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LATITUDINAL VARIATION IN POPULATION STRUCTURE AND REPRODUCTIVE PATTERN OF THE ENDEMIC SOUTH AMERICAN SHRIMP *ARTEMESIA LONGINARIS* (DECAPODA: PENAEOIDEA)

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ABSTRACT

Population structure and reproductive maturity of females were investigated in the shrimp *Artemesia longinaris* Bate, 1888 from coastal waters of northern São Paulo State (Brazil, 23°S) and Mar del Plata (Argentina, 38°S) from June 2001 to May 2002. Monthly collections were taken by commercial shrimp fishing boats equipped with bottom trawl nets. Population parameters from size frequency distributions and size (carapace length = CL) of female reproductive maturity were analyzed and compared from the two sampling areas. Latitudinal trends in reproductive parameters of *A. longinaris* were shown in overall body size and size of reproductive maturity, both of which were smaller in females from the tropical location than those from the cold-temperate sampling area. Largest females ($>$ 30 mm CL) were collected in Argentina, while Brazilian specimens reached maximum size at 27 mm CL. The smallest size of female sexual maturity was estimated at 13.6 mm CL in Brazilian samples compared to 22.1 mm CL calculated for those from Argentina. Populations from both regions exhibited a bimodal size distribution in the spring, with the peak at small body size probably corresponding to recent recruits and the peak at larger body size to reproductive females or shrimps migrating in from deeper waters or other latitudinal regions. In late spring and summer, an intrusion of the cold South Atlantic Coastal Water mass was observed which lowered water temperature and stimulated plankton production, the primary food source for the larvae of a typically cold-temperate species such as *A. longinaris*. The trend of increasing body size and delay of sexual maturity with increasing latitude appears to be correlated with the decreasing water temperature and increasing plankton productivity at higher latitudes.

Introduction

One of the principal objectives in the study of the reproductive ecology of benthic invertebrates is to describe latitudinal trends in population structure and their reproductive seasonality. Description and analysis of such trends may reveal the causal factors responsible for these latitudinal trends (Bauer, 1992). Knowledge of the magnitude and scale of causal factors affecting reproduction and population structure is important for effective fisheries management of crustacean species (Bauer and Rivera Vega, 1992; Kuhlmann and Walker, 1999).

Latitudinal differences in benthic communities come about through evolutionary changes brought on by the movement, transport, isolation, and mixing of species caused mainly by ocean circulation patterns and tectonic activity. Factors that cause evolutionary changes are variation in hydrographics (temperature, salinity, and oxygen concentration), hydrodynamics (horizontal and vertical mixing), primary production, geological processes affecting terrestrial runoff, aeolian deposition, and sedimentation, as well as an array of other abiotic and biotic factors. At all latitudes, temporal and spatial variability in community patterns on ecological time scales is driven mainly by variation in primary production, sediment type, disturbances, and biotic interactions (Lenihan and Micheli, 2001).

Boschi (2000) stated that between the Argentinean and Brazilian Biogeographic Provinces there is a transitional region with mixture of water masses where euryhaline and eurythermal species have become established. In this latitudinal gradient (23°S to 43°S), the shrimps *Artemesia longinaris* Bate, 1888 and *Pleoticus muelleri* (Bate, 1888) have adapted to the different environmental conditions of the tropical-subtropical and temperate regions within these latitudes. The geographical distribution of *A. longinaris* is restricted to the Western Atlantic, from Rio de Janeiro, Brazil (23°S) to Rawson, Argentina (43°S). This shrimp lives exclusively in the marine environment throughout its life cycle (Boschi, 1997).

Beginning in 1965, several studies of this species were conducted in Argentinean waters where this species is important, not only for commercial fisheries, but also as a major component of marine food webs (Boschi, 1969; Boschi and Scelzo, 1977; Petriella and Bridi, 1992; Boschi, 1997 and Gavio and Boschi, 2004). However, still relatively little is known about the reproductive biology and population structure of *A. longinaris*. Fransozo et al. (2004), Castilho (2004), and Costa et al. (2005) studied aspects of its ecological distribution. In Brazil, studies of this species are increasing because of the decline in landings of commonly exploited crustacean species such as the pink shrimps

