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Effects of the Southern brown shrimp, *Penaeus subtilis*, predation and artificial feeding on the population dynamics of benthic polychaetes in tropical pond enclosures

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Abstract

In less intensive shrimp culture systems, polychaetes are known to be a major food item of several penaeid species. Under these conditions, very little is known about their population dynamics and the possible interactions with penaeid predation and artificial feeding. This work examined the effects of *Penaeus subtilis*, predation, stocking density and supplemental feeding on the population dynamics of polychaetes in pond enclosures. The work was conducted in a shrimp pond, where forty-five 9-m^2 open-bottom enclosures were built. The study consisted of four treatments: enclosures with feed and shrimp (i.e., FS); enclosures without feed and shrimp (NFNS, control); enclosures with shrimp and no feed (NFS); and, enclosures with feed, but no shrimp (FNS). For enclosures with shrimp, four initial shrimp stocking densities were used (i.e., 5, 10, 15 and 20 shrimp/m^2). Benthic polychaetes were collected 2 days prior to shrimp stocking and were sampled every 10 days over the complete rearing cycle. A total of 1,631 substrate samples of 20.43 cm^2 containing 20,283 polychaetes were collected for analysis. Overall, polychaete density and dry biomass over the production cycle varied from 956 to 11,921 polychaetes/m^2 and 1.17 to 2.58 g/m^2, respectively. Six polychaete families were identified and ranked relative to their numerical occurrence and frequency (Cn) as follows: (1) Spionidae (Cn = 52.3%), (2) Capitellidae (Cn = 37.9%), (3) Eunicidae (Cn = 6.8%), and (4) Nereidae (Cn = 2.7%), Pilargidae (Cn = 0.3%) and Sabellidae (Cn < 0.1%). *P. subtilis* final body weight varied from a minimum of 4.2 g to a

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maximum of 9.3 g, with final survival ranging from 42 to 69%. Shrimp predatory pressure produced a reduced polychaete growth in NFS and FS enclosures when compared to other treatments. Polychaete numerical abundance and biomass were greatly affected by higher shrimp stocking densities, while their population patterns appeared to be governed by other environmental and endogenous cues. Artificial feeding promoted higher polychaete levels even when shrimp were present, but it was not effective in alleviating *P. subtilis* grazing pressure at increased stocking densities (i.e., 15 and 20 shrimp/m^2). Results showed that *P. subtilis* predation, shrimp stocking density and external food supply are major factors to be considered when establishing sustainable limits for polychaete use as a naturally occurring food source in aquaculture systems.

Keywords: Polychaete; Shrimp; *Penaeus*; Food; Feeding; Aquaculture

1. Introduction

In extensive and semi-intensive marine shrimp culture systems, natural food can comprise most to all of the shrimp’s diet (Boddeke, 1983; Reymond and Lagardère, 1990; Nunes et al., 1997; Focken et al., 1998). In these organically rich pond bottoms, penaeid shrimp graze on a variety of naturally occurring food sources, including detritus, plant material and animal prey (Boddeke, 1983; Reymond and Lagardère, 1990; Nunes et al., 1996, 1997; Focken et al., 1998). Under these conditions, benthic fauna can be diverse, consisting of several potential shrimp prey species (Rubright et al., 1981; Moriarty et al., 1987). In many areas, polychaetes are reported to be the most predominant benthic macrofauna (Maguire et al., 1984; Ordner and Lawrence, 1987; Martins, 1994; Nunes and Parsons, 1999), occurring at high densities throughout the initial stages of the growth cycle (Crockett et al., 1988). While in marine and brackish water environments, these animals have been extensively used as active indicators of anthropogenic pollution (Lewbell, 1985; Ansari et al., 1986; Tsutsumi, 1987), in commercial penaeid aquaculture operations, polychaete abundance reflects pond productivity and availability of natural food (Crockett et al., 1988; Nunes et al., 1997; Nunes and Parsons, 1999), assisting farmers in the optimisation of shrimp stocking, feeding and harvest (Nunes et al., 1997).

In the fine pond sediments, benthic polychaetes feed on particulate organic matter (Olivier et al., 1995) and function in the mixing of substrate particles (Madsen et al., 1997) and recycling of nutrients (Mayer et al., 1995), increasing degradation rates and gas exchange between the substrate and water. Under confined shrimp culture systems, polychaetes have been recognised as the most important prey item of several penaeid species (Boddeke, 1983; Nunes et al., 1997), accounting for as much as 33% of their total diet (*P. subtilis*, Nunes et al., 1997). In the wild, polychaetes are known to compose the diet of many fish and crustaceans (Sheridan et al., 1984; Freire and Gonzalez-Gurriaran, 1995), including several commercially important *Penaeus* spp. (George, 1974; Marte, 1980; Gleason and Wellington, 1988; Stoner and Zimmerman, 1988). Due to their high nutritional value, particularly in polyunsaturated fatty acids (Dall et al., 1991), they have been employed in penaeid compounded maturation diets to promote female ovarian development (Bray and Lawrence, 1992).

Penaeid shrimp can consume polychaetes throughout all stages of their juvenile and adult life (Stoner and Zimmerman, 1988; Nunes et al., 1997), but grazing rates are thought to progressively increase as larger shrimp body sizes are attained. Although polychaetes are described as having a rapid life-cycle (George, 1984; Tsutsumi, 1987), combined with an exceptional capacity of recolonisation (Chesney and Tenore, 1985a; Tsutsumi, 1987), in aquaculture ponds, shrimp predation generally results in significant declines in polychaete abundance (Allan and Maguire, 1992, Nunes and Parsons, 1999), requiring larger amounts of supplemental feed inputs to sustain shrimp growth and survival.

Polychaete population dynamics have been studied under laboratory conditions (Chesney and Tenore, 1985a,b), but mainly in organically polluted environments (Lewbell, 1985; Ansari et al., 1986; Tsutsumi, 1987). In mariculture, most studies have focused on their response to benthic disturbance and organic and inorganic enrichment arising from fish, shrimp or bivalve cultivation (Tsutsumi, 1987; Spencer et al., 1996; Hargrave et al., 1997). In shrimp ponds, very few previous investigations have addressed thoroughly their population patterns and the possible interactions with penaeid predation and artificial feeding. This information is essential for developing management strategies for natural food in penaeid ponds, particularly in less intensive culture systems. The present work examined the impacts of *Penaeus subtilis* predation and stocking density, and the growth promoting effects of artificial feeding on the population dynamics of polychaetes in tropical pond enclosures.

2. Materials and methods

2.1. Study site and experimental design

This work was conducted at a commercial semi-extensive marine shrimp farm (Artemisa Aquicultura, Acaraú, CE), located in the northeastern region of Brazil. A 10-ha grow-out pond was used for the study (Fig. 1), where 9-m^2 (3×3 m) open-bottom enclosures were built using a grey polyethylene 2.0-mm diameter mesh net with 1.50-m height. Enclosure construction followed the methodology described by Nunes et al. (1996) and Nunes and Parsons (1999). The pond had an irregular shape and operated with a water depth between 0.70 to 0.90 m. Enclosures were lined up in three columns (R, right; C, centre; L, left), each composed of 15 pens, arranged 40 m apart and between 30 to 140 m from the pond walls. They were spaced 30 m from the outlet system and positioned at every 20 m towards the central section of the pond.

The study was composed of four treatments: enclosures with feed supply and shrimp (i.e., FS); enclosures without feed supply and shrimp (NFNS, control); enclosures with shrimp, but without feed supply (NFS); and, enclosures with feed supply, but without shrimp (FNS). For enclosures with shrimp (i.e., FS and NFS), four initial shrimp stocking densities were used (i.e., 5, 10, 15 and 20 shrimp/m^2 or FS_5, FS_{10}, FS_{15}, FS_{20} and NFS_5, NFS_{10}, NFS_{15}, NFS_{20}).

Feeding rates were constant among FNS and FS enclosures, but the amount distributed varied according to each of the initial shrimp stocking densities of FS treatment.

