

Feeding habits of John Dory, *Zeus faber*, off the Portuguese continental coast

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The feeding habits of John Dory (*Zeus faber*) were studied, based on the analysis of stomach contents from fish sampled in five groundfish surveys. These surveys were carried out off the Portuguese coast during different seasons between 1990 and 1992. The main aspects of feeding biology analysed in this paper are: ontogenetic diet changes, temporal variations in food composition and feeding intensity. Multi-variate methods were used to investigate ontogenetic diet shifts. Two main length groups were identified: 8.0–24.9 cm fish, feeding mainly on dragonets and silvery pout, and 25.0–55.9 cm fish whose diet was mainly composed of blue whiting and snipefish. A transitional phase (24.0–30.9 cm fish) with a mixed food composition was observed. This ontogenetic diet shift does not seem to correspond to any important change in body morphology but it does coincide with the onset of sexual maturity in the species.

John Dory switched from a diet of small prey species with more pronounced benthic behaviour to a diet of larger schooling pelagic species. This suggests parallel evolution to more pelagic foraging behaviour. However, John Dory feeding habits appear to be largely controlled by the availability and accessibility of prey species: (i) the diet of adult John Dory is dominated by very abundant species; (ii) shifts in the main prey items between different times of the year and between different areas seem to be related both with their absolute and relative abundance in the environment and with the overlap between the depth distribution of predator and prey.

INTRODUCTION

The study of the feeding habits of fish contributes to the knowledge of intra- and interspecific trophic relationships and thus leads to a better understanding of the structure and dynamics of marine communities. When commercially exploited species are involved, as predators and/or as main prey species, the study of their feeding habits is a basic step for multispecies assessment approaches.

The trophic status of a fish in the community may change during its development and ontogenetic diet shifts are a common feature in the life history of most fish species. Among piscivores the most well documented ontogenetic diet shift is probably the transition from invertebrate feeding as juveniles to fish feeding as adults (e.g. Gibson & Ezzi, 1987; Winemiller, 1989; Smale, 1992). The terms 'feeding stanzas' (Paloheimo & Dickie, 1965) and 'threshold lengths' (Parker & Larkin, 1959) are often used in the literature to, respectively, refer to the size groups with common diets and to the length at which dietary changes are observed.

Some of the factors that may determine these shifts include changes in the mouth and gut morphology (e.g. Ross, 1978), seasonality of prey in relation to the occurrence of juvenile stages (e.g. Winemiller, 1989), intra- and interspecific competition (e.g. Robb & Hislop, 1980), and energy maximization (e.g. Stergiou & Fourtouni, 1991). John Dory's (*Zeus faber* L.) shift from a zooplankton and small benthic fish diet to a demersal fish diet at a threshold length of 14 cm, has been associated with energy maximization (Stergiou & Fourtouni, 1991).

The study of food habits and dietary shifts also contributes to the knowledge of physiological and behavioural changes during fish development.

John Dory is a demersal fish that is moderately abundant off the Portuguese coast (Silva, 1992a). It is exploited by trawl and artisanal fishing fleets. Although annual landings seldom exceed 450 tons it has a high market price which is similar to that of hake (*Merluccius merluccius* L.) and monkfish (*Lophius* spp.) (Silva, 1992b). Little more is known about the biology and ecology of this species than the general information given in textbooks. Franca et al. (1970) studied the distribution and population structure of John Dory off the coast of Angola, Janssen (1979) described its population structure off the Dutch coast, and more recently Righini & Voliani (1996) studied John Dory distribution and growth in the Mediterranean.

The only study on the feeding biology of John Dory has been carried out by Stergiou & Fourtouni (1991) who examined the feeding habits, ontogenetic diet shifts and prey selectivity of this species in the eastern Mediterranean.

In this paper data are presented on the food habits and ontogenetic diet shifts of John Dory in Portuguese waters. Temporal changes in food composition and feeding intensity are also presented and discussed.

MATERIALS AND METHODS

John Dory stomachs were sampled during five groundfish surveys carried out off the Portuguese continental coast on board of the RV 'Noruega' belonging to the Portuguese Fisheries Research Institute (Instituto de Investigação das Pescas e do Mar—IPIMAR). Sampling was carried out during October/December 1990, October/November 1991 and February/March, July, October/November 1992 (hereafter respectively designated as autumn 90, autumn 91, spring 92, summer 92 and autumn 92).

Table 1. Length-classes, mean length (standard deviation within brackets) and number of full stomachs in each length class, *Zeus faber*, Portuguese waters 1990–1992.