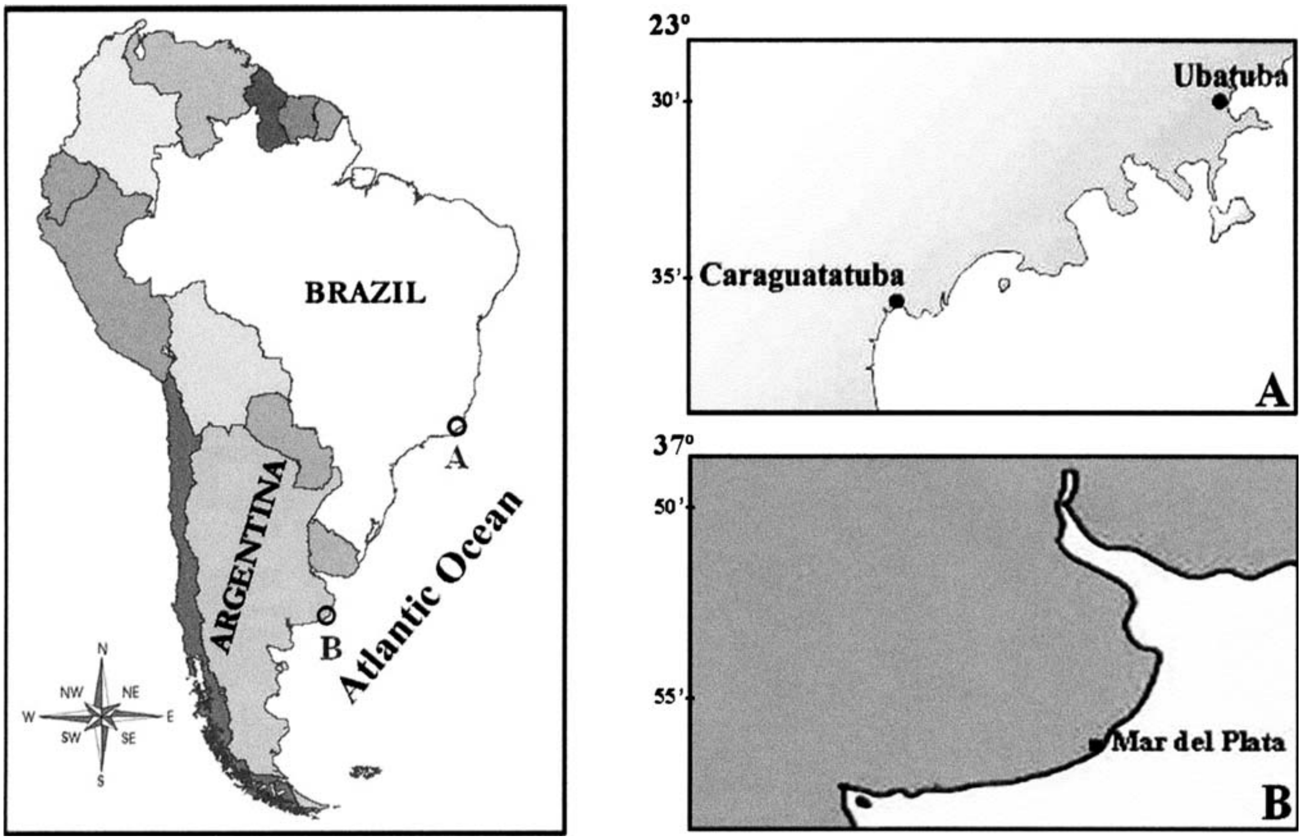

Fig. 1. Study areas: A, Northern coast of São Paulo state; B, Coast of Mar del Plata.

Farfantepenaeus brasiliensis (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967), the white shrimp *Litopenaeus schmitti* (Burkenroad, 1938) and the "seabob," *Xiphopenaeus kroyeri* Heller (1862) (D'Incao et al., 2002; Costa et al., 2005). Recently, Castilho et al. (in press) investigated the reproductive periodicity of *A. longinaris* from southeastern Brazil.

Thus, the objectives of the present study are to compare differences in the population structure and size of reproductive maturity in females of *A. longinaris*, as well as to discuss probable causal factors, or selective pressures, affecting the population dynamics of this species in the Brazilian and Argentinean coasts.

