Diet comparison of four ray species [*Raja clavata* Linnaeus, 1758; *Raja brachyura* Lafont, 1873; *Leucoraja naevus* (Müller & Henle, 1841) and *Raja montagui* Fowler, 1910] caught along the Portuguese continental coast

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Abstract

In NE Atlantic, skates and rays represent more than 40 % of elasmobranch landings. In Portugal, as in most European countries, these species are commonly landed under the generic designation *Raja* spp.. After a sampling program for the identification of species composition of *Raja* spp. landings along the Portuguese continental coast, *Raja clavata* and *Raja brachyura* were found to be the most common species, followed by *Leucoraja naevus* and *Raja montagui*, which represented nearly 40 % of the remaining sampled specimens. Diet studies are important for the comprehension of biological and ecological interactions and its subsequent information can be integrated in stock assessment methods. The present paper analyses the diets of four rajid species (*Raja clavata*, *R. brachyura*, *Leucoraja naevus* and *R. montagui*), caught in mainland Portugal, based on the examination of stomach contents. Food items were identified to the minimum *taxon* possible. For a quantitative analysis, the index of relative importance, the percentage frequency of occurrence and the percentages by number and by weight were determined for the major taxonomic groups found, namely Polychaeta, Crustacea (divided into 9 categories), Cephalopoda and Osteichthyes. Results indicated the

existence of ontogenetic dietary shifts in all species. Despite some differences in feeding habits between species, Crustacea: Decapoda and Osteichthyes were the most frequent preys.

Introduction

In the last decades, the commercial interest on cartilaginous fishes has increased worldwide mainly due to the depletion of many commercial bony fish stocks, as a consequence of over-exploitation and absence or fallible regulation of its fisheries, together with an increasing interest on elasmobranch muscle, cartilage, liver oil and fins (Stehmann, 2002).

In North-eastern Atlantic, skates and rays represent more than 40 % of elasmobranch landings. The order Rajiformes is one of the most important among elasmobranchs mainly for its species diversity and economical value (Walker, 1999). Although landings have been relatively stable along the years, this trend can be deceiving since ray species exhibit different levels of resilience to exploitation and the present statistical information is limited by the fact that most European countries record their landings without differentiation by species (Walker, 1999). The same happens in Portuguese ports where, with the exception of *Leucoraja naevus*, species are commonly landed under the generic designation *Raja* spp..

After a sampling program for the estimation of species composition of *Raja* spp. landings along the Portuguese continental coast, *Raja clavata* and *Raja brachyura* were found to be the most common species, whereas *Leucoraja naevus* and *Raja montagui* represented nearly 40 % of the remaining sampled specimens (Machado *et al.*, 2004).

The quality and quantity of food are important exogenous factors that directly affect growth and, indirectly, maturation and mortality (Wootton, 1990, *in* Stergiou & Karpouzi, 2002).

Diet studies are important for the comprehension of some population phenomena, such as migrations, competition and physiological variations, and consequently for the interpretation of fluctuations in stock production (Assis, 1992). Nowadays the compilation of existing stomach content data for various aquatic organisms seems to be one among many necessary steps for the development of ecosystem models through the use of various modelling tools (Stergiou & Karpouzi, 2002). In recent ecosystem approaches for the evaluation of stock status, the integration of information on diet and trophic relationships is fundamental (Hérran, 1988).

In fishes, the study of feeding ecology by direct methods is usually difficult or even impossible. Analysis of the digestive tract contents of collected specimens is the most common technique to overcome the difficulty of making direct observations and allows obtaining qualitative and quantitative information on the variety and abundance of digested preys (Assis, 1992).

Rajids are benthic (Cunha *et al.*, 1987) nocturnal predators that locate their preys by smell, touch and electro-reception (Steven, 1930; Kalmijn, 1966; Ajayi, 1982; Walker, 1999). Certain species have semi-benthic feeding habits, presenting the ventral surface dark grey or blue instead of white, as benthic species do (Walker, 1999).

The objective of the present study was to analyse the diets composition and feeding strategies of four rajids species, namely *Raja clavata*, *R. brachyura*, *L. naevus* and *R. montagui*, present along the Portuguese continental coast, based on stomach contents analysis and performing intra and interspecific comparisons by size, sex and geographic and seasonal distribution.

Methodology

For this study, 159 stomachs of *Raja clavata*, 97 of *Raja brachyura*, 135 of *Leucoraja naevus* and 127 of *Raja montagui* were analysed. Samples were collected from commercial landings and both pelagic and bottom trawl surveys.

For each specimen, the geographic area and date of capture, total length to the nearest mm, total weight to the nearest g, sex and maturity were registered. Maturity stages were assigned based on Stehmann's (2002) scale, which combines external and internal sexual characteristics. Stomachs were weighted with their contents to the nearest 0.01 g and frozen for posterior analysis. Later, stomach's total contents were determined as the difference in weight between the unfrozen stomach and the stomach wall.

The vacuity index was calculated for each species and sex as the percentage of empty stomachs in the whole sample of stomachs. A stomach was considered to be empty when it only contained a small amount of digested and unidentified material, sediment or specimens belonging to the filo Nematoda. Although relatively frequent, these animals were excluded from the analysis because they are common parasites of the digestive tract of many species and are, therefore, highly improbable food items.

Each stomach was dissected by cutting along the antero-posterior axis and the contents were classified to the lowest possible identifiable taxonomic level. Specimens were further separated into the major taxonomic groups found: (a) Polychaeta; (b) Crustacea; (c) Crustacea: Amphipoda; (d) Crustacea: Mysidacea; (e) Crustacea: Isopoda; (f) Crustacea:

Decapoda; (g) Crustacea: Decapoda: Dendrobranchiata + Caridea; (h) Crustacea: Decapoda: Anomura; (i) Crustacea: Decapoda: Macrura; (j) Crustacea: Decapoda: Brachyura; (k) Cephalopoda; and (l) Osteichthyes. For each food category, weight and degree of digestion were also registered. Specimens belonging to *taxa* Algae, Cnidaria, Sipuncula, Mollusca: Bivalvia, Mollusca: Gastropoda and Echinodermata were categorized as "Others", weighted and counted as a unique prey item. Unidentified material was excluded from the analysis since its occurrence was negligible.

For an ontogenetic analysis of the predators' diets, the relative importance of each food item was determined using the mean partial fullness index (PFI):

$$PFI_i = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{ij}}{(TL_j)^3}\times 10^4 \text{ ,}$$

where W_{ij} is the weight of the i^{th} prey in the j^{th} stomach, TL_j is the total length of the j^{th} predator (in cm) and n is the total number of stomachs (Lilly & Rice, 1983). Dietary trends were graphically evaluated for each sex by plotting Mean PFI *vs.* TL class (10 cm classes).

For comparing species feeding strategies, the following indices were determined: (a) percentage by number (%N), that corresponds to the fraction of the total number of specimens from a certain prey-*taxon* relatively to the total number of identified specimens; (b) percentage by weight (%W), that corresponds to the total weight of a given prey-*taxon* divided by the total weight of all contents; and (c) percentage frequency of occurrence (%O), which is the number of stomachs where a specific prey-*taxon* occurs divided by the total number of analysed stomachs.

Within each sex, individuals were separated into two length groups: "small" (< 50 cm) and "large" (≥ 50 cm). The value 50 cm is close to the length at maturity for *Raja clavata*, *R. montagui* and *Leucoraja naevus*. Even though *R. brachyura* matures at a much larger total length – around 90 cm (Walker, 1999) –, the limit was also set on 50 cm because larger individuals were underestimated and, as will be seen further on in this work, a dietary shift was observed around this size.

