

Growth and reproductive pattern of the caridean shrimp *Palaemonetes argentinus* Nobili, 1901 (Decapoda: Palaemonidae) in the south of Rio Grande do Sul, Brazil

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Abstract

In crustaceans, due to the absence of permanent hard parts which can be used for age determination, methods based on length-frequency distributions (e.g., Modal Progression Analysis – MPA) are commonly employed for ageing. However, the linkage of the cohorts followed during a period of time, brings uncertainty to the analysis. The present study suggests inclusion of biological aspects to validate the parameters estimated by the von Bertalanffy growth model (VBGM). The population of *Palaemonetes argentinus* analyzed here inhabits a closed lagoon near the Patos Lagoon (Lagoa dos Patos) estuary. Samples were collected fortnightly from June/1996 to December/1997 and carapace growth was estimated by using the VBGM. Biological aspects such as reproductive season, sex ratio and maximum carapace length were used to validate VBGM parameters. The growth parameters estimated were $L_{\infty}=8.00$; $k=0.29/\text{month}$; $t_0=-0.34$ for females and $L_{\infty}=6.67$; $k=0.34/\text{month}$; $t_0=-0.38$ for males. The main reproductive season is spring, and brooding females were observed along the year, except on June-July/1996 and May-June/1997. The mean size of first maturity estimated was 6.5 (CL-mm). The validation of the VBGM parameters by using biological aspects has showed coherent results, reducing the uncertainty in choosing the modal groups that really describe the individual growth of the species.

Key words: *Palaemonetes argentinus*, growth, reproduction, biology, von Bertalanffy

Introduction

The caridean shrimp *P. argentinus* Nobili, 1901 is distributed along the east coast of South America, inhabiting salt, fresh and brackish water environments. The northern limit of occurrence is considered the Santa Catarina State (Brazil), and the southern Buenos Aires Province (Argentina) (Holthuis, 1952; Boschi, 1981; Buckup and Bond-Buckup, 1989). This species tolerates a wide range of salinity, but is physiologically better adapted to low and very low salinity environments (Charmantier and Anger, 1999). All developmental stages are usually found inside the coastal lagoons, indicating larval development within the parental habitats (Anger *et al.*, 1994).

The larval development of freshwater species of Palaemonidae is usually abbreviated, presenting only three stages. However, *P. argentinus* has nine larval stages, suggesting that this species is a recent fresh water habitant (Menú-Marque, 1973) and therefore is likely to be under heavy selection pressure. Due to its high abundance and small size, this species seems to be very important in the intermediate trofic level in the estuarine zone of the Patos Lagoon, since it regulates the larval and juvenile abundance of several species (Bemvenuti, 1997).

Despite of evolutionary and ecological importance, the population dynamics of *P. argentinus* is poorly understood, particularly in the southern coastal lagoons of the Rio Grande do Sul

State (RS). The studies currently available include estimation of growth parameters and reproductive pattern for the northern RS populations (Gonçalves and Fontoura, 1999); determination of the reproductive season and temporal variation of the abundance of a population from Santa Catarina State (SC) (Müller and Araújo, 1994); molt, reproductive behavior and growth in laboratorial conditions (Setz and Buckup, 1977; Souza and D'Incao, 1996) as well as the growth (Setz and Buckup, 1977). Several investigations were performed in Argentinean populations, such as life history parameters (Capitulo, 1992; Capitulo and Freyre, 1989; Schuldt and Damborenea, 1987), ecological (Donati, 1986) and reproductive analysis (Goldstein and Cidre, 1974).

The aim of this paper is to estimate growth parameters by fitting the von Bertalanffy growth model (VBGM), and to estimate mean length at sexual maturity of RS southern population of *P. argentinus*, providing information to support comparison between different populations. Reproductive pattern, sex ratio and maximum lengths were used to validate the growth parameters, in the attempt of reduce uncertainty on length-based analysis.

Material and Methods

Samples were obtained from June/1996 to December/1997 in the Pond of Marrecas (31° 55'13"S, 52° 09'16"W), Island of Torotama, district of Rio Grande, Rio Grande do Sul State, Brazil. This pond is a closed water body, except in periods of high pluviosity when a small channel is formed linking the pond to the estuarine zone of the Patos Lagoon (Fig. 1).

Samples were taken fortnightly, using a manual net with 2mm mesh size. Due to the small size of the pond (80 m²), and the homogeneity in sediment and vegetation composition only one sample station was established, in which were performed three manual trawls with standardized sampling effort. Salinity and temperature (°C) were measured with a termosalinometer. The collected shrimps were taken to the laboratory, fixed in formalin (10%) and preserved in ethanol (70%).

Sex determination of the specimens was based on secondary sexual characters. Carapace length (CL-mm) was measured as the distance from the postorbital margin to the mid-dorsal posterior edge of carapace. Wet weight was measured with an analytical scale with an accuracy of 0.001g.

Mean size at sexual maturity was estimated as the class interval in which 50% of females were carrying eggs on pleopods. A logistic curve was fitted to the percentage of brooding females by an automated (Solver) least squares fitting procedure, considering all the samples that contained reproductive females. The frequency of reproductive females in the largest class interval was verified in attempt to identify different reproductive patterns in the pond. Frequencies of reproductive females lower than 100% in largest length class interval may suggest that part of population is not breeding at the same time or different populations are sharing the same area (King, 1997).

Individual growth was estimated for males and females following the cohorts, represented by CL modal groups, along the study period (Modal Progression Analysis-MPA). The class interval adopted to perform the length frequencies analysis was 0.5mm. The modal groups were determined by the equation proposed by Spiegel (1970): Modal value = $CI + [(N_i - N_{i-1}) / (N_i - N_{i-1}) + (N_i - N_{i+1})]^{int}$, where CI is the length class interval, N_{i-1} is the precedent class frequency, N_{i+1} is the posterior class frequency and *int* is the length interval adopted, in this case 0.5mm. The largest lengths (male and female) observed in each sampling were considered as a modal group, since crustaceans generally, present high natural mortality rates, which causes a reduced number of organisms in the older age groups. Therefore, the identification of these modal groups is usually hindered, causing underestimation of the growth coefficient (k) in several growth curves obtained for crustaceans (D'Incao and Fonseca, 2000).

