

Ontogenetic dietary shift and feeding strategy of *Raja undulata* Lacepède, 1802 (Chondrichthyes: Rajidae) on the Portuguese continental shelf

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SUMMARY: Under the scope of an ecosystem approach to fisheries, the understanding of trophic interactions is important for the assessment and consequently the proposal of suitable management measures. *Raja undulata*, like other rajids, is an important demersal predator in the Portuguese coastal community for which the biological and ecological information is still scarce. The ontogenetic dietary shift was investigated. Major length groups were defined through cluster analysis of the mean abundance of prey items. Prey diversity and feeding strategy were evaluated by length group. Multivariate analysis of variance was performed to test the influence of the factors sex, season and maturity on the diet of this species. It was concluded that *R. undulata* has a dietary ontogenetic shift within the definition of three major length groups (MLGs): 200-550 mm; 550-750 mm and 750-1000 mm. Diet varied from small and semi-pelagic to large and benthic prey. The feeding strategy of the species also changed from a generalised to a specialised diet. The decapod *Polybius henslowi* was the main prey item, especially for larger predators. Differences were found between sexes, maturity stages and seasons in each MLG.

Keywords: diet, feeding strategy, *Raja undulata*, *Polybius henslowi*, Portuguese continental shelf.

RESUMEN: VARIACIÓN ONTOGÉNICA EN LA DIETA Y ESTRATEGIA ALIMENTARIA DE *RAJA UNDULATA* LACEPÈDE, 1802 (CHONDRICTHYES: RAJIDAE) EN LA PLATAFORMA CONTINENTAL PORTUGUESA. – En el ámbito de la aproximación ecosistémica a las pesquerías, la comprensión de las interacciones tróficas es esencial para llevar a cabo una adecuada evaluación y gestión de los recursos. *Raja undulata*, al igual que otros rajiformes, es un importante depredador demersal que está presente en las costas portuguesas y sobre el que existe poca información biológica y ecológica. Se estudió la variación ontogenética en la dieta. Para determinar grupos de tallas se ha realizado un análisis de clusters empleando datos de abundancia media de presas. La diversidad de las presas y su estrategia alimentaria fueron evaluadas por grupos de tallas. Para comprobar la influencia de los factores sexo, estación del año y madurez en la dieta de esta especie se llevó a cabo un análisis multivariante de la varianza. Los resultados obtenidos indican que *R. undulata* presenta variaciones ontogenéticas en la dieta, habiéndose definido tres grupos de tallas (MLG): 200-550 mm; 550-750 mm and 750-1000 mm. La dieta varió desde organismos pequeños semipelágicos a presas bentónicas de mayor tamaño. Asimismo, se observó un cambio en la estrategia alimentaria de la especie, desde una dieta generalizada a otra más especializada. El decápodo *Polybius henslowi* constituyó, en concreto para los depredadores de mayor tamaño, la presa principal. Se detectaron diferencias por sexo, estado de madurez y estación del año en cada MLG.

Palabras clave: dieta, estrategia alimentaria, *Raja undulata*, *Polybius henslowi*, plataforma continental portuguesa.

INTRODUCTION

Most Rajidae are positioned at high trophic levels (Lawson *et al.*, 1998) and play an important role in the regulation of marine ecosystems at lower trophic levels (Cortés, 1997; Stevens *et al.*, 2000; Schindler *et al.*, 2002). As such, their removal from coastal ecosystems could cause a trophic cascading effect within the remaining community, possibly altering the abundance of species that hold lower trophic levels and are also targeted by fisheries (Jennings and Kaiser, 1998). An ecosystem approach to fisheries management requires the understanding of the dependencies in the diet of fish species at all stages of the life cycle. Monitoring ecosystem interactions involves the knowledge of trophic relationships between species, through diet analysis, classification of main prey, and identification of ontogenetic dietary shifts and feeding strategies (Stergiou and Karpouzi, 2002). Together with these monitoring studies, the development of conceptual models of food webs for each distinct ecosystem is an important tool for exploring possible ecosystem responses to different management measures (Busch *et al.*, 2003).