To test the null hypotheses of no differences between sexes in the number of stomachs where a certain prey item occurs (O) on each length group, χ^2 tests were performed with a significance level of 5 %. To test the null hypothesis of no differences between sexes in the weight of each prey group (W), a univariate test of significance was performed with a p-value > 0.05.

Based on Cortés (1997), feeding strategy plots were constructed for each predator species displaying the stomach contents in terms of %N, %W and %O in a three-dimensional diagram. The two defined length groups were presented in different plots.

This graphical approach consents classifying diet in terms of prey importance, distinguishing dominant from rare *taxa*, and of predator feeding strategy, which can be either generalist or specialist. In this three-dimensional graphic any point located close to 100 % in the three axis represents a dominant food item whereas any point located near the origin corresponds to a rare prey. The other six vertices can be regarded as extreme cases that point to either generalized or specialized diets. Thus a cluster of points located close to 100 % O and the origin of at least one of the other axis represents a generalized diet. Alternatively, a cluster near 100 % O and 100 % for at least one of the other indices corresponds to a specialized diet.

Percent index of relative importance (%IRI) was determined for each food category, according to the equation:

$$\%IRI = \frac{\%O \times (\%W + \%N)}{\sum [\%O \times (\%W + \%N)]} \times 100 \cdot$$

Schoener's (1970) diet overlap index was determined using percentage by weight (%W) as diet measure (Wallace, 1981). A cluster analysis approach was applied in order to get some insight about trophic differences between the four species further divided by length group. In this analysis, Schoener's (1970) dissimilarity index and Ward's clustering method were used.

Results

Table I summarizes the number of analysed stomachs and the vacuity index for each species, by sex and length group. All species, except for *Leucoraja naevus*, present very low values of vacuity index. In males of *Raja clavata* and of *R. brachyura* the vacuity index is higher than in females, whereas the opposite is registered for the other two species. In *L. naevus*, the value for females is almost two times the one for males and is much higher than for the other species.

The identified prey-items for each predator species and information on their distribution and habitat are listed in Annex I.

Mean PFI *versus* Predator's total length class graphical representations (Fig. 1) suggest ontogenetic shifts in diets at length classes around 45-50 cm for both sexes and for the four predator species. In calculating this index, length was used in preference to weight as a measure of predator size because the former is not influenced by changes in muscle, liver, gonads and stomach contents (Lilly & Rice, 1983).

Table I. Number of stomachs sampled (n), by species, sex (F - females; M - males) and length group (S - small; L - large) and vacuity index estimates (%V.I.).

			Raja clavata	***Raja brachyura***	***Leucoraja naevus***	***Raja montagui***
F	n	S	11	5	27	32
		L	62	56	55	33
	%V.I.		0	1.6	17.1	4.6
M	n	S	11	5	20	34
		L	75	31	33	28
	%V.I.		3.5	2.8	9.4	1.6

In *Raja clavata* (Figs. 1-A and B), the shift is not only quantitative but also qualitative. Small individuals feed mainly on Mysidacea and Polychaeta and also indiscriminate Crustacea and Decapoda, but the mean PFI values are low. For specimens larger than 45 cm, the values of mean PFI increase and individuals feed mainly on Cephalopoda, Osteichthyes and Decapoda: Brachyura. The highest values are registered for specimens in 60 to 70 cm length classes. The values of mean PFI of Decapoda: Dendrobranchiata + Caridea in females are higher than in males.

In *Raja brachyura* (Figs. 1-C and D), Osteichthyes were excluded from the graphical analysis since this *taxon* shows very high values in all the size classes comparatively to the remaining preys thus causing an underestimation of their importance. In this species, the ontogenetic shift is more evident in qualitative term. In comparison to small females around 45 cm, the values of mean PFI of Mysidacea and indiscriminate Crustacea decrease and higher values are registered for Polychaeta and Dendrobranchiata + Caridea. A second change occurs at around 70 cm – Polychaeta become rare preys and Cephalopoda the second most important prey-*taxon*. Brachyura, Dendrobranchiata + Caridea and Polychaeta show high values for females between 30 and 45 cm, but for specimens larger than 50 cm Cephalopoda are the second most important preys for both sexes.

In *Leucoraja naevus* (Figs. 1-E and F), the most evident ontogenetic shift occurs with the emergence of Osteichthyes as dominant preys (showing very high values of mean PFI) in stomachs of individuals larger than 45 cm. Females with lengths between 25 and 35 cm present high values for Mysidacea, which only appear among males with 45-50 cm. In this species, few differences on diet are observed between sexes.