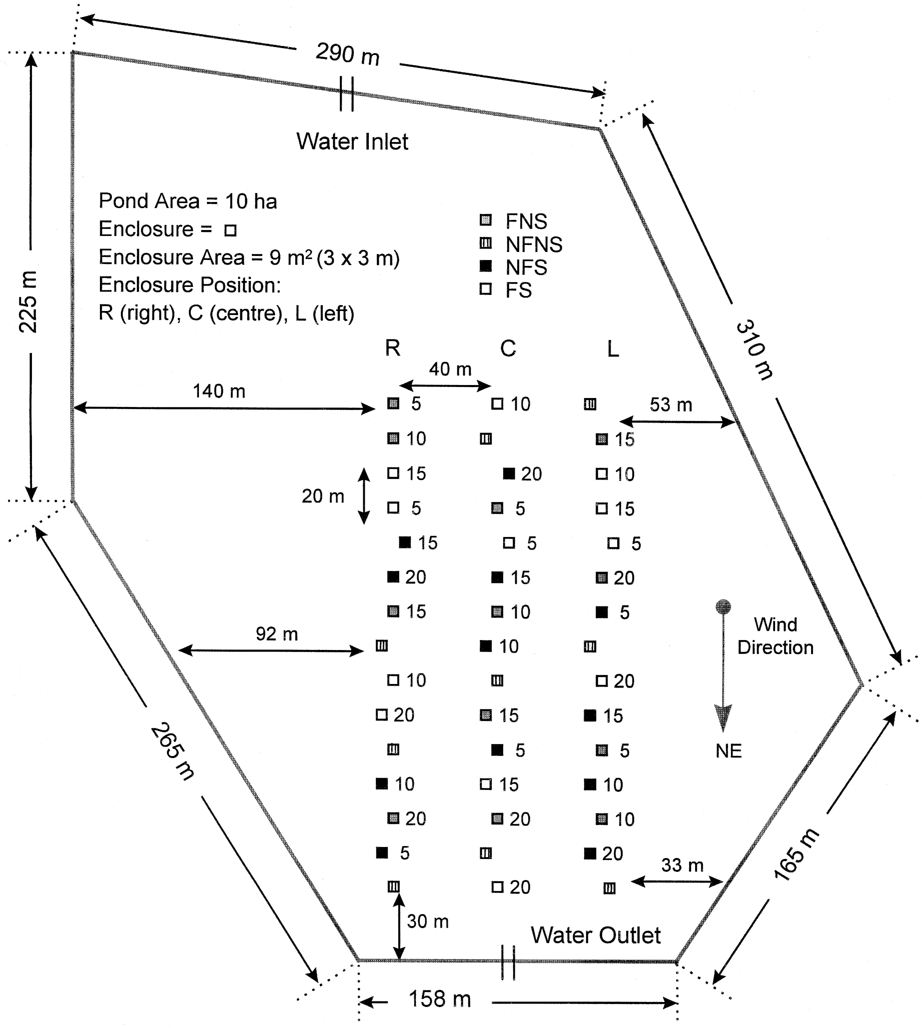

Fig. 1. Arrangement of enclosures in the grow-out pond used for the study. Shrimp stocking densities (5, 10, 15 and 20 shrimp/m^2) and respective feeding regimes are indicated by numbers next to each enclosure (FNS = feed, no shrimp; NFNS = no feed, no shrimp; NFS = shrimp, no feed; FS = feed, shrimp).

To examine the possible effects of the amount of feed administered on polychaetes, four feeding regimes were assigned to FS and FNS enclosures (i.e., FNS$_5$, feeding for 5 shrimp/m^2; FNS$_{10}$, feeding for 10 shrimp/m^2; FNS$_{15}$, feeding for 15 shrimp/m^2; and, FNS$_{20}$ feeding for 20 shrimp/m^2). Triplicate enclosures (except NFNS, 9 enclosures) were used for each treatment, shrimp density and (or) feeding regime, giving a total of 45 enclosures [i.e., 4 shrimp stocking densities × 3 treatments (FNS, FS, NFS) × 3 replicates + 9 controls (NFNS)]. Enclosures were distributed in a random fashion throughout each column of the experimental lay-out (Fig. 1), installed prior to fertilisation procedures, but after pond sterilisation.

2.2. Pond preparation

After a shrimp harvest from a previous growth cycle, the pond was sun-dried for one week in order to eradicate undesirable species, such as crabs and small fish. Remaining water puddles were sterilised with 500 l of hypochlorite for 2 days. Initial examination of pond substrate indicated depletion to very low levels of polychaete abundance. Under these conditions, inoculation of polychaetes was carried out following local commercial practices.

A total of 0.14 m^3 of substrate with 31,163 ± 11,852 (mean ± S.D.; $n = 3$) polychaetes was uniformly broadcast to each enclosed area. Animals were transplanted from nearby brackish water lagoons [8.35 ± 0.04 pH (mean ± standard deviation; $n = 3$), 20 ± 1‰ ($n = 3$) salinity and 25°C temperature] during a 7-day period. To allow sufficient time for polychaete settling and growth, pond water was exchanged after sterilisation and water level kept between 10 to 20 cm for 15 days. Subsequently, water depth was gradually increased to 50 cm for fertilisation with 240 kg of water-dissolved chicken manure. Five days after organic fertilisation, water level was raised between 80 and 90 cm and exchanged at a constant rate until shrimp stocking.

2.3. Shrimp stocking, feeding and pond management

Initially, shrimp larvae of *P. subtilis* were captured in the estuary of Acaraú River and reared during 30 d in a round 0.25-ha nursery earthen pond. Throughout this period, shrimp were fed twice daily with a mixture of a commercial formulated feed and minced fish flesh. The study started on 28 May 1998 (shrimp stocking) and extended until 30 July 1998 (harvest). Postlarvae (PL) of 0.20 ± 0.04 g (mean ± S.D.; $n = 11$) were slowly acclimated and released in FS and NFS enclosed areas at early morning. The external area of the enclosures was also stocked with PL of *P. subtilis* at a density of 2 PL/m^2. No artificial feeding was carried out during rearing of shrimp in the outside region.

A dried commercial pelleted food, type Ralston Purina MR-35 (Agribrands Purina do Brasil, São Lourenço da Mata, PE, Brazil), was broadcast by hand twice daily at 1000 and 1500 h (enclosures FNS and FS only). In the initial 19 days of culture, only feed in powder form was used. This was followed by a mixture (1:1 ratio) of powder and granules [1.9-mm diameter; from D_{20} (i.e., 20 days after shrimp stocking) to D_{30}], 70% pellets (1.3-mm length by 2.3-mm diameter) and 30% granules (from D_{31} to D_{40}), and only pellets for the remainder of the culture cycle. Feed proximate analysis indicated the following chemical composition: 9.01 ± 1.00% (mean ± S.D.; $n = 18$) moisture, 40.39 ± 1.25% protein ($N \times 6.25$, dry basis; $n = 6$), 7.53 ± 1.23% lipid ($n = 6$), 11.02 ± 0.26% ash ($n = 6$) and 32.04 ± 1.13% carbohydrate ($n = 18$). Feed quantities were adjusted at each 12-day period based on shrimp average body weight. Feeding amounts increased proportionally to the rearing period, with rates as follows: from D_1 to D_{19}, 15% shrimp body weight/day; 8% shrimp body weight/day from D_{20} to D_{40}; and, 5%

shrimp body weight/day from D_{41} to D_{60}. Shrimp growth measurements (post-orbital carapace length, CL) were only conducted with a small number of enclosures, in order to reduce disturbance to the pond substrate and the cultured population. Shrimp were sampled with a cast net at each 10-day rearing period, starting on D_{29} of culture. All collected animals were returned to their respective culture areas following measurements.

