Callionymus maculatus</i>	3.3461	2.0668	0.5298	0.0000	0.6860
<i>Cepola rubescens</i>	0.0000	0.5815	0.1105	0.5602	0.2241
Other fishes	2.2193	0.9674	0.6023	0.4923	0.6073
TFI	9.3786	4.9660	3.1057	2.6464	3.5258
No. fishes	39	90	350	168	647
Empty stomachs (%)	25.64	37.78	37.71	52.38	40.80

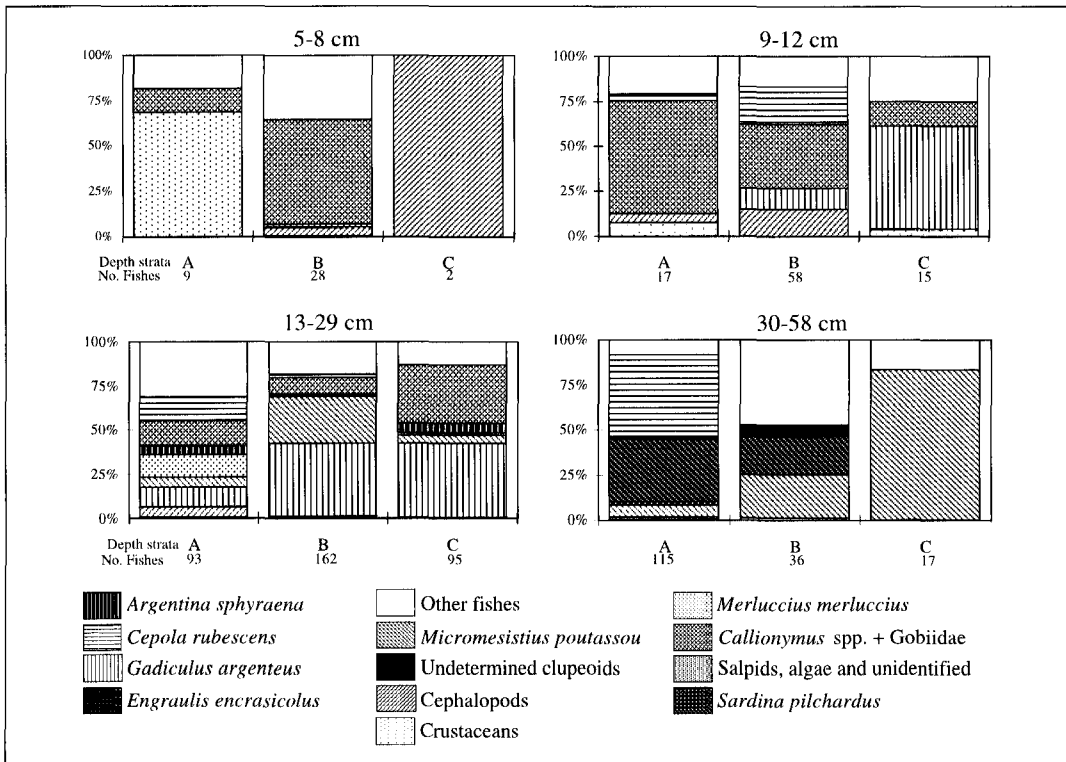


Figure 5. Diet composition in PFI % per length range and depth strata

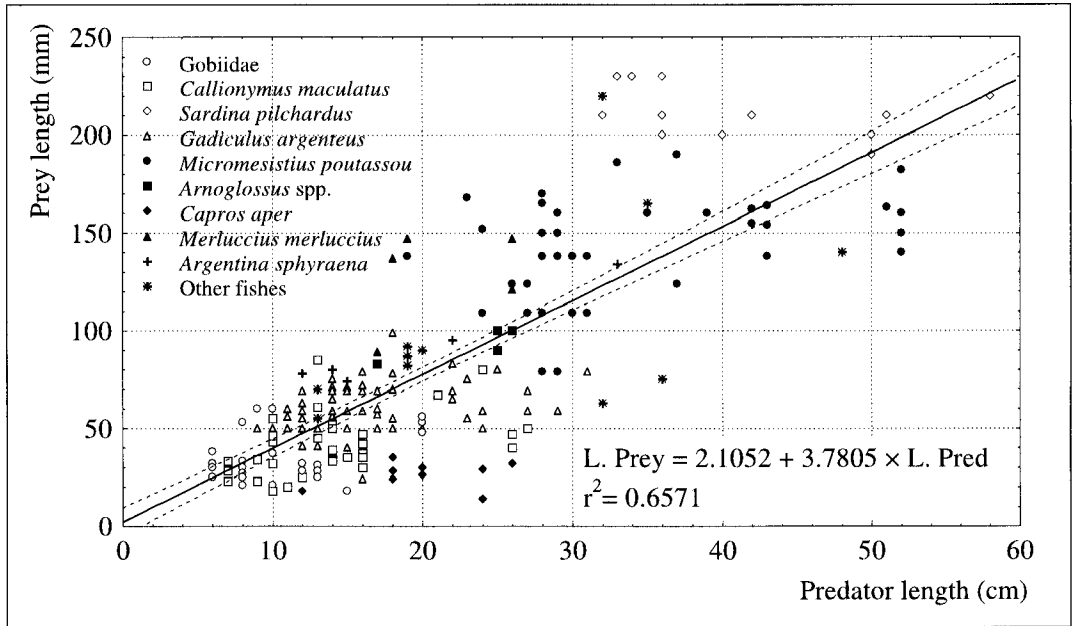


Figure 6. Regression of the prey length versus the predator length

Table V. Number of fish analysed, mean length of fish, percentage of empty stomachs and TFI per depth strata

Depth strata (m)	A: 44-100	B:100-150	C:150-225
No. fishes	234	284	129
Mean length	28.78	18.38	19.12
Empty stomachs (%)	44.02	43.31	29.46
TFI	3.2552	3.7068	3.4993

feeding mainly on small fishes, e.g., gobiids, dragonets, silvery pout, *Capros aper* (Linnaeus, 1758) or *Arnoglossus* spp.; on the other, we have a diet comprising larger fishes with a more pelagic behaviour, mainly blue whiting and sardine, but also *Scomber scombrus* Linnaeus, 1758 or *Ingraulis encrasicolus* (Linnaeus, 1958). Regarding the predators, the shift from one group of prey to the other occurs at approximately 30 cm, i.e., at the same point of the change from length range 12-30 cm to length range 30-58 cm.

DISCUSSION

In the Cantabrian Sea and off Galicia, *Z. faber* is a highly ichthyophagous species,

which starts feeding on fishes from a very small size, even earlier than reported in studies from other regions (Stergiou and Fourtouni, 1991). Size is the main factor determining *Z. faber* feeding pattern, and four different length ranges can be defined, by diet composition: first, a length range in which invertebrates and small benthic fishes play the dominant role; then, around 9 cm, there is a shift to more ichthyophagous behaviour, with invertebrates being replaced by *G. argenteus* –these groups correspond to the two smaller ones of Stergiou and Fourtouni (1991), which they place in a single group, but with larger fish percentages. From 