

Feeding strategy and trophic ontogeny in *Scorpaena maderensis* (Scorpaeniformes: Scorpaenidae) from the Azores, NE Atlantic

by

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Received: 8 Nov. 2013
Accepted: 11 Jul. 2014
Editor: E. Dufour

Abstract. – Feeding habits of *Scorpaena maderensis* Valenciennes, 1833 from the Azores archipelago were investigated. The stomach contents of 245 specimens, collected between August 1997 and July 1999, were analysed. Decapod crustaceans and teleost fishes constitute the main food items, revealing a high level of specialization by *S. maderensis*. Ontogenic shifts and seasonal changes in the diet composition were observed, unveiling the adaptability and opportunistic predatory behaviour of this scorpaenid.

Résumé. – Stratégie alimentaire et ontogénie trophique de *Scorpaena maderensis* (Scorpaeniformes: Scorpaenidae) des Açores, Atlantique NE.

Les habitudes alimentaires de *Scorpaena maderensis* Valenciennes, 1833 de l'archipel des Açores ont été étudiées. Les contenus stomacaux de 245 spécimens, récoltés entre août 1997 et juillet 1999, ont été analysés. Les crustacés décapodes et les téléostéens sont les principales proies de *S. maderensis*, indiquant un fort degré de spécialisation chez cette espèce. Des changements ontogénétiques et saisonniers de la composition du régime alimentaire révèlent l'adaptabilité et le comportement prédateur opportuniste de ce scorpaenidé.

Key words

Scorpaenidae
Scorpaena maderensis
ANE
Azores
Trophic chains
Feeding behaviour

Stomach content analyses are a fundamental tool to examine feeding habits and to define the role of a particular fish species in the food chain (Barreiros and Santos, 1998).

Scorpaenidae are carnivorous fish that usually live in solitary on hard bottom zones. They are widely known as “Scorpion” fish due to the well-developed venom glands present in the dorsal, anal and pelvic fins (Poss and Eschmeyer, 2002; Nelson, 2006; Vieira and Barreiros, 2010). Beyond poison defences, they have large heads with numerous spines and a terminal and strongly protractile mouth used to capture prey by suction, a characteristic common to many teleost fishes (Hureau and Litvinenko, 1986; Gerking, 1994).

Around the Azores, 11 species of Scorpaenidae are found, six of those belonging to the genus *Scorpaena* (Santos *et al.*, 1997). The species studied, *Scorpaena maderensis* Valenciennes, 1833, is easily distinguished from congeners by the lack of an occipital furrow. *S. maderensis* is

a widespread species in the Azores where individuals have been recorded up to 196 mm total length (Azevedo, 1997). It is also common in Madeira and Canary islands (Doolley *et al.*, 1985; Patzner *et al.*, 1992; Patzner and Santos, 1993; Brito *et al.*, 2002), however less common in Portugal, Morocco (Boutière, 1958), Adriatic and in the whole Mediterranean basin (Tortonese and Hureau, 1979). *S. maderensis* is an epibenthic species inhabiting rocky bottom coastal areas down to ca. 40 m depth (Hureau and Litvinenko, 1986; Patzner *et al.*, 1992; Saldanha, 1995). Despite their solitary habits, it is not uncommon to find many individuals relatively close to each other (Patzner and Santos, 1993).

The feeding habits of *S. maderensis* are largely unknown, although some authors refer to a diet based on crustaceans and small fish (e.g. Hureau and Litvinenko, 1986; Azevedo, 1997; Silva, 1997; La Mesa *et al.*, 2007). This study was undertaken to detail the feeding ecology of *S. maderensis*, including a complete diet description, analyses of feeding strategy and ontogenic shifts.

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In this paper, which belongs to a series of publications describing food webs and predator-prey relationships in the Azores (e.g. Morato *et al.*, 2001; Barreiros *et al.*, 2002, 2003; Figueiredo *et al.*, 2005; Ávila *et al.*, 2014), we examine and describe the feeding habits of *S. maderensis*, providing the first accurate description of the place of this species in the Azorean rocky coastal food webs.

MATERIAL AND METHODS

Sampling

Collecting was carried out between August 1997 and July 1999 in different sites of the islands of Santa Maria, Faial and Corvo, Azores Archipelago, Portugal (Fig. 1). We collected 276 specimens by spear fishing, a method that is selective and reduces regurgitation (Barreiros *et al.*, 2002, 2003). Collected specimens were weighed to the nearest g and measured to the nearest mm. In order to stop prey digestion, the stomachs were removed as fast as possible in the laboratory, weighed to the nearest 0.001 g and preserved in 4% formalin. The “stomach” comprised all organs between the oesophagus and the pyloric valve.