Materials and Methods

Artemesia longinaris was collected monthly from June 2001 to May 2002 along the northern coast of São Paulo State, located in Ubatuba (23°30′S) and Caraguatatuba (23°37′S) (Fig. 1A). During each month, seven 2-km transects were trawled over a 30-min period in depths between 5-35 m. Trawling was done from a shrimp fishing boat equipped with two double rig nets (mesh size 20 mm and 15 mm in the cod end). At Mar del Plata (37°59′S) (Fig. 1B), shrimp were caught by commercial fishing boats of 9-12 m length equipped with bottom trawl nets at 5-10 m depth. A mesh size of 20 mm in the cod end used by fishermen was utilized for this study. Fishermen, in general, retain shrimp that attain commercial size, but here all specimens collected were kept for further analyses and for comparison of both populations.

Carapace length (CL), a standard measure of body size in shrimps, was measured to the nearest 0.1 mm in females, and is defined as the distance between the posterior margin of the eye orbit and the posterior margin of the carapace. Size frequency distributions were constructed using 1 mm CL size classes. Parameters from size frequency distributions were calculated using the method of MacDonald and Pitcher (1979) with the program MIX, which identifies modes in overlapping polymodal size distributions using maximum likelihood to calculate the components of each distribution.

Adult females were determined by macroscopic observation of the degree of ovarian development (color and volume occupied by the gonads). Ovaries categorized as immature varied from thin, transparent strands to thicker strands. The reproductive status of males was assessed by examining the shape of the petasma, which is fused in adult individuals (Boschi and Scelzo, 1977; Castilho et al., in press).

The relative frequency (%) of adult females in each size class were plotted and the logistic function $y = 1/1 + e^{r(CL - CL_{50})}$ was fitted to data, where $CL_{50\%}$ corresponds to the size at which 50% of the individuals are considered mature and r stands for the slope of the slope. Fitting to the curve was carried out following the least squares method (Aguillar et al., 1995; Vazzoler, 1996), which reveals a size range overlap of adults and young of at least two size classes. The hypothesis of no difference in the proportion of females between two populations was tested with the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1995).

Results

A total of 3202 females were analyzed in this study, from which 2423 were sampled in the northern coast of Sao Paulo State (Brazil) and 779 in the Mar del Plata coast (Argentina). Overall, largest individuals up to 30 mm carapace length (CL) were collected in Argentina, while Brazilian specimens reached maximum size at 27 mm CL. The smallest adult female from Brazilian samples was 6.3 mm CL while the smallest from Argentina was 8.0 mm CL.

The proportion of adult females in 1 mm size classes increased logistically with carapace length in both regions studied (Fig. 2). The estimated onset of sexual maturity was markedly different at regions increasing further south. It

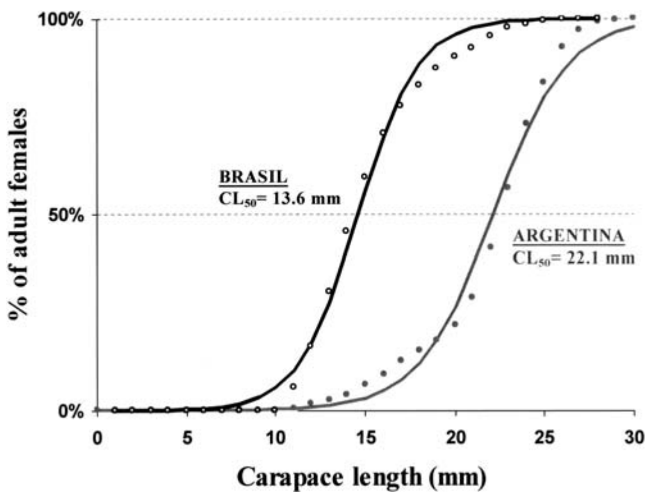

Fig. 2. *Artemesia longinaris*. Sexual maturity based on the $CL_{50\%}$ (carapace length) of females sampled in northern coast of Sao Paulo State (Brazil) and Mar del Plata coast (Argentina), from fall/2001 to summer/2002.

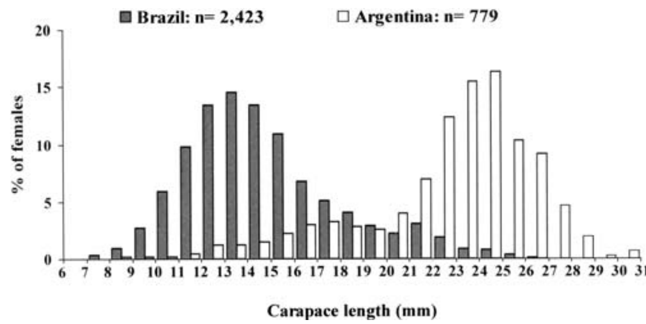

Fig. 3. *Artemesia longinaris*. Size frequency distributions of females sampled in northern coast of Sao Paulo State (Brazil) and Mar del Plata coast (Argentina).

clearly occurred at smaller sizes in Brazilian waters with $CL_{50\%} = 13.6$ mm, while in samples from Argentina $CL_{50\%} = 22.1$ mm (Fig. 2).

