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Feeding habits of the deep-sea shrimp *Aristaeopsis edwardsiana* (Johnson 1867) (DECAPODA: ARISTEIDAE) on the Southeastern and Southern Brazilian coast

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ABSTRACT. The purpose of this paper is to present the first data concerning the diet of *Aristaeopsis edwardsiana*, an abundant deep-water predator off Southeastern and Southern Brazilian coast. The diet of *A. edwardsiana* is composed mainly of benthic and benthopelagic organisms. Crustaceans were the most important prey item in the diet, followed by sediment, fishes, cephalopods, anthozoans, polychaetes, and echinoderms. A redundancy analysis (RDA) was used to assess the relative importance of different environmental and biological variables influencing the feeding habits of *Aristaeopsis edwardsiana*. Cephalopods are mostly ingested during the spring, inversely, sediment was more important during the summer. Fishes are preferentially ingested by large and sexually mature individuals, while anthozoans are preferred by small individuals. Espiríto-Santo coast presented more individuals that prefer to eat more sediment than fishes or cephalopods. The majority of the stomachs were moderately empty or moderately full and few stomachs were full or very full. Significant differences were found in the percentage of stomach fullness between sex, size and female maturation. Males, small individuals and immature females had the highest values of stomach fullness. The variation in diet appears to be related to gonad development, driving temporal changes in feeding strategy.

Keywords: Deep-sea shrimp; continental slope; crustacean; diet; scarlet-shrimp

RESUMO. Hábitos alimentares do camarão-de-profundidade *Aristaeopsis edwardsiana* (Johnson 1867) (DECAPODA: ARISTEIDAE) na costa Sudeste e Sul do Brasil. O Objetivo deste trabalho é apresentar os primeiros dados no que concerne à dieta de *Aristaeopsis edwardsiana*, um abundante predador de águas profundas da costa Sul e Sudeste brasileira. A dieta de *A. edwardsiana* é composta principalmente por organismos bentônicos e bentôpelágicos. Os crustáceos foram o mais importante item da dieta, seguido por sedimentos, peixes, cefalópodes, antozoários, poliquetas e equinodermos. Foi realizada uma análise de redundância (RDA) para verificar a importância relativa das diferentes variáveis que influenciam o hábito alimentar de *Aristaeopsis edwardsiana.* Os cefalópodes são principalmente ingeridos durante a primavera, inversamente, sedimentos são mais importantes durante o verão. Os peixes são preferencialmente ingeridos por indivíduos maiores e sexualmente maturos, enquanto os antozoários são preferência dos pequenos indivíduos. A costa do Espiríto-Santo apresentou indivíduos que preferem comer mais sedimentos que peixes ou cefalópodes. A maioria dos estômagos estavam moderadamente vazios ou moderadamente cheios e poucos estômagos estavam cheios ou muito cheios. Foi encontrada diferença estatística na plenitude estomacal entre sexo, tamanho e estágio de maturação das fêmeas. Os machos, pequenos indivíduos e fêmeas possuíram estômagos mais cheios. A variação na dieta parece estar relacionada com o desenvolvimento gonadal, levando a alterações temporais na estratégia alimentar.

Palavras-chave: camarão-de-profundidade; talude; crustáceos; dieta; camarão-carabineiro

Introduction

Five species of three genera from Aristeidae family (*Aristeus, Aristeaeopsis* and *Aristaeomorpha*) are valuable resources in many parts of the world, supporting important commercial fisheries, especially in Europe (Belcari *et al*. 2003). In Brazilian waters these deep-sea shrimps, *Aristaeopsis edwardsiana* (Johnson 1867), *Aristaeomorpha foliacea*, and *Aristaeus antillensis* have become valuable targets of the Brazilian deep-water trawling fishery as a result of a government support to exploit fishery resources in areas of the continental slope (Pezzuto *et al.* 2006). *Aristaeopsis edwardsiana* is the main component of the catches, comprising 88.4% of the total shrimp production conducted by chartered trawlers off Brazilian coast between 2000 and 2004 (Pezzuto *et al.* 2006). Also known as "carabineiro" or the scarlet shrimp, *Aristaeopsis edwardsiana* is predominantly a deep-water species, and is often found at depths between 400 and 900 m (D'Incao 1998), however, most of the catch is restricted to depths between 700 and 750 m (Pezzuto *et al.* 2006).

