Annual population dynamics of the opossum shrimp *Neomysis americana* Smith, 1873 (Crustacea: Mysidacea) from an estuarine sector of the Argentine Sea*

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SUMMARY: The opossum shrimp *Neomysis americana* Smith, 1873 (Crustacea: Mysidacea) is abundant in coastal and estuarine sectors of the southwest Atlantic (30ºS-40ºS) where it plays a key role as food for fish. In the present work the population dynamics of the species in Samborombón Bay (Río de la Plata estuary, Argentina) during an annual cycle is analyzed. Samples were obtained from March 1987 through to March 1988 with a small Bongo net (20 cm diameter, 200 μm mesh size). *N. americana* occurred all year round with maximum densities in austral spring and summer. Three annual generations were identified. The overwintering generation had a growth rate of about 0.037 mm day^{-1} and duration of 4.9 months, the spring generation grew at a rate of 0.146 mm day^{-1} during 1.5 months, the summer generation had a growth rate of 0.076 mm day^{-1} and matured in 1.5 months. The sex ratio was favourable to females, which had a higher growth rate and a larger size than males. The species reproduced constantly throughout the year. The proportion of gravid females was higher during spring and summer but the brood size was larger in winter (20-25 embryos female^{-1}) than in spring and summer (10-15 embryos female^{-1}). The results obtained were related to the environmental conditions. The implications of the spatial and temporal distribution patterns of *Neomysis americana* for the local food web were discussed.

Keywords: *Neomysis americana*, abundance, biomass, annual generations, growth, Samborombón Bay, Río de la Plata estuary, southwest Atlantic.

RESUMEN: DINÁMICA POBLACIONAL ANUAL DEL CAMARÓN MARSUPIAL *NEOMYSIS AMERICANA* SMITH, 1873 (CRUSTACEA: MYSIDACEA) EN UN SECTOR ESTUARIAL DEL MAR ARGENTINO. – El camarón marsupial *Neomysis americana* Smith, 1873 (Crustacea: Mysidacea) es abundante en sectores costeros y estuariales del Atlántico Sudoccidental (30ºS-40ºS) donde juega un rol clave como alimento para peces. En el presente trabajo se analiza la dinámica poblacional de la especie en la Bahía Samborombón (estuario del Río de la Plata, Argentina) durante un ciclo anual. Las muestras se obtuvieron durante el período marzo 1987-marzo 1988 con una red Bongo, modelo reducido (20 cm de diámetro, 200 μm de tamaño de malla). *N. americana* estuvo presente durante todo el año con máximas densidades en la primavera y el verano austral. Se identificaron tres generaciones anuales. La generacion invernal tuvo una tasa de crecimiento de aproximadamente 0.037 mm día^{-1} y una duración de 4.9 meses, la primaveral creció a una tasa de 0.146 mm día^{-1} durante 1.5 meses y la de verano mostró un crecimiento de 0.076 mm día^{-1} y maduró en 1.5 meses. La proporción de sexos fue favorable a las hembras que tuvieron mayor tasa de crecimiento y mayor talla que los machos. La especie se reprodujo continuamente durante el año. La proporción de hembras grávidas fue superior durante la primavera y el verano pero el tamaño de la progenie fue mayor en invierno (20-25 embriones hembra^{-1}) que en primavera y verano (10-15 embriones hembra^{-1}). Los resultados obtenidos se relacionaron con las condiciones ambientales. Se discutieron las implicancias que el patrón de distribución espacial y temporal de *Neomysis americana* tiene para la trama trófica local.

Palabras clave: *Neomysis americana*, abundancia, biomasa, generaciones anuales, crecimiento, bahía de Samborombón, estuario del Río de la Plata, Atlantic suroccidental.

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INTRODUCTION

Mysids are important in the ecosystem due to their capability to transform the organic detritus—which is very abundant in their habitats—into available biomass for higher trophic levels (Corey, 1988). Their largest concentrations undoubtedly occur in coastal regions where they constitute an important potential food resource for coastal fishes (Mauchline, 1980).

The opossum shrimp *Neomysis americana* (Crustacea, Mysidacea) is the most abundant shallow living mysid inhabiting the coastal and estuarine waters of eastern United States, from 55ºN to 35ºN (Hopkins, 1965; Wigley and Burns, 1971; Williams *et al*., 1974; Corey, 1988). Its presence in the southwest Atlantic was reported for several coastal and estuarine sectors of the Argentine, Uruguayan and Brazilian Sea (González, 1974; Mianzan *et al*., 1989; Hoffmeyer, 1990; Gomes Tavares and Bond-Buckup, 1991; Bond-Buckup and Gomes Tavares, 1998; Calliari *et al*., 2001; Freitas and Montú, 2001). In the Samborombón Bay (36ºS and 57ºW), within the Río de la Plata estuary, *N. americana* constitutes one of the few dominant species of the net zooplankton community (Mianzan *et al*., 1989; Viñas *et al*., 1994). The bay is the main nursery area for many of the fish species inhabiting the Río de la Plata estuary and which contribute substantially to coastal fisheries of Argentina and Uruguay (Lasta, 1995).