Modal groups were tentatively linked to visualize modal progression along the sampling period. The criteria used to accept a cohort was based on biological coherence with the longevity and the maximum length observed in the samples. To estimate growth parameters all the chosen cohorts were fitted to von Bertalanffy growth model (VBGM) (1938) by an automated (Solver) least squares fitting procedure. The von Bertalanffy equation is as follows: $CL_t = CL_\infty [1 - e^{-k(t-t_0)}]$, where CL_t is length at the time t , CL_∞ is asymptotic length, k the coefficient of growth and t_0 the theoretical age at length zero. Longevity (t_{max}) was estimated by inverted von Bertalanffy (1938) equation, considering maximum longevity (t_{max}) as reached at 99% of the asymptotic length (D'Incao and Fonseca, 2000). To test possible differences between growth parameters of males and females a F test was applied (Cerrato, 1990).

A stabilized normal probability was applied to assure that errors (e.g., in the chosen modal groups) are normal. The SNP was inspected before attempting to use the parameter confidence statistics or prediction intervals in growth analysis.

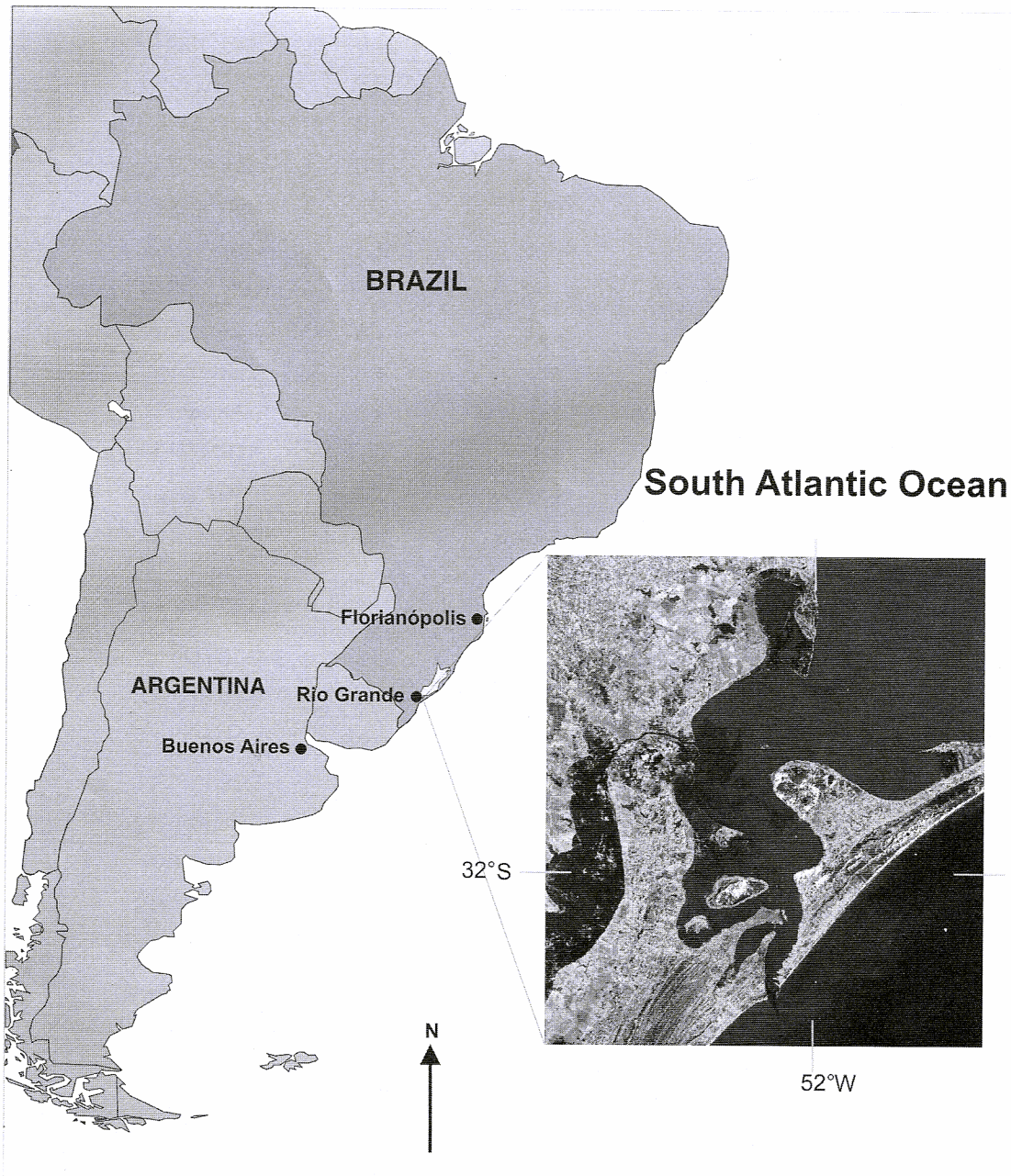


Figure 1: Distribution area of *Palaemonetes argentinus* Nobili, 1901 in South Atlantic coastal environments, from Florianópolis (Santa Catarina, Brazil) to Buenos Aires (Argentina). The box shows a detailed view from the study area in the estuarine zone of Patos Lagoon (RS) (Source: DHN).

Results

Mean temperature value on the pond was 19.2 °C. Lowest temperature was annotated during winter (9.2 °C) and the highest in summer (28.9 °C). Mean salinity was 1.6, being 0 the lowest and 6.5 the highest value (fig. 2). A total of 5575 individuals was collected (2578 males and 2817 females).

The highest absolute abundance was verified on July/1997 (494 ind.) the lowest on December/1997 (4 ind.) (Tab. I). The low abundance during December/1997 may be due to high pluviosity rates during the spring, linking the pond to the Patos Lagoon estuary and providing a way of escape to the organisms.

