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NATURAL DIET OF THE CRAB *HEPATUS PUDIBUNDUS* (BRACHYURA: CALAPPIDAE) IN FORTALEZA BAY, UBATUBA (SP), BRAZIL

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ABSTRACT

The natural diet of *Hepatus pudibundus* in Fortaleza Bay, Ubatuba (SP), Brazil, was determined, based on two methods: Frequency Occurrence and Percentage Points. Foregut contents of 219 specimens collected from November 1988 to October 1989 in 7 different areas of Fortaleza Bay were analyzed. *Hepatus pudibundus* had varied recognizable food categories, in decreasing order: crustaceans, fish, sediment (a facultative scavenger), and molluscs. Other food categories were in low percentage: bryozoans, algae, annelids, foraminiferans, cnidarians, and echinoderms ranked fifth through tenth on the basis of the methods utilized. A significant difference was found in the amount of food in the diet during seasonal analysis (autumn > summer > winter > spring) and among the 7 sampling areas of Fortaleza Bay. We suggest that the crab *H. pudibundus* is an opportunistic omnivorous crustacean, and is not exclusively molluscivorous.

Different methods have been used to quantify food items, such as Frequency of Occurrence (McLaughlin and Hebard, 1961; Gonzaléz-Gurriarán, 1978), Percentage Points (Wear and Haddon, 1987; Woods, 1993), Relative Importance Index (Stevens *et al.*, 1982; Haefner, 1990), volumetric estimates (Hill, 1976; Choy, 1986), wet weight (Jewett and Feder, 1982), and dry weight of the food item in relation to the dry weight of the brachyuran crab (Freire *et al.*, 1991).

Williams (1981) considered Frequency of Occurrence and Percentage Points to be the only methods that can be rapidly applied to the analysis of gastric contents in crabs. The Frequency Occurrence method indicates the percentage of occurrence of a given prey item in the stomach contents and is appropriate for most foods. However, this method tends to overestimate items with hard parts and small items such as foraminiferans, which contribute little to the relative volume of the stomach (Williams, 1981; Stevens *et al.*, 1982).

The calappid crab *Hepatus pudibundus* (Herbst, 1785) is a common inhabitant of the northern shore of São Paulo State, where it is very abundant among the crab fauna of the Ubatuba region (Fransozo *et al.*, 1992; Hebling *et al.*, 1994). The species is nocturnal and reaches depths of 155 m (Melo, 1985).

According to Melo (1985), this species is widely distributed in the West Atlantic from Florida to Brazil (from Amapá to Rio Grande do Sul) and in the East Atlantic (from Guinea to South Africa). The few papers that have been published concerning the biology of *H. pudibundus* have dealt primarily with population structure (Mantelatto *et al.*, 1995a), occurrence (Fransozo *et al.*, 1992; Hebling *et al.*, 1994), and distribution related to environmental factors in Fortaleza Bay (Mantelatto *et al.*, 1995b).

Mantelatto and Fransozo (1992, 1994) described the morphometry/weight ratio and relative growth, respectively, of a population inhabiting Fortaleza Bay, Ubatuba (SP), and fecundity was studied by Reigada and Negreiros-Fransozo (1995). No previous analysis of the foregut contents of *H. pudibundus* has been published, except that Petti (1990) referred to previous accounts of the diet of this species and to its omnivorous characteristics.

The present study examines the composition of the natural diet of *H. pudibundus* in Fortaleza Bay. Temporal (season of the year) and spatial (seven different locations) variation in the diet are described.

MATERIALS AND METHODS

Specimens were collected in 7 different areas (each area to a length of 1 km) in Fortaleza Bay, Ubatuba, São Paulo State (23°31'S, 45°09'W) (Fig. 1).