Stomach contents were macroscopically examined, and prey items identified to the lowest possible taxonomic level using identification guides. The level ultimately depended upon prey type and the degree to which it had been digested (e.g. Barnes, 1990; Saldanha, 1995; Wirtz 1995). Wet weights to the nearest 0.001 g were recorded for each prey item after excess water was removed with blotting paper.

A vacuity index of 11.2% was observed for all stomachs from the original sample of 276 specimens. Stomach con-

tents of 245 specimens between 49 and 135 mm SL (mean 93.9 mm; S.D. = 17.4) were then analysed, yielding 602 prey belonging to 41 different taxa. From the total of the 245 stomachs containing food 39 were in size class < 75, 102 in size class 76-95, 71 in size class 96-115 and 33 in size class 116-135.

Sample representativeness

To evaluate the adequacy of the sample size, we used the pooled quadrat method (Pielou, 1966; Hurtubia, 1973; Pierce and Boyle, 1991) where the cumulative numbers of randomly pooled stomachs are plotted against the cumulative trophic diversity. The Shannon Index (Magurran, 2004) was employed to measure the diversity:

$$H' = - \sum_{i=1}^n Pi(\log_e Pi)$$

where P_i is the proportion of individuals of the i^{th} species. Because the cumulative diversity curves are based on random orders of quadrats, 1000 random orders of stomachs for each sample were calculated. The mean curve for each sample was then estimated and plotted. Each diversity curve was considered asymptotic if at least two previous values of the total sample trophic diversity (H') were in the range $H' \pm 0.05H'$ (Alonso *et al.*, 2002).

Diet description

Traditional indices were employed to analyse the general diet composition (Hyslop, 1980): frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) were calculated for each prey item i ; %F $_i$ = (number of stomachs where prey i occurs / number of stomachs with food) x 100; %N $_i$ = (total number of prey item i / total

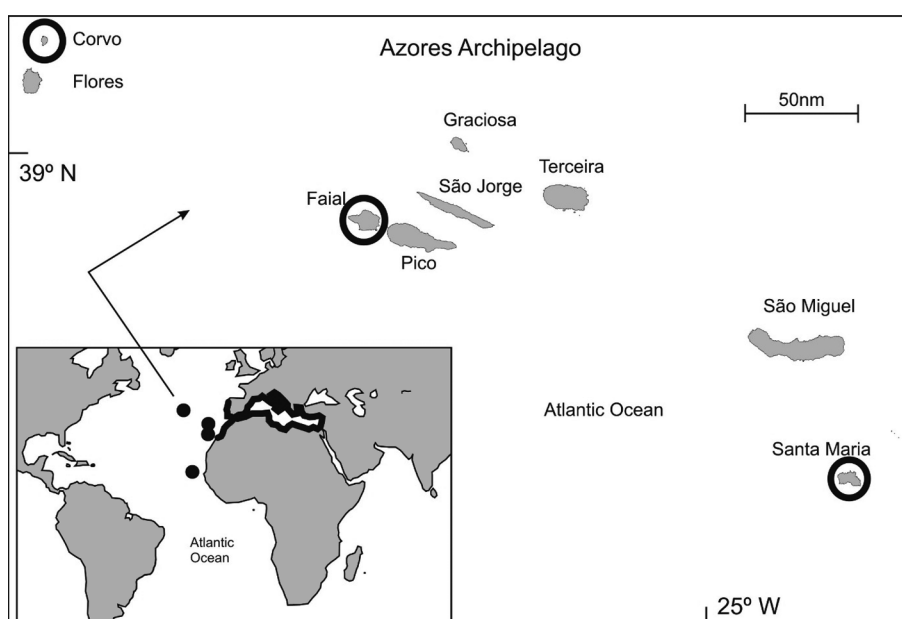


Figure 1. - Geographic distribution of *Scorpaena maderensis* and location of sampled Azorean islands.

number of prey items of all taxa) x 100; %W_i = (total weight of prey item *i* / total weight of prey items of all taxa) x 100.

Importance of prey items was identified using the index of relative importance (IRI; Cortes (1997):

$$IRI = \%F \times (\%N + \%W)$$

The general feeding strategy was analyzed following Costello's (1990) method with the modifications suggested by Amundsen *et al.* (1996). The diagram generated by this method is based on a two-dimensional representation, in which each prey point is obtained by plotting %F_i against prey-specific abundance (P_i), calculated according to the following formula:

$$P_i = (\sum S_i / \sum S_{ij}) \times 100$$

where S_i is the stomach content (weight) of prey item *i* and S_{ij} is the total stomach content (weight) of only those predators with prey item *i* in their stomach. Feeding strategy and prey importance can be determined by examining the distribution of points along the axes and the diagonal of the diagram: (1) feeding strategy is represented in the vertical axis from bottom (generalization) to top (specialization); (2) relationship between feeding strategy and between- or within-phenotype contribution to the niche width is represented in the diagonal from the lower right (high within-phenotype) to upper left (high between-phenotype); (3) prey importance is represented in the diagonal from lower left (rare prey) to upper right (dominant prey).

