

ECOLOGICAL ASPECTS AND SEXUAL MATURITY OF A SOUTHWESTERN ATLANTIC POPULATION OF THE PLANKTONIC SHRIMP *LUCIFER FAXONI* (DECAPODA: SERGESTOIDEA)

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ABSTRACT

The demographic structure and morphological sexual maturity of the shrimp *Lucifer faxoni* Borradaile, 1915 are described here. The studied specimens came from Ubatuba Bay, in the north littoral of São Paulo State, Brazil. In each month of capture, 14 stations, 7 offshore and 7 inshore, were sampled with neuston nets during high tide periods. Relative growth was analyzed by observing the change in growth patterns of certain parts of the body in relation to somite length and total length (TL). *Lucifer faxoni* was most abundant in offshore regions. The relationship that best showed the size at the onset of the sexual maturity was the length of the 6th somite of the abdomen vs. TL. The external morphology of the petasma evidenced three development stages and such characteristic was also used to estimate sexual maturity for males using the P₅₀ technique. Our results show there is a preference of *L. faxoni* for offshore areas, probably explained by differences in abiotic factors. Both estimates of maturity (relative growth and petasma stage) were very similar. In this context, we propose the search for new structures for the analysis of the maturity of *L. faxoni*, thus promoting a wider study of what is related to the maturation of sergestoid shrimps.

KEY WORDS: Brazilian coast, distribution, Luciferidae, neuston, tropical waters

DOI: 10.1163/1937240X-00002240

INTRODUCTION

The genus *Lucifer* Thompson, 1829 usually occurs in the surface waters of tropical and subtropical areas, and are an important component of the planktonic fauna (Omori, 1992). According to Costa et al. (2000), there are two luciferid species occurring along the Brazilian coast: *Lucifer faxoni* Borradaile, 1915 and *L. typus* H. Milne-Edwards, 1837. The species *L. faxoni* is one of the few holoplanktonic decapod crustaceans (Harper Jr., 1968). It occurs from 6 to 55 meters deep, but it is usually found in coastal waters (D'Incao, 1997) and presents an epipelagic habit, remaining close to the substrate during the day (Woodmansee, 1966).

As mentioned by Vega-Pérez et al. (1996), the role of the species *L. faxoni* in the trophodynamic pathways is very important, since it is one of the most found food items in the stomach contents of coastal fishes (Pascual et al., 2002), such as the cutlass fish *Trichiurus lepturus* Linnaeus, 1758 (Martins et al., 2005) and the whale shark *Rhincodon typus* Smith, 1828 (Motta et al., 2010). Furthermore, the zooplanktonic communities to which *Lucifer* belongs play a

key role in marine food web dynamics and biogeochemical cycling (Almeda et al., 2013).

Studies on species of *Lucifer* have often focused on the occurrence of each species (Omori, 1977, 1992; Costa et al., 2000; Xu, 2010; Grave, 2012; Radhakrishnan et al., 2012) or the population dynamics of the zooplanktonic community (Fernandes et al., 2002; Coyle and Pinchuk, 2004; Mackas et al., 2005; Koettker and Freire, 2006). With respect to *L. faxoni*, some studies can be found regarding its geographical and/or ecological distribution (Bowman and McCain, 1967; Harper Jr., 1968; Troost, 1975; Alvarez, 1976; Sankarankutty and Barca, 2000; Fernandes et al., 2002; Pascual et al., 2002) and about its feeding behavior (Vega-Pérez et al., 1996). However, there are few studies concerning the reproductive biology of this species, such as López (1966) and Lee et al. (1992).

Examining the dynamics of decapod larvae at Guanabara Bay, Fernandes et al. (2002) suggested a seasonal pattern for *L. faxoni*, where in the winter larval stages would be transported into Guanabara Bay to complete their development inside the estuary and, in the summer, non-reproductive adults would be exported to the shelf waters. Studying this

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same shrimp, but at shallower waters in Ubatuba Bay (SP), Teodoro et al. (2012) reported a sex ratio favoring males and the presence of juveniles in the inshore area of that bay.

This study analyzes the demographic structure of a population of *L. faxoni*, as well as the size at onset of its sexual maturity, based on the external morphology of the individuals. Additionally, a comparison of the population structure between inshore and offshore areas and the association between abiotic factors and the distribution of this species were accomplished in order to evaluate the possibility of displacement of the shrimp in this region.

MATERIALS AND METHODS

Study Area and Sampling

The species *L. faxoni* presents a wide geographic distribution, occurring from Nova Scotia, Canada, to Rio Grande do Sul, Brazil (Pérez-Farfante and Kensley, 1997). Ubatuba Bay, in the state of São Paulo, Brazil is a biologically important area as it has a very diverse crustacean decapods community (Costa and Fransozo, 1999, 2004; Costa et al., 2000), beyond other benthic organisms, mainly demersal fishes, and it is usually exploited as a fishery place. According to Castro-Filho et al. (1987), this region is strongly influenced by three water masses: the South Atlantic Central Water (SACW), with low temperature and salinity ($T < 20^{\circ}\text{C}$; $S < 36$ psu); Tropical Water (TW), with high temperature and salinity ($T > 20^{\circ}\text{C}$; $S > 36$ psu); and Coastal Water (CW), with high temperature and low salinity ($T > 20^{\circ}\text{C}$; $S < 36$ psu). These water masses interact to modify the temperature, salinity and nourishment conditions during the seasons (Castro et al., 2004).