Water was exchanged on a daily basis in accordance to tidal fluctuations at a rate of 3% of total pond volume/day. All water supply passed through a 1.0-mm diameter mesh net in the inlet gate, but fine screening was only carried out in the initial stages of culture. Water quality was monitored daily at 1030 and 1530 h. Dissolved oxygen (DO), temperature, salinity and pH measurements were taken in triplicate twice daily (morning and afternoon). Water transparency was measured in triplicate once daily at 1030 h with a Secchi disk. After harvest, shrimp from each enclosed area were counted and measured. Carapace length (CL) measurements were converted to body weight (BW) by using the following equation: $\mathrm{BW} = 0.0008\mathrm{CL}^{2.9619}$ ($r = 0.991$).

2.4. Polychaete collection, examination and identification

Benthic polychaetes started to be collected 2 days prior to shrimp stocking (i.e., D_{stock}). Sampling continued every 10 days throughout the complete rearing cycle. Polychaetes together with other existing macrobenthic fauna were collected from the upper 15-cm sediment layer using a soil sampler operated from a boat and measuring 5.1 cm of inner diameter ($A = 20.43$ cm^2). At each sampling period, a total of 5 to 6 substrate samples were taken randomly from individual enclosures, starting at 0530 h. Core samples were transferred to plastic bags containing seawater and immediately brought to a laboratory for analysis. In the laboratory, each substrate sample was elutriated and sieved through three mesh size nets of 2.83 mm, 1.83 mm and 500 μm. Polychaetes from the retained 500-μm portion of the sample were individually counted (n_{A}) and stored in 70% ethanol for subsequent analysis.

Later, samples were re-examined (×20 or ×40 magnification) for taxonomic identification (Fauchald, 1977) and recounting (n_{B}). Concurrently, separated animals from replicates were mixed, oven-dried to a constant weight and weighed to the nearest milligram. Polychaete biomass (except for D_{stock}) was calculated by dividing the total dry weight (g) obtained from mixed samples by the total number of replicates collected for each enclosure at each sampling period. Polychaete density was determined by calculating the average number ($n_{\mathrm{A/B}}$) of collected animals (n_{A} and n_{B} countings, including replicates). Both polychaete biomass and density were converted from the sample size of 20.43 cm^2 to m^2.

From this data and after taxonomic classification of polychaetes and the determination of their numerical abundance in each enclosure, the following indices were calculated (Reymond and Lagardère, 1990; Nunes et al., 1997): (i) family frequency (%): $\mathrm{Cn} = (100 \times p)/P$, where: p = total number of each specific polychaete family and P = total number of polychaetes observed in all samples; (ii) family occurrence index (%): $f = (100 \times N_{\mathrm{p}})/N'$, where N_{p} is the number of enclosures with each specific polychaete family and N' is the total number of enclosures. From f, it was determined three categories of family: prevalent or main family, where $f \geq 50\%$; secondary family ($10\% < f < 50\%$); and, accidental family ($f \leq 10\%$).

2.5. Soil analysis

A day prior to shrimp harvest (D_{63}), three replicates or more of substrate samples (15-cm deep each) were randomly collected from each enclosure for chemical analysis. Prior to examination, replicates were mixed thoroughly amounting to 1 kg of wet sediment/enclosure. Soil pH, total carbon, Kjeldahl nitrogen, phosphorus and organic matter were measured following the methodology described by Nunes and Parsons (1999). Particle size composition was determined by sieving soil samples for particles coarser than 0.05 mm. The pipette method was applied to silt and clay-sized particles. Dispersion was accomplished by the addition of 1 N NaOH. Soil particle-size texture was classified using the triangular diagram according to USDA (1951).

2.6. Statistical analyses

Statistical analyses were performed with the Statistical Package for Social Sciences Windows version, release 7.5.1. (SPSS, Chicago, IL, USA). Homogeneity of variance was examined for all data by using Bartlett-Box F and Cochran's C tests. Kurtosis and skewness and their standard error (i.e., S.E. kurtosis and S.E. skewness) were applied to the data as measures of asymmetry and tests of normality. Based on these results, data were transformed to a $\log(x+1)$ scale in order to normalise and homogenise the variances and to meet statistical assumptions. Probability of type I error was set at $\alpha = 0.05$.

3. Results

3.1. Shrimp growth and survival, and water and soil quality

P. subtilis final body weight varied from a minimum of 4.2 g (NFS_{20}) to a maximum of 9.3 g (FS_5, Table 1). Final survival ranged from 42 (FS_{10}) to 69% (FS_{15}, Table 1). Shrimp growth performance changed in accordance to the treatment used, but overall survival showed similar levels among treatments. On average, a higher mean growth

Table 1
Mean final growth (g) and survival (%, values in parentheses) of *P. subtilis* for treatments NFS (shrimp and no feed) and FS (feed and shrimp) at four stocking densities

Treatment[a]	Shrimp initial stocking density			
	5 shrimp/m^2	10 shrimp/m^2	15 shrimp/m^2	20 shrimp/m^2
NFS	6.2 g (66%)	7.4 g (58%)	6.1 g (48%)	4.2 g (54%)
FS	9.3 g (42%)	8.2 g (42%)	7.1 g (69%)	8.5 g (43%)

[a] Sample size of 272 (NFS) and 264 (FS) shrimp.

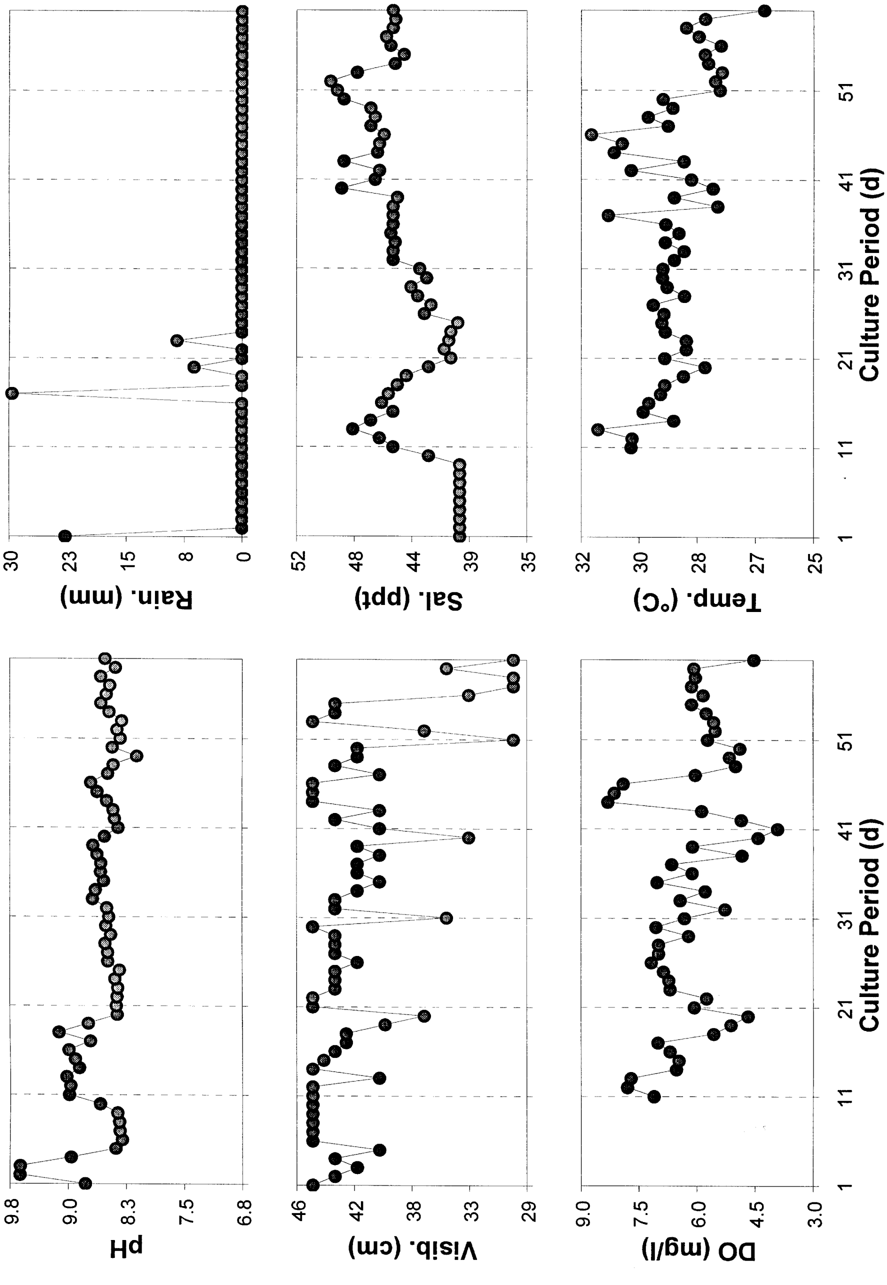
Rain. (mm)
30
23
15
8
0
Sal. (ppt)
52
48
44
39
35
Temp. (°C)
32
30
28
27
25
pH
9.8
9.0
8.3
7.5
6.8
Visib. (cm)
46
42
38
33
29
DO (mg/l)
9.0
7.5
6.0
4.5
3.0
1
11
21
31
41
51
Culture Period (d)