It was suggested that one of the conditions that most favours the bay as a nursery ground for fish is food availability (Lasta, 1995). In several previous papers it was stated that *N. americana* is the main prey for most juvenile fish (Giangiobbe and Sánchez, 1993; Sánchez *et al*., 1991; MS; Giberto *et al*., 2001), including whitemouth croaker (*Micropogonias furnieri*), the species with the highest commercial value for regional coastal fisheries (Sánchez *et al*., 1991; Macchi *et al*., 1996). In spite of the key role mysid plays in the local food web, no studies concerning its life cycle in Samborombón Bay have been conducted to date.

In the present work the population dynamics of *N. americana* during an annual cycle was analyzed. Abundance and biomass at different developmental stages, the number, timing and growth rates of seasonal generations as well as other population parameters such as sex ratio, proportion of gravid females, fecundity and size variations of adults were also studied. Results concerning the life cycle of *N. americana* in the bay were linked to the hydrographical conditions that prevailed during the study year. The implications of the spatial and temporal distribution pattern of *Neomysis americana* for the local food web were discussed.

MATERIALS AND METHODS

Study area

Samborombón Bay (SB) extends from Punta Piedra to Punta Rasa (Fig. 1 A and B), and constitutes the main coastal accident of the Río de la Plata estuary. It has a maximum depth of 10 m and a depth/width ratio of 1/10000 which traduces in high influence of winds and tides (Guerrero *et al*., 1997). Its northern zone, from Punta Piedras to the mouth of the Salado and Samborombón rivers (Fig. 1 B), is under the influence of the Río de la Plata runoff. The almost permanent influx of marine waters is a feature of the southern sector. Salt marshes are well developed all along the shore of the bay, with a maximum covered surface in the southern sector.

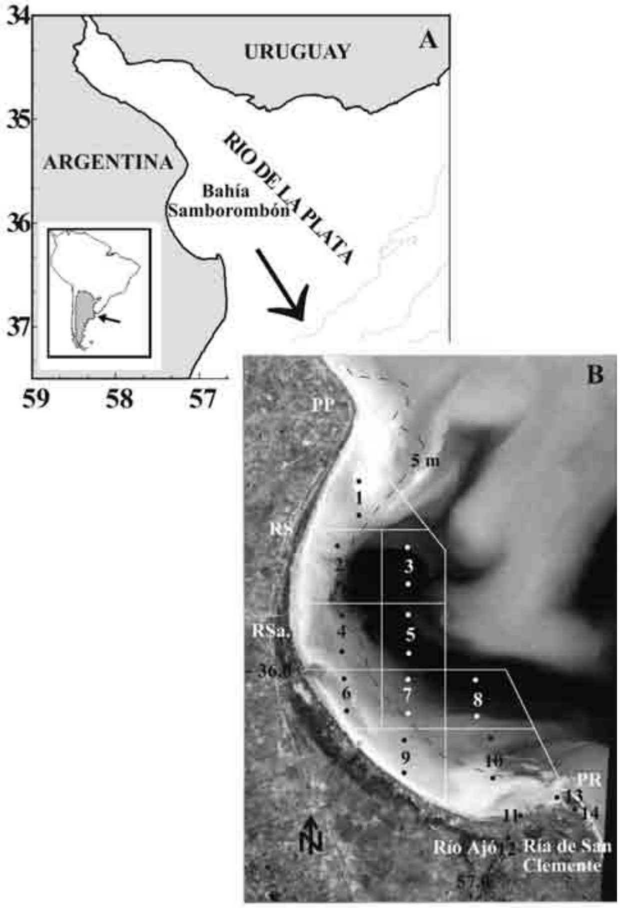

FIG. 1. – (A) Study area and (B) location of the sampling stations. LANDSAT TM image showing the turbidity front location. (PP) Punta Piedras, (RS) Río Salado, (Rsa.) Río Samborombón, (PR) Punta Rasa.

Abundant halophyte plants, predominantly *Spartina* spp., that cover the coast and the salt marshes are responsible for most of the primary productivity. They provide the main source of organic matter and detritus to the bay (Boschi, 1988). Suspended sediments, mostly originating from the Río de la Plata river, are usually observed in the littoral fringe (Fig. 1B). The most abundant herbivorous organism in the *Spartina*-dominated marshes is the burrowing crab *Chasmagnathus granulata* (Boschi, 1964; Iribarne *et al*., 1997). The intricate physiography of these habitats provides a refuge for juveniles of many fish species (Lasta, 1995).

Field sampling and sample laboratory analysis

Samples were obtained during 9 research cruises carried out in the bay between March 1987 and March 1988 (Fig. 1 B) with a small Bongo net with a 20 cm diameter and 200 μm mesh size (Smith and Richardson, 1977). Fourteen fixed stations were designed for fisheries research purposes. Two zooplankton samples were taken in each and their averages used here. In stations 11 through to 14 only one sample was obtained. The trawls were oblique from the bottom to the surface. The filtered water volume was estimated by means of a mechanical flowmeter. Samples were preserved in a 4 % formaldehyde solution.

Temperature (ºC) and salinity (PSU) data were obtained in each sampling station with a portable YSI S-C-T meter, model 33. Salinity samples were calibrated with an inducted Beckman RS9 salinometer and IAPSO sea-water P92 (29/10 1981). The final precision was 0.2 in temperature and 0.2 in salinity.

