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Diet comparison of four ray species (*Raja clavata, Raja brachyura, Raja montagui* and *Leucoraja naevus*) caught along the Portuguese continental shelf

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Abstract – Data on the diet of species are important for understanding ecosystem dynamics and are fundamental for the implementation of recent approaches in stock assessment and consequently for the establishment of more ecological management measures. In mainland Portugal, as in most European countries, skates and rays represent an important proportion of commercial landings. The four main species landed are *Raja clavata* and *Raja brachyura*, followed by *Leucoraja naevus* and *Raja montagui*. This paper analyses their diets based on the examination of stomach contents. Food items were identified to the lowest identifiable taxon and were further assembled into major taxonomic groups designated as prey. Intra- and interspecific comparisons were made according to size and sex. All four species had generalized diets with differences in prey preference among them. Decapods and bony fish were the most frequent prey. Furthermore, an ontogenetic dietary shift was evident in all species at around 45−55 cm total length. Both intra- and interspecific differences observed seem to be related to size and morphological characteristics of the species, as well as type of dentition. These variations allow different species, as well as small and large specimens from the same species, to exploit a larger diversity of habitats.

Key words: Feeding ecology / Dietary composition / Ontogenetic dietary shift / Ray / Skate / Elasmobranch fish / Atlantic Ocean

Résumé – Étude comparative des régimes alimentaires de quatre espèces de raies (*Raja clavata, Raja brachyura, Raja montagui* et *Leucoraja naevus*) capturées le long du plateau continental du Portugal. Les données sur le régime alimentaire sont importantes pour comprendre la dynamique des écosystèmes, et sont fondamentales pour mettre en œuvre les approches récentes de gestion des stocks, et donc pour établir des mesures de gestion plus écologiques. Au Portugal, comme dans les autres pays européens, les raies représentent un part importante des débarquements commerciaux. Les quatre espèces principales débarquées sont *Raja clavata* et *Raja brachyura*, suivies de *Leucoraja naevus* et *Raja montagui*. Cet article analyse leur régime alimentaire en se basant sur les contenus stomacaux. Leurs aliments sont identifiés au taxon le plus précis possible, puis regroupés par groupes taxonomiques désignés comme proies. Les comparaisons intra- et interspécifiques des raies sont faites selon leur taille et leur sexe. Les quatre espèces présentent des différences dans leur préférence alimentaire. Les Décapodes et les poissons osseux sont les proies les plus fréquentes. De plus, un changement ontogénique est évident au niveau alimentaire, et pour les quatre espèces, autour de 45−55 cm (longueur totale). Les différences intra- et interspécifiques observées semblent liées à la taille et aux caractéristiques morphologiques de l'espèce, ainsi qu'à la dentition. Ces variations leur permettent quelle soit la taille d'exploiter une plus grande diversité d'habitats.

1 Introduction

Diet studies are important for the understanding of species biology and ecology, since the quality and quantity of food are exogenous factors that directly affect species growth and, indirectly, their maturation and mortality (Stergiou and Karpouzi 2002; Wootton 1990). Feeding ecology studies are commonly based on the analysis of stomach contents of collected specimens, since the use of direct methods is usually difficult or even impossible for fish species (Assis 1992; Cortés 1997).

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These studies also represent an essential tool for the comprehension of some population phenomena, such as migrations, competition and physiological variations, and consequently for the understanding of fluctuations in stock abundance (Assis 1992). The quantification of diets and trophic relationships are also fundamental inputs for the implementation of ecosystem models (Hérran 1988; Stergiou and Karpouzi 2002).

The commercial interest in cartilaginous fishes has increased worldwide in recent decades, mainly due to the depletion of many commercial bony fish stocks together with an increasing interest on elasmobranch muscle, cartilage, liver oil and fins (Stehmann 2002). In the North-eastern Atlantic, skates and rays represent more than 40% of elasmobranch landings and within these the order Rajiformes is particularly important due not only to their diversity but also to their economical value (Walker 1999).

In Portugal, as in most European countries, rays and skates landings are recorded as aggregate landings, and are not usually differentiated into species. A sampling program on skates and rays landings carried on along the Portuguese continental shelf showed that *Raja clavata* and *Raja brachyura* were the most commonly landed species, whereas *Raja montagui* and *Leucoraja naevus* represented nearly 40% of the remaining sampled specimens (Machado et al. 2004). In previous diet studies carried out at North European waters, the main prey for *R. clavata* were shrimps and brachyuran crabs, for *R. brachyura* were bony fish and shrimps, for *R. montagui* were mysids and other small crustaceans, and for *L. naevus* were small crustaceans and bony fish (Ajayi 1982; Du Buit 1978-1979; Ellis et al. 1996; Holden and Tucker 1974). In African Atlantic waters, *R. clavata* was found to feed mostly on lobsters and fish (Ebert et al. 1991). Former studies along the Portuguese coast pointed out shrimps and brachyuran crabs as the most common prey for the four species, being fish also important in *L. naevus* (Cunha et al. 1987; Marques and Ré 1978). In the Azorean waters, fish, brachyuran crabs and mysids were identified in *R. clavata* stomachs (Gomes et al. 1998).

