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Lifespan and population dynamics of the endemic South American shrimp *Artemesia longinaris* (Crustacea: Penaeidae) in southeastern Brazil

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ABSTRACT

The present study investigated the growth, longevity and reproductive dynamics of *Artemesia longinaris* in the southeastern coast of Brazil over a two-year period. Monthly collections were conducted in Ubatuba and Caraguatatuba using a shrimp fishing boat equipped with “double-rig” nets. Each region was divided into 7 sampling stations up to 35 m deep. Size frequency distributions, growth, longevity, sex ratio, and abundance of individuals in each demographic class, were compared. The relationship between abiotic factors and abundance of each demographic class was assessed using a Canonical Correlation Analysis. A total of 64,641 individuals were collected (6,928 measured) with an estimated longevity of 1.30 (Ubatuba) and 1.14 (Caraguatatuba) years for females and 1.03 years for males in both regions. There was a statistically significant bias in sex ratio toward females (Chi-squared test, $p < 0.05$) in both regions. The Canonical Correlation Analysis resulted in a canonical correlation coefficient of 0.31 ($p = 0.00002$). Salinity and temperature showed high correlation mainly with the presence of reproductive females. In general, this demographic class was most common in conditions of low temperature and high salinity. These findings, as well as other studies carried out in colder regions with the same species, are consistent with classical latitudinal paradigm.

Key words: habitat selection, latitudinal variation, longevity, Penaeoidea, reproductive dynamics.

INTRODUCTION

An accurate portrayal of population dynamics is fundamental to an understanding of recruitment processes and reproductive stock development in penaeid shrimps. These studies are essential to implement sustainable fishery techniques, especially because reproductive patterns can differ according to distinct environmental conditions among geographical latitudes (Bauer 1992, Castilho et al. 2007a). The increase of the fishing fleet and the decrease of landings of commonly exploited species have contributed to the expansion of the *Artemesia longinaris* Spence Bate, 1888 fishery (D´Incao et al. 2002, Costa et al. 2005).

Artemesia longinaris is a monotypic and endemic species of the South American coast and presents geographical distribution restricted to the Western Atlantic, being recorded from Atafona

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(Rio de Janeiro, Brazil) to the province of Chubut, Argentina (Castilho et al. 2007b).

To date, investigations on *A. longinaris* have focused on aspects of its ecology (Fransozo et al. 2004, Costa et al. 2005, Castilho et al. 2008a, Carvalho-Batista et al. 2011, Sancinetti et al. 2014), diel variation in the abundance and size (Carvalho-Batista et al. 2012), population and reproduction biology (Castilho et al. 2007a), and latitudinal variation in population structure, reproductive pattern and phylogenetic relationships (Castilho et al. 2007b, Costa et al. 2010, Carvalho-Batista et al. 2014). However, virtually nothing is known about the growth, lifespan and spatial-temporal dynamics in reproduction of *A. longinaris* along the southeastern coast of Brazil.

Our goals in this study were to analyze and characterize the periodicity and spatial scales of variation in reproductive activity (gonadal development) and recruitment, to estimate growth rates and lifespan, based on analysis of population structure, and to estimate the size of morphological sexual maturity and the sex ratio for *A. longinaris* in Ubatuba and Caraguatatuba regions, southeastern coast of Brazil. Once growth parameters were assessed, we were able to estimate, utilizing mean size of individuals in the main cohorts, various of their life history characteristics, such as age of recruitment, sexual maturity, and lifespan of the average individual in these cohorts. Environmental factors such as bottom water salinity and temperature, sediment texture, and organic matter were measured and analyzed in relation to the abundance of each demographic class.

MATERIALS AND METHODS

COLLECTION OF SAMPLES

Shrimp collections were carried out monthly between July 2001 and June 2003 in two locations - Ubatuba (UB) and Caraguatatuba (CA), northern coast of the state of São Paulo, southeastern Brazil (UB: -23º26’27”, -45º03’18”; CA: -23º36’09”, -45º20’25”). Seven collection stations were sampled in each location at varying depths, from 5 to 35 m (Fig. 1). A shrimp-fishing boat equipped

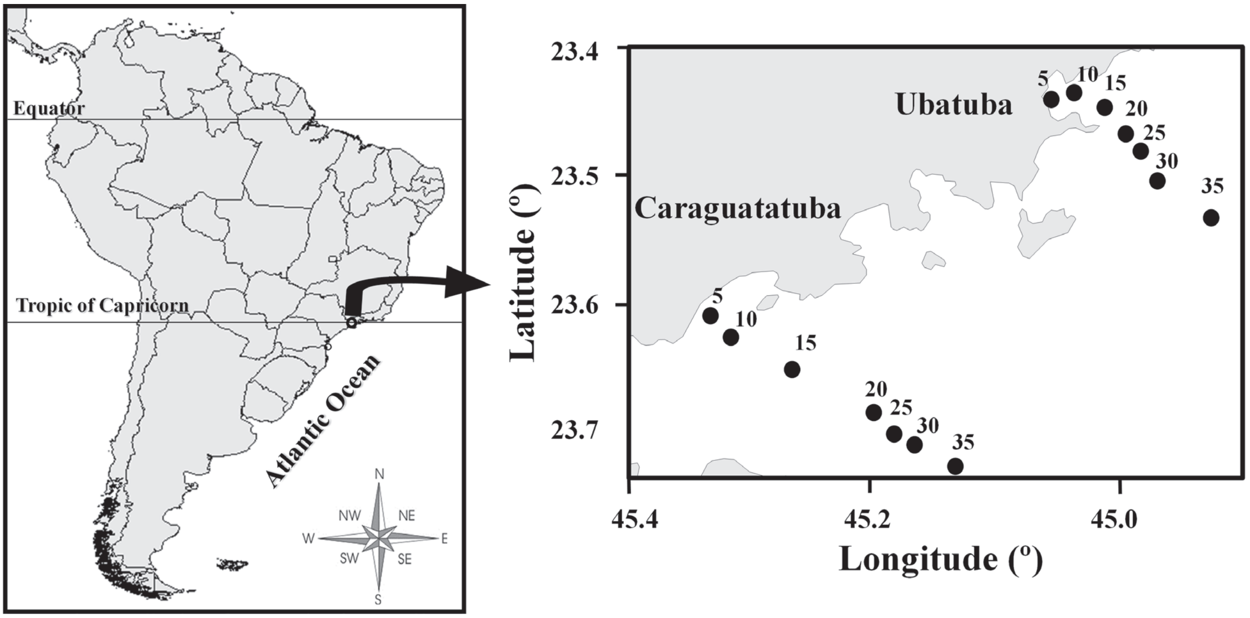

Figure 1 - Location of the Ubatuba and Caraguatatuba regions, indicating the collection stations.

with double-rig nets (mesh size 20 mm and 15 mm in the cod end) was used for trawling, which lasted for 30 min in each station, sampling a total area of approximately 18,000 m^2. When a given trawl yielded considerable biomass, the data was extrapolated from a 200 g random subsample to evaluate the descriptive and inferential statistics of the abundance (individuals per period or station) in each sex or demographic class.

