BIOGEOGRAPHY OF THE FRESHWATER DECAPODS IN THE LA PLATA BASIN, SOUTH AMERICA

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ABSTRACT

The distributions of freshwater fauna in the La Plata Basin, including decapods, are dynamic; their actual distributions depend on not only their movements but also on environmental fluctuations. The La Plata system has a diverse range of environments, which are colonized by crustaceans with complex evolutionary histories. Our aim was to elucidate the distribution patterns and relationships of current freshwater decapod fauna in terms of the different geo-climatic processes at work in the La Plata system. We recognized 13 zones based on their unique environmental characteristics. Species lists were assembled through field samples, examination of museum collections, and literature analysis. Faunistic similarity was evaluated using the Jaccard index and cluster analysis. A parsimony analysis of endemicity (PAE) was applied to determine the most parsimonious of all possible tree topologies. There were 69 species freshwater decapods analyzed in the La Plata Basin. The Mata Atlántica (MA), Paraná Superior (PS), and Uruguay Superior (US) zones are distinguished by their high species richness values, whereas the western and southern basin regions exhibit the lowest species richness values. The Paraguay-Pantanal (PP) and Paraguay-Pilcomayo-Bermejo (PPB) zones share some prawn taxa with the Amazon Basin. The eastern zones of the La Plata Basin were grouped by the presence of several species of the genera *Parastacus, Aegla*, and *Trichodactylus*. The northern, central, and western zones were characterized by species of the genera *Dilocarcinus*, *Sylviocarcinus*, and *Zilchiopsis*. According to the PAE analysis, two major zones were recognized in relation to the presence of freshwater decapods (eastern and western-central zones). In the western-central zones, three sub-areas were identified; one shares species with the Amazon basin the others have a relationship with the eastern and northern regions and represents a region that is strongly influenced by a temperate climate and therefore possesses diminished species richness values.

KEY WORDS: Aeglidae, freshwater decapod distributions, PAE, Palaemonidae, Parastacidae, Sergestidae, species richness, Trichodactylidae

INTRODUCTION

The distributions of freshwater fauna, including decapods, are dynamic, and their actual distributions depend not only on their movements but also on environmental fluctuations (Ringuelet, 1961). In the Southern Hemisphere, there are several major aquatic basins with intense histories of orogenic and climatic activities in which fauna have evolved jointly with the dynamics imposed upon them. South of the latitude 20°S, which includes the Tropic of Capricorn, the largest basin in the hemisphere is the La Plata basin. In this hydrosystem, five decapod families (Sergestidae, Palaemonidae, Parastacidae, Aeglidae, and Trichodactylidae) are present and are a subset of the seven families that are found in freshwater environments of the Neotropical region (Manning and Hobbs, 1977; Rodriguez, 1992; Magalhães and Türkay, 1996a, b, c; Martin and Davis, 2001; Morrone and Lopretto, 2001; Collins et al., 2007; Magalhães and Türkay, 2008). The biogeography of this group in the La Plata Basin is not well known. To this end, it is necessary to consider that the actual diversity and distribution of this group are products of historical and ecological actions that are the result of millions of years of evolution along with intense relationships with geological and hydrographic events that have occurred from the time of the breakup of Gondwana to the present.

Geo-Climatic History

Several geo-climatic events have occurred in the Neotropical region between the Mesozoic Era and the present time. The more relevant events include continental drift between South America and Africa, uplift of the Andes mountains, climate changes, marine ingressions (the product of sea level fluctuations), megadome uplifts, and rifting. These events affected, in different ways and degrees, the Amazon, Magdalena, La Plata, and Orinoco basins as well as the paleo-drainages of smaller rivers of the eastern margin of the South America Platform (Potter, 1997; Ribeiro, 2006).