In the laboratory, taxonomical identification and sex determination were made with a binocular microscope following Tattersall (1951), and Williams *et al.* (1974). Specimens were classified into four categories based on sexual characteristics: (1) juveniles without visible sexual characteristics; (2) males with elongated fourth pleopods or papilla; (3) ungravid females with empty *marsupium*; (4) gravid females with eggs or larvae in the *marsupium*.

The sex ratio, estimated as the proportion of females in relation to the total amount of adults, and the size structure of the population were determined in each cruise. The total length (TL) of at least 100 individuals was measured (0.1 mm) from the *rostrum* to the end of the *telson*. Mysids tend to curl when preserved, so before measuring them individuals were put in a dorsal position and stretched slightly. Five consecutive 2 mm size classes were established; the first (2-4 mm) corresponded to juveniles. From 4 mm on, each size class was subdivided into the three following categories: males, ungravid females and gravid females. After the sex and measurements were established, individuals were included in one of the above mentioned categories. The standing crop was calculated indirectly for each sampling date from the size structure of the population and the length-weight relationship proposed by Richards and Riley (1967), for the species. The equations are:

$$\text{Log}\,(DW + 1) = 0.975\ \text{Log}\,TL - 0.598$$

for individuals collected in autumn-winter and

$$\text{Log}\,(DW + 1) = 0.742\ \text{Log}\,TL - 0.813$$

for individuals collected in spring-summer.

Total length (TL) in mm and dry weight (DW) in mg.

The mean fecundity estimate was obtained following Clutter and Theilacker (1971). To make this estimate only gravid females with an undamaged *marsupium* were selected from each sample. The number of eggs or young stages was recorded without discriminating their developmental stage.

The number and duration of the annual generations were estimated taking into account the peaks of relative abundance of juveniles occurring after a pulse of relative abundance of ovigerous females and the corresponding next relative peak of ovigerous females. To support this observation, the absolute abundance of juveniles and adults was also considered.

The growth rates and growth curve of males and females of each generation were constructed considering the size increase from juveniles to adults during the generation time.

The statistic significance of sexual ratios was tested using the G-test (Sokal and Rohlf, 1995).

RESULTS

Temperature and salinity

During the study period, temperature and salinity showed a vertically homogeneous pattern in the water column. Consequently, surface data were employed as representatives of the whole water column.

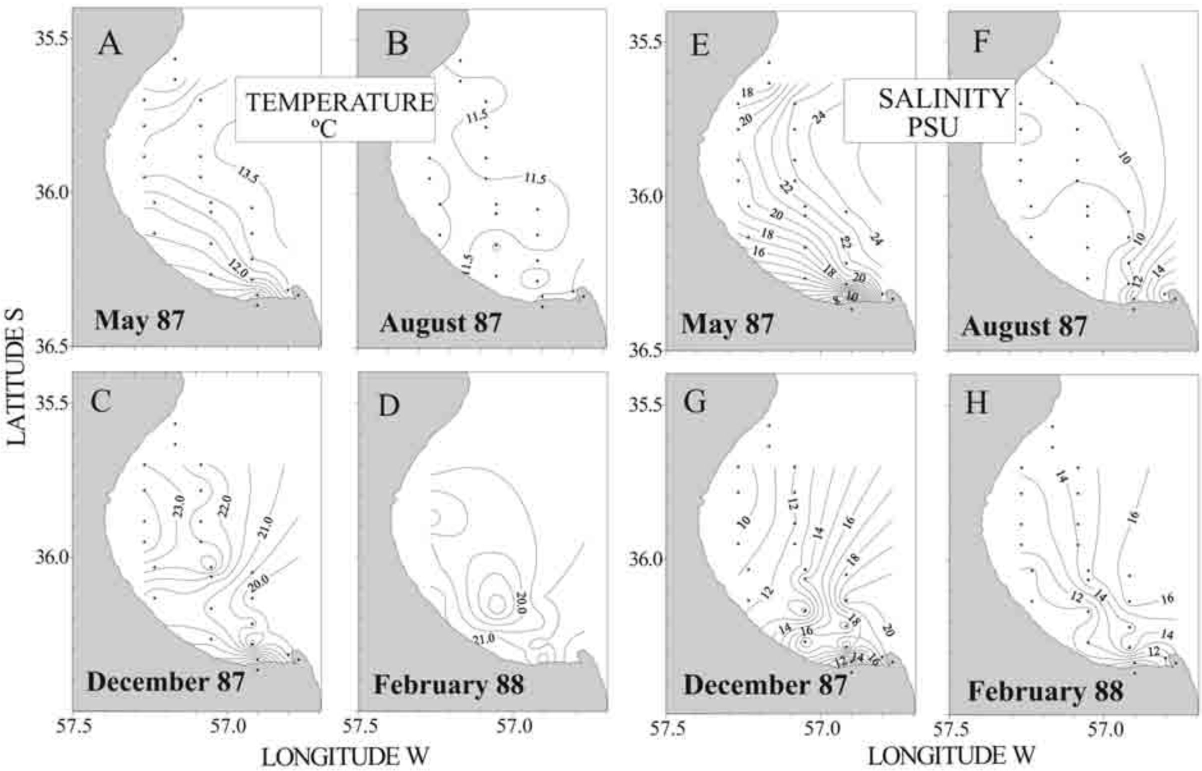

FIG. 2. – Horizontal distribution of surface temperature, expressed in ºC (A, B, C, D), and salinity, expressed in PSU (E, F, G, H) in 4 sampling dates representative of four typical hydrographic patterns occurring in the bay.