The present paper studies the diet composition and feeding habits of four of the most important rajid species landed in Portuguese ports: *Raja clavata* Linnaeus 1758; *R. brachyura* Lafont 1873; *R. montagui* Fowler 1910; and *Leucoraja naevus* (Müller & Henle 1841). This study is based on stomach contents analysis and includes intra- and interspecific comparisons according to size and sex.

2 Materials and methods

Sampling

For this study, stomachs of *Raja clavata* (n = 159), *R. brachyura* (n = 97), *R. montagui* (n = 127) and *Leucoraja naevus* (n = 135) were analysed. Samples were collected from commercial landings and from scientific trawl surveys carried out by IPIMAR, between 2001 and 2005. For each specimen, the following information was recorded: total length (*TL*, mm), total weight (*g*), and sex.

The food categories that composed the stomach contents were identified to the lowest possible taxonomic level, counted and weighted. The main prey categories were grouped into major taxonomic groups and assembled to the following prey: polychaetes (Polychaeta); unidentified crustaceans (Crustacea); amphipods (Crustacea: Amphipoda); mysids (Crustacea: Mysidacea); isopods (Crustacea: Isopoda); decapods (Crustacea: Decapoda); shrimps (Crustacea: Decapoda: Dendrobranchiata and Caridea); anomurans (Crustacea: Decapoda: Anomura); lobsters (Crustacea: Decapoda: Macrura); brachyuran crabs (Crustacea: Decapoda: Brachyura); cephalopods (Cephalopoda); and bony fish (Osteichthyes). Minor prey-taxa: Algae, Cnidaria, Sipuncula, Bivalvia, Gastropoda, and Echinodermata were categorized as "Others", and weighted and counted as a unique food category. Each food category was further designated as prey. Unidentified material was excluded from the analysis since its occurrence was negligible.

Specimens from each sex were grouped into two major length groups designated as "small" (TL < 50 cm) and "large" ($TL \geq$ 50 cm). This value is close to the length at first maturity of *R. clavata*, *R. montagui* and *L. naevus*. Although the length at first maturity of *R. brachyura* is estimated at about 90 cm (Walker 1999), the size limit used was also 50 cm due to the insufficient number of large individuals available in the samples.

Data analysis

Overall diet

For each species, the index of vacuity (%IV) was determined, by sex, as the percentage of empty stomachs in the whole sample of stomachs. A stomach was considered to be empty when it only contained either nothing or only a small amount of digested and unidentified material, sediment or endoparasites.

To evaluate the importance of each prey, the following indices were determined: (a) percentage by number (%N); (b) percentage by weight (%W); (c) percentage frequency of occurrence (%O); and (d) percent index of relative importance (%IRI). By expressing the IRI as a percentage, it constitutes a robust estimator of the relative importance of each prey and facilitates comparisons between different prey (Cortés 1997).

A χ^2 test was used to test the null hypothesis of no differences between sexes on the number of occurrence of each prey for each predator species. A univariate t-test was used to test the null hypothesis of no differences on the weight of each prey between sexes. In both tests, a 5% significance level was adopted.

Prey importance and feeding strategy

Three-dimensional diagrams were constructed for each predator species and major length group by displaying the stomach contents in terms of %N, %W and %O (Cortés 1997). This approach illustrates the diet in terms of prey importance, by distinguishing between dominant and rare prey, and also according to predator feeding strategy, by differentiating between generalist and specialist diets. In this graphical approach any point located close to 100% O, 100% N and 100% W corresponds to a dominant food item, whereas a point located near the origin of axes corresponds to a rare food item. Furthermore the existence of a cluster of points located close to 100% O and the origin of at least one of the other two axes corresponds to a generalized diet. Alternatively, a cluster near 100% O and 100% for at least one of the other indices corresponds to a specialized diet.

To evaluate ontogenetic dietary shifts, plots of mean partial fullness index (PFI) vs. *TL* class (10 cm length classes) were done by sex (Lilly and Rice 1983). PFI was determined according to:

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

where W_{ij} is the weight of the ith prey in the jth stomach, TL_j is the total length of the jth predator (in cm) and n is the total number of sampled stomachs. Length was used instead of weight since the former is not influenced by changes in muscle, liver, gonads and stomach contents. This index has the advantage of not being strongly influenced by either the frequent occurrence of small prey or by the rare presence of large prey (Lilly and Rice 1983).