The early Tertiary periods (Paleocene-Eocene), marine transgressions occurred in the South American continent, one of which enabled an effective connection between the Caribbean Sea and the South Atlantic Ocean, forming the Tethys Sea (del Río and Martinez Chiappara, 1998; Ortiz-Jaureguizar and Cladera, 2006) (Fig. 1). The connection between the northern and southern regions of the continent provoked a flow of Caribbean fauna south along with an increase in water temperature. Those warm environments

Fig. 1.   Probable paleobiogeographic situation showing water (marine transgression events) (clear area) and land (dark area). (a) Final and complete separation of Africa and South America (Mesozoic), gray arrows indicate the Andes Mountain chain, (b), (c) and (d) Different moments of marine transgressions in Cenozoic (modified from Lundberg et al., 1998; Ortiz-Jaureguizar and Cladera, 2006).

subsequently underwent cooling when the Drake Passage and Scotia arch were opened during the late Oligocene epoch and early Miocene epoch (Aceñolaza, 2000). This event caused the entrance of diverse taxa from the Pacific region to the eastern Neotropical region along with cold polar water (del Río and Martinez Chiappara, 1998). Before the Tertiary period, the terrestrial isthmus between Antarctica and Patagonia favored faunal exchange between the eastern and western sides of the continent. During the Quaternary period, the region experienced wet and dry periods along with several marine transgressions and a high temperature gradient (Iriondo, 2004; Ortiz-Jaureguizar and Cladera, 2006). More recently, orogenic movements and extreme climatic conditions caused variations in freshwater volumes and their drainage areas. These changes can be recognized in the Paraná and Uruguay sub-basins with respect to the expansion of extensive lacustrine habitats and consequently smaller marine transgressions (Fig. 1) (Lundberg et al., 1998; Ortiz-Jaureguizar and Cladera, 2006). A series of six marine transgressions were important in recent times, leading to the present shape and dynamics of the La Plata Basin (Lundberg et al., 1998). This environment has been affected by tides and southern wind (Iriondo, 2004). Consequently, during those periods of marine transgression, it is possible that the continental fauna needed to move toward regions where the marine environment did not directly affect them.

Decapod Fauna of South America

Decapods in the continental aquatic environments of South America are not monophyletic, each family presents a temporally and spatially distinct evolutionary history with respect to the conquest of freshwater environments (Feldmann and Schweitzer, 2006). Moreover, several species, genera, and families are endemic to South America (Morrone and Lopretto, 1995), and their histories likely began during the time of Pangaea. During this time, continental aquatic environments were populated by decapods exploiting different opportunities (Schram and Koenemann, 2004), and there were several possible vicariance or dispersal events. The fossil records of freshwater crustaceans are scarce and incomplete. Nevertheless, the evolutionary histories of some groups have been described (Ortmann, 1902; Ringuelet, 1949; Villalobos, 1969; Feldmann and Schweitzer, 2006; Bond-Buckup et al., 2008; Crandall and Buhay, 2008; Yeo et al., 2008).

Four decapod morphotypes are recognized in the La Plata basin: prawns, crayfish, pseudo-crabs, and crabs. With respect to the prawn and shrimp families in South America, *Macrobrachium* Bate, 1868 is the most species-rich genus and has a pantropical-subtropical distribution (Jayachandra, 2001). The species of *Macrobrachium* diversified during the late Oligocene and early Miocene from an ancestral Tethyan biota and have effectively dispersed through marine barriers (Murphy and Austin, 2004). Villalobos (1969) argued that migrations of some species in South America could have occurred from the Caribbean to the southern region. However, there is evidence of multiple invasions due to the presence of these species in many biogeographical regions (De Grave et al., 2008).

Parastacidae is a crayfish group that originated in Australia, probably in the early Mesozoic Era (Hobbs, 1988). Scholtz (2002) proposed that this group invaded freshwater environments during the Triassic period and that diversification occurred due to vicariant events, originating Astacoidea and Parastacoidea (Rode and Babcock, 2003; Crandall and Buhay, 2008).

For the pseudo-crabs of Aeglidae, the first registered species was found in marine sediments of Mexico (*Protaegla minuscula* Feldmann et al., 1998, from the middle Cretaceous, approximately 110 million year ago (m.y.a.) and New Zealand (*Haumuriaegla glaessneri*; Feldmann, 1984, from the upper Cretaceous, approximately 70 m. y. a.). *Aegla* Leach, 1820 in South America came from a marine group with a radiation center in the Indo-Pacific region. This genus dispersed effectively in South America during the late Oligocene epoch; this dispersion was associated with continental drift. In the Pleistocene, aeglids were located in southern South America, although differences of opinion exist regarding the direction of ingression (Ortman, 1902; Schmitt, 1942; Ringuelet, 1949; Feldman, 1986; Perez-Losada et al., 2004).