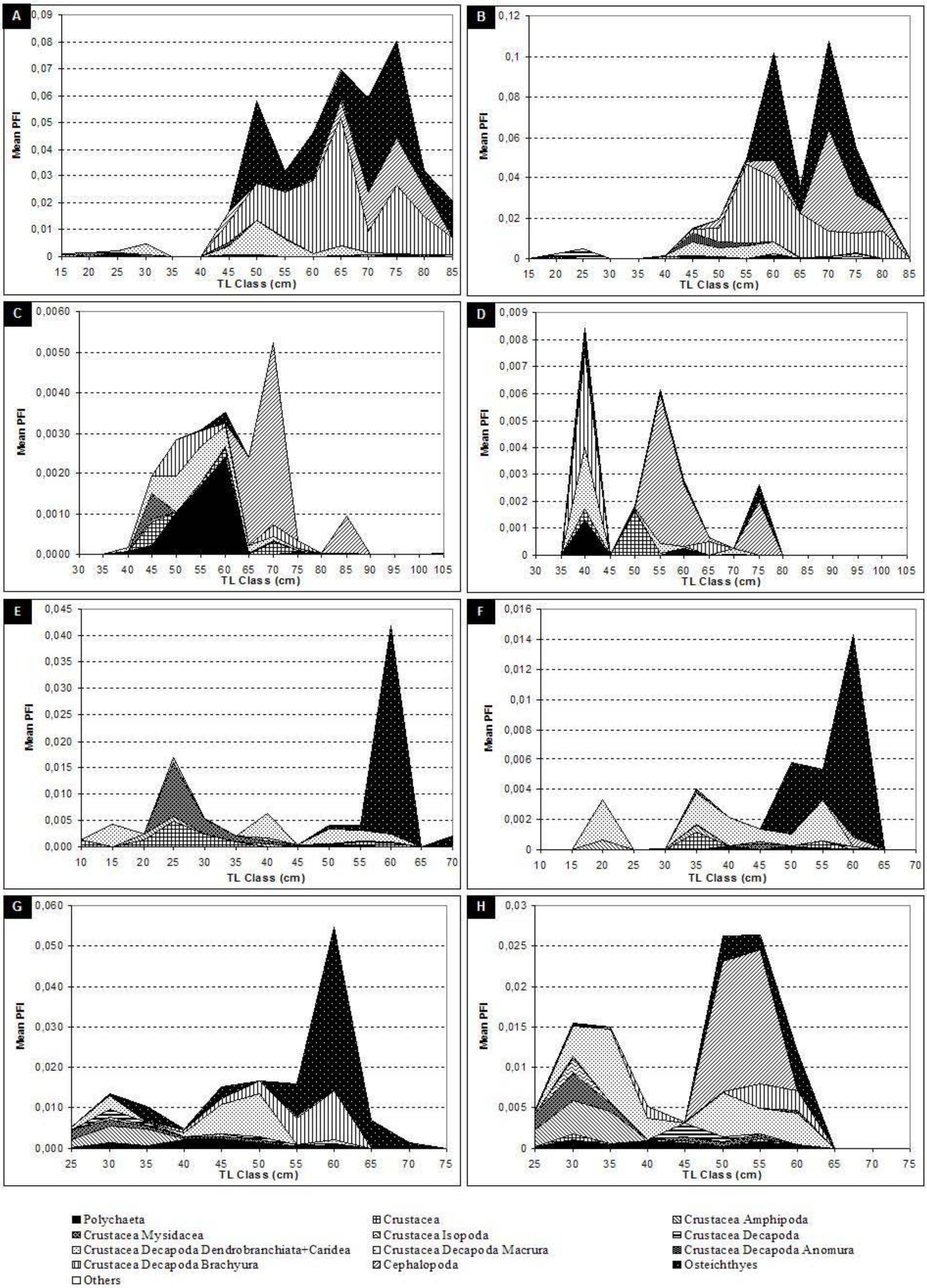

Figure 1. Mean partial fullness index (PFI) *versus* total length class (cm). A - *Raja clavata* females; B - *R. clavata* males; C - *R. brachyura* females; D - *R. brachyura* males; E - *Leucoraja naevus* females; F - *L. naevus* males; G - *R. montagui* females; H - *R. montagui* males.

In *Raja montagui* (Figs. 1-G and H), the detected ontogenetic changes are both quantitative and qualitative and similar for females and males. In small individuals, the most important preys are Dendrobranchiata + Caridea, Isopoda, Mysidacea, Amphipoda and Polychaeta (besides indiscriminate Crustacea). Small females also feed on Osteichthyes but the values of mean PFI are very low. In large females, Osteichthyes are the dominant preys followed by Decapoda: Brachyura. In males, Dendrobranchiata + Caridea are equally important in large as in small predators. In large males, Cephalopoda, Decapoda: Brachyura and Osteichthyes show high values of mean PFI, in descending order. In this species, prey diversity decreases from small to large females and large males show the most diversified diet of all predators in analysis.

Results of the statistical comparison between sexes of O and W by length group are presented in Table II.

Table II. Estimated statistics comparing sexes for each length group (S - small; L - large). χ^2=20.03 with α=0.05 for O. p>0.05 for W. r - H_0 is rejected; nr - H_0 is not rejected.

Index	*R. clavata*				*R. brachyura*				*L. naevus*				*R. montagui*			
	S		L		S		L		S		L		S		L	
O	7.78	nr	12.23	nr	10.24	nr	14.43	nr	12.52	nr	7.69	nr	11.11	nr	10.33	nr
W	0.39	nr	0.24	nr	0.37	nr	0.80	nr	0.16	nr	0.16	nr	0.24	nr	0.43	nr

Based on these results, no significant differences were found between sexes. Therefore the feeding strategy plots were constructed combining data from females and males, for all predators and for each length group. Figure 2 represents the feeding strategy three-dimensional plots based on stomach content analysis for each rajid species, which is briefly summarized in Table III.

Table III. Feeding strategies by species and length group.

Length group	*Raja clavata*	*Raja brachyura*	*Leucoraja naevus*	*Raja montagui*
small	Dominance of Crustacea. Most important preys are Decapoda: Dendrobranchiata + Caridea.	Preponderance of Decapoda: Dendrobranchiata + Caridea; Osteichthyes; and Crustacea.	Most important preys are Decapoda: Dendrobranchiata + Caridea, Mysidacea and Crustacea.	Dominant preys: Polychaeta, Amphipoda and Mysidacea.
large	Decapoda: Brachyura are the dominant preys. Osteichthyes, Crustacea and Decapoda: Dendrobranchiata + Caridea also important.	Osteichthyes are the dominant preys. Decapoda: Dendrobranchiata + Caridea and Crustacea also important.	Osteichthyes are the dominant preys. Polychaeta, Crustacea and Decapoda: Dendrobranchiata + Caridea also important.	Preponderant preys: Polychaeta; Crustacea and Osteichthyes.

