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Salinity preferences and habitat partitioning between dominant mysids at the Río de la Plata estuary (Uruguay)

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Mysids are common and abundant organisms in estuaries and coastal waters, where they have a central role in the functioning of food webs. The Río de la Plata (RdlP) is a major estuary that affects biogeographic patterns of marine coastal organisms in the south-west Atlantic, but studies of the plankton in the RdlP are scarce. Knowledge of the mysid fauna in particular is very limited with a single species (likely alien, *Neomysis americana*), traditionally known to inhabit this 38,000 km^2 estuary, and a second one, *Mysidopsis tortonesei*, only recently reported. The purpose of this paper is to contribute with the knowledge of the mysid fauna of this ecosystem by exploring the spatial distribution and *in situ* salinity preferences of *N. americana* and *M. tortonesei* in the mixohaline region of the RdlP during austral autumn, 2001. Both species showed clear and contrasting haline affinities that resulted in an almost perfect spatial segregation within the study area. *Neomysis americana* occurred preferentially in oligo- and meso-haline conditions (range <1 to 33.37, but most abundant at salinities <28), while *M. tortonesei* occurred at salinities >28. Temperature range was quite narrow and it was unlikely that it affected mysid distribution in the estuary. Temporal variability in observed patterns, as well as the role of biological interactions in shaping spatial distribution of *N. americana* and *M. tortonesei* within the estuary are subjects that deserve further attention in future studies.

INTRODUCTION

Mysidaceans are common and very abundant components of estuarine and coastal ecosystems including sandy beaches (Mauchline, 1980; Takahashi & Kawaguchi, 1998). They are adaptable consumers that feed on detritus, phytoplankton and animal food (Takahashi, 2004). They are in turn prey for larger consumers such as fish (Wooldridge, 1989; Takahashi et al., 2004), thus forming an important link to large sized consumers. Typically, mysids stay near the bottom of the water column during light hours and migrate to surface layers at night in order to reduce predation losses (Gall et al., 1999; Takahashi et al., 2004).

The Río de la Plata (RdlP) is a major estuary in the subtropical-temperate transition zone (34–36°S 55–58°W) and represents the largest freshwater input into the south-west Atlantic; low salinity waters can extend north-east for several hundred km (Piola et al., 2000) and constitute a major biogeographic barrier for coastal marine organisms (Escofet et al., 1979; Gianuca, 1983; Boltovskoy et al., 1999). The Subtropical Confluence affects external RdlP and adjacent shelf, subjecting the area to alternating influence of Brazil (warm) and Malvinas (cold) waters during summer–autumn and winter–spring periods, respectively (Ortega & Martínez, in press).

Knowledge of the distribution and environmental affinities of animals inhabiting the RdlP and adjacent areas can help to understand how species cope with environmental variability and how their distribution patterns arise. The planktonic fauna of the RdlP, and in particular the mysid components, is poorly known. That contributes to an anomalous large-scale latitudinal pattern, as compared to several other planktonic taxa (Boltovskoy, 1999; Murano, 1999); however, regional interest for this taxon has increased in the last few years (Calliari et al., 2001; Schiariti et al., 2004, 2006; Viñas et al., 2005). The first record of mysids in the RdlP was *Neomysis americana* Smith, 1873 (González, 1974), a presumed invasive species in South America (cryptogenic, *sensu* Orensanz et al., 2002). This species is now a regular component of the plankton in coastal areas of Uruguay, Brazil, and Argentina (Hoffmayer, 1990; Viñas et al., 2005; Cervetto et al., 2006) and until recently still the single mysid known for the RdlP. *Mysidopsis tortonesei* was recently reported for this ecosystem (Schiariti et al., 2004) but environmental information associated with its occurrence and regarding distribution is extremely sparse.

In this paper we explore the environmental affinities and spatial partitioning between *M. tortonesei* and *N. americana*. These were the dominant species within the mysid assemblage during austral autumn when other mysidacean species were also collected in very low numbers (i.e. *Promysis atlantica* and two further species not yet identified; Cervetto et al., in preparation). With regard to environmental affinities, we pay special attention to the effect of salinity since it presents the widest spatial variability in the study area, and also for its general relevance in modulating the distribution of marine zooplankton (Cervetto et al., 1999, Calliari et al., 2006), including mysids (Moffat & Jones, 1993).

