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Feeding of *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) (Crustacea: Penaeidae) inside and outside experimental pen-culture in southern Brazil

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Abstract. We assessed the value of benthic macroinvertebrates to the diet of *Farfantepenaeus paulensis* juveniles in experimental pen-cages after three independent rearing periods of 20, 40 and 60 days each. For each time period we initially stocked 3 pen-cages with 60 shrimps m^{-2} supplemented with ration (treatment RS), and 3 pen-cages with 60 shrimps m^{-2} without ration (WR). The diet of captive shrimps was compared with the diet of free shrimps (C). Shrimps fed preferentially on benthic preys. Captive shrimps extended their activity to daylight hours and consumed a significant amount of vegetation, likely in response to a severe decrease of macroinvertebrate density passed 20 and 40 days. After 60 days, the diet of the few survivors of *F. paulensis* in pen-cages without ration (WR) approached the diet of shrimps in the natural environment (C). These similarities were explained by the recovery of macroinvertebrates populations to relaxation from high predation pressure during the last 20 days of the experiment in WR pens. Considering the strong predatory control of *F. paulensis* over the benthic invertebrate assemblages we concluded that the value of natural production as food source for shrimps reared in pens is limited to the initial stage of the culture.

Key words: *Farfantepenaeus paulensis;* Penaeid shrimp; prawn predation; diet; pen culture; benthic invertebrate.

Resumen: **Alimentación de *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) (Crustacea: Penaeidae) dentro y fuera de corrales de cultivo experimentales en el sur de Brasil.** Comparamos la importancia de macroinvertebrados bentónicos en la dieta de juveniles del camarón *Farfantepenaeus paulensis* en corrales de engorde experimentales tras tres periodos independientes de cultivo de 20, 40 y 60 días cada uno. Al inicio de cada período se incluyeron 60 camarones m^{-2} en 3 corrales suplementados con ración (tratamiento RS), y 60 camarones m^{-2} en 3 corrales sin la provisión de ración (WR). La dieta de los camarones cautivos se comparó con la de camarones capturados en el ambiente natural (C). Los camarones consumieron preferentemente presas bentónicas. Los camarones cultivados extendieron la búsqueda de alimento durante horas de luz y consumieron una fracción importante de vegetación, probablemente en respuesta a una fuerte reducción de la densidad de macroinvertebrados al cabo de 20 y 40 días de experimento. Luego de 60 días de cultivo, la dieta de los pocos camarones supervivientes en los corrales sin suplemento alimenticio (WR) se aproximó a la de los camarones en el ambiente natural (C). Estas similitudes fueron atribuidas a la recuperación de las poblaciones de macroinvertebrados, liberadas de la fuerte presión de depredación de los camarones durante los últimos 20 días en los corrales WR. Considerando el fuerte control de depredación de *F. paulensis* sobre las asociaciones de macroinvertebrados concluimos que el valor de la producción natural como fuente de alimento para camarones en sistemas de engorde está limitado a la etapa inicial del cultivo.

Palabras clave: *Farfantepenaeus paulensis*; camarón; depredación; dieta; acuacultura en corrales; invertebrado bentónico.

Introduction

Aquaculture development is particularly useful as an alternative source of food production for commercially important species that are subjected to intense fishing practices. This is the case of the shrimp *Farfantepenaeus paulensis.* An increase of small-scale fishing on juvenile populations of this species in Patos Lagoon is partly responsible for the depletion of resources (D'Incao 1991, D'Incao *et al.* 2002). This circumstance, in conjunction with the unpredictability of the shrimp harvests in the region (Castelo & Möller 1978, Reis & D'Incao 2000), emphasized the need for repopulation studies, as well as the improvement of low cost technologies for the culture of shrimps in estuarine inlets of Patos Lagoon (*e.g.* pens and cages) (Wasielesky *et al.* 1995).

Unlike cages, pens allow direct contact of shrimps with sediments in aquatic systems. These sediments provide refuge by promoting burrowing (Moller & Jones 1975), and offer a source of natural food available within culture environment (Wickins 1976, Angell 1989). Even with ration addition, the shrimps consume and use natural sources of carbon for their growth (Nunes *et al.* 1997, Nunes & Parsons 1999, Soares *et al.* 2005). Contributions of commercial ration usually constitute a small fraction of shrimps diet (Reymond & Langardère 1990) though it may slightly increase during growth (Soares *et al.* 2005). In contrast, benthic invertebrates can particularly play an important role in penaeid nutrition (Rubright & Harrell 1981, Moriarty *et al.* 1983, Soares *et al.* 2005).

For shrimp growth, the availability and use of the natural food and the environmental conditions originated in the culture will be of importance in the evaluation of the rearing method. The penaeid shrimps have been broadly classified as omnivorous and detritus feeders (Dall 1968), although some genus (*e.g. Metapenaeus*) were considered more vegetarian than *Farfantepenaeus* (Hall 1962). Studies analyzing stomach content of both free and captive *F. paulensis* supported the omnivorous diet described for other penaeids, since it has been reported that *F. paulensis* feeds on algae, live plant tissues and detritus, besides crustaceans, mollusks, polychaetes, and others invertebrates (Asmus 1984, Silva & D'Incao 2001, Albertoni *et al.* 2003, Soares *et al.* 2005). However, variations in the proventriculus contents of *F. paulensis* are likely influenced by variations in composition and abundance of benthic macrofauna (Asmus 1984).