Five environmental features were recorded at each collecting station and location (UB and CA), namely: bottom water salinity and temperature, organic matter content, depth, and sediment grain size. Bottom water was sampled using a Nansen bottle. The salinity was measured with an Atago S/1000 optic refractometer, whereas the temperature (ºC) was measured using a thermometer attached to the bottle. An ecobathymeter coupled with a GPS was used to record depth (m) at sampling sites. Sediment samples were collected at each station with a Van Veen grab (0.06 m^2) and after, in laboratory, the organic matter and grain size were measured (more detail see Castilho et al. 2008a).

Laboratory Analyses

Grain size categories followed the American standard, and fractions were expressed on the phi (φ) scale, i.e. using the formula $\varphi = -\log_2 d$, where d = grain diameter (mm) (Tucker 1988), e.g., $-1 = \varphi < 0$ (very coarse sand); $0 = \varphi < 1$ (coarse sand); $1 = \varphi < 2$ (intermediate sand); $2 = \varphi < 3$ (fine sand); $3 = \varphi < 4$ (very fine sand) and $\varphi \geq 4$ (silt + clay). Finally, φ was calculated by cumulative particle-size curves that were plotted on a computer using the φ scale, with values corresponding to 16th, 50th, 84th percentiles being used to determine the mean diameter of the sediment using the formula $Md = (\varphi_{16} + \varphi_{50} + \varphi_{84})/3$ (Castilho et al. 2008a).

The shrimp were sexed and measured to nearest 0.1 mm. Due to the high number of individuals captured in each trawl, a 200 g subsample was separated randomly for examination: sex, reproduction condition and carapace length (CL, excluding the rostrum).

Female reproductive condition was determined by macroscopic observation of the degree of ovarian development (color and volume occupied by the gonads) (more details see Castilho et al. 2007a, b). Ovaries categorized as immature (= recruit or juvenile) varied from thin, transparent strands to thicker strands. Ovaries of adult females were classified as spent, if they were white and much larger and thicker than the immature females, as developed if they were light green, or as ripe if they were green to olive green.

Sexual maturity of males in penaeids is usually indicated by fusion of the petasmal lobes (gonadal endopods), whereas juvenile males have separate petasmal lobes (Boschi 1989, Bauer and Rivera Vega 1992). The maturity of adult males was classified according to the development of spermatophores in the terminal ampoule (ejaculatory duct). This was convenient because spermatophores were visible through the exoskeleton (Chu 1995). When the spermatophores were not visible by macroscopic observation, the adult male was classified as lacking spermatophores. If spermatophores were visible and occupied part (developing) or all (developed) of the terminal ampoule, males were classified as spermatophore-bearing males (Castilho et al. 2012, 2015). Thus, the reproductive activity of the population was estimated by the abundance of reproductive females [with developing and fully developed (mature) gonads] and spermatophore-bearing males. In the present study, recruit refers to the youngest individuals (juvenile males and females) which may be vulnerable to fishing gear (Sparre and Venema 1998).

Growth and Longevity Analyses

For each sample month, the length frequency (CLmm = the distance from the orbital angle to the posterior margin of the carapace) was distributed in size classes of 1 mm, and the modes were calculated using the program PeakFit. The specimen growth was identified for each sex, and the chosen cohorts were fitted in a Growth Model proposed by Von Bertalanffy (1938), given by $CL_\infty = [1 - \exp^{-k(t - to)}]$, where CL_∞ is the asymptotic length, k is the coefficient of growth and t_0 is the theoretical age when the size is equal to 0. The growth parameters were estimated for the different cohorts using the 'Solver' tool, varying the equation parameters ($CL_{\infty,}$ k and t_0). The criteria used to validate a cohort were the biological coherence with the life cycle of the species (the coherent estimate of longevity based on the duration of a cohort in time and values suggested in the literature). Comparisons of the growth curves were made using an F test ($p = 0.05$), in accordance to Cerrato (1990).

Longevity (= lifespan) was estimated by inverted Growth Model (Von Bertalanffy 1938) with the modification suggested by D'Incao and Fonseca (1999), considering $t_0 = 0$ and $CLi/L_\infty = 0.99$. The equation of longevity is given by: longevity $= 0 - (1/k) \text{ Ln } [1 - (CL_i/CL_\infty)]$.

The age of recruitment of those cohorts with smaller individuals and the age at which 50% of males and females became sexually mature was calculated by using the inverse of the growth equation: $t = t0 - (1/k) \ln [1 - CLt/CL_\infty]$ (King 1995).

SEXUAL MATURITY

Size at sexual maturity for males and females was determined using the proportion of juvenile and adult individuals in size classes of 1.0 mm CL. The procedure used here to estimate sexual maturity was based on fitting the sigmoid logistic curve (see Almeida et al. 2012). We used the equation $y = 1 / (1 + e^{[-r\,(CL - CL50)]})$, where y is the estimated proportion of adult shrimp, CL_{50} is the carapace size at the onset of sexual maturity, and r is the coefficient for the slope of the logistic curve. The logistic curve was fitted by least squares to the previously mentioned proportions per size class of all the individuals and samples using maximum-likelihood iterations. After adjusting the regression model, sexual maturity (CL_{50}) was estimated as the size at which 50% of males and females reached maturity.

STATISTICAL ANALYSES

For all analyses, in the station collection in which trawl yielded considerable biomass, the abundance in each sex and/or demographic class was extrapolated based on 200 g random subsample obtained for examination of carapace length, sex and reproduction condition.