Lagardère (1972) and Rainer (1992) studied the diet of *A. edwardsiana* along the coasts of Morocco and Australia, respectively, and recorded a diverse diet for this species, mostly composed of fishes, crustaceans, and squids. The diet and feeding habits of other aristeid shrimps, such as *Aristaeomorpha foliacea* and *Aristeus antennatus*, have been extensively studied (Chartosia *et al*. 2005, Cartes *et al.* 2008 Kapiris *et al*. 2010, Nouar *et al*. 2011). Aristeids are among the megabenthic predators whose diet is composed of a wide variety of organisms (i.e. benthic and zooplanktonic crustaceans; mobile prey, such as fishes or cephalopods; detritus; echinoderms; and polychaetes), being important in the trophic chains of deep-sea communities (Cartes 1994, Cartes & Carrassón 2004, Kapiris *et al.* 2010).

Trophic relationships is an important approach for understanding the organization of communities, as interactions with biological and environmental variables can influence the choice of food resources exploited by species, like changes in feeding strategy related to sexual development (Kapiris & Thessalou-Legaki 2011, Kapiris 2012). Additionally, many deep-sea species shows feeding patterns that is related with the temporal and seasonal distributions of their prey (Gartner *et al*, 1997). However, there is a lack of studies on the feeding habitats of aristeid shrimps in Brazilian coastal waters. The aim of the present study was to provide a first description of the diet and feeding habits and to assess the relative importance of different environmental and biological variables influencing the feeding habits of *Aristaeopsis edwardsiana* inhabiting the continental slope of the southeastern and southern sectors of the Brazilian coast.

Methods

The shrimps were collected by observers aboard commercial vessels that operated on the continental slope off the Southeastern and Southern Brazilian coasts (18°S-28°S, 665-766 m deep) (Fig. 1) between February 2003 and January 2007. The study area was subdivided into three regions: the Espírito Santo coast (18°S-21°S), the Rio de Janeiro - São Paulo coast (23°S-25°S), and the Paraná - Santa Catarina coast (26°S-27°S). The Espírito Santo coast is known to possess diverse background morphology, with the presence of significant submarine canyons and a series of protuberances (cones and plateaus) between 100 and 1000 m in depth; however, the regions of the Rio de Janeiro - São Paulo coast and the Paraná - Santa Catarina coast are less irregular (MMA, 2006).

Data on the position, date, hour, depth (m) of each trawl were recorded. After each tow, the stomachs were fixed in formalin (10%) and stored in 70% alcohol to keep preserved and enable a better manipulation. Sex was determined macroscopically by the presence of a petasma in males and a thelycum in females. Carapace length (CL) was measured (accuracy, 1 mm) from the orbit to the dorsal mid-point of the posterior margin of the carapace using sliding calipers. Males were classified according to maturation stage: terminal ampullae empty (immature) or filled with sperm (mature) (Sardà & Demestre 1989). Females were classified according presence (impregnated; mature) or absence (not impregnated; imature) of spermatophores plugged in their telicum (Sardá & Demestre 1989) and to a macroscopic examination of the gonads: I-immature, translucent ovary; II-incipient maturity, orange ovarian; and III-mature, brown ovary (Guéguen 1998). The percentage of stomach fullness (%SF) was estimated as %SF = (SWW/BWW) * 100, where SWW is the stomach (with contents) wet weight (g) and BWW is the shrimp body wet weight (g) (Héroux & Magnan 1996). One-way ANOVA was used to verify if the percentage of stomach fullness varied according to sex, size, season, maturation stage, and area. The data were transformed (log10(x+1)) to satisfy the assumptions of normality and homoscedasticity.