Population densities of benthic invertebrates may be strongly reduced by shrimp predation (Leber 1985, Nelson & Capone 1990, Beseres & Feller 2007), potentially limiting shrimp growth and survival under pen-culture. Hence, the capacity of *F. paulensis* to overcome reductions in the availability of animal food sources would be critical to the success of culture methods such as pens. To assess the degree of dependence on prey availability and the importance of omnivory in the trophic behavior of *F. paulensis* we compared the diet of shrimps in their natural environment and inside experimental pen-cultures simultaneously.

Experiments designed to assess culture methods at relatively large spatial scales in the field usually suffer of statistical dependence problems, segregation of sample units, etc. (see Hurlbert 1984). In the present study we assessed the potential contribution of natural production to the diet of *F. paulensis* in a replicated experiment. We reinforced conclusions from parallel results that advised on poor shrimp growth and survival in highly stocked pens supplemented with low quality rations (Jorgensen & Bemvenuti 2001), explained by the drastic reduction of benthic invertebrate populations through shrimp predation within pen-cages (Jorgensen 1998).

Material and methods

Study area: The study was carried out in the estuarine region of Patos Lagoon, located in Rio Grande do Sul's coastal plain at southern Brazil (Fig. 1a, b). In this region there are shallow, semi-closed and vegetated areas locally known as "sacos". The Saco do Justino is a small mixohaline inlet of 2 km diameter and an approximate surface of 250 ha (Fig. 1c). Maximum depth in its central part is 1.5 m. Sandy and sand-muddy sediments constitute its bottom. Unlike other sectors of the lagoon, the inlet is unaffected by direct input of any anthropogenic nutrients (Baumgarten *et al.* 2005).

High levels of primary and secondary production in the "sacos" envisioned the aquaculture potential of the region for commercial rearing of native penaeid shrimps (*e.g.* Jorgensen & Bemvenuti 2001, Soares *et al.* 2006). However, precipitation produce abrupt variations of salinity in the Patos Lagoon (Garcia *et al.* 2004), and may affect growth and survival of shrimps (Tsuzuki *et al.* 2003, Soares *et al.* 2006). Environmental conditions during the present study were summarized in Jorgensen and Bemvenuti (2001). For the study season (Summer 1997), low salinities (< 5) were rare and never occurred during long periods (> 5 days). Furthermore, the total production of *Farfantepenaeus paulensis* for 1997 was the highest reported for the period 1989-1999 (D'Incao *et al.*

2002). Thus, it is inferred that growth and survival were not affected by environmental parameters in this study (Jorgensen 1998, Jorgensen & Bemvenuti 2001).

Experimental procedure: The population of *F. paulensis* included in the pens had an initial mean individual biomass of 4.25 g (± 0.40 s.e.) (Jorgensen & Bemvenuti 2001). Cage inclusions were prolonged for three different periods, or stages, of 20, 40 and 60 days length (herein referred to as Period 1, Period 2 and Period 3 respectively), all initiated on February 1st, 1997. The following treatments were applied independently for each period: RS, 1 m^{-2} pens stocked with 60 shrimps supplemented with a daily ration of by-catch local fishing (80% fish + 20% crustaceans) that amounted to about 10% the initial shrimp biomass in the pens; WR, pens with 60 shrimps but without ration addition; C, shrimps captured in the natural environment (uncaged areas), as control of the general conditions of the experiment. Three replicates for period-treatment combination were disposed in the field following a totally randomized design. Additional details are available in Jorgensen and Bemvenuti (2001).

The shrimps included in the pens were captured in the natural environment the night before the beginning of cultures. Between 5 and 6 pm of the corresponding sampling day of each period, 6 pens were retired from the initial 18 pens (three for each treatment) and the shrimps collected were fixed and preserved in 5% formalin for ulterior analysis of their stomach content. This experimental procedure ensured the complete independence of treatment means (Underwood 1997). The same days of samplings, but at night (10 pm), shrimps were collected in the natural environment with a beam-trawl net.

