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REPRODUCTION AND RECRUITMENT OF THE BROWN SHRIMP *Penaeus subtilis* IN THE AMAZON RIVER CONTINENTAL SHELF

Reprodução e recrutamento do camarão-rosa *Penaeus subtilis* na plataforma continental amazônica

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ABSTRACT

This paper analyzes the pattern of the reproduction and recruitment of the pink shrimp *Penaeus subtilis* in the Amazon River continental shelf. Biostatistics samples obtained on board of industrial fishing vessels and in the estuaries of the northeastern state of Para were use in the analysis as well as monthly data on landings processed by commercial category. The sex ratio, for female and male respectively, was 61% to 39%, in the samples of commercial fishery, and 54% to 46%, in the samples of the estuary. The size at first maturity of females was estimated at 142.6 mm. The period of highest intensity of reproductive activity ranges from May to September. The settlement of post-larvae and residence period of juveniles in the estuary occurs with more intensity between June and September and the period of highest intensity of recruitment to the fishing areas begins in September extending until January of the following year. The main period of developing and maturing of the individuals ranges from November to July. It was observed a strong relationship between the hydrological cycle in the region, mainly the flow of Amazon River, and the life cycle of the species.

Keywords: brown shrimp, sexual maturity, reproduction period, juvenile recruitment, Amazon.

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RESUMO

Este trabalho analisa o padrão de reprodução e recrutamento do camarão-rosa Penaeus subtilis na plataforma continental do rio Amazonas. Amostras bioestatísticas obtidas a bordo de embarcações de pesca industrial e nos estuários do nordeste do Pará foram utilizadas na análise, bem como dados mensais sobre os desembarques processados por categoria comercial. A proporção sexual foi de 61% de fêmeas para 39% de machos, nas amostras da pesca comercial, e 54% de fêmeas para 46% de machos, nas amostras do estuário. O tamanho de primeira maturação das fêmeas foi estimado em 142,6 mm. O período de maior intensidade de atividade reprodutiva vai de maio a setembro. O assentamento de pós-larvas e o período de residência dos juvenis no estuário ocorrem com maior intensidade entre junho e setembro e o período de maior intensidade de recrutamento para as áreas de pesca se inicia em setembro, estendendo-se até janeiro do ano seguinte. O principal período de desenvolvimento e posterior maturação dos indivíduos se situa, portanto, entre novembro e julho. Observou-se uma forte relação entre o ciclo hidrológico da região, especialmente a vazão do rio Amazonas, e o ciclo de vida das espécies.

Palavras-chave: *maturidade sexual, período de reprodução, recrutamento juvenil.*

INTRODUCTION

The brown shrimp *Penaeus subtilis* (Pérez-Farfante, 1967) has a wide distribution in the tropical coastal waters of the eastern Atlantic, extending from Cuba to the State of Rio de Janeiro, Brazil (Pérez-Farfante, 1969). In northern Brazil the species supports important industrial fisheries carried out with bottom trawls, especially between the coast of the States of Pará and Amapá, at depths generally ranging between 40 and 80 meters. Industrial landings reached a record 6,900 t of tails in 1987/1988, declined since then mainly due to economic reasons, and in the last five years have oscillated around 1,500 t. Belém, the capital city of the State of Pará, is the main landing port and hosts the processing industry in the region (Aragão; Cintra & Silva, 2004).

Landing oscillations are largely related to stock abundance changes. So the knowledge of penaeidae reproduction dynamics is essential to understand its life cycle, especially issues as stock-recruitment relationships and predictability of recruitment pattern and success (Bauer & Lin, 1994). The complex seasonality of reproductive and recruitment pattern of penaeidae shrimps has been described by several authors and it depends on the species and might be affected by environmental factors including rainfall, temperature and depth, inducing inter-annual changes in timing and duration of the reproductive period in relation to the optimum conditions (Garcia, 1985; Crocos, 1987; Crocos & Van der Velde, 1995; Crocos & Coman, 1997; Leal-Gaxiola *et al*., 2001).

Spawning season for penaeidae shrimps has been determined in previous studies by changes in gonad index or by changes in the percentage of ripe females (Thomas, 1974; Kennedy Júnior & Barber, 1981; López-Martínez *et al*., 2005). These approaches do not consider the effect of large seasonal fluctuation in abundance of adults, and hence numbers of spawners, which are characteristic of penaeidae populations (Crocos & Kerr, 1983).

Studies carried out in the Amazon River continental shelf concerned to *P. subtilis* based on the former criteria suggest reproduction and recruitment throughout the year with two peaks in periods that are not coincidental in the two analysis (Isaac; Dias-Neto & Damasceno, 1992; Cintra; Aragão & Silva, 2004).

The present paper is a comparative review of these studies using fisheries dependent data series from a wider area, combined with samples from the small-scale fisheries at estuaries of the region, as well as monthly data on landings processed by commercial category, in order to more accurately identify the main reproductive period, determine the size of first maturation as well as obtain indicative of the period of greatest intensity of recruitment.

MATERIAL AND METHODS

The shrimp fishery in the North of Brazil is carried out along the area located between Parnaíba River mouth (02º53′ S), in the border of States of Piauí and Maranhão, and the Oiapoque River mouth (04º23′ N), in the border of the State of Amapá and the French Guyana. It is part of an important shrimp fishing ground which extent until the mouth of Orinoco River, covering an area of about 223.000 km^2, known as Guianas-Brazil area (Ibama, 1994).

The industrial fleet operates in three main well defined subareas whose general characteristics are (Aragão *et al*., 2001): Maranhão – located between the Parnaíba River mouth (02º53′ S) and Gurupí Cape (00º53′ S), with a substrate composed of mud and sand and the fishing grounds are close to the coast; Amazonas – situated between latitudes of 00º50′ N and 02º30′ N, mainly in the coast of Pará, with a substrate composed mainly of mud; Amapá – located between the latitudes 02º30′ N and 04º23′ N (Orange Cape), in the coast of Amapá, where hard and rocky grounds predominate.

In recent years the fleet has concentrated its operations mainly between the latitudes 00º15′ S and 04º50′ N, correspondent to the Amazon River continental shelf (Amazonas and Amapá area), at depths ranging mainly from 40 to 80 m.

The data used in this analysis result from monthly samples collected onboard of commercial vessels operating in the industrial shrimp fishing on the continental shelf of the Amazon River from 2000 to 2004. Monthly samples were also taken in the estuaries in the Northeastern state of Pará from 1997-2005, as well as monthly data on landings processed by commercial category from 1982-2006.