Length-classes			
Code	Length range (cm)	Mean \pm SD length	No. full stomachs
L1	8.0–12.9	11.0 \pm 1.5	28
L2	13.0–16.9	15.1 \pm 0.9	26
L3	17.0–18.9	17.6 \pm 0.6	46
L4	19.0–20.9	19.8 \pm 0.6	38
L5	21.0–22.9	21.9 \pm 0.6	28
L6	23.0–24.9	23.9 \pm 0.7	31
L7	25.0–26.9	26.0 \pm 0.6	26
L8	27.0–28.9	27.5 \pm 0.6	16
L9	29.0–30.9	29.8 \pm 0.5	31
L10	31.0–32.9	31.9 \pm 0.7	21
L11	33.0–34.9	34.0 \pm 0.6	24
L12	35.0–36.9	35.9 \pm 0.6	30
L13	37.0–38.9	36.8 \pm 0.5	22
L14	39.0–40.9	39.5 \pm 0.6	22
L15	41.0–43.9	42.4 \pm 0.9	28
L16	44.0–46.9	44.7 \pm 0.5	17
L17	45.0–55.9	50.8 \pm 2.6	21

At each station the fish were sorted into 1 cm length-classes. Total length was recorded and the stomach was dissected and immediately frozen at -18°C . Data on sex, maturity stage and individual fish weight were also collected in the 1992 surveys. In the laboratory empty stomachs were recorded and, for those containing food, the contents were blotted dry with absorbent paper and total stomach weight was recorded. Prey were identified to the lowest possible taxonomic level, counted, weighed and measured (total length for fish and carapace length for decapod crustaceans) whenever possible.

To investigate dietary shifts related to the size of fish, samples from all surveys were pooled. This meant a detailed study of temporal changes in diet could not be made but it was essential to ensure an adequate sample size. Fish were grouped into 17 length-classes (codes L1–L17) and the number of full stomachs analysed per length-class ranged from 16 to 46 (Table 1).

From the full list of prey obtained (Table 2), some prey were grouped in higher taxonomic levels (e.g. Phylum, Class, Family or Genera levels) to increase the chances of finding similarities between the different predator length-classes. Prey groups that occurred only once (*Anthozoa*, *Paracentrotus lividus* Lamarck and *Ammodytes* sp.) were excluded from the analysis. Unidentified fish remains were also excluded from the analysis to prevent length groups being considered similar. Fourteen different prey groups were established (Table 2): molluscs (MOL), crustacea (CRU), fish larvae (LAR), *Sardina pilchardus* Walbaum (SAR), *Argentina sphyraena* L. (ARG), *Macrorhamphosus scolopax* L. (MAC), *Gadiculus argenteus* Guichenot (GAD), *Micromesistius poutassou* Risso (MIC), *Cepola macrophthalma* L. (CEP), *Trachurus* spp. (TRA), *Boops boops* L. (BOO), *Callionymus* spp. (CAL), pleuro-nectiforme (PLE) and Gobiidae (GOB).

In order to discuss possible ontogenetic changes in John Dory foraging behaviour, prey were classified as pelagic

or benthic (Table 2) based on Fischer et al. (1981) and Whitehead et al. (1984).

In the study of dietary shifts, statistical methods similar to those used by Stergiou & Fourtouni (1991) were used so that the results are more comparable. Classification methods (cluster analysis) and ordination techniques (multidimensional scaling, MDS) were applied in order to identify groups with similar diets (Legendre & Legendre, 1979; Field et al., 1982).

The number and the weight of each prey group in each of the 17 predator length-classes was computed and then normalized using a $\log(x+1)$ transformation. Dissimilarity matrices for prey numbers and prey weights were computed with the software NTSYS-Pc (version 1.6, Applied Biostatistics, Inc., 1990), using the Bray–Curtis index (Bray & Curtis, 1957):

$$\delta_{jk} = \frac{\sum_{i=1}^s |Y_{ij} - Y_{ik}|}{\sum_{i=1}^s (Y_{ij} + Y_{ik})} \quad (1)$$

where Y_{ij} = number/weight of prey i in length class j ; Y_{ik} = number/weight of prey i in length class k ; δ_{jk} = dissimilarity between the diets of length classes j and k summed over all s prey categories. δ_{jk} = ranges from 0 (identical diets) to 1 (no prey categories in common).

The software Statistica (version 5.1 for Windows, Statsoft Inc., 1995) was used for the multivariate analysis. Cluster analysis was performed using the UPGMA algorithm and an arbitrary level of 60% dissimilarity was assumed to separate groups. The number of dimensions for MDS was chosen after preliminary analysis of the solutions with two and three dimensions. Stress (a measure of the goodness-of-fit) was used as a guide according to the suggestion made by Kruskal & Wish (1981). Both its absolute value and the way stress decreased with the increase in the number of dimensions were considered. In the plot of stress against the number of dimensions, the ‘elbow’ of the curve suggested a 3-D solution with a very low stress value (0.07). However, the 3-D configuration did not add much information to that provided by the 2-D solution and it has the disadvantage of being more difficult to interpret. Therefore, two dimensions were chosen for the analysis of both prey numbers and prey weights with associated stress values of 0.11 and 0.12, respectively. The scatterplot of the observed against the reproduced distances (Shephard diagram) was examined to evaluate the fit of the final 2-D configuration.