Negreiros-Fransozo *et al.* (1991) gave detailed descriptions of Fortaleza Bay, with an emphasis on environmental factors and the geographic description of the 7 sites. The sampling areas included 2 exposed areas located at the entrance of the bay (I and VII), 3 relatively sheltered enclosed areas (II, III, and V) where organic material is abundant, 1 river-dominated area with lower salinity located in the lower estuary (IV), and 1 area with intermediate characteristics (VI).

Collections were made monthly over a period of 1 year (November 1988 to October 1989) in all areas. They were

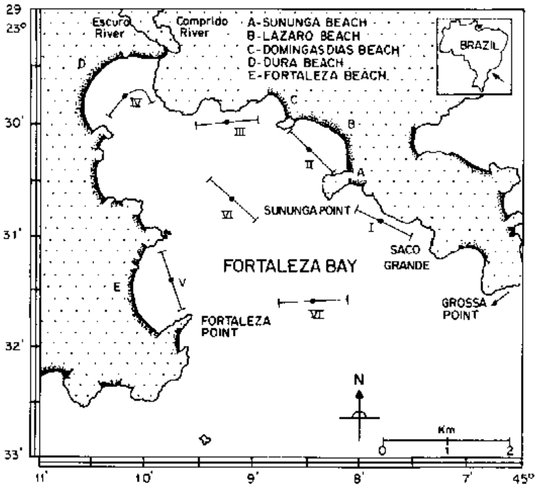

Fig. 1. Forteleza Bay, Ubatuba (SP), Brazil, indicating the seven areas sampled. (Map modified from Negreiros-Fransozo and Fransozo, 1995).

made by means of a shrimp fishery vessel equipped with paired otter trawls. In each area 1 tow was made per month during the daylight at high tide. The trawl track lasted 20 min at a constant speed of 1.47 knots. Each monthly collection was made on the same day in each area.

Months were grouped in seasons during the study: summer (December, January, February), autumn (March, April, May), winter (June, July, August), and spring (September, October, November).

Immediately after capture, all crabs were stored in an insulated box with ice cubes to slow digestion and stop the maceration by the gastric mill. After approximately 6 h, the crabs were stored in a freezer. In the laboratory, analyses were performed after thawing at room temperature.

Analysis of foregut contents.—The relative degree of fullness of the foreguts was determined immediately after removal from the crabs and was assessed visually by the method of Wear and Haddon (1987). Each foregut was assigned to 1 of 6 ordered classes as follows: Class 5, 100% full foreguts; Class 4, 75% (<100% but >65% full); Class 3, 50% (<65% but >35% full); Class 2, 25% (<35% but >5% full); Class 1, <5% full or only a trace of food; and Class 0, empty foreguts. Visual assessment was made possible by the fact that the foregut of *H. pudibundus* is a thin-walled translucent bag. After this analysis, the foreguts were preserved in 10% Formalin.

Observations of the contents of foreguts were made with a binocular dissecting microscope with the contents spread on 40-mm diameter Petri dishes. Only guts from classes 5–2 (N = 219) were used in our analyses of foregut contents; these were identified and separated into major taxa.

Preliminary analysis carried out by a pilot project showed similar components in the dietary composition of male and female *H. pudibundus*; the feeding data from both sexes were, therefore, pooled. The quantitative scoring method used for the analysis of foregut contents was Percentage Points (Williams, 1981; Wear and Haddon, 1987).

The relative contribution of each prey category to the total volume of material in each foregut was subjectively assessed as follows: a category representing 95–100% of foregut contents was awarded 100 points; 65–95% = 75 points; 35–65% = 50 points; 5–35% = 25 points; 5% or less = 2.5 points; empty = 0 points. The number of points that each prey category received was then weighted by multiplying them by a value dependent on the degree of foregut fullness: full = 1; 75% = 0.75; 50% = 0.5; 25% = 0.25; trace = 0.02 (Wear and Haddon, 1987).

The maximum weighted points possible for a single category in a single foregut are 100 (100 × 1), and the minimum weighted points possible are 0.05 (2.5 × 0.02).