Variation in male and female proportions in space and time were compared using a Chi-square test. The relationship between the demographic categories and the environmental factors was assessed using a Canonical Correlation Analysis (CCorrA). This is a multivariate statistical procedure that directly measures the strength of relationships between two sets of variables. The first set, used during the CCorrA, comprised the environmental characteristics (bottom water salinity and temperature, organic matter content, and φ), whereas the second set of variables included the abundance of the demographic classes (spent females, reproductive females, adult males without spermatophore, spermatophore-bearing males and recruits). Alternative data transformations were tested with respect to their capacity to improve the normality of the data, and the ln(1+x) was the most appropriate transformation based on the lowest Kolmogorov-Smirnov's D (more details see Castilho et al. 2008a).

All samples from both locations were incorporated into the same analysis. This approach is justified given that the goal of the present abiotic-biotic analysis was not to characterize each sampling location. Instead, by including the widest possible variation in environmental parameters, one would expect that the effects of these parameters on the demographic categories would become more apparent. The environmental factor and the demographic class that were correlated according to the CCorrA, were combined in each geographic coordinate sample using Surfer software (Version 10.4.799, Golden software, Inc.).

RESULTS

GROWTH AND LIFESPAN

A total of 64,641 individuals (39,358 in UB and in 25,283 CA) were collected during the present study, of which 6,928 were measured (3,604 from UB and 3,324 from CA, respectively). In UB, the mean size recorded was 14.5±2.8 mm CL, ranging from 6.3 to 27.1 mm in females, and 12.2±1.9 mm CL, ranging from 7.0 to 21.1 mm in males. Whereas in CA, 14.8±3.3 mm CL (6.7 to 27.3 mm) and 12.6±2.1 mm CL (6.7 to 21.2 mm) was observed in females and males, respectively. Juvenile size classes range by definition from 6-9 mm. Spent and reproductive females were distributed in the size classes from 10-27 mm, while adult males with or without spermatophores in the terminal ampoule were found in the size classes 10-24 mm (Fig. 2).

As a result of the variation in the calculated modes, eight cohorts of females and six of males were selected from UB (Figs. 3 and 4) and six cohorts of females and five of males from CA (Figs. 5 and 6).

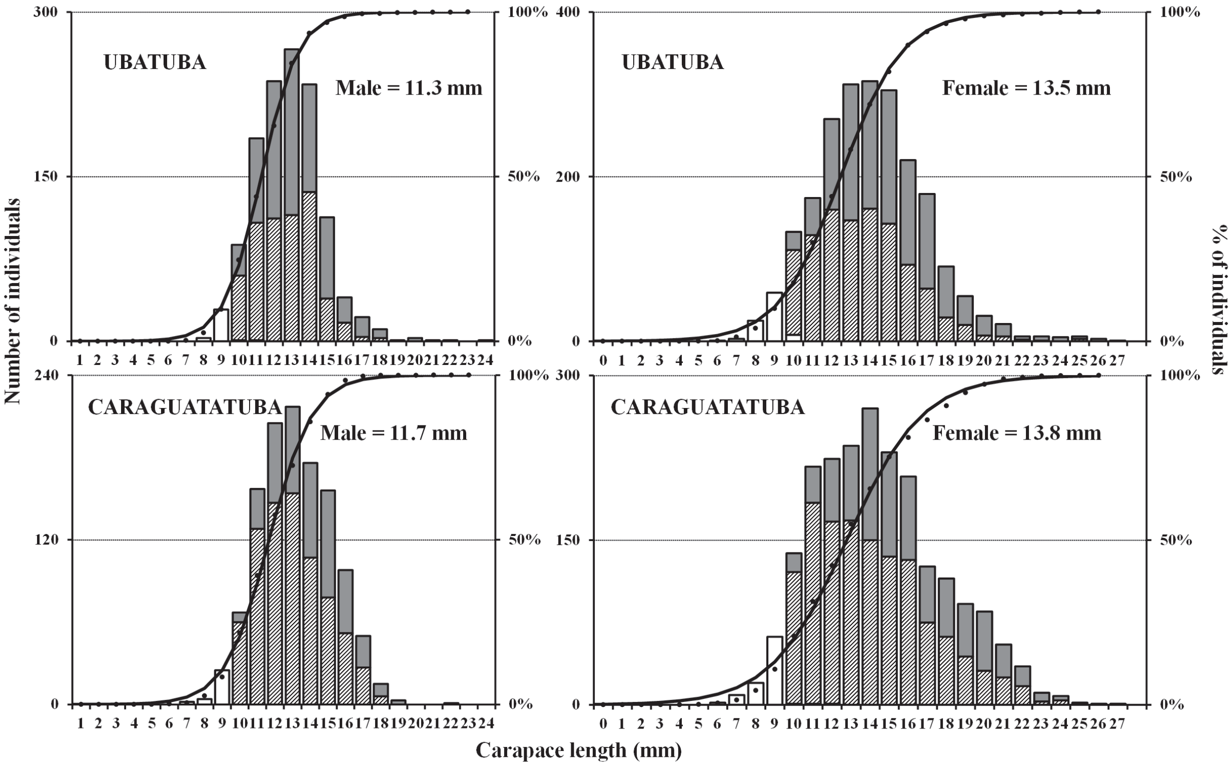

Figure 2 - Size frequency distributions and sexual maturity based on the CL50 (carapace length) of males and females sampled in Ubatuba and Caraguatatuba regions, northern coast of the state of São Paulo (Brazil). Unfilled bars: juvenile males and females; hatched bars: spermatophore-lacking males and spent females; shaded bars: spermatophore-bearing males and reproductive females.