The undulate ray, *Raja undulata* Lacepède, 1802 (Elasmobranchii, Rajidae) is a benthic species that occurs in the subtropical and temperate waters of the northeast Atlantic Ocean, from the Gulf of Guinea (Schneider, 1990) to southern England (Stehmann and Burkel, 1984), including the Canary islands (Brito, 1991). It has also been recorded in the Mediterranean and West Africa (ICES, 2006) and in a localised population on the southwest coast of Ireland, with occasional records in the English Channel (ICES, 2005; ICES, 2006). It is found on continental shelf coasts at depths of up to 200 m but is most commonly found at depths of less than 30 m (ICES, 2006). In mainland Portugal the undulate ray is caught by commercial fishing vessels and is landed together with other ray species under the general designation of *Raja* spp. This group constitutes an important by-catch from various Portuguese mixed fisheries, particularly from the artisanal and trawl segments (Machado *et al.*, 2004).

Some aspects of the biology of the undulate ray are already documented from the Portuguese continental shelf. Age was assigned using both caudal thorns and vertebrae and no differences were detected in growth between males and females (Coelho and Erzini, 2002; Moura *et al.*, 2007). As with most other skates, this is an oviparous species, character-

ised by the production of an egg capsule surrounding a fertilised egg that develops and hatches externally to the female progenitor (Hamlett *et al.*, 2005). It is a seasonal breeder, in which egg laying occurs preferentially from March to June (Coelho and Erzini, 2006; Moura *et al.*, 2007). Early stages of juveniles of this species occur within specific coastal zones, particularly in estuaries (Moura *et al.*, 2007) and coastal lagoons (Coelho *et al.*, 2002).

The objectives of this study were to investigate aspects of the biology and ecology of *R. undulata* in Portuguese continental waters, and particularly to understand the role of this species in the ecosystem through the characterisation of its diet, the identification of the main ontogenetic dietary shifts and the characterisation of its feeding strategy in relation to special aspects of its life cycle.

MATERIALS AND METHODS

Specimens of *R. undulata* were sampled off the Portuguese coast from three sources (Fig. 1): i) commercial trawlers, multi-purpose vessels using either gill nets or trammel nets and operating in Peniche (sampling period: December 2003 to September 2006); ii) bottom research surveys conducted on the Portuguese continental coast (sampling period: October 2003 and July 2004); iii) a beam trawl sampling

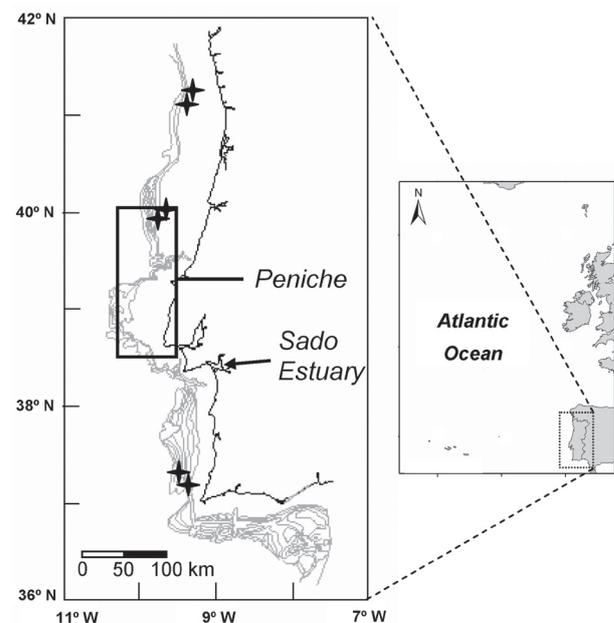


FIG. 1. – Sample collection locations: Sado Estuary, fishing grounds nearby Peniche (square) and position of the research survey hauls with occurrence of specimens of *R. undulata* (+). The depth range of isobaths varies from 300 to 1000 m (100 m between isobaths).

TABLE 1. – Scale adopted for male and female maturity stage assignments, based on Stehmann (2002) with indication of the number of sampled specimens.