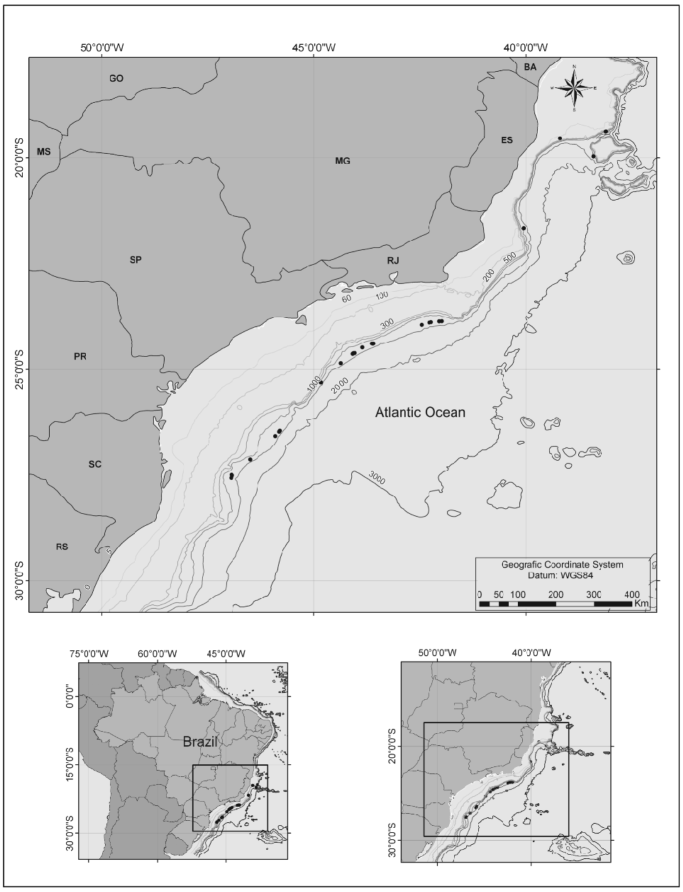

Figure 1. Study area, Southeastern and Southern regions of the Brazilian coast, with emphasis on the continental slope between 500 m and 1000 m depth, and latitudinal limits of the fishing sectors of Aristaeopsis edwardsiana. Dots represent the locations of capture.

The statistical package used was Statistica 7.0. The degree of stomach fullness was estimated based on the highest value of %SF, which was considered as 100% full, resulting in the following classes: very full (<100% and >75%), full (<75% and >50%), moderately full (<50% and >25%), moderately empty (<25%), and empty (<1%). Exceptions were stomachs with no contents, which were visually classified as empty. Tukey's Multiple Range Test was used to determine significant differences between group means.

The food items were examined under a stereoscopic microscope and identified to the lowest taxonomic level possible. The quantification of food items was performed using two methods: the relative frequency of occurrence and the points method (Williams 1981, Wear & Haddon 1987). The index of food importance (IAi) (Kawakami & Vazzoler 1980) was also used as a complementary index to indicate the relative importance of certain food categories.

The diet composition was summarized by the relative frequency of occurrence of the food item i (FO%) and was calculated as the ratio between the number of stomachs containing a food item i (FO) and the total number of stomachs with food content (n):

$$FO\% = (FO \div n) \times 100$$

(Williams 1981). Empty stomachs were eliminated from this analysis. The relative contribution of each food item i (RCi) in a stomach was evaluated by the points method, and was subjectively classified into five categories: 0-5% = 2.5 points, 5.1-35% = 25 points, 35.1-65% = 50 points, 65.1-95% = 75 points, and 95.1-100% = 100 points. Further, RCi was weighted according to the degree of fullness of stomachs in which a food item i was found, as follows: moderately empty, 0.25; moderately full, 0.5; full, 0.75; and very full, 1.00 (Wear & Haddon 1987). This resulted in the absolute frequency of points for a food item i found in the foregut j (PFaij). The relative frequency of points (FP%) of a food item was estimated as

$$FP\% = \sum_{j=i}^{n} (PFaij \div A) \times 100$$
,

where A is the total number of points for all food items found in all stomachs, aij is the total number of points found for the item i in all stomachs, and n is the number of stomachs (Williams 1981).

Multivariate analysis was used to determine the relationships between the diet composition and biological and environmental variables (sex, size, season, male and female maturation stage, and area). A detrended correspondence analysis (DCA) revealed that the ordination axes were smaller than one and a half standard deviations, suggesting that redundancy analysis (RDA) was the proper method to relate two sets of variables. The inflation factor calculated during RDA showed that the variable sex presented high collienarity. Strong collinearity may affect the ability to correctly estimate model parameters, therefore dataset was reduced by leaving out the sex (Legendre & Legendre 1998). The statistical significance of the variables extracted from the RDA was estimated by a Monte Carlo permutation test (1000 simulations) (Lepš & Šmilauer 2003). As in Magnan *et al*. (1994) a cut-off point of p=0.10 was used in this routine.

Results

The most conspicuous components of the diet of Aristaeopsis edwardsiana were sediment, carapaces of crustaceans and molluscs shells, corals, sponge spicules, hard parts of cephalopods (beaks, sucker rings, sucker hooks, and eye-lens), and fish vertebrae. Items that could not be identified were classified as undetermined organic matter (UOM).

According to the ranking of IAi, crustaceans were the main prey item in the diet of Aristaeopsis edwardsiana, followed by sediment, fishes, cephalopods, anthozoans, polychaetes, and echinoderms (Table I; Fig. 2). The ranking of the frequency of occurrence was in agreement with the ranking of IAi for most food items, with the exception of cephalopods, which have a greater frequency of occurrence than the fishes.