Table 2
Polychaete density (mean number/m^2 × 10^2 ± S.D.) in the bottom of FNS, FS, NFS and NFNS enclosures. Values in parentheses indicate minimum and maximum values (n refers to number of observations for each treatment). Common letters denote non-significant differences at the $\alpha = 0.05$ level by Scheffé's multiple range test. Lower and uppercase letters refer to vertical and horizontal comparisons, respectively

Culture period (days)	Polychaete Density (number/m^2 × 10^2)			
	FNS	FS	NFS	NFNS
D_{stock}	10 ± 8 A	11 ± 9 A	8 ± 8 aA	9 ± 8 A
	(< 1–39)	(< 1–34)	(< 1–34)	(< 1–29)
D_{10-12}	61 ± 53 aA	52 ± 39 aA	34 ± 36 bB	33 ± 33 aB
	(< 1–220)	(< 1–176)	(< 1–201)	(< 1–127)
D_{20-22}	52 ± 42 aA	49 ± 43 aA	25 ± 27 ab	42 ± 33 abA
	(< 1–201)	(< 1–220)	(< 1–98)	(< 1–108)
D_{30-32}	57 ± 42 aA	54 ± 67 aAB	33 ± 33 bB	45 ± 38 abAB
	(< 1–191)	(< 1–333)	(< 1–137)	(< 1–157)
D_{40-42}	109 ± 89 bA	57 ± 65 aBC	55 ± 77 bC	72 ± 54 bAB
	(< 1–357)	(< 1–323)	(< 1–279)	(< 1–230)
D_{50-52}	141 ± 108 bA	100 ± 125 aB	60 ± 71 bB	125 ± 65 cA
	(< 1–470)	(< 1–563)	(< 1–333)	(< 1–289)
D_{60-62}	154 ± 113 bA	125 ± 166 aB	73 ± 99 b	127 ± 80 cAB
	(< 1–519)	(< 1–636)	(< 1–396)	(< 1–348)
n	435	435	436	325

was found for shrimp in FS treatment (8.3 g) when compared to NFS (6.0 g). Both *P. subtilis* growth and survival were reduced as initial stocking density increased (except NFS_{10} and FS_{20}, Table 1).

Rainfall was scarce during the complete rearing cycle (Fig. 2). A total of only 67.0 mm of precipitation fell over the 2.5-month study period, decreasing salinity levels at some instances. While temperatures remained relatively uniform during the rearing cycle [29.2 ± 2.6°C (mean ± S.D.); $n = 280$], salinity (44 ± 2‰; $n = 335$) varied significantly ($P < 0.001$), showing an increasing trend as the culture period progressed. DO (6.13 ± 1.61 mg/l; $n = 282$), water visibility (42 ± 5 cm; $n = 184$) and pH (8.57 ± 0.34; $n = 334$) presented no clear patterns or pronounced variations over the rearing cycle.

Since sediment physical profile is known to affect polychaete abundance (Decho et al., 1985), statistical tests were performed to assess variations among treatments. One-way ANOVA conducted for each chemical and physical variable of pond sediment indicated no significant differences among enclosures ($P > 0.05$; 8.1 ± 0.1 pH; 0.86 ± 0.28% total C; 0.08 ± 0.003% Kjeldahl N; 10 ± 1 C:N; 4 ± 5‰ P; 1.49 ± 0.48% organic matter; mean ± S.D., $n = 45$ samples/variable). In general, soil texture fell within the sandy clay loam class (33 ± 13% coarse sand, 16 ± 9% fine sand, 27 ± 13% silt and 25 ± 9% clay; $n = 45$).

Fig. 2. Daily mean physical and chemical water quality parameters (i.e., pH, salinity, dissolved oxygen, temperature and water visibility) of shrimp pond enclosures over the rearing cycle of *P. subtilis*. Measurements were taken at least once a day. Rainfall data provided by Fundação Cearense de Meteorologia e Recursos Hídricos (FUNCEME).

3.2. Polychaete analysis

A total of 1,631 substrate samples of 20.43 cm^2 containing 20,283 polychaetes were collected for analysis. All samples were numerically dominated by polychaetes, although amphipods were sometimes observed at very low numbers. Examination of polychaete density (PD) prior to shrimp stocking indicated mean levels of 954 ± 832 polychaetes/m^2 (mean ± S.D.; $n = 269$). Initial PD did not differ statistically among treatments (Table 2), but changed significantly during the culture period.

3.2.1. Trends over the rearing cycle

Lowest PD was measured just prior to shrimp stocking, in contrast to the highest obtained in the end of the rearing period (Fig. 3). Transformed PD was statistically different among sampling periods ($P < 0.001$). A posteriori analysis showed that differences concentrated mainly among three stages of culture, an initial (D_{stock}, D_{10-12}, D_{20-22} and D_{30-32}), an intermediate (D_{40-42}) and a final period (D_{50-52} and D_{60-62}). While the control treatment (i.e., NFNS) displayed PD changes similar to the overall trend, other treatments presented different variations. PD pattern for FNS was limited to two stages, initial (D_{10-12}, D_{20-22} and D_{30-32}) and final (D_{40-42}, D_{50-52} and D_{60-62};

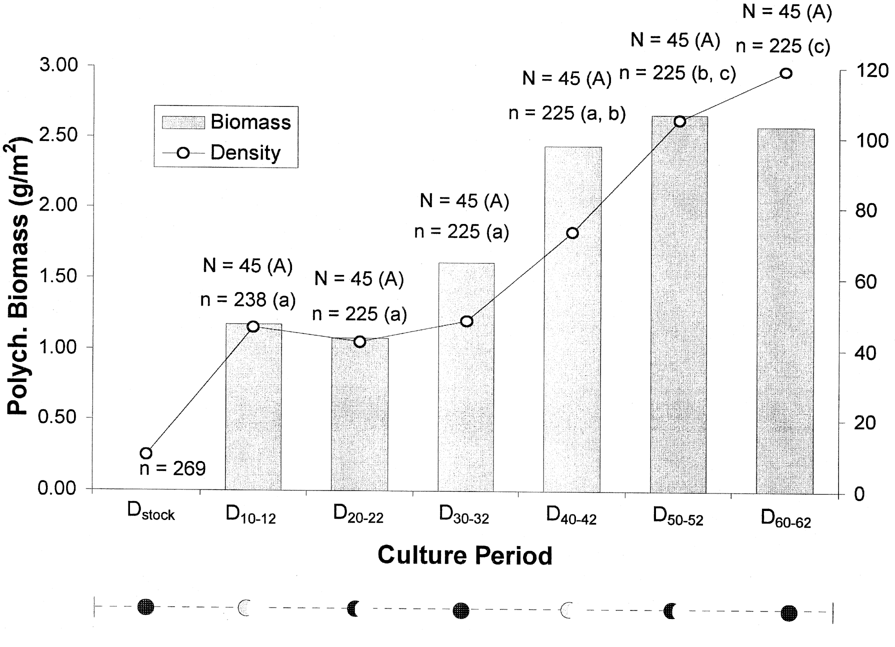

Fig. 3. Overall mean polychaete density (number/$m^2 \times 10^2$) and biomass (g of dried polychetes/m^2) in relation to the rearing period. Common letters in parentheses indicate non-significant differences at the $\alpha = 0.05$ level by Scheffé's multiple range test. Uppercase letters refer to comparisons for biomass and lowercase for density. Number of observations at each culture period are indicated by N (biomass) and n (density). Moon phases are shown on the bottom.