Temperature values fluctuated between minimum values (10ºC-11ºC) in winter and maximum values (23ºC-24ºC) in summer (Fig. 2A-D).

As expected, salinity values in the range of 10 to 24 PSU showed strong variability due to the influence of the Río de la Plata river and tributaries or to the incoming marine waters (Fig. 1A and B). Therefore, the bay offered two conditions: high influence of freshwater runoff with values of 10 PSU or influence of marine waters that reached values higher than 20 PSU. However, the southern zone, between Punta Rasa (PR) and San Clemente "ría", was permanently influenced by shelf marine waters. The influx of marine waters penetrated into the bay from the south and reached the low depth littoral area, including rivers and streams (Figs. 2E-H).

Abundance and standing crop

N. americana was found in SB throughout the study year (Fig. 3), with the highest densities of adults and juveniles recorded in winter (June 1987) and summer (February 1988). Most of the year, mysid abundance in stations 11 through to 14 outnumbered those in the rest of the bay.

The biomass distribution pattern showed the same trend (Fig. 4), with maximum values recorded in summer (December 1987 and February 1988) and in winter (June 1987) in the southernmost stations.

Sex ratio, proportion of gravid females and female fecundity

Sexes were distinguished from 4 mm TL. The mean proportion of females in relation to the total number of adults was 0.59 (Fig. 5A). However, a significant difference in the proportion of females between the months was detected ($G = 118.34^{**}$, $p < 0.0000$). Maximum values were observed in March (0.78), June (0.68) and September (0.73) 1987.

The presence of gravid females all year long, indicated a continuous reproductive activity (Fig. 5B). However, proportions of gravid females on the total females reached their maximum in spring (0.6) and summer (0.4) and were close to 0.2 during the rest of the year.

The mean number of embryos per female fluctuated between 7.25 (s.e. 1.05) and 26.82 (s.e. 1.59) during the year (Fig. 5C). At the beginning of the study period the lowest values corresponded to autumn (May 1987) and the highest to winter (August and September).

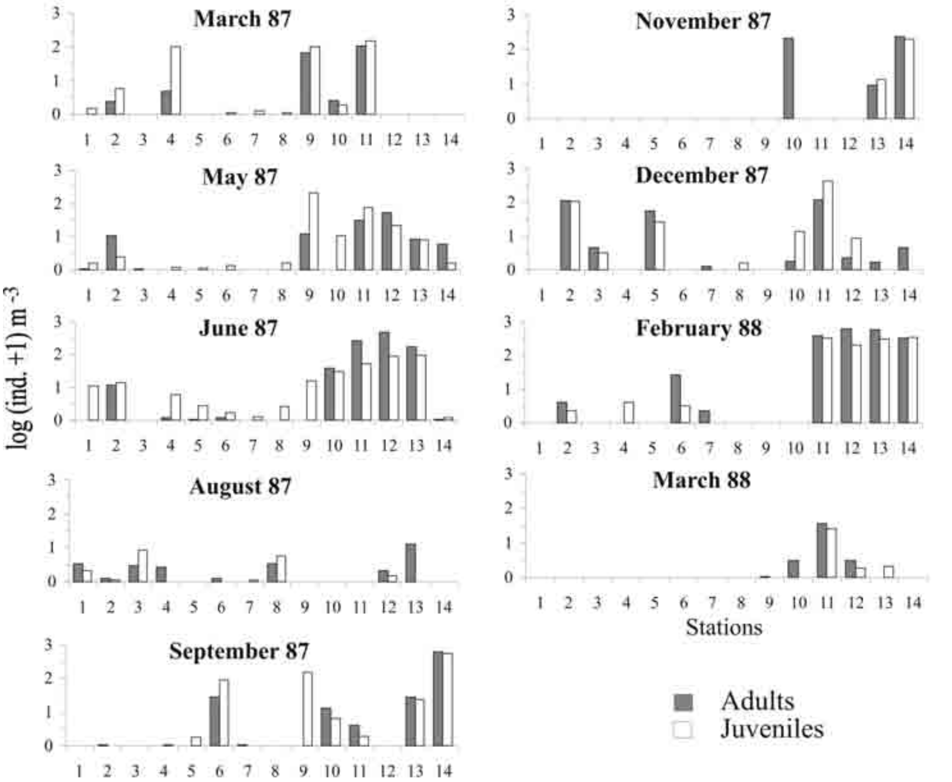

FIG. 3. – Seasonal variation of abundance (ind. m^{-3}) of *Neomysis americana* in SB during the study year. White bars: juveniles; grey bars: adults.