The sampling on board was carried by scientific observers, mainly in the subareas of Amazonas and Amapá. Random samples composed of at least 300 individuals were drawn from each of the trawls sampled during the trips, recording the geographical position (latitude and longitude) and depth of the operation. The total length was measured with the individuals gently stretched over an ichthyometer covered with a special scaled paper, with the tip of the rostrum touching the headboard. The paper was then stuck to the nearest millimeter with a kind of needle at end of the telson. The sex of individuals was identified and the gonad development stage of females was assigned according to a scale described in the next section.

Monthly samples in the estuaries were collect through experimental fishing carried out with hand operated trawl nets, from 1996 to 2007. For each trawl it was registered the duration, the water temperature and salinity and the catch was transported to analyses at laboratory where it was registered sex, total length (mm) and total weight (g) of the individuals.

The data on the monthly composition of the industrial landings by commercial categories are registered for each trip and were collected at the processing plants in Belém for the period from 1980 to 2006. In general shrimps are assigned to 10 different commercial categories, according to the individual weight/length of the tail. Each category corresponds to a number of tails with an approximated uniform weight in pounds and the main categories are: 10/15; 16/20; 21/25; 26/30; 31/40; 41/50; 51/60; 61/70; 71/90; 91/120. The relative composition of the landings by commercial categories allows identifying the periods when smaller shrimps are caught as an indicative of the recruitment to the fishery.

The analysis of gonadal development and reproductive activity is limited to the samples from the industrial fishing and refers only to adult females. Males were not examined due to some difficulties to handle with the maturation stages for both sexes on board.

Sex ratio

Initially, the proportion of individuals by sex we estimated pooling the data for all years on a monthly basis by interval length of 10 mm for the samples of the industrial and experimental fisheries in the estuary. A chi-square test (χ^2) was conducted to assess the difference between the monthly and annual proportions between sexes for each habitat separately.

Gonadal development

The gonadal maturation of penaeid shrimp females is characterized by changes in the morphology and staining intensity of the ovaries making it possible to identify with accuracy in the field work the stage of gonadal development. Several authors have described similar morfocromatic scales for identifying the gonadal stages (King, 1948; Thomas, 1974; Quintero & Gracia, 1998). In the present study, the maturation stages of females were classified according to a scale proposed by Porto and Santos (1996) in four stages:

Stage I (undeveloped or spent) – translucent or slightly whitish filiform ovaries (immature) or flaccid, brownish, occupying a small volume in the region of cephalothoraxes not reaching the abdomen;

Stage II (early development) – ovaries more stout, pale yellow or yellow-green, smooth edges and surfaces or with a little roughness;

Stage III (late development) - bulky ovaries, with rough surface and edges, strongly greenish color, extending the length of the abdomen, reaching the telson;

Stage IV (ripe stage) – bulky and completely developed ovaries, extending along the dorsal part of the abdomen, reaching the telson, with rough surface and edges, dark green color, granulation of the eggs distinguished by the naked eye.

For purposes of identification of the period of higher incidence of immature and mature females, individuals with undeveloped ovaries and early development (stages I and II) were grouped as immature. Those in development and in advanced stage (stages III and IV) were grouped as mature (Thomas, 1974; Bauer & Lin, 1994; López-Martínez *et al*. 2005).

Size at first maturation

The size at first maturation was estimated by the accumulated relative frequency plot of mature females (P_{L_t}) versus the total length (L_t). A logistic curve was fitted to the data via nonlinear regression using the software *R*. The logistic model is described by the following equation (King, 2007; Quinn & Deriso, 1999):

$$P_{L_t} = \frac{1}{1 + \exp(a + bL_t)}$$

Where (P_{L_t}) is the proportion of mature females (stage IV), L_t is its respective total length (mm), *a* and *b* are parameters to be estimated.

The size at first maturation is determined as the length where the proportion of mature females (P_L) corresponds to 50% of the logistic curve ($L_{50\%}$), which is considered a good indication of the size of the individuals during the large-scale spawning period in the population. The minimum size at first maturity is estimated as the length where the proportion of mature females (P_L) corresponds to 1% of the logistic curve ($L_{1\%}$). Individuals with size below ($L_{50\%}$) are considered juveniles or sub-adults (Crocos & Kerr 1983; Crocos 1987).

Reproductive activity and pattern

The breeding season of penaeid has often been determined by assessments of the gonadal maturation index and the percentage of mature females (Thomas 1974; Kennedy Júnior & Barber, 1981; López-Martínez *et al.* 2005). A more accurate measure of female reproductive intensity named "population fertility index" (PFI), was proposed by Penn (1980) and Crocos and Kerr (1983). This index is estimated taking into account also the individual fecundity, given by the contribution in terms of the number of eggs, and the abundance of mature females, namely the population spawning size calculated by the expression:

$$PFl = \frac{1}{n} \sum_{i=1}^{n} p * a * f$$

Where represents the percentage of females in stage IV, the numerical abundance of females, the number of eggs produced and the number of individuals in the area.

Courtney, Dredge and Masel (1989) also used the abundance of adult females in each month and the female relative proportion in different length classes to determine the PFI as the egg production is influenced by their size. The relationship between ovarian weight and carapace length in early maturing females (stage III) and mature (stage IV) is given by:

$$Ovarian\ weight = aC_L^{\,b}$$

Where $C_L^{\,b}$ is the carapace lenght (mm).

The proportion of females preparing to spawn (stages III and IV) in each month also influences population fecundity and, therefore, this ratio should be incorporated into the index:

$$PFl = n * p * \sum_{f_m}^{m_S} s * (aC_L^{\ b})$$

Where *n* represents the adult females standardized abundance, *p* represents the proportion of mature adult females (stages III and IV) and *s* is the proportion of adult females in the size classes between the size at first maturity and maximum size in the sample.

Although estimates of the individual fecundity of females of *P. subtilis* are not available for the present analysis, some inferences regarding the period of greatest reproductive intensity were made considering the monthly accumulated relative frequency of females with sizes larger than the size at first maturity and the rate of monthly abundance of the population as whole throughout the year.

Rate and pattern of recruitment to the estuary

Due to the lack of data to determine an appropriated index of abundance, we tried to identify the period of highest intensity and pattern of recruitment in the estuary taking into account the average length variation throughout the year as well as the composition of the length frequency distributions of individuals of the samples of all years grouped on a monthly basis. An obvious limitation of this procedure is not to consider the intra-annual variations.

The length frequency distributions inspection allows detecting distinct age groups of individuals, by identifying modes along the months (Bauer & Lin, 1994). The modes identification and decomposition were carried out using the Bhattacharya method through the program FiSAT II (Gayanilo-Júnior & Pauly, 1997). A multinomial distribution was also adjusted to the monthly frequency distributions, using the criterion of maximum likelihood as indicative of better fit and the results of the two methods compared and matched. Finally, the likely period of greatest reproductive activity of the species was matched with the arrival of post-larvae and the residence time of juveniles in the estuaries.