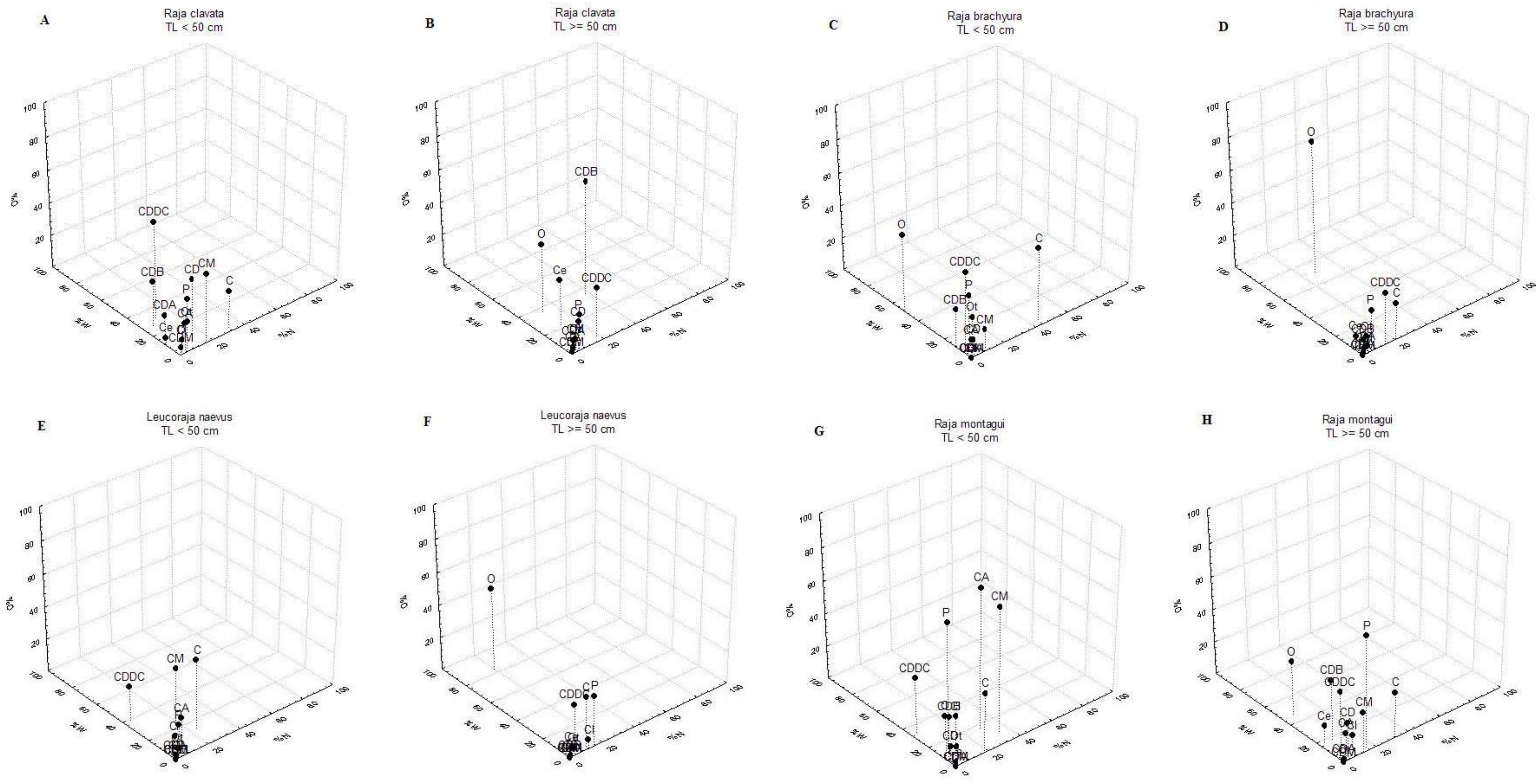

Figure 2. Feeding strategy three-dimensional representations of: (A) Small *Raja clavata*; (B) Large *R. clavata;* (C) Small *R. brachyura*; (D) Large *R. brachyura*; (E) Small *Leucoraja naevus*; (F) Large *L. naevus*; (G) Small *R. montagui*; (H) Large *R. montagui*. Prey codes: P - Polychaeta; C - Crustacea; CA - Crustacea: Amphipoda; CM - Crustacea: Mysidacea; CI - Crustacea: Isopoda; CD - Crustacea: Decapoda; CDDC - Crustacea: Decapoda: Dendrobranchiata + Caridea; CDA - Crustacea: Decapoda: Anomura; CDM - Crustacea: Decapoda: Macrura; CDB - Crustacea: Decapoda: Brachyura; Ce - Cephalopoda; O - Osteichthyes; Ot - Others.

The results for %IRI are graphically represented in Figure 3. Expressing the IRI as a percentage allows obtaining a robust estimate of the relative importance of each prey-*taxon* and, therefore, facilitates comparisons between them (Cortés, 1997). This index is essentially a mean of the three included diet measures for each food category (Wallace, 1981).

In *Raja clavata*, Crustacea: Decapoda: Dendrobranchiata + Caridea are the most important preys in small specimens, while Crustacea: Decapoda: Brachyura are in the larger ones. In *R. brachyura*, the most important preys are Osteichthyes followed by Crustacea (indiscriminate) and Decapoda: Dendrobranchiata + Caridea for both length groups. In small *Leucoraja naevus*, indiscriminate Crustacea and Crustacea: Mysidacea are the main prey types, changing to Osteichthyes in the "large" length group. *R. montagui* show the highest %IRI values for Crustacea Amphipoda and Mysidacea, in the small specimens' group, and for Osteichthyes and Polychaeta, in the other one.

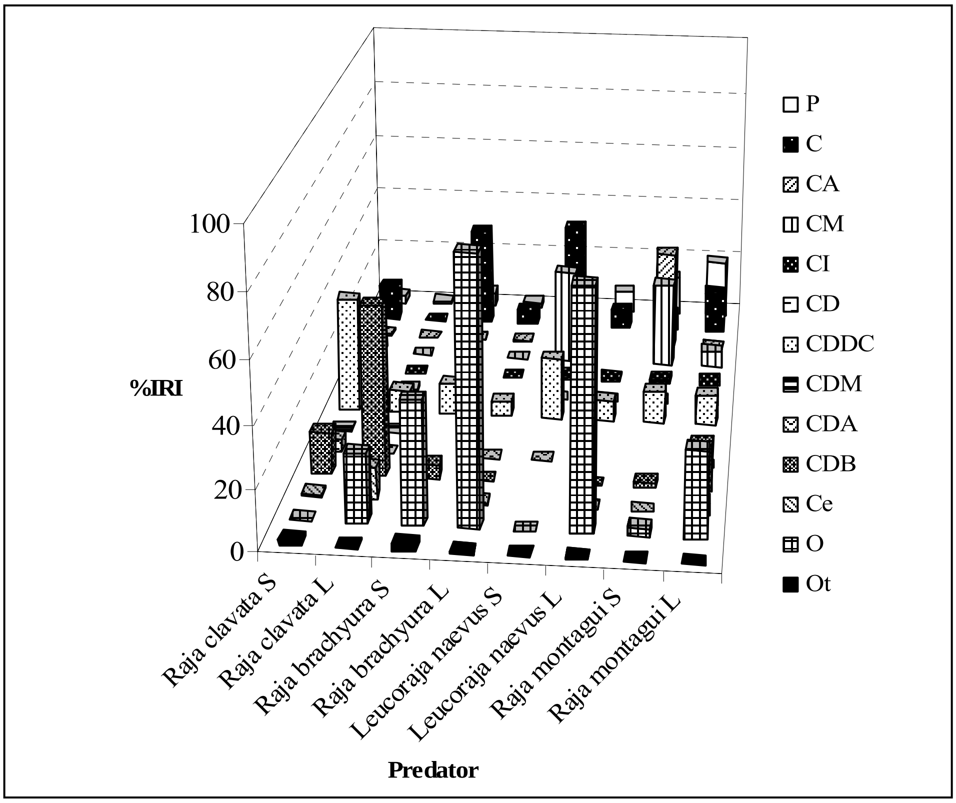

Figure 3. Index of relative importance (%IRI) by species and length group (S - small; L - large). Prey codes: P - Polychaeta; C - Crustacea; CA - Crustacea: Amphipoda; CM - Crustacea: Mysidacea; CI - Crustacea: Isopoda; CD - Crustacea: Decapoda; CDDC - Crustacea: Decapoda: Dendrobranchiata + Caridea; CDA - Crustacea: Decapoda: Anomura; CDM - Crustacea: Decapoda: Macrura; CDB - Crustacea: Decapoda: Brachyura; Ce - Cephalopoda; O - Osteichthyes; Ot - Others.

The dendrogram (Fig. 4) relates small and large individuals of the four analysed species in terms of diet similarity. In this graphical representation, the smallest the linkage distance the biggest the similarity between the diets. Results from cluster analysis indicate that large and small length groups are separated into two different clusters.

Large *Raja brachyura* and *Leucoraja naevus* present the most similar diets. Small *R. brachyura* are posteriorly linked to this pair. Large *R. clavata* and *R. montagui* are grouped together. Small *L. naevus*, small *R. montagui* and later small *R. clavata* are group apart from the previous ones. Further ahead, all large individuals plus small *R. brachyura* are clustered together.

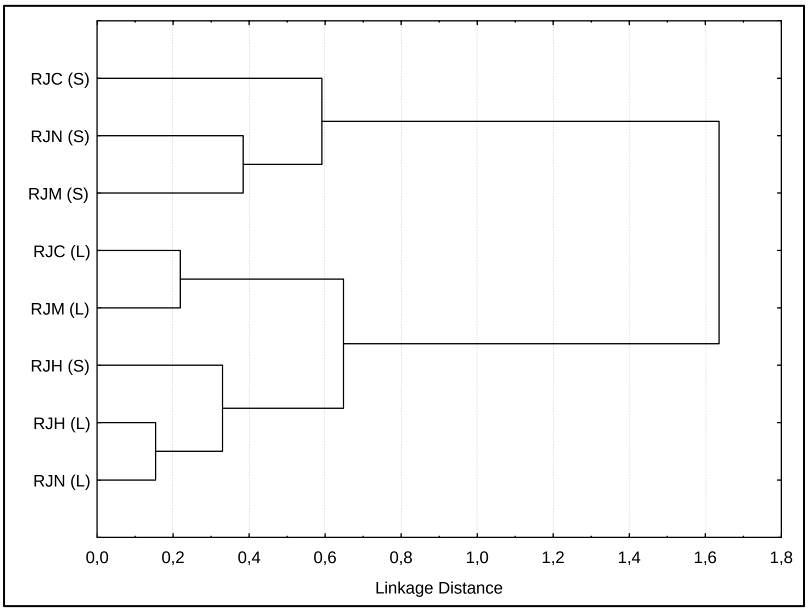

Figure 4. Cluster analysis of prey similarity between species divided by length group (S - small; L - large) [Ward's method; dissimilarity matrix based on Schoener's (1970) method]. Similarity was determined from percentage by weight of prey categories. RJC - *Raja clavata*; RJH - *Raja brachyura*; RJN - *Leucoraja naevus*; RJM - *Raja montagui*.