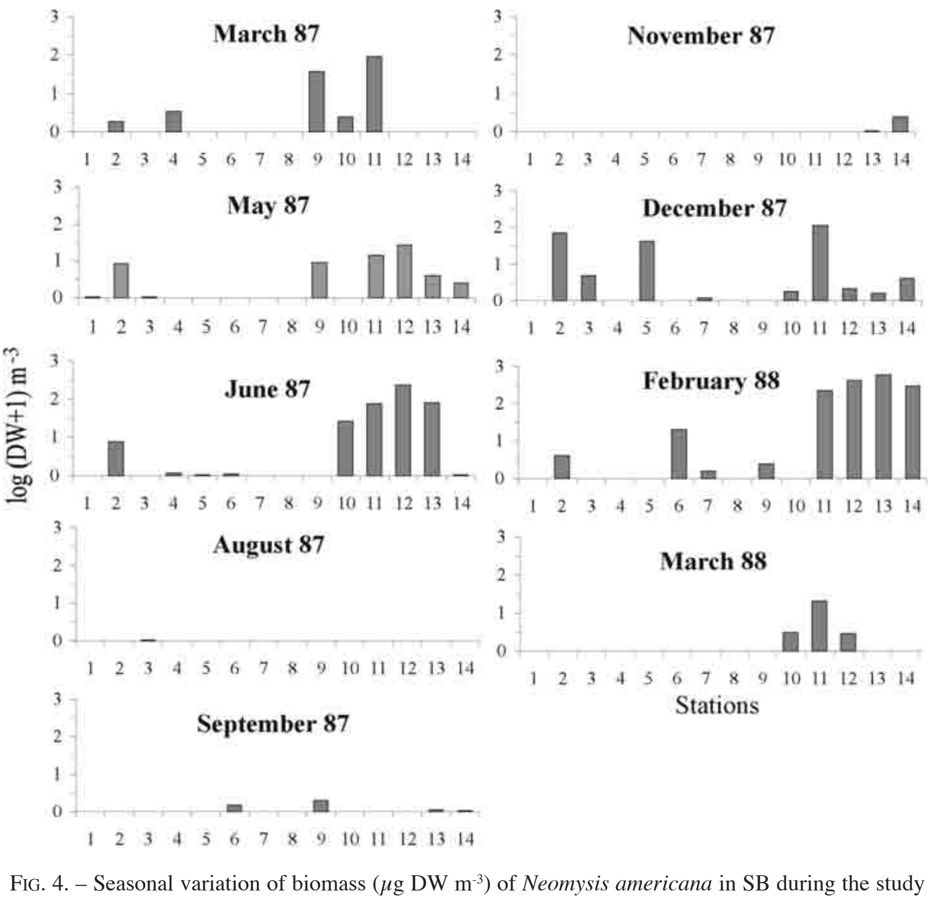

FIG. 4. – Seasonal variation of biomass (μg DW m^{-3}) of *Neomysis americana* in SB during the study year.

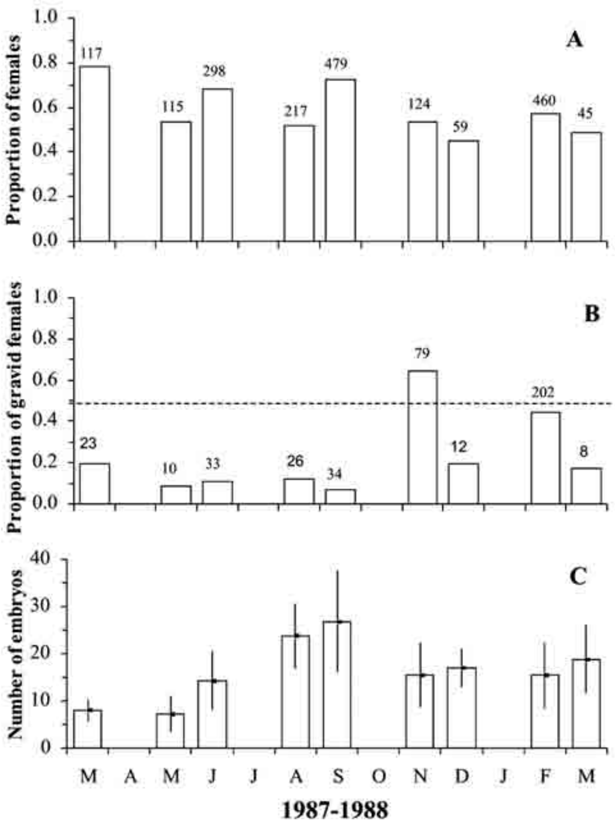

FIG. 5. – Annual variation of: (A) the sex-ratio, (B) the proportion of gravid females in the total females and (C) the mean number of embryos (± SD) per female of *Neomysis americana*. Figures on top of the bars in (A) and (B) indicate the number of observations.

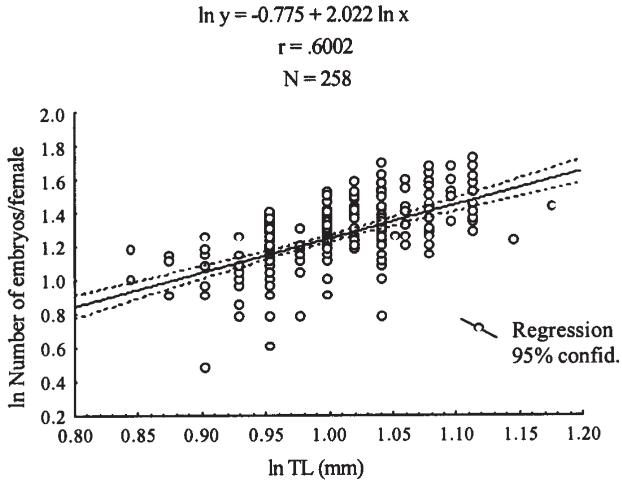

FIG. 6. – Relationship between the number of embryos per female of *Neomysis americana* and female size.