Temporal variations in John Dory diet and feeding intensity were investigated for the groups identified by multivariate analysis. The percentage of the main prey groups, in number and weight, in each survey was compared with the corresponding values estimated from the pooled surveys data. For the prey groups whose importance in the diet seemed to present temporal variations, an index of abundance in the study area was estimated and the respective depth range distribution calculated from data obtained from the same surveys.

Feeding intensity was evaluated by the percentage of empty stomachs and by an index of mean stomach weight (I_{sw}), corrected to account for differences in fish size:

Table 2. Number and weight of prey identified in John Dory stomachs, classification of prey as benthic or pelagic and grouping of prey for the analysis of dietary shifts.

Prey group	Prey	Benthic/Pelagic	Number	Weight (g)
	Anthozoa	—	—	1.0
	<i>Paracentrotus lividus</i>	—	1	0.4
MOL	<i>Sepia</i> sp.	B	1	1.5
	<i>Sepia elegans</i>	B	2	5.4
	LOLIGINIDAE	P	2	0.2
	<i>Allotheutis subulata</i>	P	1	3.2
CRU	Crustacea	B	4	1.7
	Euphausiacea	—	3	0.0
	PANDALIDAE	B	5	3.0
	CARIDAE	B	—	1.5
	<i>Pandalina</i> sp.	B	2	0.1
	<i>Pandalina brevirostris</i>	B	6	2.2
	<i>Plesionika</i> sp.	B	3	1.3
	<i>Plesionika heterocarpus</i>	B	11	21.4
	<i>Parapandalus</i> sp.	B	2	1.6
	Fish	—	10	915.6
LAR	Fish larvae	P	2	0.1
SAR	<i>Sardina pilchardus</i>	P	20	944.8
ARG	<i>Argentina sphyraena</i>	P	22	276.5
MAC	<i>Macroramphosus scolopax</i>	P	63	312.4
GAD	<i>Gadiculus argenteus</i>	P	47	145.3
MIC	<i>Micromesistius poutassou</i>	P	89	1727.4
CEP	<i>Cepola macrophthalmia</i>	B	8	83.8
TRA	<i>Trachurus trachurus</i>	P	12	329.0
	<i>Trachurus picturatus</i>	P	1	93.0
BOO	<i>Boops boops</i>	B	2	86.0
AMM	<i>Ammodytes</i> sp.	—	2	14.1
CAL	<i>Callionymus</i> sp.	B	17	11.9
	<i>Callionymus lyra</i>	B	28	49.1
	<i>Callionymus maculatus</i>	B	1	8.2
	<i>Callionymus reticulatus</i>	B	22	40.6
PLE	<i>Pleuronectiformes</i>	B	11	39.3
	<i>Lepidorhombus</i> sp.	B	1	3.5
	<i>Lepidorhombus whiffiagonis</i>	B	1	10.8
	<i>Citharus macrolepidotus</i>	B	1	38.6
	<i>Arnoglossus</i> sp.	B	10	67.5
	GOBIDAE	B	3	18.8
GOB	<i>Gobius niger</i>	B	2	2.1
	<i>Pomatoschistus minutus</i>	B	10	10.3
	<i>Dentelosteus quadrimaculatus</i>	B	1	3.3
	Unidentified remains	—	—	47.1

MOL, Molluscs; CRU, Crustacea; LAR, fish larvae; SAR, *Sardina pilchardus*; ARG, *Argentina sphyraena*; MAC, *Macroramphosus scolopax*; GAD, *Gadiculus argenteus*; MIC, *Micromesistius poutassou*; CEP, *Cepola macrophthalmia*; TRA, *Trachurus* spp.; BOO, *Boops boops*; AMM, *Ammodytes* sp.; CAL, *Callionymus* spp.; PLE, pleuronectiformes; GOB, Gobidae.

$$I_{sw} = \frac{1}{N} \sum_{i=1}^N \frac{\text{stomach weight}_i}{\text{body weight}_i - \text{stomach weight}_i} \quad (2)$$

where stomach weight_{*i*}=stomach (wet) weight of fish *i*; body weight_{*i*}=body weight of fish *i*; N=number of fish in each group and survey.

RESULTS

Food composition and ontogenetic diet shifts

In total, 777 stomachs were examined, of which 323 (42%) were empty and 454 contained food. Table 2 presents the full list of food items identified in the stomachs.