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

$$S = \sum_{i=1}^{n}\inf(W_{ip}, W_{iq})$$

where W_{ip} is the weight of prey item i found in stomach p relative to the total weight of prey items, W_{iq} is the same for predator q and $\inf(W_{ip}, W_{iq})$ is the infimum between the two values. When resource availability data are absent, this index appears to be the most accurate to estimate diet overlap (Wallace 1981). It has been demonstrated that cluster analyses provide an efficient and relatively simple way of comparing data from feeding studies (Ross 1978). In this graphical representation, the smallest linkages indicate the greatest similarities between the diets.

3 Results

Overall diet

Stomach composition of the four ray species is presented in Table 1, which also includes, if available, information on the main prey's habitat. Some prey were highly digested and consequently difficult to identify. Some of the brachyuran crabs, cephalopods and fish presented marks of teeth on the carapaces and bodies. *L. naevus* presented indices of vacuity both by sex higher than in the other three species (Table 2). In *R. clavata* and *R. brachyura*, the index was higher in males, whereas was it greater in females of the other two species. In *L. naevus*, the value of the index for females was almost twice that for males. Few specimens had everted stomachs (two of each of *R. clavata* and *R. montagui* and one of *L. naevus*).

Prey importance and feeding strategy

For the four ray species, no significant differences in occurrence and weight were found between sexes (Table 3) and therefore feeding strategy plots were constructed by combining data from females and males. Feeding strategy three-dimensional plots for each rajid species are presented and summarized with information on frequently identified species and their habitats (Fig. 1, Table 4). These results are further supported by %IRI values (Fig. 2). For small *R. clavata*, the most important prey were indiscriminate crustaceans and shrimps, namely the benthic shrimp *Solenocera membranacea*. Besides these prey, large specimens fed also on bony fish and brachyuran crabs, within which *Polybius henslowi* (pelagic) was the most common item. For *R. brachyura*, bony fish followed by indiscriminate crustaceans and shrimps were the main prey both for small and large individuals (Fig. 2). For the former, *Crangon crangon* (benthic shrimp that lives in shallow waters) was the most common item, while large specimens fed predominantly on benthic offshore prey like the smooth sandeel *Gymnammodytes semisquamatus* and the small shrimp *Processa canaliculata* (Fig. 1; Table 4). Polychaetes and small intertidal crustaceans (e.g. *Ampelisca* spp. and *Lophogaster typicus*) were the most important prey for *R. montagui*, and showed the highest values of %IRI (Fig. 2). Large specimens also fed on bony fish like *Micromesistius poutassou* (mesopelagic). For *L. naevus*, indiscriminate and small crustaceans, like *L. typicus* and *S. membranacea*, were the most important prey for small specimens. For large individuals, polychaetes and the bony fish *G. semisquamatus* were also important food items (Figs. 1 and 2; Table 4).

For all ray species, the plots of mean PFI versus predator's total length class (Fig. 3) suggested ontogenetic shifts in their diets at lengths of about 45−55 cm in both sexes. Smaller males and females of *R. clavata* fed mainly on polychaetes, mysids, and various other small crustaceans, but with low values of mean PFI. For specimens larger than 45 cm, the values of mean PFI increased and cephalopods, bony fish and brachyuran crabs were the main prey. For females, two modal peaks were evident at lengths of about 50 and 75 cm. For males, there are also two marked peaks but at around lengths of 60 and 70 cm.

Fish were a major prey item for all sizes of *R. brachyura* (Fig. 3). Excluding bony fish, polychaetes were the most common prey for females with lengths from 45 to 65 cm, and shrimps and brachyuran crabs prevailed in males from 35 to 45 cm. Cephalopods were the most important prey for both sexes for specimens larger than 50 cm.

For small females of *R. montagui* (Fig. 3), the most important prey were various crustaceans and polychaetes, while large females predated primarily on fish. For males, although shrimps were equally important for large and small specimens, for the former, cephalopods, brachyuran crabs and fish also showed high values of mean PFI.

Table 1. Overall diets of the four ray species (*Raja clavata*, *R. brachyura*, *R. montagui* and *Leucoraja naevus*) identified to species level, with available information on the main habitat of prey.