The items such as porifera spicules, foraminiferans, and shells of bivalves and gastropods (all around 1 mm) were considered as incidental prey, because we assumed that these items were passively ingested along with the substratum. This conclusion was based on the fact that such items were recorded mainly in stomachs containing large quantities of sediment. Plastic intake was observed in stomachs filled with various food items, indicating incidental ingestion (Rezende et al. 2011).

The carapace length ranged from 26.80 to 99.30 mm in females (128 females examined) and from 31.35 to 69.45 mm in males (98 males examined). For statistical analyzes four size classes were used: < 49.9 mm; 50-64.9 mm, 65-79.9 mm, >80 mm. A total of 226 individuals were analysed, table II summarize the number of individuals for each variable examined.

The RDA performed shows that spring, small individual (> 50 mm), impregnate females, summer and Espiríto Santo coast are the most important environmental variables ($p < 0.10$) influencing the diet composition (Table III, Fig. 3). The forward selection procedure has not retained the remaining variables. However, the non-significant variables were included in the final ordination diagram of the RDA due to their importance in explaining the diet variations. The first two RDA ordination axes account for 81.8 % of total variance.

According to RDA graph (Fig. 3) it was possible to observe that during spring cephalopods were the most important item and sediment seems to have little importance. However, in summer the opposite takes place, with shrimps feeding mostly on sediment. As females become mature (impregnate and stage III of gonad development), fishes become more important, while immature individuals ingest more sediment. Yet, small individuals prefer anthozoans and sediments, and large shrimps prefer cephalopods and fishes. Regarding to the area, the individuals captured from the Espírito Santo coast consumed more sediment and fewer fishes and cephalopods than the individuals captured from the Rio de Janeiro - São Paulo and Paraná - Santa Catarina coasts.

The highest value of percentage stomach fullness (%SF) found in *Aristaeopsis edwardsiana* was 5.95%, and this value corresponded to a 100% full stomach. Of the 202 individuals analysed, 10 had their degree of fullness visually determined as empty. According to the degree of fullness, it was observed that the majority of the stomachs were moderately empty (63.4%), followed by moderately full (24.3%). A few stomachs were between full (3.9%) and very full (1.9%), whereas empty stomachs were present in 6% of individuals.

Table I. Composition of stomach contents of 226 individuals of *Aristaeopsis edwardsiana*, in which appeared empty 13 stomachs.

	FO	FO%	FP	FP%	IAi
Undetermined Organic Matter (UOM)	**167.00**	**82.67**	**3274.50**	**33.14**	**0.41**
Crustacea	**167.00**	**82.67**	**2963.50**	**29.99**	**0.36**
Crustacea n.i.	165.00	81.68	2903.50	29.39	0.36
Pleocyemata n.i	1.00	0.50	45.00	0.46	0.00
Munida n.i.	1.00	0.50	15.00	0.15	0.00
Sediment	**130.00**	**64.36**	**940.50**	**9.52**	**0.09**
Teleostei	**89.00**	**44.06**	**1390.00**	**14.07**	**0.09**
Teleostei n.i.	89.00	44.06	1390.00	14.07	0.09
Cephalopoda	**100.00**	**49.50**	**517.50**	**5.24**	**0.02**
Cephalopoda n.i.	81.00	40.10	329.00	3.33	0.02
Oegopsina n.i.	11.00	5.45	81.50	0.82	0.00
Heteroteuthis atlantis	2.00	0.99	65.00	0.66	0.00
Sepiolida n.i.	2.00	0.99	32.50	0.33	0.00
Ommastrephidae n.i.	1.00	0.50	5.00	0.05	0.00
Octopodidae n.i.	1.00	0.50	2.50	0.03	0.00
Argonauta nodosa	1.00	0.50	1.50	0.02	0.00
Pyroteuthis margaritifera	1.00	0.50	0.50	0.01	0.00
Anthozoa	**46.00**	**22.77**	**422.00**	**4.27**	**0.01**
Scleractinia n.i.	46.00	22.77	422.00	4.27	0.01
Polychaeta	**4.00**	**1.98**	**38.00**	**0.38**	**0.00**
Polychaeta n.i.	4.00	1.98	38.00	0.38	0.00
Echinodermata	**2.00**	**0.99**	**5.00**	**0.05**	**0.00**
Crinoidea n.i.	2.00	0.99	5.00	0.05	0.00
Incidental prey	**89.00**	**44.06**	**329.50**	**3.33**	**0.01**
Porifera n.i.	18.00	8.91	52.50	0.53	0.00
Mollusca n.i.	46.00	22.77	238.50	2.41	0.01
Foraminifera n.i.	21.00	10.40	28.50	0.29	0.00
Plastic debris	4.00	1.98	10.00	0.10	0.00

Bold font means large groups; FO, frequency of occurrence; FP, frequency of points; IAi, index of food importance; n.i., not indentified.