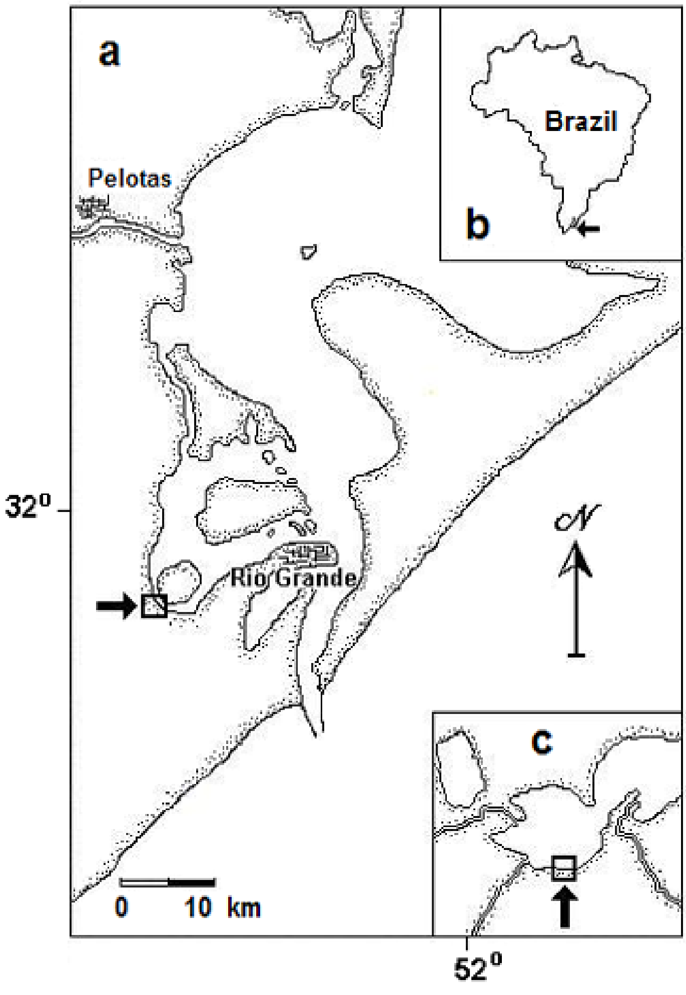

Figure 1. Geographic location of the sampling area within the Patos Lagoon estuary (a), at southern Brazil (b). The experimental units were located in an embayment known as Saco do Justino (c).

Content analysis of the anterior proventriculus: Five shrimps per pen and 15 among those captured in the natural environment in each sampling period were randomly chosen prior stomach content analysis. During dissection, the anterior proventriculus was separated and weighted; then, it was emptied and the wall of the proventriculus was weighted. The content mass was quantified by difference (error = 0.001 g). The percentage of stomach repletion index, R(%), was estimated from the categorical visual inspection of the proventriculus volume occupied by food, *sensu* Nunes *et al.* (1997). Finally the percentage frequency of food items occurrence, FO(%), was calculated on a total of 15 individuals analyzed for all period-treatment levels combinations.

The number of survival shrimps per pen did not reach in the third period the quantity fixed for the comparisons of weight content, R(%) and FO(%) among the experimental treatments. After 60 days of culture, only 1 individual was captured in one of the enclosures belonging to the treatment RS. In the same sampling period (Period 3), 3, 3 and 1 shrimp were collected in the three WR pens, respectively. Estimates of variables in this last period were then carried out basing on the number of survivors.

Data analysis: The comparative analysis of the growth in weight of cultured shrimps (RS and WR enclosures) was carried out through a 3-way nested ANOVA (treatment-period-pen) by Jorgensen and Bemvenuti (2001), so the observed results will be synthetically referred here. Variations in the content weight and in the repletion percentage, R(%), of the shrimps proventriculus among treatments RS, WR and C were estimated in a similar way. The factor 'pen' was nested in the factor 'treatment' and was ignored only after differences among the replicated pens were found to be not significant, justifying the use of the shrimps as experimental units in the comparisons (Underwood 1997). Statistical comparisons of the mentioned variables were limited to the periods 1 and 2 as a consequence of the reduced number of shrimps that survived after two months of culture. The relationship among the proventriculus-wall weight and the shrimp biomass was studied by a regression analysis.

The significance level of the statistical tests performed was preset at 5% ($\alpha = 0.05$). Cochran's test was used to test homogeneity of variances; data normality was verified through diagrams of observed and expected residuals for a normal distribution and box-plots of the medians distribution of the samples groups. When necessary, were carried out the transformation of variables to $x' = \log_{10}(x+1)$, or to $x' = \arcsin(x\%/100)^{1/2}$ in the case of data expressed in percentages (Sokal & Rohlf 1981). *A posteriori* multiple comparisons of means among periods-treatments combinations were analyzed with Tukey´s HSD test when significant differences were indicated by general ANOVA.

Differences in the diet of shrimps were evaluated by applying multivariate methods in non-transformed data of percentage frequency of food items occurrence in stomachs contents. In order to assess that a sufficient number of proventriculus were analyzed for each period-treatment combination, we plotted the cumulative number of species per number of proventriculus examined (*i.e.* species accumulation curves). We performed hierarchical classification of the samples by the use of UPGMA algorithm on the Bray-Curtis similarity matrix. The contribution of the items in the formation of groups defined by the classification analysis was determined through the SIMPER method (Clarke & Warwick 1994). The result of the groups' formation was evaluated by a samples ordination plot using NMDS (Non-metric Multidimensional Scaling) (Clarke & Warwick 1994). Ordinations were based on the rank similarity matrix among pairs of samples, defined by the Bray-Curtis index, and assessed through the stress value. Stress is a measure of quality of the ordination in the representation of the dissimilarity of matrix. Stress values < 0.1 indicate a good representation of the structure of the community without real risk of misinterpretation. The stress value interval 0.1 - 0.2 indicate a useful ordination, although little emphasis should be put on details for values of stress close to the upper limit of the interval (0.2). Computational routines used in multivariate analysis are part of statistical package PRIMER (Clarke & Gorley 2001).

