

POPULATION ECOLOGY OF THE PLANKTONIC SHRIMP *Lucifer faxoni*
BORRADAILE, 1915 (CRUSTACEA, SERGESTOIDEA, LUCIFERIDAE)
OF THE SOUTHEASTERN COAST OF BRAZIL

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ABSTRACT

Luciferid shrimps have short life spans and a rapid turnover of generations, engage in sequential spawning, and protect their eggs during incubation. This study investigates the ecology of *Lucifer faxoni* Borradaile, 1915 in the littoral zone, Ubatuba region, São Paulo. Sampling was conducted monthly from July 2005 to December 2006 using a Renfro net trawled over a distance of 50 m for a total sampling effort of 50 m² at each station. Nine stations were sampled, ranging from 1 to 15 m deep. Three stations each were grouped into zones 1, 2 and 3 (Z1, Z2 and Z3). Monthly values of salinity, temperature and rainfall were recorded at each station. The pre-buccal somite length (SL) of each specimen was measured. The results showed that in shallower zones (Z1 and Z2), 6306 individuals were captured, whereas in the deeper zone (Z3), 3808 specimens were captured, but no significant differences in SL was detected between the specimens from Z1 and Z2 and those from Z3 (ANOVA, p=0.25). The abundance of shrimps did not differ significantly between seasons (Tukey's test, p=0.02) except in the spring. The sex ratio differed significantly over the seasons (χ^2 , p<0.05). The results were closely associated with environmental factors with respect to the spatial and seasonal distribution of *L. faxoni*. Rainfall affected salinity directly, and contributed to the displacement of these shrimps to deeper areas.

RESUMO

Este estudo analisa a ecologia de *Lucifer faxoni* Borradaile, 1915 em Ubatuba, São Paulo. Os indivíduos foram coletados mensalmente de julho de 2005 a dezembro de 2006, com uma rede de Renfro, arrastada por uma distância de 50 m, totalizando um esforço amostral de 50 m² em cada ponto de coleta. Nove pontos foram amostrados, variando de 1 a 15 m de profundidade. Cada 3 pontos foram agrupados em 3 zonas (Z1, Z2 e Z3). Os valores de salinidade, temperatura e pluviosidade foram registrados mensalmente em cada transecto. Os espécimes foram medidos quanto ao comprimento do somito pré-bucal (SL). Os resultados mostram que nas zonas mais rasas (Z1 e Z2) foram coletados 6306 indivíduos, enquanto que na mais profunda (Z3) obteve-se 3808 espécimes, não havendo diferença estatística entre as zonas (ANOVA, p=0.25). A abundância não diferiu estatisticamente entre as estações do ano (Tukey, p=0.02), exceto para a primavera. Em todas as estações amostradas, o sex ratio diferiu estatisticamente (χ^2 , p< 0.05). Os fatores ambientais aqui analisados apresentaram relação estreita com a distribuição espaço-temporal de *L. faxoni*. A pluviosidade influenciou diretamente a salinidade, que provocou o deslocamento dos camarões *L. faxoni* para áreas mais profundas.

Descriptors: Abundance, Population structure, Ecologic distribution, South Atlantic, Decapoda.

Descritores: Abundância, Estrutura populacional, Distribuição ecológica, Atlântico Sul, Decapoda.