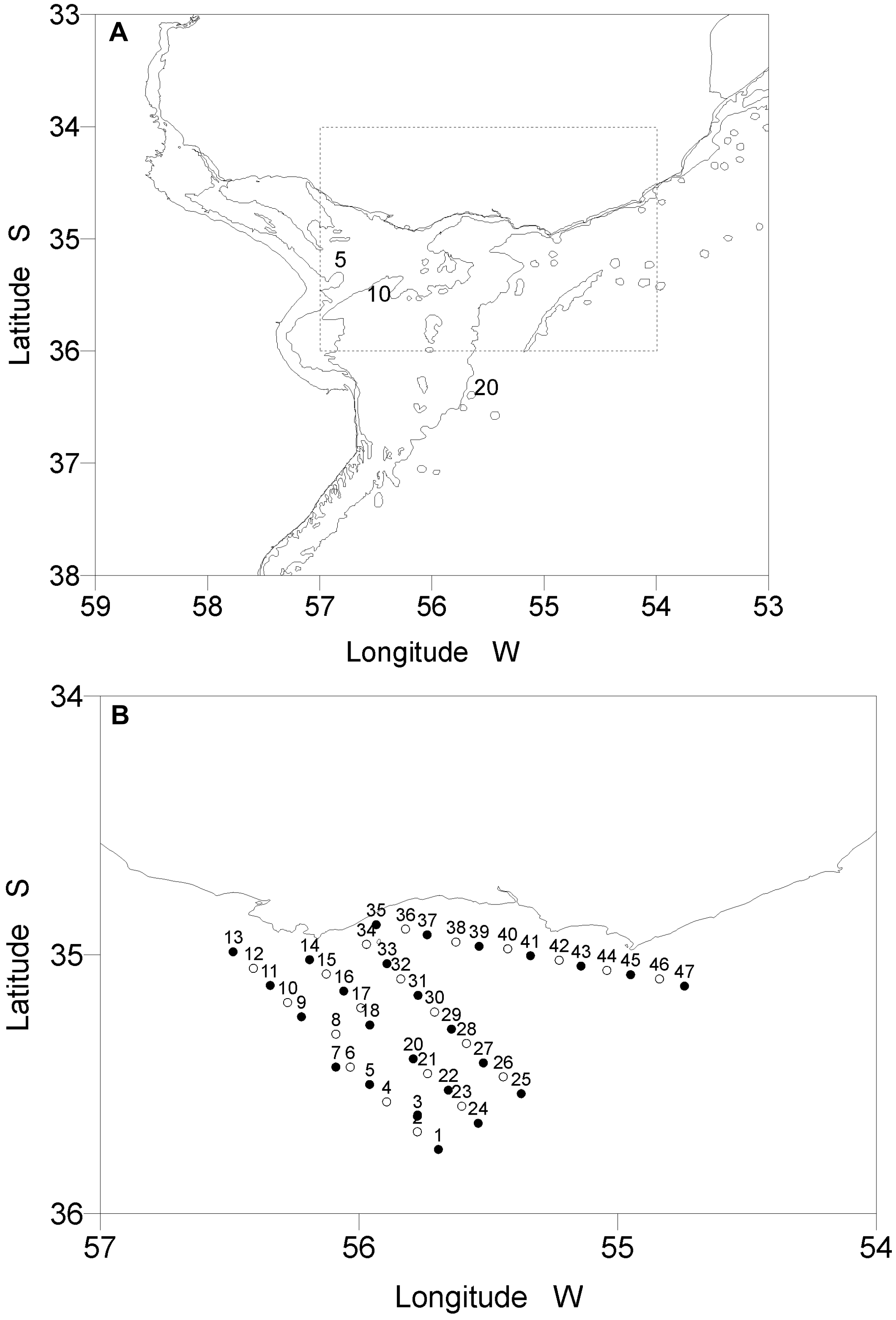

Figure 1. (A) Map of the study area showing depth contours and (B) location of sampling stations and their corresponding station number. In B, open circles correspond to hydrographic (CTD) stations and full circles correspond to hydrographic and plankton stations.

MATERIALS AND METHODS

Study site

The study area corresponds to the Uruguayan sector of the external RdlP; this encompasses the entire mixing zone between fresh and marine waters (Figure 1). The RdlP is a funnel shaped, drowned river valley estuary ~350 km long and 230 km wide at the mouth. It drains the second largest basin in South America and has a mean annual flow of ~23,000 $m^3 s^{-1}$, shallow depths (average <10 m, maximum 25 m at the mouth) and highly turbid waters (Nagy et al., 1996). The estuary tends to be salinity-stratified in the external region, and vertical gradients result from combined