	Males	Females
1 Immature	Claspers flexible and shorter than the anterior margin of the pelvic fin; testes small. (n=17)	Ovaries small, granulated, without follicles differentiated. Uterus narrow and oviducal gland undifferentiated. (n=29)
2 Maturing	Claspers flexible but longer than the anterior margin of the pelvic fin; testes larger. (n=16)	Ovaries enlarged with follicles in many stages of development, sometimes restricted to the anterior part of the ovary. Uterus larger than the previous stage and oviducal gland differentiated. (n=15)
3 Mature	Claspers rigid, longer than the anterior margin of the pelvic fin. Testes enlarged; Sperm vesicles can be distinguished (n=12)	Ovaries with large follicles that can reach 40 mm diameter. (n=7)
4 Active	Claspers rigid; clasper glans dilated and redish; clasper groove with sperm. Testes identical to stage 3. (n=5)	Large yolk-egg present in both Fallopian tubes. (n=0)
5 Advanced	---	Formation of the egg capsule in the oviducal gland. Capsules may be fully formed but remain in the anterior part of the oviduct. (n=1)
6 Extruding	---	Capsules totally formed, in the posterior part of the uterus, ready for extrusion. (n=1)

programme carried out in the Sado estuary (sampling period: November 2004 and November 2005). From each specimen information on total length (TL, in cm) was recorded. Sex was determined and maturity stage was assigned according to Stehmann's maturity scale for oviparous elasmobranchs (Stehmann, 2002) (Table 1).

Stomachs were extracted and then frozen. Stomach contents were analysed and prey items were classified to the lowest possible identifiable taxonomic level.

The vacuity index was estimated as the percentage of empty stomachs in the sample. Dietary ontogenetic shift was investigated using cluster analysis (Ward's method, Manhattan distance) of the mean weight of each prey item by predator length class of 50 mm. According to the different prey spectra, results suggested that specimens could be divided into three major length groups, henceforth referred to as MLGs.

Cumulative prey curves, which can be used to determine whether the number of digestive tracts analysed is appropriate to describe the diet (Cailliet *et al.*, 1988), were constructed for each MLG. The order of digestive tracts was randomised five times and the mean cumulative number of prey taxa found was plotted against the number of digestive tracts (Ferry and Cailliet, 1996). The relative importance of each prey item in each MLG was quantified through the estimation of dietary indexes (Hyslop, 1980; Cortés, 1997) by prey item and prey items aggregated by higher taxa: i) frequency of occurrence (%O); ii) percentage by number (%N); and iii) percentage by weight (%W). The percent index of relative impor-

tance (%IRI) was given by the %O of each prey category multiplied by the sum of %W and %N, and expressed on a percent basis (1):

$$\%IRI_i = 100IRI \left/ \sum_{i=1}^n IRI_i \right. \quad (1)$$

where n stands for the total number of foods considered at a given taxonomic level and i is the food category (Cortés, 1997).

The feeding strategy by MLG was examined through graphical representation as proposed by Cortés (1997) and using the most representative prey items aggregated by higher taxa: amphipods (Crustacea: Amphipoda), mysids (Crustacea: Mysidacea), shrimps (Crustacea: Decapoda Natantia), brachyuran crabs (Crustacea: Decapoda Brachyura), cephalopods (Mollusca: Cephalopoda) and teleosts (Osteichthyes: Teleostei). The diversity of prey-items between MLGs was evaluated through the estimation of Shannon-Wiener diversity index (H') of prey items by MLG (Legendre and Legendre, 1998).

Multivariate analysis of variance (MANOVA) was used to study the diet of the undulate ray. The weight of the more representative prey categories (divided into higher taxa and with more than 10 occurrences) was considered the dependent variable, and season (winter, spring, summer and autumn), sex (F or M) and maturity stage (1, 2, 3, 4 and 5; females in stages 5 and 6 were grouped) were defined as factors. All these three factors and their interactions were analysed within each MLG. The multivariate F value (Wilks' lambda) based on a comparison of the error variance/covariance matrix and the effect vari-

TABLE 2. – Number of sampled specimens (n) and their total length (TL) and range (in mm) in each sample source.

	Males		Females	
	n	TL range	n	TL range
Peniche	40	467-945	40	540-905
Sado Estuary	4	275-651	5	237-430
Research surveys	6	480-639	8	524-885
TOTAL	50	275-945	53	237-905

ance/covariance matrix was applied to test differences in the diet within each MLG at a significance level of 5%. An ANOVA was further performed to identify the main prey groups responsible for the major differences among factors: sex, season and maturity. The significance level adopted was 5%.