Rate and pattern of recruitment to the fishery

The period and intensity of the recruitment to the fishery was initially determined by evaluating the proportion of juvenile females by subarea in monthly samples collected onboard of the industrial fleet (Bauer & Lin, 1994). A general conclusion about the recruitment pattern, considering both sexes, was then obtained from the relative share of the smaller monthly commercial categories in the industrial processing (Bauer & Lin, 1994; Ehrhardt & Legault, 1999) combined with the catch rate in kilograms per day at sea of the smaller shrimps (Garcia; Lemoine & Lebrum, 1985).

The analysis was performed on a monthly basis with data for all years grouped into three main categories: (1) small – comprising the commercial categories "51/60" to "91/120"; (2) medium – comprising the categories "26/30" to "41/50"; (3) large – comprising the categories "10/15" to "21/25". The monthly relative share of each group was determined as the periods with higher catch of smaller individual. Only the processing data for the years when closed season was not established, from 1980-1986 and from 1998-2000, were considered in this analysis.

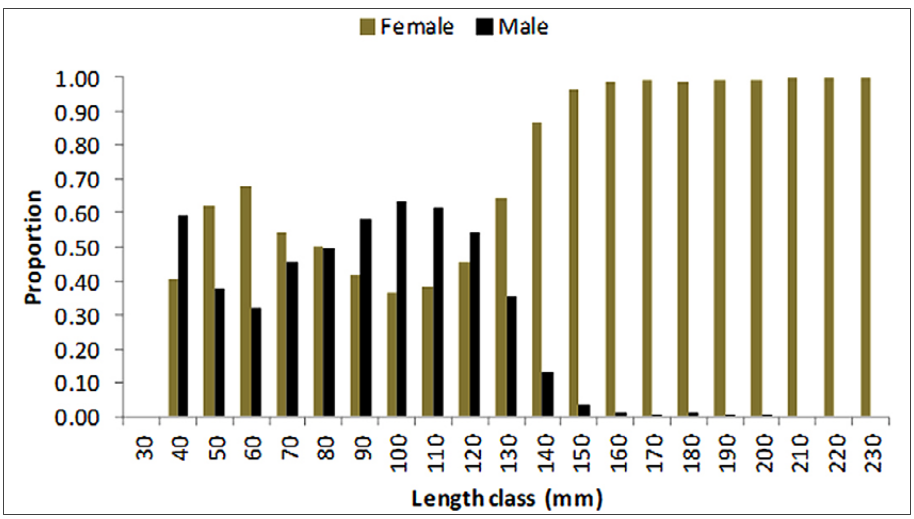
RESULTS

Sex ratio

As females reach much larger sizes than males, the sex ratio in the upper length classes in the samples from the industrial fishery was uneven, with a complete dominance of females in length classes above 160 mm, along the months. Below this value, the sex ratio shows oscillations, with a predominance of males in some intervals of length classes and females in others (Figure 1).

These oscillations are due to the fact that males in the smaller length classes are, probably, in a phase of life where they growth faster and have reached larger sizes than females, being relatively more vulnerable to trawling. In classes above 130 mm, the females begin to predominate, for their growth rate is relatively high, reaching larger sizes and being more vulnerable to the trawl net.

Figure 1 – Proportion of sexes of *P. subtilis* caught by the industrial fishery in the Amazon River continental shelf, from 2000 to 2004



In general, the annual average sex ratio in samples from the industrial fishery showed a highly significant difference, with females accounting for 61% of the catches, versus 39% of males (X^2= 13513,67; gl = 1; p < 2.2e-16). Along the months the sex ratio fluctuated around the annual pattern, always showing a predominance of females. It should be noted, however, that in December and January the relative participation of males increases, coinciding with greater participation of smaller individuals in the catches (Table I).

There is also a predominance of females (54%) in the juvenile population in the estuary (Table II). The difference between sexes, however, is numerically lower than in industrial catches for the smaller sizes in the estuary and changes in the vulnerability of the individuals, which should contribute to an increased catch of males.

Table I – Number and monthly sex ratio of *P. subtilis* in the industrial fisheries carried out in the Amazon River continental shelf, from 2000 to 2004

	Number		Sex ratio (%)	
Months	Female	Male	Female	Male
Jan	2.348	1.797	0,57	0,43
Feb	6.465	3.683	0,64	0,36
Mar	19.750	12.678	0,61	0,39
Apr	18.479	11.031	0,63	0,37
May	21.781	14.908	0,59	0,41
Jun	18.214	10.690	0,63	0,37
Jul	31.679	20.091	0,61	0,39
Aug	17.538	12.322	0,59	0,41
Sep	21.862	14.933	0,59	0,41
Oct	13.764	8.946	0,61	0,39
Nov	4.177	2.362	0,64	0,36
Dec	1.913	1.602	0,54	0,46
Total	177.970	115.043	0,61	0,39

Table II – Number and sex ratio in monthly samples of *P. subtilis* in the estuaries in the NE of the state of Pará, from 1997 to 2005

	Number		Sex ratio	
Month	Female	Male	Female	Male
Jan	2.789	2.312	0,55	0,45
Feb	2.983	2.613	0,53	0,47
Mar	2.888	2.070	0,58	0,42
Apr	2.686	2.283	0,54	0,46
May	3.185	2.378	0,57	0,43
Jun	2.840	2.090	0,58	0,42
Jul	5.331	4.071	0,57	0,43
Aug	3.862	3.641	0,51	0,49
Sep	4.594	3.922	0,54	0,46
Oct	5.097	4.164	0,55	0,45
Nov	4.107	3.242	0,56	0,44
Dec	3.825	3.196	0,54	0,46
Total	14.572	12.371	0,54	0,46

