

# Population biology of *Palaemon (Palaeander) northropi* Rankin, 1898 (Crustacea, Decapoda, Palaemonidae) in a tropical South American estuary.

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**ABSTRACT: Population biology of *Palaemon (Palaeander) northropi* Rankin, 1898 (Crustacea, Decapoda, Palaemonidae) in a tropical South American estuary.** The population biology of the palaemonid shrimp *Palaemon (Palaeander) northropi* was studied for one year in the Ubatumirim estuary, Ubatuba, state of São Paulo, Brazil. Sampling was carried out monthly from April 2003 through March 2004. The shrimp were collected with a sieve from under the bordering vegetation, during ebb tide. All specimens were measured for carapace length, and allocated to 17 size classes. Based on analyses of the allometric growth of some body dimensions (carapace length vs. pleura length), all females smaller than 4.41 mm carapace length were considered juveniles. Based on the body structures analyzed, in males the growth pattern was not differentiated between juveniles and adults, and therefore the size at sexual maturity of males could not be determined. Only salinity showed a significant correlation with the abundance of shrimp at the sampling site. The size-frequency distribution of *P. northropi* was unimodal. Median lengths of males and females were 3.77 ( $\pm$  0.49) mm and 4.46 ( $\pm$  1.19) mm carapace length, respectively. Males predominated in the population, with an overall sex-ratio of 1.39:1. Oviparous females occurred only during winter and spring. Shrimp were not obtained during summer, because of low salinity in the estuary at that season; the shrimp migrated to other areas near the sea, where the salinity was higher. The estimated individual mean fecundity was 165  $\pm$  12.3 eggs per female; the smallest oviparous female was 4.49 mm in carapace length. Because some size classes were not collected in this study, further studies are needed to improve understanding of the dynamics of this population of *P. northropi*.

**Key-words:** Allometry, population structure, sex ratio, fecundity.

**RESUMO: Biologia populacional de *Palaemon (Palaeander) northropi* Rankin, 1898 (Crustacea, Decapoda, Palaemonidae) em um estuário tropical sul-americano.** A biologia populacional de *Palaemon (Palaeander) northropi* foi investigada durante um ano no estuário do Rio Ubatumirim, Ubatuba (SP), Brasil. As coletas foram realizadas mensalmente, de Abril de 2003 a Março de 2004. Os camarões foram coletados com peneira, próximo à vegetação marginal, no período de maré baixa. Baseando-se nas análises do crescimento alométrico de algumas dimensões corporais (comprimento do cefalotórax vs. comprimento da pleura), todas fêmeas com tamanho de comprimento do cefalotórax (CC) menor que 4.41mm foram consideradas juvenis. Baseado nas estruturas corporais analisadas, machos não apresentaram um padrão de crescimento diferencial entre juvenis e adulto, portanto, o tamanho da maturidade sexual dos machos não pôde ser determinado. Apenas o fator salinidade apresentou correlação significativa com a abundância de camarões no local de coleta. O comprimento do cefalotórax dos camarões foi registrado e estes foram agrupados em 17 classes de tamanho. A distribuição de frequência por classes de tamanho indica que a população apresenta unimodalidade. O tamanho médio de machos e fêmeas foi de 3,77 ( $\pm$ 0,49) mm e 4,46 ( $\pm$ 1,19) mm de comprimento de cefalotórax, respectivamente. Houve uma predominância de machos na população, que foi expressa por uma razão sexual de 1,39 : 1. Fêmeas ovígeras ocorreram no inverno e primavera. Os camarões não foram encontrados durante o verão devido à baixa salinidade no estuário. Ocorreu uma migração dos camarões para outras áreas próximas ao mar, onde a salinidade é mais alta. A fecundidade individual média obtida foi de 165  $\pm$  12,3 ovos por fêmea e a menor fêmea ovígera coletada tinha 4,49mm de CC. Estudos mais detalhados são necessários para um melhor entendimento da dinâmica da população de *P. northropi*, considerando que algumas classes de tamanho não foram detectadas neste trabalho.

**Palavras-chave:** Alometria, estrutura populacional, razão sexual, fecundidade.

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## Introduction

During the evolutionary history of the Palaemonidae, different developmental and reproductive patterns were evolved. As a result, this family has a wide geographical distribution and its representatives occupy diverse habitats including fresh, estuarine, and sea waters (Holthuis, 1952). According to Bond-Buckup & Buckup (1989), the three most species-rich genera of this family in Brazil are *Macrobrachium* Bate, 1868; *Palaemonetes* Heller, 1869; and *Palaemon* Weber, 1795.