INTRODUCTION

According to Costa et al. (2000), the genus *Lucifer* Thompson, 1829, includes only two species that occur along the Brazilian coast: *Lucifer faxoni* Borradaile, 1915, and *L. typus* Milne-Edwards, 1837. *L. faxoni* occurs throughout the western Atlantic Ocean, with its northern limit in Nova Scotia, Canada, and its southern limit in the State of Rio Grande do Sul, Brazil. This species exhibits a planktonic habit, occurring from depths of 6 to 55 meters, but is usually found in coastal waters (D'INCAO, 1997). *L. faxoni* also has a short life span and high growth rates, engages in sequential spawning and protects its eggs during incubation (LEE et al., 1992). This species is not pleopodal like other decapods but incubates its eggs under the thoracic somites. Few studies have investigated this species, and most studies have focused on the occurrence of the *Lucifer* genus (OMORI, 1977; D'INCAO, 1997; COSTA et al., 2000). Specific studies on *L. faxoni* have investigated its geographical and/or ecological distribution (BOWMAN; MCCAIN, 1967; HARPER JR, 1968; TROOST, 1975; ALVAREZ, 1985; SANKARANKUTTY; BARCA, 2000; FERNANDES et al., 2002; PASCUAL et al., 2002). López (1966) reported that *L. faxoni* is the most frequent decapod in planktonic collections.

The relationship among environmental factors and the abundance of penaeoidean shrimps have been studied by several authors. Costa et al. (2005 a,b; 2007) emphasized the importance of parameters such as salinity, temperature and sediment texture, in habitat selection by commercially exploitable penaeid shrimps such as *Xiphopenaeus kroyeri* Heller, 1862 and *Artemesia longinaris* Bate, 1888. Luciferid shrimps exhibit an epipelagic habit, remaining close to the substrate during the day (WOODMANSEE, 1966). As a result of this epipelagic behavior, sediment texture likely does not influence the distribution of this species.

Lucifer faxoni is an important component of the pelagic and coastal ecosystem (LEE et al., 1992), and the importance of the communities of which this species is a member is irrefutable. This species is part of the diet of coastal fishes (PASCUAL et al., 2002) such as the cutlassfish *Trichiurus lepturus* Linnaeus, 1758 (MARTINS et al., 2005) and large filter feeders such as the whale shark *Rhincodon typus* Smith, 1828 (MOTTA et al., 2010). Moreover, the zooplanktonic communities to which *Lucifer* belongs are among the most important components of marine ecosystems because of their role in nutrient recycling and the distribution of organic matter (VEGA-PÉREZ, 1993). Zooplankton are also important for their use as a research tool to investigate the impact of pollutants on marine communities (EPOPEM, 1979; SIOKOU-

FRANGOU; PAPATHANASSIOU, 1991). In this context, additional studies on the biology of *Lucifer faxoni* are extremely important. These studies will add to knowledge on this species but can also contribute to studies on the conservation and ecology of *L. faxoni* and the food chain to which it belongs. The aim of the present study is to provide an ecological analysis of the shrimp *L. faxoni* in Ubatuba Bay on the northern coast of the State of São Paulo, Brazil.

MATERIAL AND METHODS

Sampling was conducted at Ubatuba Bay on the northern coast of the State of São Paulo (23°25' – 23°27'S; 45°00' – 45°03'18''W) (Fig. 1). Sampling was performed using a small fishing boat with a 25-HP stern-drive engine. The specimens of *L. faxoni* were sampled monthly from July 2005 to December 2006 with a Renfro net (RENFRO, 1963) measuring 1 m at the mouth aperture and with a 1-mm mesh size, that was trawled over a distance of 50 m for a total sampling effort of 50 m² per station. Nine stations were sampled, ranging from depths of 1 to 15 m. Three stations each were grouped into zones 1, 2 and 3, named Z1 (closed areas with little or no wave influence), Z2 (open areas influenced by wave action) and Z3 (deeper waters). Each sampling site was subdivided in 3 areas, each including 3 stations (Z1, Z2 and Z3). In the laboratory, all samples were identified in accordance with D'INCAO (1997) and PÉREZ-FARFANTE (1997) and measured, sexed, and stored in 10% formaldehyde.

Measurements were taken with a microscope stereoscope equipped with an ocular micrometer with a resolution of 10/100 mm. For each month sampled, frequency distributions of the pre-buccal somite length (SL) were made, on the basis of size classes of 0.8 mm. At each station, the bottom temperature and salinity were recorded monthly using a Van Dorn bottle for water sampling. Rainfall rates in the region were provided by the "Instituto Agrônômico" (IAC) through the official website of the institute (<http://www.iac.sp.gov.br/>).