Gonadal development

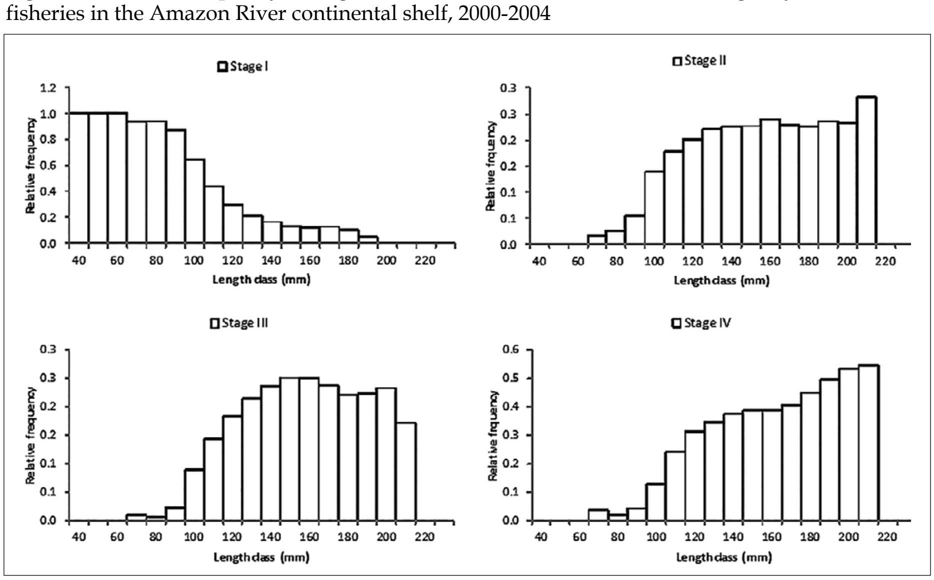
The frequency of the different maturation stages of females per length class is shown in Table 3 and the Figure 2 presents the relative frequency of occurrence and evolution of the four maturation stages of females by length class. Actually, mature females are found at low proportions from classes as small as 60-70 mm with the frequency of occurrence increasing gradually with the increase in size, reaching higher levels from 140 mm, when females reach full sexual maturation, and at the maximum level in the upper classes.

It is observed in Figure 2 that the frequency of females in stage I (immature) declines sharply from the class of 100-110 mm, while the stage II (early maturation) begins to increase at about the same proportion from this class, stabilizing after the 130 to 140 mm class. The frequency of occurrence of stage III (developing) resembles somewhat a bell-shaped curve and the frequency of occurrence of stage IV (mature) is positively asymmetric, reflecting the high proportion of mature and older individuals.

Table III – Frequency of gonadal maturation stages of females of *P. subtilis* in the industrial fisheries carried out in the Amazon River continental shelf, 2000-2004

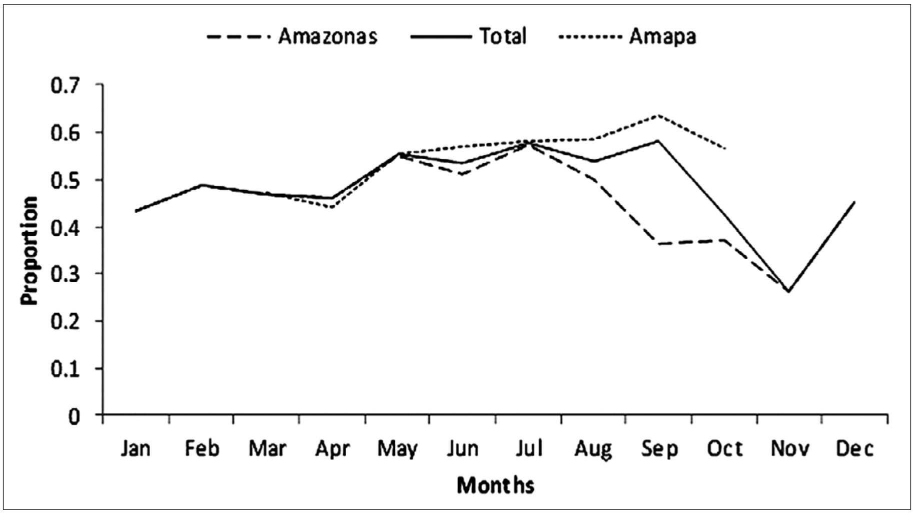
	Absolut frequency					Relative Frequency			
Class	I	II	III	IV	Total	Stage I	Stage II	Stage III	Stage IV
40	3				3	1,00	0,00	0,00	0,00
50	18				18	1,00	0,00	0,00	0,00
60	89				89	1,00	0,00	0,00	0,00
70	389	7	4	15	415	0,94	0,02	0,01	0,04
80	1.988	57	13	42	2.100	0,95	0,03	0,01	0,02
90	4.928	318	131	250	5.627	0,88	0,06	0,02	0,04
100	6.745	1.453	928	1.319	10.445	0,65	0,14	0,09	0,13
110	7.398	2.996	2.436	4.097	16.927	0,44	0,18	0,14	0,24
120	7.366	4.918	4.488	7.642	24.414	0,30	0,20	0,18	0,31
130	6.262	6.354	6.144	9.995	28.755	0,22	0,22	0,21	0,35
140	4.797	6.618	6.892	10.967	29.274	0,16	0,23	0,24	0,37
150	3.412	5.759	6.341	9.781	25.293	0,13	0,23	0,25	0,39
160	1.961	3.819	3.972	6.191	15.943	0,12	0,24	0,25	0,39
170	979	1.765	1.834	3.128	7.706	0,13	0,23	0,24	0,41
180	306	643	634	1.283	2.866	0,11	0,22	0,22	0,45
190	52	272	257	572	1.153	0,05	0,24	0,22	0,50
200		116	116	265	497	0,00	0,23	0,23	0,53
210		31	19	60	110	0,00	0,28	0,17	0,55

Figure 2 – Relative frequency of stages of maturation of females *P. subtilis* caught by the industrial fisheries in the Amazon River continental shelf, 2000-2004



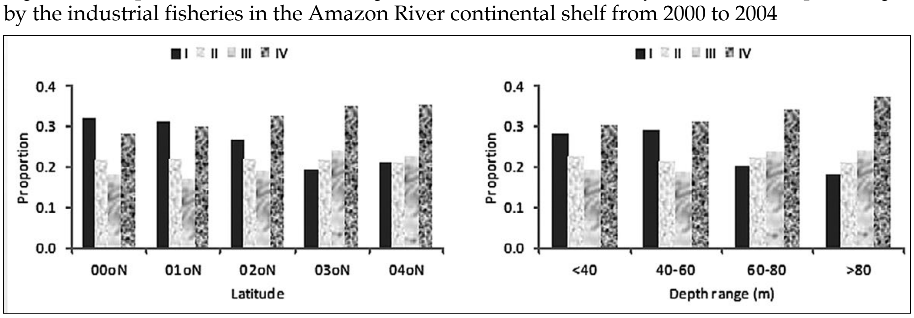
The monthly proportion of mature females (stages III and IV) in the catches is higher from May to August in Amazonas subarea and from May to October in Amapá subarea, being higher from May to September in the whole area, as can be seeing in Figure 3.