Results

The mean shrimp weight increased significantly with time, and particularly during the first 20 days of the experiment ($p = 0.006$, Table I). Although the mean final growth was greater in the pens with food supply (Table II), this difference was not significant ($p = 0.212$, Table I). However, general differences among treatments were detected when the weight of the empty proventriculus of the shrimps was compared (RS = 0.233 g > C = 0.166 g and WR = 0.163 g; $F = 18.81$, $p = 0.000$). We found a significant direct relationship between the proventriculus-wall weight and the shrimp biomass ($n = 123$; $r = 0.7$; $p = 0.000$).

Table I. Summary of the 3-way nested ANOVA for differences among periods (Period 1: 20 days; Period 2: 40 days; Period 3: 60 days) and experimental treatments (RS: shrimps supplied with ration; WR: shrimps without ration supply; C: natural environment) in the mean weight of shrimps, stomach repletion index R(%), and weight of proventriculus content in *Farfantepenaeus paulensis*; n = 15 for period-treatment combination, except in Period 3; factor cage nested in factor treatment (see Material and methods). Significant values at p < 0.05 in bold.

Variable	Source	gl	MS	F	p
Shrimp weight [1]	Period	2	0.37	5.35	**0.006**
	Treatment	1	0.11	1.58	0.212
	Period x Treatment	2	0.15	2.12	0.126
	Residual	102	0.07		
R(%)	Period	1	1173.6	4.13	**0.045**
	Treatment	2	1265.6	4.46	**0.014**
	Period x Treatment	2	158.0	0.56	0.575
	Residual	84	284.0		
Proventriculus content	Period	1	0.000014	1.99	0.162
	Treatment	2	0.000025	3.47	**0.035**
	Period x Treatment	2	0.000053	7.37	**0.001**
	Residual	84	0.000007		

[1] shrimp weight comparisons among initial weight (day 0) and periods 1 and 2, and treatments RS and WR.

The amount of material ingested by *F. paulensis* (Tables III and IV) varied significantly across experimental treatments (R(%): p = 0.014; proventriculus content: p = 0.035, Table I). Shrimps included in WR pens, in which the only source of available food was the natural production of the system, consistently presented fuller proventriculus than in the other treatments (R(%), Period x Treatment: p = 0.575) (Table I). Furthermore, measures of stomach repletion, R(%), tended to decrease with the amount of time under captivity (p = 0.045, Tables I and III). In contrast with R(%), differences in the mass of material ingested by *F. paulensis* among treatments levels depended on the length of time under culture (Period x Treatment: p = 0.001, Table I). However, shrimps within RS pens presented both the lowest values of R(%) and mass content in their proventriculus after 60 days of culture (40% ± 21 s.e., Table III; 0.006 g ± 0.003 s.e. Table IV).

Samples classification and ordination based on frequency of occurrence of food items ingested by *F. paulensis* reflected important differences in the diet of shrimps under treatments RS, WR and C (Fig. 2). Species accumulation curves indicated that the number of proventriculus analyzed was adequate to characterize the diet of *F. paulensis* in the experimental treatments (Fig. 3). Indeed, in most situations the analyses of additional proventriculus would provide only small increases in the number of items (species) ingested.

Two homogeneous groups of samples were defined in the dendrograme at 75% similarity cut level in response to natural (group I) and culture (group II) conditions predefined in the experimental treatments (Fig. 2). Group I showed an average similarity of 83.3% and was constituted by animals captured in the natural environment, independently of the period of sampling, plus those belonging to WR pens subjected to two months of rearing. Group II (similarity average = 81.0%) was conformed by individuals in both pens RS and WR sampled at the end of the first two experiment periods (20 and 40 days of culture). Shrimps maintained in pens with food supply (RS) after two months of culture did not conform any group (Fig. 2).

Table II. Mean (s.e.) weight (g) of *Farfantepenaeus paulensis*, among periods (Period 1: 20 days; Period 2: 40 days; Period 3: 60 days) and experimental treatments (RS: shrimps supplied with ration, WR: shrimps without ration supply); n = 15 for period-treatment combination, except in Period 3 (see Material and Methods). Initial mean weight (s.e.): 4.25 g (0.40).