Prey-taxon	Habitat	*Raja clavata*	*Raja brachyura*	*Raja montagui*	*Leucoraja naevus*
ANNELIDA					
POLYCHAETA					
Glycera spp.	shallow sublittoral	x		x	
Nephthys spp.	shallow to deep water	x	x	x	x
Sigalion spp.	low water		x	x	
Leanira spp.		x		x	
Eupanthalis kinbergi				x	
ARTHROPODA					
CRUSTACEA					
OSTRACODA	most benthic		x		
COPEPODA			x		x
MALACOSTRACA		x	x	x	x
CUMACEA					x
EUPHAUSIACEA					x
AMPHIPODA			x		
Ampelisca brevicornis	intertidal and sublittoral	x		x	
Ampelisca spinipes		x		x	
Ampelisca unidentata		x		x	
Ampelisca armoricana				x	
Ampelisca spooneri				x	
Ampelisca sarsi				x	
Hippomedon denticulatus	sublittoral; shallow water			x	x
Hippomedon oculatus					x
MYSIDACEA					
Lophogaster typicus		x		x	x
Gastrosaccus normani			x		
Paramysis arenosa				x	
ISOPODA					
Conilera cylindracea	sublittoral	x		x	
Cirolana cranchi	offshore			x	
Eurydice pulchra	intertidal	x		x	x
Eurydice spinigera	sublittoral		x	x	x
Eurydice affinis	intertidal			x	
DECAPODA					
DENDROBRANCHIATA					
Solenocera membranacea	20–700 m deep	x		x	x
CARIDEA					
Pasiphaea sivado	10–600 m deep	x			
Alpheus glaber	30–40 m deep	x		x	
Alpheus macrocheles	littoral or sublittoral		x		
Athanas nitescens	phanerogamic prairies	x			
Processa canaliculata	70–600 m deep	x	x		x
Processa edulis	phanerogamic prairies	x			
Processa intermedia	rare	x			
Processa macrophthalma	shallow water	x		x	
Processa mediterranea	about 200 m deep	x	x		
Processa elegantula	rare; 30–40 m deep		x		
Processa nouveli holthuisi	rare; 20–230 m		x		
Processa modica				x	
Chlorotocus crassicornis	50–600 m deep	x		x	x
Pandalina brevirostris	20–30 m to 100 m deep		x		
Aegaeon lacazei	200–400 m deep	x			x
Pontophilus spinosus	10–200 m deep	x			
Pontophilus norvegicus	200–500 m deep			x	
Crangon crangon	benthic; shallow water		x	x	

Table 1. Continued.

Prey-taxon	Habitat	*Raja clavata*	*Raja brachyura*	*Raja montagui*	*Leucoraja naevus*
MACRURA					
Callianassa tyrrhena	shallow water to 1 m deep	x			
Scyllarus arctus				x	
ANOMURA					
Pagurus bernhardus	coastal to 500 m deep	x			
Anapagurus spp.		x			
Galathea intermedia	30–40 m deep	x	x		
Munida rutlanti	80–500 m deep	x			x
Munida intermedia	300–400 m deep			x	
BRACHYURA					
Corystes cassiveluanus	10–20 m deep	x			
Atelecyclus rotundatus	20–90 m deep	x		x	
Atelecyclus undecimdentatus	shallow water to 30 m deep			x	
Thia scutellata	4–20 m deep	x	x	x	
Pirimela denticulata	near coast to up to 200 m deep			x	
Polybius henslowi	shallow water to 200 m deep	x	x	x	
Liocarcinus depurator	shallow water to 300 m deep	x		x	
Liocarcinus marmoreus	shallow water to 200 m deep	x			
Liocarcinus pusillus	shallow water to 200 m deep		x		
Pinnotheres pinnotheres	commensal with bivalves and ascids	x		x	
Goneplax rhomboides	shallow water to 400 m deep	x		x	
Eurynome aspera	10–550 m deep	x			
MOLLUSCA					
BIVALVIA		x		x	x
GASTROPODA		x	x	x	x
CEPHALOPODA					
Sepia spp.	demersal	x			
Alloteuthis subulata	neritic and demersal; sandy bottoms	x	x	x	
Loligo vulgaris	nectobenthic; surface to 550 m deep	x	x		x
Loligo forbesii	nectobenthic; surface to 400 m deep		x		
Histioteuthis spp.	oceanic	x			
Illex coindetii	neritic; surface to 1100 m deep	x	x		
Todarodes sagitattus					x
Eledone cirrhosa	benthic; 45–580 m deep	x			
ECHINODERMATA		x			x
CHORDATA					
OSTEICHTHYES					
Sardina pilchardus	coastal pelagic; 25−55 m deep		x	x	x
Argentina sphyraena	continental shelf to 450 m or deeper	x		x	
Belone belone	epipelagic; neritic	x			
Micromesistius poutassou	mesopelagic; 160–3000 m deep	x	x	x	x
Trisopterus luscus	adults offshore; 30–100 m deep	x	x		
Merluccius merluccius	semi-benthic; 100–300 m deep	x			
Trachurus trachurus	sandy bottom in 100–200 m deep	x	x	x	
Pomatoschistus minutus	inshore; sand; to about 20 m deep	x			
Scomber scombrus	pelagic; up to 200–250 m deep	x			
Lepidotrigla cavillone	muddy sands; 30–450 m deep	x			
Echiichthys vipera	littoral and benthic		x		
Trachinus draco	littoral and benthic			x	
Gymnammodytes semisquamatus	offshore over shell-gravel		x	x	x
Callionymus maculatus	benthic; sandy bottoms; 45–650 m deep		x		
Citharus linguatula	benthic or continental shelf		x		
Lepidorhombus boscii	depths down to 700–800 m		x		
Arnoglossus spp.	benthic			x	