RESULTS

The smallest specimens were caught in the Sado Estuary, where lengths ranged from 237 to 651 mm (4 males and 5 females) (Table 2). In the second data source, specimens sampled from catches held in coastal areas near Peniche consisted of 40 males with lengths ranging from 467 to 945 mm, and 40 females with lengths ranging from 540 to 905 mm. 14 specimens were collected during research surveys, 6 males with TL ranging from 480 to 639 cm and 8 females with TL ranging from 524 and 885 cm.

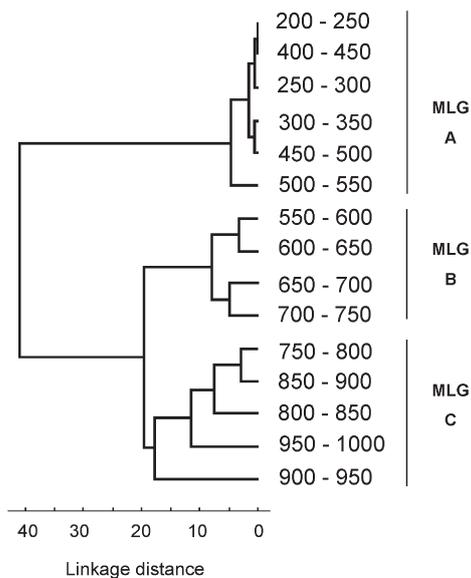


FIG. 2. – Dendrogram resulting from the hierarchical cluster analysis of the mean weight of each prey item by predator length class of 50 mm using Ward's method and Manhattan distances. Three major length groups (MLGs) were defined: A) 200-550 mm, B) 550-750 mm, and C) 750-1000 mm.

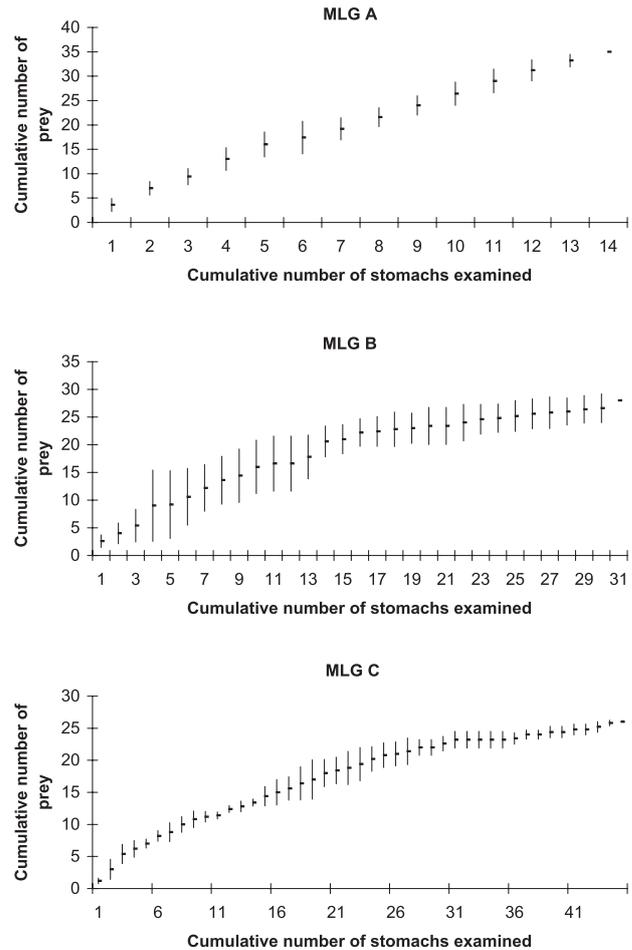


FIG. 3. – Cumulative prey curves for each major length group (MLG): A) 200-550 mm, B) 550-750 mm, and C) 750-1000 mm.

In the overall sample, all the maturity stages were covered, with the exception of females in maturity stage 4 (Table 1). However, females with egg capsules were scarce (n=2).