Shrimp weight	RS	WR
Period 1	5.49 (0.46)	5.62 (0.36)
Period 2	5.68 (0.38)	4.33 (0.38)
Period 3	6.99 (0.79)	5.27 (0.55)

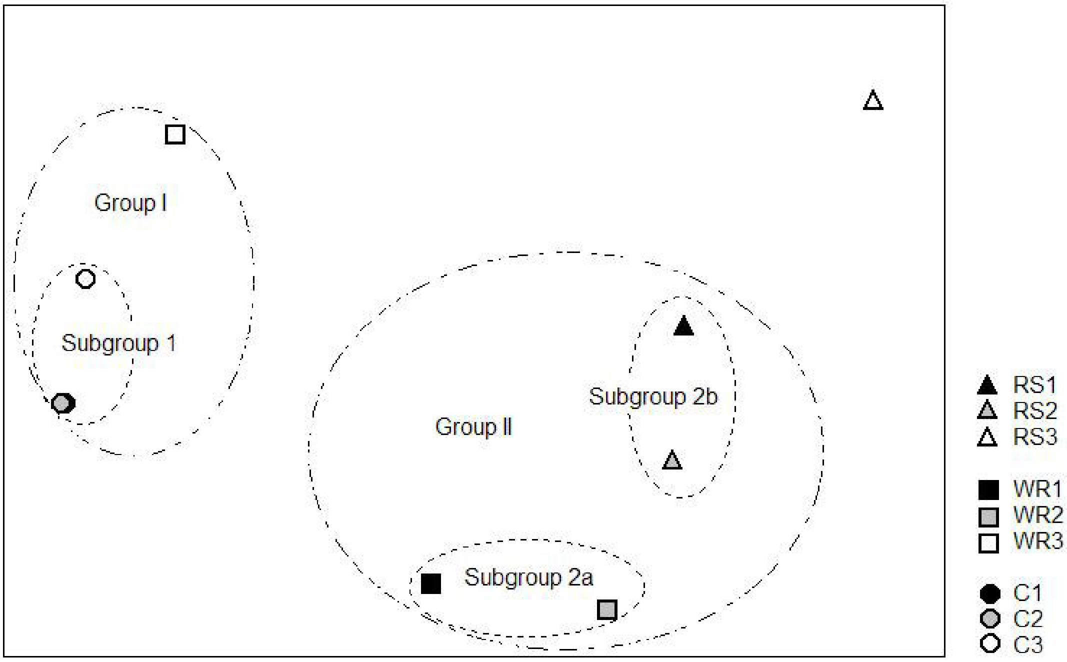

Figure 2. Non-metric Multidimensional Scaling (NMDS) ordination of the samples by frequency of food items occurrence, FO(%), in the anterior proventriculus of *Farfantepenaeus paulensis* (stress = 0.017). Letters and numbers of samples code (e.g. RS1) identifies experimental treatments (RS: shrimps supplied with ration, WR: without ration supply; C: natural environment) and period (Period 1: 20 days; Period 2: 40 days; Period 3: 60 days), respectively. The dotted lines define the groups and subgroups discriminated by the analysis of classification (dendrograme not shown).

Table III. Mean (s.e.) repletion, R(%), of the anterior proventriculus of *Farfantepenaeus paulensis*, among periods (Period 1: 20 days; Period 2: 40 days; Period 3: 60 days) and experimental treatments (RS: shrimps supplied with ration; WR: shrimps without ration supply; C: natural environment); n = 15 for period-treatment combination, except in Period 3 (see Material and methods).

R(%)	RS	WR	C
Period 1	64.2 (4.2)	77.5 (5.0)	61.7 (4.6)
Period 2	56.7 (5.1)	65.8 (1.7)	59.2 (3.6)
Period 3	40.0 (20.5)	71.4 (24.6)	61.7 (3.0)

Table IV. Mean (s.e.) wet weight content (g) in the anterior proventriculus of *Farfantepenaeus paulensis*, among periods (Period 1: 20 days; 2: 40 days; 3: 60 days) and experimental treatments (RS: shrimps supplied with ration; WR: shrimps without ration supply; C: natural environment); n = 15 for period-treatment combination, except in Period 3 (see Material and methods).

Weight (g)	RS	WR	C
Period 1	0.013 (0.001)	0.020 (0.004)	0.010 (0.002)
Period 2	0.014 (0.002)	0.011 (0.000)	0.012 (0.001)
Period 3	0.006 (0.003)	0.026 (0.010)	0.013 (0.001)

Table V. Frequency of food items occurrence, FO(%), in the anterior proventriculus of *Farfantepenaeus paulensis*, and their contribution to mean global dissimilarity (δ_{global}) among groups I and II, discriminated by the classification of samples in the dendrogram; δ_i%: percentual of dissimilarity contribution of the item *i* to the mean global dissimilarity among the two groups.

Item	FO(%)	FO(%)	δ_i%	δ_i% Acumulated
	I	II	I-II	I-II
Vegetation	7.5	100.0	24.1	24.1
Insect eggs	12.5	76.7	16.5	40.6
Laeonereis acuta	65.0	16.7	13.1	53.7
Ration	0.0	41.7	11.2	64.9
Ostracoda	43.3	55.0	5.7	70.6
Tanais stanfordi	0.0	20.0	5.2	75.8
Nematoda	21.7	6.7	4.9	80.7
Unidentified	15.0	21.7	4.5	85.2
Foraminifera	25.0	33.3	4.3	89.5
Kalliapseudes schübartii	92.5	78.3	4.1	93.6
Heleobia australis	0.0	6.7	1.6	95.2
Sand	94.2	98.3	1.5	96.7
Nepthys fluviatilis	8.3	5.0	1.5	98.2
Detritus	100.0	95.0	1.3	99.5
Decapoda	0.0	1.7	0.5	100.0
δ_{global}			33.7	