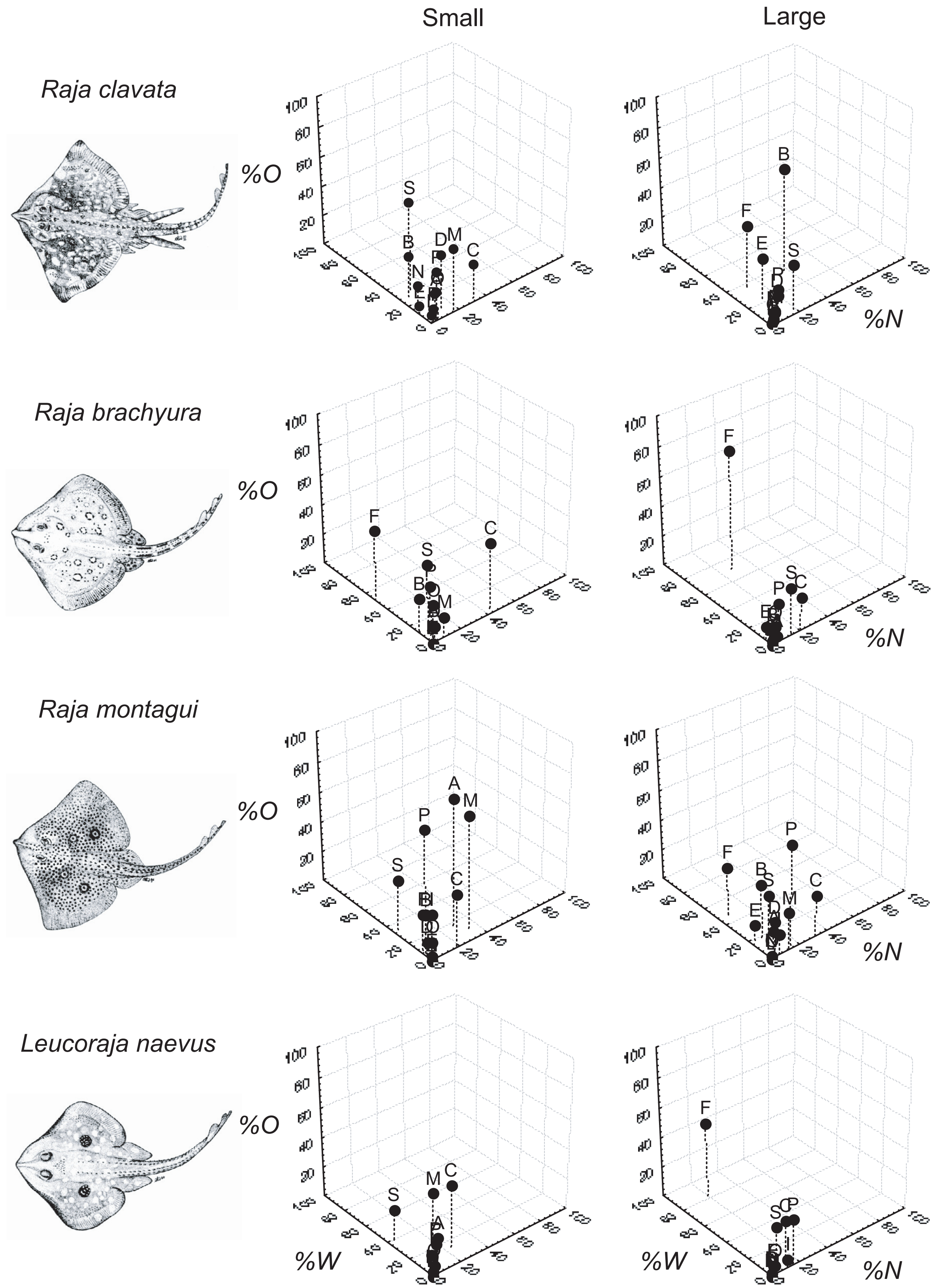

Fig. 1. Three-dimensional representations of the feeding habits of small (*TL* < 50 cm) and large (*TL* ≥ 50 cm) *Raja clavata*, *R. brachyura*, *R. montagui* and *Leucoraja naevus*. Prey codes – P: Polychaetes; C: Unidentified crustaceans; A: Amphipods; M: Mysids; I: Isopods; D: Decapods; S: Shrimps; L: Lobsters; N: Anomurans; B: Brachyuran crabs; E: Cephalopods; F: Bony fish; O: Others. Fish drawing adapted from Bauchot (1987). Percentage by number (%N), by weight (%W) and frequency of occurrence (%O).