From the 103 stomachs analysed, 13 were empty, giving a vacuity index of 12.6%. In the remaining stomachs, 52 different prey items were identified (Table 3). The majority were considered to be benthic prey, although pelagic were also found. The cluster analysis enabled to identify the following MLG groups: group A, 200-550 mm (n=14); group B, 550-700 cm (n=31); and group C, 750-1000 mm (n=45). Within each MLG the diets were similar among different specimens (Fig. 2).

The cumulative prey curves results by MLG showed that the number of digestive tracts sampled in MLGs B and C was adequate to describe the diet (Fig. 3). For MLG B the cumulative curve reached the asymptote at 15 digestive tracts and in MLG C the asymptote was attained at 21 digestive tracts. In MLG A the number of items did not clearly stabilise

TABLE 3. – Stomach contents of *R. undulata* expressed as frequency of occurrence (%O), percentage by number (%N), percentage by weight (%W) and percent index of relative importance (%IRI) for each major length group (MLG) (A: 200-550 mm; B: 550-750 mm and C: 750-1000 mm). Subtotals are presented in bold for higher taxonomic levels.

ITEM	MLG A				MLG B				MLG C			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
CRUSTACEA												
Euphausiacea	7.14	0.61	0.01	0.3								
Misidacea	7.14	14.11	0.00	6.2	3.23	0.36	0.00	0.07				
<i>Gastrosaccus spinifer</i>	7.14	14.11	0.00	6.2	3.23	0.36	0.00	0.07				
Isopoda	7.14	0.61	0.12	0.05					0.02	0.61	0.01	0.00
<i>Eurydice pulchra</i>	7.14	0.61	0.12	0.3								
Isopoda NI									2.22	0.60	0.01	0.05
Amphipoda	14.29	2.45	0.01	0.36	6.45	0.71	0.00	0.02				
<i>Ampelisca</i> sp.	7.14	0.61	0.01	0.3	3.23	0.36	0.00	0.07				
Amphipoda NI	7.14	1.84	0.00	0.8	3.23	0.36	0.00	0.07				
Natantia	71.43	39.88	6.21	32.32	25.81	46.98	2.84	6.09	0.16	5.45	2.39	0.58
<i>Parapenaeus longirostris</i>					3.23	0.36	0.06	0.09				
<i>Processa canaliculata</i>	14.29	11.66	2.72	5.8	16.13	42.35	2.52	11.75	2.22	0.60	0.14	0.11
<i>Processa edulis</i>	7.14	3.68	0.34	1.7								
<i>Processa</i> sp.	21.43	10.43	1.09	4.9	9.68	1.78	0.08	0.38				
<i>Crangon crangon</i>									2.22	0.60	0.01	0.05
<i>Philoceras</i> sp.	7.14	4.29	0.10	1.9								
<i>Philoceras trispinosus</i>	7.14	0.61	0.00	0.3	6.45	1.78	0.02	0.35				
Crangonidae	14.29	3.68	0.10	1.6					2.22	1.20	0.00	0.08
Natantia NI	7.14	4.29	0.28	2.0	3.23	0.71	0.16	0.21	2.22	0.60	0.01	0.05
Reptantia Macrura									6.67	2.40	1.75	0.99
<i>Scyllarus arctus</i>									6.67	2.40	1.75	0.99