The carapace length ranged from 2.3 to 8.4 mm in females and from 2.5 to 6.9 mm in males. The mean sex ratio value, considering all the samples, was 1.09 (F:M). However, the seasonal analysis of the sex ratio values showed variations in this parameter. The highest F:M values were observed during the summer (2.14) and the lowest during winter (0.18) (Fig. 3).

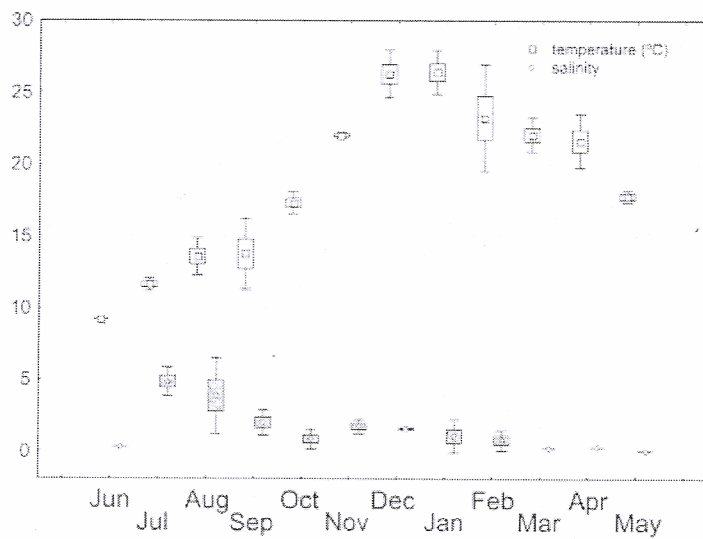


Figure 2: Monthly variation in temperature (°C) and salinity (%) in the study area. Central points are mean values, boxes are standard error and lines, standard deviations.

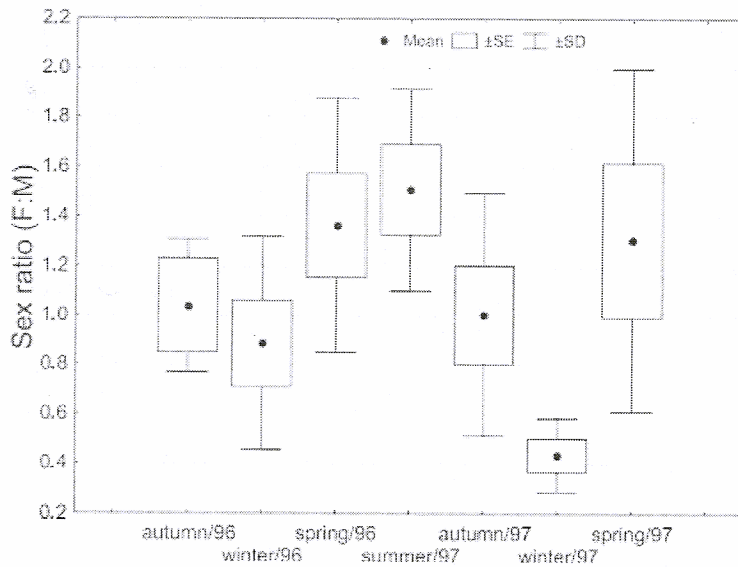


Figure 3: Seasonal variation in the sex ratio (F:M) of *P. argentinus*. Central points are the mean values, boxes are standard error and lines, standard deviations.

Table I: Summary of sampling information containing the absolute number of females, males and reproductive females observed in each sampling cruise. The symbol X was attributed to a discarded sample.

Date	Males (n°)	Females (n°)	RF (n°)	Total
4/6/1996	201	247	0	448
26/6/1996	124	105	0	229
10/7/1996	52	65	0	117
30/7/1996	150	109	0	259
13/8/1996	96	76	0	172
27/8/1996	41	64	10	105
10/9/1996	49	25	8	74
27/9/1996	42	20	13	62
11/10/1996	52	65	32	117
22/10/1996	41	60	34	101
12/11/1996	36	17	15	53
26/11/1996	84	145	6	229
6/12/1996	58	75	2	133
26/12/1996	40	79	3	119
14/1/1997	81	174	2	255
28/1/1997	154	220	21	374
6/2/1997	75	122	7	197
3/3/1997	63	76	2	139
17/3/1997	61	69	9	130
1/4/1997	102	79	6	181
22/4/1997	59	33	0	92
5/5/1997	76	37	0	113
2/6/1997	92	124	0	216
16/6/1997	72	126	0	198
30/6/1997	163	180	0	343
16/7/1997	44	8	0	52
29/7/1997	320	174	1	494
12/8/1997	121	57	7	178
26/8/1997	62	27	2	89
9/9/1997	68	37	10	105
23/9/1997	X	28	12	28
7/10/1997	38	43	10	81
21/10/1997	5	10	5	15
18/11/1997	16	32	16	48
2/12/1997	18	7	5	25
16/12/1997	2	2	1	4
total	2758	2817	249	5575

The main reproductive season is the spring, when the highest abundances of brooding females (*e.g.*, October/1996 – 34) were recorded. After the spring, the abundance of brooding females decreases towards the summer. In summer a second smaller peak of ovigerous females

was verified, suggesting a new reproductive event. No breeding female was sampled during the months of May, June, and July; April/97 and early August/97. After these periods a new increase in frequency of reproductive females were observed, reaching the highest value in October (Fig. 4).

The mean length at first maturity estimated was 6.5 mm (CL). All females in the largest length class interval were reproductive, meaning that reproduction is synchronized and that there is only one population in the pond. The smallest length class interval with brooding females was 5.0 mm (CL) and the largest 8.0 mm (CL) (Fig. 5).