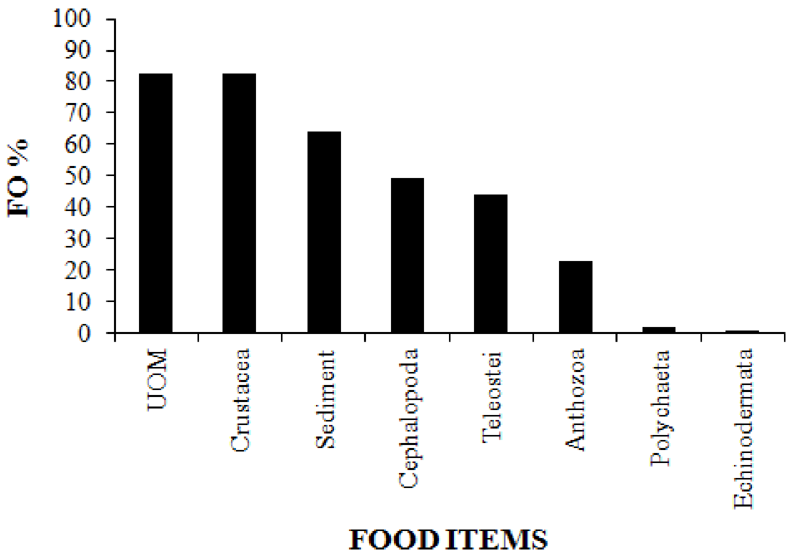

Figure 2. Frequency of occurrence of food items (large groups) found in the stomachs contents of *Aristaeopsis edwardsiana*.

Table II. Number of individuals (excluding the empty stomachs) for each variable (n) used to determine the relationships between the diet composition of *Aristaeopsis edwardsiana* and biological and environmental variables.

	Variables	n
Sex	Female	128
	Male	98
Size	< 49.9 mm	46
	50-64.9 mm	98
	65 -79.9 mm	47
	> 80 mm	35
Season	Summer	50
	Autumn	5
	Winter	43
	Spring	128
Male Maturation	Empty ampullae (immature)	67
	Full ampullae (mature)	17
Female Maturation	Not impregnated (immature)	44
	Impregnated (mature)	83
	I (immature)	60
	II (incipient maturation)	31
	III (mature)	32
Area	Espírito Santo	25
	Rio de Janeiro - São Paulo	138
	Paraná - Santa Catarina	40

Table III. Results of Canonical Redundancy Analysis (RDA) used to determine the relationships between the diet composition and biological and environmental variables. Where * mark the significant variables (p < 0.10) influencing the diet composition.

	Variables	p-value
Size	< 49.9 mm	0.0030*
	50-64.9 mm	0.5265
	65-79.9 mm	0.8302
	> 80 mm	0.8302
Season	Summer	0.0490*
	Autumn	0.2867
	Winter	0.2867
	Spring	0.0010*
Male Maturation	Empty ampullae (immature)	0.4855
	Full ampullae (mature)	0.9650
Female Maturation	Not impregnated (immature)	0.1499
	Impregnated (mature)	0.0160*
	I (immature)	0.6114
	II (incipient maturation)	0.1918
	III (mature)	0.1988
Area	Espírito Santo	0.0839*
	Rio de Janeiro - São Paulo	0.3207
	Paraná - Santa Catarina	0.1359
Summary	**Axes 1**	**Axes 2**
Eigenvalues	0.062	0.017
Species- environment correlations	0.518	0.29
Cumulative percentage variance of species data	6.2	7.9
Cumulative percentage variance of species- environment relation	64.3	81.8