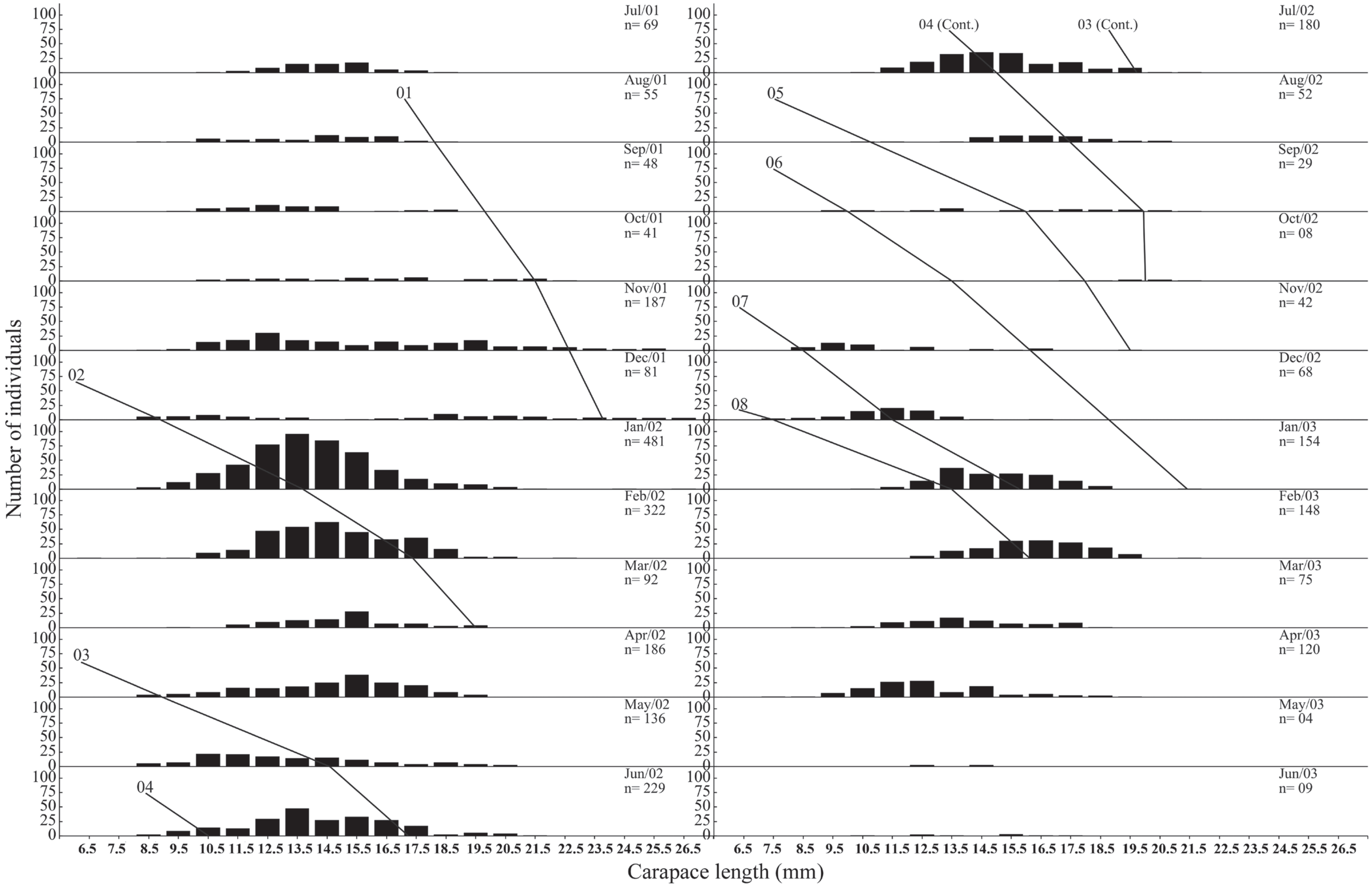

Figure 3 - Carapace length (CL) frequency histograms of female *Artemesia longinaris* in the Ubatuba region from July 2001 and June 2003. Lines represent the cohorts followed during the studied period to describe the individual growth.

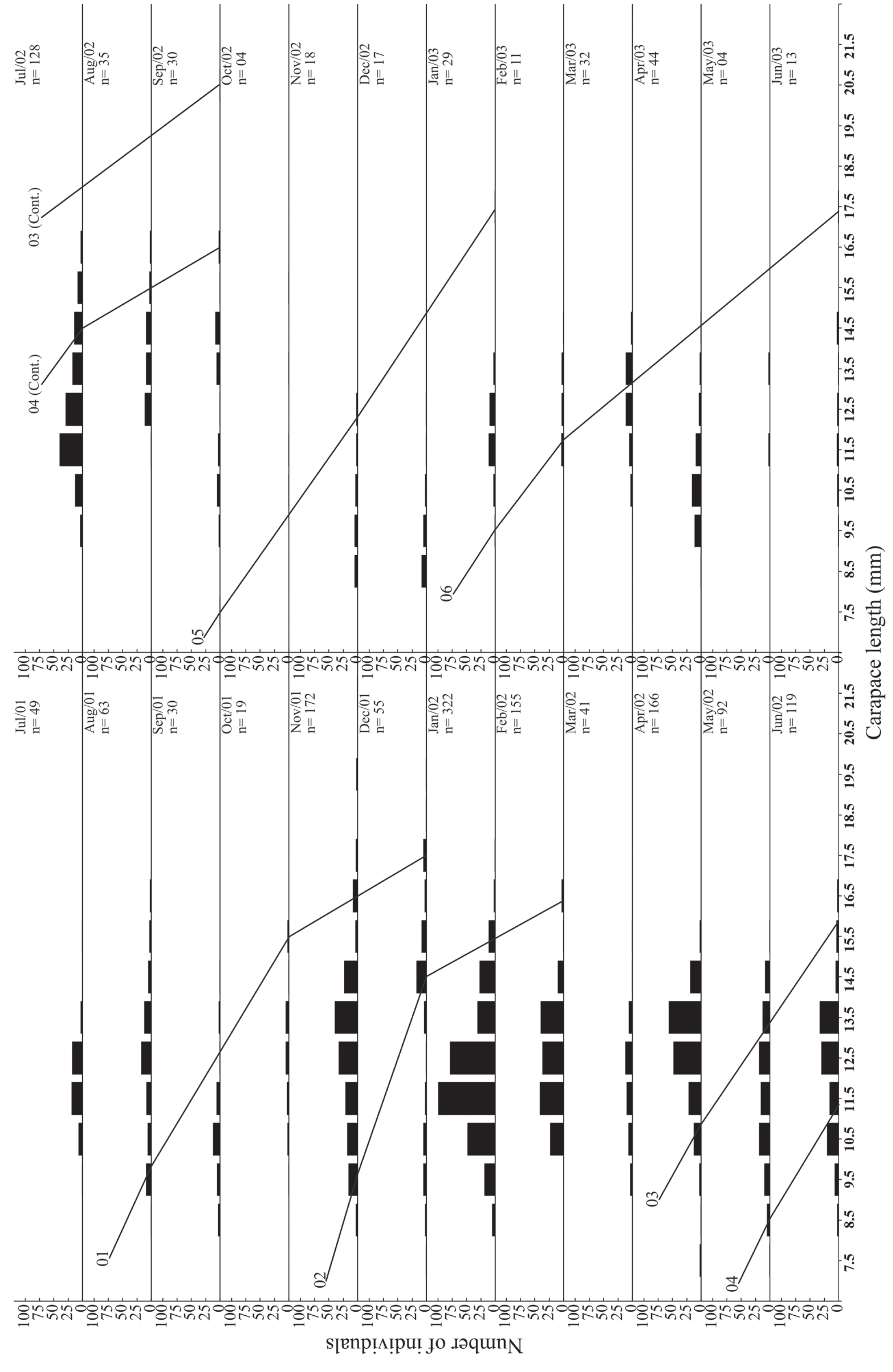

Figure 4 - Carapace length (CL) frequency histograms of male *Artemesia longinaris* in the Ubatuba region from July 2001 and June 2003. Lines represent the cohorts followed during the studied period to describe the individual growth.