Samples were collected in Ubatuba Bay (Fig. 1), in the north littoral of the state of São Paulo ($23^{\circ}25'S$ and $45^{\circ}00'W$; $23^{\circ}27'S$ and $45^{\circ}03'18''W$), in November 2005, January, April, October and November 2006 and January 2007. The samplings were performed during the spring and summer as those are very productive periods for planktonic organisms (Vega-Pérez, 1993). In each month of collection, 14 stations were sampled during high tide, using neuston nets with a $250\ \mu\text{m}$ mesh size, and 1 m wide by 70 cm high. Seven of those stations were located in offshore regions, where the depths were 20-40 meters (numbered 1 to 7), while the other seven stations were located in inshore regions (numbered 8 to 14), with depths shallower than 20 meters. Samples were performed in the surface water, where neuston net picks up the water from the surface to a layer of about 70 cm, below surface only. During sampling, the temperature and salinity of the water surface were assessed; the exact location of sampled stations was determined using a Global Positioning System device. The volume of seawater filtered in the trawls was calculated using a flow meter adhered to the mouth of the neuston net.

Shrimp were collected and stored in ethanol (80%) and then transported to the laboratory (Group of Studies on Biology, Ecology and Culture (NEBECC)) located at Departamento de Zoologia, Universidade Estadual Paulista (UNESP), Botucatu municipality. Samples were incorporated to

the NEBECC scientific collection. The obtained material was subsampled using a Motoda splitter. All subsampled specimens were identified according to Pérez-Farfante and Kensley (1997) and then quantified (total number of captured shrimp and also the number of shrimps per 1000 liter), sexed and measured. All individuals in the subsample were measured for pre-buccal somite length (SL), carapace length (CL), merus length of the 3rd pereopod (ML), the length of the 6th somite of the abdomen (6SL) and total length (TL) (Fig. 2).

Density and Spatio-temporal Distribution

The total number of the captured individuals in each month was counted. Density was defined as the number of *L. faxoni* individuals per 1000 liter of water, based on the seawater volume filtered in each trawling. Values of density were calculated by year and by month. All the subsampled data were scaled up to the sample size and subsequently to the total density. The specimens' distribution was analyzed as a function of environmental factors by means multiple linear regression. Data were log-transformed prior to this analysis, to improve their normality (Zar, 1996). The comparison of this species density (number of shrimp per 1000 liter) among the months of the year and among the sampled stations was performed using analysis of variance (ANOVA), complemented by Tukey's multiple comparisons test, at the 5% probability level. Homogeneity of data variance was verified by the Levene test. Shrimp were separated by sex and grouped into size classes, where the number of classes was determined according to the Sturges equation (Sturges, 1926).

Measurements were taken using a microscope/stereoscope, equipped with a micrometric ocular 10/100 mm. Deviation from the 1:1 sex-ratio was checked using the χ^2 square test ($p < 0.05$) (Sokal and Rohlf, 1995).

Relative Growth and Determination of Morphological Sexual Maturity

The analysis of relative growth was based on the morphometric data, to assess the change in growth patterns of certain parts of the body in relation to the independent variables SL and TL. The data were plotted on dispersion graphs and fitted to the allometric equation $y = ax^b$, in which y = the dimension studied; x = total length or somite length; b = allometric coefficient of the studied structure, and a = the intercept of the curve on the ordinate axis. The parameters were estimated by linear regression of the log-transformed data, i.e., with the linear version of the model ($\log y = \log a + b * \log x$). The allometric state of each structure was analyzed ($b > 1$, positive allometry; $b < 1$, negative allometry; $b = 1$, isometry), testing the null hypothesis $H_0: b = 1$, with a t -test for the linear regression coefficient ($\alpha = 0.05$) (Zar, 1996).

A non-hierarchical K-means clustering analysis was carried out on the transformed data (\log_{10}) for the morphometric relationships that best showed differences in the relative growth pattern. This method distributed the data into a previously determined number of groups by an interactive process that minimizes the variance within groups and maximizes the variance between them. The result of the K-means classification was refined by applying a discriminant analysis. The break point between the groups identified by discriminant analysis was considered as the size limits of the maturity categories (morphologically immature and morphologically mature). This statistical procedure is based on Sampedro et al. (1999).