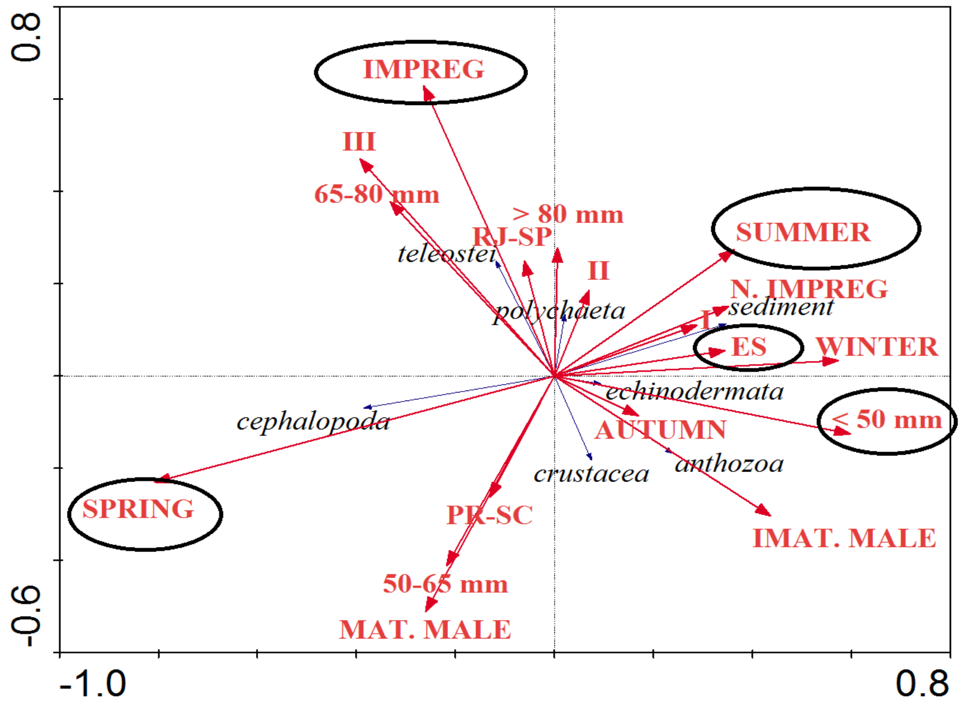

Figure 3. Redundancy analysis (RDA) ordination diagram based on the diet composition of *Aristaeopsis edwardsiana* and enviromental and biological variables. The most significant variables ($p < 0.10$) in the diet are circled, the others were included to better understanding the diet variations. Where, IMPREG: impregnate female; N. IMPREG: not impregnate female; I: immature-translucent ovary; II: incipient maturity-orange ovarian; III: mature-brown ovary; ES: Espírito Santo coast; RJ-SP: Rio de Janeiro - São Paulo coast; PR-SC: Paraná - Santa Catarina coast.

According to the one-way ANOVA results, significant differences were found in the percentage of stomach fullness between sex, size and female maturation (Table IV). Relating the percentage of stomach fullness values to the degree of fullness classes, all variables presented, on average, moderately empty stomachs. Males, small individuals (< 50mm and 50-65 mm) and immature females had the highest values of stomach fullness. While, females, large individuals (65-80 mm and >80 mm) and mature females presented less stomach fullness (Fig. 4).

Discussion

In Brazilian waters, *Aristaeopsis edwardsiana* has a diet similar to that previously to aristeid shrimps. Lagardère (1972) and Rainer (1992) recorded a similar diet for this species. The diet of two other species of aristeid shrimps, *Aristeus antennatus* and *Aristaemorpha foliacea,* is also mainly composed of crustaceans, fishes, and cephalopods, with some quantities of polychaetes, echinoderms, gastropods, and bivalves (Chartosia *et al*. 2005).

The stomach contents recorded in *Aristaeopsis edwardsiana* usually contained only hard parts highly fragmented. Lagardère (1972) also point out this problem, saying that the species grind their food and ingest only small fragments. Since the state of preys most of the items could only be identified at a higher taxonomic level. The retention time for these is likely to be greater than that for soft tissues, which could explain why soft tissues and other prey items were not frequently found in the low-level digestion conditions.

It was not possible to provide more precise information about the habitat of the prey, i.e. whether they are pelagic or benthic. However, the high frequency of occurrence of fishes and cephalopods in the diet, in addition to the morphological characteristics of *Aristaeopsis edwardsiana*, such as light exoskeletons and long pleopods, suggesting good swimming ability (Guéguen 1997), is evidence that the specie feeds on pelagic forms. As well as on benthic forms, by the frequent occurrence of sediment, anthozoa and other benthic forms depending of the life time.

Table IV. Summary of the statistical analysis, one-way ANOVA, used to verify if differences occurred in the percentage of stomach fullness of *Aristaeopsis edwardsiana* according to sex, size, season, male and female maturation stage, and area. The table shows the number of individuals (excluding those with empty stomachs) for each factor (n), the degrees of freedom, and the p-value (* <0.005) for each analysis.