The following percentages were calculated for each prey type (Williams, 1981):

$$\text{Percentage Points for prey } i^{\text{th}} = \left(\sum_{j=1}^{n} aij/\text{A}\right)100,$$

$$\text{Percentage Occurrence for } i^{\text{th}} \text{ prey} = (bi/N)100,$$

where aij is the number of points of prey item i in the foregut of the j^{th} crab; A = total number of points for all crabs and all foods in the sample; N is the number of crabs in the sample (all with food in the foregut); and bi is the number of crabs whose gastric mills contained prey type i.

Since point score is a quantitative measure commonly used in other investigations, this measure was used in statistical analysis in the present study. The Kruskal-Wallis test (Zar, 1974) was used in determining feeding differences between sampling periods of the year and areas. A

Table 1. Composition of the natural diet of *Hepatus pudibundus* from Fortaleza Bay expressed as points (Pts) and percentage points (% Pts) score in seasonal sampling period. For more details see Materials and Methods.

	Summer (N = 28)		Autumn (N = 125)		Winter (N = 37)		Spring (N= 29)		Total	
Diet components	Pts	% Pts	Pts	% Pts	Pts	% Pts	Pts	% Pts	Pts	% Pts
Crustacea	658.12	55.28	4,654.35	56.18	814.00	49.42	831.87	54.33	6,958.34	54.96
Decomposition material	263.11	22.08	1,980.61	23.90	446.87	27.11	398.12	25.98	3,088.71	24.39
Pisces	126.86	10.65	769.99	9.28	317.50	19.26	143.75	9.38	1,358.10	10.74
Sediment	51.80	4.34	391.72	4.72	38.05	2.30	65.58	4.28	547.15	4.34
Mollusca	89.36	7.50	175.62	2.11	12.50	0.75	25.00	1.63	302.48	2.38
Bryozoa	0.00	0.00	225.00	2.71	13.12	0.79	8.75	0.57	246.87	1.95
Annelida	0.00	0.00	48.75	0.58	0.00	0.00	56.25	3.67	105.00	0.82
Algae	1.87	0.15	36.20	0.43	5.61	0.34	2.50	0.16	46.18	0.37
Foraminifera	0.00	0.00	6.24	0.07	0.00	0.00	0.00	0.00	6.24	0.04
Cnidaria	0.00	0.00	1.25	0.01	0.62	0.03	0.00	0.00	1.87	0.01
Echinodermata	0.00	0.00	1.25	0.01	0.00	0.00	0.00	0.00	1.25	0.01

Table 2. Composition of the natural diet of *Hepatus pudibundus* from Fortaleza Bay expressed as Frequency Occurrence (FO) and Percentage Occurrence (%O) in seasonal sampling period.

	Summer (N = 28)		Autumn (N = 125)		Winter (N = 37)		Spring (N = 29)		Total	
Diet components	FO	%O	FO	%O	FO	%O	FO	%O	FO	%O
Crustacea	24	85.11	118	94.40	29	78.37	26	89.65	197	89.95
Decomposition material	28	100.00	120	96.00	34	91.89	28	96.55	210	95.89
Pisces	11	39.28	51	40.80	22	59.45	10	34.48	94	42.92
Sediment	26	92.85	115	92.00	28	75.67	24	82.75	193	88.12
Mollusca	8	28.57	13	10.40	1	2.70	2	6.89	24	10.95
Bryozoa	0	0.00	16	12.80	2	5.40	3	10.34	21	9.58
Annelida	0	0.00	6	4.80	0	0.00	1	3.44	7	3.19
Algae	1	3.57	23	18.40	6	16.21	2	6.89	32	14.61
Foraminifera	0	0.00	4	3.20	0	0.00	0	0.00	4	1.82
Cnidaria	0	0.00	1	0.80	1	2.70	0	0.00	2	0.91
Echinodermata	0	0.00	1	0.80	0	0.00	0	0.00	1	0.45

second procedure was employed to make multiple comparisons using the rank sums (Dunn, 1964), where the rank is based on the percentage points for each separate gut.