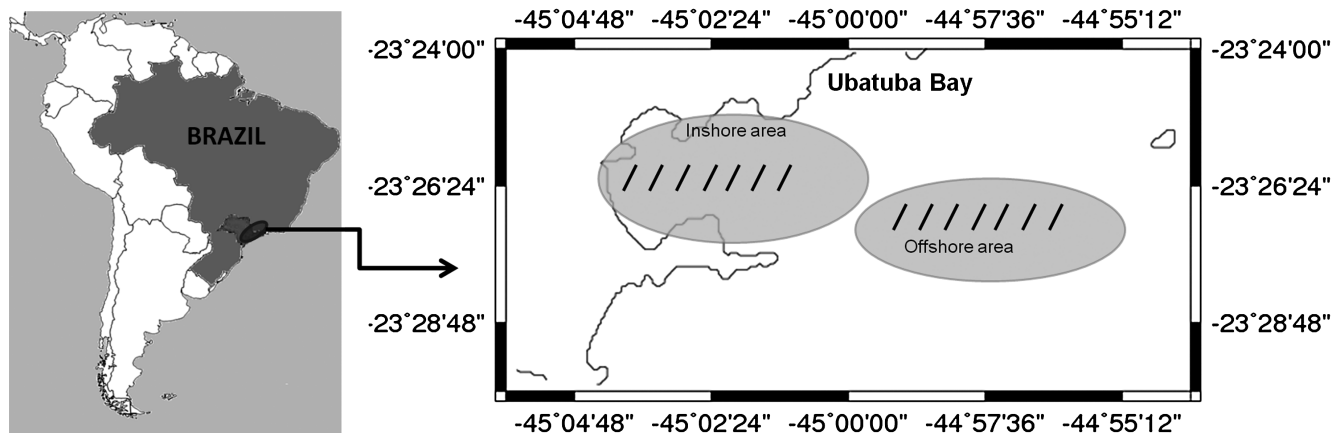


Fig. 1. A map of Ubatuba Bay, Brazil indicating the sampled region.

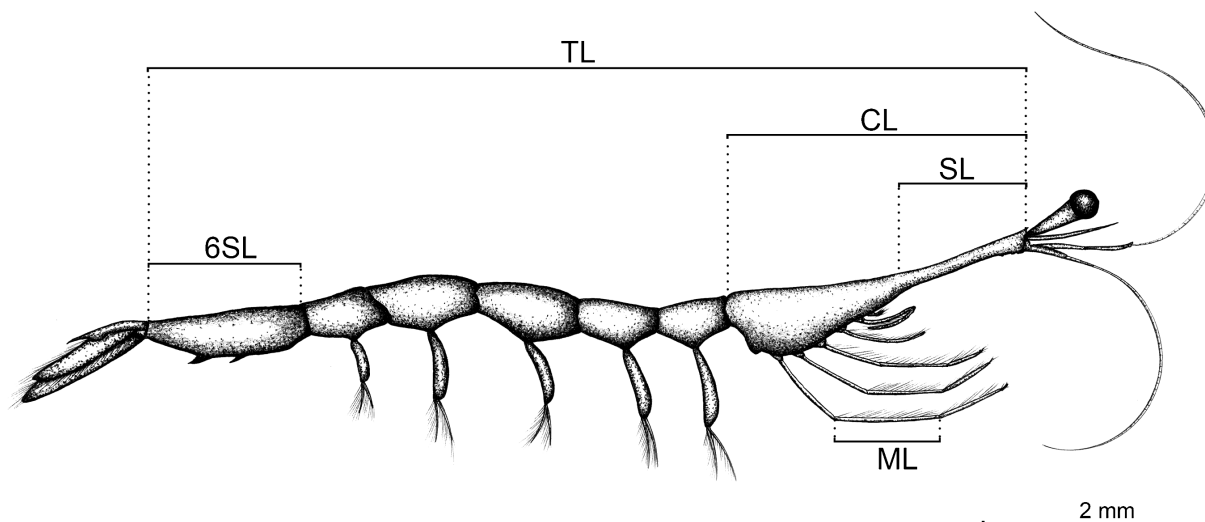


Fig. 2. *Lucifer faxoni* Borradaile, 1915. Dimensions used in morphometric analyses. Pre-buccal somite length (SL), carapace length (CL), merus length of the third pereopod (ML), sixth somite abdominal length (6SL) and total length (TL). Scale bar = 2 mm.

Once the size categories were correctly determined, the log-transformed data for each category were submitted to a covariance analysis (ANCOVA) to test the angular and linear coefficients between groups (juveniles and adults). This procedure showed whether the data for each relationship were better adjusted to a single straight line, or if the size categories should be represented by different linear equations.

López (1966) suggested that the petasma can be a good indicator of sexual maturity, considering it can be observed in several development stages. Thus, for the present work, three development stages of the petasma of *L. faxoni* were determined using the indications by López (1966), as follows: 1) just a hint of petasma, with a straight free end; 2) a small petasma, but with a curved free end; and 3) a large petasma and a small spermatophore. The maturation stages of the *L. faxoni* petasma were determined and described so as to verify a possible association of this structure with the sexual maturity of the shrimp. For this, the P_{50} technique was used, i.e., an estimation of the size at which 50% of the individuals of the studied population had a petasma at stage III, i.e., the external morphology indicates that they are mature regarding reproduction. This technique analyses the distribution of individuals according to their size classes based on SL. A graph based on the logistic curve equation ($y = 1/(1 + \text{er}(\text{SL} - \text{L50}))$) was plotted to relate the SL, the independent variable, to the relative frequency of mature individuals (petasma at stage III), the dependent variable. The size at sexual morphological maturity is defined by the interpolation point corresponding to a relative frequency of 50% on the graph. The equation of the logistic curve was fitted to the data by the method of least squares (Vazzoler, 1996).

