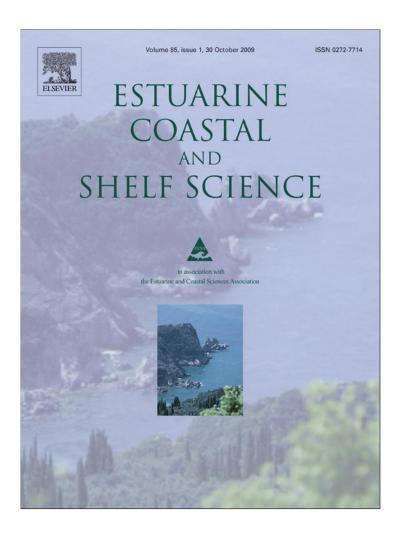
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Estuarine, Coastal and Shelf Science 85 (2009) 82-88



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Temporal variation in abundance and fecundity of the invading copepod Eurytemora americana in Bahía Blanca Estuary during an unusual year

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ARTICLE INFO

Article history: Received 4 December 2008 Accepted 8 March 2009 Available online 14 March 2009

Keywords: Eurytemora americana abundance and fecundity invading copepod unusual annual cycle

ABSTRACT

Eurytemora americana has been only reported as invader in Bahía Blanca Estuary, Argentina within the South Hemisphere. There are a few experimental researches under laboratory conditions done with this species and its reproductive behaviour around the world is very scarce. Consequently, it is still not possible to completely understand its population dynamics. In the present study, E. americana reproductive temporal behaviour and relationships among abundance, female size, egg production and hatching success were examined in the Bahía Blanca Estuary, during 2007 pulse. In order to determine the potential relationships between these variables and the environmental variables, experimental incubations were conducted in the laboratory simulating natural conditions. Spearman's rank correlation was used to analyze the relationships among all variables. Temporal change of biotic and environmental variables was corroborated by a Mann-Whitney/Kruskal-Wallis non-parametric tests, with significant differences ($p \ll 0.01$) in all variables throughout the study. Abundance population results showed very high values in relation to those recorded in recent years in Bahía Blanca Estuary. This response could be due to the unusual combination of environmental factors (polar wave with temperatures \leq 6 °C and a drought period with high salinities, 32.7–36.6) recorded during the studied winter period. Significant positive correlations between abundance and salinity (p < 0.01, n = 226), and hatching success (p < 0.01, n = 25) as well as a significant negative correlation between abundance and chlorophyll a (p < 0.01, n = 226) were found. Although E. americana shows a k-strategy within its annual pulse, it presented two markedly distinct behaviours depending on temporal environmental variability. From July to early september, when the estuary evidenced high salinity, low temperature and high food availability, E. Americana showed large females, large clutch size and high hatching success. When environmental conditions became unfavorable from September to October, small females, small clutch size and very low hatching success were observed. The latter is associated with diapause egg laying which ensures population recruitment. According to our findings the particular combination of low temperatures, high salinities and high available food (i.e. variables which each year modulate its pulse) during 2007 winterspring, favored the great development of E. americana. This invading species in its opportunistic role has managed to exploit a vacant niche in the estuary, developing two different behaviours within the k-strategy depending on change in environmental conditions.

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Eurytemora americana (Williams, 1906) is an estuarine copepod native to the northern hemisphere (Kos, 1977) which is generally observed in relatively low abundance (40–1250 ind m⁻³) in comparison to other copepods like Eurytemora affinis, Eurytemora hirundoides, Acartia tonsa and Acartia clausi (Jeffries, 1962; Heron,

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1964; Sage and Herman, 1972; Avent, 1998). This species is adapted to cold-intermediate temperatures (<1–15 °C) and intermediate salinity with values (in Practical Salinity Scale) ranging between 10 and 33 (Avent, 1998) or around an average of 24 or less (Sage and Herman, 1972).