Table 2. Number of sampled stomachs (n) by species, sex (F: females; M: males) and major length group (S: small, $TL < 50$ cm; L: large, $TL \geq 50$ cm) and index of vacuity estimates (%IV).

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

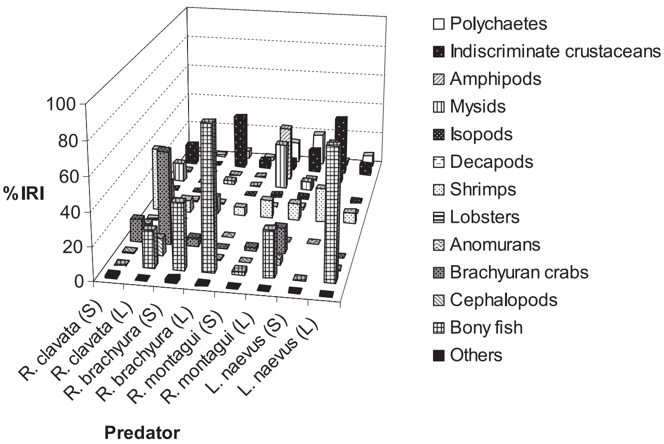

Fig. 2. Index of relative importance (%IRI) by species and major length group (S: small, $TL < 50$ cm, L: large, $TL \geq 50$ cm) of *Raja clavata*, *R. brachyura*, *R. montagui* and *Leucoraja naevus*.

For *L. naevus* specimens larger than 45 cm (Fig. 3), fish were the dominant prey, with high values of mean PFI. Mysids were important for females with lengths ranging from 25 to 35 cm. Shrimps also showed relatively high values for females with 10−20 and 35−60 cm length and for males with about 15−25 and 30−60 cm length.

The dendrogram (Fig. 4) illustrates the similarity in the diets of small and large rays of the four species analysed. "Large" and "small" length groups were separated into two major clusters. Small *L. naevus*, small *R. montagui* and small *R. clavata* were grouped into one cluster. Large *R. brachyura* and large *L. naevus* were clustered together, showing a high level of similarity. Small *R. brachyura* was further linked to this cluster. Large *R. clavata* and *R. montagui* had similar diets and were relatively similar to the diets of the preceding group.

4 Discussion

The occurrence of large prey, like brachyuran crabs, cephalopods and bony fish, with marks of teeth on their carapaces and bodies may suggest that they had been chewed prior to ingestion. This feeding strategy is known to occur in *R. clavata*, *R. montagui* and *L. naevus* (Daan et al. 1993). Furthermore it was observed that small and soft prey, like polychaetes and some small crustaceans, were more easily digested. The most obvious consequences of the occurrence of highly digested prey were the difficulty in identifying some specimens, and the underestimation in weight of some prey.

The high index of vacuity recorded for *L. naevus* has also been reported in other diet studies of this species (Holden and Tucker 1974; Ellis et al. 1996). Piscivorous species are generally found to possess a relatively high index of vacuity, and this may be because fish have a higher nutritional value than crustaceans and so it is not necessary to feed so frequently; are digested more rapidly than invertebrates; or because feeding is restricted by success in prey capture (Ellis et al. 1996). Despite the small proportion of everted stomachs observed, the full stomach eversion, followed by its swallowing, could also be a factor contributing for the occurrence of empty stomachs. This mechanism has been described for rays and other elasmobranchs and allows removing parasites, indigestible material, toxic food and remains of gastric mucosa and mucus (Brunnschweiler et al. 2005; Sims et al. 2000).

The analysis of feeding strategy plots highlighted the generalized diets exhibited by all four ray species with a higher incidence of benthic preys. In general, results were similar to those presented for the species in other Atlantic areas (Ajayi 1982; Cunha et al. 1987; Du Buit 1978-1979; Ebert et al. 1991; Ellis et al. 1996; Gomes et al. 1998; Holden and Tucker 1974; Marques and Ré 1978). Cephalopods and fish, especially Gadiformes and Clupeiformes, were more frequent in the diets of larger specimens and in species that attain larger maximum lengths, like *R. clavata* and *R. brachyura*. This may result from the fact that larger individuals are more active predators and their swimming capacities allow to catch faster prey and also to forage along the water column (Ebeling 1988).