Crabs of Trichodactylidae are also considered to be pangenic, originating in the Cretaceous, possibly in the southern Tethys Sea (von Sternberg et al., 1999; Cumberlidge and Ng, 2009). Their initial dispersion contrasts with that of Pseudothelphusidae, the other freshwater crab family that inhabits South America. One group of Gondwanan crabs could be considered to be a hypothetic ancestral assemblage formed by the families Potamoidea + Trichodactylidae, with a wide littoral distribution, resulting in the origin of the true lowland crabs of the Neotropical region, Trichodactylidae (Yeo et al., 2008). However, uncertainty remains regarding their origin (Cumberlidge and Ng, 2009; Schubart and Reuschel, 2009).

The La Plata system has a diverse range of environments that are colonized by crustaceans with complex evolutionary histories that have been shaped by various geo-climatic events. The aim of the present work was to elucidate the distributions and relationships of decapod fauna in terms of different geo-climatic processes as a model of evolution for freshwater crustaceans in the continent.

MATERIALS AND METHODS

The description of the biogeographical distribution of freshwater decapods in the La Plata Basin was made according to the data of the absence/presence binary matrix of species and area (Garzón-Orduña et al., 2008). For this reason, a multivariate (cluster) analysis and parsimony analysis of endemicity (PAE) were used (Crisci et al., 2000). The multivariate analysis was performed for each family with a similar relationship within each group, and the PAE served to view the relationships among all families due to the fact that they have distinct evolutionary histories.

Study Area

The La Plata Basin is mainly formed by the Paraná, Paraguay, and Uruguay rivers and has an approximate area of 3,100,000 km^2 (Bonetto and Wais, 1995). This area is located between 14°05′S and 37°37′S and 67°00′W and 43°00′W, corresponding to the area from the Bolivian plateau to the Atlantic Ocean and from the Pantanal (Matto Grosso) to the
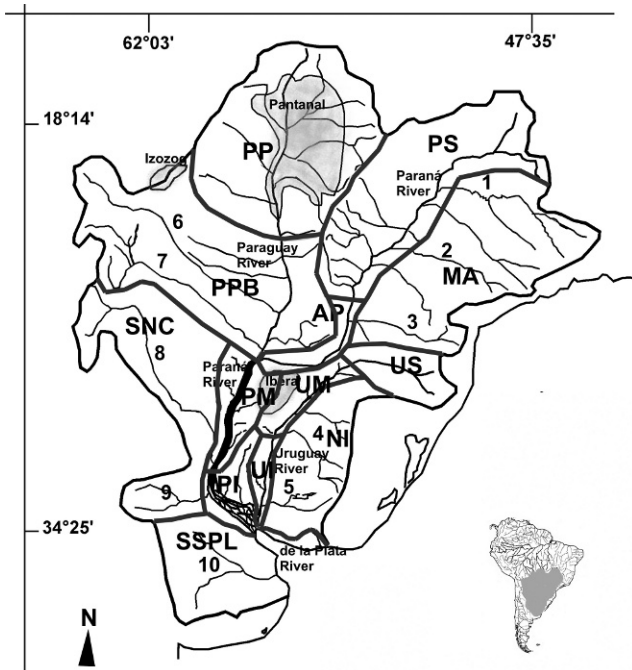
Fig. 2.   La Plata Basin and their determined zones. Paraná Superior (PS), Alto Paraná (AP), Paraná Medio (PM), Paraná Inferior (PI), Mata Atlántica (MA), Uruguay Superior (US), Uruguay Medio (UM), Uruguay Inferior (UI), Negro-Ibicuí (NI), Paraguay-Pantanal (PP), Paraguay-Pilcomayo-Bermejo (PPB), Salado Norte-Carcarañá (SNC) and Salado Sur-Río de La Plata (SSLP). Numbers indicate some main rivers: 1, Grande River; 2, Paranapanema River; 3, Iguazú River; 4, Ibicuí River; 5, Negro River; 6, Pilcomayo River; 7, Bermejo River; 8, Salado Norte River; 9, Caracaraña River; 10, Salado Sur River.