*Palaemon* (*Palaeander*) *northropi* Rankin, 1898 is a marine palaemonid shrimp, easily found in intertidal sand and mudflat pools, on reef pools during ebb tide, and in the lower portions of estuaries, near mangrove areas (Anger & Moreira, 1998; Coelho, 1963/4). According to Holthuis (1952), *P. northropi* is found along the eastern coasts of the Americas from the Bermudas to Uruguay (in Brazil, from the states of Ceará to Santa Catarina). The few published studies of this species deal mainly with its population biology. Anger & Moreira (1998) studied the growth and some aspects of the reproduction of a population at São Sebastião, state of São Paulo, Brazil; and Coelho (1963/4) reported observations of its ecology in the state of Pernambuco, Brazil.

Studies on population dynamics provide the foundations for improved knowledge of the ecological establishment of populations, focusing on certain aspects such as seasonal abundance, population density, frequency distribution, dispersion, and demographic dynamics (Negreiros-Fransozo et al., 1999). In a biological environment, the non-sessile animal populations show a dynamic behavior that changes over time. Changes in the population size raise complex ecological questions, which are better understood when species-habitat relationships are investigated (Silva & Chacur, 2002).

The lack of consistent data concerning the population biology of *P. northropi* was the main reason for the present study. We examined the population biology of the population living in the Ubatumirim estuary, Ubatuba, state of São Paulo.

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## Material and methods

The investigation was carried out monthly from April 2003 through March

2004, in the Ubatumirim estuary, Ubatuba, São Paulo (23°20'54" S; 44°53'48" W). The seasons of the year were considered as follows: autumn in April, May, and June; winter in July, August, and September; spring in October, November, and December; and summer in January, February, and March. One collector working for 60 minutes caught the shrimps with sieves (approximately 2-mm mesh size) among the bordering vegetation. The marginal vegetation was composed of grasses of the genus *Spartina* Schreb. and mangrove trees such as *Avicennia* Gaertn. F., *Laguncularia* (L.), and *Rhizophora* (L.). The area sampled was about 10 m<sup>2</sup> along the riverbank.

All the specimens obtained were identified, stored in appropriately labeled glass containers, and preserved in 70% ethanol. In the laboratory, several morphometric dimensions were measured by use of a stereomicroscope with a calibrated ocular micrometer, to the nearest 0.01 mm. Carapace length (CL) was defined as the shortest distance from the rear margin of the eye orbit to the median posterior edge of the carapace. Total body length (TBL) was measured from the rear margin of the eye orbit to the base of the median distal telson spine. Abdomen length (AL) was defined as the difference between TBL and CL. Pleura length (PL) was measured from a lateral part of the second abdominal pleura to the other. Propodus length (PRL) was taken from the proximal border to the tip of the fixed finger of the propodus of the second pereopod until the posterior region. To determine the presence of an appendix masculina, the second pleopod was dissected off and inspected under a dissecting microscope. This procedure allowed identification of the minimum body size at which individuals could be sexed (termed "minimum sexable size," MSS). Because smaller individuals were morphologically similar to young females, these were counted as NS (not sexable, individuals with CL less than 2.1 mm), distinguishing these from reliably identified males and females. Theoretically, juvenile males below the MSS that were erroneously "sexed" as females may have introduced a statistical error into our morphometric data for female shrimp. However, it was assumed that this bias did not significantly change the morphometric or other regressions given herein, because juveniles smaller than the MSS probably show no significant

sexual dimorphism, and this size group constituted only a small fraction of our material overall (22 individuals).

The relative growth and morphological sexual maturity of *P. northropi* was evaluated through allometric analyses (Huxley, 1950), with CL used as the independent variable. The relationships obtained were linearized to the form  $\log Y = \log a + b \log X$ , where  $Y$  = independent variable,  $X$  = dependent variable, and  $a$  and  $b$  are constants. The computer software Mature II (Somerton, 1980) was used to delimit growth phases, for females only, in those cases where fitting more than a single regression line significantly decreased the total residual sum of squares. The significance of the linear regression equations was tested by Analysis of Variance (ANOVA), and the equality of regression coefficients was compared by Student's *t*-test (Zar, 1996). The fit of the data to the equations was analyzed by the determination coefficient ( $r^2$ ) in association with a *t*-test ( $\alpha = 5\%$ ).