A total of 12 cohorts was followed (6 females – 6 males) (fig. 6,7), resulting in the curves shown in figures 8 and 9. Cohorts hatched in all reproductive seasons were accompanied. The longevity was estimated in 15.9 and 13.5 months for females and males, respectively. Males presented higher k values and consequently smaller asymptotic lengths. A detailed numeric summary of the growth parameters estimated is available in table 2. The growth curves of females and males were significantly different ($F_{\text{calc}} = 45554$; $F_{\text{tab}} = 5.4$), pointing out the sexual dimorphism related to growth. The SNP test shown that none of the chosen modal groups violated the 99% critical limit (fig. 10, 11).

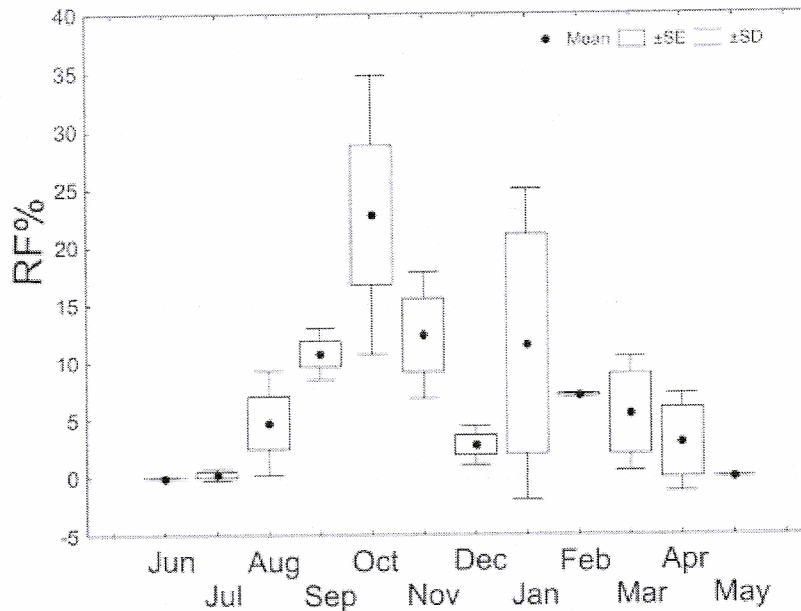


Figure 4: *P. argentinus*. Mean, standard deviation and standard error of monthly grouped abundance (number) of reproductive females (RF). Dot line indicates the length class interval at which 50% of females are reproductive.

Discussion

The investigation of reproductive season showed that the main event occurs during spring (October) and a second peak of reproduction during summer (January). The length-frequency data confirms it, since it was verified that very clear modal groups recruited to the stock during these periods. Two recruitment events were observed in spring, one at the beginning and another at the end of season. The next reproductive event is in summer. This event seems to be less important to the maintenance of the stock due to the low abundance of reproductive females and the absence of the largest females.

Similar reproduction pattern was observed in northern population of RS with a slight anticipation in reproductive event, since the highest abundance of reproductive females was observed in September (Gonçalves and Fontoura, 1999). This difference is likely related to higher water median temperature measured in northern lagoons (20.75 °C), than that recorded in the present study (19 °C).

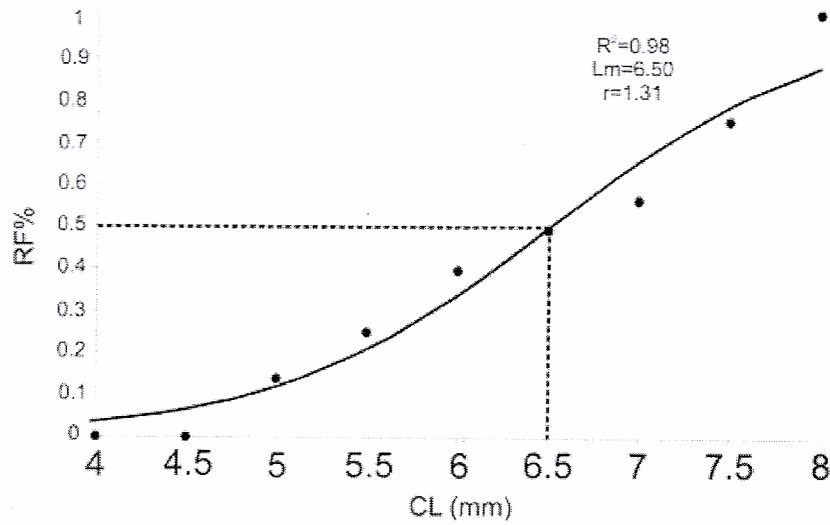


Figure 5: *P. argentinus*. Mean length of sexual maturity (L_m), coefficient of determination (R^2) and slope (r) estimated by logistic maturation curve. Dot line indicates the length class interval at which 50% of females are reproductive (RF).

