

Life history of a brackish-water population of *Palaemonetes argentinus* (Decapoda : Caridea) in Argentina

E.D. Spivak¹

Keywords : Caridea, *Palaemonetes argentinus*, breeding period, fecundity, life history, brackish-water, Argentina.

The life cycle of a brackish-water population of *Palaemonetes argentinus*, a normally freshwater shrimp from the warm temperate region of eastern South America, was studied in Mar Chiquita coastal lagoon, Argentina. In 1995, recruitment took place in January, followed by two growth periods, the first at the beginning of summer and the second from the end of winter through most of spring. Females reached a larger size than males. Ovigerous females, probably belonging to two cohorts, were found from October 1995 to February 1996, with a maximum number in November (93 %). Their average size and fecundity varied during the breeding period. The sex ratio did not significantly differ from 1:1 except in November. Evidence of mature oocytes in the ovaries was found in ovigerous and postovigerous shrimps, suggesting that they breed twice a year. However, only some females of the first cohort produced a second hatch in 1995. The maximum number of undifferentiated embryos carried by a female was 250; there was a positive relationship between fecundity and size. Larvae were collected together with adults from November to March. The life history is similar to that described in several freshwater populations. Differences are restricted to chronological aspects such as a shorter unimodal breeding period and are probably related to climatic factors, since Mar Chiquita is near the southern limit of the geographic range of the species. Data presented here suggest interannual variations in reproductive patterns that lead, sometimes, to a longer bimodal breeding period.

Cycle de vie de la population de *Palaemonetes argentinus* (Decapoda : Caridea) dans les eaux saumâtres en Argentine

Mots clés : Caridea, *Palaemonetes argentinus*, période de reproduction, fécondité, cycle de vie, eau saumâtre, Argentine.

Le cycle de vie de la crevette d'eau saumâtre *Palaemonetes argentinus* vivant normalement en eau douce dans la région chaude du sud-est américain, a été étudié dans la lagune côtière de Mar Chiquita en Argentine. En 1995, le recrutement a eu lieu en janvier suivi par 2 périodes de croissance ; la première au début de l'été et la seconde à la fin de l'hiver jusqu'à une période avancée du printemps. Les femelles ont une meilleure croissance que les mâles. Les femelles ovigères appartiennent probablement à 2 cohortes que l'on a trouvé d'octobre 1995 à février 1996, avec un maximum d'effectifs (93 %) en novembre. La taille moyenne et la fécondité varient durant la période de reproduction. Le sex-ratio est de 1 : 1, sauf en novembre. Des ovocytes matures ont été trouvés dans les ovaires des crevettes ovigères et post ovigères dont on suppose, qu'elles se reproduisent 2 fois dans l'année. Par contre, quelques femelles de la première cohorte seulement se sont reproduites une seconde fois en 1995. Le nombre maximum d'embryons non différenciés par femelle est de l'ordre de 250 ; il existe une relation positive entre la taille et la fécondité. Les larves ont été récoltées en même temps que les adultes de novembre à mars. Le cycle de vie est similaire à celui écrit dans la plupart des populations de crevettes d'eau douce. Les différences sont limitées à des aspects chronologiques, telles qu'une reproduction de type unimodal plus courte, et qui sont probablement liées à des facteurs climatiques, du fait que Mar Chiquita est proche de la limite sud de l'aire de répartition de l'espèce. Les données de ce travail présentent une variation interannuelle dans le mode de reproduction, ce qui conduit quelque fois à une période de reproduction, de type bimodal, plus longue.

1. Introduction

Shrimps of the family Palaemonidae (Decapoda Caridea) inhabit marine, brackish and freshwater habi-

tats. *Palaemonetes argentinus* (Nobili, 1901) lives in the north and center of Argentina, Uruguay and southern Brazil and is considered a typical freshwater species (Boschi 1981). However, it has been found in several brackish coastal lagoons extending along the coasts of the warm temperate southwestern Atlantic Ocean: Lagoa dos Patos, laguna Castillos and laguna Mar Chiquita (Capitoli et al. 1978, Nión 1980, Anger et al. 1994).

1. Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. Casilla de Correo 1216, 7600 Mar del Plata, Argentina.

The geographic distribution of *P. argentinus* in Argentina ranges from streams of the Paraná-La Plata system located in the north-eastern region of the country to a small river near Bahia Blanca (Cazzaniga & Sitjar 1986, Bisbal 1987, Pettovello 1992). The size structure, growth and reproductive biology of limnetic populations of this species were studied in an artificial pond in Buenos Aires city, in the Canal Villa Elisa and the Laguna Chascomus (both in Buenos Aires province), and the Embalse San Roque (an artificial lake in Córdoba province; Goldstein & Lauria 1974, Schuldt & Damborenea 1987, Rodrigues Capitulo & Freyre 1989, Donatti 1986). The larval development of *P. argentinus* was studied from laboratory reared material by Menu-Marque (1973).

Mar Chiquita is a coastal lagoon connected to the sea by a narrow opening, consequently, its salinity changes both daily and seasonally. Larvae, juveniles and adults of *P. argentinus* were found in several creeks that flow into the lagoon. Larvae were also collected in the main body of the lagoon, with salinity values higher than 25 ‰ (Anger et al. 1994). In the laboratory, larvae survive and successfully complete their development in 30 ‰ (pers.obs.). In the present study, the annual variation in some population traits were investigated in the brackish-water population of Mar Chiquita.

2. Material and methods

2.1. Study area

Mar Chiquita, the southernmost in the series of coastal lagoons of southern Brazil, Uruguay and Argentina, is a shallow body of water that runs parallel to the sea from 37°32' to 37°45'S. It is separated from the shore by dunes and flows into the sea through a narrow channel at its southern end, 35 Km north from Mar del Plata, Argentina. The southern part of the lagoon is influenced by the sea, showing daily salinity variations, depending on tidal amplitude, direction and wind speed. However, physical conditions are highly variable and oligohaline waters may predominate over extended periods of time (Anger et al. 1994). Seasonal variation of freshwater input and evaporation increases (in summer) or reduces (in winter) the area that is influenced by the sea. Although information on water temperatures in the Mar Chiquita system is scarce, some data on air temperatures are available. January is the warmest month, July the coldest (the average maxima and minima are 26-15° and 12-4° C, respectively). Frosts occur from June to September, with a maximum frequency in July.

Samples were collected in Arroyo Sotelo, a shallow creek (< 1m deep in the channel) that flows into the wi-

de central part of the lagoon. The sampling site (Fig. 1) is situated 1 Km from the lagoon, the bottom is muddy and without submerged vegetation. Salinity (measured with a hand refractometer) oscillated between 1 and 8 ‰, only three times it was > 5 ‰ (August 1995, January and March, 1996).