For size analyses, measurements (in mm) of the pre-buccal somite length (SL) of *L. faxoni* were used. In samples with a large number of captured individuals, only 100 individuals of each sample were utilized in the analysis. When the number of *L. faxoni* was lower than 100, all the individuals in the sample were measured. The SL was measured as the distance from the labrum anterior margin to the base of the eyestalk. This parameter appears to be applicable for analyses of the developmental stages of *L. faxoni*, as shown by López (1966), Woodmansee (1966), Costa and Prandi (1971) and Alvarez (1988). The abundance was compared among stations and seasons of the year using analysis of

variance (two-way ANOVA with interaction, $p < 0.05$), complemented by Tukey's multiple-comparisons test, at the 5% probability level. For the environmental factor association in relation to species abundance, a multiple linear regression was used. Data were log-transformed prior to the analysis to improve their normality (ZAR, 1996). The sex ratio during the period sampled was tested using the chi-squared test (χ^2) at a 5% level of significance.

RESULTS

A total of 10,114 individuals were captured, 6306 in waters shallower than 5 meters (Z1 and Z2) and 3808 in regions with depths of 10 to 15 meters (Z3), with no significant differences between the

number of individuals captured in each zone (ANOVA, $p = 0.25$). The comparison of abundance revealed a significant difference only among seasons of the year (two-way ANOVA with interaction, $p = 0.002$). Only winter and spring seasons differed significantly (Tukey's test, $p = 0.002$). There were no significant differences among the stations sampled (two-way ANOVA with interaction, $p = 0.305$) (Table 1).

Of the total number of shrimps captured, 2784 were measured and sexed. With the exception of spring 2006 (October, November and December), males outnumbered females in all of the sampling periods. In all seasons of the year, the sex ratio differed significantly (χ^2 , $p < 0.05$), with the male to female ratio at 1.48:1 (Fig. 2).

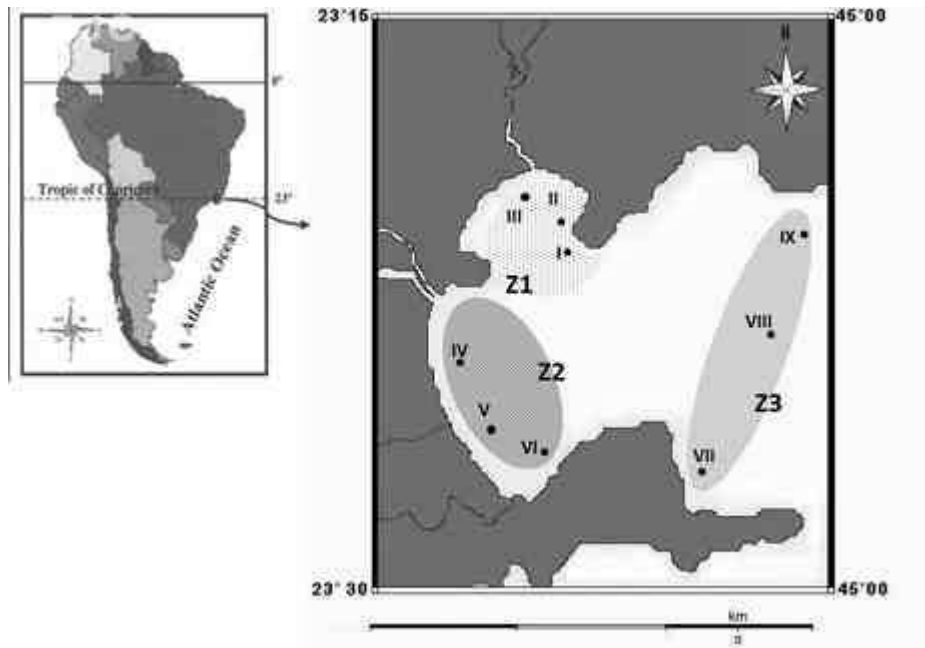


Fig. 1. Map of Ubatuba Bay, Brazil, indicating the sampled stations and the zones established (Z1, Z2 and Z3).