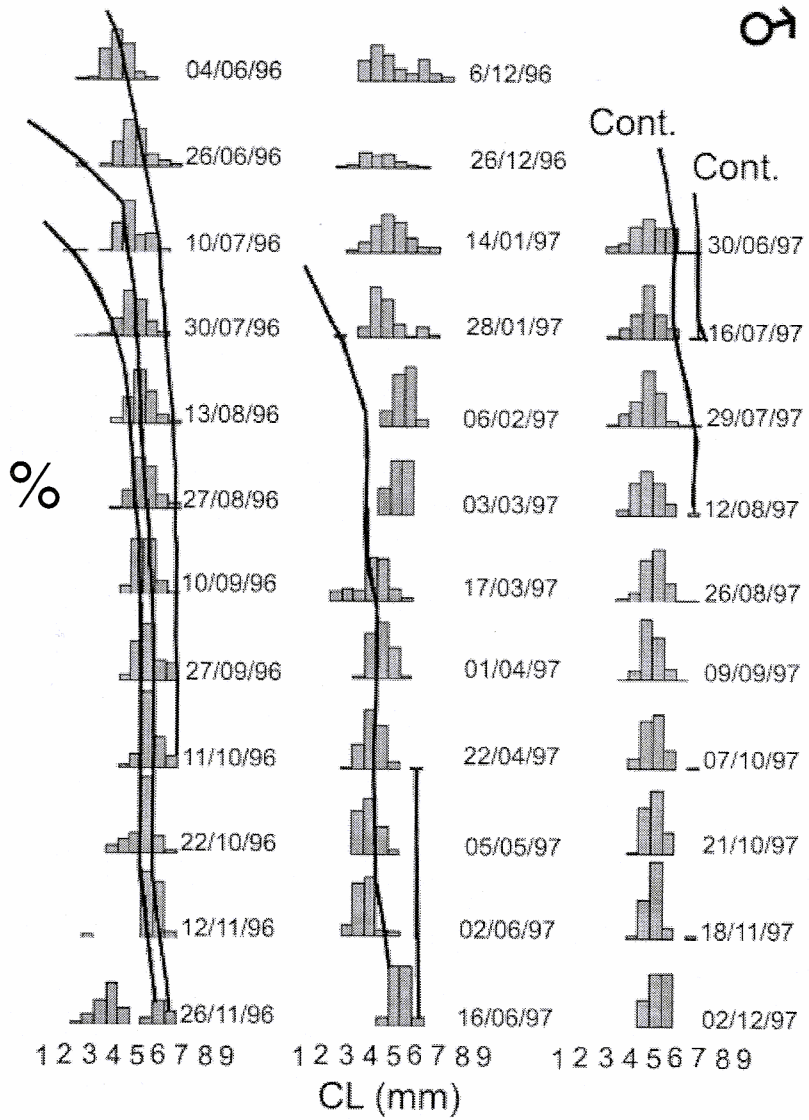


Figure 6: *P. argentinus*. Modal progression analysis (MPA) of male cohorts. Bold lines are the linked cohorts used to describe the individual growth.

Nauplius

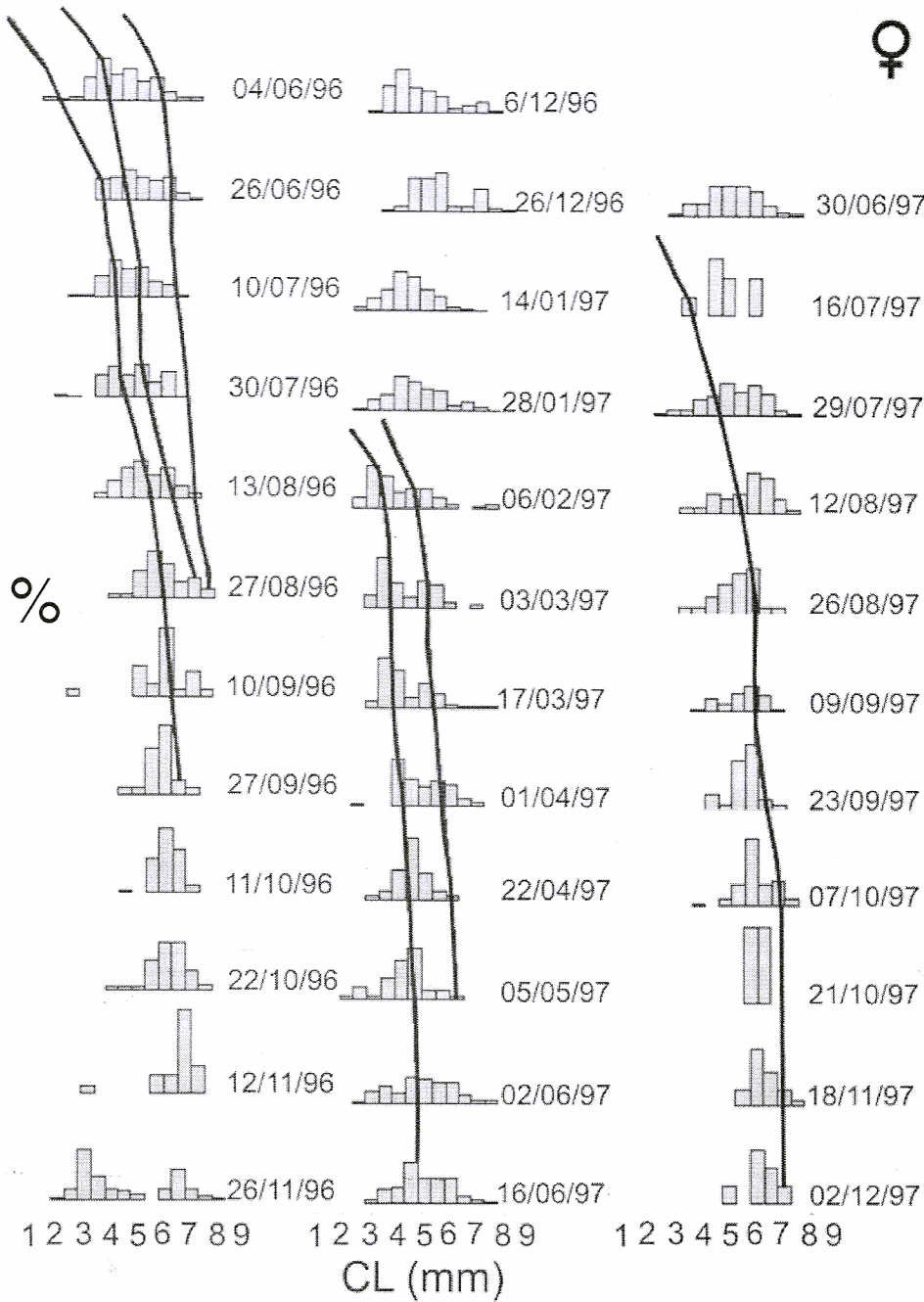


Figure 7: *P. argentinus*. Modal progression analysis (MPA) of females cohorts. Bold lines are the cohorts linked along the period of study used to describe the individual growth.

Table II: *P. argentinus*. males. Growth curves estimated for the southern population from the Rio Grande do Sul State.