The overall size-frequency distributions of *A. longinaris* from the two sampling areas were significantly different (Kolmogorov-Smirnov two-sample test; $d_{max} = 0.73$, $P < 0.01$). The Argentinean population showed a modal peak at 24-25 mm CL, 11 mm larger than that of the Brazilian population, which peaked at 13-14 mm (Fig. 3). Both populations exhibited a unimodal size-frequency distribution in autumn and summer. However, size frequency distributions were bimodal in spring samples (Fig. 4). The peak of smaller individuals in the spring size-frequency distributions is indicative of a recruitment event. A marked increase in carapace length of modes was observed from autumn to winter, indicating growth in size (Fig. 4, Table 1), but largest Brazilian's individuals corresponding to the older size class disappeared from spring to summer (Fig. 4).

Discussion

Several authors have suggested a paradigm of latitudinal trends in the population dynamics of penaeoidean shrimps (Bauer, 1992; Bauer and Rivera Vega, 1992; Boschi, 1997; Gavio and Boschi, 2004; Costa and Fransozo, 2004; Costa et al., 2005; Castilho, 2004; Castilho et al., in press). In Chubut Province, Argentina (43°S), Boschi and Mistakidis (1966) found females as large as 37 mm CL, 7 mm larger than the largest specimens collected in Mar del Plata waters (37°S) (Boschi, 1997). In contrast, females taken along the Brazilian coast at Rio Grande do Sul (32°S) reached 28 mm CL (Dumont, 2003), while the largest specimens of *A. longinaris* captured in Northern Littoral of São Paulo state (23°S) were even yet smaller (27 mm CL).

A similar trend in decreasing body size with decreasing latitude was observed in the size of sexual maturity, which was estimated at 22.1 mm CL at 37°S, 17 mm CL at Rio Grande do Sul (32°S) (Dumont, 2003), and 13. 6 mm CL at 23°S. Bauer (1992) compared the longevity and size of females of *Sicyonia* spp. from tropical, subtropical, and cold-temperate regions, and found that cold-temperate females live longer and grow larger than tropical sicyoniids. Based on our results, we confirm that Bauer's hypothesis on female body size and sexual maturity applies to *A. longinaris*. In a tropical region (São Paulo State), females are smallest and mature at smaller sizes compared to a more southern temperate region as Mar del Plata. Life span was calculated to last 20-22 months in this coastal area (Boschi, 1969), but we have as yet no age estimates for the northern (lower latitude) Brazilian population. However, we suggest that variations in life history parameters such as longevity, body size and size at sexual maturity are modified by habitat conditions correlated with latitude, such as water temperature, nutrient supply, and resultant primary productivity that forms the basis of the larval food supply.

The bimodal structure of both populations in spring is predictable and related to the reproductive and migratory behavior of this species. In a 5.5 year study on *A. longinaris* from the northern littoral of São Paulo State, Castilho et al. (in press) describe, from changes in size frequency distributions, one peak at smaller body size that corresponds to recruitment events and another peak composed of larger individuals migrating from deeper waters and other latitudinal regions. On other hand, the unimodal peak verified only in the Ubatuba region confirms the hypothesis of Costa et al. (2005) that *A. longinaris* migrates farther north along the Brazilian coast (like Rio de Janeiro littoral) during the intrusions of the SACW in summer.

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 of interest by suggesting 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 is the annual cycle of larval food supply (spring plankton bloom).