Table 1. *Lucifer faxoni*. Results of the analysis of variance (two-way ANOVA with interaction) of the mean catch by season and station.

Source of variation	dF	MS	F	P
Season	5	267406.8	4.642	<0.001
Station	8	69230.4	1.202	0.305
Season x Station	40	62691.7	1.088	0.358
Residual	108	57609.1		
Total	161	65964.8		

df = degrees of freedom, MS = mean square, F = MS factor/MS residual and p = probability of significance; $\alpha = 0.05$.

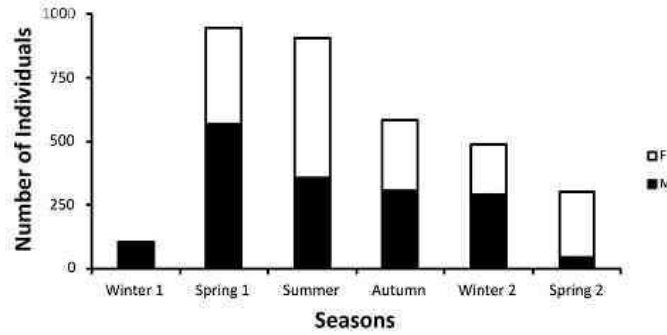


Fig. 2. The sex ratio of *Lucifer faxoni* in each season during the sampling period.

Spatially, Zone 1 (areas shallower than 5 meters) exhibited the highest abundance (1,101 measured shrimps), followed by Zones 2 (859) and 3

(794). The sex ratio for each size class in each zone is shown in Figure 3. Once again, the predominance of males compared to females can be clearly observed.