<i>Upogebia pusilla</i>	7.14	1.23	1.58	1.0								
Brachyura	78.57	27.61	78.05	61.26	90.32	35.94	86.11	90.10	0.87	73.94	87.50	96.00
<i>Ebalia tuberosa</i>	7.14	1.23	0.60	0.7								
<i>Ebalia</i> sp.					3.23	0.36	0.02	0.08				
<i>Atelecyclus undecimdentatus</i>	14.29	1.84	7.54	2.8	9.68	2.49	1.33	1.04	22.22	16.77	8.15	8.05
<i>Atelecyclus</i> sp.					3.23	0.36	1.23	0.59	2.22	0.60	0.17	0.12
<i>Polybius henslowi</i>	21.43	5.52	58.99	45.9	74.19	21.35	79.48	72.01	57.78	48.50	57.81	73.42
<i>Liocarcinus acuatius</i>					3.23	0.36	0.05	0.09				
<i>Liocarcinus depurator</i>	7.14	1.84	1.01	2.2								
<i>Liocarcinus marmoratus</i>	7.14	0.61	0.43	0.4	9.68	3.20	1.55	2.86	4.44	1.80	0.43	0.46
<i>Liocarcinus pusillus</i>	7.14	0.61	0.15	0.3	3.23	0.36	0.08	0.10				
<i>Liocarcinus</i> sp.	14.29	2.45	1.60	1.5	3.23	0.71	0.14	0.20	2.22	0.60	0.13	0.10
<i>Liocarcinus</i> spp.	14.29	4.29	1.40	2.3								
<i>Necora puber</i>									6.67	2.40	1.95	1.08
Portunidae	14.29	1.23	0.55	0.7					4.44	1.20	0.67	0.40
<i>Pilumnus hirtellus</i>	7.14	1.23	2.52	1.2	3.23	1.07	0.80	0.54				
<i>Monadaeus couchii</i>					3.23	0.36	0.05	0.09				
Xanthidae	7.14	0.61	0.14	0.3					2.22	0.60	0.48	0.27
<i>Goneplax rhomboides</i>	7.14	0.61	0.07	0.3	3.23	0.36	0.29	0.19				
Brachyura NI	42.86	5.52	3.06	3.9	22.58	4.63	0.77	1.22	2.22	0.60	0.01	0.05
Decapoda NI	7.14	0.61	0.20	0.3	6.45	1.07	0.37	0.36	2.22	0.60	0.17	0.12
Crustacea (larvae)	7.14	1.84	0.00	0.8								
Crustacea NI	7.14	4.91	0.01	2.2	12.90	2.14	0.42	0.59	8.89	2.40	0.78	0.53
MOLLUSCA												
Bivalvia	7.14	0.61	0.00	0.3					2.22	0.60	0.01	0.05
Cephalopoda	14.29	3.07	10.23	1.38	12.90	3.20	6.38	0.98	0.07	1.82	0.14	0.03
<i>Loligo vulgaris</i>	14.29	2.45	7.91	3.2	12.90	3.20	6.38	3.33	2.22	0.60	0.09	0.09
<i>Alloteuthis</i> sp.	7.14	0.61	2.32	0.9								
Cephalopoda NI									4.44	1.20	0.02	0.09
PISCES												
Teleostei	35.71	3.68	5.15	2.52	25.81	7.12	2.70	1.49	0.27	12.12	7.69	2.90
<i>Merluccius merluccius</i>									2.22	0.60	5.02	2.40
<i>Echiichthys vipera</i>									6.67	2.99	0.13	0.27
<i>Hyperoplus lanceolatus</i>					3.23	2.14	0.19	0.50	6.67	4.79	0.06	0.36
<i>Pagellus acarne</i>									2.22	1.20	20.23	9.58
<i>Gobius niger</i>	7.14	0.61	3.60	1.2	3.23	0.36	0.01	0.07				
<i>Pomatoschistus minutus</i>	7.14	0.61	0.08	0.3	6.45	2.85	2.20	1.49				
<i>Arnoglossus imperialis</i>					3.23	0.36	0.00	0.07				
Teleostei NI	28.57	2.45	1.47	1.5	12.90	1.42	0.29	0.40	11.11	3.59	0.93	0.68
Chondrichthyes									2.22	0.60	0.21	0.14
Unidentified tissue					9.68	1.07	0.04	0.22	2.22	0.60	0.01	0.05