Table 2), whereas in FS, polychaete densities were uniform throughout the rearing period (except for D_{stock}; Table 2). Similarly, PD was maintained almost uniform in NFS enclosures, except for a significant drop detected at $D_{20\text{-}22}$ (Table 2). In all cases, PD increased as the rearing cycle progressed.

Similarly to PD, polychaete biomass differed statistically among culture periods, but only slightly. Analysis of correlation between PD and PB indicated a significant, but poor relationship at the 1% level (Pearson coefficient of correlation = 0.375; $n = 534$). Although population growth (i.e., PD and PB) appeared to be synchronous with the moon phase, particularly the new moon, no statistically significant increments were detected during these stages (Fig. 3).

3.2.2. Effects of shrimp predation

Overall, polychaete numerical abundance and biomass differed significantly among treatments ($P < 0.001$, Fig. 4). NFS enclosures showed statistically lower levels in PD when compared to the remainder treatments (Fig. 4). This indicated a strong shrimp predation effect on polychaetes, particularly when feed was not provided. This effect was also clear in an early stage of culture (Table 2). NFS also showed a significantly lower PB when compared to FNS, but it did not differ from NFNS and FS (Fig. 4). On the other hand, FS presented a statistically lower PD than FNS enclosures (Fig. 4).

Shrimp predation effects on polychaetes were confirmed by contrasting treatments with shrimp and without (Fig. 5). In general, there was a significantly higher PD and PB in treatments without shrimp when compared to treatments with shrimp. Comparisons

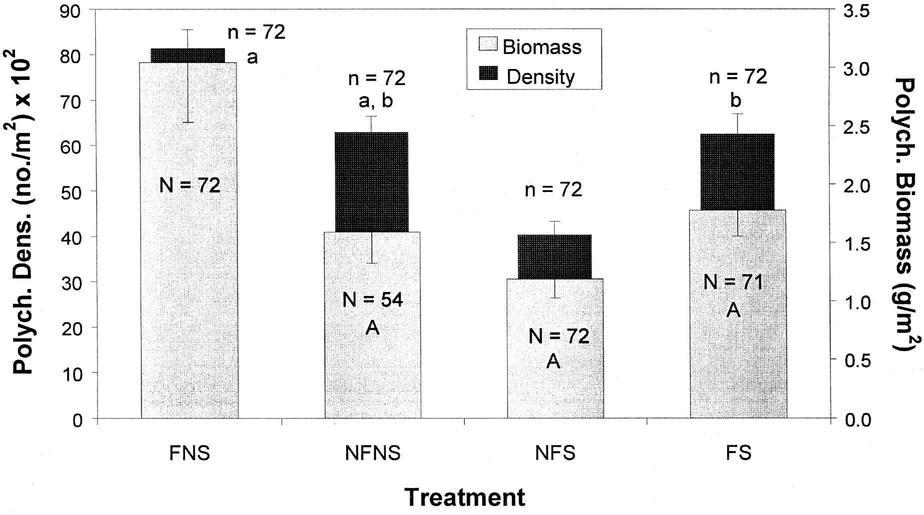

Fig. 4. Differences in total mean polychaete density (number/m^2 $\times 10^2$) + standard error (S.E.) and biomass (g of dried polychaetes/m^2)-S.E. among treatments FNS (feed and no shrimp), NFNS (no feed and no shrimp), NFS (shrimp and no feed) and FS (feed and shrimp). Number of observations are indicated by N (biomass) and n (density). Common letters (uppercase refers to biomass and lowercase refers to density) denote no significant difference at the $\alpha = 0.05$ level by Scheffé's multiple range test.

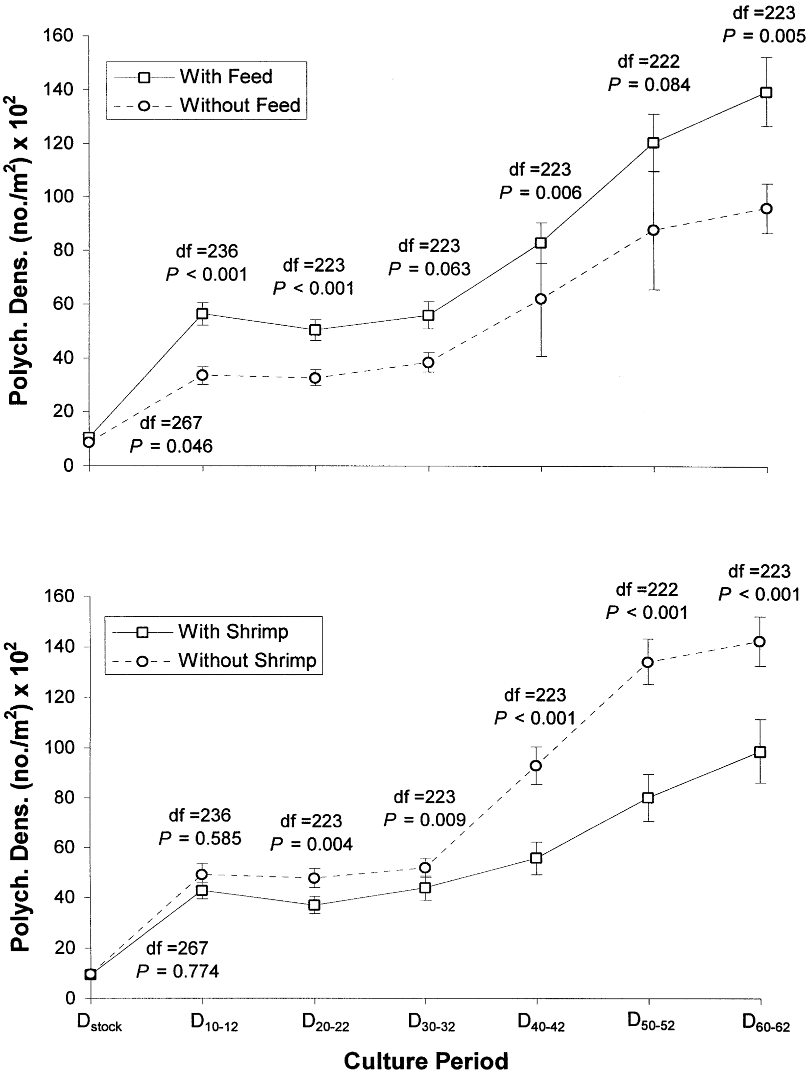

Fig. 5. Changes in mean polychaete density (number/m^2 $\times 10^2$)$\pm$S.E. in enclosures with (NFS and FS) and without (FNS and NFNS) shrimp and with (FNS and FS) and without (NFS and NFNS) feed. Days represent culture period after shrimp stocking (D$_{stock}$). Numbers next to lines indicate level of significance from two-tailed *t*-tests.

among shrimp stocking densities indicated significant differences in FS enclosures (Fig. 6). On average, the higher the shrimp density, the lower PD was found, although a similar effect could not be observed in NFS enclosures (Fig. 6). No statistical differences were found in PB among shrimp densities in enclosures FS ($P = 0.214$) and NFS ($P = 0.094$).