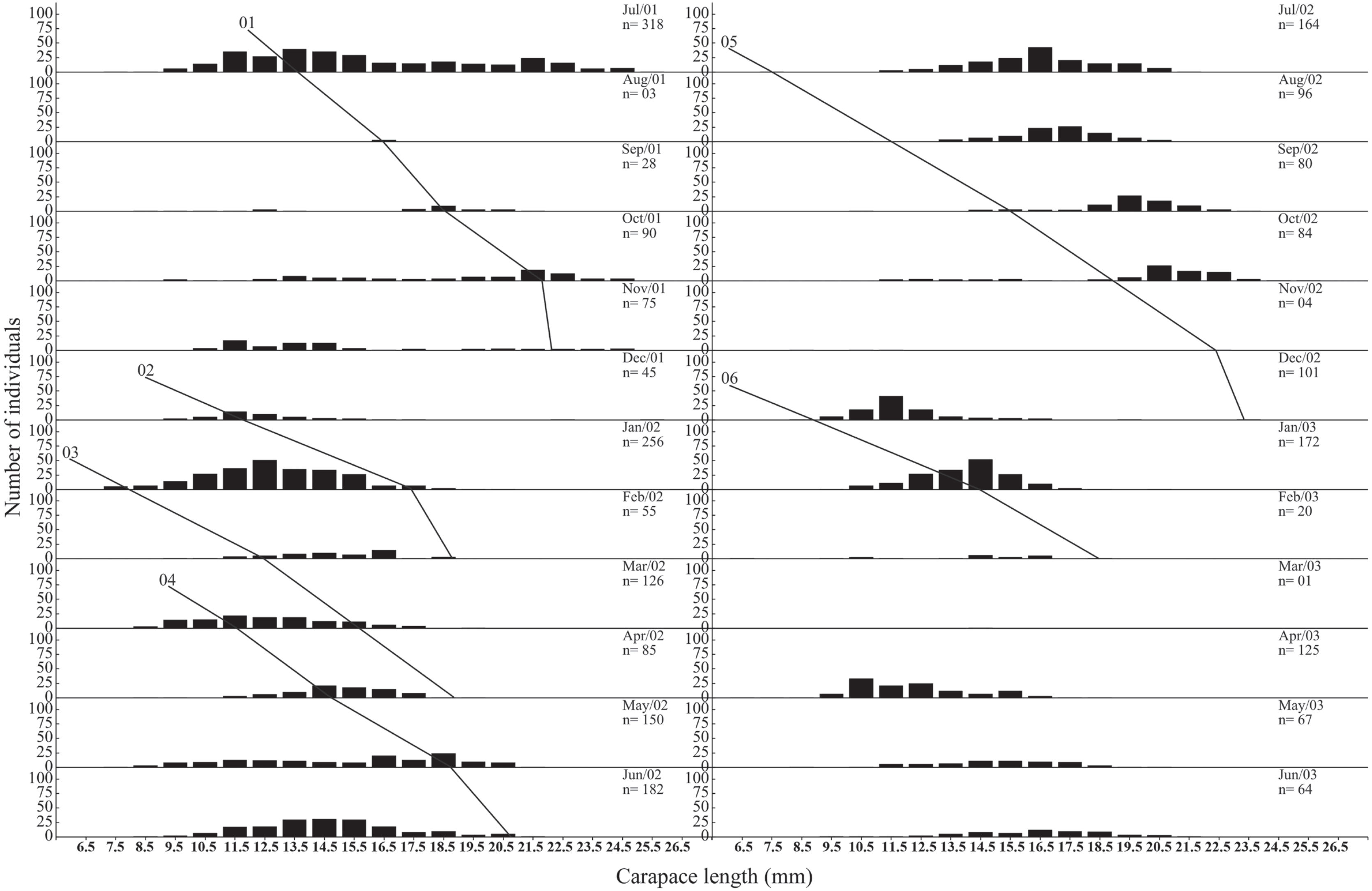

Figure 5 - Carapace length (CL) frequency histograms of female *Artemesia longinaris* in the Caraguatatuba region from July 2001 and June 2003. Lines represent the cohorts followed during the studied period to describe the individual growth.