Trophic ontogeny

Specimens were classified into four size classes (TL in mm): < 75, 76-95, 96-115 and 116-135. The pooled quadrat method mentioned above was applied to these classes in order to generate cumulative trophic diversity curves for the evaluation of sampling adequacy for each size class.

The Tokeshi graphical method (Tokeshi, 1991) was used to determine the feeding strategy of the different size classes. The feeding strategy is interpreted by the position of data points on the graph, where the mean individual prey diversity (D_I) is plotted against the population prey diversity (D_P). The values of D_I and D_P, based on the Shannon-Wiener diversity index (H), were calculated according to the following formulas:

$$D_I = (-\sum P_{ij} \ln P_{ij}) / N$$

$$D_P = -\sum P_i \ln P_i$$

where N = total number of stomachs per size class, P_{ij} = the proportion of prey-type *i* in the *j*th stomach, P_i = the proportion of the prey-type *i* in all size classes. These diversity indexes were calculated using the weight proportions. According to this method, in the graphical interpretation it is considered that: a) size classes with a low value for both population and mean individual prey diversity can be described as specialists; b) size classes with a generalist strategy present high population prey diversity, and either high mean individual prey diversity (where homogeneous

and/or similar feeding is apparent) or low mean individual prey diversity (where heterogeneous and/or variable feeding is apparent).

Dietary overlap between size classes was evaluated by the Schoener's index, R_o (Schoener, 1970):

$$R_o = 1 - 0.5 \times \sum_{i=1}^{i=n} |P_{xi} - P_{yi}|$$

where P_{xi} and P_{yi} are the numerical proportion (%N) of item *i* in the size classes *x* and *y*. The index ranges from 0, which indicates no overlap, to 1 indicating a complete overlap. Based on previous studies (Zaret and Rand, 1971; Wallace, 1981) results from the Schoener index above 0.6 were considered as a significant dietary overlap.

The three traditional indices (Hyslop, 1980) used in the general approach were also applied to *S. maderensis* in different size classes. The homoscedasticity of variances were tested by Kolmogorov-Smirnov method. As the homoscedasticity was not verified in all cases, the Kruskal-Wallis test was used to analyse the relationships between length data and mean number and weight of preys (Zar, 1998).

RESULTS

General diet composition

The number of stomachs examined appeared sufficient to study the general diet of *S. maderensis*, with a trophic diversity curve reaching an asymptote after 10 stomachs (Fig. 2). The analysis of *S. maderensis* feeding strategy showed this species to be a predator with a narrow trophic niche and a specialization towards decapod crustaceans. Most individuals consumed this prey group, while smaller proportions of other prey types were included in the diet of some specimens (Fig. 3). Amongst decapod taxa, brachyurans were the most ingested prey type. They occurred in 27.7% of stomachs, representing 12.8% of the total number of ingested prey and 41.1% of total prey weight (Tab. I). The genera *Liocarcinus* Stimpson, 1870 and *Xantho* Leach, 1841 were the most commonly recorded.

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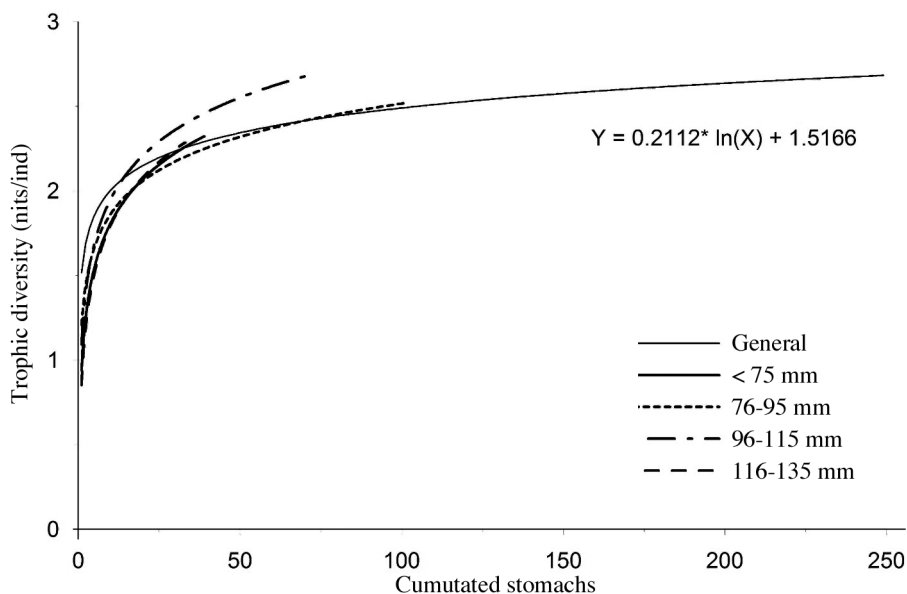


Figure 2. - Cumulative trophic diversity curves of *Scorpaena maderensis* specimens sampled from the Azores by size classes.