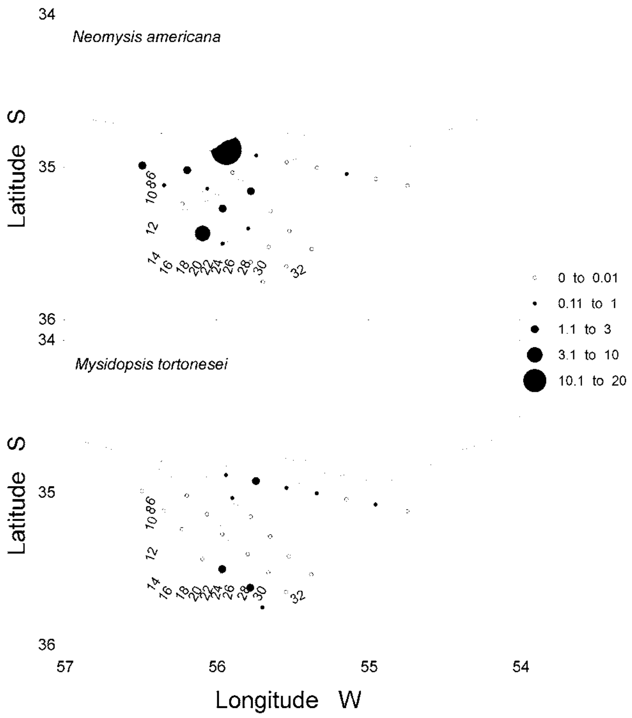

Figure 2. Spatial distribution of *Neomysis americana* (upper pannel) and *Mysidopsis tortonesei* (lower pannel) at the Río de la Plata during May 2001. Abundances are expressed as individuals m^{-3}; salinity contours at intervals of 2 units are superimpossed as reference.

effects of topography, freshwater run-off, and wind stress (Nagy et al., 1996). At the external area the horizontal salinity ranges from ~0 to >30.

Sampling design

A total of 46 stations arranged in four transects were occupied during an oceanographic cruise from 17 to 19 May 2001 on board the RV 'Aldebarán' (Figure 1), which was primarily intended to survey abundance and distribution of mesozooplankton at meso and small scales. For that reason, some sampling methods (type of nets employed) were not particularly suited for larger zooplankton (see below). Station depths ranged between 6 and 36 m. At each station salinity and temperature profiles were obtained with a CTD (Seabird SBE 19). Salinity values thus correspond to the practical salinity scale and are reported without units. Zooplankton samples were collected at alternating stations (i.e. one plankton station every two hydrographic ones) by oblique tows of a Bongo-type net (19 cm diameter) fitted with a 68 μm pore-size mesh and a General Oceanics flowmeter to estimate the volume of water filtered; length and angle of the cable were manipulated to ensure the net sampled most of the water column, i.e. from 1 to 2 m above the bottom and upwards. Tows were always short (~2 min) in order to avoid excessive clogging of the mesh in the turbid waters. Samples were preserved in buffered formaldehyde (~5% final concentration) and at the laboratory mysids were picked out from the samples, identified, staged as juveniles or adults, sexed (only adults), and counted. Adult females were further classified as brood-carrying or not brood-carrying. Identifications were based on Almeida-Prado (1974), González (1978), Mauchline (1980), and Murano (1999).

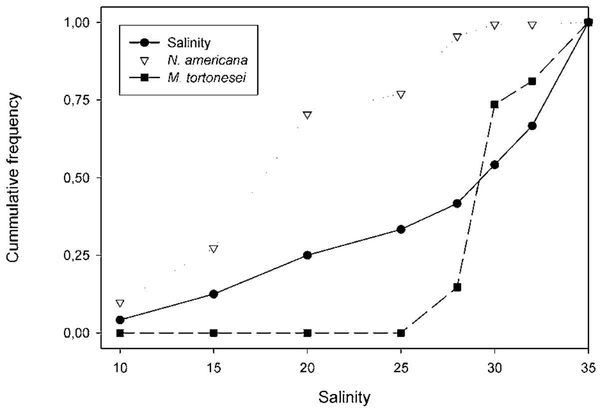

Figure 3. Estimated cummulative distribution functions for salinity data (dots), *Neomysis americana* abundance (open triangles), and *Mysidopsis tortonesei* abundance (squares) at the Río de la Plata during May 2001.