2.2. Sampling

Samples were collected monthly from January 1995 to March 1996 from the shore (fortnightly on November and December), using a hand net with 1 mm mesh size. Larvae, juveniles and adults of both sexes (including ovigerous females) were found together, with no evidence of net selection by size, sex or developmental stage. Apparently, the shrimps show a variable patchy spatial distribution (pers. obs.). Consequently, the net was dragged for different times on the sampling dates in order to catch a similar number of specimens (juveniles + adults) and therefore the obtained results cannot be used to estimate the density of the population.

Samples were preserved in 4 % formaldehyde. A random subsample of about 200 shrimps was sized and sexed. Carapace length (CL), from the orbital margin, behind the eyestalk, to the dorso-posterior border was chosen as a measure of individual size. The rostrum was excluded from the measurements because break and regeneration were often observed. Measurements were taken under a SZ40 Olympus stereomicroscope furnished with a micrometer eyepiece (magnification: 5.4X). Male and female size frequency distributions (SFD) were determined for each subsample with 0.5 mm size intervals.

Sex was determined from pleopod 1 and 2 morphology. Specimens with at least 2.75 mm (CL) can be sexed in agreement with observations by Dávila (1996), smaller shrimps were classified as «undifferentiated».

The sex ratio and the percentage of ovigerous females within the total number of females were calculated for each sample. Ovigerous shrimps were classified in three groups according to the developmental stage of their embryos, defined on the basis of microscopical examination. Stage 1: no evidence of segmentation or organs; Stage 2: eyes visible as a dark dot; Stage 3: eyes well developed. An additional group included the few females with embryos immediately before hatching. Pleon morphology did not change after hatching, allowing to differentiate postovigerous from non-ovigerous females.

Fecundity was defined as the number of stage 1 embryos carried by a female (in order to reduce errors due to embryonic lost during development). The relation-

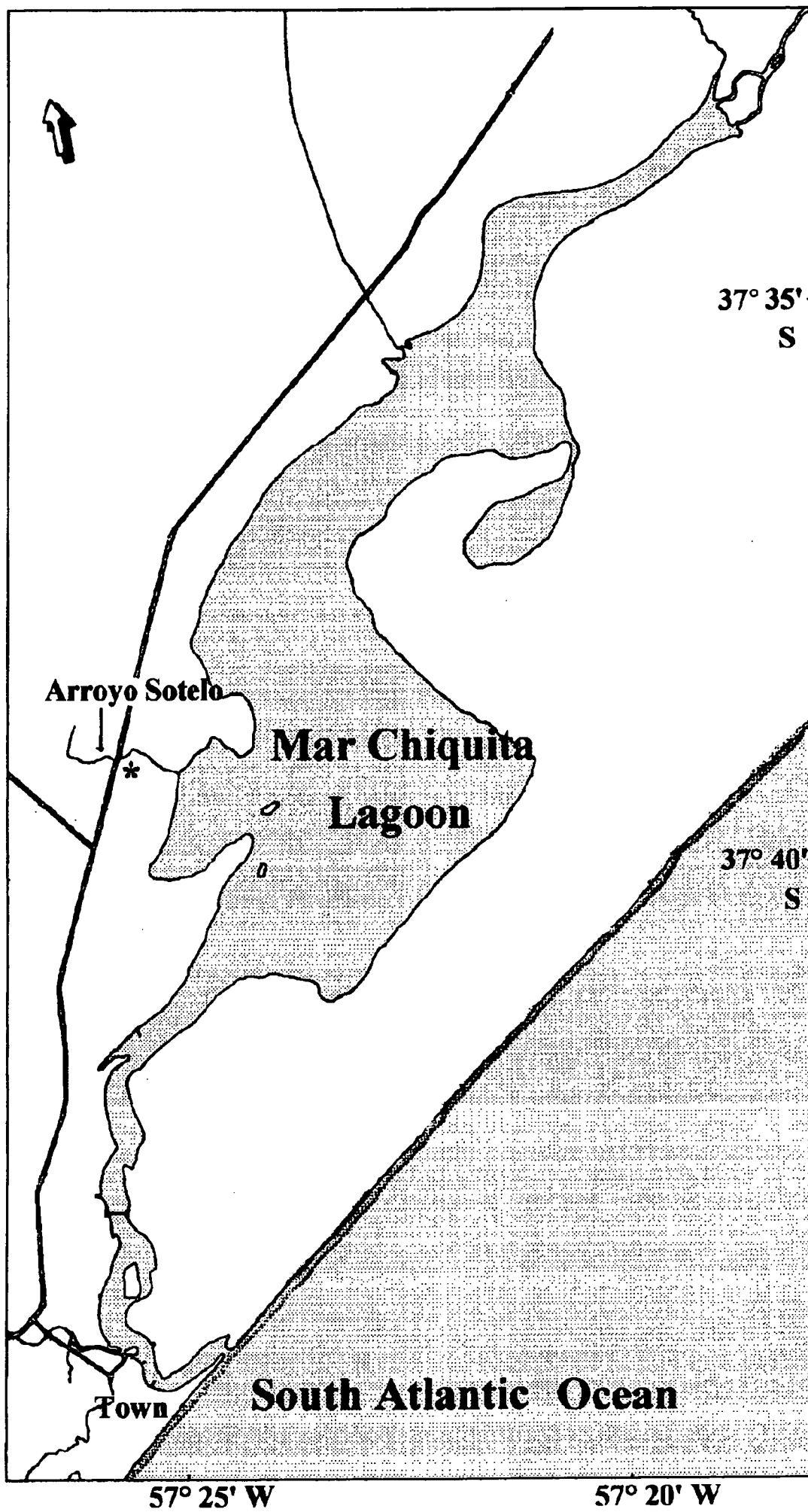


Fig. 1. Mar Chiquita lagoon, Argentina. The sampling site is indicated with *.
Fig. 1. Lagune Mar Chiquita, Argentine. Le site d'échantillonnage est indiqué par *

ship between fecundity and size of females was estimated, disregarding those which carried less than 50 embryos (probable embryonic loss). Carapace or total length, including the rostrum, were chosen as a measure of individual size in other studies (CL_R and TL, respectively; Donatti 1986, Schuldt & Damborenea 1987). For comparative purposes, the relationship between CL_R and CL was estimated from 25 ovigerous females ($CL_R = 1.67CL + 1.08$; $R^2 = 0.84$) and the relationship between TL and CL was recalculated from Dávila (1996) ($TL = 1.95 + 3.07 CL$; females only).