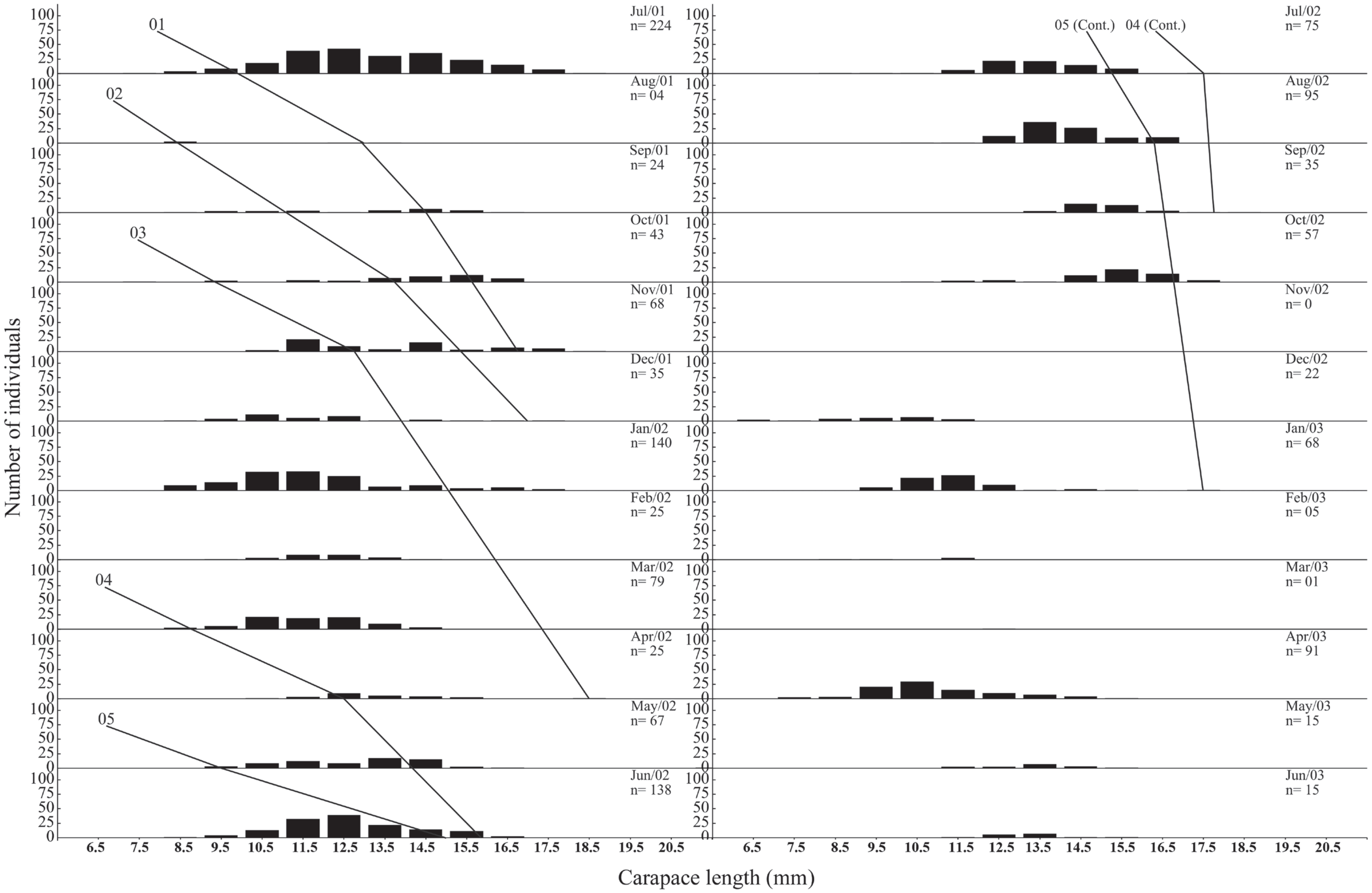

Figure 6 - Carapace length (CL) frequency histograms of male *Artemesia longinaris* in the Caraguatatuba region from July 2001 and June 2003. Lines represent the cohorts followed during the studied period to describe the individual growth.

The average growth curve, combining cohort curves for each sex in UB, resulted in the formulas: $CL_{\infty} = 26.1[1 - e^{-0.0097\,(t\,-\,0.0165)}]$ ($R^2 = 0.96$; $CL_{\infty} = 26.1$ mm; K= 0.0097/day; $t_0 = 0.0165$) for females and $CL_{\infty} = 19.7[1 - e^{-0.0122\,(t\,+\,0.0408)}]$ ($R^2 = 0.94$; $CL_{\infty} = 19.7$ mm; K = 0.0122/day; $t_0 = -0.0408$) for males. On the other hand, equations for the CA samples were: $CL_{\infty} = 26.4[1 - \exp^{-0.0110\,(t\,+\,0.0563)}]$ ($R^2 = 0.96$; $CT_{\infty} = 26.4$ mm; k= 0.0110/day, and $t_0 = -0.0563$) for females and $CL_{\infty} = 19.7[1 - \exp^{-0.0122\,(t\,-\,0.0125)}]$ ($R^2 = 0.89$; $CL_{\infty} = 19.7$ mm; k= 0.0122/day and $t_0 = 0.0125$) for males.

The calculated longevity, based on growth curves, was estimated as 475 days (1.3 years) for females, and 377 days (1.03 years) for males in UB, and 417 days (1.14 years) for females, and 376 days (1.03 years) for males in CA. The F test comparing the estimated curves from females and males showed significant differences between UB ($F_{calculated} = 70.88 > F_{critical} = 3.17$, p = 0.00) and CA ($F_{calculated} = 252.56 > F_{critical} = 3.20$, p = 0.00).

Sexual Maturity

In UB, the size at sexual maturity estimates (CL50) was 11.3 mm for males and 13.5 mm for females, which correspond to ages of 70 and 74 days, respectively. Whereas in CA, 11.7 mm CL50 males and 13.8 mm CL50 females was observed, which correspond de ages of 74 and 68 days (Fig. 2).

Reproductive Dynamics

Spent females showed the highest abundance (20,042 inds.), followed by reproductive females (19,130), adult males without spermatophore (12,991 inds.), spermatophore-bearing males (9,172 inds.), and recruits (3,306 inds.). In general, females were more abundant than males (Chi-square test, $p < 0.05$), mainly from January to February of each period, when the number of reproductive females was higher when compared to other months. The main reproductive period of January to February 2002 in both regions occurred after the coldest period registered in October to November 2001 (Table I).

A more evident inflow of male and female recruits (6-9 mm CL) on the population took place during spring-summer (December, 2001 and 2002 in UB, and January, 2002 December, 2002 in CA) and autumn-winter (April and May, 2002 in UB, and July, 2002 in CA) (Figs. 3, 4, 5 and 6). The minimum mean length of shrimp forming a cohort recorded was 7.41 mm (July 2002, Fig. 4) and 7.5 mm (December 2002, Fig. 2), which corresponds to a converted age of 30 and 42 days, respectively.

The CCorrA resulted in a canonical correlation coefficient of 0.31 (p = 0.00002), with 100% of the variance being extracted from the dataset of the environmental variables (total redundancy of 4.22%), whereas 96.46% of the variance was extracted from the dataset with information on the demographic class (total redundancy of 4.23%). The first root was statistically significant (p = 0.01), and salinity was the environmental variable with the highest factor loading (0.64), followed by temperature, which showed opposite sign in relation to salinity (-0.56). In addition, both factors showed high and opposite canonical weights (0.51 and -0.50, respectively), indicating a greater variation in these two variables. In the demographic class, reproductive females revealed high factor loadings (0.44) and canonical weight (2.42), followed by recruited juveniles (0.27 and 0.65).