RESULTS

Density and Distribution

During the sampling period, 104,386 individuals of *L. faxoni* were captured. A total of 5133 shrimp were subsampled, measured and sexed. The highest densities were recorded in April 2006 and November 2006 (18.33 and 11.12 individuals per 1000 liter, respectively), while the lowest amounts of *L. faxoni* were captured in October and January 2006 (4.22 and 3.7 shrimps per 1000 liters, respectively). The density found at each sample area and months of the year can be seen in Table 1. Excepting April 2006, *L. faxoni* was most abundant in offshore regions throughout the entire sampling period, when compared with the shrimp density captured in inshore areas. The difference in the mean values among inshore and offshore areas were greater than would be expected by chance, so there was a statistically significant difference

(ANOVA, $p = 0.008$). On the other hand, considering the sampled months, there was no statistically significant difference (ANOVA, $p = 0.624$). Considering only inshore areas, differences among the sampled months were not statistically significant (ANOVA, $p = 0.295$), as well as for considering only offshore areas among the sampled months (ANOVA, $p = 0.296$). The mean values of abiotic factors (temperature, salinity and precipitation) for each sampled month are shown in Table 2. The highest density (18,33 individuals/1000 l) occurred in April 2006, when the lowest average precipitation was also recorded (Tables 1 and 2). Multiple linear regression did not show a significant difference ($p < 0.05$) in the density or environmental factors both for inshore and offshore areas (Table 3).

In all sampled seasons, the proportion between males and females differed statistically (χ^2 , $p < 0.05$), where the calculated sex ratio was $1\text{♀}:0.64\text{♂}$. Excepting January 2007, females were more abundant than males in all sampled months, mainly in November 2006 ($1\text{♀}:0.48\text{♂}$), followed by October 2006 ($1\text{♀}:0.48\text{♂}$) and November 2005 and January 2006 (both $1\text{♀}:0.58\text{♂}$). Excepting station 08-in, females

Table 1. *Lucifer faxoni* Borradaile, 1915. Densities found in the sampled area during all the study period at Ubatuba Bay, Ubatuba (SP). All the subsampled data were scaled up to the sample size, and subsequently to the total density.

Month	Area	<i>Lucifer</i> /1000 l	Mean
November 2005	Offshore	17.6	8.4
	Inshore	1.8	
January 2006	Offshore	5.5	3.7
	Inshore	1.4	
April 2006	Offshore	6.2	18.3
	Inshore	79.1	
October 2006	Offshore	5.8	4.2
	Inshore	1.4	
November 2006	Offshore	14.5	11.1
	Inshore	4.6	
January 2007	Offshore	9.2	7.4
	Inshore	4.4	

Table 2. Mean values of the environmental factors analyzed in the present study, except for pluviocity, which is expressed in monthly values.

Month	Area	Mean temperature (°C)	Mean salinity (‰)	Pluviocity (mm)
November 2005	Inshore	25.4 ± 0.5	36.6 ± 2.4	221.8
	Offshore	25.1 ± 0.5	35.8 ± 1.3	
January 2006	Inshore	26.5 ± 0.6	33.5 ± 1.1	154.0
	Offshore	25.7 ± 0.4	34.7 ± 0.7	
April 2006	Inshore	25.0 ± 0.0	38.0 ± 0.0	148.3
	Offshore	26.0 ± 0.4	37.0 ± 0.7	
October 2006	Inshore	23.4 ± 0.8	34.8 ± 1.4	260.3
	Offshore	22.8 ± 0.4	35.9 ± 0.7	
November 2006	Inshore	27.0 ± 0.0	35.5 ± 0.7	335.4
	Offshore	24.8 ± 2.2	36.9 ± 0.4	
January 2007	Inshore	26.0 ± 0.0	35.0 ± 0.0	270.3
	Offshore	26.0 ± 0.0	35.0 ± 0.0	

were also more abundant than males at all sampled stations. Only six ovigerous females were captured, four of them in January 2006. The reproductive analysis was not possible, as the eggs unfasten easily.

Individuals were separated into 10 size classes. The range of the pre-buccal somite length (SL) varied from 0.3 mm to 2.4 mm. The smallest female had a 0.39 mm SL, while the smallest male had a 0.58 mm SL. The largest female SL was 2.17 mm and the largest male SL was 2.08 mm. When both sexes were analyzed together, the mean value of SL was calculated as 1.22 mm ± 0.34. The sex ratio found for each size class can be seen in Fig. 3. Although there were individuals in basically all size classes in the offshore and inshore regions, it can be easily observed that the smallest individuals (mean SL 1.06 mm) were found in inshore regions, while the largest shrimp (mean SL 1.49 mm) were found in offshore areas (Fig. 4).

Relative Growth and Determination of Morphological Sexual Maturity

The relationships studied in the relative growth and allometric levels of *L. faxoni* are presented in Table 4. According to the K-means analysis, for the relationships 6SL vs. TL, 6SL vs. CL, ML vs. TL and ML vs. CL, a significant difference was observed between the ontogenetic stages of growth in males, after the size categories were separated. For females, significant values were found for the relationships 6SL vs.

TL, ML vs. TL and ML vs. CL (between the categories of juveniles vs. adults) (Table 5). The relationship that best evidenced a change in the growth pattern for males and females was 6SL vs. TL. The results obtained from this relationship were used to estimate sexual maturity. Based on this relationship, the size at sexual maturity was estimated as a somite length of 1.24 mm and 1.05 mm for males and females, respectively (Figs. 5 and 6).