New oocytes can mature while *P. argentinus* females are still ovigerous, during this process ovaries became yellow and visible in the cephalothorax (Goldstein & Lauria de Cidre 1974, Schuldt & Damborenea 1987). The percentage of females with maturing oocytes within the ovigerous and postovigerous females was calculated for each sample.

2.3. Statistical procedures

SFDs were used to detect growth and recruitment periods from displacement of modal classes. Sex ratios were tested for deviations from a hypothetical 1:1 ratio employing a goodness-of-fit (Chi-square) test. Mean size of ovigerous and postovigerous females was compared by means of Student-t or Mann-Whitney Rank Sum tests. Regressions of fecundity vs. size were estimated after checking for normality and homoscedasticity of the data, and tested with ANOVA. Differences in slopes and intercepts between regressions were tested with ANCOVA

3. Results

3.1 Recruitment and growth periods

Adult SFD had one modal class in most samples. A remarkable exception was in January 1995 and 1996 when small males and females predominated, but coexisted with larger animals (Figs. 2 and 3). The smallest and undifferentiated shrimps were collected in summer (January to March, 1995; January and February, 1996) (Fig. 2).

The analysis of SFD shows two growth periods in females, at the beginning of summer and at the end of winter through most of spring (Fig. 2). The modal class increased from January to February, 1995 (3 to 3.5 mm) remaining in this position until April. In May, and specially in June and July, a few larger females appeared (reaching 6.5 mm). The modal class increased from July to November, from 3.5 to 5.5 mm. During the end of spring, all females were large (modal class: 5.5 mm). They disappeared almost completely at the beginning of summer (December). In January 1996,

small animals (modal class: 2.5 mm) were again collected, they grew during summer and the modal class reached 3.5 mm in March.

Males showed a similar pattern (Fig. 3). Modal classes increased from January to February 1995 (3 to 3.5 mm), from October to December 1995 (4 to 4.5 mm), and from January to March 1996 (2.5 to 3.5 mm). Most large adults disappeared during the period from December 20, 1995, to January 8, 1996, when a new group of small shrimps was recruited.

Females reached larger size than males. The largest female measured 7 mm CL (collected on November 21, 1995), the largest male had 5 mm CL (December 20, 1995).

3.2. Sex ratio

During most of the year (January to October), sex ratio did not significantly differ from 1:1 (Fig. 4). In November, this ratio was strongly biased, with females predominating. At the beginning of December, sex ratio was again near 1:1, but by the end of this month, 93 % of the adults were males.

3.3. Breeding cycle

Females carrying eggs were found from the beginning of October to February. The percentage of ovigerous females within the total number of females, reached a maximum in early November (93 %), continued high until the end of this month (87 %), and then diminished (Fig. 5). During the breeding period, the proportion of females that carried embryos in different developmental stages changed (Fig. 6). On October 12, all ovigerous females carried stage 1 embryos. One month later, females with stage 3 embryos amounted to more than 40 % (November 8), later reaching 60 % (November 21). Few females with stage 1 embryos were found in December, none in January and February.

Ovigerous females measured from 4.2 to 7 mm CL. The mean size of females with stage 1 embryos diminished during the first part of the breeding period and reached a minimum value on November 21, which was significantly different from those of the preceding and the following samples (Mann-Whitney test $p=0.0465$ and t test $p=0.0071$ respectively, Fig. 7a). Females with stage 3 embryos showed a similar pattern, with significant differences between November 8 and 21 (Mann-Whitney test $p<0.0001$, Fig 7b). Postovigerous females were found in samples from the end of spring (November 21, December 6 and 20). The mean size of postovigerous females significantly decreased between the two first samples (Mann-Whitney test $p<0.0001$, Fig. 7c).