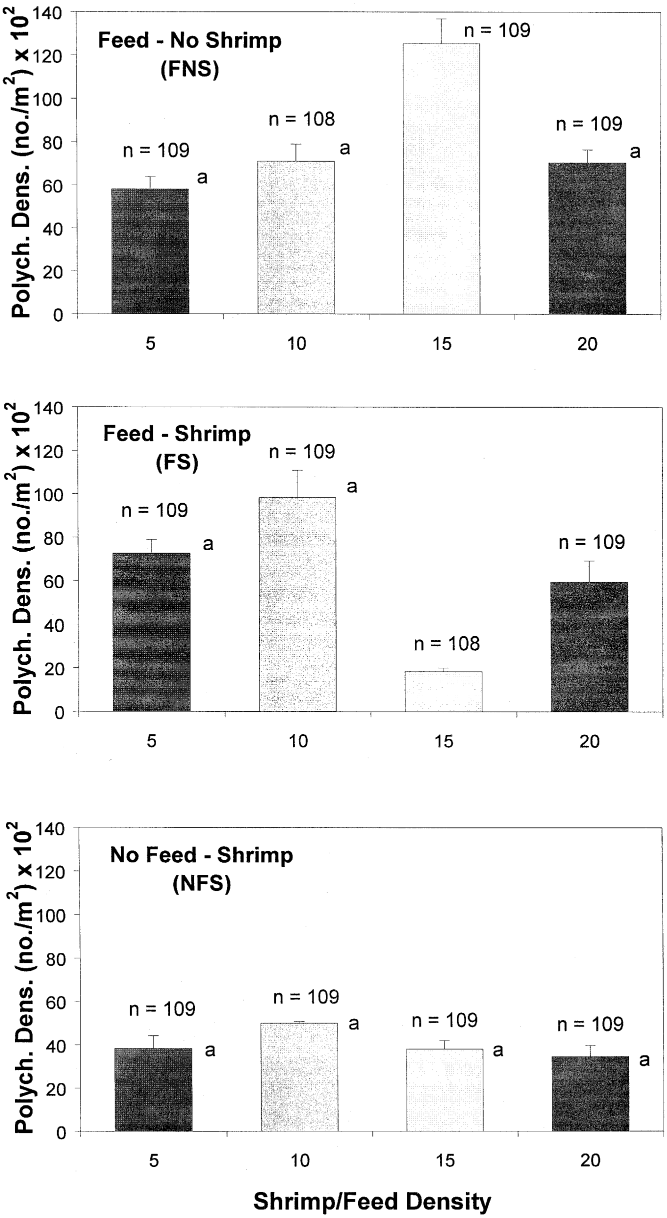

Fig. 6. Comparison of total mean polychaete density (number/m^2 $\times 10^2$) ± S.E. in relation to four shrimp and (or) feed densities among treatments FNS (feed and no shrimp), FS (feed and shrimp) and NFS (shrimp and no feed). Feed density refers to feeding regime used for each respective shrimp stocking density (number of shrimp/m^2). Values (n) on top of bars indicate number of substrate samples analysed. Common letters denote no significant difference at the $\alpha = 0.05$ level by Scheffé's multiple range test.

3.2.3. Effects of artificial feeding

In contrast to enclosures without feed supply, treatments with feed presented a statistically higher PD (Fig. 5) and PB ($P = 0.002$). PB was also significantly greater in treatments with feed (2.40 ± 0.28 g of dried polychaetes/m^2) than without feed (1.36 ± 0.15 g of dried polychaetes/m^2). Overall, PD showed higher levels for FNS and FS enclosures when compared to the NFS treatment (Fig. 4). In the case of PB, the effect of artificial feeding was highest when shrimp were not present (i.e., FNS, Fig. 4). Within FNS enclosures, the effect of artificial feeding on PD was highest for FNS$_{15}$

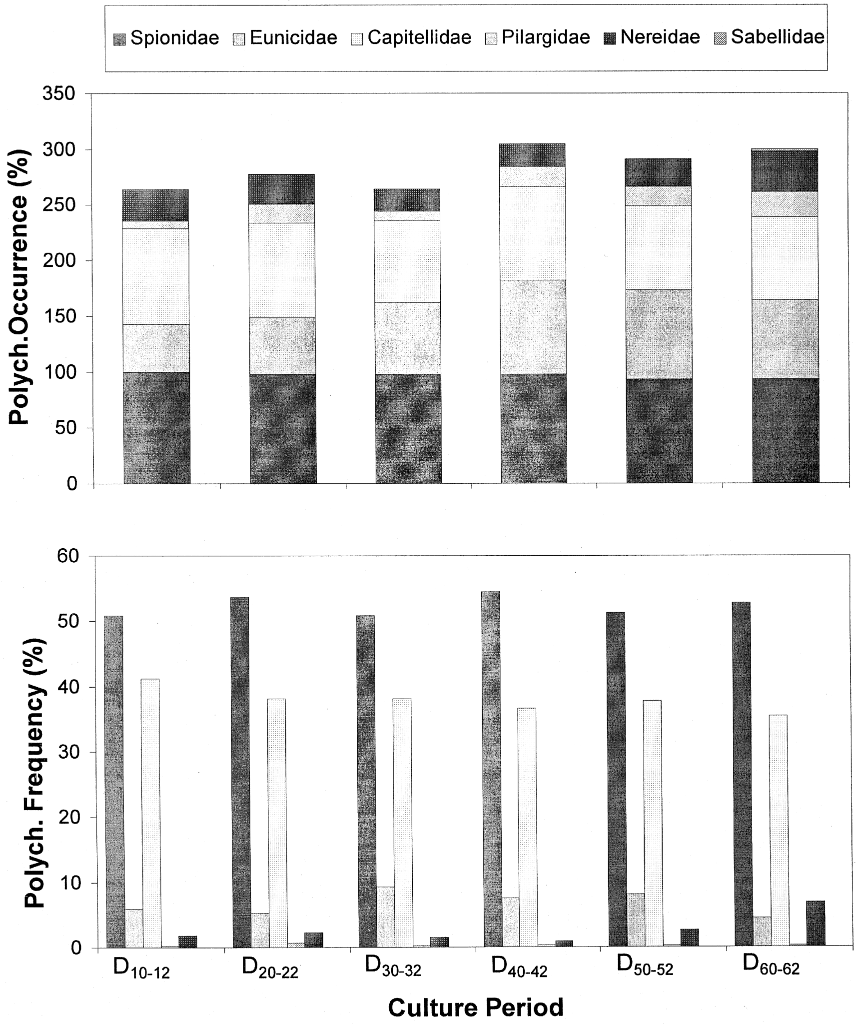

Fig. 7. Polychaete family frequency (Cn, %) and occurrence (f, %) relative to the culture period of *P. subtilis* in pond enclosures. Cn is the percentage of a specific polychaete family in all samples, while f refers to the recurrence of a specific family relative to all enclosures under investigation.

Table 3
Numerical representation of polychaetes [(number/m^2) ± S.D.] by family over a 62-day shrimp rearing cycle ($n = 45$ observations/culture period). Each observation represents a mixture of five to six substrate samples of 306 cm^3. Common letters denote non-significant differences at the $\alpha = 0.05$ level by Scheffé's multiple range test. Lowercase letters indicate horizontal comparisons among culture periods for each family, while uppercase letters refer to vertical comparisons among families at each culture period

Family	Polychaete density (number/m^2)					
	Culture period					
	D_{10-12}	D_{20-22}	D_{30-32}	D_{40-42}	D_{50-52}	D_{60-62}
Spionidae	1968 ± 1170 a	1987 ± 1204 a	2178 ± 1375 a	3583 ± 3152 ac	4914 ± 3891 bc	5986 ± 4851 bc
Eunicidae	235 ± 685 aA	196 ± 377 aA	396 ± 573 abA	494 ± 700 ab	773 ± 803 bc	514 ± 578 acA
Capitellidae	1610 ± 2286 a	1410 ± 1694 a	1630 ± 2159 a	2413 ± 3186 a	3627 ± 4371 a	4023 ± 5521 a
Pilargidae	8 ± 33 aA	24 ± 54 aA	9 ± 28 aB	26 ± 64 aA	20 ± 45 aA	29 ± 59 aAB
Nereidae	73 ± 157 abA	83 ± 196 abA	64 ± 162 abAB	64 ± 230 aA	250 ± 881 abA	778 ± 2242 bAB
Sabellidae	< 1 aA	< 1 aA	< 1 aB	< 1 aA	< 1 aA	2 ± 15 aB

treatment (Fig. 6). Under the same feeding regime, FS_{15} enclosures produced the lowest PD levels among all other shrimp densities (Fig. 6). No statistical differences could be detected in PB among feeding regimes in enclosures FNS ($P = 0.459$).