Discussion

The analysis of stomach contents is not an easy task because some food items appear very digested, complicating their identification and quantification. In fact, some predators, like *Raja clavata*, *Leucoraja naevus* and *R. montagui*, can chew food prior to ingestion (Daan *et al.*, 1993). This situation was particularly evident in the case of large preys such as Crustacea: Decapoda and Osteichthyes. Other preys present relatively high digestion rates. For example, small preys like Polychaeta and Crustacea other than Decapoda are more promptly digested and are therefore hardly identifiable. The most obvious consequence of those difficulties was the impossibility of identifying many crustaceans, causing an overestimation in number and an underestimation in weight of the prey-group Crustacea, since it included all indiscriminate preys belonging to this filo.

Leucoraja naevus was found to have a much higher vacuity index than the other species, fact that is in agreement with previous similar works (Holden & Tucker, 1974; Ellis *at al.*, 1996). The vacuity index can be related to the time that a specific item takes to be digested. Piscivorous species are generally found to possess a relatively high index of vacuity, whether because Osteichthyes have a higher nutritional value than Crustacea and are more rapidly digested or because feeding is restricted to success in prey capture (Ellis *et al.*, 1996). Nonetheless, *Raja brachyura* is a piscivorous species and yet shows a relatively low vacuity index. Another explanation for the occurrence of empty stomachs could be the full stomach eversion, a mechanism described for some elasmobranchs. Stomach eversion, followed by its swallowing, allows removing parasites, indigestible material, toxic food and remains of gastric mucosa and mucus (Sims *et al.*, 2000).

There is a wide range of indices and statistical methodologies that can be applied in the study of feeding strategy and behaviour. Among many others, number, weight and percent frequency are of the most commonly used, mainly due to their simple interpretation. Abundance indices reflect the density-dependent prey acquisition by predators, thus providing some insight into their feeding behaviour. Volume and weight indices reflect prey species nutritional value, being preferably used when prey items are too numerous to be counted. Percent frequency of occurrence gives an indication of prey species variability in diets, thus being particularly appropriate when there are not many food categories. (Macdonald & Green, 1983)

The stomach fullness index can provide more insightful comparisons than the previous methods, since it is not strongly influenced by the frequent occurrence of small prey which contribute little to total weight, as is the percentage frequency of occurrence index, neither by the rare presence of large prey which leads to an overestimation of the prey category importance, as is the percentage by weight index (Lilly & Rice, 1983). Plotting mean PFI against the predators' total length class put in evidence the existence of ontogenetic dietary shifts at around class 45-50 cm for all the four rajids. Comparing between species, *Raja clavata* show the highest maximum values, followed by *R. montagui*, *R. brachyura* and *Leucoraja naevus*, in decreasing order. On another hand, *R. brachyura* and *R. montagui* show the most diversified diets of the four species in study.

Further, the fact that that shift is apparent at the same total length class in *Raja brachyura*, the species which attains the largest maximum length, than in the other species suggests that this characteristic is only dependent on size and not on other life history characteristics, such as maturity stage. This link is probably mainly due to the close direct relationship between predator's size and mouth dimensions, swimming capacity and visual accuracy (Scharf *et al.*, 2000). It has been frequently stated that size, shape and mechanisms of mouth, teeth and head of predators are correlated with their diets and their degree of prey specialization (Du Buit, 1978-79; Walker, 1999;

Scharf *et al.*, 2000). Furthermore, diet is also dependent on the size, motility and abundance of preys (Walker, 1999; Scharf *et al.*, 2000).

On a quantitative perspective, for most fishes, the larger the predator the bigger the consumed preys, comprising a wider range of prey sizes. Although studies on rajids' diets show no evidence of a specialist feeding, many authors agree that in general, as these predators grow, there is a shift to larger and faster preys, from benthic to semi-pelagic feeding habits and from Crustacea to Osteichthyes (Ajayi, 1982; Daan *et al.*, 1993; Holden & Tucker, 1974; Steven, 1930; Walker, 1999).

In all the presently studied predator species, the feeding strategy plots pointed towards a generalized diet. In small *Raja clavata*, Crustacea: Dendrobranchiata + Caridea, Mysidacea, Brachyura and Decapoda detach from the other preys. Conversely, Decapoda: Brachyura are dominant preys in the diet of large specimens, followed by Osteichthyes. In *R. brachyura* diets, Osteichthyes are dominant preys, while most of the other items are concentrated near the plots' origins. In *Leucoraja naevus*, small individuals feed mainly on small Crustacea like Mysidacea and Decapoda: Dendrobranchiata + Caridea, whereas Osteichthyes are dominant preys for the larger predators. *R. montagui* present the most generalized diets, with Polychaeta and Crustacea being the main preys.

The four rajid species analysed in this study feed mainly on benthic preys that live from shallow waters to depths of 500 to 700 m. Pelagic Cephalopoda and Osteichthyes, especially Gadiformes and Clupeiformes, are more frequent in diets of large specimens and in species that attain larger dimensions, like *Raja clavata* and *R. brachyura*. This can be explained by the fact that commonly larger individuals are more active predators and can move to a semi-pelagic habitat to feed (Ebeling, 1988). Besides that, large specimens' swimming capacity is better and their vulnerability to predation is lower than in small predators.

Moreover, there is a close relationship between teeth morphology and diet. Thus piscivorous species, like *Leucoraja naevus* and *Raja brachyura*, present more cusped teeth, whereas the ones that feed mainly on Crustacea possess molariform teeth. Considering that the shape of teeth influences the mandible apprehension capacity, cusped teeth are more efficient avoiding the escape of a caught fish, favouring piscivorous species. (Du Buit, 1978-79)

Teeth morphology resemblances between species may also account for the grouping results from the cluster analysis. It has been demonstrated that cluster analyses provide an efficient and relatively simple way of comparing data from feeding studies (Ross, 1978). When resource availability data are absent, Schoener's (1970) index appears to be the most accurate to estimate diet overlap (Wallace, 1981).

Large *Raja brachyura* and *Leucoraja naevus* have the same teeth shape and feed mainly on Osteichthyes; therefore are clustered together. Small *R. brachyura* are further clustered with the former two because they also feed mainly on Osteichthyes. *R. clavata* and *R. montagui* both show molariform teeth (Du Buit, 1978-79). These species' large individuals are clustered together and both show relatively similar values of %W for Osteichthyes and Decapoda: Brachyura preys. *R. clavata*, *L. naevus* and *R. montagui* belonging to small length group are clustered together in a separate branch. Such result was expected since small individuals generally present narrow diets, limited by mouth and body size and by swimming capacity and scarcely dependent on prey availability, and these species share the same habitat.