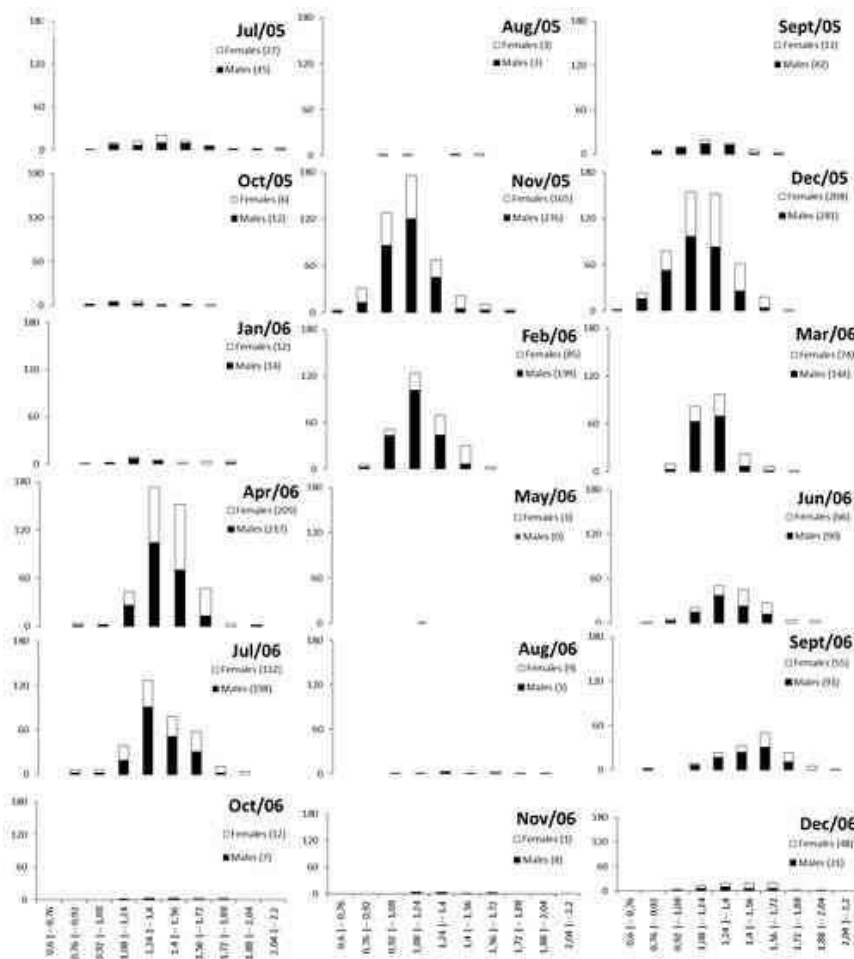


Fig. 3. The sex ratio in each size class (mm) of *Lucifer faxoni* found in each zone sampled in the study period. M= males; F= females.

The average of pre-buccal somite length (SL) found for *L. faxoni* was 1.28 mm. The sex ratio for each size class and for each sampled month is presented in Figure 4. In July and December 2005, individuals were found in all size classes. Individuals classified in the smallest size classes were found in 2005 (July, October and December) and 2006 (January, February, March, July and September). Shrimps with average SL were observed in all months of the year except May 2006. The smallest male and the smallest female had an SL of 0.70 mm; the largest individuals of each sex had an SL of 2.11 mm. Females exhibited a mean SL of 1.32 mm, whereas males exhibited a mean SL of 1.24 mm.

A positive correlation between the abundance of *L. faxoni* and rainfall was found

(multiple linear regression, $p=0.00$) (Table 2), whereas other factors did not present a positive correlation. The same test was conducted – excluding rainfall – and temperature and salinity were not significant factors affecting *L. faxoni* distribution. In fact, *L. faxoni* abundance was higher when rainfall values increased. When these values decreased, this shrimp's abundance also decreased, except in the spring (October, November and December) of 2006 (Fig. 5).

Only 4 females with egg masses were found, 2 of which were in summer 2005 (Table 3). A reproductive analysis of ovigerous females was not possible because the eggs are too easily released from the females. The SL of ovigerous females ranged from 0.94 to 1.41 mm, but the number of females with eggs was not high enough for a reliable analysis.

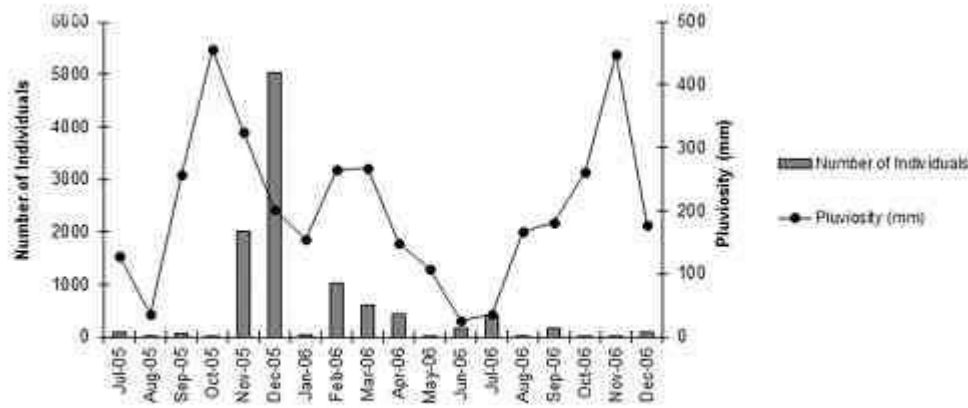


Fig. 4. Monthly distribution of males and females of *Lucifer faxoni* in each size class based on somite length.

Table 2. Multiple Linear Regression of the mean catch of *Lucifer faxoni*, by environmental factors, considering and not considering rainfall.