Based on the diet composition of the 17 length-classes, two main groups were identified by cluster analysis (Figure 1): group A formed by 8.0–24.9 cm fish (length-classes L1–L6) and group B formed by 25.0–55.9 cm fish (length-classes L7–L17). These groups were linked at high dissimilarity values (about 80%) both for prey numbers (Figure 1A) and for prey weights (Figure 1B) analysis. A similar picture was clear for the MDS plots for both the prey numbers (Figure 2A) and prey weights analyses (Figure 2B). Exactly the same cluster, identified as group A in the dendrograms, was formed. On the other hand, some of the elements of group B in the cluster analysis now occupy a transitional position. In terms of prey numbers, fish with lengths 25.0–30.9 cm and 35.0–36.9 cm (length-classes L7–L9 and L12) were located between the main groups (Figure 2A). These length

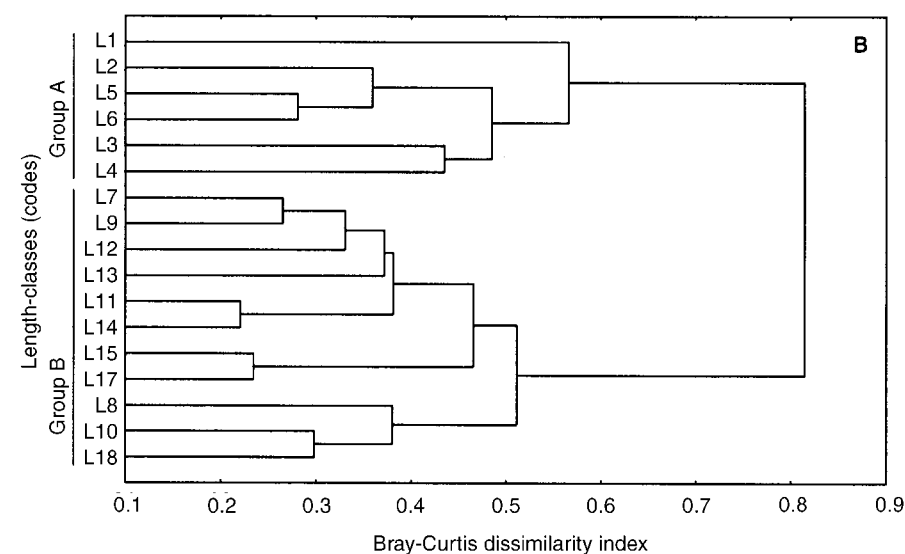
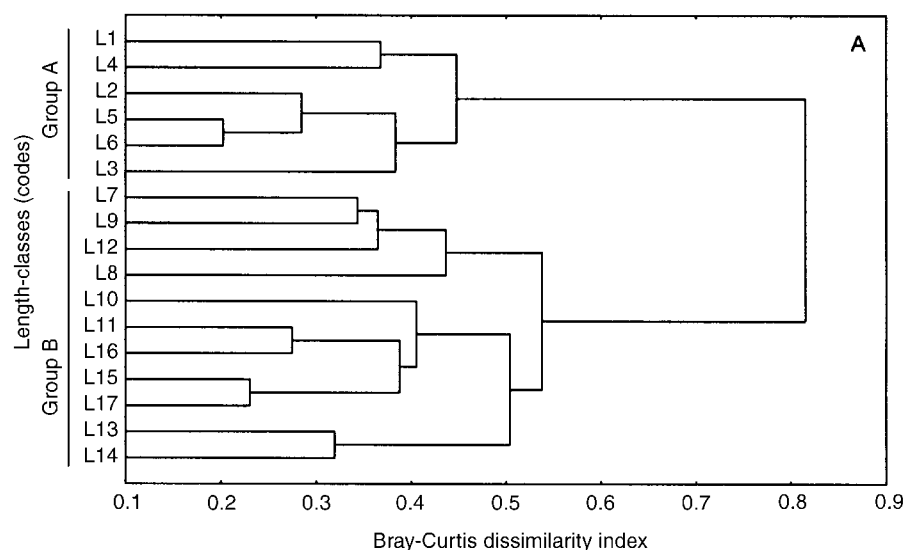


Figure 1. Dendrograms showing the results of classification of John Dory into size groups with similar diets, based on cluster analysis of prey numbers (A) and prey weights (B).

L1 = 8.0–12.9 cm, L2 = 13.0–16.9 cm, L3 = 17.0–18.9 cm, L4 = 19.0–20.9 cm, L5 = 21.0–22.9 cm, L6 = 23.0–24.9 cm, L7 = 25.0–26.9 cm, L8 = 27.0–28.9 cm, L9 = 29.0–30.9 cm, L10 = 31.0–32.9 cm, L11 = 33.0–34.9 cm, L12 = 35.0–36.9 cm, L13 = 37.0–38.9 cm, L14 = 39.0–40.9 cm, L15 = 41.0–43.9 cm, L16 = 44.0–46.9 cm, L17 = 45.0–55.9 cm.