La Pampa region. A wide variety of habitats can be found in this region, ranging from tropical forest to cold mountain climates. These sub-basins have a great diversity of aquatic environments, including streams and rivers with rapids, riffles, falls (Paraná Superior, Iguazú Falls, Mocona Falls), floodplains, and extensive swamps (Paraná medio, Pantanal, Izozog, Iberá).

In our study, the La Plata Basin was divided into 13 zones (Fig. 2) according to differences in their physical characteristics and coinciding with areas of decapod endemism indicated by several studies (Morrone and Lopretto, 1994; Bonetto and Waiss, 1995; Morrone and Lopretto, 1995; Morrone, 1996; Lundberg et al., 1998; Morrone, 2001; Morrone and Lopretto, 2001). The zones are Paraná Superior (PS), Alto Paraná (AP), Paraná Medio (PM), Paraná Inferior (PI), Mata Atlántica (MA), Uruguay Superior (US), Uruguay Medio (UM), Uruguay Inferior (UI), Negro-Ibicuí (NI), Paraguay-Pantanal (PP), Paraguay-Pilcomayo-Bermejo (PPB), Salado Norte-Carcarañá (SNC), and Salado Sur-Río de La Plata (SSLP). The general characteristics of the zones are as follows: Paraná Superior (PS) ranges from the birth of the Parana River to Guayra Falls. It consists of a river with abundant rapids, riffles, and falls. The substrate is characterized by basaltic rocks. At the present time, several dams modify the water regime and main channels. The climate is tropical and has abundant rain. Alto Paraná (AP) ranges from Guayra Falls to the Paraguay River, with a sand bed and a progressive diminution in slope. Streams that drain into this zone are short and have low water discharge levels. The climate is subtropical. Paraná Medio (PM) includes the region from the Paraguay River to 32°S and is characterized by an important floodplain wider than 30 km with abundant islands, secondary rivers, shallow lakes, and ponds. The bottom is mainly formed by sand and clay. The climate is warm, temperate, and wet. Paraná Inferior (PI) consists of the last section of this river and, together with the Uruguay River, forms the La Plata River. This region includes a large deltaic area more than 60 km in width. The climate is temperate. Mata Atlántica (MA) consists of tropical rivers and streams with a basaltic substrate, and these rivers flow into the Alto Paraná section. The Uruguay Superior (US) is the area from the origins of tributary

streams of the Uruguay River to the "Saltos del Mocona" waterfalls. All of these tributary streams have characteristics of subtropical boxed rivers. Uruguay Medio (UM) is the section that ranges from "Saltos del Mocona" to "Salto Grande." This region is geomorphologically similar to the previous region (MA, and US) but has a temperate climate. The Uruguay Inferior (UI) has a small floodplain with a sand substrate. In this zone, there are islands with internal shallow lakes. The climate is temperate. The aquatic vegetation has a lower diversity and density than in the Parana River. Negro-Ibicuí (NI) refers to an area drained by the Negro and Ibicuí Rivers. Along with their tributaries, both rivers flow into the UM and UI zones. The climate is temperate. Paraguay-Pantanal (PP) corresponds to the northern section of the Paraguay River, with an interior delta known as Pantanal. During periods of abundant rain, this zone is connected to several tributaries of the Amazon River (Iriondo and Paira, 2007). In the southern part of this zone, the Paraguay River presents lotic environments with defined channels and sand banks. Paraguay-Pilcomayo-Bermejo (PPB) corresponds to the inferior section of the Paraguay River, where several important tributaries are found. This area also includes an important floodplain. These tributaries originate in the Andes Mountain chain (Pilcomayo and Bermejo rivers) and introduce a large amount of dissolved and suspended material. Smaller rivers make smaller contributions, with origins in the highlands near the Paraguay River (middle and inferior). In the origins of these tributaries, there are temporary connections with rivers of the Amazon basin; these occur during rain events, e.g., through the Izozog swamp (Iriondo and Paira, 2007). The climate is tropical/subtropical, but near the birthplaces of the tributaries, the climate is mountainous. Salado Norte-Carcarañá (SNC) corresponds to rivers that flow into the Paraná Medio and Inferior River. The rivers origins in SNC occur in the "Precordillera de los Andes" and "Sierras de Cordoba" mountains, respectively, and the water volume is lower than that of the Paraná River. The climate is temperate. Salado Sur-Río de La Plata (SSLP) corresponds to an area with short rivers that flow directly into the Rio de La Plata River. The climate is temperate (Bonetto and Wais, 1995).