The NMDS successfully depicted details on subgroups discrimination in response to the inclusion of high initial densities of *F. paulensis* (RS and WR vs. C), the addition of ration (RS vs. WR), and the length of time under culture (represented by periods 1, 2 and 3) (Fig. 2). During periods 1 and 2 the samples of treatments RS and WR presented separately a similar disposition in the plane defined by the multivariate analysis. In contrast, RS and WR samples in the third period showed a different location compared with the position of the samples of the respective treatments in the previous periods (Fig. 2). Differences in samples disposition among periods 1 and 2 relative to period 3 indicated that an important change in the *F. paulensis* diet took place when shrimps at initial densities were subjected to more than 40 days of culture.

The degree of percentage dissimilarity among the groups discriminated by the classification analysis was useful in the identification of the variables that had a major contribution to the observed results (Table V). This method showed that the vegetation was the most important item in the differentiation among the group conformed by treatments RS and WR (groups II), on one hand, and the group of control samples (group I) on the other. Still green vegetal remains (mainly from fanerogame *Ruppia maritima*) and insect eggs were frequently observed inside the proventriculus of animals in captivity (treatments RS and WR of the first and second periods, and RS of the third). In contrast, these items were ingested with low frequency by shrimps in the natural environment or under treatment WR after 60 days of culture (Table VI).

Among animal preys, the polychaete *Laeonereis acuta* and the tanaid *Kalliapseudes schübartii* presented high frequencies of occurrence inside the proventriculus of the penaeid and were in general consumed in higher proportion by the shrimps captured in the natural environment (Tables V and VI). Meiofauna components did not show clear patterns of occurrence in the proventriculus during the first two experimental periods. Only in period 3 foraminifers and nematodes were present in higher frequency in the ration addition treatment (Table VI).

Detritus fragments and sand grains were identified in most of the proventriculus examined, both in captivity and control C. On the other hand, the ingestion of the ration given in RS was verified. The presence of this item was observed in more than 80% of the proventriculus of the shrimps maintained in RS pens (Tables V and VI). Other items were less important in the diet of *F. paulensis*. *Nephtys fluviatilis*, *Heleobia australis* and decapods were consumed occasionally because of their low palatability, or else in function of their availability or accessibility.