This study was based on samples collected from commercial landings and both pelagic and bottom trawl surveys. As the sample numbers were limited, the collected data wasn't sufficient to perform consistent spatial or seasonal analyses. The periodical collection of stomach content data would allow searching for spatial and temporal trends in species' trophic levels and for correlations with other parameters such as fishing effort (Stergiou & Karpouzi, 2002).

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ANNEX I: List of identified preys

Table I. List of preys identified in the stomachs of *Raja clavata* and corresponding information on their distribution and habitat.

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
ALGAE					
Phaeophyta					
ANIMALIA			animals		
CNIDARIA					
Hydrozoa					
NEMATODA			nematods		
SIPUNCULA					
ANNELIDA			annelids		
Polychaeta			polychaets		
	Glyceridae				
		Glycera spp.			shallow sublittoral
	Nephthyidae				
		Nephthys spp.			shallow to deep water
	Polynoidae				shallow sublittoral
	Sigalionidae				
		Leanira spp.			
ARTHROPODA					
CRUSTACEA			crustaceans		
MALACOSTRACA					
AMPHIPODA			amphipods		
	Ampeliscidae				
		Ampelisca brevicornis			intertidal and sublittoral
		Ampelisca spinipes			
		Ampelisca unidentata			
MYSIDACEA			mysid shrimps		
	Lophogastridae				
		Lophogaster typicus			
ISOPODA			isopods		
	Cirolanidae				
		Conilera cylindracea			sublittoral
		Eurydice pulchra			intertidal
DECAPODA			decapods		
DENDROBRANCHIATA					
	Solenoceridae				
		Solenocera membranacea		Atlantic; Bristish Islands, Mediterranean	20-700 m deep
CARIDEA					
	Pasiphaeidae				
		Pasiphaea sivado		Eastern Atlantic; British Islands; Mediterranean	10-600 m deep
	Alpheidae				
		Alpheus glaber		Atlantic; meridional British Islands; Mediterranean	30-40 m deep

Table I. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
		Athanas nitescens		Atlantic; British Islands; Norway; Mediterranean; Black Sea	fanerogamics prairies
	Processidae				
		Processa canaliculata		Atlantic; England; Mediterranean	70-600 m deep
		Processa edulis		Mediterranean	fanerogamics prairies
		Processa intermedia		Portugal; meridional Atlantic	rare
		Processa macrophthalma		Mediterranean	shallow water
		Processa mediterranea		Atlantic (England and France); western Mediterranean	about 200 m deep
	Pandalidae				
		Chlorotocus crassicornis		Atlantic, below Biscay Gulf; Mediterranean	50-600 m deep
	Crangonidae				
		Aegaeon lacazei		Atlantic, below Ireland; Mediterranean	200-400 m deep
		Pontophilus spinosus		Atlantic, below England and Norway; Mediterranean	10-200 m deep
MACRURA					
	Callianassidae				
		Callianassa tyrrhena		Atlantic; Mediterranean	shallow water to 1 m deep
ANOMURA					
	Paguridae				
		Pagurus bernhardus		Atlantic; British Islands; Norway; western Mediterranean	coastal to 500 m deep
		Anapagurus spp.			
	Galatheidae				
		Galathea intermedia		Mediterranean; Cadiz Gulf	30-40 m deep
		Munida rutllanti		Atlantic; western Mediterranean	80-500 m deep
		Munida sp.			
BRACHYURA Corystoidea			crabs		
	Corystidae				
		Corystes cassiveluanus		Atlantic; British Islands; Norway; Mediterranean	10-20 m deep
		Atelecyclidae			
		Atelecyclus rotundatus		Atlantic; British Islands; Norway; Mediterranean	20-90 m deep
		Atelecyclus sp.			
	Thiidae				
		Thia scutellata		Atlantic; British Islands; North Sea; Mediterranean	4-20 m deep
Brachyrhynca					
	Portunidae				
		Polybius henslowi		Atlantic; meridional British Islands; western Mediterranean	shallow water to 200 m deep

Table I. (cont.)

		FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
			Liocarcinus depurator		Atlantic, below Norway; Mediterranean	shallow water to 300 m deep
			Liocarcinus marmoreus		Atlantic, below British Islands; Mediterranean	shallow water to 200 m deep
			Liocarcinus spp.			
		Pinnotheridae				
			Pinnotheres pinnotheres		Atlantic; British Islands; Mediterranean	commensal with bivalves and ascids
		Goneplacidae				
			Goneplax rhomboides		Atlantic, below England; Mediterranean	shallow water to 400 m deep, also found at 700 m
	Oxyrhyncha					
		Majidae				
			Eurynome aspera		Atlantic; British Islands; Norway; Mediterranean	10-550 m deep
MOLLUSCA						
	BIVALVIA			bivalves		
	GASTROPODA			gastropods		
	CEPHALOPODA			cephalopods		
	Sepioidea					
		Sepiidae		cuttlefishes		
			Sepia spp.		Mediterranean Sea, eastern Atlantic, common in Iberian coasts	demersal
	Teuthoidea			squids		
		Loliginidae				
			Alloteuthis sp.			
			Alloteuthis subulata		Rare in Mediterranean Sea; common in North-eastern Atlantic from 60ºN to 10ºS, North Sea and south-western Baltic	neritic and demersal, sandy bottoms
			Loligo vulgaris		Mediterranean Sea; Eastern Atlantic from 55ºN to 20ºS; common in Iberian coast	nectobenthic, from surface to 550 m deep
		Histioteuthidae				
			Histioteuthis spp.		Known for few species; northern Atlantic and some species in the Mediterranean Sea	oceanic
		Ommastrephidae				
			Illex coindetii		Mediterranean Sea; eastern Atlantic from 60ºN to 17ºS and 30ºO	oceanic and neritic, from surface to 1100 m deep
	Octopoda			octopuses		
		Octopodidae				
			Eledone cirrhosa		Mediterranean Sea; north-eastern Atlantic from 67ºN to 33ºN	benthic, depths of 45-580 m

Table I. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
ECHINODERMATA			echinoderms		
Ophiuroidea			sea-serpents		
Echinoidea			sea-urchins		
CHORDATA			chordates		
Craniata					
Vertebrata					
Gnathostomata					
Osteichthyes			bony fishes		
Sarcopterygii					
Teleostei					
Clupeiformes					
	Argentinidae				
		Argentina sphyraena	herring smelts	Atlantic coasts southward from northern Norway to 24º N, Mediterranean	continental shelf to 450 m or deeper
Beloniformes					
	Belonidae				
		Belone belone	garpike	north-eastern Atlantic	epipelagic, neritic
Gadiformes					
	Gadidae				
		Micromesistius poutassou	blue whiting	North Atlantic from Barents Sea to Morocco, western Mediterranean	mesopelagic, over depths of 160-3000 m
		Trisopterus luscus	pouting	North Sea, British Islands, southward to Morocco, western Mediterranean	adults offshore, from depths of 30-100 m
	Merluccidae				
		Merluccius merluccius	European hake	northe-eastern Atlantic, Mediterranean and Black Sea	midwater or at bottom, 100-300 m deep, at edge and slop of continental shelf
Perciformes					
	Carangidae				
		Trachurus trachurus	Atlantic horse mackerel	north-eastern Atlantic from Iceland to Cape Verde Islands, Metiterranean and Marmara Seas	sandy bottom in 100-200 m deep
	Gobiidae				
		Pomatoschistus minutus	sand goby	eastern Atlantic, Mediterranean and Black Sea	inshore sand and muddy sand, to about 20 m deep
	Scombridae				
		Scomber scombrus	Atlantic mackerel	from Norway to the Azores and Morocco, Mediterranean and Black Seas	epipelagic or mesopelagic, in depths to 200-250 m
	Triglidae				
		Lepidotrigla cavillone	large-scaled gunard	eastern Atlantic from southern coast of Portugal to Mauritania, Mediterranean except Black Sea	muddy sands and gravel, between 30 and 450 m deep

Table II. List of preys identified in the stomachs of *Raja brachyura* and corresponding information on their distribution and habitat.