The water temperature was recorded monthly with a mercury thermometer, the salinity was measured by means of a hand refractometer, and the precipitation data were obtained from the Brazilian Meteorological Monitoring System, in order to test the correlation of the abundance of individuals with the median values (point measurements) of these physical factors (Spearman correlation,  $p < 0.05$ ).

The shrimp were separated according to the following demographic groups: males, females, ovigerous females, and not sexable. Next, the shrimp were allocated to 17 size classes with amplitude of 0.5 mm, determined by Sturges' equation (Sturges, 1926). Student's "*t*" test was used to compare the size between males and females ( $\alpha = 5\%$ ). The Kruskal-Wallis test was used to compare the population median size among seasons, complemented by the Dunn test ( $\alpha = 5\%$ ) (Zar, 1996).

A  $\chi^2$  test for goodness of fit ( $\alpha = 5\%$ ) was performed to assess whether the sex ratio in the population, in each season, departed significantly from 1:1 (Sokal and Rohlf, 1995). The proportion of sexes by size class was evaluated in the same way.

The proportions of ovigerous females and juveniles in each season were compared by statistical software MANAP (Curi & Moraes, 1981), which analyzed differences between and within multinomial proportions ( $p < 0.05$ ).

For fecundity analyses, the eggs were carefully removed from the pleopods and counted under a stereomicroscope, by means of a manual counter. All the eggs were counted, independent of the stage of development of the embryos, but they were first classified as follows: (initial) more than two-thirds of the egg volume occupied by yolk, no eye pigments visible, embryo showing little or no differentiation; (intermediate) phase of eye formation and embryonic differentiation (segmentation, development of appendices), heartbeat visible but often irregular, yolk occupying more than one-third of egg volume; (final) eye fully developed, heartbeat regular, differentiation of appendages in final phase, yolk occupying less than one-third of egg volume. The relationship fecundity ( $F$ ) / carapace length (CL) was expressed by a potential equation ( $F = a CL^b$ ), where  $F$  = number of eggs per female, CL = carapace length, and  $a$  and  $b$  are constants.

## Results

A total of 508 specimens of *P. northropi* were obtained, of which 283 were males, 203 females, and 22 not sexable. The sizes varied from 2.5 to 7.4 mm and 2.1 to 9.6 mm (CL) of males and females, respectively.

Table I shows the results for allometry of different body parts. Males showed isometry for the relationship PL vs. CL, whereas juvenile and adult females showed positive allometry for the same relationship. Relative growth analysis of this relationship indicated that the puberty molt occurs when females reach 4.4 mm (CL) (Fig. 1). Fig. 2 corresponds to the size at which 50% of females are morphologically mature. Males did not show a structure that indicated allometric growth from which the sexual maturity could be determined. Therefore, we present the size at sexual maturity only for females. The relationships AL vs. CL and TBL vs. CL showed exactly the same pattern of growth, with juvenile and adult females showing isometric growth and negative allometric growth, respectively; whereas males showed positive allometric growth for both relationships. For the relationship PRL vs. CL, males showed isometric growth, whereas juvenile and adult females showed positive allometric growth and isometric growth, respectively.

The water temperature at the sampling site varied from 21.97 to 26.83 °C ( $\pm 2.44$ ).

Table 1: Result of the regression analysis of the morphometric data for the population of *Palaemon (Palaeander) northropi* in the Ubatumirim River, with carapace length (CL) as an independent variable.

Variable	Category	N	Power function ( $Y = aX^b$ )		$r^2$	t (b=1)	Allometry
			a	b			
AL	JF	82	2.570	0.982	0.887	0.47	0
	AF	97	3.118	0.847	0.701	2.73 *	-
	TM	265	2.530	1.057	0.842	2.04 *	+
TBL	JF	82	4.187	0.994	0.939	0.22	0
	AF	97	4.731	0.904	0.798	2.08 *	-
	TM	265	4.073	1.058	0.903	2.77 *	+
PL	JF	82	0.386	1.147	0.893	3.37 *	+
	AF	99	0.260	1.421	0.768	5.38 *	+
	TM	266	0.463	1.047	0.818	1.56	0
PRL	JF	82	0.442	1.236	0.769	3.06 *	+
	AF	97	0.590	1.050	0.540	0.56	0
	TM	267	0.559	0.982	0.592	0.35	0

(\*) Significant by student's t test ( $\alpha = 0.05$ ); AL= Abdomen Length; TBL= Total Body Length; PL= Pleura Length; PRL= Propodus Length; JF= Juvenile Females; AF= Adult Females; TM= Total Males; N= Number of shrimps;  $r^2$ = Determination coefficient; 0= isometry; + = positive allometry; - = negative allometry; A and B, constants.