3.2.4. Family classification and abundance

Six polychaete families were identified and ranked according to Scheffé's multiple range test as follows: (1) Spionidae (Cn = 52.3%), (2) Capitellidae (Cn = 37.9%); (3) Eunicidae (Cn = 6.8%); and, (4) Nereidae (Cn = 2.7%), Pilargidae (Cn = 0.3%) and Sabellidae (Cn < 0.1%). Visual observations indicated that most spionids, capitellids and nereids had comparatively smaller body sizes than the eunicids. Some eunicids reached 10 cm or more in length.

There were only small changes in polychaete family frequency and occurrence patterns throughout the production cycle (Fig. 7). The dominance of Spionidae and Capitellidae over other families was evident starting in the early stages of culture, while Eunicidae became more numerically abundant from D_{40-42} on (Table 3). The overall density of Spionidae and Capitellidae was also statistically greater than the remainder families, regardless of the treatment used (Table 3). In general, Spionidae, Capitellidae and Eunicidae fell within prevalent or main families, Pilargidae and Nereidae as secondary families and Sabellidae as an accidental family. Within each family, Capitellidae, Pilargidae and Sabellidae showed a constant numerical abundance over the rearing cycle (Table 3). A significant increase was observed for Spionidae and Eunicidae in the final stages of culture, while Nereidae had only slight changes (Table 3).

4. Discussion

4.1. Environmental parameters and shrimp performance

All water quality parameters analysed were within normal levels for penaeid shrimp culture (Boyd and Fast, 1992; Boyd and Tucker, 1998). In some instances, salinity was higher than desirable levels, but average values (44 ± 2‰; $n = 335$) were within limits found in other studies conducted in the same site and season (Nunes et al., 1996). It is also unlikely that the increasing salinity levels over the production cycle depressed polychaete growth, since increments in their population size were observed.

Similarly, chemical analysis of the pond sediment revealed results comparable to other investigations in shrimp ponds (Boyd et al., 1994; Boyd and Pippopinyo, 1994; Smith, 1996; Nunes and Parsons, 1999). The general soil textural classification (i.e., sandy clay loam) suggests a good water retention capacity by the substrate. The observed silt (25%) and sand (49%) content balance reflect a normal soil structure (Guillet and Rouiller, 1982), with textural characteristics similar to other aquaculture ponds (Boyd and Pippopinyo, 1994; Smith, 1996). The absence of significant variations in soil particle size indicates that sediment physical profile did not have an effect in the differences found for polychaete abundance among treatments.

P. subtilis average survival observed in NFS and FS treatments are comparable to normal figures obtained in the industry (between 54.0 and 88.1% after 60 days of culture; Jory, 1995). In NFS, some of the low growth and survival values found for *P. subtilis* (NFS_{15} and NFS_{20}) were the result of higher shrimp stocking densities used, coupled with the absence of external food supply. In general, shrimp mean body weights increased with feed inputs and at lower shrimp stocking densities. Maguire and Leedow (1983) and Allan and Maguire (1992) observed a similar shrimp density and growth interaction for *Metapenaeus macleayi* and *P. monodon*, respectively. In both studies, the authors reported that as shrimp density increased, average shrimp weight gain was reduced, although survival was unaffected by stocking density. However, Apud et al. (1981) found that stocking density affected both shrimp survival and growth.

4.2. Polychaete families

Taxonomic representation of polychaetes in the pond bottom was not diverse. Data indicated the predominance of spionids and capitellids over other families throughout all stages of the growth cycle. The prevalence of these two families have also been reported elsewhere (Ordner and Lawrence, 1987; Martins, 1994; Nunes and Parsons, 1999). These observations also agree with other studies that show the high capacity of spionids and capitellids to recolonise defaunated azoic areas and to rapidly restore previous population sizes (Tsutsumi and Kikuchi, 1983; Chesney and Tenore, 1985a; Tsutsumi, 1987).

Capitellids, spionids and nereids have all been found in the stomach of penaeid shrimp (Gleason and Wellington, 1988; Stoner and Zimmerman, 1988; Reymond and Lagardère, 1990). In the present study, the disproportional larger body sizes observed for eunicids may explain why this family has not been reported to occur in the diet of penaeids. Although *Penaeus* spp. are known to consume a wide range of prey sizes (Marte, 1980; Stoner and Zimmerman, 1988; Reymond and Lagardère, 1990; Nunes et al., 1997), in the presence of various food sizes they discriminate against large items (Nunes and Parsons, 1998a). Overall, results suggest that further investigations aimed at increasing polychaete population levels in shrimp ponds should mainly focus on opportunistic families, such as spionids and capitellids. Their ability to restore and maintain high population sizes during the growth cycle, even under continuous shrimp predation pressure was confirmed in the present study. Their apparent adequate body sizes for shrimp handling and consumption should also bring more favourable results.

4.3. Polychaete population patterns

Variations in polychaete density (956 to 11,921 polychaetes/m^2) and biomass (1.17 to 2.58 g/m^2) over the production cycle are comparable to estimates by Crockett et al. (1988), which indicated densities varying between 1,919 to 22,311 polychaetes/m^2 and dry biomass between 0.119 to 3.870 g/m^2. The trend in polychaete density for the control treatment indicated that if left undisturbed (i.e., without shrimp predation or addition of feed inputs), pond polychaete populations have the potential to significantly increase over a rearing cycle (NFNS, Table 2). According to Chesney and Tenore (1985a) when conditions favour development, populations of opportunistic polychaetes tend to overshoot the carrying capacity of the environment, resulting in an explosive population growth.

However, in the present study, increases in population number did not produce higher levels in total polychaete biomass. Although size-frequency distribution data were not collected, these results lead to speculations that natural polychaete population recruitment occurred over the study period. New recruits probably originated from within the enclosures, although distribution of polychaete eggs and larvae from the supply water or external enclosure area may have also occurred. Within a 2.3-month period, Tsutsumi (1987) reported two large recruitments in a population of *Capitella capitata* growing nearby fish cages. George (1984) indicated that some mangrove-dwelling capitellid polychaetes may become gravid in 3 to 5 weeks after larval metamorphosis and spawn 1.5 weeks later.

In the present study, peaks observed in the overall polychaete density suggest that spawning occurred by the intermediate towards the final stages of culture (i.e., D_{40-42} to D_{60-62}; Fig. 3). In other investigations (Martinez-Cordova et al., 1998; Nunes and Parsons, 1999), a similar effect was found between 5 to 10 weeks after initial shrimp stocking. Nunes and Parsons (1999) reported a significant peak in polychaete density on the 68th day of a shrimp rearing cycle after observing continual 12-day declines. It appears that in shrimp ponds, prominent increases in polychaete density are mainly the result of their reproductive cycle, although factors such as low survival of adults due to predation has been suggested to accelerate this process (Nunes and Parsons, 1999).