Figure 3 – Relative frequency of female maturation of stages III and IV of *P. subtilis* caught by the industrial fisheries in the Amazon River continental shelf



Along the months of the year there is a clear temporal and spatial size stratification, with the largest mean sizes in the second and third quarters of the year and at greater depths and latitudes (Aragão; Pretere-Júnior & Cintra, 2017). Considering this stratification and the ratio of mature individuals per month (Figure 3) and per latitude and depth range (Figure 4), it can be concluded that female maturation occurs concurrently with migration of pre-adult population to high sea, which will intensify from of October/November, as well as the displacement of adults towards the Northwest areas.

Figure 4 – Proportion of maturation stages of females of *P. subtilis*, by latitude and depth, caught by the industrial fisheries in the Amazon River continental shelf from 2000 to 2004



Size at first maturity

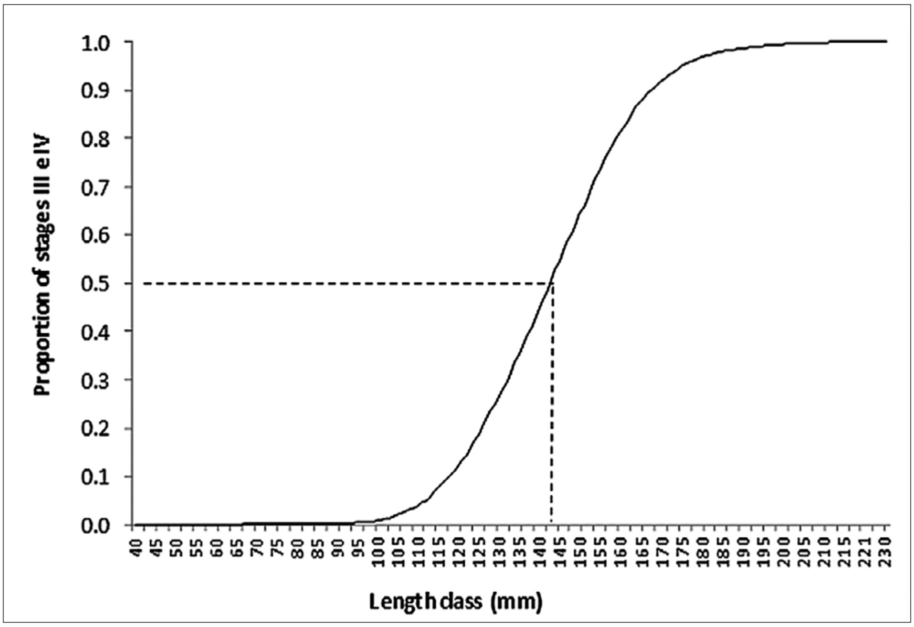
The size at first maturity was determined by nonlinear regression, adjusted by the least squares method with numerical algorithmic (Hilborn & Mangel, 1997). The equation below describes the curve of sexual maturation for *P. subtilis* in the Amazon continental shelf, represented by the logistic curve, and its estimated parameters:

P_Lt =1/(1+exp(12,37931-0,086797*Lt)) standard error = 0,007867 (168 df)

Where P (L_t) is the proportion of mature females (stage IV) and L_t is its respective total lenght (mm).

From this equation and the criteria suggested by Crocos and Kerr (1983), the mean size at first maturation of *P. subtilis* in the Amazon River continental shelf was estimated to be 142.6 mm while the minimum size of first maturity was estimated at 89.7 mm (Figure 5).

Figure 5 – Proportion of ovaries of *P. subtilis* in stages III and IV caught by the industrial fisheries in the Amazon River continental shelf, from 2000-2004



Reproductive activity and reproduction pattern

The proportion of females with sizes larger than the size at first maturation along the months is shown in Figure 6, being higher from May to September. Although it is also observed a relatively high proportion of mature individuals in September, it should be noted that much of the data are originated from the subarea of Amapá, where the proportion of adults is always greater. In relation to the intensity of reproductive activity, however, it should be taken into account that the level of abundance of the population in this period is already quite low, being much higher from March to August (Ehrhardt; Aragão & Silva, 1999).

Although it is not possible, based on the available data, to determine objectively the index of population fecundity (PFI), as defined by Penn (1980) and Crocos and Kerr (1983), the combination of these results allow to infer that there is only one long main pulse of higher intensity of reproductive activity, with indications that this occurs in the area as a whole, from May to August/September.

Index and settlement pattern of post-larvae

A mixture of sizes is always observed at the estuary, due to the continued reproduction and long main pulse, but mean lengths are larger in the second half of the year and the length frequency distribution suggest the existence of two distinct groups from July/ August on (Figure 7), suggesting a pattern of settlement in the estuary.

Figure 6 – Female proportion of *P. subtilis* with sizes higher than the mean size at first maturation classes caught by the industrial fisheries in the Amazon River continental shelf, 2000-2004

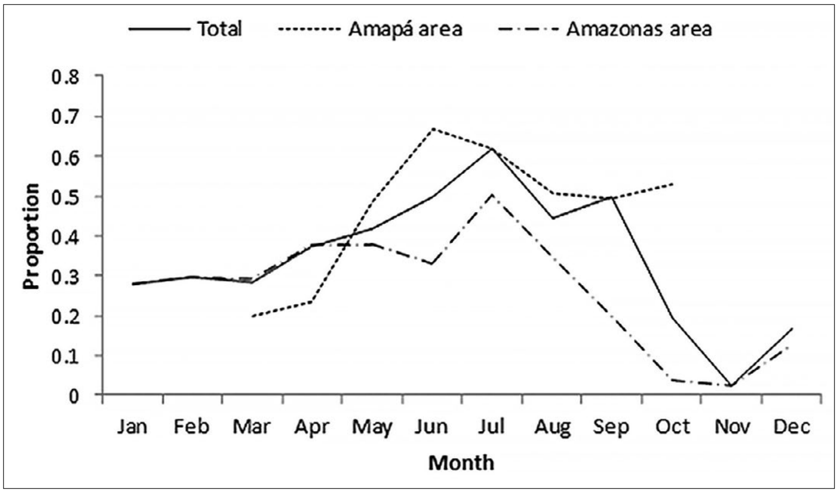
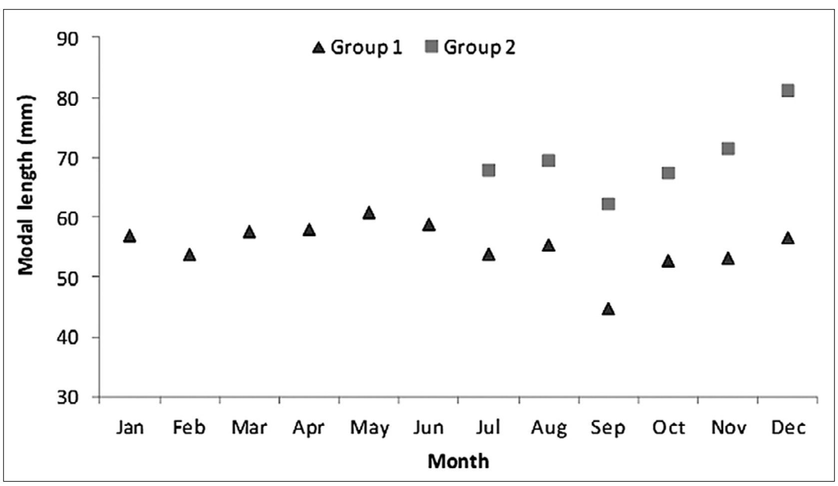


Figure 7 – Modal monthly sizes (mm) in the length frequency of *P. subtilis* caught in the estuaries in the NE of the State of Pará



One group would be composed by individuals originated from settlement in previous months which have already reached larger sizes and are starting the migration phase for the high seas being more vulnerable to trawling in this period. The other group would be composed of smaller individuals from more recent settlements, which gradually start to become vulnerable to trawling.