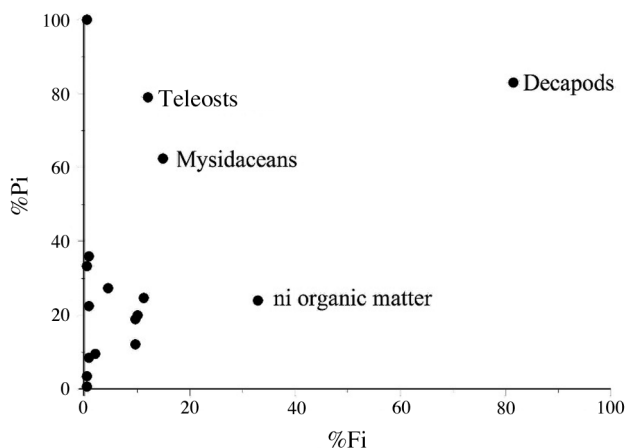


Figure 3. - General feeding strategies plot based on Amundsen *et al.* (1996) for *Scorpaena maderensis* from the Azores. %Fi = frequency of prey i occurrence; %Pi = specific prey abundance

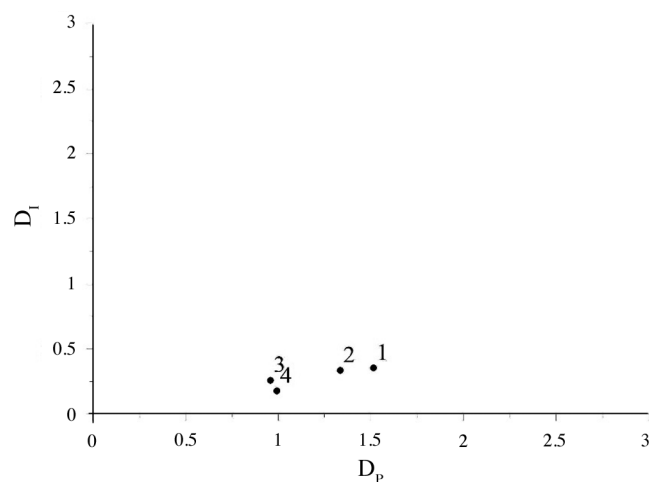


Figure 4. - Tokeshi plot of the feeding strategy of each size class (1 = < 75 mm; 2 = 76-95 mm; 3 = 96-115 mm; 4 = 116-135 mm) of *Scorpaena maderensis* from the Azores. D_i = mean individual prey diversity; D_p = population prey diversity.

these stomach contents was high, thus indicating a possible individual specialization. Other prey types besides decapods, teleosts and mysidaceans can be considered as occasional prey (Tab. I).

Trophic ontogeny

Sampling adequacy curves for the whole sample showed asymptotic tendencies between the 13th (76-95 mm) and the 18th (> 135 mm) stomach with food (Fig. 2). As the smallest number of stomachs analysed in one class was 33 (> 135 mm), we considered the sample sufficient to undertake an ontogeny analysis.

The low values of mean individual prey diversity (D_i) and prey population diversity (D_p) suggest a tendency toward a specialist feeding strategies in all size classes. However,

there was also an ontogenetic shift to more generalist feeding in younger specimens, mainly in the first two size classes (Fig. 4).

The index of diet overlap was highest between consecutive size classes. The smaller size class displayed significant dietary overlap ($R_o \geq 0.60$) only with the subsequent group (76-95mm), while between the last three size classes the diet overlap was always significant (Tab. II).

In terms of weight, decapods dominated the diet of *S. maderensis* during its entire life cycle, while mysidaceans and teleosts revealed inverse ontogenetic tendencies. Mysidaceans were most important for small individuals, while teleosts became more important in larger specimens (Tab. III).

Table I. - Diet composition of *Scorpaena maderensis* (n = 249 stomachs with contents), from Azores. Values of frequency of occurrence (%F), numerical proportion (%N), weight proportion (%W) and index of relative importance (%IRI) for each food item are presented. + : values < 0.1%.