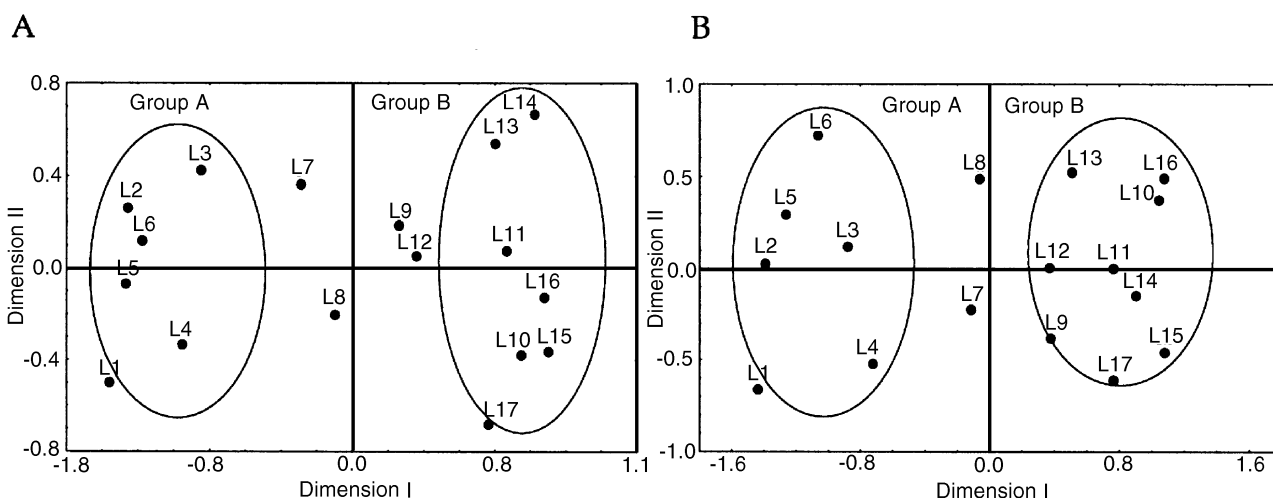


Figure 2. Multidimensional scaling final configuration based on the analysis of prey numbers (A) and prey weights (B) showing the ordination of John Dory into size groups with similar diets. L1 = 8.0–12.9 cm, L2 = 13.0–16.9 cm, L3 = 17.0–18.9 cm, L4 = 19.0–20.9 cm, L5 = 21.0–22.9 cm, L6 = 23.0–24.9 cm, L7 = 25.0–26.9 cm, L8 = 27.0–28.9 cm, L9 = 29.0–30.9 cm, L10 = 31.0–32.9 cm, L11 = 33.0–34.9 cm, L12 = 35.0–36.9 cm, L13 = 37.0–38.9 cm, L14 = 39.0–40.9 cm, L15 = 41.0–43.9 cm, L16 = 44.0–46.9 cm, L17 = 45.0–55.9 cm.

Table 3. Percentage of prey in number (%N) and weight (%W) in the length groups identified by multivariate analysis.

Prey group	Group A (8.0–24.9 cm)		Group B (25.0–55.9 cm)	
	%N	%W	%N	%W
MOL	2.3	0.5	0.8	0.2
CRU	17.6	6.1	2.1	0.2
LAR	1.1	0.0	0.0	0.0
SAR	0.6	5.4	7.9	23.5
ARG	2.8	6.4	7.1	6.4
MAC	0.6	0.2	25.8	7.9
GAD	23.9	28.0	2.1	0.7
MIC	0.0	0.0	37.1	44.0
CEP	1.1	10.7	2.5	1.0
TRA	0.0	0.0	5.4	10.7
BOO	0.0	0.0	0.8	2.2
CAL	34.7	22.3	2.9	0.4
PLE	6.3	12.1	5.4	2.8
GOB	9.1	8.3	0.0	0.0

MOL, Molluscs; CRU, Crustacea; LAR, fish larvae; SAR, *Sardina pilchardus*; ARG, *Argentina sphyraena*; MAC, *Macroramphosus scolopax*; GAD, *Gadiculus argenteus*; MIC, *Micromesistius poutassou*; CEP, *Cepola macrophthalmia*; TRA, *Trachurus* spp.; BOO, *Boops boops*; CAL, *Callionymus* spp.; PLE, pleuronectiformes; GOB, Gobiidae.

classes were also linked in a subgroup, branching from group B in the prey numbers dendrogram. In terms of prey weights, only fish with lengths 25.0–28.9 cm (length-classes L7 and L8) appeared as transitional length-classes

in the Dimension I direction. Thus, predator length increases along Dimension I direction.

Table 3 presents the percentage in number (%N) and weight (%W) of the prey in the diet of the two predator groups identified from the pooled surveys data. *Callionymus* spp. (dragonets) and *Gadiculus argenteus* (silvery pout) represented about 50% of group A prey, both in numbers and in weight. On a numbers basis, Crustacea, Gobiidae and pleuronectiformes were also important food items. However, Crustacea were relatively less important when weight was considered and *Cepola macrophthalmia* (redband fish) increased in importance despite being represented by only two individuals.

For group B, *Micromesistius poutassou* (blue whiting) and *Macroramphosus scolopax* (snipefish) were the most important prey in numbers basis (37.1 and 25.8% respectively). In terms of weight, snipefish was replaced by *Sardina pilchardus* (sardine). *Trachurus* spp. (horse mackerel and Jack mackerel) and *Argentina sphyraena* (argentine) were also of moderate importance for this length group.