	<i>Coefficients</i>	<i>Standard Error</i>	<i>Stat t</i>	<i>P-value</i>
Intercept	-0.403	2.502	-0.161	0.872
Temperature	-0.527	1.480	-0.356	0.722
Salinity	0.506	0.662	0.764	0.446
Rainfall	0.529	0.067	7.887	0.000
	<i>Coefficients</i>	<i>Standard Error</i>	<i>Stat t</i>	<i>P-value</i>
Intercept	-1.41	2.94	-0.48	0.63
Temperature	1.38	1.72	0.81	0.42
Salinity	0.08	0.78	0.10	0.92

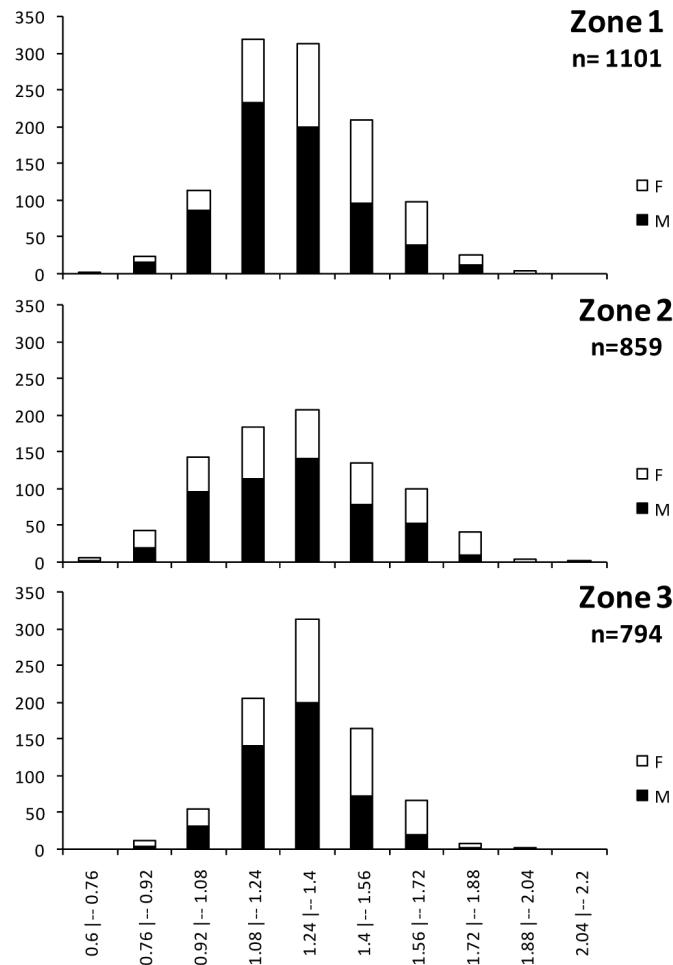


Fig. 5. Variation in number of individuals and mean monthly rainfall during the sampling period.

Table 3. Distribution of the breeding females of *Lucifer faxoni* on the depth zones.

Date	Zone	Breeding Females	Somit Length (mm)	Number of eggs
Oct-05	Z1	1	1.41	13
Nov/05	Z2	1	1.17	1
Aug/05	Z1	1	1.64	4
Jul/06	Z3	1	0.94	1

DISCUSSION

With regard to the correlation observed between *L. faxoni* abundance and rainfall, we suggest that this factor may have influenced salinity values in shallow regions, causing the shrimps to move to deeper areas. López (1966) reported that *L. faxoni* did not occur in regions under the influence of

waters with salinity levels lower than 36 psu. In contrast, Alvarez (1985) and Bowman and McCain (1967) found that *L. faxoni* has a preference for salinities close to 30 psu, a similar value to that recorded in the present study. The difference in abundance observed in these studies may have resulted from the year-round variability in rainfall. With less rain and a consequently lower variation in salinity in shallow areas, winter would be the most consistent

season for the larval development of *L. faxoni*, which would lead to an increase in population the following spring. Surface waters exhibit a higher fluctuation in salinity in the summer due to the greater amount of rainfall. *Lucifer* larvae hatched under these conditions would have a lower survival rate, i.e., they could not complete their life cycle, and this fact would reduce the shrimp population in the subsequent seasons.