Studies done on *A. longinaris* suggest that this species can be considered a typical warm-temperate marine species. Boschi (1969), Ruffino and Castello (1992), Fransozo et al. (2004), Costa et al. (2005) and Castilho et al. (in press)

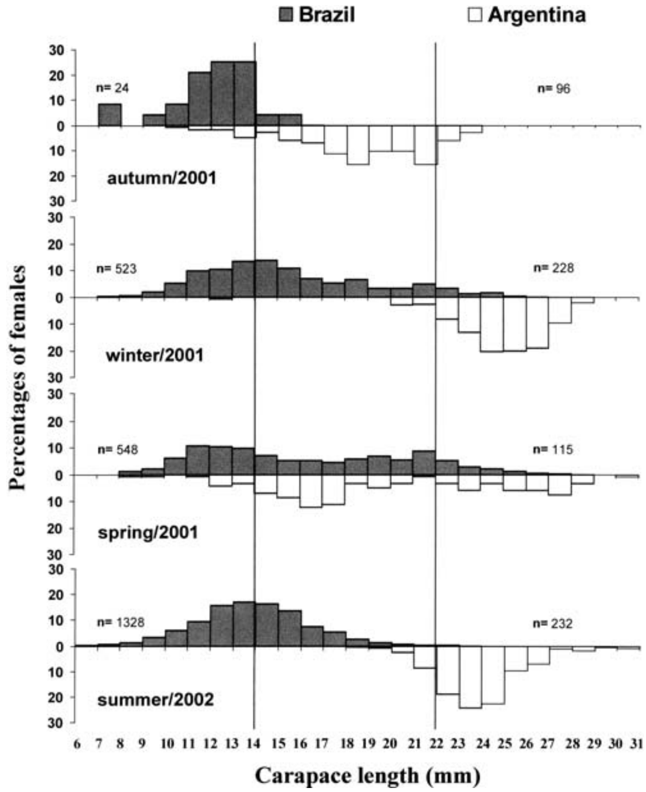

Fig. 4. *Artemesia longinaris*. Seasonal size frequency distributions of females sampled in the northern coast of Sao Paulo state (Brazil), and females collected in Mar del Plata coast (Argentina; inverted bars). Lines: estimated sexual maturity (CL_{50}).

showed that this species prefers temperatures ranging from 15-21°C. In laboratory studies, Lopez and Fenucci (1988) reported that those temperatures were optimal for best growth and longevity, while the intermolt period decreased at higher temperatures.

In southeastern Brazil, the upwelling current of the South Atlantic Central Water (SACW) is responsible for the decrease of the coastal water temperature during spring and the first months of summer, with minimum values of 15°C, among other changes in the bottom water characteristics (Castro-Filho et al., 1987). According to Vega-Pérez (1993), during the intrusion of SACW in the Ubatuba region, there are higher values of chlorophyll, reflecting increases in phytoplankton production. This increased primary production may stimulate subsequent production of herbivorous zooplankton. Highest densities of planktonic organisms was found during summer, while lowest values were observed during winter.

In the Mar del Plata coast, Christiansen and Scelzo (1971) and Petriella and Bridi (1992) observed a highly seasonal breeding and spawning period in *A. longinaris*, from which the percentage of mature females was high from October to January (spring to early summer) while breeding apparently ceases during the rest of the year. Sea surface water temperature increases from November peaking in February at 21°C, with the highest chlorophyll concentration present in the area in spring (Carreto et al., 1995; Hoffmann et al., 1997).

Table 1. Parameters obtained by the MIX program from size frequency distributions of *Artemesia longinaris* females from the northern coast of Sao Paulo state (Brazil) and from Mar del Plata coast (Argentina). Prop: proportion, SD standard deviation, *d.f.* degrees of freedom. χ^2: Chi square test. A, autumn; W, winter; Sp, spring; S, summer.

Season	Prop.	Mean	SD	Prop.	Mean	SD	χ^2	*d.f.*	*P*
Brazil									
A/2001	1.00	11.03	1.98				8.92	6	0.18
W/2001	0.74	12.72	2.14	0.26	19.15	2.36	16.64	13	0.22
Sp/2001	0.50	11.56	1.79	0.50	19.13	2.78	11.57	14	0.64
S/2002	1.00	12.90	2.34				11.41	14	0.65
Argentina									
A/2001	1.00	17.52	3.05				13.42	11	0.27
W/2001				1.00	23.97	1.80	11.51	6	0.07
Sp/2001	0.63	15.34	2.67	0.37	24.81	0.40	19.27	20	0.31
S/2002	1.00	22.80	1.70				11.73	13	0.23

The 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 in this species (Castilho et al., in press). We suggest that the population structure and size of female maturity in *A. longinaris* are a result of reproductive adaptations to environmental factors, mainly temperature, nutrient supply, and subsequent plankton production as constrained by intrinsic physiological limitations.

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