A significant positive relationship (F (1, 256) = 144.15, p<0.000000)) was found between the ln number of embryos and the ln TL of females (Fig. 6), with a higher dispersion of values in the intermediate size classes.

Number, timing and growth rates of the generations

The estimate of the number and duration of annual generations was based on the mean data obtained in the southern stations (9 through to 14) where the population was better represented in number and size classes throughout the year.

At the beginning of the sampling period, during March and May 1987 (Figs. 3 and 7), juveniles dominated the *N. americana* population. Individuals of the overwintering generation (G1) continued growing during winter (June and July) to reach their maximum size in August. In September, a new generation (G2) of juveniles occurred, preceded by an increasing percentage of gravid females. Growth of this generation finished in November with maximum sizes of both sexes. Figure 3 clearly shows that the highest annual percentage of gravid females that occurred that month gave place to a new peak of juveniles in December (G3). A high percentage of juveniles was also observed in February 1988 as a result of a period of intense reproduction that coincided with the highest temperatures of the year. This fact was confirmed by the absolute abundance of juveniles during the period (Fig. 3). In March 1988 the population was composed of very few individuals of different sizes (Figs. 3 and 7).

The growth curve (Fig. 8 and Table 1) that relates the mean TL of adults belonging to each of the three generations to their duration showed a rapid growth of G1 in autumn followed by a growth decrease during winter; males and females matured in about 5 months and grew to an average size of 8.4 and 9.6 mm respectively. The growth rates were 0.037 and 0.039 mm day^{-1} for males and females respectively. G2, present during spring, showed a marked increase in growth, which was faster in females (0.188 mm day^{-1}) than in males (0.105 mm day^{-1}). Adults of this generation matured in 1.5 months and reached an average size of 7.8 mm for males and 8.7 mm for females. Sexes of G3, present during summer, showed intermediate values (0.074) for males and (0.078) for females, and also matured in 1.5 months. Adults were the smallest of the year, with a mean size of 6.5 mm and 6.7 mm for males and females respectively.

DISCUSSION

Throughout the study period three annual generations of *Neomysis americana* were recorded in SB,

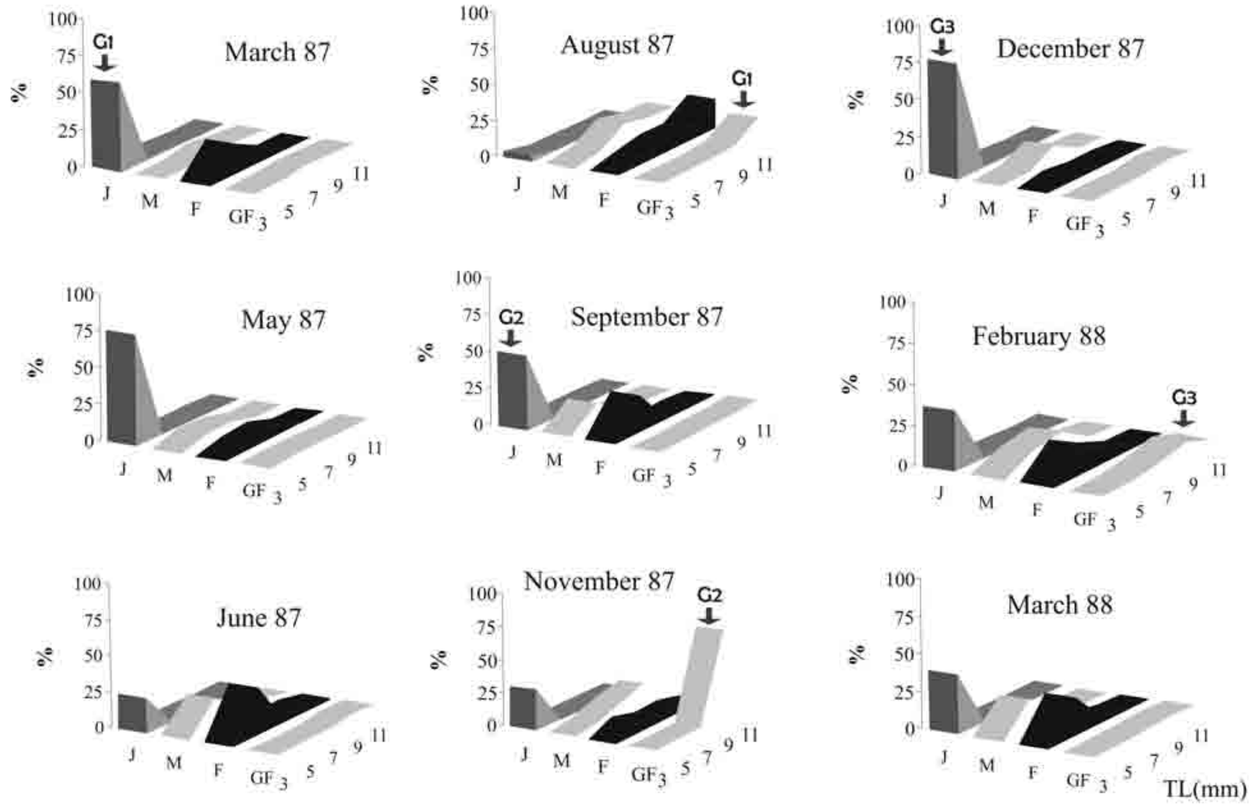

FIG. 7. – Relative abundance of the different developmental stages of *Neomysis americana* during the study period, with indication of the start of each new generation. (J) juveniles, (M) males, (F) females, GF (gravid females), G (generation).