Results

The crabs that were examined for foregut fullness ranged from 13–78 mm in carapace width (Mantelatto *et al.*, 1995a). The 219 foreguts examined were as follows: 42 (class 5), 29 (class 4), 73 (class 3), and 75 (class 2); 106 (32.61%) were "empty" (class 0 and 1, <5%), and consequently not included in analysis.

While most of the food ingested by *H. pudibundus* was fragmented due to mastication, the remains of animals with hard parts were readily identified. Foraminifera were recognized from whole tests. Cnidaria were recognized by hydrozoan polyps and Bryozoa from small pieces of calcified colonies. Crustacea (shrimps, crabs, hermit crabs, isopods) were identified by the carapace and fragments of appendages (chelae, telson). The presence of pieces of shell, opercula, radulae, and beak-like jaws aided in the identification of Mollusca (gastropods, bivalves, cephalopods). Annelida (polychaetes) were recognized from jaws, setae, and intact portions of the head and body. Echinodermata (ophiuroids, sea urchins) were identified from ossicles, pieces of test and body wall. Pisces were recognized from scales and bones, including vertebrae and otoliths. Algae were recognized from small pieces.

In this study we assigned all unrecognizable tissue, amorphous particles, algal and animal fragments in decomposition, and unidentifiable organic material to a category entitled "decomposed material."

Diet Composition

Hepatus pudibundus fed on a wide variety of diet components. Crustaceans, fish, sediment, and molluscs ranked as the four most common recognizable prey items, with a cumulative Percentage Points index of 72.4% (Table V). Bryozoans, algae, annelids, foraminiferans, cnidarians, and echinoderms were also present in the foregut contents but were of minor importance. Of the four main food categories, crustaceans had both a high frequency of occurrence and a high percentage point score, with penaeid shrimps being the predominant taxa.

Seasonal Diet

The Frequency Occurrence and Percentage Point score revealed that the same pattern occurred for the total diet. Crustaceans, fish, sediment, and molluscs composed the primary diet. The combined Percentage Points index (Table 1) of the four principle diet components was 77.8% (summer), 72.3% (autumn), 71.7% (winter), and 69.6% (spring), with practically no percentage variations during the study year. Of the four main recognizable food categories, Crustacea had both a high Frequency Occurrence and a high Percentage Point score (Table 2).

A significant difference was found in the amount of food in stomachs between seasons of the year (Table 3). In general, crabs from autumn months contained significantly more food than crabs from summer, winter, and spring months.

Area Diet

The combined Percentage Points indices for the four recognizable diet components re-

Table 3. Kruskal-Wallis one-way ANOVA for food points score in *Hepatus pudibundus* relative to seasonal sampling periods of year.

Sampling period	Stomachs with food *N*	Stomachs with food %	Rank sum of contents[a]	Average rank sum of contents
Summer	28	75.7	1,191.1	108.3
Autumn	125	70.6	8,291.0	753.7
Winter	37	52.1	1,648.3	149.8
Spring	29	72.5	1,531.8	139.3

Pairs significantly different ($P < 0.05$)[b]. Autumn > Summer, Autumn > Winter, Autumn > Spring, Spring > Summer, Spring > Winter, and Winter > Summer.
[a]Calculated test statistic = 21.8; calculated *P*-value; ≈ 0 assuming a χ^2 distribution with 3 *d.f.*
[b]Multiple comparison test (Dunn, 1964).

vealed no difference in diet based on area of capture: 69.5% (area I), 65.3% (II), 78.2% (III), 75.6% (IV), 69.1% (V), 69.4% (VI), and 76.1% (VII) (Tables 4, 5). The food items of minor importance (lower Frequency and Points) presented heterogeneous oscillations among the areas. The food points score shows significant differences in diet based on areas of capture for several pairs, with emphasis on area VII (Table 6).