	Variables	N	Degrees of freedom	p-value
Sex	Female	105	186	0.0400*
	Male	83		
Size	< 49.9 mm	29	184	0.0052*
	50-64.9 mm	89		
	65 -79.9 mm	39		
	> 80 mm	31		
Season	Summer	39	105	0.7697
	Autumn	5		
	Winter	16		
	Spring	128		
Male Maturation	Empty ampullae (immature)	58	68	0.4140
	Full ampullae	12		
Female Maturation	Not impregnated (immature)	32	102	0.0080*
	Impregnated (mature)	72		
	I (immature)	48	110	0.0013*
	II (incipient maturation)	23		
	III (mature)	32		
Area	Espírito Santo	25	162	0.9554
	Rio de Janeiro-São Paulo	101		
	Paraná-Santa Catarina	40		

Since cephalopods, fishes, and some crustacean species have great swimming ability, the presence of these items in the stomach contents may indicate that these deep-sea shrimps are effective predators. Bello & Pipitone (2002) have pointed out that *Aristeomorpha foliacea* fed on small and very small specimens of cephalopods, including early juveniles, and that the prey size was found to be positively correlated with shrimp size. However, a pattern of mass spawning, followed by the death of the spawners, is known in many cephalopods (Boyle & Rodhouse, 2005). This indicates that it is likely that the consumption of demersal decapods is achieved by feeding on dead or dying cephalopods.

Comparison of diet composition of this species on the Brazilian coast reveals that this shrimp species undergoes changes in feeding habits with increasing body size. With an increase in size, individuals cease to consume sediment and anthozoans, and switch their diet to larger and more energetic prey, such as fishes and cephalopods. Ontogenetic shifts in diet were also apparent in *Aristaeomorpha foliacea*, despite high dietary overlaps among small, medium, and large females. Large individuals, who are more efficient predators, selected highly mobile prey (e.g. fishes), whereas small individuals consumed low-mobility prey (e.g. copepods, ostracods, tanaids, and sipunculans) (Kapiris *et al*. 2010).

In aristeid shrimps, sexual and ontogenetic segregation have been observed along different bathymetric gradients, in which the largest catch of mature spawning females occurs along the open slope, and juveniles and males are caught in abundance near the canyons (Sardà & Cartes 1993, Sardà *et al*. 1994, Relini *et al.* 1999, Tudela *et al.* 2003). This ontogenetic and sexual segregation could explain the difference found in the diet between the individuals of the Espírito Santo coast, Rio de Janeiro - São Paulo coast, and Paraná - Santa Catarina coast. Additionally, it was observed that along the Espírito Santo coast, of the females captured, only 6% were mature, whereas along the Rio de Janeiro - São Paulo coast and the Paraná - Santa Catarina coast, 17% and 20% of captured females, respectively, were mature. A diet rich in fish and cephalopods, appropriate for mature females, was found in the stomachs of the shrimps along the Rio de Janeiro - São Paulo coast and Paraná - Santa Catarina coast, where we found the greatest abundance of mature females. However, there are no previous studies in the area that attest this hypothesis. Seasons have an influence on the diet of the deep-sea megafauna, and this is possibly related to the period of highest abundance of each prey group in the environment (Cartes 1994, Fanelli & Cartes 2008).