Prey items	%F	%N	%W	%IRI
Algae				
Unidentified	9.6	-	1.0	-
Bryozoa				
Unidentified	0.4	0.3	0.4	-
Anthozoa				
Unidentified	0.4	0.2	+	-
Platyhelminthes				
Unidentified	0.8	0.3	0.1	-
Nematoda				
Unidentified	0.4	0.2	-	-
Crustacea	85.5	69.7	75.2	49.1
Mysidacea unidentified	14.9	10.5	8.4	1.1
Caprellidea unidentified	6.8	4.3	0.4	0.1
Gammaridea unidentified	1.2	0.7	+	-
Amphipoda unidentified	2.0	0.8	0.2	+
Isopoda unidentified	4.4	2.8	0.3	+
Decapoda total	66.7	46.3	63.9	29.1
<i>Stenopus spinosus</i>	0.4	0.2	1.2	-
Palinuridae unidentified	1.2	0.5	1.0	+
<i>Scyllarus arctus</i>	2.0	0.8	1.1	+
<i>Galathea</i> sp.	0.4	0.2	1.1	+
Anomura unidentified	1.2	0.5	0.7	+
Decapoda Brachyura total	27.7	12.8	41.1	5.9
Homolidae unidentified	1.2	0.5	0.4	-
<i>Ebalia tuberosa</i>	0.4	0.2	0.1	-
Majidae unidentified	1.2	0.5	0.2	-

Prey items	%F	%N	%W	%IRI
<i>Acanthonyx lunulatus</i>	0.4	0.2	0.7	-
<i>Achaeus cranchii</i>	1.6	0.8	0.9	+
<i>Liocarcinus</i> sp.	6.4	3.0	7.3	0.3
<i>Liocarcinus corrugatus</i>	3.2	1.3	5.9	0.1
<i>Liocarcinus pusillus</i>	0.4	0.2	0.1	-
<i>Lophozozymus</i> sp.	6.4	2.8	7.7	0.3
<i>Lophozozymus incisus</i>	5.2	2.2	11.1	0.3
<i>Grapsus grapsus</i>	0.4	0.2	0.6	-
<i>Pachygrapsus marmoratus</i>	2.4	1.0	6.0	0.1
Decapoda unidentified	47.4	31.3	17.7	9.2
Crustacea unidentified	11.2	4.8	1.9	0.3
Echinoidea				
Unidentified	0.8	0.3	0.2	-
Mollusca	9.6	5.3	1.8	0.3
Bivalvia unidentified	2.0	1.0	+	+
<i>Loligo forbesi</i>	0.4	0.2	-	-
<i>Calliostoma lusitanium</i>	0.4	0.2	-	-
Patellidae unidentified	1.2	0.5	0.4	-
Prosobranchia unidentified	6.4	2.8	0.9	0.1
Gastropoda unidentified	1.6	0.7	0.4	+
Teleostei				
Syngnathidae unidentified	0.4	0.2	+	-
Teleostei unidentified	11.7	5.3	16.1	1.0
Unidentified fish larvae	0.8	0.3	+	-

Table II. - Schoener's index of diet overlap between the four size classes of *Scorpaena maderensis* from the Azores.

Size groups (mm)	< 75	76-95	96-115
76-95	0.6	-	-
96-115	0.5	0.7	-
116-135	0.4	0.7	0.7

The frequency and number data analysis revealed a great importance of occasional prey in small specimens, evidencing a more generalized feeding. However, while *S. maderensis* grew, the importance of these mixed prey decreased and the specialization upon decapods became more evident (Fig. 5).

The Kruskal-Wallis test revealed non-significant relationships ($H_{(3, 245)} = 0.7679$; $p = 0.8571$) of size and number of prey captured among size classes. However, there was a significant increase in mean prey weight ($H_{(3, 592)} = 67.35$; $p < 0.01$) with *S. maderensis* size. Mean prey weight increased from 0.023 to 0.109 g per stomach from the smallest (< 75 mm) to the largest (116-135 mm) size class (Tab. IV).

DISCUSSION

Diet characterization

Our study reveals a high level of feeding specialization in *S. maderensis*, with decapod crustaceans and teleost fish being its main food items in the studied area, as also observed by Silva (1997). However, Mysidacea appeared to have a relatively high importance (%Rw) in the stomach contents analysed. This pattern of preferred prey was also verified for other Scorpaenidae in the Mediterranean Sea (Harmelin-Vivien *et al.*, 1989) and the Indian Ocean where, amongst a guild of 17 species, only one did not follow this feeding pattern (Harmelin-Vivien and Bouchon, 1976). Prey of *S. maderensis* are essentially rocky bottom dwellers (Saldanha, 1995; Morton *et al.*, 1998) a tendency that Bradai and Bouain (1990) spread to all Scorpaenidae. Since the occurrence of *S. maderensis* in the Azores is limited to rocky bottoms (Morton *et al.*, 1998) the species may be classified as an opportunistic predator of "passing by" prey (Shpigel and Fishelson, 1989). Similarly to our study, minor prey items were found in high proportions in the stomachs

Table III. - Diet composition of four *Scorpaena maderensis* size classes, from Azores. Values of frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) for each food item are presented. +: values < 0.1.