A different pattern in area IV, with low indices, should be noted. There were not sufficient specimens for a precise analysis (N = 1). This area was located near an estuary. According to Mantelatto *et al.* (1995b), this species shows no correlation with low salinities, with preference for areas with high salinities (35‰).

When crabs from the seven sampling areas were compared, a significant difference in total food points score was detected, i.e., crabs from area VII contained significantly more food than crabs from other areas (Table 6).

Discussion

All previous food data on *H. pudibundus* were based on the Frequency of Occurrence method, a technique that assesses feeding trends, but often fails to give an accurate interpretation of the importance of a given food item.

The diversity of food items eaten by these crabs suggests that they are opportunistic predators. Our results are similar to those obtained in studies on the diets of other species of calappid crabs, such as *Matuta lunaris* (Forskål) (see Perez and Bellwood, 1988), *H. pudibundus* (see Petti, 1990), and *Acanthocarpus alexandri* Stimpson (see Haefner, 1981). Several authors have recognized the importance of crustaceans in the diet of Brachyura (Paul, 1981; Choy, 1986). We believe that the food items in the foreguts of *H. pudibundus* are directly related to the relative abundance of these diet components in the environment, as mentioned for *Callinectes sapidus* Rathbun by Laughlin (1982) and *Callinectes ornatus* Ordway by Haefner (1990). Most crabs are foraging omnivores, although certain families show tendencies toward a more specialized diet (Warner, 1977).

Calappid crabs are reported as being mainly molluscivorous, because the most specialized morphological and behavioral adaptations for opening mollusk shells yet discovered are found in oxystomatous crabs of this family (Shoup, 1968; Haefner, 1981; Hughes and Elner, 1989). The inferred molluscivorous diet of *H. pudibundus* is not supported by the diet observed in the crabs from our sample, similar to the study of Haefner (1981) on *Acanthocarpus alexandri*.

Brachyurans are known to influence the distribution and abundance of prey populations (Virnstein, 1977; Seed, 1980; Perez and Bellwood, 1988). According to Choy (1986), the diets of tropical and subtropical portunid crabs are relatively uniform because of the high diversity and regular availability of diet components. In contrast, the diets of temperate species change markedly as a result of lower diversity and seasonal changes in the availability of prey species. The feeding habits of *H. pudibundus* appear to fit the latter context, with the availability of prey in Fortaleza Bay suggesting that this species is omnivorous, with a strong tendency to eat crustaceans. This may be the major factor responsible for the homogeneous pattern of the main diet components in the seven areas.

The species of the present study shows a greater capacity for feeding during autumn (Table 3). This pattern was observed in the period immediately after the peak of reproduction (in the summer) studied by Mantelatto *et al.* (1995).

In connection with the fish component in the diet, our results are similar to those obtained in studies on the diets of portunid crabs (Laughlin, 1982; Haefner, 1990; Stoner and Buchanan, 1990; Hsueh *et al.*, 1992). However, the high percentage of fish in the diet of *H. pudibundus* in Fortaleza Bay may also reflect scavenging on fish remains that are discarded by shrimp trawlers. Fishes, there-

Table 4. Composition of the natural diet of *Hepatus pudibundus* from Fortaleza Bay expressed as Frequency of Occurrence analyzed in seven areas.