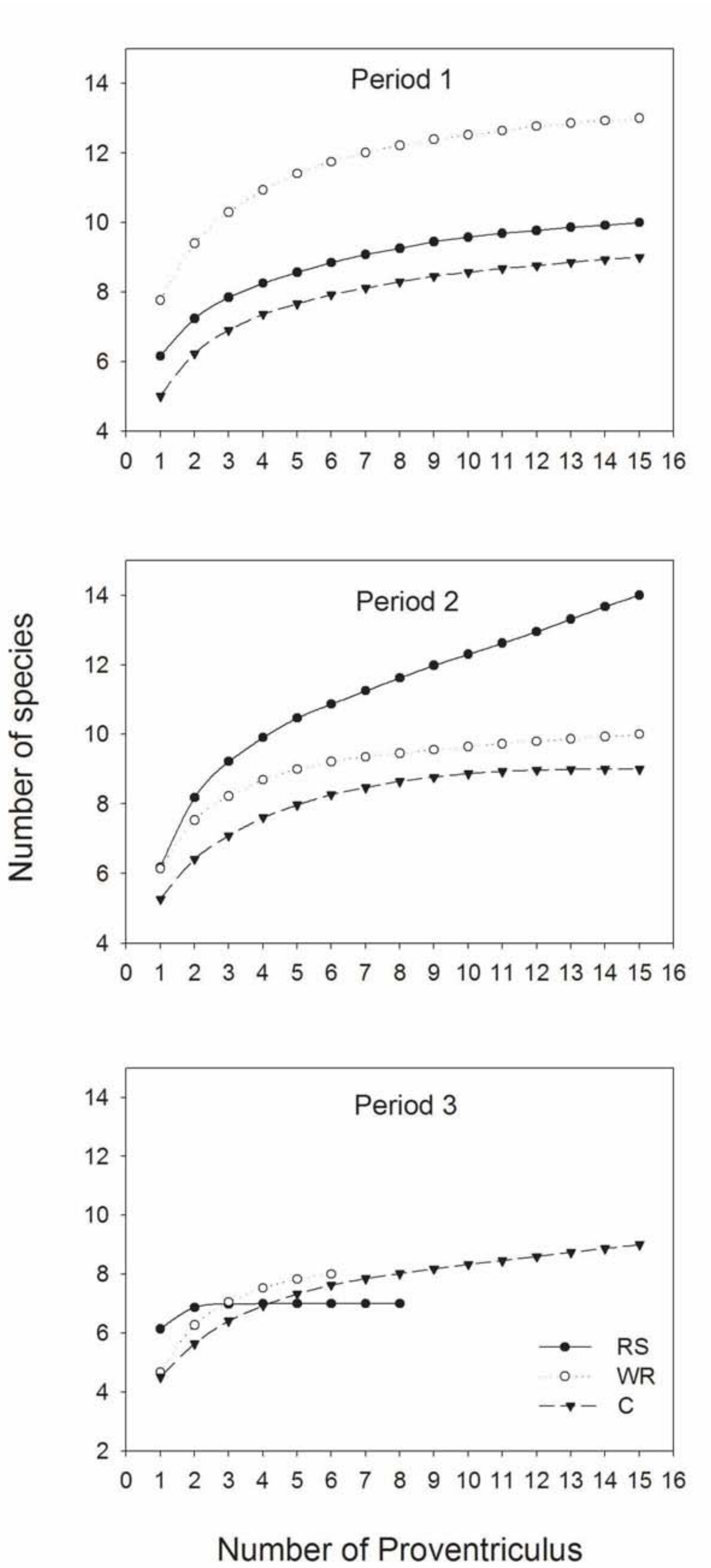

Figure 3. Cumulative number of items ingested (species) relative to the number of anterior proventriculus of *Farfantepenaeus paulensis* analyzed for the three periods, Period 1: 20 days; Period 2: 40 days; Period 3: 60 days, and experimental treatments RS: shrimps supplied with ration; WR: without ration supply; C: natural environment.

Table VI. Frequency of the food items occurrence, FO(%), in the anterior proventriculus of *Farfantepenaeus paulensis*, among periods (Period 1: 20 days; Period 2: 40 days; Period 3: 60 days) and experimental treatments (RS: shrimps supplied with ration; WR: shrimps without ration supply; C: natural environment); n = 15 for period-treatment combination, except in Period 3 (see Material and Methods).

Item	Period 1			Period 2			Period 3		
	RS	WR	C	RS	WR	C	RS	WR	C
Vegetation	100.0	100.0	6.7	100.0	100.0	0.0	100.0	16.7	6.7
Insect eggs	73.3	100.0	0.0	53.3	80.0	0.0	75.0	50.0	0.0
Laeonereis acuta	13.3	53.3	73.3	0.0	0.0	73.3	0.0	66.7	46.7
Ration	93.3	0.0	0.0	73.3	0.0	0.0	87.5	0.0	0.0
Ostracoda	33.3	86.7	46.7	60.0	40.0	66.7	0.0	33.3	26.7
Tanais stanfordi	0.0	26.7	0.0	6.7	46.7	0.0	0.0	0.0	0.0
Nematoda	0.0	13.3	0.0	6.7	6.7	20.0	62.5	33.3	33.3
Unidentified	0.0	40.0	26.7	26.7	20.0	33.3	0.0	0.0	0.0
Foraminifera	20.0	40.0	46.7	33.3	40.0	20.0	87.5	0.0	33.3
Kalliapseudes schübartii	73.3	93.3	93.3	66.7	80.0	100.0	0.0	83.3	93.3
Heleobia australis	0.0	20.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0
Sand	100.0	100.0	93.3	93.3	100.0	100.0	100.0	83.3	100.0
Nepthys fluviatilis	6.7	6.7	13.3	6.7	0.0	13.3	0.0	0.0	6.7
Detritus	100.0	93.3	100.0	86.7	100.0	100.0	100.0	100.0	100.0
Decapoda	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0

Discussion

The trophic habit of penaeid shrimps have been broadly classified as omnivorous and detritivorous (Dall 1968). In the present study, developed between mid summer and the beginning of autumn, detritus particles occurred on average in more than 90% of the examined contents, both in the natural environment and under culture. Though we did not quantify the volumetric contribution of ingested items, detritus is usually in relatively constant low amount in guts of free *Farfantepenaeus* (*e.g.* Schwamborn & Criales 2000, Albertoni *et al.* 2003). Larger amounts of detritus may be observed, however, in response to low prey abundance (Stoner & Zimmerman 1988). This seems to be the case for *F. paulensis* in Patos Lagoon, where variability in their proventriculus content is strongly influenced by variations in composition and abundance of benthic macrofauna. For example, organic detritus only comprised a large proportion in the diet of free shrimps when prey availability diminished during winter, while in summer *F. paulensis* consumed mainly ostracodes and the digger polychaete *Laeonereis acuta* (Asmus 1984). Similarly, detritus was the main food component of *F. paulensis* diet inside pen-cultures, likely in response to a severe decline of prey availability through consumption (Soares *et al.* 2004, Soares *et al.* 2005).