This may also be indicative that from August begins a period of greater abundance of residents in the estuary as a result of settlements that began in May/June and become more intense over the months, peaking between September and November and then decreasing until January of the following year. We can assume then that although the entry of post-larvae in the estuary occurs throughout the year, a higher input intensity from the end of the first half and the first months of the second half allows identifying the two groups.

As the period of higher reproductive intensity occurs between May and September and, according to Garcia (1988), the larvae settle in the estuary about 20 to 30 days after hatching at sea, larger amounts of post-larvae would be actually entering the estuary from

June/July, when the waters of the rivers of the region begin to fall, and in the following weeks the juveniles would have reached sufficient size to begin to be caught by trawls. So the period of greatest settlement of post-larvae and juveniles residence in the estuary would be from June/July to September/October.

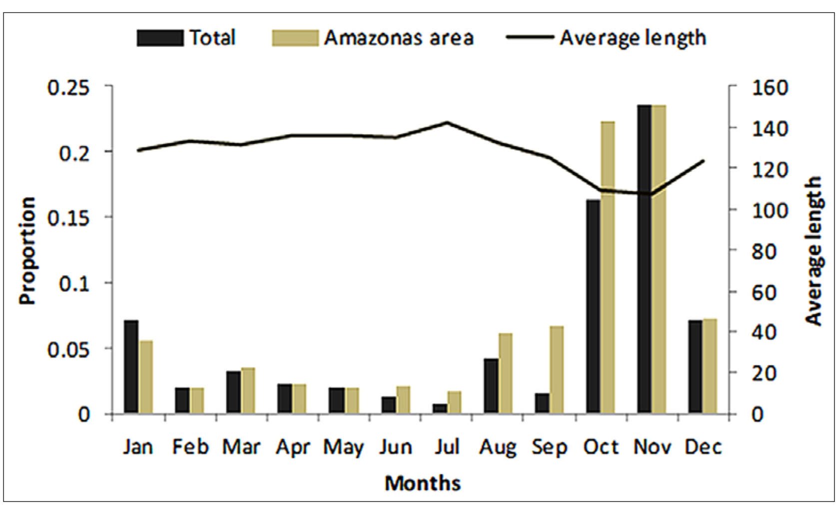
Recruitment to the fishing grounds

Consistent with the previous findings, the analysis of the samples of commercial fisheries and data on industrial processing clearly identified a period of higher intensity of recruitment to the fishing area. Considering that the minimum size at first maturity of females was estimated in 89.7 mm, it is assumed that the share of the population recruited to the fishing areas is composed of young and immature individuals below this size.

Garcia (1985) suggests that, in most cases, the penaeid shrimp begin to appear in the catches on the high seas less than a month after performing the migration towards the ocean. Ehrhardt and Legault (1999) reached similar conclusions, suggesting that sub-adults shrimps of the species *F. duorarum* are recruited to the fishery in the Bay of Florida in sizes that correspond to the commercial category of 67+ tails per pound, 4-5 months after the larval stage.

Taking into account these criteria, Figure 8 shows that the participation of immature individuals in the industrial fisheries begins to rise from August/September, accentuates in October and November, and continuing relatively high in December and January, in the area as a whole but with greatest intensity in the subarea of the Amazon, where it also starts earlier.

Figure 8 – Relative proportion and average monthly length of juveniles *P. subtilis* caught by industrial fisheries in the Amazon River continental shelf, 2000-2004



The relative share of the commercial categories at the industrial processing, considering an average lag of 20-25 days between catches and landings, shows similar results, with an increasing participation of commercial categories “small” from September/October to January/February of the next year, decreasing thereafter. The share of commercial categories of class “large” behaves exactly opposite, while the proportion of the category “medium” are relatively stable, but slightly higher between April/May and August/September (Figure 9).

Figure 9 – Average monthly proportion of commercial categories of *P. subtilis* caught by the industrial fishery in the Amazon River continental shelf, 1982-2006

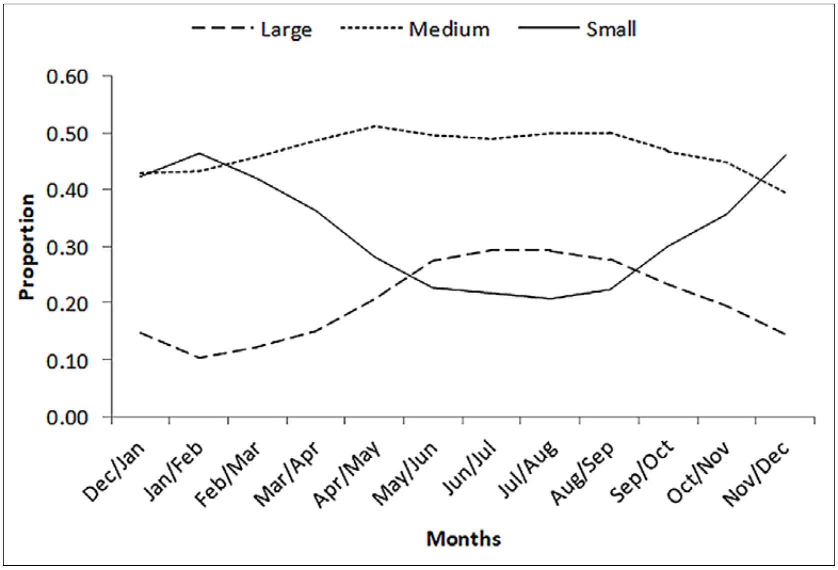
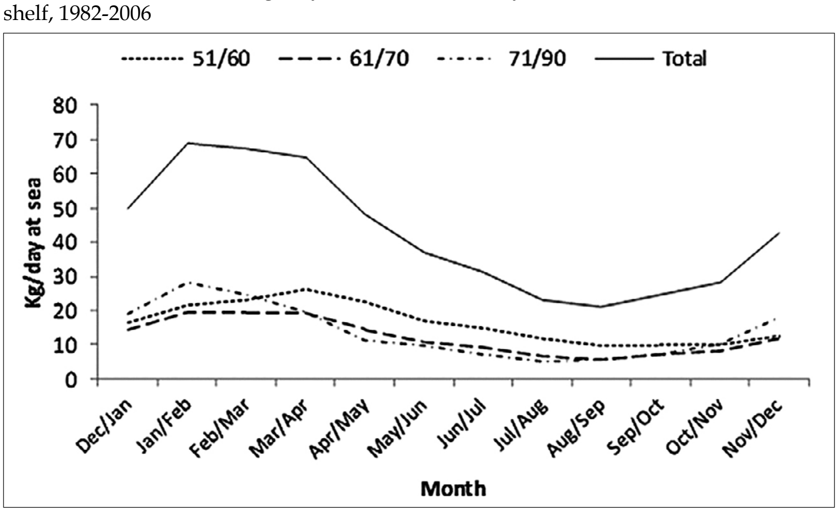