	I (N = 29)		II (N = 40)		III (N = 23)		IV (N = 1)		V (N = 25)		VI (N = 27)		VII (N = 74)	
Diet components	FO	%O	FO	%O	FO	%O	FO	%O	FO%	O	FO	%O	FO	%O
Crustacea	26	89.65	35	87.50	22	95.65	1	100	21	84.00	20	74.07	72	97.29
Decomposition material	29	100	39	97.50	22	95.65	1	100	22	88.00	25	95.59	72	97.29
Pisces	9	31.03	22	55.00	15	65.21	0	0.00	12	48.00	13	48.14	23	31.08
Sediment	29	100	39	97.50	23	100	1	100	13	52.00	19	70.37	69	93.24
Mollusca	4	13.79	3	7.50	2	8.69	0	0.00	1	4.00	4	14.81	10	13.51
Bryozoa	0	0.00	8	20.00	5	21.73	0	0.00	6	24.00	1	3.70	1	1.35
Annelida	0	0.00	1	2.50	4	17.39	0	0.00	1	4.00	0	0.00	1	1.35
Algae	7	24.13	12	30.00	5	21.73	0	0.00	1	4.00	5	18.51	2	2.70
Foraminifera	2	6.89	1	2.50	0	0.00	0	0.00	0	0.00	0	0.00	1	1.35
Cnidaria	2	6.89	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Echinodermata	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	1.35

Table 5. Composition of the natural diet of *Hepatus pudibundus* from Fortaleza Bay expressed as points and percentage points score analyzed in seven areas.

	I (N = 29)		II (N = 40)		III (N = 23)		IV (N = 1)		V (N = 25)		VI (N = 27)		VII (N = 74)	
Diet components	Pts	%Pts	Pts	%Pts	Pts	%Pts	Pts	%Pts	Pts	%Pts	Pts	%Pts	Pts	%Pts
Crustacea	800.62	54.03	978.73	43.91	738.37	55.34	56.25	73.18	532.50	50.22	500.62	41.30	3351.25	63.72
Decomposition material	431.25	29.09	596.24	26.72	238.12	17.83	18.75	24.39	254.36	23.96	328.74	27.11	1221.25	23.20
Pisces	150.62	10.16	364.99	16.35	192.50	14.41	0.00	0.00	145.62	13.72	226.25	18.66	278.12	5.28
Sediment	51.80	3.49	98.05	4.39	93.73	7.01	1.87	2.43	41.85	3.94	45.59	3.76	214.26	4.07
Mollusca	27.49	1.85	13.74	0.61	18.75	1.40	0.00	0.00	12.50	1.17	68.75	5.67	161.25	3.06
Bryozoa	0.00	0.00	150.00	6.72	36.25	2.71	0.00	0.00	16.87	1.58	37.50	3.09	6.25	0.11
Annelida	0.00	0.00	12.50	0.56	11.25	0.84	0.00	0.00	56.25	5.30	0.00	0.00	25.00	0.47
Algae	15.61	1.05	15.61	0.69	6.23	0.46	0.00	0.00	1.25	0.11	4.99	0.41	2.49	0.04
Foraminifera	3.12	0.21	1.25	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.87	0.03
Cnidaria	1.87	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.02

Table 6. Kruskal-Wallis one-way ANOVA for food points score in *Hepatus pudibundus* relative to sampling areas in Fortaleza Bay.

Sampling area	Stomachs with food *N*	Stomachs with food %	Rank sum of contents[a]	Average rank sum of contents
I	29	64.4	1,482.4	134.8
II	40	56.3	2,231.1	202.8
III	23	67.6	1,335.2	121.4
IV	01	33.3	76.9	6.9
V	25	60.9	1,061.9	96.5
VI	27	61.4	717.4	65.2
VII	74	85.1	5,263.0	478.5

Pairs significantly different ($P < 0.05$)[b]

I > III	II > V	VI > V
I > IV	II > VI	VII > I
I > V	III > IV	VII > II
I > VI	III > V	VII > III
II > I	III > VI	VII > IV
II > III	V > IV	VII > V
II > IV	VI > IV	VII > VI

[a]Calculated test statistic = 28.6; calculated P-value = 0.0971 assuming a χ^2 distribution with 6 *d.f.*
[b]Multiple comparison test (Dunn, 1964).

fore, presumably represent a diet component of opportunity.

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