Until now, *Eurytemora americana* has been only reported as invader in Bahía Blanca Estuary within the South Hemisphere (Hoffmeyer, 1994; Hoffmeyer et al., 2000). This copepod develops a planktonic pulse beginning in June and lasting until October,

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during which it coexists with A. tonsa and Balanus glandula larvae, maintaining a competitive relationship between them (Hoffmeyer, 1994, 2004). After this, E. americana disappears from the water column and remains as resting eggs in bottom sediments (Hoffmeyer, 2004). Over approximately the last twenty years E. americana has became the most abundant calanoid copepod in the estuary from August to October (Hoffmeyer et al., 2009). Its population density has increased during the last years associated with environmental changes and its dominance over A. tonsa population has been observed (Hoffmeyer, 2004; Hoffmeyer et al., 2008, 2009). Partial exclusion of A. tonsa in the co-occurring period could be attributed to the fact that E. americana (herbivory) assimilates the phytoplankton bloom more efficiently than A. tonsa (Hoffmeyer and Prado-Figueroa, 1997). Eurytemora americana has presented low abundance (30.33 ind m $^{-3}$ at 5–7 °C and 34–35 of salinity) during the 1990-1991 pulse and a higher abundance (6330 ind m⁻³ at 10.90 °C and 17.23 of salinity) in the 2002 pulse in the Bahía Blanca Estuary (Hoffmeyer, 2004). Recent research on this population has shown positive significant correlations of abundance of its developmental stages with chlorophyll a (Chl-a) and salinity as well as negative correlations with temperature and photoperiod (Hoffmeyer et al., 2009).

Generation time of *E. americana* is approximately 40 days at 4 °C (Grice, 1970) and its reproductive strategy appears to be similar to that of E. affinis. The latter species produces subitaneous eggs during favourable environmental conditions and diapausal during unfavourable conditions (Marcus et al., 1994; Chen and Marcus, 1997; Katajisto, 2006). Preliminary studies performed in Bahía Blanca Estuary provide evidence that, during the population growth period, E. americana produces only subitaneous eggs which are ready to hatch in a few days (Berasategui et al., 2009). In contrast, at the beginning of population decline, females start to produce resting eggs (Diodato et al., 2006; Hoffmeyer et al., 2008; Berasategui et al., 2009). Research conducted with E. affinis has shown an inverse correlation of temperature with body length and clutch size, with the consequent direct relationship between the last two variables (Hirche, 1974, 1992). Similarly, in a study carried out with E. americana females from Bahía Blanca Estuary, body size and volume (biomass) decrease was detected at the end of the population pulse, associated with higher temperatures and less available phytoplankton but the probable relationship with the clutch size was not addressed (Hoffmeyer and Torres, 2001). At present, there are a few experimental researches under laboratory conditions done with E. americana (Grice, 1970; Berasategui et al., 2009). In addition, knowledge about its reproductive behaviour around the world is very scarce. Consequently, it is still not possible to completely understand its population dynamics. Taking into account the results of research conducted with Eurytemora spp. we predict that (1) egg production, and hatching success vary temporally during the population pulse, and (2) these variables have a direct relationship with salinity and Chl-a and an inverse relationship with temperature. To test these hypotheses and reconfirm already established results, we examined the relationship between E. americana field abundance, egg production (clutch size), hatching success (hatching percentage) and female size (prosome length) during the 2007 population pulse in Bahía Blanca Estuary. We also analyzed the possible relationships between these biotic variables and environmental conditions such as temperature, salinity and Chl-a. The present paper will contribute to a better understanding of population dynamics of this species and to comprise how such dynamics is affected by environmental variability which constitutes scarcely known matters.

Sampling and measurements were conducted at Cuatreros Port from July to October 2007, with an approximate fortnight frequency (nine sampling dates) during the *E. americana* annual pulse (Fig. 1).