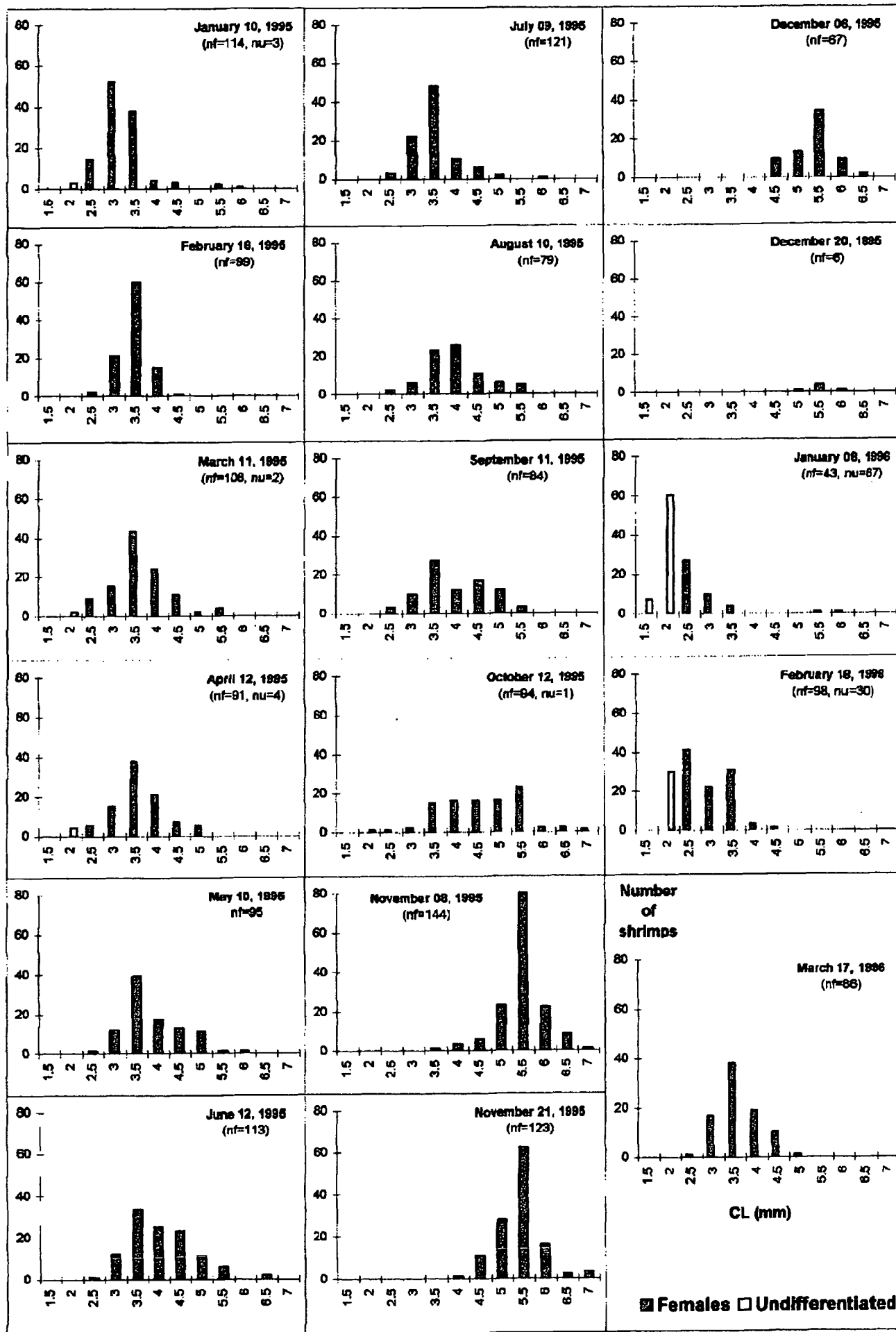


Fig. 2. Size frequency distributions (CL = carapace length) of female and undifferentiated *Palaemonetes argentinus*. Numbers below x-axis indicate the midpoint of each size interval. nf: number of females; nu: number of undifferentiated shrimps.

Fig. 2. Distributions Taille-Fréquence (CL = longueur de la carapace) des femelles et les immatures.

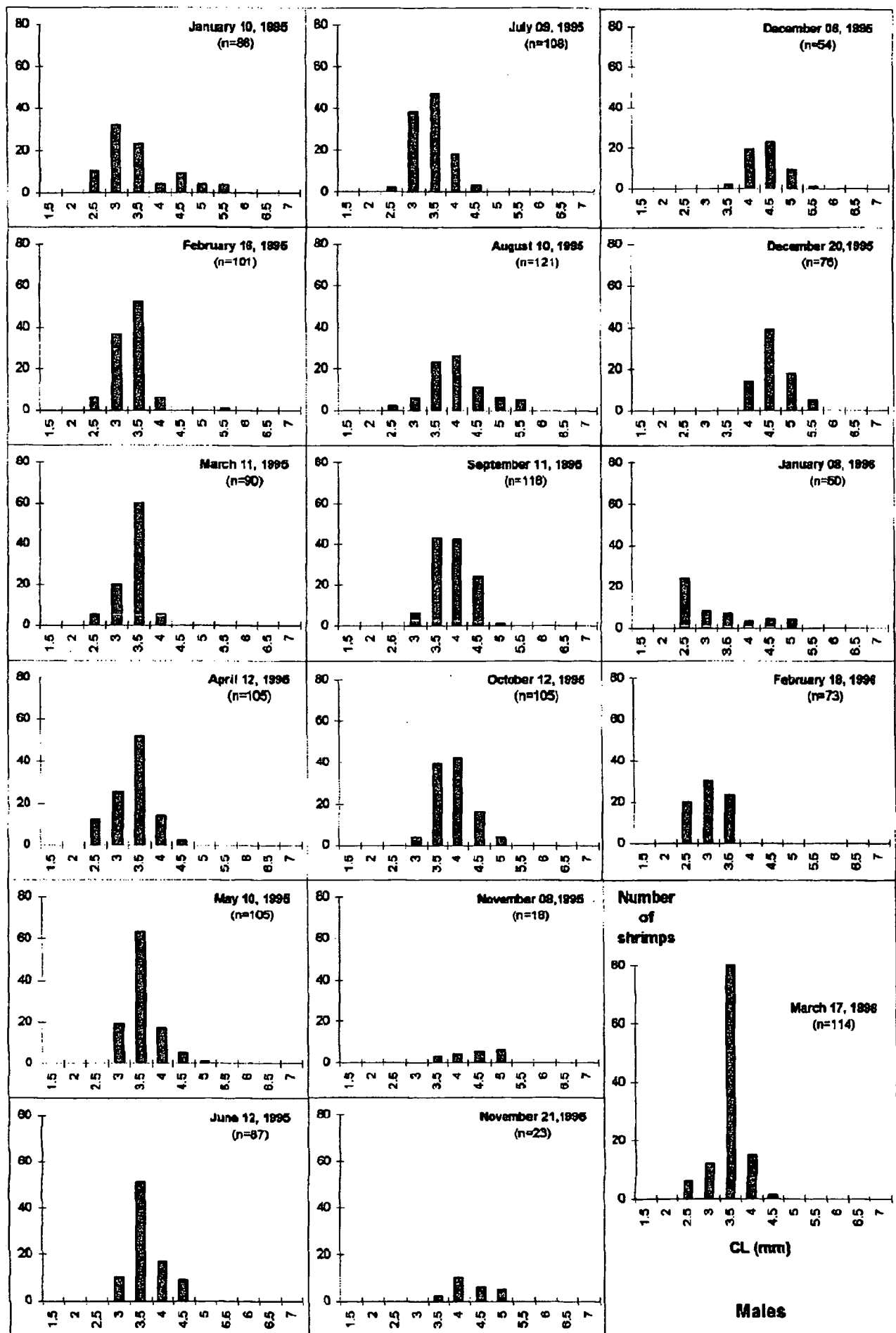


Fig. 3. Size frequency distributions (CL = carapace length) of *Palaemonetes argentinus* males. Numbers below x-axis indicate the midpoint of each size interval. n: number of males.

Fig. 3. Distributions Taille-Fréquence (CL = longueur de la carapace) de *Palaemonetes argentinus* mâles. Les nombres au dessous de l'axe de x indiquent le point médian de l'intervalle de chaque taille. n : nombre de mâles.