Parameters(♂)	Value	Std Error	t-value	90% Confidence Limits		P> t
L_{∞}	6.67	0.24	28.05	6.27	7.07	0.00000
k	0.34	0.04	7.90	0.26	0.40	0.00000
t_0	-0.38	0.12	-3.20	-0.58	-0.18	0.00291
Parameters(♀)	Value	Std Error	t-value	90% Confidence Limits		P> t
L_{∞}	8.00	0.30	26.26	7.49	8.51	0.00000
k	0.29	0.03	9.64	0.23	0.34	0.00000
t_0	-0.34	0.08	-3.98	-0.48	-0.19	0.00023

Nauplius

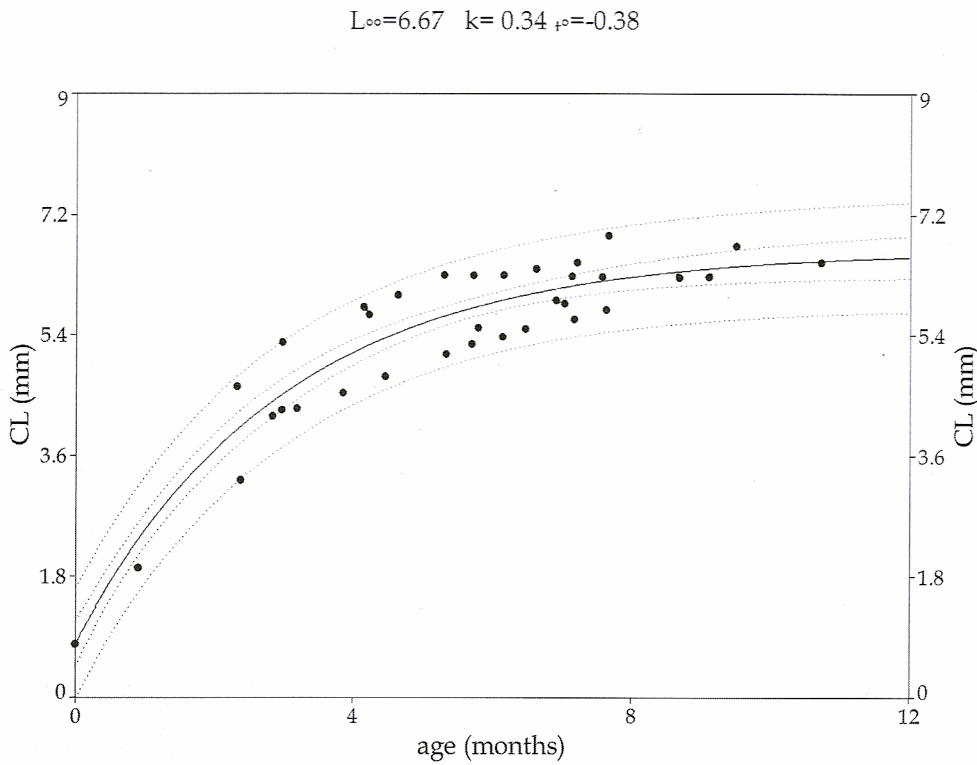


Figure 8: Males *P. argentinus*. Growth curves estimated for the southern population from the Rio Grande do Sul State.

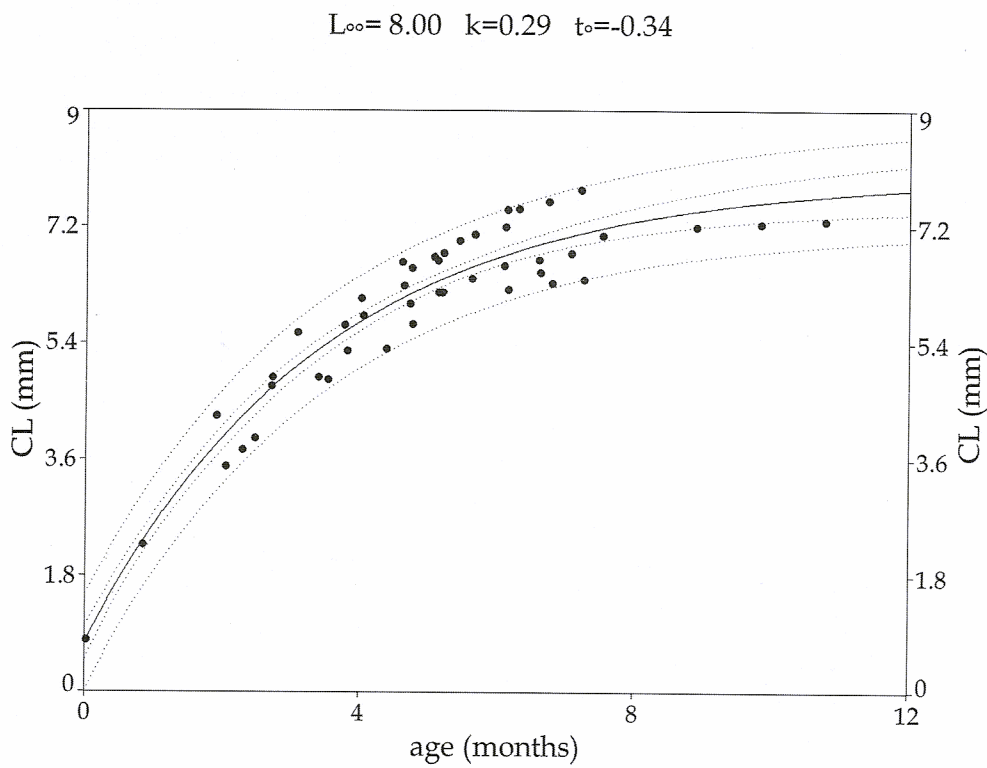


Figure 9: Females *P. argentinus* Growth curves estimated for the southern population from the Rio Grande do Sul State.