15-29 cm, there is a group that feeds on gadoids, with a declining importance of gobiids and dragonets; and from 30 cm, predation on clupeoids, mainly *S. pilchardus*, begins, as well as *C. rubescens* and *M. poutassou*, with an important increase in prey size, as can be seen in prey size distribution. These groups are similar to those found by Silva (in press) in Portuguese waters. The existence of this larger group, not found in the Mediterranean by Stergiou and Fourtouni (1991), is confirmed by the predator-prey size rela-

tionship, with a very different prey length distribution in those two groups.

There is also a shift from benthic towards pelagic feeding behaviour, covering almost the entire length distribution, which was also reported by Silva (in press). There are three different levels in these benthic-to-pelagic behaviour: the smallest range is almost completely benthic; from 9 to 12 cm there is a transitional stage; from 12-30 cm, *Z. faber* preys on benthic and pelagic preys in similar proportions; and in the largest range, it needs larger preys and goes up the water column searching for pelagic fishes (e.g., sardine or anchovy) – except for *C. rubescens*, its diet in this stage is almost completely pelagic.

Despite the importance of size, depth also has a marked effect on diet composition within each length range, an effect that has not been studied previously. This influence seems to be due to the abundance of preys and their length distribution within each depth strata, as suggested by the variation in abundance of clupeoids or gadoids in the diet with depth: in the largest length range, *S. pilchardus* is replaced by *M. poutassou* as depth increases, and ingestion of *G. argenteus* is always larger in the two deeper strata than in the shallowest one; these results agree with the bathymetric distribution of these species (Sánchez, 1993). Therefore, we can conclude that *Z. faber*, depending on its size, selects its preys according to their size among those available in its different habitats.