It is now apparent from stable isotope studies tracing food webs of coastal ecosystems that penaeids are mainly carnivorous and not detritivorous (Stoner & Zimmerman 1988, Primavera 1996, Schwamborn & Criales 2000), in contrast to earlier conclusions on penaeid diets. In our study *F. paulensis* consumed food of animal origin whenever it was available, even in culture conditions when macrobenthic preys density was reduced in 80% as a consequence of the high number of shrimps included initially in the pens (Jorgensen 1998). However, diet differences among captive shrimps and those from the natural environment were clearly reflected in our study, for example, through differences in the frequency of vegetation ingestion. These contrasts could hardly have originated from discrepancies in the hour of sampling of shrimp populations. Instead, we think the major reason for the frequent consumption of vegetation observed in the culture environment derived from the significant reduction of the density of macrobenthic invertebrates in pens RS and WR. The ingestion of vegetation likely occurred as an opportunistic feeding strategy to overcome deficiencies in the diet due to shortage of animal preys. Similarly, Soares *et al.* (2005) reported consumption of plant material by *F. penaeus* under culture conditions. Weidenbach (1980) showed that increases in vegetal material consumption by shrimps of considerable size occurred under the absence of balanced food.

The ingestion of vegetation does not imply that its digestion really happens (Dall *et al.* 1990). It is possible that epibionts in *Ruppia maritima* are in fact the source of nutrition. A recent stable isotopes study indicated that microorganisms living in the organic matrix attached to submersed surfaces enhanced growth of *F. paulensis* kept in floating cages and unable to feed on benthic invertebrates (Abreu *et al.* 2007). Hence, omnivory (*i.e.* consumption at more than one trophic level) such as detritivory appears to be important only when the abundance of primary consumers is low, such as in least productive seasons (*e.g.* Asmus 1984), or when the predation pressure reduce availability of invertebrates to sustain the shrimps stocked in rearing systems (*e.g.* Soares *et al.* 2005, this study). In fact, wild *F. paulensis* in Saco do Justino have a high trophic position in the food chain, as indicated by a stable isotopic study that positioned the shrimp in a similar trophic level as predatory fishes (Abreu *et al.* 2006).

The ingestion of vegetation was not the only difference between the trophic habits of captive and free shrimps. The observation of *F. paulensis* behavior inside the pens during the experiment showed surprisingly high activity levels during the day (mainly in treatment WR). Daytime feeding of juveniles of free *F. paulensis* in the Patos Lagoon estuary has been described, although feeding activity mostly occurs during the dark period (Santos 2003). In densely stocked cultures, shrimps increased their feeding frequency in the unavailability of food of high nutritious quality (Reymond & Langardère 1990). Increments of activity, described as a tendency of shrimps to emerge off the substratum during daylight hours, were observed in *F. esculentus* after six days of starvation (Hill & Wassenberg 1987). A similar behavior was reported for *Metapenaeus macleayi* (Racek 1959). The extension of shrimp activity to daylight hours in our study was likely related to an increase in food search time in response to the reduction of benthic preys density (Jorgensen 1998). This would also explain why the animals included in the non-supplemented treatment (WR) showed consistently fuller proventriculus.

Inclusion of *F. paulensis* in cages or pens indicated that the shrimp functions at a predator level, having its greatest effect on benthic invertebrates (Jorgensen 1998, Soares *et al.* 2004, Rodríguez-Gallego *et al.* 2008). In parallel studies Jorgensen (1998) and Jorgensen and Bemvenuti (2001) showed that the densities of benthic macroinvertebrates within enclosures were significantly depressed soon after introduction of shrimps, and depletion of prey populations derived in their low survival, particularly in WR cages. The extremely low survival of *F. paulensis* in WR cages (7%) determined the recovery of some invertebrate populations, and the structure of the macrobenthic assemblage approached that of the natural environment during the last twenty days of culture (Jorgensen 1998, Jorgensen & Bemvenuti 2001). The numerical response of prey populations to relaxation of the predation pressure associated with a severe reduction in *F. paulensis* density was also reflected in the proventriculus content of shrimps (Table VI). The tight relationship between the macroinvertebrates species abundance matrix in the pen-cultures, and the matrix of benthic invertebrates frequency inside the anterior proventriculus of *F. paulensis* was indicated by a multivariate correlation analysis performed by the RELATE routine, included in PRIMER (Clarke & Gorley 2001). The null hypothesis of non-existence relationship between both groups of variables was rejected with a probability error below 0.1% (Rho = 0.405, $p < 0.001$). The vicinity of samples WR of the third period with the samples C (natural) in the NMDS plane (Fig. 2) could then be explained as a return to the ‘natural conditions’ in the availability of the preys preferred by *F. paulensis* in its diet.

The marked preference of *F. paulensis* for benthic invertebrate preys contrasts with least carnivorous habits of other penaeid species, such as *Litopenaeus vannamei* (see references in Lemos *et al.* 2004). The dominant carnivorous behavior of *F. paulensis* explained the high protein demand of this species in captivity, and why the commercial culture of *F. paulensis* in ponds drastically decreased due to the lack of adequate feeds to sustain profitable growth (references in Lemos *et al.* 2004). Hence, the trophic preferences and the strong functional role of *F. paulensis* must be considered when determining the density of shrimps to be included in culture pens and in the adoption of rations of high nutritional value (*i.e.* protein content and digestibility). Although preys population recover may be possible at densities < 10 ind. m^{-2}, dominance of the macrobenthic assemblage of Saco do Justino by preys with direct development (*e.g. K. schübartii*) would retard recovery time.

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