Biological Data

Registered species in all zones were determined through field samples (420 sites), analysis of museum collections, and literature analysis (Appendix 1). Decapod species were determined according to Boschi (1981), Bond-Buckup and Buckup (1994), Magalhães and Türkay (1996a, b, c), Melo (2003), and Magalhães and Türkay (2008). Other sources of information were bird regurgitate rest as well as bird and mammal feces from different sites.

The sample sites were representative of all zones and habitats (open river, coast with or without vegetation, lakes, ponds, water column, bottoms with sand, clay, and/or rock, rapids, waterfalls, and caves). The museum samples came from the Natural Sciences Museum "Bernardino Rivadavia" from Buenos Aires (Argentina), the Natural Sciences and Museum of the National University of La Plata (Argentina), the Provincial Museum of Natural Sciences "Florentino Ameghino" from Santa Fe (Argentina), the Provincial Natural Sciences and Anthropological Museum "Prof. Antonio Serrano" from Paraná (Argentina), the Crustacean Collection of Miguel Lillio Institute from Tucumán (Argentina), the Crustaceans Laboratory of UFRGS Porto Alegre (Brazil), and the Senckenberger Museum (Germany).

The analysis was based on a data matrix built with taxa (columns) versus areas (rows). The character states are the presence/absence of taxa in previously described zones. The presence or absence of taxa in several areas was coded as (1) or (0), respectively. Next, faunistic similarities were evaluated using the Jaccard association index. This evaluation was performed with the construction of a similarity matrix, and UPGMA (unweighted pair-group method using arithmetic averages) was applied to obtain the dendrogram (cluster analysis). This analysis was performed for each family or morphotype group with the PAST computer program (Hammer et al., 2001). The degree of distortion was evaluated between the matrix and the dendrogram, computing the cophenetic coefficient (Sokal and Rohlf, 1962). A species percentage analysis of each area was conducted along with a specific richness analysis.