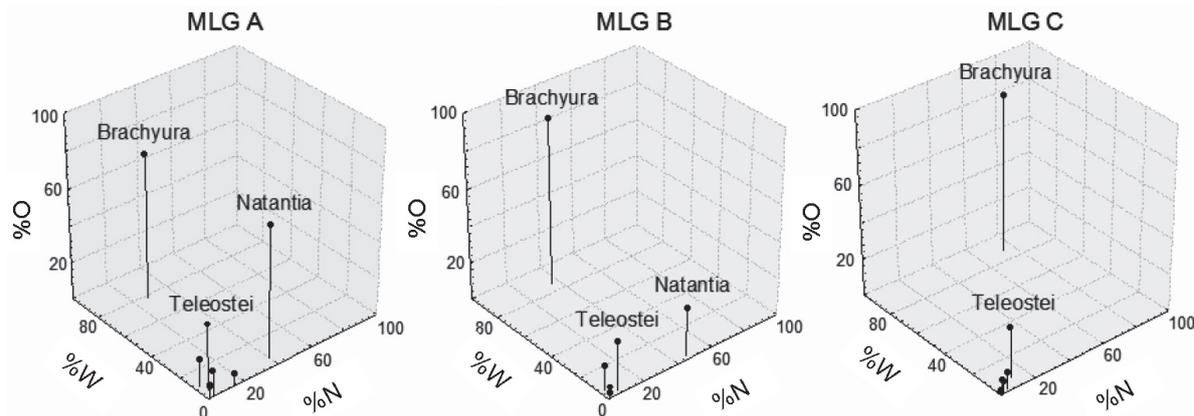


FIG. 4. – Three-dimensional representation of the feeding strategy of *R. undulata* by major length group (MLG): A) 200-550 mm; B) 550-750 mm; and C) 750-1000 mm.

after 14 stomachs. This is a relatively small sample and the possibility of finding new prey groups if more specimens were analysed cannot be discarded.

The index estimates of %O, %N and %W by MLG (Table 3) showed that: i) MLG A fed on pelagic prey, namely, the mysid *Gastrosaccus spinifer* and the shrimp *Processa canaliculata*. Small benthic brachyuran crabs, particularly species of the genus *Liocarcinus* and the pelagic crab *Polybius henslowi*, were also important prey items. In this length group, the small dimensions of most of the prey and probably the fast digestion rates made it impossible to identify prey at genus or species level in some cases. For larger specimens belonging to MLGs B and C the major prey was *P. henslowi*, which was identified in most of the stomachs sampled (high %O) and in relatively high number and weight (high %N and %W). In some specimens from these two MLGs *P. henslowi* was the only prey found in stomachs. Although present in all MLGs, the high degree of digestion of most of the teleosts made their taxonomic identification to species or genus impossible.

The analysis of %IRI by MLG group showed that the Brachyura were the most important prey items in all MLGs, while the importance of Natantia decreased in MLG C. %IRI estimates for Teleosts remained similar in all three MLGs. The Shannon-Wiener diversity index (H') was estimated as 4.43, 3.12 and 2.96 for MLGs A, B and C, respectively.

The three-dimensional graphical representation of the diet by MLG (Fig. 4) indicated that smaller specimens had a generalised diet, consuming a fairly large variety of different prey. The medium-sized predators (MLG B) had a more specialised diet, with *P. henslowi* being the most important prey species. In larger specimens (MGL C) the diet was more specialised than in the two other groups: *P. henslowi* was the main prey and the remaining prey were all considered rare.

The MANOVA results demonstrated the existence of differences in the diet within each MLG according to season, sex and maturity (Table 4). The ANOVA performed for each dependent variable (group *taxa*) indicated that Teleostei were responsible for the statistically significant interaction

TABLE 4. – MANOVA table of Wilks' lambda and group response to ANOVA. (df = degrees of freedom; Wilks = value of Wilks statistic; Approximate F = approximate F value; num df = numerator degrees of freedom; den df = denominator degrees of freedom; Pr (>F) = p value; significance codes: *** 0.001; ** 0.01; * 0.05)

	Df	Wilks	MANOVA results				Pr (>F)	Group response to ANOVA				
			approx F	Num Df	Den Df			Brachyura	Natantia	Misidacea	Teleostei	Cephalopoda
Season	3	0.614	1.890	15	146.71	0.0284*	0.006**	0.039*	0.867	0.270	0.526	
Sex	1	0.673	5.151	5	53.00	0.00064***	4.421e-05***	0.041*	0.364	0.074	0.415	
Maturity	4	0.559	1.692	20	176.73	0.0383*	0.432	0.032*	0.980	0.001**	0.808	
Season*Sex	3	0.658	1.599	15	146.71	0.08	0.016*	0.187	0.856	0.256	0.853	
Season*Maturity	8	0.429	1.251	40	233.82	0.158	0.0005***	0.340	1.00	0.051	0.995	
Sex*Maturity	2	0.399	6.188	10	106.00	2.165e-07***	0.016*	0.112	0.775	1.273e-10***	0.588	
Season*Sex*Maturity	3	0.586	2.087	15	146.71	0.013*	0.122	0.381	0.956	9.402e-06***	0.869	
Season*Sex*Maturity*MLG	8	0.425	1.268	40	233.82	0.144	0.0014**	0.030*	0.894	1.000	0.876	