Variations in food composition and feeding intensity between surveys

The percentage of each prey item per survey is presented in Figures 3A (group A John Dory) and 3B (group B John Dory). For group A, dragonets were considerably more important in the summer and spring surveys than in the autumn surveys. The opposite can be observed for Crustacea. This is however less clear when looking at weights. Silvery pout is particularly important in the autumn 91 survey and represented a very low

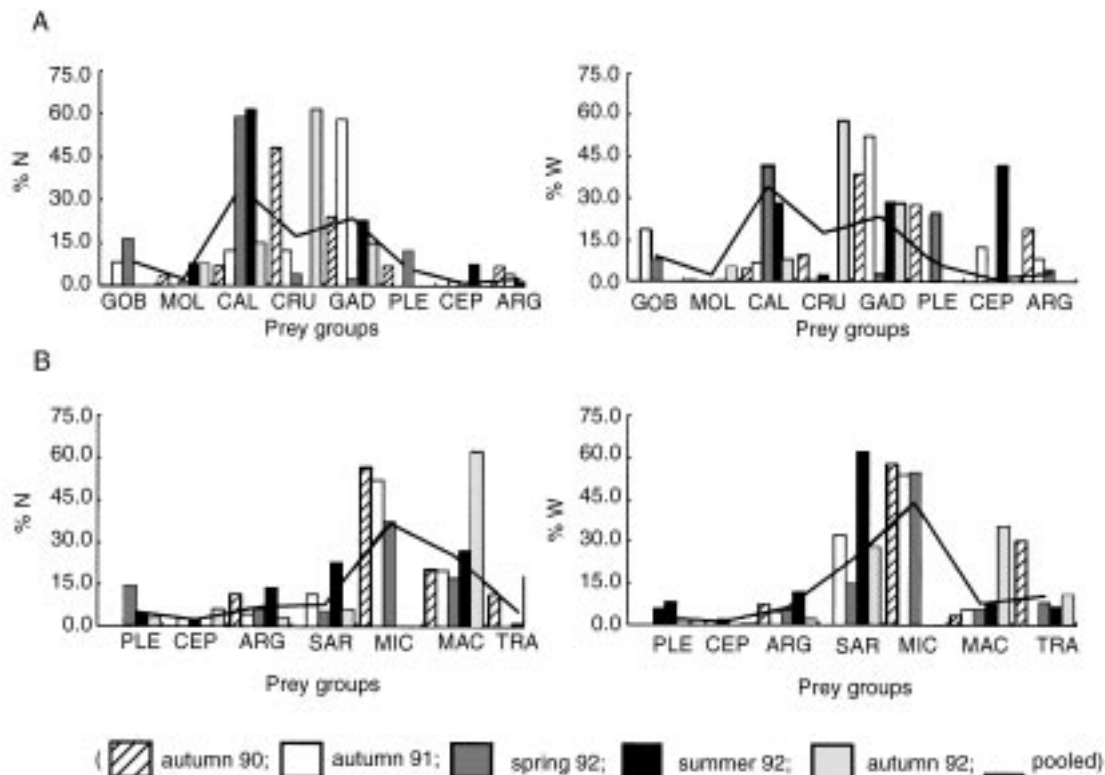


Figure 3. Percentage of each prey category in numbers and weight in group A and group B (A and B respectively) diet in each survey and for pooled surveys data. ARG, *Argentina sphyraena*; BOO, *Boops boops*; CAL, *Callionymus* spp.; CEP, *Cepola macrophthalmia*; CRU, Crustacea; GAD, *Gadiculus argenteus*; GOB, Gobiidae; LAR, fish larvae; MAC, *Macroramphosus scolopax*; MIC, *Micromesistius poutassou*; MOL, molluscs; Cephalopodes; PLE, pleuronectiformes; SAR, *Sardina pilchardus*; TRA, *Trachurus* spp.

Table 4. *Percentage of prey in John Dory diet, index of prey abundance in the environment, depth range distribution of prey and depth range distribution of John Dory in each survey. These data are presented for the main prey items in the diet of group A and group B John Dory.*

Group A (8.0–24.9 cm)	CAL					GAD				
	Aut 90	Aut 91	Spr 92	Sum 92	Aut 92	Aut 90	Aut 91	Spr 92	Sum 92	Aut 92
Percentage prey in the diet (%)	6.9	12.5	58.9	61.5	15.4	24.1	58.3	2.7	23.1	15.4
Prey abundance in the environment (mean no. h ⁻¹)	3.8	1.9	1.6	3.4	6.7	6.2	8.7	0.9	1.8	0.2
Prey depth range distribution (m)	15–224	40–456	34–518	41–320	38–302	100–590	125–546	298–558	106–511	225–550
John Dory depth range distribution (m)	34–300	60–208	73–244	41–355	56–242	34–300	60–208	73–244	41–355	56–242
Group B (25.0–55.9 cm)	MIC					MAC				
	Aut 90	Aut 91	Spr 92	Sum 92	Aut 92	Aut 90	Aut 91	Spr 92	Sum 92	Aut 92
Percentage prey in the diet (%)	56.8	52.2	37.3	0	0	20.4	20.3	17.3	27.3	62.5
Prey abundance in the environment (mean no. h ⁻¹)	3700	2700	1800	1500	1400	10,000	42,000	12,000	98,000	100,000
Prey depth range distribution (m)	68–708	50–700	86–706	65–558	63–680	73–265	85–241	76–255	44–244	70–242
John Dory's depth range distribution (m)	39–242	50–240	54–244	43–355	46–180	39–242	50–240	54–244	43–355	46–180