ACKNOWLEDGEMENTS

This work resulted from a revision of the stomach contents database during the EU FAIR project CT-95-0604, while the first author was contracted under this project, and it received financial support from the FAIR programme.

REFERENCES

- Bowering, W. R. and G. R. Lilly. 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). *Neth. J. Sea Res.* 29 (1-2): 211-222.
- Field, J. G., K. R. Clark and R. M. Warwick. 1982. A practical strategy for analysing multi-species distribution patterns. *Marine Ecology-Progress Series* 8: 37-52.
- Kruskal, J. B. and M. Wish. 1978. *Multidimensional scaling*. Sage University Series on Quantitative Applications in the Social Sciences: 11. Sage Publications. Beverly Hills, EE UU.
- Olaso, I. 1990. Distribución y abundancia del megabentos invertebrado en fondos de la plataforma cantábrica. *Publicaciones Especiales. Instituto Español de Oceanografía* 5: 128 pp.
- Olaso, I., F. Velasco and N. Pérez. 1998. Importance of blue whiting (*Micromesistius poutassou*) discarded in the diet of lesser-spotted dogfish (*Scyliorhinus canicula*) in the Cantabrian Sea. *ICES Journal of Marine Science* 55: 331-341.
- Pereda, P. and B. Villamor. 1991. Relaciones biométricas en peces de la plataforma cantábrica. *Informes Técnicos. Instituto Español de Oceanografía* 92: 39 pp.
- Righini, P. and A. Voliani. 1996. Distribution and estimates of growth parameters of *Zeus faber* L. in the Tuscan Archipelago. *Biol. Mar. Mediterr.* 3 (1): 567-568
- Robb, A. P. 1992. Changes in the gall bladder of whiting (*Merlangius merlangus*) in relation to recent feeding history. *ICES Journal of Marine Science* 49: 41-436.
- Sánchez, F. 1993. Las comunidades de peces de la plataforma del Cantábrico. *Publicaciones Especiales. Instituto Español de Oceanografía* 13: 137 pp.
- Sánchez, F. 1994. Campaña de evaluación de recursos pesqueros demersales 0991. *Informes Técnicos. Instituto Español de Oceanografía* 155: 51 pp.
- Sánchez, F., F. de la Gándara and R. Gancedo. 1995. Atlas de los peces demersales de Galicia y el Cantábrico. Otoño 1991-1993. *Publicaciones Especiales. Instituto Español de Oceanografía* 20: 100 pp.
- Silva, A. 1992. Distribution and abundance of John Dory (*Zeus faber*, Linnaeus 1758) in the Portuguese continental waters (ICES Div. IXa) during 1986-1991. *ICES C.M.* 1992/G: 68. Demersal Fish Committee: 18 pp.
- Silva, A. In press. Feeding habits of John Dory (*Zeus faber*, Linnaeus 1758) off the Por-

- tuguese continental coast (ICES Div. IXa). *J. Mar. Biol. Assoc. UK*.
- Stergiou, K. I. and H. Fourtouni. 1991. Food habits, ontogenetic diet shift and selectivity in *Zeus faber* Linnaeus, 1758. *J. Fish Biol.* 39: 589-603.
- Velasco, F. and I. Olaso. 1998. European hake *Merluccius merluccius* (L., 1758) feeding in the Cantabrian Sea: seasonal, bathymetric and length variations. *Fisheries Research* 38: 33-44.
- Velasco, F., I. Olaso and F. de la Gándara. 1996. Alimentación de veintidós especies de peces demersales de la división VIIIc del ICES. Otoños de 1992 y 1993. *Informes Técnicos. Instituto Español de Oceanografía* 164: 62 pp.
- Wheeler, A. 1969. *The Fishes of the British Isles and Northwest Europe*. Michigan State University Press. East Lansing, Michigan: 613 pp.
- Whitehead, P. J., M. L. Bauchot, J. C. Hureau, J. Nielsen and E. Tortonese. 1986. *Fishes of the North-eastern Atlantic and the Mediterranean*. Vols I-III: 1 473 pp. Unesco. Paris.
- Received June 1998. Accepted December 1998.