Prey items/size groups (TL, mm)	%F				%N				%W			
	≤ 75	76-95	96-115	116-135	≤ 75	76-95	96-115	116-135	≤ 75	76-95	96-115	116-135
Algae												
Unidentified	7.7	8.8	9.9	12.1	-	-	-	-	2.9	0.5	0.2	3.0
Bryozoa												
Unidentified	-	-	1.4	-	-	-	1.2	-	-	-	1.1	-
Anthozoa												
Unidentified	-	-	1.4	-	-	-	0.6	-	-	-	+	-
Platyhelminthes												
Unidentified	-	1.0	1.4	-	-	0.4	0.6	-	-	0.2	0.1	-
Nematoda												
Unidentified	-	1.0	-	-	-	0.4	-	-	-	+	-	-
Crustacea	79.5	82.4	93.0	91.0	69.3	69.2	72.1	68.8	84.0	72.5	76.9	75.8
Mysidacea unidentified	28.2	16.7	7.0	9.1	23.9	12.7	3.0	3.8	18.8	17.7	0.6	2.5
Caprellidea unidentified	18.0	2.0	10.0	3.0	13.7	1.6	5.4	1.3	3.3	0.2	0.6	0.1
Gammaridea unidentified	2.6	2.0	-	-	1.1	1.2	-	-	+	+	-	-
Amphipoda unidentified	-	3.0	1.4	3.0	-	1.2	0.6	1.3	-	0.3	+	0.6
Isopoda unidentified	7.7	4.9	2.8	3.0	4.6	2.3	1.2	1.3	2.7	0.3	0.1	0.3
Decapoda total	41.0	65.7	80.3	72.7	19.3	46.2	55.8	58.8	51.8	52.7	73.4	71.3
<i>Stenopus spinosus</i>	-	-	1.4	-	-	-	0.6	-	-	-	3.3	-
Palinuridae unidentified	2.6	1.0	1.4	-	1.1	0.4	0.6	-	9.2	1.3	0.1	-
<i>Scyllarus arctus</i>	5.1	1.0	1.4	3.0	2.3	0.4	0.6	1.3	14.8	0.5	0.4	0.7
<i>Galathea</i> sp.	-	-	1.4	-	-	-	0.6	-	-	-	3.2	-
Anomura unidentified	-	2.0	1.4	-	-	0.8	0.6	-	-	2.0	+	-
Decapoda Brachyura total	7.7	25.5	38.0	33.3	3.4	11.9	17.6	15.0	18.0	33.4	48.0	45.0
Homolidae unidentified	-	1.0	2.9	-	-	0.4	1.2	-	-	0.6	0.5	-
<i>Ebalia tuberosa</i>	-	-	1.4	-	-	-	0.6	-	-	-	0.3	-
Majidae unidentified	-	-	2.8	3.0	-	-	1.2	1.3	-	-	0.4	0.6
<i>Acanthonyx lunulatus</i>	-	-	1.4	-	-	-	0.6	-	-	-	1.9	-
<i>Achaeus cranchii</i>	-	1.0	2.9	3.0	-	0.8	1.2	1.3	-	1.9	0.5	0.2
<i>Liocarcinus</i> sp.	5.1	11.8	1.4	3.0	2.3	5.4	0.6	1.3	17.8	15.7	0.9	1.1
<i>Liocarcinus corrugatus</i>	-	2.0	5.6	3.0	-	0.8	2.4	1.3	-	1.3	9.3	2.2
<i>Liocarcinus pusillus</i>	-	1.0	-	-	-	0.4	-	-	-	0.2	-	-
<i>Lophozozymus</i> sp.	2.6	5.9	4.2	15.2	1.1	2.3	1.8	7.5	0.2	6.3	6.2	14.3
<i>Lophozozymus incisus</i>	-	2.9	12.7	3.0	-	1.2	5.5	1.3	-	3.7	25.3	3.5
<i>Grapsus grapsus</i>	-	-	1.41	-	-	-	0.61	-	-	-	1.83	-
<i>Pachygrapsus marmoratus</i>	-	2.0	4.2	3.0	-	0.8	1.8	1.3	-	2.2	2.3	23.2
Decapoda unidentified	28.2	50.0	53.5	54.6	12.5	32.7	35.2	42.5	9.9	15.6	18.4	25.7
Crustacea unidentified	15.4	10.8	12.7	6.1	6.8	4.2	6.1	2.5	7.5	1.4	2.3	1.0
Echinoidea												
Unidentified	-	-	2.8	-	-	-	1.2	-	-	-	0.5	-
Mollusca	2.6	10.8	8.5	15.2	1.1	6.2	3.6	10.0	0.1	0.9	1.5	3.1
Bivalvia unidentified	2.6	3.9	-	-	1.1	1.9	-	-	0.1	0.1	-	-
<i>Loligo forbesi</i>	-	-	-	3.0	-	-	-	1.3	-	-	-	+
<i>Calliostoma lusitanium</i>	-	1.0	-	-	-	0.4	-	-	-	+	-	-
Patellidae unidentified	-	1.0	2.8	-	-	0.4	1.2	-	-	0.3	1.0	-
Prosobranchia unidentified	-	7.8	4.2	15.2	-	3.1	1.8	7.5	-	0.5	0.4	2.8
Gastropoda unidentified	-	1.0	1.4	3.0	-	0.4	0.6	1.3	-	0.1	0.1	0.3

Table III. - Continued.