Finally, variation in salinity and temperature were the environmental parameters with the highest influence on the demographic classes, particularly for reproductive females, such that their population size was correlated positively with salinity and inversely correlated with temperature (Fig. 7). Reproductive females and recruits were most common in depths greater, or over 10 m, greater salinity, and lower temperatures. However, a progressive decrease of the percentage of

TABLE I

Abundance, sex ratio, number of reproductive females and recruits (Recr.), and mean bottom temperature and salinity collected monthly in each region during July 2001 to June 2003. ♂:♀ = sex ratio; * = significant difference according to χ^2 test ($p < 0.05$); ♀♀ = reproductive females; Recr = recruits, Temp (°C) = temperature.

	UBATUBA						**CARAGUATATUBA**					
Months	N	♂:♀	♀♀	Recr	Temp °C	Sal	N	♂:♀	♀♀	Recr	Temp °C	Sal
Jul/01	182	1:1	71	0	21.4	34.8	147	1:1	19	3	20.9	35.0
Aug	118	1:1	45	7	19.8	34.5	7	1:1	2	2	20.9	36.7
Sep	268	1:2*	95	24	21.9	36.1	250	1:2*	145	2	20.7	36
Oct	65	1:2*	37	1	17.9	36.2	450	1:2*	124	14	19.0	36.3
Nov	822	1:1	94	34	16.7	35.1	163	1:1	25	0	19.0	35.9
Dec	308	1:3*	165	22	22.0	35.0	1,115	1:1	112	56	20.9	35.1
Jan/02	13,753	1:1	4,304	562	22.5	34.7	3,946	1:2*	613	801	21.1	36.8
Feb	11,164	1:4*	6,042	60	23.7	35.2	4,527	1:2*	905	113	23.3	35.3
Mar	1,061	1:3*	180	11	26	33.7	932	1:2*	120	67	22.7	35.3
May	3,126	1:1	906	32	20.4	34.7	1,833	1:3*	715	36	21.2	36.4
Apr	1,698	1:1	322	210	23.1	36.4	5,199	1:2*	463	384	23.9	36.0
Jun	1,355	1:2*	176	115	23.1	36.2	717	1:1	142	15	22.9	34.7
Jul	808	1:1	213	4	22.6	34.9	2,027	1:2*	354	18	22	35.3
Aug	109	1:1	0	73	22.4	34.6	484	1:1	113	4	22.1	32.3
Sep	73	1:1	25	6	19.9	35.1	189	1:2*	96	0	20.9	34.4
Oct	20	1:2	8	8	22.6	35.3	178	1:1	44	0	22.9	35.7
Nov	109	1:2*	9	53	22.5	35.1	5	100%♀	1	2	22.9	35.0
Dec	376	1:4*	178	103	20.0	35.9	320	1:5*	70	26	21.4	35.0
Jan/03	2,642	1:3*	1,232	1	21.0	35.0	1,769	1:2*	536	29	20.4	35.9
Feb	376	1:14*	154	0	21.5	36.5	25	1:4*	5	1	22.9	34.6
Mar	651	1:2*	216	2	24.6	34.0	3	1:2	2	0	24.5	36.0
May	238	1:3*	27	29	25.4	35.1	829	1:1	0	367	25.6	35.0
Apr	14	1:2	2	0	23.4	35.5	89	1:4*	4	7	22.7	35.3
Jun	22	1:1	3	1	23.6	33.5	79	1:4*	12	1	23.3	32.7
Total	**39,358**	**1:2***	**14,504**	**1,358**			**25,283**	**1:2***	**4,622**	**1,948**		

demographic classes was noticed at depths superior to 25 m in both regions. Reproductive females concentrated mainly at 15 m and 20 m of UB region and higher abundances of recruits were collected at 20 m and 15 m of UB and CA, respectively (Fig. 7).

DISCUSSION

The shrimp *A. longinaris* showed variation in the spatio-temporal distribution, sex-ratio, population growth, and age structure among sexes, with the observation of all demographic classes, from juveniles to adults. These results corroborate the assertion by Castilho et al. (2007a) that this species completes its life cycle in the southeastern coast of Brazil. The observed differences among sexes in the growth analysis reflects the biology of *A. longinaris* and confirms the existence of sexual size dimorphism, with females showing larger

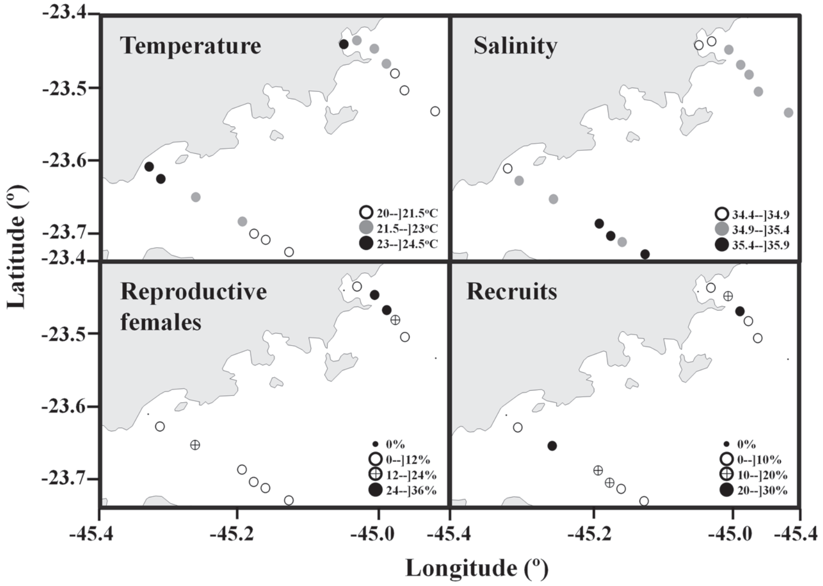

Figure 7 - Spatial variation of the abiotic factors (temperature and salinity) and percentage of *Artemesia longinaris* (N) in each demographic groups (reproductive females and recruits), at each region sampled, from July 2001 to June 2003.

dimensions, smaller growth rates, and greater longevity (Boschi 1969). According to Boschi (1989), sex-related differences in body length are a general rule among penaeoid shrimp. Costa and Fransozo (2004), Castilho et al. (2007a, 2008b, c, 2015), Grabowski et al. (2014) reported smaller sizes in males of *Rimapenaeus constrictus* Stimpson, 1874, in *A. longinaris*, in *Pleoticus muelleri* (Spence Bate, 1888), in *Sicyonia dorsalis* Kingsley, 1878, and in *Xiphopenaeus kroyeri* (Heller, 1962). Gab-Alla et al. (1990), Yamada et al. (2007) and Simões et al. (2013) suggested that this sexual dimorphism is probably a result of the exponential increase in female fecundity with body size, i.e. the large body size of females may be an adaptation to increase egg production.