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
ANIMALIA			animals		
CNIDARIA					
Anthozoa					
Hydrozoa					
SIPUNCULA					
NEMATODA			nematods		
ANNELIDA			annelids		
Polychaeta			polychaets		
	Sigalionidae				
		Sigalion spp.			low water
	Nephthyidae				
		Nephthys spp.			shallow to deep water
	Lumbrinidae				
	Polynoidae				
ARTHROPODA			arthropods		
CRUSTACEA			crustaceans		
OSTRACODA					most benthic, some free swimming and few planktonic
COPEPODA			copepods		
MALACOSTRACA					
AMPHIPODA			amphipods		
MYSIDACEA					
	Mysidae				
		Gastrosaccinae			
		Gastrosaccus spp.			
		Gastrosaccus normani			
ISOPODA			isopods		
	Cirolanidae				
		Eurydice spinigera			sublittoral
DECAPODA			decapods		
CARIDEA					
	Alphidae				
		Alpheus macrocheles		Atlantic; meridional England; Mediterranean; Black Sea	littoral or sublittoral
	Processidae				
		Processa spp.			
		Processa canaliculata		Atlantic; England; Mediterranean	70-600 m deep
		Processa elegantula		Atlantic; Mediterranean	rare; 30-40 m deep
		Processa mediterranea		Atlantic (England and France); western Mediterranean	about 200 m deep
		Processa nouveli holthuisi		Northern Atlantic; Mediterranean	rare; 20-230 m
	Pandalidae				
		Pandalina brevirostris		Atlantic; British Islands; Norway; Mediterranean	20-30 m and up to 100 m deep

Table II. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
	Crangonidae				
		Crangon crangon		Atlantic, below Baltic Sea; Mediterranean; Black Sea	benthic, shallow water
ANOMURA					
	Galatheidae				
		Galathea intermedia		Mediterranean; Cadiz Gulf	30-40 m deep
BRACHYURA			crabs		
Corystoidea					
	Thiidae				
		Thia scutellata		Atlantic; British Islands; North Sea; Mediterranean	4-20 m deep
Brachyrhynca					
	Portunidae				
		Liocarcinus pusillus		Atlantic, below Norway	shallow water to 200 m deep
		Polybius henslowi		Atlantic; meridional British Islands; western Mediterranean	shallow water to 200 m deep
MOLLUSCA			molluscs		
GASTROPODA			gastropods		
CEPHALOPODA			cephalopods		
Teuthoidea			squids		
	Loliginidae				
		Loligo vulgaris		Mediterranean Sea; Eastern Atlantic from 55ºN to 20ºS; common in Iberian coast	nectobenthic, from surface to 550 m deep
		Loligo forbesii		Mediterranean Sea; Eastern Atlantic from 63ºN to 20ºN, excluding the Baltic Sea; occidental limit in the Azores	nectobenthic, from surface to 400 m deep
		Alloteuthis subulata		Rare in Mediterranean Sea; common in North-eastern Atlantic from 60ºN to 10ºS, North Sea and south-western Baltic	neritic and demersal, sandy bottoms
	Ommastrepidae				
		Illex coindetii		Mediterranean Sea; eastern Atlantic from 60ºN to 17ºS and 30ºO	oceanic and neritic, from surface to 1100 m deep
CHORDATA			chordates		
CEPHALOCHORDATA			cephalochordates		
CRANIATA					
Vertebrata					
Gnathostomata					
Chondrichthyes			cartilaginous fishes		
Osteichthyes			bony fishes		
Sarcopterygii					
Teleostei					

Table II. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
Clupeiformes					
	Clupeidae				
		Sardina pilchardus	European pilchard	Atlantic coasts southward Senegal to North Sea, Mediterranean	coastal pelagic, 25-55 m deep
Gadiformes					
	Gadidae				
		Gadinae			
		Micromesistius poutassou	blue whiting	North Atlantic from Barents Sea to Morocco, western Mediterranean	mesopelagic, over depths of 160-3000 m
		Trisopterus luscus	pouting	North Sea, British Islands, southward to Morocco, western Mediterranean	adults offshore, from depths of 30-100 m
Perciformes					
	Trachinidae				
		Echiichthys vipera	lesser weever	Mediterranean, Adriatic, eastern Atlantic from Great Britain to the Canaries	littoral and benthic
	Carangidae				
		Trachurus trachurus	Atlantic horse mackerel	north-eastern Atlantic from Iceland to Cape Verde Islands, Metiterranean and Marmara Seas	sandy bottom in 100-200 m deep
	Ammodytidae				
		Gymnammodytes semisquamatus	smooth sandeel	eatern North Atlantic from the southern coast of Norway and the Shetlands to Spain	offshore over shell-gravel
	Callionymidae				
		Callionymus maculatus	dragonet	whole Mediterranean except Black Sea, Atlantic from southern and western Iceland and Norway south to Senegal	benthic, sandy bottoms, 45-650 m deep
Pleuronectiformes					
	Citharidae				
		Citharus linguatula	Atlantic spotted flounder	Mediterranean, eastern Atlantic from Portugal southward to Morocco	benthic or continental shelf
	Scophtalmidae				
		Lepidorhombus boscii	fourspotted megrim	from the British Islands to Cape Bojador, Mediterranean	depths down to 700-800 m

Table III. List of preys identified in the stomachs of *Leucoraja naevus* and corresponding information on their distribution and habitat.

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
ALGAE					
Phaeophyta					
ANIMALIA			animals		
PLATYHELMINTES					
NEMATODA			nematods		
ANNELIDA			annelids		
Polychaeta			polychaets		
	Aphroditidae				
	Polynoidae				
	Sigalionidae				
	Nephthyidae				
		Nephthys spp.			shallow to deep water
ARTHROPODA			arthropods		
CRUSTACEA			crustaceans		
OSTRACODA					
MALACOSTRACA					
CUMACEA					
EUPHAUSIACEA					
AMPHIPODA			amphipods		
	Lysianissidae				
		Hippomedon denticulatus			sublittoral, shallow water
		Hippomedon oculatus			
MYSIDACEA					
	Lophogastridae				
		Lophogaster typicus			
	Mysidae				
		Gastrosaccinae			
		Gastrosaccus spp.			
ISOPODA			isopods		
	Cirolanidae				
		Eurydice pulchra			intertidal
		Eurydice spinigera			sublittoral
DECAPODA			decapods		
DENDROBRANCHIATA					
	Solenoceridae				
		Solenocera membranacea		Atlantic; Bristish Islands, Mediterranean	20-700 m deep
CARIDEA					
	Processidae				
		Processa spp.			
		Processa canaliculata		Atlantic; England; Mediterranean	70-600 m deep
	Pandalidae				
		Chlorotocus crassicornis		Atlantic, below Biscay Gulf; Mediterranean	50-600 m deep
	Crangonidae				
		Aegaeon lacazei		Atlantic, below Ireland; Mediterranean	200-400 m deep