Cuatreros Port is located in the innermost area of Bahía Blanca Estuary, Argentina (30°30′-39°25′S; 61°15′-63°00′W). On the basis of mainly water dynamics and temperature-salinity variation, in general this estuary is defined as vertically homogeneous (Perillo and Piccolo, 1999; Freije and Marcovecchio, 2004). Water exchange is driven by semidiurnal tides and the estuary receives a low freshwater input from Sauce Chico River and Napostá Grande Stream, with an annual mean discharge of 1.9 and $0.8 \text{ m}^3 \text{ s}^{-1}$, respectively (Piccolo et al., 1990). Subsurface water temperature, salinity and Chl-a concentration were monitored to determine their temporal variation. Temperature and salinity were measured (in Practical Salinity Scale) with an HORIBA® multiparameter probe, and subsurface water samples were collected for spectrophotometrically determining Chl-a and phaeopigment concentrations according to Lorenzen (1967). Additional subsurface water (0.5-1 m depth) samples were collected for the experimental laboratory incubations. A total of 18 live mesozooplankton samples (two for each sampling date) were collected with a 200-µm mesh plankton net (0.30 m mouth diameter) by means of subsurface horizontal tows. Two series of experiments were conducted in the laboratory. In the first series, live samples were filtered using a 1.7-mm mesh filter to reject macrozooplankton while the mesozooplankton fraction was retained on a 0.2-mm mesh filter. Immediately after this, the concentrated mesozooplankton was put into two plastic containers filled with 5 L of filtered seawater (60-µm mesh) for diminishing density and was incubated for 24 h. Copepod egg production observed in the first 24 h after sampling reflects the in situ egg-laying behaviour (Runge and Roff, 2000). During experiments, we used similar temperature values as those measured in situ. After incubation, samples were preserved in 4% formalin for later determining abundance, egg production (clutch size) and female body size (prosome length) according to Hoffmeyer and Torres (2001). Thus, during each sampling date, females (10-30) with complete egg sacs and empty oviducts were selected to measure prosome length and count the number of eggs per sac. A total of 226 females were measured along the study period. In the second series, egg-carrying females were selected from the live mesozooplankton samples and were individually incubated to examine hatching success. Each female was sorted from the sample under a stereomicroscope, washed with 0.45-µm mesh filtered estuarine water and placed on a dish with 100 ml water ($<60 \mu m$). Two to four dish replicates were incubated for each sampling date, by suspending the dishes in a culture water bath under simulated in situ temperature and photoperiod conditions. Hatching of initial eggs (15-60 eggs per dish) was monitored with controls every 24-48 h. Estuarine water with natural food (<60 μm) was changed every 48 h and 14–15 h of dark were provided. Hatching percentage was calculated in relation to the initial egg number by: [(No. of nauplii/No. of initial eggs) × 100] according to Runge and Roff (2000). To facilitate counting of nauplii and non-hatched eggs in each control, both were retained in a 60-µm mesh and preserved in 4% formalin. General appearance of non-hatched eggs was also observed. Hatching success was evaluated in a total of 25 experimental units along the sampling period. Mean comparisons of biotic variables between sampling dates were performed by the Mann-Whitney/Kruskal-Wallis tests with Bonferroni's correction. These statistical non-parametric tests were applied because the studied variable data have not been able to meet the normality/ variance's homogeneity assumptions. On the other hand Spearman's rank correlation analysis was used to describe and analyze the relationships among all variables.

Results on temporal variation of salinity, temperature and Chla showed two clear trends (Fig. 2a). From July to mid-August, low temperatures (5.2-7 °C) and high salinity (32.7-36.6) were recorded. In September, a temperature increase (11.9-15.8 °C) and

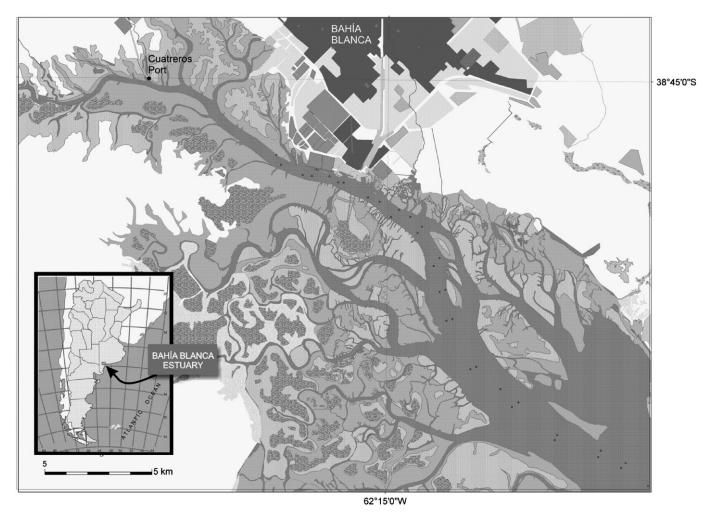


Fig. 1. Map of the Bahía Blanca Estuary, Argentina, with location of the sampling station (Cuatreros Port).