Growth in Penaeoidea is influenced by environmental factors. As such, higher temperatures in tropical regions would be expected to induce an increase in the growth coefficient through higher metabolism, but a decrease in CL. Castilho et al. (2007b) verified differences in sizes of *A. longinaris* along the South American coast indicating a latitudinal shift to larger sizes (CL) with increasing latitude. Hartnoll (2001) suggests that the increase in temperature can have an opposite effect in relation to the growth rate due to the reduction in the intermolt period, i.e. with the increase in temperature, the growth rate increases due to the shortening of the intermolt interval and the consequent decrease in its increment. The longevity obtained here (latitude 23º S) of 1.03 – 1.14 years is smaller than the 1.7 – 1.8 years verified in Mar del Plata region (Argentine, latitude 37º S) for Boschi (1969). Therefore, the results of the present study for *A. longinaris* confirm the paradigm of the latitudinal effect, i.e. congener or conspecific populations tend to reach larger sizes and, consequently, live longer with increasing latitude (Bauer 1992, Castilho et al. 2007b). However, the growth coefficient (K) did not show any apparent variation according to region of origin in either sexes, possibly because the geographical proximity between regions establishes a migratory connection between groups that are part of the same population.

Artemesia longinaris lives exclusively in the marine environment throughout its life cycle with individuals usually migrating from inshore to offshore areas during their ontogeny (Boschi 1997). Moreover, shrimp migration is not restricted to the inshore-offshore axis, as individuals are able to use marine currents throughout their life cycle. *Litopenaeus setiferus* (Linnaeus, 1767) is able to migrate up to 580 km through the Atlantic coast, whereas *Melicertus plebejus* (Hess, 1865) can move 930 km along the Australian coast (Fenucci 1988). The shrimp *A. longinaris*, together with *P. muelleri*, can be considered as indicator species of the inbound cold water and these species use the South Atlantic Central Water (SACW) to migrate along the São Paulo coast (Costa et al. 2004, 2005). The SACW intrudes throughout late spring and summer, causing decreases in temperature (< 20º C) (Castro-Filho et al. 1987). The studied species shows abundance peaks associated with the arrival of the SACW, mainly in the first year when the bottom water temperature was colder. Pires-Vanin et al. (1993) recorded thermal seasonality caused by SACW similar to the annual variation reported in this study, being characterized by a reduced penetration in December 1986 and an intense one in December 1988. The limited influence of SACW on the second year of research probably resulted in a reduction in the population of *A. longinaris*, especially of reproductive females. According to Vega-Pérez (1993), during the intrusion of SACW there were higher values of chlorophyll, reflecting in increases on phytoplankton production. This increased primary productivity may stimulate subsequent production of herbivorous zooplankton. In coastal marine animals, spawning events typically coincide with springtime production of phytoplankton, upon which the newly spawned larvae feed. From the point of view of chronobiology, repeatability of annual spawning dates is interesting because it suggests that crustaceans and fish possess endogenous circa-annual biological clocks that control spawning (Naylor 2005). These biological clocks, along with abiotic factors such as photoperiod and temperature which may constrain them, are proximate factors controlling spawning while the ultimate factor to which spawning is timed by the annual cycle of larval food supply (spring plankton bloom). Variation of plankton production is correlated with high and low frequencies of females with mature gonads, suggesting that food availability for protozoeal larvae (indicated by phytoplankton production) may be an important selective factor shaping the seasonal breeding pattern of this species. In a 5.5 years of study, Castilho et al. (2007a, 2008b, c, 2012, 2015) found the same reproductive investment in summer months with the shrimp *A. longinaris*, *P. muelleri*, *S. dorsalis*, and *X. kroyeri*, demonstrating that the primary production is an essential resource by penaeid shrimp in a match/mismatch theory of Cushing (1975), where the maximum reproductive investment of marine planktotrophic species coincides with the seasonal maximum abundance of phytoplankton.

Several authors have suggested that the distribution of penaeoid shrimp is strongly modulated by the texture and organic content of the substrate (Boschi 1969, Dall et al. 1990, Castilho et al. 2008c). However, no correlation in CANONICA analysis was detected between demographic classes and characteristics of the substrate. The present study found few specimens in coastal areas (depth smaller than 15 m), even when abiotic characteristics such as sediment type were favorable to their establishment. We suggest that the combination of lower salinity and high temperature in shallow coastal waters may prevent this species from entering sites shallower than 15 m. This proposition corroborates the record of Costa et al. (2005) that salinity and temperature might play a role in determining the ecological distribution of

A. longinaris, a species typical of colder regions, occurring in a temperature range from 15 to 21º C and salinity above 33.

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RESUMO

O presente estudo investigou o crescimento, longevidade e dinâmica reprodutiva de *Artemesia longinaris* na costa sudeste do Brasil, durante um período de dois anos. Coletas mensais foram conduzidas em Ubatuba e Caraguatatuba, usando um barco de pesca de camarão equipado com redes “doublerig”. Cada região foi dividida em sete estações amostrais com profundidades de até 35 m. Frequência de classes de tamanho, crescimento, longevidade, razão sexual e abundância de indivíduos em cada classe demográfica foram comparadas. A relação entre os fatores ambientais e a abundância de cada classe demográfica foi analisada utilizando a Análise de Correlação Canônica. Um total de 64.641 indivíduos foi coletado (6.928 analisados), com longevidades estimadas de 1,30 (Ubatuba) e 1,14 (Caraguatatuba) anos para fêmeas e 1,03 anos para os machos de ambas as regiões. Houve um desvio estatisticamente significativo na razão sexual a favor das fêmeas (teste Qui-quadrado, $p < 0,05$) em ambas as regiões. A Análise de Correlação Canônica resultou em um coeficiente de correlação canônica de 0,31 ($p = 0,00002$). A salinidade e a temperatura apresentaram alta correlação principalmente com a presença de fêmeas reprodutivas. Em geral, esta classe demográfica foi mais comum em condições de baixa temperatura e alta salinidade. Estes resultados, tal como outros obtidos em estudos abordando regiões de temperaturas mais frias com a espécie, encontram-se em conformidade com o padrão proposto pelo clássico paradigma do efeito latitudinal.

Palavras-chave: seleção por habitat, variação latitudinal, longevidade, Penaeoidea, dinâmica reprodutiva.

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