Prey items/size groups (TL, mm)	%F				%N				%W			
	≤ 75	76-95	96-115	116-135	≤ 75	76-95	96-115	116-135	≤ 75	76-95	96-115	116-135
Teleostei												
Syngnathidae unidentified	–	1.0	–	–	–	0.4	–	–	–	0.1	–	–
Teleostei unidentified	10.3	10.8	10.0	21.2	4.6	4.62	4.9	10.0	3.9	19.7	14.6	17.2
Unidentified fish larvae	2.6	1.0	–	–	1.1	0.4	–	–	0.1	+	–	–
Unidentified organic matter	46.2	37.3	26.8	15.2	–	–	–	–	9.1	6.1	5.2	1.0

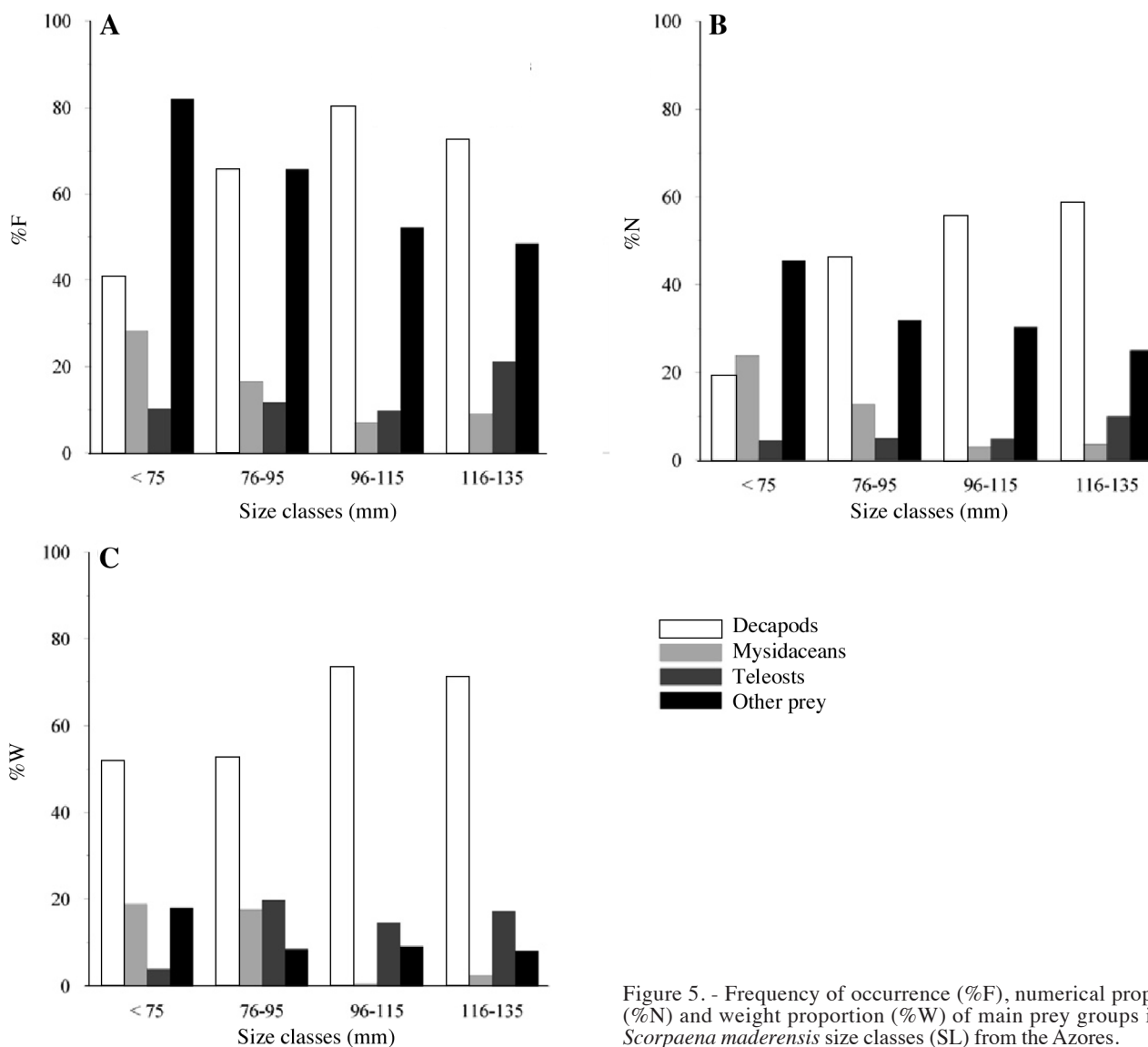


Figure 5. - Frequency of occurrence (%F), numerical proportion (%N) and weight proportion (%W) of main prey groups in four *Scorpaena maderensis* size classes (SL) from the Azores.