Aut, autumn; Spr, spring; Sum, summer; CAL, *Callionymus* spp.; GAD, *Gadiculus argenteus*; MAC, *Macroramphosus scolopax*; MIC, *Micromesistius poutassou*.

percentage in the spring 92 survey. Blue whiting, identified as the main group B prey from pooled data, disappeared from the summer and autumn 92 surveys. It was replaced by sardine and snipefish in the summer and exclusively by snipefish in the autumn.

Variations in the dietary importance of dragonets and silvery pout for group A John Dory seem to be associated with both their absolute and relative abundance. The estimated index of abundance of dragonets was generally higher in the summer and autumn surveys and lower in the spring survey (Table 4). This agrees with the findings of Safran (1990) for the French coast. Thus, the greater proportion of dragonets in the diet of John Dory in the summer survey seems to reflect their availability during that season. In spite of their low abundance in spring, dragonets were also very important in John Dory diet in this season. This may be due to the decrease in the relative abundance of silvery pout. This decrease seems to be mainly a consequence of the non-overlapping depth distributions of silvery pout and John Dory. According to Albert (1993), silvery pout exhibits seasonal variations in depth distribution occurring in deeper waters in winter, shallower waters in summer and even shallower waters in autumn off the Norwegian coast. With the exception of the autumn 92 survey, the depth distribution of silvery pout in the Portuguese waters is also shallower in the autumn and deeper in the winter (bearing in mind that the spring 92 survey took place in February/March, i.e. late winter). When silvery pout and John Dory occur at

Table 5. *Feeding intensity indices of group A and group B John Dory in each survey.*

	Survey	I _{SW} ± SD	% empty stomachs	N
group A	autumn 91	0.036 ± 0.043	52	25
	spring 92	0.025 ± 0.029	32	51
	summer 92	0.039 ± 0.060	32	20
	autumn 92	0.025 ± 0.017	30	7
group B	autumn 91	0.024 ± 0.030	42	38
	spring 92	0.021 ± 0.022	43	43
	summer 92	0.030 ± 0.037	32	26
	autumn 92	0.022 ± 0.040	23	17

I_{SW}, index of mean stomach weight (±SD); N, number of fish in each group and survey.

the same depths, the percentage of this prey in the diet also reflects its abundance.

The proportion of blue whiting and snipefish in group B John Dory diet is not limited by depth distributions since for both species a high overlap is observed in all surveys (Table 4). The abundance of blue whiting decreases from autumn 90 to autumn 92 survey. Its importance in John Dory diet also decreases gradually until spring 92 and then disappears completely in the summer and autumn of the same year. Snipefish abundance increased almost ten-fold in these two surveys and

this is reflected in its dietary importance particularly in the autumn survey.

The index of mean stomach weight and the percentage of empty stomachs in each survey for group A and group B fish are presented in Table 5. Observed variations do not suggest a consistent pattern in feeding intensity between surveys. Furthermore, there is no clear trend in feeding intensity between the two groups.

DISCUSSION

The results of this study indicate that, at around a length of 25 cm, John Dory undergoes a major dietary change. It gradually moves from a diet characterized by small fish species such as dragonets, silvery pout, Gobiidae and crustaceans (mainly Pandalidae), to a diet dominated by larger fish species such as blue whiting and sardine. Snipefish, although a relatively small fish, is also numerically an important prey for larger John Dory. This is probably more due to the great abundance of this species in the Portuguese waters than the reflection of a true food preference.

Stergiou & Fourtouni (1991) studied the food habits and ontogenetic diet shifts of John Dory in the eastern Mediterranean. Based on a similar range of fish lengths, they identified a single dietary shift around 14 cm total length. This corresponds to the transition from a diet dominated by mysids, *Callionymus maculatus* Rafinesque and *Deltentosteus quadrimaculatus* Valenciennes to a diet dominated by *C. macrophthalmus*, *Spicara flexuosa* Rafinesque and *Serranus hepatus*. The smaller length group was also divided into a zooplanktophagous stage (5.1–8.0 cm fish) and a transitional stage to piscivory (8.1–14.0 cm fish). In a sample of nine individuals in the length range 2.7–11.7 cm from the west coast of Scotland, Gibson & Ezzi (1987) also found that mysids and small benthic fish were the main prey of John Dory.