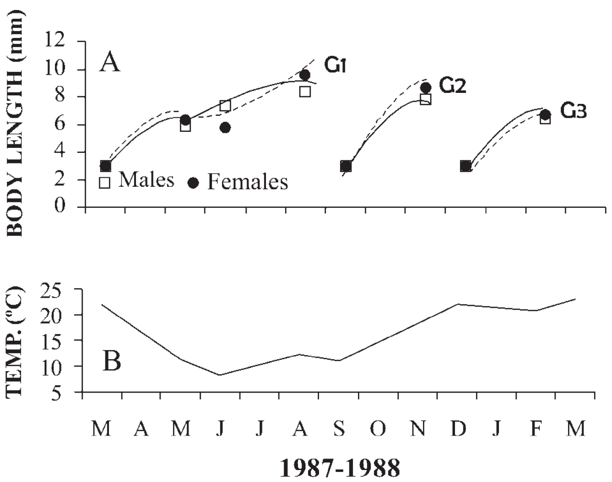

FIG. 8. – (A) Oversimplification of the growth curve of the three annual generations (G1, G2 and G3) estimated for *Neomysis americana*. (B) Evolution of temperature values during the study year. See Table 1 for more details.

TABLE 1. – Mean size (± SD) of males and females of the three annual generations of *Neomysis americana*. * Size of juveniles of each generation. In brackets: number of individuals measured.

Dates	Males	Females
Generation 1		
13.03.87	3* (299)	3* (299)
14.05.87	5.9 ± 0.32 (102)	6.3 ± 0.52 (117)
19.06.87	7.4 ± 0.48 (262)	5.8 ± 2.74 (300)
08.08.87	8.4 ± 0.31 (226)	9.6 ± 0.26 (291)
Generation 2		
18.09.87	3* (436)	3* (436)
04.11.87	7.82 ± 0.25 (135)	8.66 ± 0.14 (142)
Generation 3		
17.12.87	3* (375)	3* (375)
03.02.88	6.46 ± 0.26 (173)	6.68 ± 0.29 (270)

with the highest densities in spring and summer and the continuous presence of juveniles. Depending on the latitude, two or three generations a year were reported in different locations of the eastern coast of the U.S.A. (Table 2). Species of mysids producing three generations per year usually exhibit more or less continuous breeding with periods of seasonal maxima throughout the year (Mauchline, 1980). This coincides with the results obtained in SB where the highest densities of juveniles were observed in summer; only a few young specimens corresponded to winter. In other areas characterized by more severe climatic conditions, winter breeding may be absent (Pezzack and Corey, 1979 and references therein).

Previous studies and the results derived from this work show that in locations where the temperature is

TABLE 2. – Number of generations of *Neomysis americana* in different locations of the northern Atlantic compared to present results in Samborombón Bay. The maximum temperature recorded during the warmest period of the year is indicated for each location.

Location	Latitude range	Number of generations	Maximum temperature (°C)	References
St. John River	50-40° N	2	< 20	Talbot (unpublished)*
Passamaquoddy Bay	50-40° N	2	< 20	Pezzack and Corey (1979)
Georges Bank	50-40° N	2	< 20	Wigley and Burns (1971) Whitey (1948)*
Narragansett Bay	50-40° N	3	> 20	Herman (1962)*
Long Island Sound	40-30° N	2?	> 20	Richards and Riley (1967)
Inland River Inlet	40-30° N	3	> 20	Hopkins (1965)
Chesapeake Bay	40-30° N	3	> 20	Cowles (1930)*
Samborombón Bay	40-30° S	3	> 20	Present work

* From Pezzack and Corey (1979)

20ºC or over during the warm period of the year, three annual generations of *N. americana* can be expected. If the maximum temperature is lower than 20ºC, only two annual generations occur at latitudes higher than 40º (Table 2).

Growth rates of males (0.074 mm day^{-1}) and females (0.078 mm day^{-1}) of *N. americana* for the summer generation were higher than those reported for the species in other locations with lower thermal ranges (Pezzack and Corey, 1979). The strong temperature dependence found in the growth rate of this species (Pezzack and Corey, 1979), and of *N. intermedia* (Toda *et al.,* 1984), would indicate that the growth rate and generation length are controlled mainly by temperature. In our study, the summer breeding generation (December 1987-March 1988) matures rapidly and bred in about 1.5 months, a shorter period than that of other generations of the year. Coincidently, Pezzack and Corey (1979), observed that temperature had a positive effect on duration in a given location.