Under the presence of shrimp, polychaete densities and biomass were maintained relatively uniform over the rearing cycle (SNS and FS, Table 2). This pattern disagrees with the general perception that in shrimp ponds, polychaete density and biomass successively decline as the culture period progresses (Martinez-Cordova et al., 1998; Nunes and Parsons, 1998b). In fact, many cultured *Penaeus* spp., including *P. subtilis* (Nunes et al., 1997), acquire a more pronounced carnivorous habit as larger body sizes are attained [e.g., *P. monoceros* (George, 1974), *P. monodon* (Marte, 1980), *P. brasiliensis* (Stoner and Zimmerman, 1988); *P. japonicus* (Reymond and Lagardère, 1990)]. Such a behaviour combined with a larger shrimp population biomass usually result in an increased grazing pressure over naturally occurring pond prey species

(Nunes and Parsons, 1999). Ordner and Lawrence (1987) studying the benthic infaunal communities of shrimp ponds, indicated that in the presence of shrimp, polychaete densities started to decline after the third week of culture. Martins (1994) reported bi-weekly polychaete biomass measurements from 83 commercial production cycles of seven semi-extensive penaeid polyculture ponds. In agreement with the present study, the data of Martins (1994) provided no indication of meaningful reductions in polychaete biomass throughout grow-out cycles, or of a depleted polychaete biomass prior to shrimp harvest.

On the other hand, in the present study, artificial feeding could not produce progressive increments in polychaete density patterns, as it would be expected with the continual increases in feed ration. The only major temporal peak found for treatment FNS was observed from D_{30-32} to D_{40-42}. This peak appears to correspond to the event found in the same period for the control treatment (NFNS). Thus, rather than a promoting effect generated by artificial feeding, such an increase is more likely to be related with the timing of polychaete recruitment. The low feed promoting impact on polychaete growth patterns are explained by the small variations in feed quantities that occurred over the rearing cycle. Although the amount of feed given increased during the course of the study, differences among sampling dates may not have been sufficiently large to produce a significant effect on polychaete density patterns.

In general, the increases in polychaete density over the production cycle can be attributed to their initial successful colonisation prior to shrimp stocking and their reproduction. The absence of other predominant macrofauna or competitive species in the sediment may have also favoured their growth. These results indicate that in shrimp ponds, polychaetes can successfully and rapidly recolonise previously depleted areas and maintain high growth levels even under continuous shrimp grazing pressure. Such observations fit into the general description of polychaetes life-history and behaviour as opportunistic and r-strategistic animals (Grassle and Grassle, 1974; Tsutsumi, 1987).

4.4. Impact of P. subtilis predation on polychaete abundance

P. subtilis grazing pressure was the leading cause for a reduced polychaete growth in enclosures NFS and FS when compared to other treatments. This influence could be detected for both polychaete biomass (NFS vs. FNS) and density (NFS vs. other treatments; and, FS vs. FNS). Shrimp predatory effects on polychaetes have been identified in both cultured (Rubright et al., 1981; Moriarty et al., 1987; Martins, 1994) and natural environments (Kneib, 1985; Leber, 1985) and under laboratory-controlled conditions (Bonsdorff and Pearson, 1997). In shrimp ponds, polychaete populations have been reported to decline from a total of 45,000 animals/m^2 to less than 10 animals/m^2 (Hopkins et al., 1995), changing the community structure of these systems (Moriarty et al., 1987).

In the present study, *P. subtilis* predatory behaviour on polychaetes agrees with descriptions of its feeding habits and diet. Stoner and Zimmerman (1988) examining the food of *P. subtilis* in the wild, found that capitellids composed 20 to 38% of its diet. Under semi-intensive culture, this species has a benthic omnivorous opportunistic feeding habit, favouring polychaetes as its main prey during all stages of the growth cycle (Nunes et al., 1997). The authors also encountered an intense predation on polychaetes by juvenile *P. subtilis*, commensurate to the reduced polychaete levels detected within 20 to 22 days after the start of the present study.

P. subtilis grazing rates on polychaetes increased at higher shrimp stocking densities. This predator–prey effect was particularly noticeable at densities of 15 and 20 shrimp/m^2. In model farming ponds, Allan and Maguire (1992) found comparable declines in the numerical abundance of polychaetes with an increase in *P. monodon* stocking densities. Although in the present study, polychaete population was not depleted at high shrimp stocking densities, mean levels were comparable to the ones found for NFS treatment. This indicated that under increased shrimp stocking densities (i.e., FS_{15} and FS_{20}), artificial feeding could only partly reduce *P. subtilis* predatory potential on polychaetes and poorly enhance their abundance, although in these conditions, larger amounts of nutrients are expected to be produced (Briggs and Funge-Smith, 1994).

Reasons that can account for the low impact of artificial feeding on the overall culture system, include an inefficient feeding programme (e.g., through deficient amounts of formulated food), and food attractiveness. The recognition of polychaetes as an important prey for *P. subtilis*, suggests the use, in aquaculture systems, of feeds with improved attractiveness in order to allow a balance between shrimp feed consumption and polychaete predation. This is important for larger shrimp since a pronounced carnivorous habit becomes more evident (Nunes et al., 1997), possibly making polychaetes more susceptible to shrimp attacks.

Overall polychaete density and biomass in NFS treatments revealed prohibitive polychaete levels when no external food supplies were used (as also found for shrimp final body weights, Table 1), regardless of the shrimp stocking density. Under culture and natural conditions, *P. subtilis* is known to feed on other epifauna and macrobenthos (Stoner and Zimmerman, 1988; Nunes et al., 1997). In the present study, observations of the pond substrate (first 10 to 15-cm layer) showed a scarce occurrence of other potential prey items, although some epiphyte coverage was noticed on the sides of all enclosures. This may have led the species to concentrate its feeding efforts solely on polychaetes and detritus, even when reduced stocking densities were adopted (NFS).

4.5. Polychaete growth interactions with artificial feeding

Artificial feeding influenced polychaete abundance in all enclosures receiving external food supply (i.e., FNS and FS). When exposed to feed inputs, polychaete population size was higher both in terms of density (FNS and FS) and biomass (FNS). Although only a slight sediment organic and nutrient enrichment was found for the pond bottom of these treatments, polychaetes were likely to have taken advantage of external food sources by either feeding directly on fresh pellets or on decomposed food stuffs.

Organic-related polychaete growth responses have been well documented in the literature, particularly for polluted environments (Lewbell, 1985; Ansari et al., 1986; Tsutsumi, 1987). In aquaculture ponds, a feed promoting effect was reported on benthic macroinvertebrates, mainly oligochaetes (Wahab and Stirling, 1991). In shrimp ponds, artificial feeds can form the base of the food chain (Moriarty et al., 1987). It is estimated that only 10 to 15% of the organic carbon and 20 to 70% of the nitrogen and phosphorus in feed are converted to shrimp flesh and removed from ponds at harvest (Briggs and Funge-Smith, 1994; Boyd, 1995), with the remainder organic matter and nutrients deposited on the pond bed. In the present study, remains of uneaten feed in FS enclosures were possibly responsible for maintaining polychaete densities at higher levels when compared to NFS treatment.

The presence of feed in FS enclosures also appeared to have partially relieved, as discussed previously, the predatory impact of *P. subtilis* on polychaetes. Larger amounts of feed, either generated a higher polychaete density (FNS_{15}) or an equal effect in comparison to treatments with lower feed rations (FNS_{20} vs. FNS_5 and FNS_{10}).

This study has shown that *P. subtilis* predation, shrimp stocking density and external food supply are major factors to be considered when establishing sustainable limits for polychaete use as a naturally occurring food source in aquaculture systems. Shrimp stocking density greatly affected polychaete numerical abundance and biomass, while their population patterns appeared to be dictated by other environmental and endogenous cues. Artificial feeding promoted polychaete population growth even in the presence of shrimp, but it was not effective in alleviating *P. subtilis* grazing pressure at higher stocking densities (i.e., 15 and 20 shrimp/m^2). Although the present feeding regimes used could not produce differences in polychaete abundance, the amount and particularly the quality of feed should be more precisely evaluated in their potential to minimise and compensate for shrimp predation impacts on pond macrobenthic fauna. Further investigations in extensive and semi-intensive systems should concentrate efforts on developing management strategies for inoculation and restoration of polychaete populations in shrimp ponds, mainly during the various stages of the growth cycle (e.g., through alternating fencing of strategic pond areas).

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