(season*sex*maturity) from the MANOVA results. Due to the low number of samples within each factor, further analysis—in particular, new index estimations by sex, maturity and season in each MLG—could not be performed.

DISCUSSION

The findings of this study on the undulate ray support the common view that rays occupy high trophic levels. Most of the identified prey items were benthic or semi-pelagic. This is in accordance with the functional guilds assigned to this species by Mathieson *et al.* (2000), as well as the trophic guild assigned by Pinnegar *et al.* (2003) for specimens caught in the Celtic Sea.

The main diet changes, corresponding to dietary ontogenetic shifts, occurred at 550 mm and 750 mm. These shifts may be related to biological and ecological events occurring during the life cycle of this species. The first shift, at 550 mm, is probably related to juvenile migration to areas outside the nursery zones (inside estuaries), where the juvenile phase is spent (Moura *et al.*, 2007). But this shift can also be associated with changes in morphometric characteristics and swimming capacities of the species, as has been observed for other rajids caught on the Portuguese continental shelf (Farias *et al.*, 2006). The second shift, at 750 mm, may be related to the onset of sexual maturity. The length at first maturity was estimated as 838 mm for females and 781 mm for males (Moura *et al.*, 2007). Migratory patterns associated with reproduction are common among elasmobranchs and the occupation of new niches may result in differences in diet (Wetherbee and Cortés, 2004).

Ontogenetic dietary shift goes from small semi-pelagic to larger and benthic prey and from a generalised to a specialised diet. Shrimps and mysids are especially important in the diet of smaller specimens. Unlike other common rajids on the Portuguese continental shelf, there is no evidence that this species changes from a crustacean to a piscivorous diet as specimens increase in size (Farias *et al.*, 2006). In *R. undulata* the diet is characterised by the increasing importance of brachyuran crabs, with special emphasis on the decapod *P. henslowi*. This decapod, which is the fifth most abundant species in Portuguese groundfish surveys (Sousa *et al.*, 2006), attains high levels of occurrence and weight in the stomachs of larger specimens of *R. undulata*. *P. henslowi* is

also an important prey for large specimens of *Raja clavata* and is occasionally found in the stomachs of *R. brachyura* and *R. montagui* (Farias *et al.*, 2006), all sampled in the same geographical zone (Peniche) and on similar sampling dates. This tendency for a specialised diet as size increases was evident both in the three-dimensional graphical representation of stomach data and in the decrease in the diversity index of the prey items with length.

In each MLG all three factors—season, sex and maturity stage—were significant for the observed differences in the diet of this species. Seasonal differences are commonly observed in coastal species, as they reflect temporal changes at lower trophic levels, namely in planktonic communities. In Portuguese coastal waters the occurrence of seasonal (summer) upwelling involves energetic manifestations in the form of cold filaments, extending offshore hundreds of kilometres, and strong jets (Fiuza, 1983; Peliz and Fiuza, 1999). Well-developed phytoplankton structures are generally related to moderate or intense offshore transport, whereas the absence of plumes correspond to either weak offshore transport or coastal convergence (Sousa and Bricaud, 1992). The influence of sex and maturity stage is probably related to behaviour of the species and to its life cycle, which includes migrations that influence the type of prey caught. In other Rajidae species migration and aggregation have been linked to spatial and temporal variation in prey concentration or mating behaviour (Skjæraasen and Bergstad, 2000).

A community dominated by species with specialised feeding strategies may indicate a high level of interspecific competition for resources (Mihuc, 1997). The feeding strategy adopted by this species gives an interesting view that *R. undulata* has a unique trophic position in the marine food web, distinct from other Rajidae species of the Portuguese continental shelf.

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