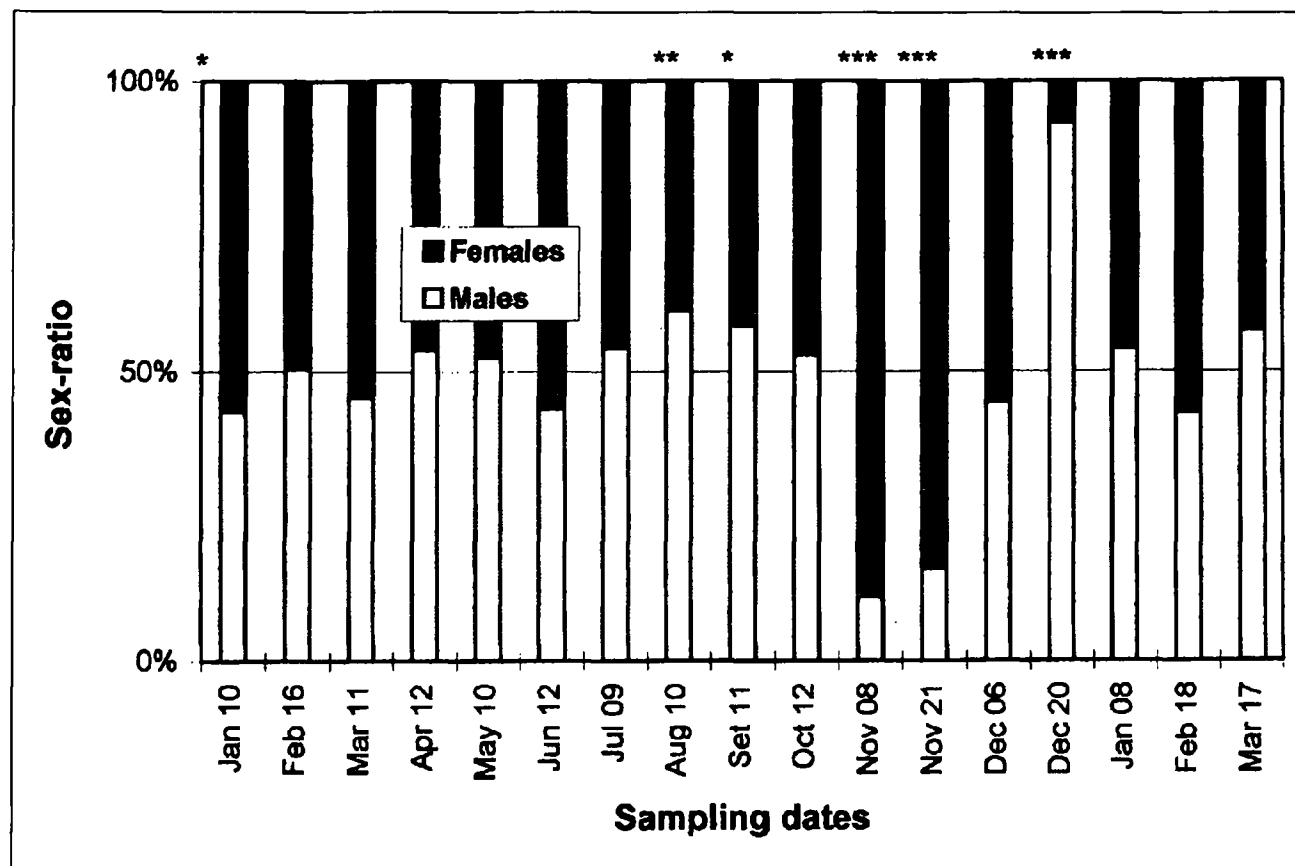


Fig. 4. Annual changes in *Palaemonetes argentinus* sex-ratio. Statistically significant differences respect an hypothesized 1:1 ratio (Independent chi-square test) are indicated as follows: * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

Fig. 4. Variations annuelles du sex-ratio de *Palaemonetes argentinus*. Différences significatives confirmées par l'hypothèse 1:1 ratio (test Chi 2) comme inciqué ci-après : * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

Evidence of mature oocytes in the ovaries was found in females with stage 3 embryos and postovigerous shrimps. 31 to 33 % of the ovigerous shrimps collected in November had yellow ovaries, this figure increased to 56 % in postovigerous females collected on December 6.

3.4. Fecundity

The maximum number of stage 1 embryos carried by a female was 250. There was a positive relationship between fecundity and size (CL) described by a linear model (all samples pooled; $r^2=0.54$, $F=89.0$, $p<0.0001$; Fig. 8) but fecundity values from October 12 were smaller than those from other samples. However, better correlations were obtained when regressions were calculated for different samples (Table 1). An ANCOVA test used to compare the regression lines showed significant differences in the intercepts (F -ratio=10.26, $p<0.001$).

3.5. Larvae

Larvae of *P. argentinus* were collected together with adults in February and March, 1995 and from Novem-

ber 1995 to February 1996. The number of larvae found in the adult subsamples increased from November 21, 1995, and reached a maximum in January 8, 1996, (87 larvae). All larvae collected on the 21st November 1995 were first stage zoea, but later samples contained stage 5-7 zoea.

4. Discussion

At Mar Chiquita, *Palaemonetes argentinus* completes its life cycle in 15 months which is comparable to the results obtained from other populations 300 Km north in Villa Elisa and Chascomús (Schuldt & Damborenea 1987, Rodrigues Capitulo & Freyre 1989). In the warm temperate region of Argentina, the presence of ovigerous females of this shrimp is restricted to a definite period that starts at the end of winter or the beginning of spring, after water temperatures have begun to rise. *Palaemonetes argentinus* breeds in Mar Chiquita from October to January but in northern populations the breeding season begins earlier, in August or September (depending on site and year), and ends in February (Goldstein & Lauria de Cidre 1974, Donatti 1986, Schuldt & Damborenea 1987).