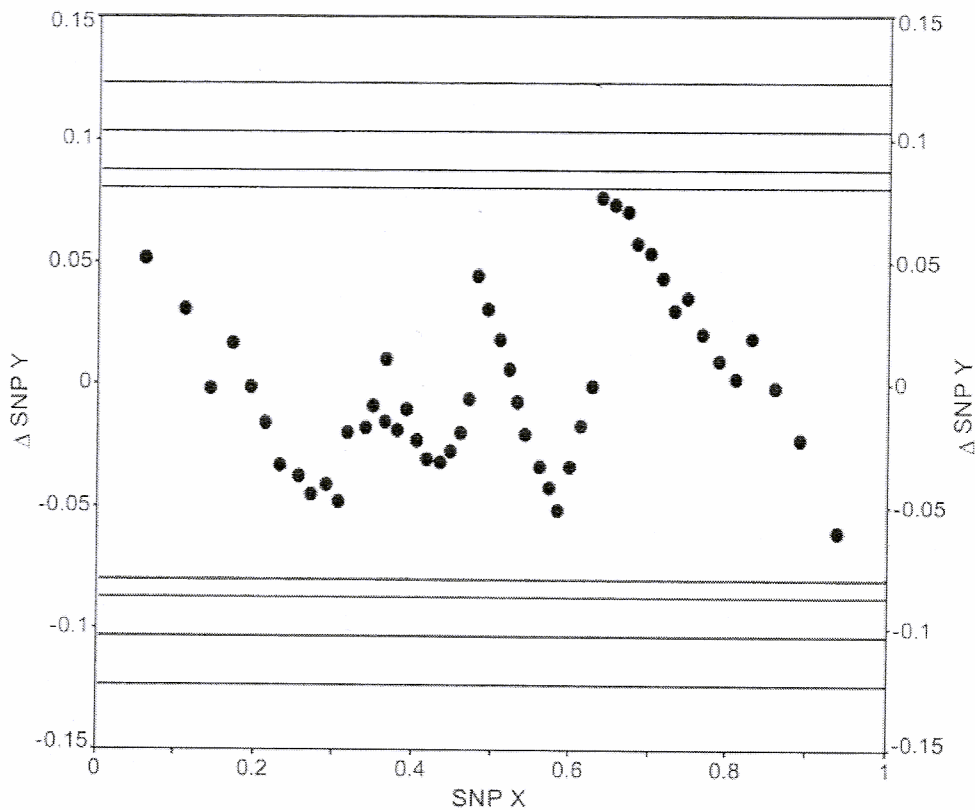


Figure 10: Males *P. argentinus*. Standardized normality plot. All the modal values used for estimate individual growth were among the critical limits adopted (99%).

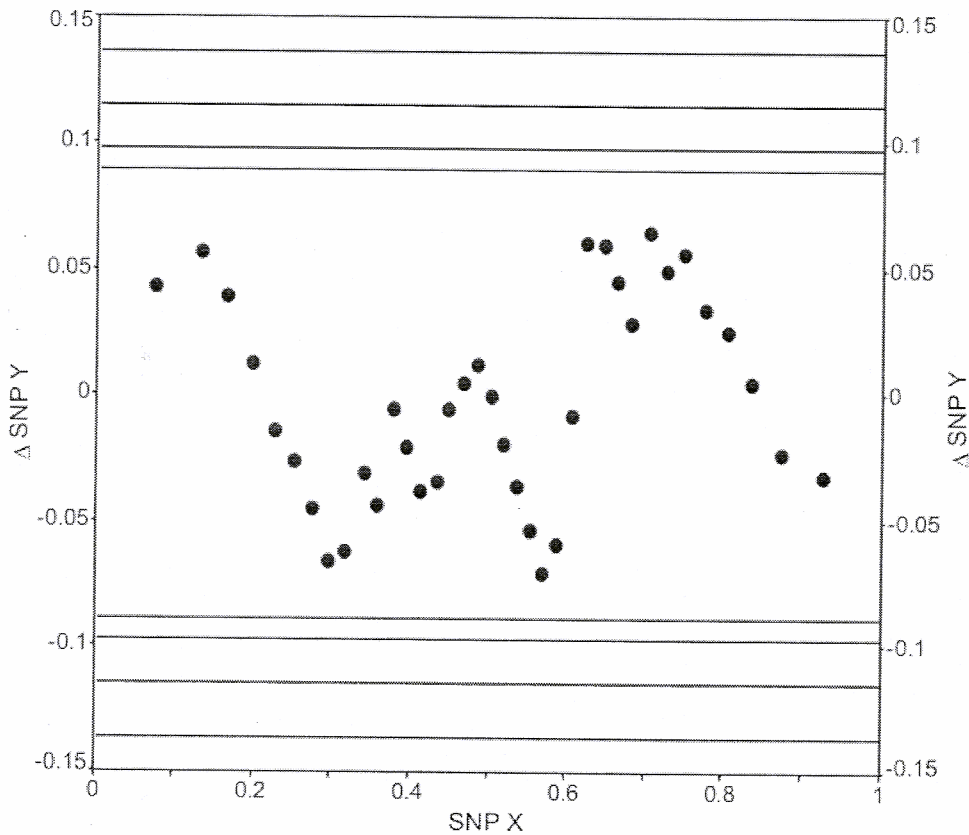


Figure 11: Females *P. argentinus*. Standardized normality plot. All the modal values used for estimate individual growth were among the critical limits adopted (99%).

Nauplius

Increase in temperature from June to August is clearly followed by increase in reproductive females abundance. Donati (1986), studying an Argentinean population of *P. argentinus*, observed that the increase in 2 °C in water temperature, in late September was followed by the appearance of brooding females. According to the same author, there is a first reproductive event in October and a second in January, which is in agreement with the results of present investigation. A shorter period of reproduction was reported to Argentinean populations, accomplished between August and February, which is likely related to lower water temperatures observed in that area, otherwise two reproductive events were also observed, first in October and second in January (Goldstein and Cidre, 1974; Donati, 1986; Schuldt and Damborenea, 1987).