Results indicated the existence of an ontogenetic dietary shift at around classes 45−55 cm for the four analysed species, despite all attaining different maximum lengths and lengths at first maturity. This fact suggests that this shift is more dependent on size than on other life history characteristics. The relationship between predator's size and mouth dimensions in rays has been frequently stated to be correlated with their diets and their degree of prey specialization (Du Buit 1978-1979; Scharf et al. 2000; Walker 1999). Small *L. naevus*, *R. montagui* and *R. clavata* had relatively narrow diets, possibly limited by mouth size and swimming capacity, being grouped together in a distinct cluster. Small and large *R. brachyura* showed a very similar diet, both feeding mainly on bony fish. The type of dentition is also accepted to affect the type of diet. Cusped teeth are prevalent in piscivorous rays, whereas molariform teeth are better suited to feeding on crustaceans and other hard invertebrates (Du Buit 1978-1979). *R. brachyura* and *L. naevus*, which mainly feed on fish and are clustered together, have both cusped teeth (Du Buit 1978-1979). Large *R. clavata* and *R. montagui*, which were included in the same cluster, feed mostly on brachyuran crabs and fish and both have molariform teeth (Du Buit 1978-1979).

In all four species, ontogenetic shifts were in general characterized by changes from small to larger and faster prey, from benthic to semi-pelagic feeding habits, from shallow to offshore waters and from crustacean-dominated diets to a more piscivorous diet. The main changes were from benthic shrimps to pelagic crabs for *R. clavata*; from benthic teleosts to offshore teleosts and occasionally pelagic