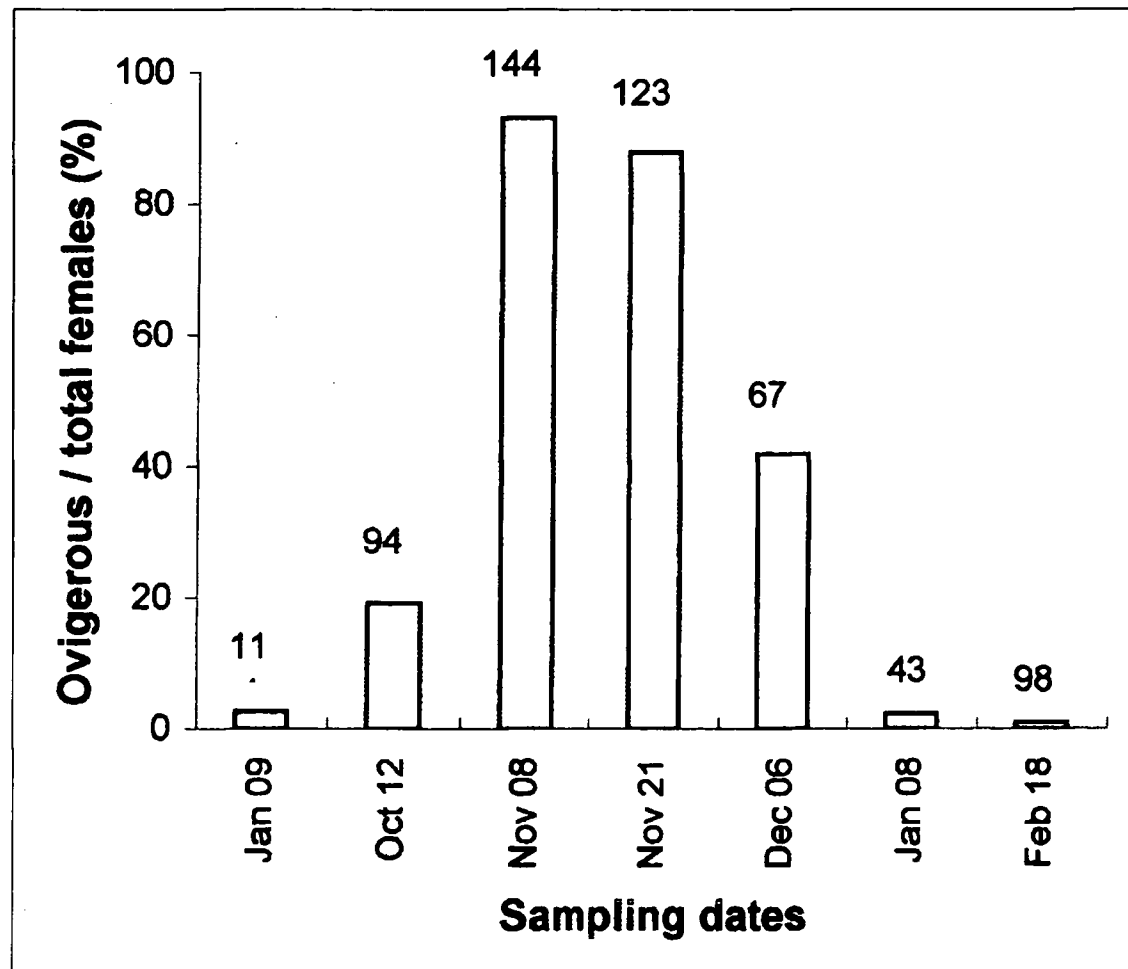


Fig. 5. Percentage of *Palaemonetes argentinus* ovigerous females with respect to total females during the breeding season. The number of ovigerous females is indicated in each column.

Fig. 5. Pourcentage de femelles ovigères de *Palaemonetes argentinus* par rapport au nombre total de femelles durant la période de reproduction. Le nombre de femelles ovigères est indiqué dans chaque colonne.

Table 1. Relationships between the number of *Palaemonetes argentinus* stage 1 embryos (NE) and the carapace length of ovigerous females (CL) from different samples (October 12, November 08 and 21) and from all samples pooled (including 7 specimens from December 06). n: number of specimens, r^2 : coefficient of determination, F: coefficient of ANOVA.

Tableau 1. Relation entre les embryons de stade 1 de *Palaemonetes argentinus* (NE) et la taille de la carapace des femelles ovigères (CL) de différents échantillonnages (12 Octobre, 8 et 21 Novembre) et à partir de tous les échantillons groupés (comprenant 7 spécimens du 6 Décembre). n : nombre de spécimens, r^2 : coefficient de corrélation, F : coefficient d'ANOVA.

Sample	Equation	n	r^2	F	p
October 12	NE = 61.9CL - 247.1	16	0.718	35.7	<0.0001
November 08	NE = 67.3CL - 251.0	34	0.653	60.2	<0.0001
November 21	NE = 40.6CL - 99.7	22	0.742	57.7	<0.0001
all samples	NE = 44.7CL - 129.0	79	0.536	89.0	<0.0001

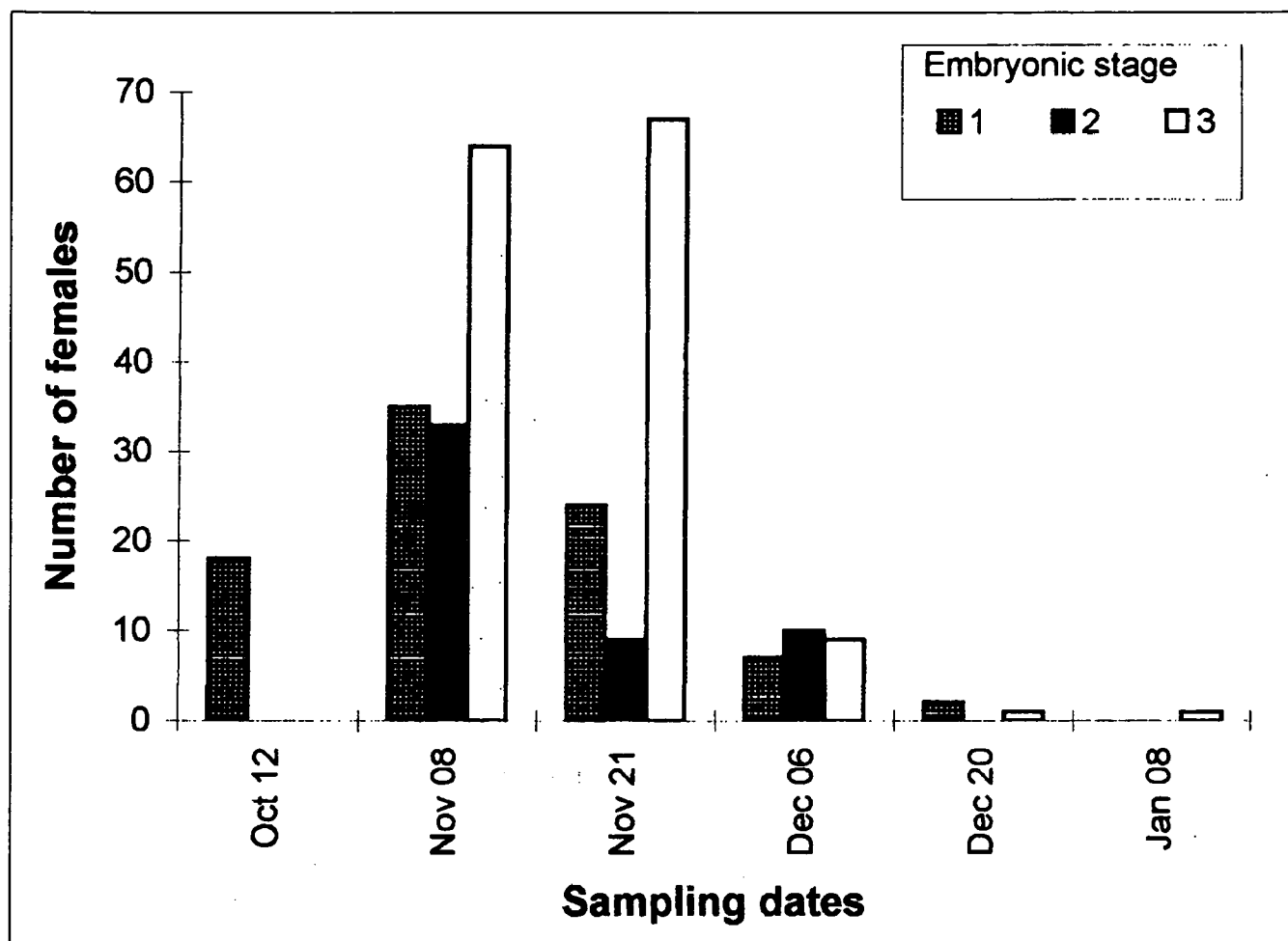


Fig. 6. Number of *Palaemonetes argentinus* ovigerous females carrying embryos in different developmental stages. Embryos without eyes (Stage 1); with incipient eyes (Stage 2); with well developed eyes (Stage 3).