Data analysis

Abundance between day and night samples was compared for each species separately using the Mann–Whitney *U*-test for independent samples (Zar, 1996). To explore salinity preferences we followed the approach proposed by Perry & Smith (1994), simplified for a single-stratum case. Briefly, the method compares the empirical cumulative distribution function (cdf) of an environmental variable (salinity in our case) and of the species abundance using a Kolmogorov–Smirnov test based on maximum vertical distance between estimated cdf's (d_{max}); d_{max} is compared with tabulated critical values $d_{P,k,N}$ for probability level P, with k (number of classes) and N (number of observations) degrees of freedom (df) under the null hypothesis of random association between organism distribution and habitat condition (Perry & Smith, 1994; Zar, 1996). Since mysids were expected to occur mostly in near bottom waters the salinity values used in the analyses were average salinities below the halocline; depth range for salinity averaging was deduced from graphical analyses of salinity profiles at each station.

RESULTS

Environmental variables

Salinity ranged from <1 to 33.42 and evidenced a clear horizontal gradient along the main axis of the estuary; vertical haline stratification occurred at all stations (maximum 2.72 m^{-1}), but at the lowest salinity (Station 13) where vertically homogeneous freshwater prevailed. Temperature range was narrow between 13.23°C and 16.43°C and correlated positively with salinity (r^2= 0.76, N=524, P<0.01) indicating slightly warmer marine waters.

Mysid abundance, population structure and relationship with salinity

Neomysis americana occurred in 50% of samples in a temperature range of 13.4–16.2°C, and maximum abundance recorded was 14 ind m^{-3}; population comprised 80% juveniles, 18% females, 2% males, and 89% of females were carrying broods. *Mysidopsis tortonesei* occurred in 38% of samples in a narrow temperature range of 15.1–16.2°C and maximum abundance recorded was 2.4 ind m^{-3}; population comprised 57% juveniles, 17% females, and 27% males, and 80% of females were carrying broods. No differences were found for either species when comparing abundances between night and day samples (U=45 for *M. tortonesei* and U=42 for *N. americana*; *P*>0.1, N=25, for both species). *Neomysis americana* was particularly abundant at low and moderate salinities up to 28 (Figure 2); in turn, *M. tortonesei* occurred at salinities 28 and higher. There were only two stations at which both species were found together (Station 5 and Station 37, Figure 2), with bottom salinities between 29 and 30. Both *N. americana* and *M. tortonesei* evidenced a significant association (*P*<0.05) of their abundance with salinity (d_{max}=12.9, and d_{max}=8.0, respectively, in both cases df=8, 24; Figure 3).

DISCUSSION

We need to draw attention to known shortcomings of our dataset arising from sampling methods, since the use of a small mouth net could have induced a significant escape effect. Also, preference for bottom layers makes mysids difficult to sample quantitatively with traditional plankton nets or benthic grabs (Mauchline, 1980; Murano, 1999). If during our sampling mysids were concentrated in near bottom waters actual abundances may have been underestimated by averaging the catch over the total water volume filtered in oblique tows. We thus note that abundances here reported should be taken cautiously since they most likely underestimate real numbers by an unknown amount. In spite of these limitations, we stress that for the purposes of the present work we are not strictly concerned about absolute abundance of organisms but with presence/absence and relative abundance data. Since the same net and general procedures were employed throughout the study the bias resulting from the sampling method is systematic, and so the information provided and the results of analyses performed should still reflect the patterns we are interested in.

Salinity preferences and spatial segregation

Neomysis americana is common in coastal waters of North America (Mauchline, 1980). It was probably introduced into South America in the late 1960s or early 1970s (Orensanz et al., 2002) and until recently it was still the single mysid reported for the RdlP, all of the Uruguayan Atlantic coastline, and small scale estuaries (Calliari et al., 2001; Cervetto et al., 2006). Our results and earlier studies support the view that *N. americana* thrives in a wide salinity range and seems well adapted to the RdlP environment, reproducing throughout the year at salinities between 10 and 24 in the Samborombon area (Viñas et al., 2005; Schiariti et al., 2006). Schiariti et al. (2006) found *N. americana* in the salinity range 0–28, but mostly concentrated near the estuarine salinity front at salinities <20; those results are also highly consistent with ours, even though Schiariti et al. (2006) did not find a significant Pearson's correlation and concluded that no relationship existed between *N. americana* abundance and salinity. However, lack of a linear fit is often observed when exploring relationships between species abundance and environmental variables and the underlying relationships are non-linear and/or only hold for narrow ranges of the environmental variable (Perry & Smith, 1994). In fact that was also the case for our own data set. In such cases alternative analyses like cdf's are particularly suited for spotting effects of environmental variables on species distribution and abundance.