of *S. maderensis* in the Mediterranean Sea (La Mesa *et al.*, 2007). Capturing prey by suction seems to be a characteristic of *S. maderensis*, as in other scorpaenids (Gerking, 1994) and this may well explain the occurrence of algae and inert detritus in some stomach contents.

As to the predominance of some crabs such as *Lopho-*

zozymus incisus (Milne Edwards, 1834) (see Figueiredo *et al.*, 2005), *Xhanto* sp. Leach, 1814, *Liocarcinus corrugatus* (Pennant, 1777), *Liocarcinus* sp. and *Pachygrapsus marmoratus* (Fabricius, 1787), it may well be a consequence of a greater availability of these preys within *S. maderensis* habitats. However, as noticed by Silva (1997), one should

Table IV. - Average number and average weight of prey items in the four *Scorpaena maderensis* classes (SL) from Azores (\pm standard error).

	< 75	76-95	96-115	116-135
Mean number	2.26	2.55	2.32	2.42
SD	1.41	2.09	1.37	2.07
Mean weight	0.02	0.07	0.10	0.11
SD	0.05	0.17	0.17	0.25

not discard the hypothesis that *S. maderensis* may present some degree of specialization towards these particular preys. Studies focused on population densities on these crabs in the Azores would be useful to give some insights into this question.

Diet composition by size classes

Frequency of distribution by size class was somewhat homogenous, undoubtedly a consequence of spear fishing being the method we used for specimen collection, which allowed the efficient capture of an adequate size range (Barreiros and Santos, 1998). Also important was the observation of significant ontogenic differences in the diet of *S. maderensis*, which may reflect a decrease of intra specific competition between different size animals. Ontogenic changes were also reflected by an increase in size of the prey captured by bigger specimens. A similar pattern was detected for this species in the Mediterranean (La Mesa *et al.*, 2007) – and this is one of the main aspects of interest between our study and the former author work on a Mediterranean population – but also for the congeneric *S. scrofa* Linnaeus, 1758 and *S. porcus* Linnaeus, 1758 (Harmelin-Vivien *et al.*, 1989; Bradai and Bouain, 1990). This increase in prey size is probably related to an increase in nutrition requirements of the predator (Wootton, 1990) although the relation between prey size and predator mouth gap may also have a role in this pattern (Ross, 1978; Stoner, 1980; Roscchi, 1983; Pallaoro *et al.*, 2006).

Seasonal variation in the abundance of decapod crustaceans and teleosts was observed for *S. maderensis* in the Mediterranean Sea (La Mesa *et al.*, 2007), as well as in other demersal fish species (Morato *et al.*, 2000). It can be speculated that *S. maderensis* responds to seasonal changes that have an effect on food availability thus reflecting its adaptability and opportunistic predatory behaviour (Morato *et al.*, 2000). The significant increase in decapod crustaceans as prey may coincide with spring periods of recruitment, the same applying to teleost fish in fall (Robertson, 1984). It is also possible that decapod crustaceans are not as abundant as fish during fall, which may explain a diet shift of *S. maderensis* towards the latter. This aspect is currently under study.

Diet composition between islands

As mentioned before, the spatial distribution of samples indicated no significant difference among the three sampling sites. This is probably due to the high environmental similarity between these islands and their relative proximity. This study allowed to characterize the diet of an important demersal/epibenthic coastal predator of the Azores. Understanding its trophic ecology within a broader and wider context of complex food webs is an important step towards the knowledge of these islands ecology, and also a valuable tool for management and stock assessment of marine life resources.

Acknowledgments. – Financial support for this study was given by the Portuguese National Science Foundation (FCT) through the PRAXIS/3/3.2/EMG/1957/95 project. We wish to thank several volunteers who helped in data collection, namely Norberto Serpa, Victor Rosa, José Branco, Frederico Cardigos, Jorge Fontes, Filipa Gomes, Carmelina Leal, Miguel Machete, Fátima Mendes, Telmo Morato, Pedro Afonso and Fernando Tempera. Rui Pedro Vieira is currently supported through a doctoral grant from the Portuguese Science Foundation (SFRH/BD/84030/2012). Leonardo F. Machado is currently supported through a postdoctoral research fellowship from FAPES/CNPq (Federal Government of Brazil). Thanks are due to the two anonymous referees whose comments and suggestions greatly improved the first versions of the manuscript.

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