Figure 10 shows that the catch rates of small individuals, considering the aforementioned gap between landings and catches, reach the lowest values in July/August, increasing rapidly thereafter. This means that the capture of juveniles is increasing since then, reaching its peak in December/January. However, the arrival of juveniles to fishing areas began to intensify between two to three months before, as is seen in Figure 8, and individuals are now slightly larger and heavier, increasing its trawling vulnerability and the catch rates in weight.

Figure 10 – Catch per unit of fishing effort (kg days-at-sea^{-1}) of the commercial categories "small" of the *P. subtilis* caught by the industrial fishery in the Amazon River continental shelf, 1982-2006

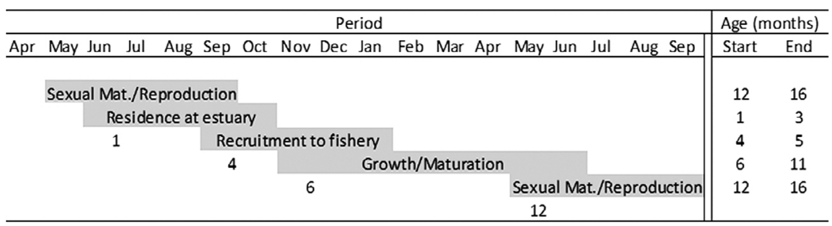


The previous results suggest that the shrimp begin to migrate from the estuary to the sea in August/September intensifying from September to December. On the other hand, if they live for 3 to 4 months in the estuary, the period of greatest post-larvae settling occurred between June/July and October, approximately one month after the period of higher reproduction intensity that takes place between May/June and August/September. This is an average pattern as environmental conditions may vary from year to year and also the recruitment.

Life cycle stages

The conclusion is that the life cycle of *P. subtilis* in the Amazon River continental shelf is characterized by periods of greater intensity with the following sequence of phases: reproduction from May/June to August/September; migration and residency in the estuary from June/July to September/October; recruitment to fishing areas in September/October to December/January; growth and sexual maturation from November/December to May/June (Figure 11).

Figure 11 – Diagram of the life cycle phases of *P. subtilis* in the Amazon River continental shelf



DISCUSSION

Sex ratio

Sexual dimorphism is common in penaeid, with females growing faster and reaching larger sizes than males (Pérez-Farfante, 1969; Gillet, 2008). Thus, individuals of the same size have different growth rates depending on their sex and size. As a result, on the catches of the industrial fishing, females have strong predominance in larger length classes while fluctuations occur in the sex ratio in smaller length classes. Throughout the year, however, the proportion of females in the catches from industrial fishing is always higher than that of males, although from October to January there is predominance of small sized males. In the estuary, where only young individuals are captured throughout the year, the difference between the proportion of males and females is numerically smaller.

In general, the sex ratio in this study, 61% for females and 39% for males in samples of the industrial fisheries, is not different from the ratio calculated by other authors. Cintra, Aragão and Silva (2004) found an almost equal proportion, while Isaac, Dias-Neto and Damasceno (1992), based on samples taken in 1986, found an annual mean of 62% for females and 38% for males. In the estuary, a ratio almost constant throughout the year, around 54% for females and 46% for males, shows also the predominance of females, however, as these are mostly juveniles, the predominance is less pronounced.

Gonadal development

Trends of relative participation of different maturation stages showed a similar pattern as detected by Crocos and Kerr (1983) for the banana prawn (*P. merguiensis*) in the Gulf of Carpentaria, Australia. Mature females of *P. subtilis* in the Amazon River continental shelf were found in all months of the year, but from May to August the proportion is higher in relation to immature individuals. The presence of mature females in the samples, throughout the years, is evidence of a continuous reproduction with an annual peak of higher intensity. The increasing proportion of mature females, with increasing depth and the displacement of individuals in a northwesterly direction, as they grow and become adults, show the timing of the migration to the high seas and the growth and maturation of individuals.

Size at first maturity

The minimum size of first maturation with which individuals begin to ripen for the first time was estimated at approximately 90 mm while the first maturation size was estimated to be 142.6 mm, when individuals would be at an age of about 10 to 12 months. However, the proportion of mature females already reaches high levels from the class of 120 mm. One must take into account some differences between the minimum size and the size at first maturation estimated for *P. subtilis* in the present analysis and those found by some authors in the Amazon River continental shelf.

Porto and Santos (1996) estimated at 117.5 mm the minimum size at first maturation for females and 91.25 mm for males. Isaac, Dias-Neto and Damasceno (1992) detected that 50% of females start their sexual maturation with 110 mm and that 50% of females are mature when they reach 140 mm. Cintra, Aragão and Silva (2004) estimated in 126.5 mm the size where 50% of females are in stage II, considering this as the minimum size of sexual maturation and estimated as 135.5 mm the size where 50 % of females are mature, considering it the mean size of first sexual maturation.

The observed differences could be attributed to the greater representativeness of the samples analyzed here with much larger sizes and wider spatial and temporal coverage, as well as the criteria used here to define the size of first maturation.

Pattern of reproduction and reproductive activity

A continuous reproduction is common in penaeid, as evidenced by simultaneous presence of shrimps with ovaries in more than one stage of maturation along the year (Thomas, 1974), but different patterns can be observed depending on the species and/or area of occurrence, being common the occurrence of one or two major peaks of reproduction, where one of them is predominant (Crocos & Kerr, 1983; Cha *et al*., 2002; Courtney; Dredge & Masel, 1989). Some species of penaeid present more than one period of higher intensity, as females spawn when reaching the minimum size of maturity at about 6 months of age, and spawn again with more intensity when they are one year old (Pauly; Ingles & Neal, 1984; Garcia, 1988; Crocos & Coman, 1997). Kennedy Júnior and Barber (1981) observed that *P. duorarum* spawn continuously on the continental shelf of the Northeast Florida, but with a major peak in the late spring and summer.