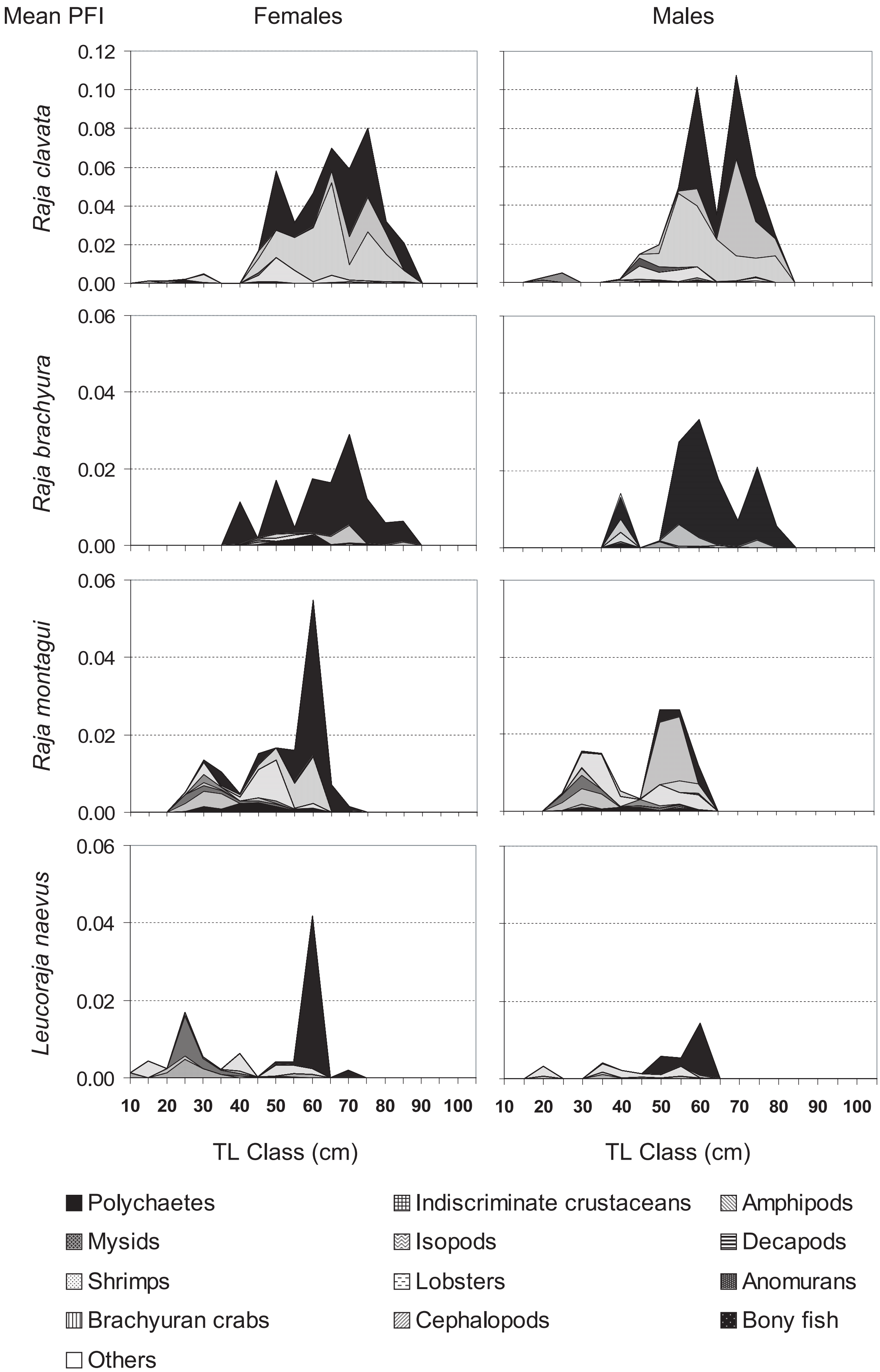

Fig. 3. Mean partial fullness index (PFI) vs. total length (*TL*, cm) class of females (left column) and males (right column) of *Raja clavata*, *R. brachyura*, *R. montagui* and *Leucoraja naevus*.

Table 3. Estimated statistics for testing differences between sexes in number of occurrence and weight for each major length group (S: small, $TL < 50$ cm; L: large, $TL \geq 50$ cm). $\chi^2 = 20.03$ with $\alpha = 0.05$ for occurrence; $p > 0.05$ for weight; * H0 is not rejected.

Index	*Raja clavata*		*Raja brachyura*		*Raja montagui*		*Leucoraja naevus*	
	S	L	S	L	S	L	S	L
Occurrence	7.78*	12.23*	10.24*	14.43*	11.11*	10.33*	12.52*	7.69*
Weight	0.39*	0.24*	0.37*	0.80*	0.24*	0.43*	0.16*	0.16*

Table 4. Feeding habits by species and major length group.

Length group		*Raja clavata*	*Raja brachyura*	*Raja montagui*	*Leucoraja naevus*
Small	Most important prey	Indisc. crustaceans Shrimps	Shrimps Bony fish Indisc. crustaceans	Polychaetes Amphipods Mysids	Shrimps Mysids Indisc. crustaceans
	Examples of identified species	*Solenocera membranacea* [1]	*Crangon crangon* [2]	*Ampelisca* spp. [3] *Lophogaster typicus* [3]	*Lophogaster typicus* [3] *Solenocera membranacea* [1]
Large	Most important prey	Brachyuran crabs (dominant) Bony fish Indisc. crustaceans Shrimps	Bony fish (dominant) Shrimps Indisc. crustaceans	Polychaetes Indisc. crustaceans Bony fish	Bony fish (dominant) Polychaetes Indisc. crustaceans Shrimps
	Examples of identified species	*Polybius henslowi* [4]	*Processa canaliculata* [5] *G. semisquamatus* [5]	*Micromesistius poutassou* [6]	*Gymnammodytes semisquamatus* [5]

Habitat: [1] benthic, [2] benthic, shallow waters, [3] suprabenthic, intertidal to sublittoral, [4] pelagic, [5] benthic offshore, [6] mesopelagic

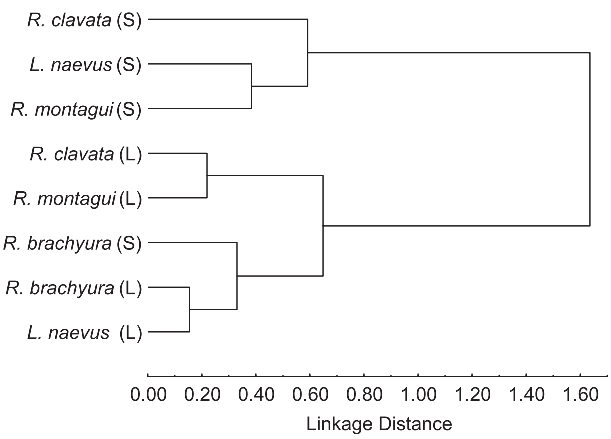

Fig. 4. Cluster analysis of prey similarity between species (*Raja clavata*, *R. brachyura*, *R. montagui* and *Leucoraja naevus*) divided by major length group (S: small, $TL < 50$ cm, L: large, $TL \geq 50$ cm). Ward's method, dissimilarity matrix based on Schoener's (1970) index. Similarity was determined from percentage by weight of each prey.

teleosts for *R. brachyura*; from sublittoral supra-benthic prey to mesopelagic teleosts for *R. montagui*; and from mysids and benthic shrimps to mesopelagic and offshore benthic teleosts for *L. naevus*. Similar shifts have been also recorded for these species in other geographic areas (e.g., Ajayi 1982; Daan et al. 1993; Holden and Tucker 1974; Steven 1930; Walker 1999).

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