The external morphology of the petasma showed three development stages (I, II and III; Fig. 7), and such a characteristic can be useful when it comes to the determination of sexual maturity. There were no males with a petasma at stage I in the largest size classes; the largest male at stage I had an SL of 1.13 mm (Fig. 8). Stage III, more developed and considered here as the closest stage to sexual maturity, was observed mainly in the largest individuals, and was seen more often with SL < 0.93 mm. Also, there were no males with an SL smaller than 0.58 mm. Males at all development stages were collected at all sampling stations, but males at stage III were more abundant in offshore regions (Fig. 9). Using the P₅₀ technique, the SL at the beginning of morphological sexual maturity (males with petasma at stage III) was estimated as 1.26 mm (Fig. 10).

Table 3. *Lucifer faxoni* Borradaile, 1915. Results of multiple linear regression on the comparison of the species and the environmental factors analyzed in this study for inshore and offshore areas. All the subsampled data were scaled up to the sample size, and subsequently to the total density.

	Coefficient	SE	tStat	p
Offshore				
Constant	-26.69	83.22	-0.32	0.75
Temperature	-0.83	1.65	-0.50	0.62
Salinity	1.43	1.85	0.77	0.45
Pluviocity	0.02	0.03	0.65	0.52
Inshore				
Constant	-87.00	100.22	-0.87	0.40
Temperature	0.96	2.72	0.35	0.73
Salinity	2.37	1.77	1.34	0.20
Pluviocity	-0.07	0.06	-1.20	0.25

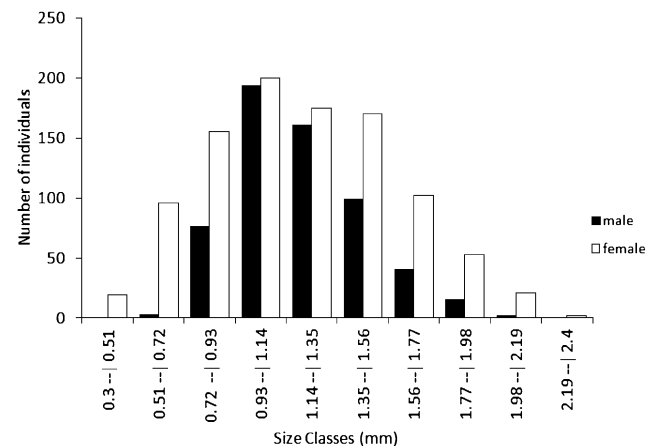


Fig. 3. *Lucifer faxoni* Borradaile, 1915. Number of measured individuals (males and females) distributed in the size classes found by this study.

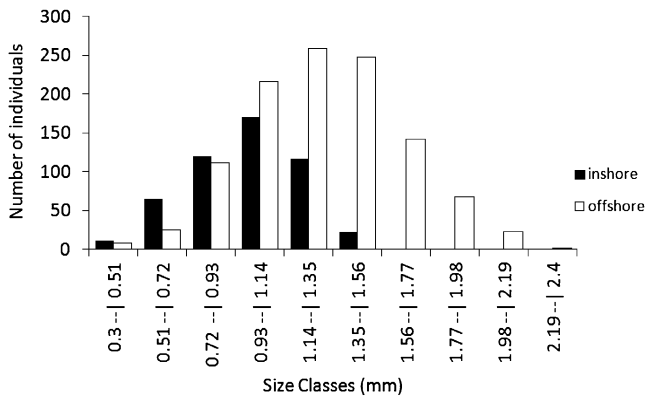


Fig. 4. *Lucifer faxoni* Borradaile, 1915. Comparison of the size classes at inshore and offshore region in Ubatuba Bay, in terms of the number of measured individuals.

DISCUSSION

According to Castro-Filho et al. (1987), the South Atlantic Central Water (SACW) is water mass characterized by salinity lower than 36‰ and temperature lower than 20°C; it penetrates intensely from the deepest layers until areas close to the coast, creating a strong thermocline. This study revealed a reflex of the SACW at the end of 2005 and 2006, once the area close to the bay mouth (15–20 meters deep) showed mean values for salinity (25‰ in January) and temperature (22.8°C), which were lower when compared

to the other sampled months. In accordance with Alvarez (1976), the thermocline associated with other parameters can be a limiting factor for the distribution of *L. faxoni*. Previous works (Costa and Fransozo, 2004; Costa et al., 2005a, b) reported a decreasing in temperature in offshore regions due to SACW entrance and the migration of other Dendrobranchiata to more favorable places.

The low number of individuals in January is likely associated to the intrusion of this water mass (Woodmansee, 1966), as the distribution and vertical migration of *L. faxoni* can be influenced by sea currents and water masses that enter into the region. Additionally, Webber et al. (1996) described *L. faxoni* as an indicator species of eutrophic waters and, in this way, it can indicate some abundance of nutrients in the region. According to Vega-Pérez (1993), the entrance of the SACW into the coastal region of São Paulo State produces a significant increase in the availability of phyto- and zooplankton food. In this way, in offshore regions, temperature and salinity were at ideal levels for *L. faxoni*, together with the possible high primary productivity due to water masses present at deeper regions; this could explain the high abundance of this species in the months after SACW entrance. Troost (1975) also found high abundance values for this luciferid in offshore samples, where high productivity and salinity were also recorded.