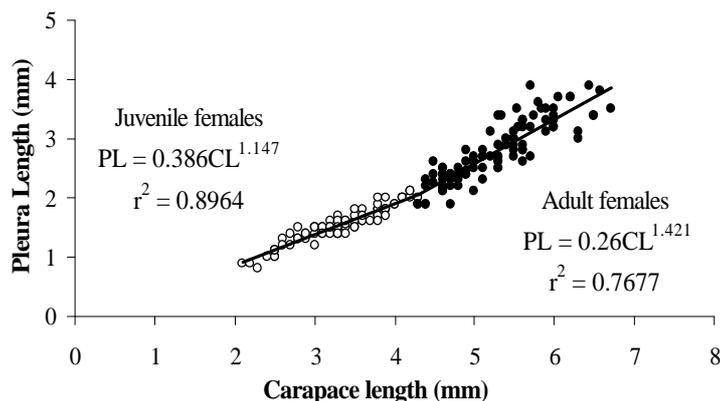


Figure 1: *Palaemon (Palaeander) northropi*. Morphometric relationship between pleura length (PL) and carapace length (CL) ( $p < 0.05$ ). ○ indicates juvenile females and ● indicates adult females.

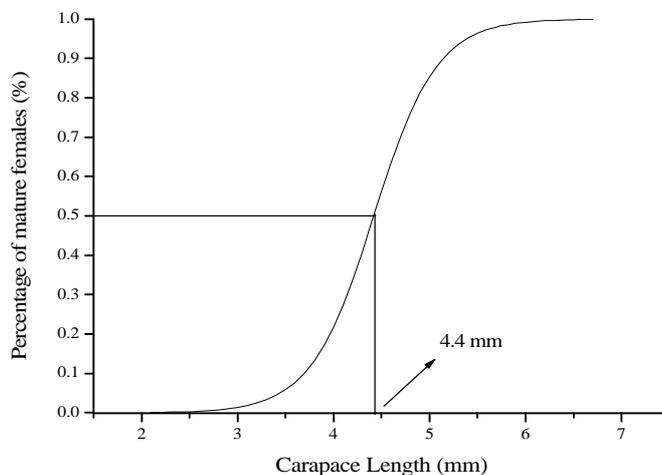


Figure 2: *Palaemon (Palaeander) northropi*. The logistic equation indicating the point at which 50% of females are mature.

Neither temperature nor precipitation showed any correlation with the species abundance in the area. However, salinity did show a significant correlation (Spearman correlation,  $p < 0.05$ ). The median salinity, in each season, is presented in Table II, as well as the shrimp abundance during the year, by seasons and precipitation.

The size-frequency distributions for

each season and during the year are shown in Fig. 3. The median size of carapace length of males ( $3.77 \pm 0.49$  mm) was smaller than that of females ( $4.49 \pm 1.19$  mm) ( $p < 0.05$ ). According to the size-frequency distribution, the average population size was similar in autumn and winter; the individuals obtained in spring were larger than the previous two seasons ( $p > 0.05$ ).

Table II: *Palaemon (Palaeander) northropi*. Abiotic factors in the sampling area in the Ubatumirim River.

Seasons	Salinity	Number of prawns	Pluviometric accumulative data (mm)
autumm	$9.7 \pm 8.58$	115	59.2
winter	$16.7 \pm 7.61$	247	73.4
spring	$3.8 \pm 2.32$	146	365.2
summer	$3.3 \pm 4.50$	0	419.2