Our results are also consistent with salinity ranges reported for some northern populations of *N. americana*: i.e. down to salinity of 0.5 at the St Lawrence river estuary (Winkler et al., 2003), and between salinities 4.5 and 26 in the Delaware river estuary (Hulburt, 1957). Interestingly, there are also important deviations to this pattern suggesting that in some cases *N. americana* might prefer open coastal waters (Mauchline, 1980), i.e. an 'oceanic population' of *N. americana* on the Georges Bank extends its distribution up to 75–100 m depth and virtually full-strength seawater (Whiteley, 1948; Wigely & Burns, 1971; *fide* Williams et al., 1974), contrasting with our findings at the RdlP.

Salinity seems to play a central role in regulating distribution of *N. americana*, but biological interactions may also contribute to modulate spatial distribution of mysids. Experimental studies suggest that intra-guild predation shapes coexistence dynamics and abundance of *Neomysis integer* and *Praunus flexuosus* in the Elbe estuary (Winkler & Greve, 2004); in spite of similar omnivorous trophic behaviour, adult and large juveniles of the latter species exert strong predation pressure on juveniles of the former, while the inverse is not true (predation of *N. integer* on *P. flexuosus*) due to better escape reactions of *P. flexuosus*. Laboratory-based experiments showed that maximum potential intra-guild predation (i.e. when alternative prey are absent) can remove >100% of secondary production by *N. integer*. In this and other cases of intra-guild predation between mysids (i.e. *Rhopalophtalamus terrenalis* and *Mysidopsis slaberri* in South Africa, Wooldridge & Webb, 1988), spatial segregation is one factor that reduces predation pressure and favours coexistence. An almost perfect spatial separation observed between dominating mysids in the RdlP suggests that biological interactions may also contribute to explain spatial distribution of both species within the estuary besides strict environmental affinities.

Comparatively, there is considerably less information about distribution and salinity ranges for *Mysidopsis tortonesei*. This species occurs in Brazilian waters off Río de Janeiro and Sao Paulo (i.e. Cananeia region), and in the Lagoa dos Patos estuary (Montú, 1980); to the authors' knowledge there are no reports for this species outside Brazilian waters, except for the recent report at the RdlP (Schiariti et al., 2004). Neither are studies of salinity preferences by *M. tortonesei*; a re-analysis of data provided by Almeida-Prado (1973, her tables 1 and 6) comparing cdf's of salinity and abundance at Cananeia indicates preference for salinities over 25, which is in close agreement with results presented here. Thus, we can tentatively regard *M. tortonesei* as a marine coastal species whose distribution is restricted by dilution of marine waters below a salinity ~25. The spatial distribution in the RdlP would thus be contingent upon saltwater penetration, but under average salinity conditions (Figure 2; Guerrero et al., 1997) *M. tortonesei* could inhabit a significant fraction of the external area in the RdlP year-round.

Need for further investigations

Experimental studies focused on physiological tolerances to salinity, and regarding potential trophic interactions (i.e. predator–prey, competence for prey) seem necessary to gain further insight into the relative importance of abiotic and biological factors in shaping distribution and coexistence dynamics between *N. americana* and *M. tortonesei* in the RdlP. Also, temporal variability of patterns here described for both species are subjects that deserve further attention. *Neomysis americana* is known to occur in the RdlP during the whole year (Viñas et al., 2005). Our data indicate similar population structures between *N. americana* and *M. tortonesei*, and are also comparable to population structure of *N. americana* during active reproducing periods (Viñas et al., 2005). That suggests that *M. tortonesei* specimens found during this study were most likely not just vagrant individuals advected from a northern population into the study area but a consistent population unit, including an important fraction of reproducing females.

Seasonal variability of salinity and temperature in the RdlP do not appear as important restrictions to the maintenance of *M. tortonesei* in the area. Bottom salinity is relatively stable seasonally, but bottom temperature varies between ∼11°C and 21°C. According to Almeida-Prado's data (1973, table 3) temperature at Cananeia ranges between 19.8 and 28.1°C, with *M. tortonesei* present over the whole year and over the entire temperature range: 19.8–27.7°C. In the RdlP *M. tortonesei* has been recorded over a broader temperature range which accounts for nearly the whole range of seasonal variability (15.1 to 16.2°C, present study; 12 to 24°C according to Schiariti et al. (2004), unfortunately without specification if values refer to surface or bottom temperature), which further supports the existence of a permanent population in the RdlP or adjacent coastal waters.

In summary, recent direct evidence and analyses of environmental affinities suggest that *M. tortonesei* constitutes a second permanent mysid species inhabiting the RdlP estuary, besides *N. americana*. These two species showed complementary spatial distributions within the estuary clearly related to differential haline affinities. Further investigations seem necessary to assess the temporal variability in the reported spatial patterns, and to verify a potential role of biological interactions in shaping distribution and coexistence dynamics of these species within the estuary.

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