Despite of similar median water temperature values, different reproduction pattern was reported to a Santa Catarina (SC) population, occurring near to the northern limit of occurrence of species. This population presents low abundance and a reproductive season restricted to the summer. A possible explanation to reduced reproductive season is the stress caused by higher salinity environment, when compared with the measures obtained in the present study, varying from 8 to 36. According to Charmantier and Anger (1999), *P. argentinus* is a strict osmoconformer in salinities of about 20-32 and survival under these conditions is limited to a few days. In addition, the shrimps tend to avoid high-salinity areas in brackish-water habitats (Anger *et al.*, 1999). At the other end of salinity spectrum, *P. argentinus* is well adapted to low and very low salinities through efficient hyper-osmoregulation, which supports a general view of this shrimp as a freshwater species (Charmantier and Anger, 1999). Another evidence of environmental stress caused by high salinity is the inferior abundance observed in SC population. Despite of possible differences in the efficiency of nets, there is a marked difference in the relative abundance (n° of individuals/trawl) between both populations, being the northernmost less abundant (mean=2.6 ind/trawl) than the population investigated in this paper (mean =51.6 ind/trawl).

The mean length at sexual maturity estimated ($L_m = 6.5$) was slightly higher than the value obtained for a RS northern population ($L_m = 6.0$) (Gonçalves and Fontoura, 1999). Carapace length of smallest brooding female in southern RS population was markedly superior (5.3 mm) to the observed in RS northern population (3.1 mm) (Gonçalves and Fontoura, 1999). Higher temperatures tend to increase growth coefficient, reduce longevity, reduce maximum length and advance the mean size of first maturity (Pauly, 1998), so the anticipation of sexual maturity in the RS northern population may be due to this factor.

The estimated longevity of females was around 16 months. Therefore, the absence of the largest females in the summer event of reproduction can be attributed to high mortality rates, reducing drastically the abundance in the oldest modal groups. The decrease of the sex ratio towards the autumn confirms it. This decrease is caused by the high mortality rates in the older individuals, since the cohort hatched in spring/96 reaches its maximum longevity at the early summer/97.

The longevity of males was estimated as 13.5 months. So the absence of largest males in the summer reproduction is even more noticeable, since most of shrimps die after a period around a year and do not reach the second reproductive event (January). The sex ratio confirms this hypothesis. During the main reproductive event (spring), sex ratio is approximately 1 (F:M). Towards the summer this figure increases to a maximum value, which can be attributed to the higher mortality rates of males that reach the t_{max} at the end of spring.

Due to the absence of permanent calcified structures in crustaceans, age can not be directly determined (Hartnoll, 1982) and growth studies are usually based on length-frequency information. The MPA brings uncertainty to the analysis, so biological parameters as reproductive season, sex ratio and the largest CL observed in the samples can be used to support the estimated growth parameters (D'Incao and Fonseca, 2000).

Biological aspects (*e.g.* reproductive season and sex ratio) can be used to validate the maximum longevity. It is reasonable to exclude cohorts which do not present values of k (coefficient of growth) coherent with the longevity estimates, based on biological information available for the species from the analysis. Growth coefficient values obtained for a population from northern RS were inferior (males= 0.21/month; females=0.11/month) (Gonçalves and Fontoura, 1999) to those estimated in the present study. Same authors suggest longevity of 16 months for both sexes, based on a visual analysis of modal progression. A population from Argentina showed k values varying between 0.85/month (males) and 1.07/month (females).

Applying the inverted VBGM ($t_{\max} = 99\% L_{\infty}$), to these k values obtained by Gonçalves and Fontoura (1999), the estimated longevity for male and female from northern population of *P. argentinus*, would be around 22 and 42 months, respectively. Considering the similarities in water temperature and salinity between these two coastal lagoons, these longevity values are biologically incoherent, provided that the present MPA analysis does not allow a lifespan longer than 16 months. Therefore, the utilization of 99% of asymptotic length to estimate longevity allows an easier identification of possible distortions in the k estimates, providing a more accurate method to evaluate t_{\max} (D'Incao and Fonseca, 2000).

Besides the coefficient of growth (k), the estimates of asymptotic length must be validated. According to Pauly (1998), a valid asymptotic length should be similar to the largest CL observed in the samples. D'Incao and Fonseca (2000) suggested an asymptotic length around 10% of the maximum carapace length observed in the samples. Estimates of L_{∞} obtained in this paper were very near to the largest lengths observed (males- $L_{\infty}= 6.67/$ maximum CL= 6.5; females- $L_{\infty}= 8.00/$ maximum CL= 8.4), which can provide support to the estimated values.

Asymptotic lengths estimated for a northern population (Gonçalves and Fontoura, 1999) were 7.8 mm (females) and 5.0 mm (males) and largest individuals measured 8 mm (female) and 6.25 mm CL (male). The L_{∞} estimated for an Argentinean population was 16 and 14 mm, for females and males respectively (Capitulo and Freyre, 1989). Largest female observed in this population showed 15 mm CL and the largest male 11.5 mm CL.

Highest L_{∞} values observed in the Argentinean population are likely related to the lowest water temperatures, resulting in a slow growth and consequently high asymptotic lengths. Asymptotic lengths estimated for a population from the north of Rio Grande do Sul State were more similar to those obtained in this study. However, a slight decrease in this parameter can be noticed towards highest latitudes.

Briefly, this investigation demonstrated that *P. argentinus* presents two main reproductive events, first in the spring and the second in summer. Sex ratio was approximately 1:1, but seasonal fluctuations were attributed to differential mortality and different growth patterns of both sexes. The present study suggests the use of biological information to validate the VBGM parameters, such as reproductive season, maximum length observed in the samples and sex ratio. Besides, the utilization of inverted curve of Bertalanffy, considering that t_{\max} is achieved at 99% of asymptotic length provided an accurate method of estimating longevity. Comparison of present population parameters with bibliography information is relatively difficult, since the methods used in estimates were significantly different. Otherwise, different patterns of reproduction and growth can be noticed along the coastal environments of Southeast Atlantic Ocean, suggesting the presence of different populations, or species, submitted to different environments. Further investigations should be developed in the field of population genetics, in an attempt to provide more accurate information about reproductive isolation of the species.

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