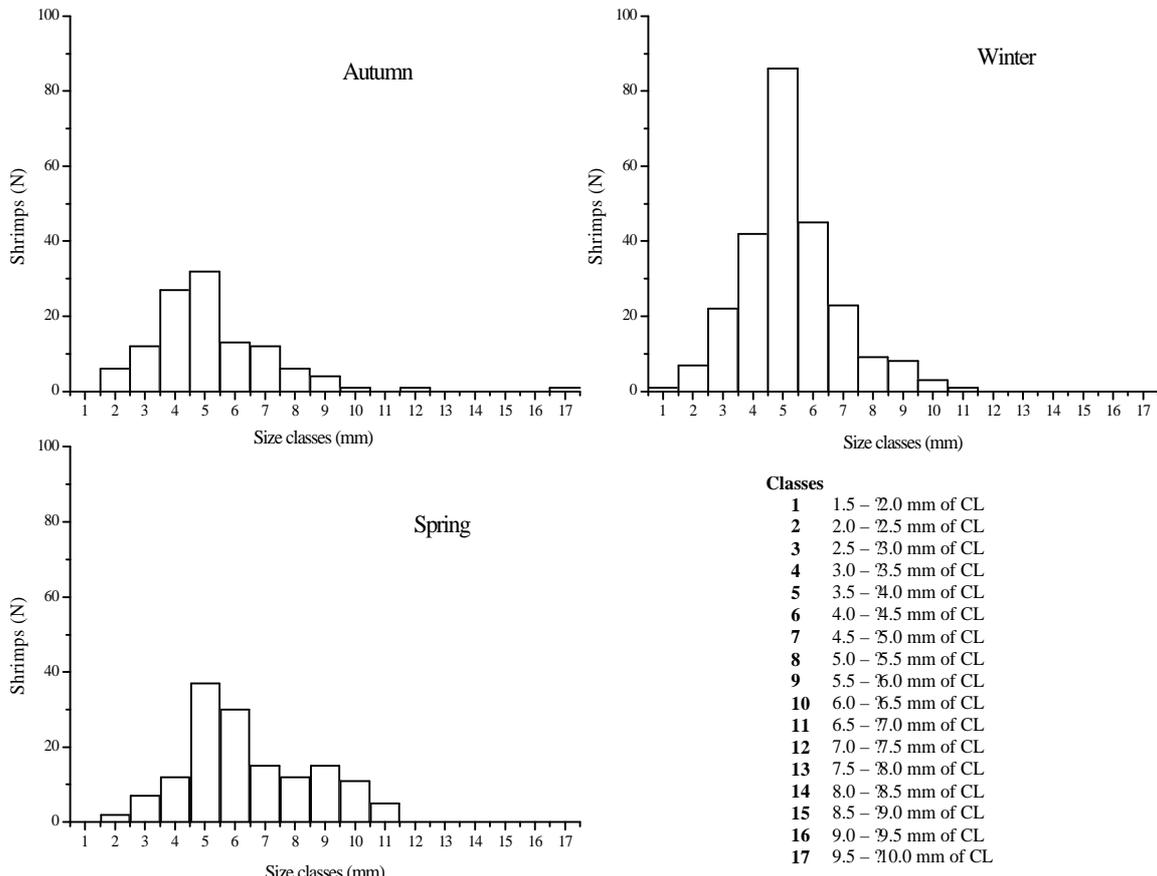


Figure 3: *Palaemon (Palaeander) northropi*. Size-frequency distribution by seasons of the year (carapace length, CL, in mm).

The overall sex ratio was skewed toward males (1.39:1). When the number of shrimp was analyzed for each season, the sex ratio did not differ from 1:1 in spring ( $\chi^2 = 0.105$ ;  $p > 0.05$ ) and in autumn  $\chi^2 = 2.53$ ;  $p > 0.05$ ); whereas in winter there was a

statistical difference between males (70%) and females (30%). The proportion of males by size classes is shown in Fig. 4.

Ovigerous females were found only in winter and spring, totaling 28 (13.7%) of 203 females collected. All 28 ovigerous females



(1995). Although females attained larger sizes, their growth rate was lower than that of males (Tab. 1). The investment of energy in reproduction inhibits growth by reducing molt increment and extending the intermolt period (Hartnoll, 1985). It is expected that female growth will be reduced during the reproductive period, because a proportion of available energy is used to develop the oocytes (Wickins & Beard, 1974).

The allometric relationship PL vs CL clearly showed a sexual dimorphism for *P. northropi* (positive allometry for juvenile and adult females, and isometry for males). This is related to the different functions that the second abdominal pleura perform in each sex (Hartnoll, 1974). In females, the second abdominal pleura will substantially increase the growth of the incubation chamber of the eggs, with the first and the third abdominal pleurae, protecting them with the pleopods (Nagamine & Knight, 1980). The isometry found in males reflects the low importance of the growth of the pleura for this sex, in which its function is simply structural.