The sex ratio found in this study (1♀:0.64♂) is similar those found in the pertinent literature for the species and

Table 4. Regression analyses of morphometric data of *L. faxoni*. Carapace length (CL) and total length (TL) were used as the independent variables. SL = pre-buccal somite length; ML = merus length; 6SL = length of 6th somite; JM = juvenile males; AM = adult males; JF = juvenile females; AF = adult females.

Relationship	Sex	N	Intercept (log)	Slope	r ²	t (b = 1)	p	Allometry
SL vs. TL	JM	34	-0.7437	0.9859	0.6971	0.122552	0.00	0
	AM	45	-0.8793	1.1324	0.8357	1.72671	0.00	+
	JF	34	-0.8767	1.1814	0.8082	1.78316	0.00	+
	AF	75	-0.8769	1.1611	0.7516	2.06661	0.00	+
SL vs. CL	JM	36	-0.2993	1.1301	0.8789	1.80801	0.00	+
	AM	44	-0.3525	1.2553	0.8359	2.97452	0.00	+
	JF	33	-0.3209	1.3226	0.8982	4.03471	0.00	+
	AF	75	-0.3224	1.199	0.8474	3.34175	0.00	+
6SL vs. TL	JM	33	-0.6404	0.8364	0.7829	2.068056	0.00	-
	AM	45	-0.7184	0.9649	0.8492	0.565967	0.00	0
	JF	30	-0.6563	0.8258	0.71	1.746606244	0.00	-
	AF	75	-0.7678	1.0168	0.8785	0.38035	0.00	0
6SL vs. CL	JM	36	-0.2993	1.1301	0.8789	1.80801	0.00	+
	AM	44	-0.3525	1.2553	0.8359	2.97452	0.00	+
	JF	30	-0.2483	0.8587	0.651	1.189039528	0.00	0
	AF	74	-0.2369	0.9457	0.7872	0.936958548	0.00	0
ML vs. TL	JM	39	-0.5884	0.5122	0.3534	4.281832946	0.00	-
	AM	39	-1.2474	1.2317	0.7181	1.82581	0.00	+
	JF	29	-0.8068	0.7409	0.4287	1.57411739	0.00	0
	AF	72	-0.7512	0.7433	0.6137	3.642965591	0.00	-
ML vs. CL	JM	38	-0.3528	0.5339	0.2411	2.952567367	0.00	-
	AM	41	-0.5876	1.1679	0.6336	1.1801	0.00	0
	JF	36	-0.424	0.6312	0.355	2.527244194	0.00	-
	AF	68	-0.3248	0.6145	0.4541	4.647583679	0.00	-
CL vs. TL	JM	36	-0.4426	0.9335	0.7935	0.814335039	0.00	0
	AM	43	-0.3877	0.8703	0.8033	1.928860278	0.00	-
	JF	33	-0.3911	0.8454	0.8127	2.121319393	0.00	-
	AF	75	-0.4523	0.9579	0.8962	1.104784375	0.00	-

Table 5. Results of the ANCOVA of morphometric data for *L. faxoni*. J = juveniles; A = adults; SL = pre-buccal somite length; ML = merus length; 6SL = length of 6th somite; a = intercept values; b = slope values. * $P < 0.05$.

Relationship	Factor (Group)	Parameter (log)	F	p
SL vs. TL	Male (J vs. A)	a	1.208	0.275
		b	1.198	0.277
	Female (J vs. A)	a	0.540	0.464
		b	0.027	0.870
SL vs. CL	Male (J vs. A)	a	0.674	0.414
		b	1.230	0.271
	Female (J vs. A)	a	3.748	0.056
		b	1.571	0.213
6SL vs. TL	Male (J vs. A)	a	4.274	0.042
		b	1.695	0.197
	Female (J vs. A)	a	—	—
		b	4.476	0.037
6SL vs. CL	Male (J vs. A)	a	14.034	0.000
		b	1.166	0.284
	Female (J vs. A)	a	3.073	0.083
		b	0.583	0.447
ML vs. TL	Male (J vs. A)	a	—	—
		b	17.273	0.000
	Female (J vs. A)	a	—	—
		b	5.053	0.027
ML vs. CL	Male (J vs. A)	a	—	—
		b	8.780	0.004
	Female (J vs. A)	a	—	—
		b	12.980	0.000
CL vs. TL	Male (J vs. A)	a	0.052	0.821
		b	0.363	0.549
	Female (J vs. A)	a	3.337	0.071
		b	2.444	0.121

for penaeids in general. López (1966) also captured a higher number of females when studying this shrimp in the Cananéia region (south of São Paulo State). However, Alvarez (1976) reported a higher abundance of males in a study performed at Santos (central region of São Paulo coast). For other penaeids, similar results can be found as for the seabob shrimp *Xiphopenaeus kroyeri* Heller, 1862 (sex ratio of 1♂:0.7♀) in a study by Cortés (1991). For the sergestid *Acetes americanus* Ortmann, 1893, a

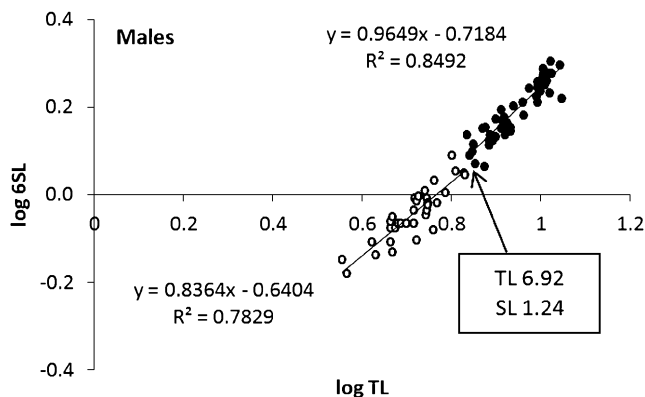


Fig. 5. Estimate of size at morphological sexual maturity for male of *Lucifer faxoni*. The estimated size of morphological sexual maturity corresponds to the SL of the smaller individual after the break point of the equations for immature and adult.