In the Gulf of California, the coffee shrimp, *F. californiensis*, showed high interannual variability during the breeding season, with two distinct patterns. In one, reproduction occurs throughout the year and in the other two major peaks were observed, one from March to May, and another of lesser intensity, from October to November. The two patterns show the environment effect, particularly the temperature over the reproductive dynamics of short living species. Continuous spawning is favored by warmer waters, probably due to the influence of El Niño, while spawning occurs in pulses in colder water (Leal-Gaxiola *et al*., 2001).

On the Amazon River continental shelf, Sudepe (1985) reports a period of greater intensity of reproductive activity of *P. subtilis* in the second half of the year, while Isaac, Dias-Neto and Damasceno (1992) indicate two periods, a longer one, from March to July, and a shorter one, from September to October. Cintra, Aragão and Silva (2004) found a higher proportion of mature females in the catch from February to April and July to August, suggesting that the major peaks of reproduction occur in these periods.

Periods mentioned above were based mainly on the proportion of mature females throughout the months of the year and do not take into account the fertility rate of the population, which peaks correspond to the period of mass reproduction. If one takes into account the abundance of the population, the period of greatest relative proportion of females in the catches and the greater fecundity of females of medium and large sizes, it can be concluded that there would only be a period of greater reproduction intensity from May to August/September.

If samples in Subarea Amapá are prevalent in the second half of the year, however, we can conclude, erroneously, that there would occur a second peak of greater reproduction intensity, in September/October. Actually, this shows only that the larger adult shrimp, which are increasingly present in the subarea of Amapá, continue to spawn, but the effective result of reproduction as a whole is of little significance due to the sharp decline in the abundance of population during this period.

It is worth noting that in the case of the North region, where the abiotic cycle is governed by the Amazon River hydrological cycle (Filizola *et al*., 2006), the assumptions of a reproductive cycle more intense from May/June to August/September are strengthened because, although there are changes in environmental conditions over the years, the overall pattern is essentially the same and there is no justification for more than one peak of highest intensity of reproduction.

Interannual variations in the reproductive dynamics of aquatic organisms are often reported, showing the adaptive capacity of species in response to extreme changes in environmental conditions, resulting in the displacement or fluctuations in the intensity of spawning (Pitcher & Hart, 1982), but no records of alterations of the penaeid modal pattern of reproductive peaks were recorded in the literature.

Recruitment index and pattern

The complex life cycle of penaeid shrimps, especially their short longevity, rapid growth, high natural mortality, highly variable recruitment, and overlapping generations, making it difficult to identify patterns of recruitment resulting in a population with complex composition by size and age (Garcia, 1988; Crocos & Coman, 1997). However, as a consequence of the reproduction pattern, several authors suggest one or two annual peaks of greater recruitment intensity.

Diop *et al*. (2007) reported a main breeding peak of the white shrimp (*L. setiferus*) in the northern Gulf of Mexico, between May and August and the recruitment of post-larvae occurring from June to September towards the estuaries of Louisiana, where they remain and grow during a period of three months. The migration of young and/or sub-adults to deep water always starts with decreasing the salinity in the estuary and covers the months from September to November and the progressive movement towards deep water continue as the shrimp grows, matures and after spawning.

In Sonda de Campeche in the southern Gulf of Mexico, the main recruitment period of the pink shrimp (*F. duorarum*) occurs between July and November, when the salinity tends to decrease and the sea surface temperature (SST) is warm and stable. The period of lower recruitment intensity ranges from December to June, while the SST and salinity reach their lowest values and begin to rise during this period (Ramirez-Rodrigues; Arrenguín-Sanches & Lluch-Belda, 2003).

Ehrhardt and Legault (1999) concluded that the recruitment of the pink shrimp (*F. duorarum*) in the Bay of Florida occurs throughout the year, but there are one or more seasonal peaks, albeit the peaks magnitude and monthly position changes over of decades. These changes can be explained by a variable breeding population resulting in different levels of egg production, by environmental changes in nursery areas, which modulate a supply of eggs almost constant, or a combination thereof.

On the Amazon River continental shelf, there is evidence that the intensity of recruitment of the brown shrimp (*P. subtilis*) to the fishing areas is also variable, although it occurs continuously throughout the year, peaking between the last quarter of year and the beginning of the first quarter of the following year, being modulated by rainfall. Thus, being in a population consisting of a main generation, the gradual decrease in abundance throughout the year is marked and accentuated by the fishing mortality (Ehrhardt; Aragão & Silva, 1999). In the present analysis, the intensity and pattern of recruitment were assessed based on the proportion of immature individuals in samples of the commercial fishing and the participation of categories "small" in the industrial processing confirm the earlier findings.

CONCLUSION

The annual mean proportion of females of brow shrimp (*P. subtilis*) in samples collected on board of industrial vessels was 62% and 38% of males. The proportion of females was also higher than that of males along the year. The ratio of males and females varied according to the length range. Males predominate in lower and intermediate length classes and females predominate markedly in the upper classes.

In the estuaries samples the predominance of females over the males in the juvenile strata is also evident, with proportions of 54% and 46% respectively. The difference between the proportion of females and males, however, is much lower than in industrial catches, a consequence of the smaller sizes found in the estuary, which should contribute to higher catches of males.

The minimum size of first maturation of *P. subtilis*, where 1% of the individuals is mature, was estimated at 89.7 mm, while the average size of first sexual maturity, wherein at least 50% of individuals are mature in the population was estimated in 142.6 mm.

The period of highest reproductive intensity of *P. subtilis*, on the Amazon River continental shelf is probably between May and August/September, which is considered the main breeding period of the species.

The post-larvae settlement and the period of residence of juveniles in estuarine areas, with suggested duration of 3 to 4 months should occur with greater intensity from July to October.

Between 3 and 4 months after the larval period, the sub-adults migrate to the sea and about a month later they are vulnerable and recruited to fishing, being the period of greatest recruitment intensity between September of the year and January of following year.

The stages of the life cycle of the pink shrimp (*P. subtilis*) in the Amazon River continental shelf are characterized by periods of greater intensity. The following sequence is suggested: reproduction from May/June to August/September; migration and residence in the estuary from June/July to August/October; recruitment to fishing grounds from September/October to November/January; development and sexual maturation from November/December to March/April.

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