a salinity decrease (<30) were also observed. Concentration of Chla from July to mid-August was generally higher (20–8.07 μ g L⁻¹) than the concentration during October owing to a phytoplankton bloom during that period (Popovich and Marcovecchio, 2008). The population's abundance increased during July to the beginning of September when the maximum value occurred (Fig. 2b). After this, there was a period of population decline until the end of the pulse in October. During the population peak, a maximum of 17402 ind m⁻³ was observed, which coincided with the maximum salinity value (37.51), temperatures of approximately 7–11.9 °C and a decrease in Chl-a (<8.07 $\mu g L^{-1}$). Significant positive correlations between abundance and salinity (p < 0.01, n = 226), and hatching success (p < 0.01, n = 25) as well as a significant negative correlation between abundance and Chl-a (p < 0.01, n = 226) were found (Table 1). Female prosome length decreased during the pulse, but there were notoriously larger prosome sizes (1.14 ± 0.009 – $0.95 \pm 0.018 \text{ mm}$) during the period of population growth than during the period of population decline $(0.72 \pm 0.012 0.67 \pm 0.012$ mm) (Figs. 2b and 3). The largest sizes coincided with high salinity (32–37.51), high Chl-a ($>8.07 \text{ mg L}^{-1}$) and low temperature (5-7 °C) conditions as well as with a high hatching success (91-100%) and large clutch size (114-101 eggs per sac) (Fig. 2a,b). Correlations showed the same trends, female prosome length was positively correlated with salinity, Chl-a, clutch size and hatching success but negatively correlated with temperature (Table 1).

Clutch size and hatching success presented high values during the period of population growth and low values in the declining period (Fig. 2c). Both variables were positively correlated with each other and with salinity, also presenting a negative correlation with temperature (Table 1). Chl-a exhibited a positive significant correlation with clutch size and a positive non-significant correlation with hatching success (Table 1). At the end of August, the number of non-hatched eggs increased, reaching 100% in October, at the end of the pulse (Fig. 2c). Although we do not present in this paper egg size measurements, these eggs were larger than those produced at the start of pulse (subitaneous) (Fig. 3). Generally, they were released forming egg masses with sac remains. Kruskal-Wallis test results determined significant differences ($p \ll 0.001$) in all mentioned biotic variables throughout the sampling dates. The latter indicates that there were clear temporal variations of them during the population pulse. The Mann-Whitney-Bonferroni analysis results determined that abundance significantly differed during all sampling dates (p < 0.05). In contrast, no significant differences in clutch size, prosome length and hatching success were found within the first and the last sampling dates by which two different behaviours of these variables could be established.

The results of this study demonstrated higher abundance values of *E. americana*, than those recorded in the last years (Fig. 4a), in Bahía Blanca Estuary (Hoffmeyer, 2004; Hoffmeyer et al., 2008, 2009). Furthermore population peak values found in this study

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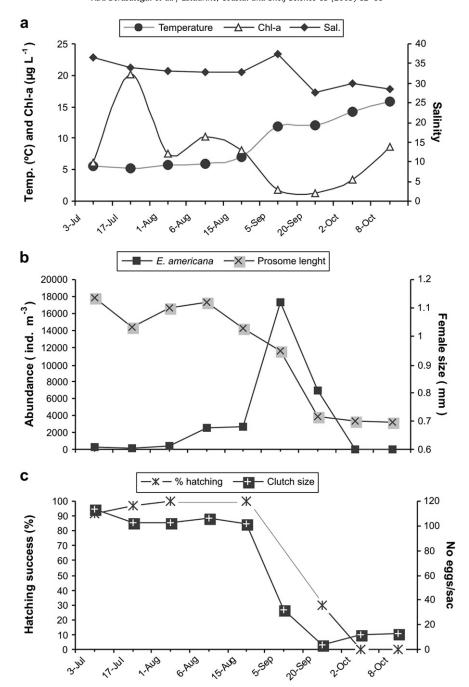


Fig. 2. Temporal variation. a) Environmental variables, b) Female size and abundance of E. americana and c) Hatching success and clutch size.