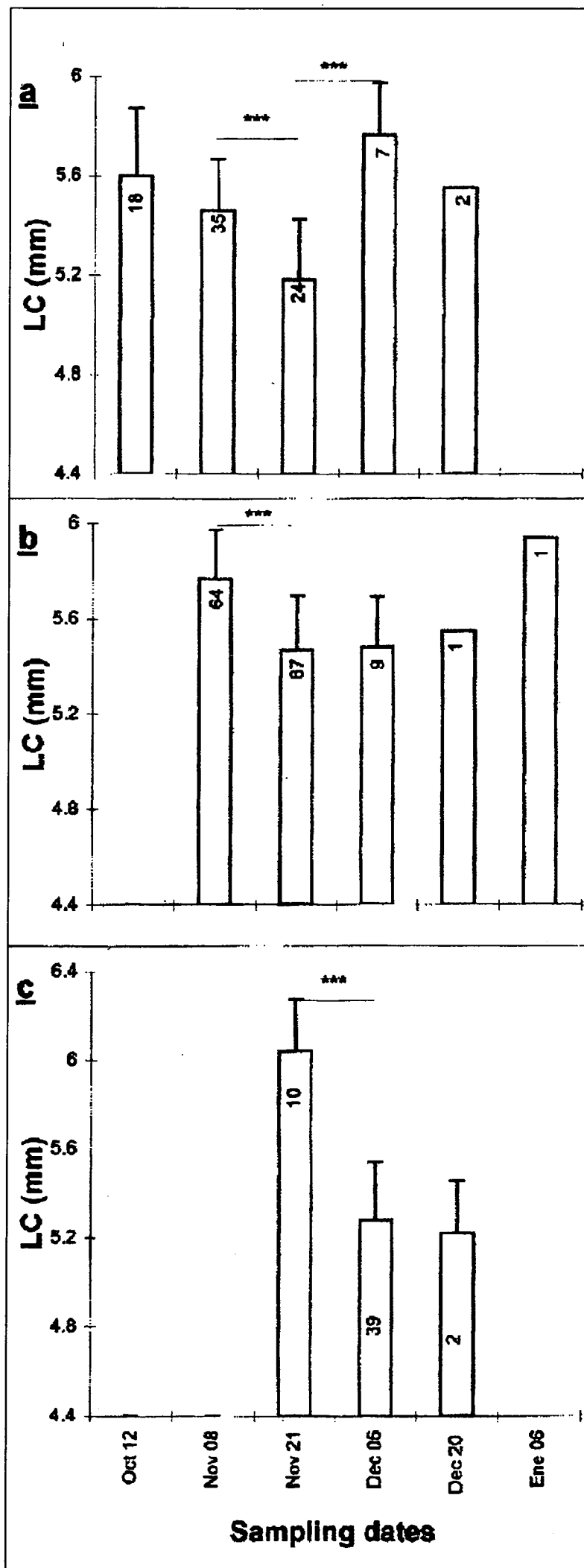
Fig. 6. Nombre de femelles ovigères de *Palaemonetes argentinus* portant des embryons de différents stades de développement. Embryons sans yeux (stade 1), avec début de développement des yeux (stade 2), avec développement complet des yeux (stade 3).

The breeding period of *P. argentinus* in Mar Chiquita was characterized by one peak in the percentage of ovigerous females (>87 %, Fig. 5) as in Villa Elisa (>83 %; Schuldt & Damborenea 1987), whereas two peaks with different intensity were found in Buenos Aires (October 93 %, January 38 %) and Córdoba, (November 67 %, January 16 %) (Goldstein & Lauria de Cidre 1974, Donatti 1986).

The sex-ratio in the Mar Chiquita population of *P. argentinus* was approximately 1:1 during most of the year (Fig. 4), whereas in other populations females predominated (Córdoba ; Donatti 1986). However, changes in sex-ratio were observed during the period of high reproductive activity: females reached >84 % in the November samples, but returned to a 1:1 sex ratio in December. These transient changes suggest changes in the spatial organization of the population, probably related with mating and hatching. On the other hand, the predominance of males at the end of December could be explained by earlier deaths of females.

In Mar Chiquita, females are larger than male *P. argentinus* and can produce more than two broods during their lives, as observed also in freshwater populations (Goldstein & Lauria de Cidre 1974, Donatti 1986, Schuldt & Damborenea 1987, Rodrigues Capitulo & Freyre 1989).

Rodrigues Capitulo & Freyre (1989) established that a freshwater population of *P. argentinus* is characterized by several cohorts per year. Donatti (1986) described the existence of two groups of females, with different sizes, in the Córdoba population. Two female cohorts were observed in Mar Chiquita during 1995, they were ovigerous at different times and varied in size and fecundity (Figs. 7, 8). At the beginning of the reproductive season, females were larger and carried comparatively less embryos. Later, smaller females appeared, but their relative fecundity was higher. Both cohorts could potentially produce two hatches per season, since many shrimps showed evidence of ovary development during egg incubation or after hatching. The present data suggest that only some females of the



first cohort were able to produce a second hatch in 1995 (Fig. 7).

The number of stage 1 embryos per female varied with sizes and samples (Fig. 8). It was possible to estimate a linear size-fecundity relationship, like Schuldt & Damborenea (1987). The maximum number of embryos (250) was higher and lower, respectively, than that observed in the populations from Córdoba (228) and Villa Elisa (300) (Donatti 1986; Schuldt & Damborenea 1987) but the former study did not distinguish between early and late embryos. A comparison of size-fecundity relationships between different populations of *P. argentinus* was possible after taking uniform measurements of individual size (see Material and Methods). Although there were no important differences in the number of embryos carried, ovigerous females from Mar Chiquita were small. e.g. The CL of females carrying 110 embryos were 5.35, 6.12 and 7.75 mm in Mar Chiquita, Villa Elisa and Córdoba, respectively. No evidence of *Probopyrus oviformis* was found in Mar Chiquita females, this isopod has been reported as a frequent parasite of the branchial chamber in the Villa Elisa population (Schuldt & Damborenea 1987).