According to Razouls and Thiriot (1968), variations in the amount of biomass represented by zooplankton taxa would be a response to variations in temperature, considering that temperature regulates the life cycle of these organisms. Although it was not significant in the present study, temperature was likely a decisive factor affecting the low abundance of *L. faxoni* found in the spring of the second study year. The present study was performed in shallow waters (< 15 meters) and, consistent with the findings of Castro-Filho et al. (1987), it can be assumed that these areas are influenced by coastal water (CW), which is characterized by salinity levels that range from 33 to 35 psu and temperatures higher than 20°C and is incorporated with tropical water (TW). In the spring and early summer, the incursion of a relatively cold (< 20°C) and less saline (< 36.4) water mass, called SACW (South Atlantic Central Water), commonly occurs. The mixing zone is observed near the coast (including the region studied), creating a strong thermocline (in the winter, there is no substantial inflow of SACW on the inner shelf) (CASTRO-FILHO et al., 1987). The presented data indicates an influx of SACW at the end of 2006, when the bottom temperature reached values below 18°C. Previous studies (COSTA et al., 2004; 2005a) showed that, due to the entrance of SACW, a decrease in the temperature of the outer region of the inlet promoted the migration of other Dendrobranchiata shrimps, such as *Pleoticus muelleri* (Bate, 1888) and *Artemesia longinaris*. Other species, such as *Sicyonia dorsalis* Kingsley, 1878, and *Xiphopenaeus kroyeri*, migrated from this region to deeper waters in the middle of the bays (e.g., Ubatuba Bay), where temperature values were higher (COSTA et al., 2005b; 2007). The low numbers of *L. faxoni* individuals recorded in January and mainly in November and December, 2006 were likely associated with the intrusion of this water mass.

The sex ratio determined in the present study differs from that described in previous studies on *L. faxoni*. For example, López (1966), studying the same species at Cananéia (SP, Brazil), found a higher number of females than males. In contrast, Alvarez (1985) obtained a higher abundance of males than females in a study undertaken on the coast of Santos. Sex ratios have been very variable in other shrimp species. For example, in a study of *X. kroyeri*, Cortés (1991) reported a sex ratio of 1♂:0.7♀, and in a study

of *Acetes americanus* Ortmann, 1893, Simões (2008) found a predominance of females over males (0.5:1).

According to Lee et al. (1992), *L. faxoni* females migrate vertically during the night, both to avoid predation and in search of more abundant food resources or for egg protection. Females may cluster in regions with more appropriate conditions, such as areas of more abundant food resources, which would account for the difference in the number of males and females found in the present study. In this case, alterations in sex ratios may result from the grouping of females in particular areas during spawning (SIMÕES, 2008). Dendrobranchiata shrimps generally move to deeper areas to spawn (DALL et al., 1990).

The fact that very few ovigerous females were found may have resulted from the fact that females lost their eggs, both during sampling and at the time of fixing (LOPÉZ, 1966). Despite the low number of ovigerous females, the sampling period found in the present study coincides with Lopéz (1966) and Alvarez's (1985) results, which likely indicates a longer reproduction period at this time, i.e., during the spring months. Females were predominant at stations 3 and 7, both of which are located close to river mouths. These locations tend to harbor a greater quantity of phytoplankton, which, according to Lee et al. (1992), is the preferred food of *Lucifer* larvae. Because the females carry the eggs, they are likely to remain in places that are more favorable for larval development until hatching, which would explain the dominance of females at these stations.