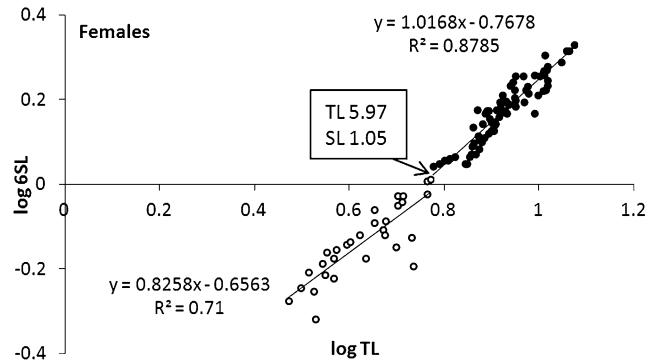


Fig. 6. Estimate of size at morphological sexual maturity for female of *Lucifer faxoni*. The estimated size of morphological sexual maturity corresponds to the SL of the smaller individual after the break point of the equations for immature and adult.

predominance of females (0.5♂:1♀) was mentioned by Simões et al. (2013). Teodoro et al. (2012), studying the ecology of *L. faxoni* in the same region as the present study, captured a higher number of males when compared to females. However, the study involved only the inshore region (until a depth of 15 meters). We suggest here that there was probably a displacement of these individuals to deeper areas in that time of the fieldwork performed by Teodoro et al. (2012). Considering that, in this paper, the largest individuals and a greater number of females were captured in the offshore areas, sizes that were not obtained in the previous study (Teodoro et al., 2012). According to Lee et al. (1992), *L. faxoni* females migrate vertically during the night, searching for both greater amounts of food and egg protection, which in some way also avoids predation. It should be emphasized that samplings of this paper was performed at night, what could influence the bias in the sex ratio favoring females in almost all sampled months and stations.

Our results related to the species distribution show that there is a major incidence of *L. faxoni* for the offshore area. Differences in abiotic factors between these two areas, such

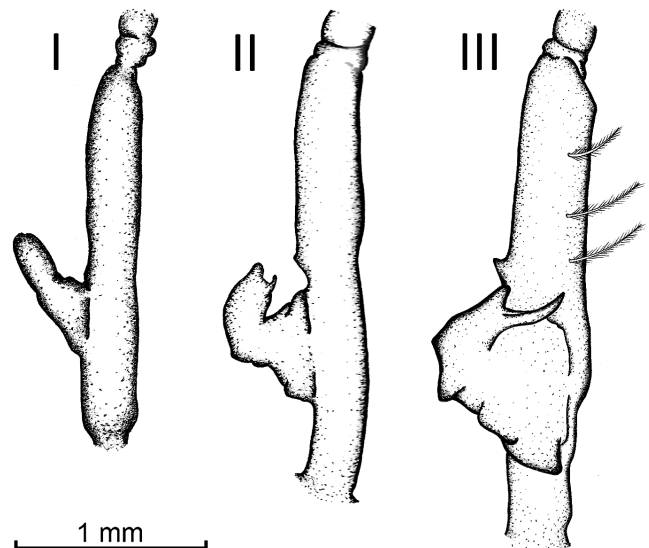


Fig. 7. *Lucifer faxoni* Borradaile, 1915. Development stages of petasma.

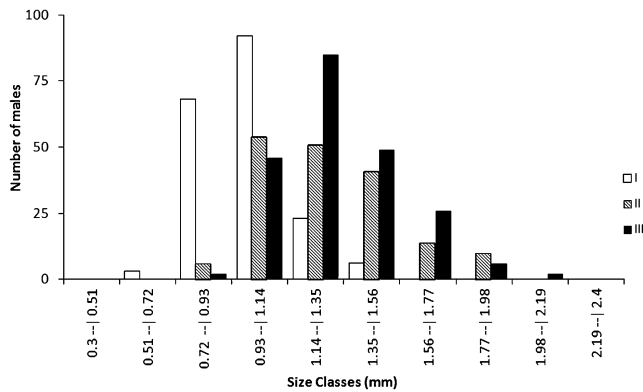


Fig. 8. *Lucifer faxoni* Borradaile, 1915. Development stages of petasma throughout the size classes found in the present study.

as temperature, depth and salinity, could explain the high abundance of *L. faxoni* in the offshore area. As mentioned by D'Incao (1974), juvenile plankton often congregates in shallower regions than those occupied by adults. The present study corroborates this affirmation, as the smallest individuals were captured in the inshore area, which coincided with the shallower zone of the sampling stations. All size classes were captured in the offshore region, but the largest shrimps were sampled only in areas located beyond the mouth of the bay, i.e., at areas away from the coast. Besides, tidal currents may exert an influence on plankton displacement, particularly considering a zooplankton faced with the problem of maintaining its center of density in a region subject to considerable tidal flow (Woodmansee, 1966), as in the region of the present study. It is likely that planktonic numbers are related to both solar and tidal cycles (Woodmansee, 1966). Another explanation is that distribution of *L. faxoni* maybe is determined by a combination of its longevity and the time required for restocking from breeding populations along the coast (Bowman and McCain, 1967).