The presence of gravid females was recorded all year long, indicating continuous reproduction of *N. americana,* as observed in other populations under favourable environmental conditions (Pezzack and Corey, 1979). In the coldest locations of its geographic distribution (*e.g*. Passamaquoddy Bay, 45ºN), only a few gravid females were observed in winter, with no evidence of young specimens being released during that season (Pezzack and Corey, 1979). In laboratory experiments, the authors did not observe any development of eggs at low temperatures (≤ 4ºC). However, in SB, high fecundity values were recorded even during winter, probably because the lowest temperatures recorded (> 10ºC) were favourable to reproduction processes.

The high number of summer juveniles and the low percentage of females during the period, when compared to the rest of the year, suggest that multiple broods per female may occur. The process was frequently observed in many mysids (Mauchline, 1980), including *N. americana,* whose summer-breeding females were able to produce two or three broods in the laboratory (Pezzack and Corey, 1979). Most females released eggs of the next brood into the *marsupium* the same night the young specimens of the previous brood were released.

A clear trend between brood size and female length was observed in *N. americana,* with the largest females producing the largest broods, as recorded in several mysid species (Mauchline, 1980). However, as expected a large variance in brood size within any given size class was observed (Mauchline, 1980; Pezzack and Corey, 1979). On a seasonal scale, the largest females producing the highest number of embryos per *marsupium* were caught in SB in winter. Accordingly, previous field observations (Wigley and Burns, 1971; Pezzack and Corey, 1979), and laboratory experiences (Toda et al., 1984), showed an inverse relationship between the brood size and the temperature in this and other species of *Neomysis*. The brood sizes observed in our specimens of *N. americana* were within the range reported for the northern populations, 6-26 (Wigley and Burns, 1971), except for that of Passamaquoddy Bay which was 32-45 (Pezzack and Corey, 1979), where lower temperature values were recorded (2-20ºC) compared to 8-23ºC in SB.

Females outnumbered males in most of the sampling months, a situation frequently found in mysid populations (Mauchline, 1980), and particularly *N. americana* (Wigley and Burns, 1971). In our study, the highest proportions of females were observed in autumn and winter, coinciding with the start of generations (*i.e*. in March and September 1987, G1 and G2). However, Pezzack and Corey (1979), found that the female:male ratio showed a trend towards higher values during summer with a maximum of 2.6:1 (June) and a minimum of 1:1 during winter. The sex ratio of mysids normally varies between samples and seasons and a consistent reason for the observed fluctuations has not been found so far (Mauchline, 1980 and references therein).

The high growth rates, the existence of three generations per year and the presence of gravid females throughout the year favour the development of an abundant population of the species in our study site. In fact, *Neomysis americana* is among the four dominant components of zooplankton in SB with the highest relative contribution (40-60 %) to the zooplankton biomass in summer and autumn (Mianzan *et al.*, 1989; Sorarrain, 1998).

The development of *N. americana* populations probably depends not only on temperature but also on food availability. The highest densities of the species were recorded in the southern stations (Ajó river, San Clemente "ría") all year long. Salt marshes are most extensive in these locations. It was observed that *Spartina,* the dominant plant in SB salt marshes (Boschi, 1964; Iribarne *et al.*, 1997), constitutes an important food item for the species in winter (Zagursky and Feller, 1985). The dynamics of the water masses with a net retention movement inside the bay during most part of the year (Lasta, 1995), could also contribute to the constant availability of detritus particles for mysids and other detritivores. Moreover, in the southern stations high densities of *Acartia tonsa,* the dominant copepod species in the bay, were also recorded throughout the year (Mianzan *et al.*, 1989; Sorarrain, 1998). This copepod is an important potential prey for *N. americana* (Fulton, 1982). The ability of *N. americana* to substantially increase its clearance rate and maintain high feeding rates at low prey densities (Fulton, 1982), combined with its omnivorous diet could explain in part why the species maintains high abundances during the whole year in the southern sector of the bay, even in winter.

At the highest trophic levels of the food web*, N. americana* constitutes an important feeding item for most juvenile fishes distributed in SB: *Macrodon ancylodon, Micropogonias furnieri*, *Pogonias cromis*, *Parona signata, Lycengraulis olidus,* etc. (Sánchez *et al.*, MS). Juveniles of whitemouth croaker (*Micropogonias furnieri*), the most abundant fish in the bay, are unable to ingest hard benthic adult prey (Giberto, 2001), and feed mostly (>73% of incidence) on mysids (Sánchez *et al.*, 1991). Feeding on *Neomysis,* juvenile fishes significantly increase their daily energy intake and growth rate (Lankford and Targett, 1997). Over the year, juveniles concentrated mostly in the southern sector (Lasta *et al.*, 1994; Carozza *et al*, in press) where *N. americana* is likely to be constantly available, even in the winter season.

Although based on small scale data, the present study provides the first insight concerning *Neomysis americana* population dynamics in the Río de la Plata estuary and suggests the key role the species plays in the trophic food web of Samborombón Bay. Some considerations about the possible influence of hydrographic conditions on the development of the species are also presented. Research currently in progress is focused on the distribution pattern of the species at a larger spatial scale within the estuary in relation to environmental factors. Abundance and distribution of particulate organic matter deserves special attention.

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