 $(17402 \text{ ind m}^{-3})$ greatly exceeded those previously recorded in estuaries of origin (Jeffries, 1962; Heron, 1964; Sage and Herman, 1972), as well as those recently reported for other places in Argentina such as Golondrina and Ushuaia bays (Fernandez-Severini and Hoffmeyer, 2005; Biancalana et al., 2007). Under similar conditions of temperature and salinity as in the present study, low abundances of *E. americana* have been reported in Duwamish River Estuary (40–150 ind m⁻³) (Avent, 1998) and Ushuaia Bay (<2 ind m⁻³) (Biancalana's unpublished data), in relation to other copepods. Taking into account these precedents, the strong response in abundance observed during pulse 2007 may be explained by an unusual combination of environmental conditions, low competition and the existence of a large egg-bank, deposited in the sediments over the years. These unusual

environmental conditions during the 2007 winter can be related to a polar wave of Antarctic origin which affected the south of South America, likely lowering the temperature of estuarine water. On the

Table 1 Spearman's rank correlation matrix. The correlation coefficients correspond to only significant correlations.**p < 0.01; *p < 0.05 and ns means no significant correlation (n = 25 for hatching success and n = 226 for the other variables).

	% hatching	Abundance	Prosome length	Clutch size
Abundance	0.475*			
Prosome length	0.874**	ns		
Clutch size	0.848**	ns	0.782**	
Temperature	-0.810**	ns	-0.786**	-0.788**
Salinity	0.675**	0.208**	0.537**	0.543**
Chl-a	ns	-0.437**	0.472**	0.657**

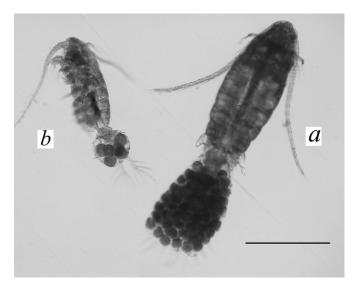


Fig. 3. Variability of *E. americana* female size and clutch size. a) Female at the beginning of pulse (August) and b) female at the end of pulse (October). The scale bar represents 700 µm.

other hand, a drought period in the temperate eastern coast of South America, postulated as an effect of an ENSO episode (La Niña) (Barros and Silvestri, 2002; Silvestri, 2005), was also recorded in 2007. This phenomenon produced a low freshwater input into the estuary generating high salinity. Although other factors such as the scarcity of competitors (low abundances of A. tonsa and B. glandula larvae) and fish larvae predation (Lopez-Cazorla et al., 2006) could be modulating the abundance of E. americana population, we believe that the combination of low temperatures and high salinities also had an important role in 2007's pulse. Furthermore, analyzing comparatively the fluctuations of the environmental conditions during the E. americana pulses in 2002, 2005 and 2007 years, there were no large differences among peak values of Chla $(17-20 \mu g L^{-1})$ but the lowest temperatures and highest salinities were observed during the 2007 pulse (Fig. 4b). According to previous studies, an inverse correlation between abundance and temperature as we expected (Hoffmeyer et al., 2009) was not found in this study. However, the high significant negative correlations between temperature and clutch size-hatching success suggest a possible indirect relationship between abundance and temperature. On the other hand, correlation analysis showed a significant direct relationship between abundance and salinity. Our findings on the maximal population abundance in Bahía Blanca Estuary suggest that this species seems to benefit from high salinity conditions (32-37) compared with those from the estuaries of