Our results did not show any stage where the zooplankton was the dominant prey (only three Euphausiacea were identified in a fish of 18 cm). This may be because of the small number of stomachs sampled from lower length-classes (only six stomachs from fish 8.0–9.9 cm). This undersampling may also explain the lower threshold length observed by Stergiou & Fourtouni (1991) when compared to that observed in the present study (14 and 25 cm, respectively).

The feeding spectra of John Dory with lengths of less than 14 cm in the eastern Mediterranean (Stergiou & Fourtouni, 1991) closely resembles that of individuals of up to 25 cm analysed in this study, i.e. main prey species correspond to small benthic fish and crustacea. The same genera and species are even observed in the two areas. On the other hand, the species composition of the diet of larger fish differs considerably in the two areas. In the eastern Mediterranean John Dory changes to a diet characterized by larger demersal fish and *C. macrophthalmus* is largely dominant, whereas in Portuguese waters John Dory feeds mainly upon larger pelagic fish and blue whiting is dominant.

The method used here to classify prey as benthic or pelagic represents a simplification and imposes a rather rigid division in a behavioural trait that is seldom very clear. In fact, some Pandalid crustaceans, that are usually

classified as benthic in general textbooks, are known to have strong swimming activity and occupy the whole water column adjacent to the sea-floor (e.g. Dauvin et al., 1994). Silvery pout, generally designated as a pelagic fish, is also found close to the sea-floor (Priede et al., 1994). Even for blue whiting, sardine and snipefish, which are often considered typical pelagic species, the classification is not fully descriptive of their behaviour. Both blue whiting and sardine exhibit vertical migrations forming dense shoals close to the sea bed in some circumstances (Bailey, 1982). Snipefish is caught in large quantities by bottom trawls (Cardador et al., 1994), which indicates that it also occurs in the lower water layers.

Nevertheless, this simplified classification enables a general pattern for John Dory feeding behaviour to be established according to fish growth. This pattern suggests that younger individuals depend mainly on bottom-dwelling or benthopelagic prey, living close to the bottom whereas, John Dory larger than 25 cm begin to exploit a wider range of the water column, preying mainly upon schooling pelagic species. In a study of trophic interactions in fish communities in South Africa, Smale (1992) observed that numerous demersal fish species exhibit vertical migrations to exploit pelagic prey. In this category he included a southern relative of John Dory, the cape dory *Zeus capensis* L.

The availability and accessibility of prey are probably the main factors determining the importance of certain species in the diet of John Dory. They explain differences in diet at different times of the year and between different areas such as the Portuguese coast and the eastern Mediterranean. The main pelagic species consumed by mature John Dory (blue whiting, sardine and snipefish) are very abundant in Portuguese waters and usually form dense schools. This behaviour is known to significantly increase the benefit/cost ratio of prey consumption. This type of opportunistic behaviour also becomes apparent from the analysis of John Dory diet in different surveys. The observed variations in the importance of the main prey for both mature and immature John Dory seems to be mainly determined by the absolute and relative abundance of prey and co-occurrence at the same depths as John Dory. This reasoning can also be applied to the differences between our results and those of Stergiou & Fourtouni (1991) regarding the diet of larger John Dory. The redband fish is an uncommon species in Portuguese waters. In groundfish surveys average catch rates (rarely exceeding one individual per hour) are several thousands of times lower than those of snipefish and blue whiting. On the other hand, snipefish was not present in the area studied by Stergiou & Fourtouni (1991) and blue whiting was present with (about) the same abundance as the redband fish (this may be because the area sampled was of a maximum depth of 135 m and blue whiting is typical of the shelf edge).

The observed threshold length (25 cm) does not seem to correspond to any important change in John Dory's mouth gape or overall body morphology (Stergiou & Fourtouni, 1991). It does however coincide with the onset of the first reproductive development in this species. Indeed data from which the analysed stomachs were obtained, show that sexually active individuals are larger

than 24 cm although the numbers of pre- and post-spawning fish are only significant beyond a length of 36 cm (fish in spawning condition are always scarce) (A.S., unpublished data).

The energy expenditure of the maturation process is widely studied in the context of annual reproductive cycles of fish (Hoar, 1969; Love, 1970). The first maturation may represent the onset of a life history stage involving much higher energetic demands and this may require a considerable change in food habits. John Dory dietary shift did not involve an increase in the number of prey consumed, so increased energetic needs seem to have been satisfied by the ingestion of larger and heavier prey. The process of sexual maturation and spawning has also been associated with an ontogenetic diet change in cod, *Gadus morhua* L. (Paz et al., 1993).

Stergiou & Fourtouni (1991) related the dietary shift from zooplankton to fish in 8 cm John Dory to a change in the growth pattern. This change was seen in the length–weight relationship as an increase in the rate of weight gain. In this study, the slope (b) of the log transformed length–weight relationship increases significantly from fish with 8–24.9 cm ($b=2.58$, $SD=0.056$) to those with 25–55.9 cm ($b=3.25$, $SD=0.046$) (test for comparison of means, $d=-103.81$, $P=0.000$). The dietary shift described in this study is therefore also reflected in a change in the length–weight relationship.

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