For *L. faxoni*, there are no studies focusing on species recruitment. However, Fernandes et al. (2002), studying the dynamics of decapod larvae in Guanabara Bay, suggest that *L. faxoni* has a seasonal distribution pattern: in the winter, larvae are imported into the bay to complete their development inside the estuary, and in the summer, non-reproductive adults are exported to coastal waters. In this way, as for the sergestid *A. americanus* studied by Simões (2008), *L. faxoni* appears to present recruitment peaks during October and November. The largest females were found in November and December, 2005 and in April and July, 2006, which suggests the occurrence of reproduction periods at these times. These results are in agreement with Lopéz (1966), who found a higher number of reproductive females during the summer and autumn. Alvarez (1985) found a higher number of *L. faxoni* of reproductive age in September.

As in the present study, Alvarez (1988) found *L. faxoni* females to be larger than males. These results are similar to the findings for other penaeid shrimps, such as *X. kroyeri*, studied by Cortés (1991), and *Litopenaeus schmitti* (Burkenroad, 1936), studied by Davant (1963) and Ewald (1967). This finding indicates that sexual dimorphism, with respect to length, is a general rule among penaeoideans, with

females larger than males. Gab-Alla et al. (1990), Rodrigues et al. (1992), Santos (2000) and Santos and Ivo (2000) found that the male carapace grows differently from that of females as a result of a process associated with reproduction. This fact has been observed for penaeid species such as *Rimapenaeus constrictus* (Stimpson, 1874), *X.kroyeri* and *A.longinaris*, which were studied by Costa and Fransozo (2004), Castro et al. (2005) and Castilho et al. (2007), respectively. With respect to sergestid shrimps, some studies have also presented similar results, including that by Oh and Jeong (2003) for *Acetes chinensis* (Hansen, 1919) and that by Simões (2008) for *Acetes americanus* and *Peisos petrunkevitchi* Burkenroad, 1945.

According to Lee et al. (1992), *L. faxoni* reaches sexual maturity at approximately 19 days and, preferentially, in locations with temperatures close to 30°C, which helps to explain the higher number of individuals found during the autumn months. As a result of the high temperatures characteristic of the summer, females experience a higher reproductive peak, and a greater frequency of spawning may occur in subsequent months. This may explain the abundance of smaller and average-sized individuals found during the period of the present study.

The low concentration of *L. faxoni* among the smallest size classes may be associated with the fact that larvae and immature juveniles of this species often concentrate more at the surface than near the bottom. This concentration of larvae at the surface generally occurs because of the greater amount of phytoplankton, which acts as a barrier to the larvae, intercepting them in such a way as to maintain them in these areas (ALVAREZ, 1985). In summary, the environmental factors monitored here have a close relation to the spatial and seasonal distribution of *L. faxoni*. The intensity of the rainfall directly affected salinity in such a way as to promote the displacement of these shrimps to deeper areas, whereas temperature mainly influenced the variation in seasonal abundance. Additional studies on reproduction and population dynamics are necessary for a better understanding of the life cycle of this species. Although there have been few studies on reproductive analyses of *L. faxoni*, the findings of the present study are in agreement with those of the existing literature. Further investigation of the vertical migration, histology and morphological descriptions of this species will make it possible to describe its reproductive biology in greater detail.

ACKNOWLEDGEMENTS

The authors are indebted to the "Fundação de Amparo à Pesquisa do Estado de São Paulo" (FAPESP) for providing financial support during field collections and laboratory activities (Grants 2004/07309-8, 2007/58094 2009/54672-4 and

2010/50188-8 to RCC and 1998/03134-6 to MLNF) and to CNPq (Research Scholarships PQ 306304/2008-2 to RCC and PQ 300481/2008-0 to MLNF). Thanks are extended to the staff at NEBECC and LABCAM for their help with sampling and laboratory activities, especially to Adilson Fransozo and Antonio L. Castilho.

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(Manuscript received 13 December 2011; revised 16 January 2012; accepted 16 February 2012)