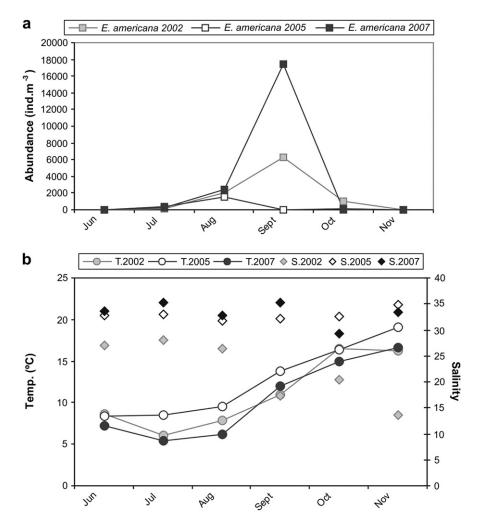


Fig. 4. Comparative analysis among *E. americana* pulses in Bahía Blanca Estuary. a) *Eurytemora americana* annual pulses and b) temperature and salinity conditions. Pulse 2002 data extracted from Hoffmeyer et al. (2009) and pulse 2005 data (M.D. Fernandez Severini, unpubl. data).

origin and also with those registered in this estuary in previous years. However, this hypothesis should be corroborated with further experimental studies on tolerance range for salinity.

Despite being considered the temperature as the main factor influencing in copepod fertility (Castro-Longoria, 2003; Holste and Peck, 2006), it is known in other estuarine copepod species that salinity can also have a direct effect on egg production, development time and survival (Castro-Longoria, 2003; Lee et al., 2003; Calliari et al., 2008). From the relationships observed in the present study between hatching percentage/clutch size and salinity coupled with temperature, it is clear that *E. americana* fecundity was positively influenced by the high salinity. On the other hand, since this species is an herbivore (Hoffmeyer and Prado-Figueroa, 1997), rich available food also plays a fundamental role in relation to its fecundity which is supported by the positive relationship found between Chl-a concentration and clutch size.

Although E. americana shows a k-strategy similar to that of E. affinis (Hirche, 1992) within its annual pulse, it presented two markedly distinct behaviours depending on temporal environmental variability. From July to early September, when there was high salinities (32–37), low temperatures (<7 °C) and high food availability in the estuary, E. americana produced large females, large clutch size (Fig. 3a) and high hatching success. When environmental conditions became unfavourable (salinity lower than 30, temperatures above 11 °C and Chl-a below $8 \mu g L^{-1}$) from September to October, small females, small clutch size (Fig. 3b) and very low hatching success were observed. As in the case of E. affinis (Ban, 1992; Katajisto, 2006), this second behaviour is associated with diapause egg laying to ensure population recruitment (Marcus, 1996; Hoffmeyer et al., 2009). On the other hand, an inverse relationship between egg size and clutch size has been mentioned for E. affinis (Hirche, 1992) and the same relationship has been observed for E. americana in this study. Temporal variation of female size and egg production (clutch size) might be well related to the use of metabolic resources (Ikeda et al., 2000) in relation to environmental changes. In this sense, the small size of females observed in this study at the end of pulse could probably be the result of a metabolic balance in favour of diapause egg production (Marcus, 1996; Belmonte, 1998; Castro-Longoria, 2001) and osmotic regulation in front of changes in water temperaturesalinity (Kimmel and Bradley, 2001), leaving little reserves to be accumulated in body mass.

In conclusion, the particular combination of low temperatures, high salinities and high available food (i.e. variables which each year modulate its pulse) during 2007 winter–spring gave rise to the highest abundance peak of *E. americana* in the last years in Bahía Blanca Estuary. This invading species in its opportunistic role has managed to exploit a vacant niche in the estuary, developing two different behaviours within the k-strategy depending on change in environmental conditions. Certainly, these two behaviours contributed to its success as invasive species in this estuary.

Acknowledgments

We are grateful to Instituto Argentino de Oceanografia and Chemistry Lab. staff for their collaboration. Particularly we thank R.O Asteasuain and L. Kaufman. This study was supported by grant PICT1713-2006 (ANPCYT) and a postgraduate fellowship (CONICET).

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