Alvarez (1976), studying the vertical migration of *L. faxoni*, found a higher abundance of individuals of larger size classes in deeper areas, which is in accordance with our results. The smallest individuals concentrated in sheltered regions, probably due to factors that enable a higher survival rate of juveniles. However, we cannot attribute such difference to only one parameter, considering that the zooplankton distribution can rarely be explained in terms of only one

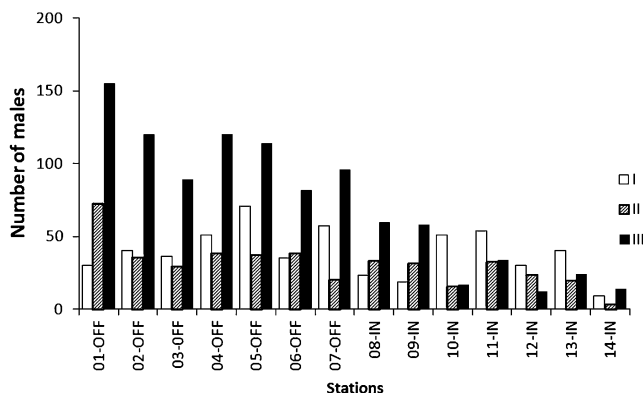


Fig. 9. *Lucifer faxoni* Borradaile, 1915. Development stages of petasma found in the present study throughout the sampled stations.

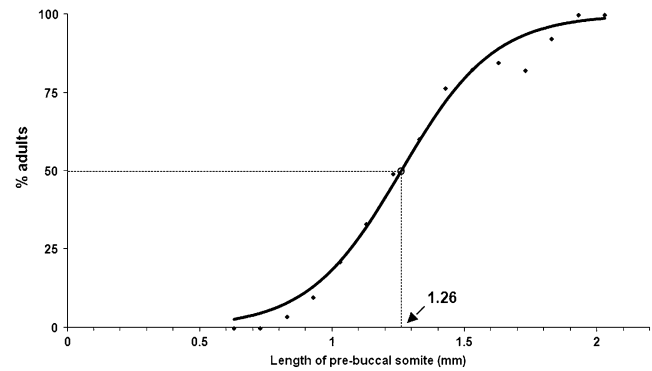


Fig. 10. *Lucifer faxoni* Borradaile, 1915. Fit of the logistic curve equation, indicating the length of the pre-buccal somite in which 50% of males present a petasma at stage III.

external condition. According to Moore and Bauer (1960), the zooplankton distribution is often a result of a complex of factors, not just from reactions to different factors, but also from the variation in responses to a factor.

Differences in the growth pattern among body structures can be related to the extension of how much they can interact with the other structures of the animal in order to function properly (Cowles, 1994). In the analysis performed here, it was observed that the length of the sixth abdominal somite (6SL) proved be significant in the calculation of the maturity of the species, i.e., there is an increase in the growth of this structure after *L. faxoni* individuals reach sexual maturity. According to Chu et al. (1996), the complex development of decapod crustaceans is followed by changes in swimming mechanisms; somites and abdominal appendages that are gradually added throughout larval development provide additional propulsion for swimming. In agreement with Iwai (1978), the movement of vertical migrations and the fluctuation of post-larvae of penaeids are effectively exerted by the well-developed sixth abdominal somite, balancing the body during vertical movements. The species *L. faxoni* exhibits a planktonic habit even in the adult stage, i.e., it is a holoplanktonic species. This fact can partially explain the significance of such a structure. Additionally, locomotion is an important component of the feeding strategy of the animal (Chu et al., 1996). In this sense, a more developed sixth abdominal somite at a mature stage can play a fundamental role in food processes and on displacement movements, both important in the life history of the species.

The results of the P_{50} technique corroborate this information, since both estimates of maturity using 6SL and petasma stage and the length of the pre-buccal somite were similar (1.24 mm and 1.26 mm, respectively). In this context, the information obtained in the present work complements previous studies performed on the reproductive biology of *L. faxoni*. We propose here a search for new parameters to analyze the process of maturation in *L. faxoni*, thus promoting a wider study of the structures that may be related to the maturation of any particular individual.

ACKNOWLEDGEMENTS

The authors are indebted to "São Paulo Research Foundation" (FAPESP) for providing financial support during field collections and visiting activities (Grants 04/07309-8, 09/54672-4, 10/50188-8 to RCC and 04/15194-6 to

M.L.N.F.) and to CNPq (Research Scholarships PQ 303371/2011-0 to R.C.C. and PQ 300481/2008-0 to M.L.N.F.). Thanks are extended to the NEBECC and LABCAM members for their help during sampling and laboratory activities, especially Dr. Adilson Fransozo.

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RECEIVED: 16 September 2013.

ACCEPTED: 3 April 2014.

AVAILABLE ONLINE: 4 June 2014.