Table III. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
ANOMURA					
	Galatheidae				
		Munida rutlanti		Atlantic; western Mediterranean	80-500 m deep
BRACHYURA			crabs		
MOLLUSCA			molluscs		
GASTROPODA			gastropods		
BIVALVIA			bivalves		
CEPHALOPODA			cephalopods		
Teuthoidea			squids		
	Loliginidae				
		Loligo vulgaris		Mediterranean Sea; Eastern Atlantic from 55ºN to 20ºS; common in Iberian coast	nectobenthic, from surface to 550 m deep
	Ommastrephidae				
		Todarodes sagitattus		Mediterranean Sea; eastern Atlantic from the Artic to approximately 13ºS and 40ºO	
ECHINODERMATA			echinoderms		
CHORDATA			chordates		
Craniata					
Vertebrata					
Gnathostomata					
Osteichthyes			bony fishes		
Sarcopterygii					
Teleostei					
Clupeiformes					
	Clupeidae				
		Sardina pilchardus	European pilchard	Atlantic coasts southward Senegal to North Sea, Mediterranean	coastal pelagic, 25-55 m deep
Gadiformes					
	Gadidae				
		Micromesistius poutassou	blue whiting	North Atlantic from Barents Sea to Morocco, western Mediterranean	mesopelagic, over depths of 160-3000 m
Perciformes					
	Ammodytidae				
		Gymnammodytes semisquamatus	smooth sandeel	eatern North Atlantic from the southern coast of Norway and the Shetlands to Spain	offshore over shell-gravel
Pleuronectiformes					benthic

Table IV. List of preys identified in the stomachs of *Raja montagui* and corresponding information on their distribution and habitat.

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
PLANTAE ANGIOSPERMAE			plants		
ANIMALIA			animals		
NEMATODA			nematods		
SIPUNCULA					
	Phascolosomatidae				
		Physcosoma granulatum			
ANNELIDA			annelids		
Polychaeta			polychaets		
	Polynoidae				
	Glyceridae				
		Glycera spp.			shallow sublittoral
Nephtyidae					
		Nephtys spp.			shallow to deep water
Sigalionidae					
		Sigalion spp.			low water
		Leanira spp.			
Polyodontidae					
		Eupanthalis kinbergi			
Eunicidae					
ARTHROPODA			arthropods		
CRUSTACEA			crustaceans		
MALACOSTRACA					
ISOPODA			isopods		
	Cirolanidae				
		Cirolana cranchi			offshore
		Conilera cylindracea			sublittoral
		Eurydice spp.			
		Eurydice pulchra			intertidal
		Eurydice spinigera			sublittoral
		Eurydice affinis			intertidal
AMPHIPODA			amphipods		
	Lysianassidae				
		Hippomedon denticulatus			sublittoral, shallow water
		Ampeliscidae			
		Ampelisca spp.			
		Ampelisca brevicornis			intertidal and sublittoral
		Ampelisca unidentata			
		Ampelisca armoricana			
		Ampelisca spooneri			
		Ampelisca sarsi			
		Ampelisca spinipes			

Table IV. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
MYSIDACEA					
	Lophogastridae				
		Lophogaster typicus			
	Mysidae				
		Paramysis arenosa			
DECAPODA DENDROBRANCHIATA			decapods		
	Solenoceridae				
		Solenocera membranacea		Atlantic; Bristish Islands, Mediterranean	20-700 m deep
CARIDEA					
	Alpheidae				
		Alpheus glaber		Atlantic; meridional British Islands; Mediterranean	30-40 m deep
	Pandalidae				
		Chlorotocus crassicornis		Atlantic, below Biscay Gulf; Mediterranean	50-600 m deep
	Processidae				
		Processa spp.			
		Processa modica			
		Processa macrophtalma			
		Processa nouveli		Northern Atlantic; Mediterranean	rare; 20-230 m
	Crangonidae				
		Crangon crangon		Atlantic, below Baltic Sea; Mediterranean; Black Sea	benthic, shallow water
		Pontophilus norvegicus		Atlantic; British Islands; western Mediterranean	200-500 m deep
MACRURA					
	Scyllaridae				
		Scyllarus arctus			
ANOMURA					
	Galatheidae				
		Munida intermedia		Atlantic; Mediterranean	300-400 m deep
BRACHYRURA Corystoidea			crabs		
	Thiidae				
		Thia scutellata		Atlantic; British Islands; North Sea; Mediterranean	4-20 m deep
	Atelecyclidae				
		Atelecyclus rotundatus		Atlantic; British Islands; Norway; Mediterranean	20-90 m deep
		Atelecyclus undecimdentatus		Atlantic; rare in the Mediterranean	shallow water to 30 m deep
	Pirimelidae				
		Pirimela denticulata		Atlantic, below Norway; Mediterranean	near coast to up to 200 m deep

Table IV. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
Brachyrhynca					
	Portunidae				
		Liocarcinus spp.			
		Liocarcinus depurator		Atlantic, below Norway; Mediterranean	shallow water to 300 m deep
		Polybius henslowi		Atlantic; meridional British Islands; western Mediterranean	shallow water to 200 m deep
	Pinnotheridae				
		Pinnotheres pinnotheres		Atlantic; British Islands; Mediterranean	commensal of bivalves and ascids
	Goneplacidae				
		Goneplax rhomboides		Atlantic, below England; Mediterranean	shallow water to 400 m deep, also found at 700 m
MOLLUSCA			molluscs		
GASTROPODA			gastropods		
BIVALVIA			bivlaves		
CEPHALOPODA			cephalopods		
Teuthoidea			squids		
	Loliginidae				
		Alloteuthis subulata		Rare in Mediterranean Sea; common in North-eastern Atlantic from 60ºN to 10ºS, North Sea and south-western Baltic	neritic and demersal, sandy bottoms
CHORDATA			chordates		
Craniata					
Vertebrata					
Gnathostomata					
Osteichthyes			bony fishes		
Sarcopterygii					
Teleostei					
Clupeiformes					
	Clupeidae				
		Sardina pilchardus	European pilchard	Atlantic coasts southward Senegal to North Sea, Mediterranean	coastal pelagic, 25-55 m deep
	Argentinidae				
		Argentina sphyraena	herring smelts	Atlantic coasts southward from northern Norway to 24º N, Mediterranean	continental shelf to 450 m or deeper
Gadiformes					
	Gadidae				
		Micromesistius poutassou	blue whiting	North Atlantic from Barents Sea to Morocco, western Mediterranean	mesopelagic, over depths of 160-3000 m
Perciformes					
	Ammodytidae				
		Gymnammodytes semisquamatus	smooth sandeel	eatern North Atlantic from the southern coast of Norway and the Shetlands to Spain	offshore over shell-gravel

Table IV. (cont.)

	FAMILY	SPECIES	COMMON NAME	DISTRIBUTION	HABITAT
	Trachinidae				
		Trachinus draco	greater weever	Mediterranean, Adriatic, Black Sea, eastern Atlantic from Norway to Morocco and Madeira	littoral and benthic
	Carangidae				
		Trachurus trachurus	Atlantic horse mackerel	north-eastern Atlantic from Iceland to Cape Verde Islands, Metiterranean and Marmara Seas	sandy bottom in 100-200 m deep
Pleuronectiformes					
	Bothidae				
		Arnoglossus spp.	(flounders)		benthic
	Soleidae				
	Pleuronectidae				