The estimated size at morphological sexual maturity of females (4.4 mm CL) is close to the size of the smallest ovigerous female sampled (4.49 mm CL), indicating that the determination of the size at the onset of maturity by allometric analyses can be appropriately used for carideans. The estimated value is similar to those found by Anger & Moreira (1998) for *P. northropi* and *P. pandaliformis* at São Sebastião, São Paulo, Brazil. However, size at the onset of egg production can vary among conspecific populations (Wenner et al., 1985). The difference in body size at the onset of sexual maturity in a variety of conspecific populations is largely due to phenotypic plasticity (Mashiko, 2000). A single analysis of relative growth, nevertheless, cannot be used to determine exactly the beginning of the sexual maturity, because sometimes morphological maturity does not occur at the same time as physiological maturity. Thus, a more detailed analysis of the gonads would define the point at which the shrimp are able to reproduce (functional maturity).

In some crustacean species, the chelipeds are an important mechanism of distinction between sexes and their morphological maturation, such as those of the fiddler crabs *Uca* and the American lobster *Homarus americanus*; however, this

does not seem to occur in *P. northropi*. The estimated relationship PRL vs CL (positive allometry for juvenile females and isometry for adult females and males) did not show an evident sexual dimorphism, nor did it demonstrate remarkable differences between the growth rates of juveniles and adults. Males did not have a structure that indicates a different growth pattern between juveniles and adults, and so the size at sexual maturity of males could not be determined. The chelipeds in males and females of *P. northropi* are equal in form and function, and are used for food searching and handling, aggression and defense, and grooming (Bauer, 2004).

The close positive correlation between salinity and shrimp abundance through the seasons found for *P. northropi* in the present study, corroborates with the findings of Coelho (1963/4) and Teixeira & Sá (1998) for *P. northropi* on the northeast coast of Brazil. *P. northropi* cannot spend much time in fresh water, being a marine species (Freire et al. 2003). It seems to find more favorable conditions for its development in locations with high salinities, although, according to Freire et al. (2003), it has a strong osmoregulatory capacity, perhaps similar to that of ancestral, marine palaemonids.

Sexual dimorphism in size is pronounced in *P. northropi*, with females reaching larger sizes than males. Guerao et al. (1994), Anger & Moreira (1998), and Cartaxana (2003) observed the same pattern in other species of the genus *Palaemon*. Females reach a greater total length than males as a function of differences between the sexes in growth rates and patterns of population structure. According to Sanz (1987), the differences in the growth rates between males and females of *P. elegans* are related to the gonad development, which in females reaches a higher stage of development than in the male. There is a reduction in energy investment for growth of males, which may decrease predation risks (Berglund, 1981). It may not be adaptive to diminish female body size beyond a certain limit, since egg number in each brood depends on cephalothorax size (Berglund, 1981). However, in *Palaemonidae*, the opposite (males reaching higher sizes than females) has also been observed, e.g., in some species of *Macrobrachium* (Anger & Moreira, 1998; Mossolin & Bueno, 2003; Fransozo et al., 2004; Mantelatto & Barbosa, 2005). This opposite pattern, according

to Mantelatto & Barbosa (2005), is a function of domination by males over females, as well as pre-adult males, during the copulation process. According to Mantelatto & Barbosa (2005), another hypothesis is the relationship with the hierarchy in favor of male size that can interfere with the growth of submissive individuals in the population. Thus, females of the genus *Palaemon* produce more tissue in the ovaries than males do in the testes (Sanz, 1987). This effect should occur also in species of *Macrobrachium*, but here it may be overcompensated by stronger sexual dimorphism in other organs, namely, by disproportionate growth of chelae in large males (Anger & Moreira, 1998). In short, *P. northropi* showed similar growth patterns to some other *Palaemon* species, such as *P. xiphias*, *P. pacificus*, and *P. gravieri* (Kim, 2005). Nevertheless, their growth coefficients and other parameters can change significantly with latitude and local environmental situations.