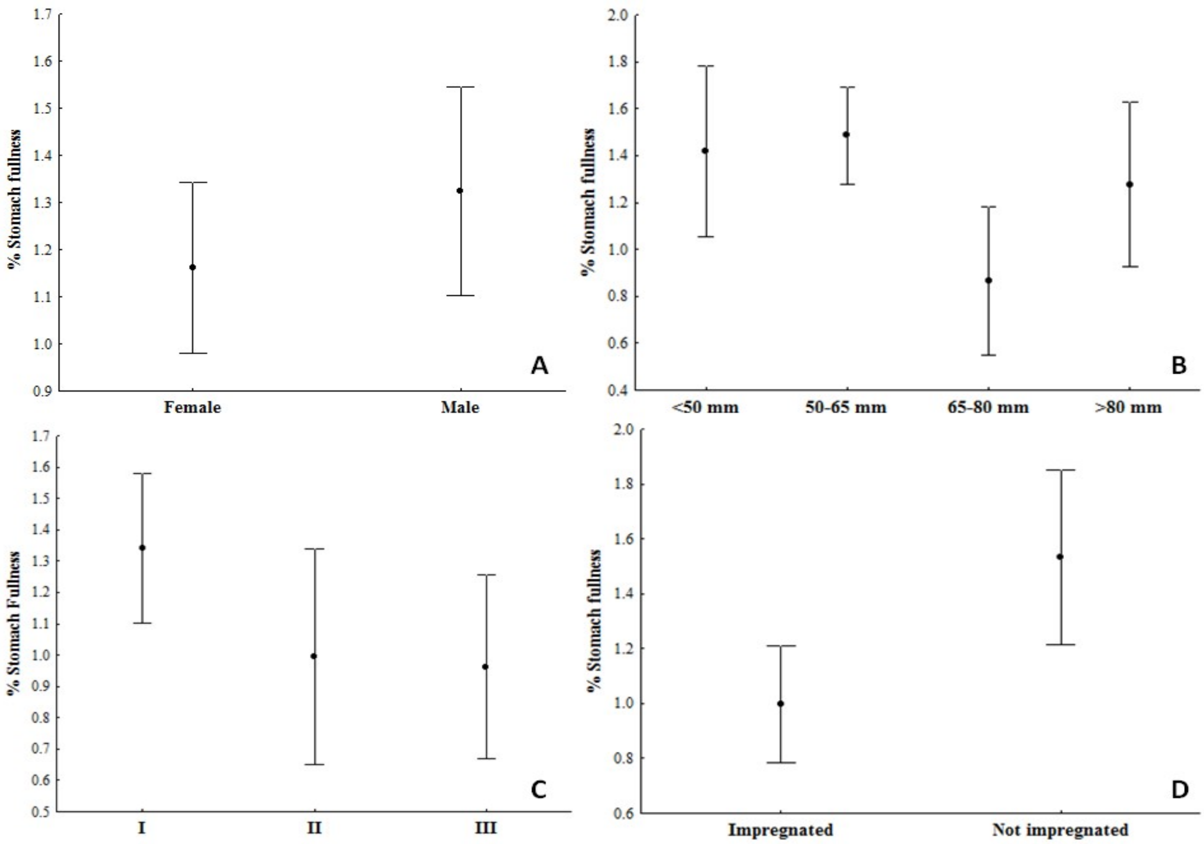

Figure 4. Percentage of stomach fullness (%SF) by sex (A), size (B) and female maturation of *Aristaeopsis edwardsiana* classified according to a macroscopic examination of the gonads (C) and the presence (impregnated) or absence (not impregnated) of spermatophores plugged in their telicum (D). The vertical bars indicate the 95% confidence interval, with the minimum and maximum values.

However, several studies have shown that biological processes, such as gonad development, are also responsible for the seasonal patterns in the diet of aristeids (Cartes *et al.* 2008, Kapiris *et al*. 2010, Nouar *et al*. 2011) During spring, RDA results showed that the ingestion of cephalopods becomes significant. Additionally, it was observed that higher proportions of mature females of *Aristaeopsis edwardsiana* occur in Brazilian waters in spring (Pezzuto & Dias 2007, Dias 2009). These facts support the finding that the seasonal feeding habits of *Aristaeopsis edwardsiana* seem to be related to reproduction. In shrimps maintained in captivity, the value of several food items for maturation and reproduction is attributed to their cholesterol content (Ravid *et al.* 1999, Wouters e*t al.* 2001, Díaz & Fenucci 2004). This is because, like most invertebrates, crustaceans are incapable of synthesizing cholesterol; thus these lipids need to be ingested along with the food (Shmidt-Nielsen 2002). Mendoza *et al*. (1997) showed that squid is a rich cholesterol source, and also contains sexual steroids that trigger shrimp vitellogenesis.

For aristeids, many authors describe higher feeding activity (higher values of stomach fullness) for large females, explained by the increased metabolic demands at the beginning of oogenesis (Maynou & Cartes 1998; Cartes *et al.* 2008, Kapiris *et al.* 2010). This work found the opposite scenario, in which males, small shrimps and immature females presented higher stomach fullness than females, large shrimps, and mature females. We believe this could be due to the high-level digestion conditions present in most analyzed stomach contents, which can interfere with the accuracy of the analysis depending on the main item ingested by each group.

Most analyzed stomach contents presented high-level digestion conditions that can interfere with the accuracy of the analysis. Higher occurrences of anthozoans, sediment and crustaceans in males, small shrimps and immature females could overestimate the stomach fullness analysis, since these items present more refractory material that may be present in the stomach for a long time before capture. Large individuals and mature females ingested more fishes and cephalopods, which are digested faster and could, therefore, be underestimated.

This could be because of the rapid digestion in midwater decapods, with food being retained in the stomach for only a few hours (Lagardère 1976, Roe 1984). However, the retention time of different food types in the guts of crustaceans may differ among the prey groups. Hard parts, such as bones or mollusc shells, may be retained in the stomach for a much longer time than fleshy tissues (Hill 1976, Joll 1982, Wassenberg & Hill 1987).

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