The adult population disappeared by the end of the year in Mar Chiquita (Fig. 2 and 3), when a new generation of recruits became evident, and a second reproductive year was not observed. This pattern is similar to that observed in the populations from Villa Elisa and Córdoba, where massive adult mortality has been reported for January and November, respectively (Donatti 1986, Schuldt & Damborenea 1987). A second reproductive year may occur in Buenos Aires and in Chascomús (Goldstein & Lauria de Cidre 1974, Rodrigues Capitulo & Freyre 1989). In Chascomús, females reach 2 years of age, but males did not live more than 1.3 years.

Fig. 7. Size of *Palaemonetes argentinus* females during the breeding period (CL = carapace length; mean and SD values). a) ovigerous females with stage 1 embryos; b) ovigerous females with stage 3 embryos; c) postovigerous females. Statistically significant differences between means belonging to successive samples (Mann-Whitney Rank Sum or Student-t test) are indicated as follows: * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

Fig. 7. Taille de *Plaemonetes argentinus* femelles durant la période de reproduction (CL = taille de la carapace, moyenne, déviation standard). a) femelles ovigères avec les embryons de stade 1; b) femelles ovigères avec les embryons de stade 3; c) femelle post ovigère. Les différences significatives entre les moyennes des échantillonnages successifs (Mann-Whitney somme des rangs ou Test Student) sont données ci-après : * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

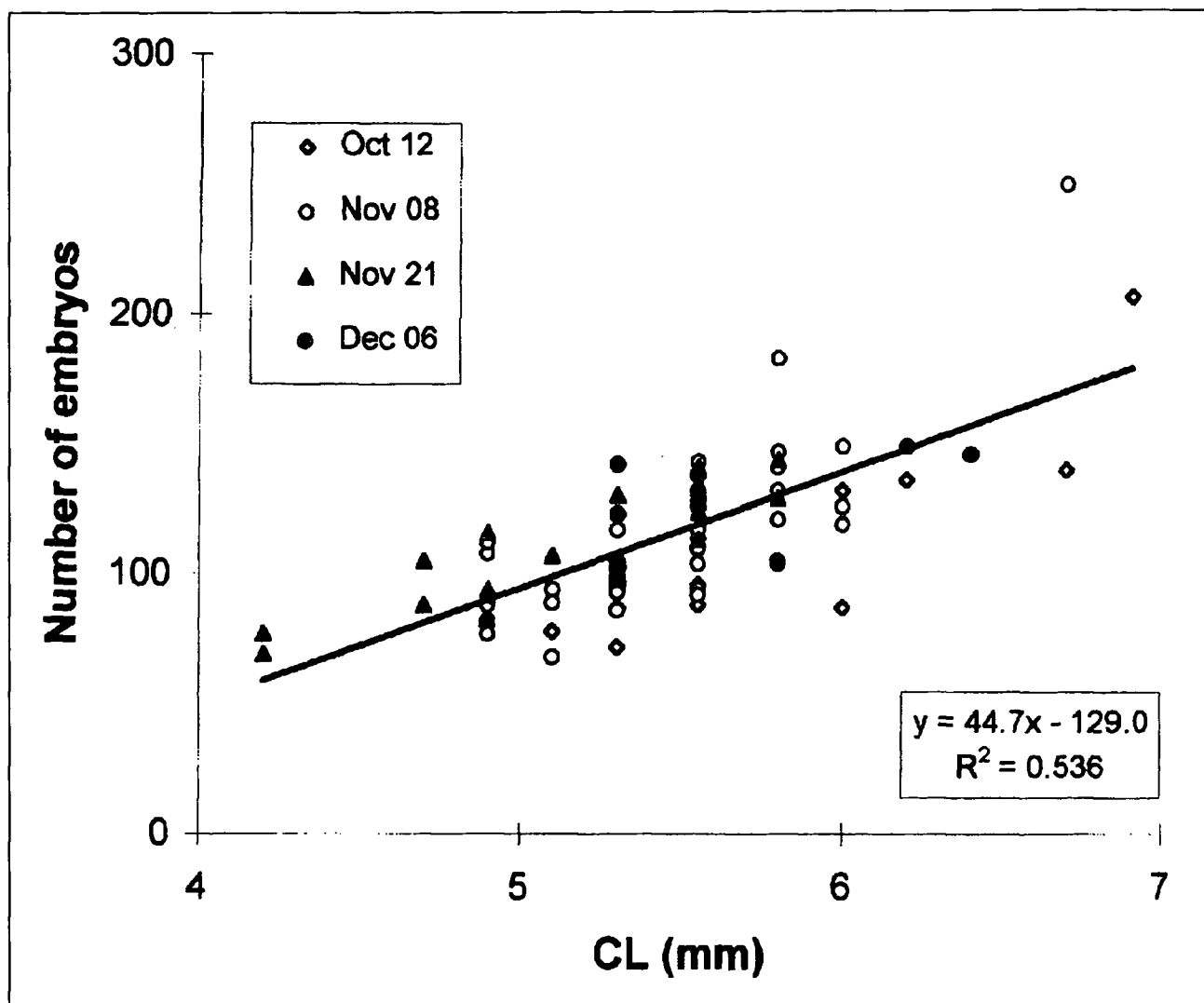


Fig. 8. Relationship between the number of *Palaemonetes argentinus* stage 1 embryos and size of ovigerous females (CL= carapace length).

Fig. 8. Relation entre le nombre des embryons de stade 1 de *Palaemonetes argentinus* et la taille des femelles ovigères (CL = taille de la carapace).

The existence of two periods of intense growth, one in spring, the other in summer, was observed in Mar Chiquita and in freshwater populations (Rodrigues Capitulo & Freyre 1989, Donatti 1986). Small shrimps grew quickly in summer, but growth of juveniles diminished in winter and restarted in spring.

Larvae were present in the same habitat as the adults from the end of November and their abundance seemed to reach a maximum at the beginning of January. These data agree with the period of 40 days of embryonic development observed in the laboratory at 21°C (Goldstein & Lauria de Cidre 1974). The small number of larvae collected in February, and their absence in March 1996, contrast with higher numbers observed in March 1995. The presence of two female cohorts in 1995, as well as larvae occurring late in the season (March), suggest that two peaks of reproductive activity have occurred in Mar Chiquita in 1994.

The life cycle of *P. argentinus* in Mar Chiquita brackish-waters is similar to that described in several freshwater populations although differences such as a shorter breeding period are probably related to climatic factors, since Mar Chiquita is near to the southern limit of the geographic range of *P. argentinus*. However, data presented here suggest interannual variations in the reproductive patterns which sometimes lead to a bimodal breeding pattern, as in northern populations.

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