According to Fisher (1958), natural selection favors the 1:1 proportion, but following birth, certain factors may cause an imbalance in the expected ratio. Mortality and growth influence males and females differently, more than any other factors such as nutrition, habitat, and seasons (Wenner, 1972). In some cases, they determine the predominance of one sex throughout the stages of development. In the present study, although males of *P. northropi* predominated in the population as a whole (1.39:1), in the larger size classes the females outnumbered the males. The proportion of males in the different size classes showed an anomalous pattern, as described by Wenner (1972), in which this ratio differed in intermediate classes, favoring one sex (males), and in the larger classes favoring the opposite sex (females). Wenner (1972) assumed that the factors causing this anomalous pattern could be attributed to one of five interpretations: longevity factor, differential migration, differential mortality, differential growth rates, and sex reversal. Kim (2005) found the same pattern in a population of *P. gravieri*, and he attributed the sex ratio skewed toward females in the higher size classes to mortality of males after mating with females. For *P. northropi* in the Ubatumirim estuary, differential growth rates between sexes seem to be the best explanation for the anomalous pattern of the

sex ratio. The predominance of males in the total number of shrimp collected has also been observed in other palaemonid populations, such as *P. adspersus* and *P. squilla* by Berglund (1981) and *M. borellii* by Collins (2001). Thus, the higher proportion of males (1.39:1) in the population studied can be considered as a reproductive strategy of *P. northropi*.

The size-frequency distribution of the shrimp was unimodal overall throughout the year. Díaz & Conde (1989) suggested that this kind of distribution indicates a population in equilibrium, with continuous recruitment and constant mortality. The result of the comparison of the median sizes of the individuals of the population among seasons shows that larger shrimp were present in spring, which was also the season with the highest frequency of ovigerous females. However, it cannot be confirmed that the present population was in equilibrium, because during summer *P. northropi* were absent from the collecting area, and also no individual was found in certain size classes between 8.0 mm and 9.5 mm (CL).

It also could not be determined whether the reproduction of *P. northropi* is seasonal, based only on the presence of ovigerous females in winter and spring, because juveniles were collected in all three seasons when shrimp were obtained, which suggests continuous recruitment. The absence of *P. northropi* in summer may be related to the low salinity in the estuary because of intense rains during that period. The population probably migrated to shallow waters near the coastal zone, where the salinity is higher. In an experiment by Moreira & McNamara (1984), the early zoeal stages of *P. northropi* had higher survival rates in salinities from 21 to 35 ‰. The larvae of *P. northropi* are stenohaline, and can survive for only a few hours in fresh water. Spawning may have occurred in summer, and the population migrated to insure survival of the larvae. This phenomenon requires further investigation.

The number of eggs produced by crustaceans varies widely (Sastry, 1983). The estimated fecundity for *P. northropi* in the Ubatuba region in this study was lower than that found by Anger & Moreira (1998) for a population of the same species at São Sebastião (SP), and also lower than the fecundity observed for most other marine-estuarine palaemonid species (Tab. III). This

Table III: Comparison of mean fecundities in marine and estuarine caridean shrimps.

Species	Egg number (mean value $\pm$ standard deviation)	Author
Palaemon (Palaeander) northropi	165 $\pm$ 62.7	Present study
Palaemon (Palaeander) northropi	172 to 418	Anger & Moreira, 1998
Palaemon (Palaeander) northropi	395.23	Corey & Reid, 1991
Palaemonetes pugio	109.62	Corey & Reid, 1991
Leander tenuicornis	452.08	Corey & Reid, 1991
Periclimenes americanus	247.33	Corey & Reid, 1991

is related, mainly, to environmental adaptations, variations in animal size, and the geographical location of the species (Mantelatto & Fransozo, 1997). Some shrimp had considerably fewer eggs than did most of the others, although they had the same carapace length. Egg loss during netting or subsequent handling may cause egg loss. Sanz (1987), studying *P. elegans*, attributed the egg loss to multiple spawning in just one reproductive cycle. According to O'Brien & Van Wyk (1985), aquatic parasites are major factors in egg loss in different groups of decapods. However, such parasites have not been found in ovigerous females of *P. northropi*, which suggests that aquatic parasites are not a factor reducing fecundity. Thus, other factors such as natural loss (i.e., abortion, contact of eggs with substrate) and any potential change in the incubation period may contribute to variability in fecundity (Oh et al., 2002). In this population, the size range of ovigerous females was too small. Consequently, fecundity showed only a weak correlation with size ( $r^2 = 0.5268$ ).

Further studies in the sampling locale and in nearby areas such as the sublittoral zone and rocky intertidal should be developed, to improve understanding of the ecology of *P. northropi*.

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