A hypothetical area-to-root tree with all taxa absent was added to the data matrix. The parsimony analysis of endemicity (PAE) classifies localities, areas or quadrants according to their shared taxa by means of a parsimony algorithm. In this analysis, the binary data matrix of all species and areas was analyzed using PAST (Hammer et al., 2001), and the branch
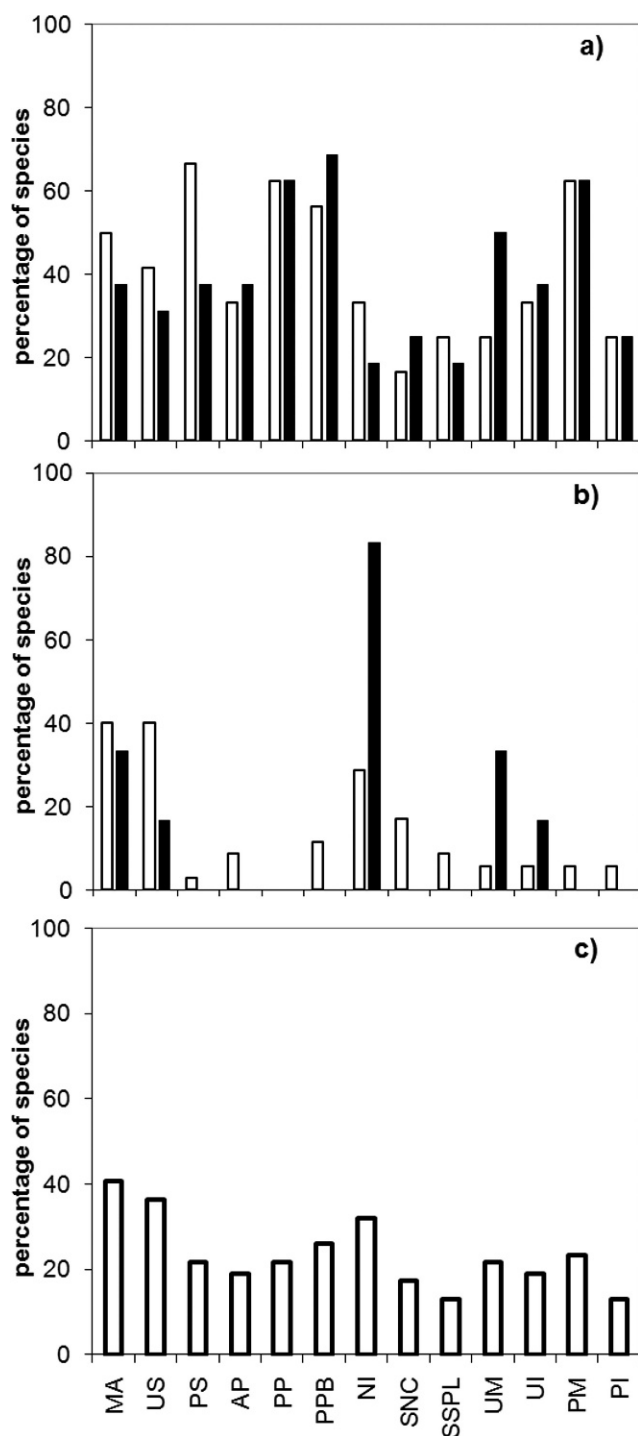
Fig. 3.   Percentage of species richness for the total decapods species from zones (a) prawns (dark bars) and freshwater crabs (Trichodactylidae) (clear bars) (b) freshwater pseudo-crabs (Aeglidae) (dark bars) and crayfish (clear bars), and (c) all freshwater decapods.

and bound algorithm was applied with the Wagner optimization to perform a search of the most parsimonious of all possible tree topologies.

RESULTS AND DISCUSSION

Decapod fauna in the La Plata Basin were characterized by 69 species of prawns, crayfish, pseudo-crabs, and crabs (see Appendix). In the first group, there are 5 genera from Sergestidae and Palaemonidae, with a total of 12 species. The genus *Macrobrachium* had the highest number of species (7). Parastacidae (crayfish) was represented by six species. Aeglidae, endemic freshwater anomurans from southern South America, includes only one genus, *Aegla*, with 35 species in the study catchment. Finally, the freshwater Trichodactylidae, endemic to the Neotropical region, is a unique family of crabs represented in this system. This group has seven genera, with *Trichodactylus* Latreille, 1828 having the greatest diversity (seven species).

Prawns

Two major areas were defined; the first, north and east of the La Plata Basin, has the highest abundance of species, where prawns with Amazon or tropical distributions were observed. The second area corresponds to areas with poorer faunal distributions; there were relicts of endemic species as well as species that could have come from the Amazon basin.

The MA, PS, PP, PPB, and PM zones are distinguished by their high species richness values, while the SNC zone had the lowest species richness value (Fig. 3). The similarities in the PM-UI and PI-SSP zones (Fig. 4), according to the presence/absence of prawns, shows the highest relationship among the studied zones due to occurrence of *Palaemonetes argentinus* Nobili, 1901 and *M. borellii* (Nobili, 1896). All of these areas were associated with the NI-UM group, whereas the latter was linked with AP-PPB (Fig. 4). The PP, PPB, and AP zones have some taxa that are also present in the Amazon Basin, e.g., *Acetes paraguayensis* (Hansen, 1919), *M. jelskii* (Miers, 1877), *M. amazonicum* (Heller, 1862), and *P. ivonicus* Holthuis, 1950.

Among palaemonids, *M. borellii* could be considered the most ancestral species in the La Plata Basin (Boschi, 1981). The origin of this species could have occurred in the Miocene epoch as a consequence of multiple invasions of a caridean ancestor into freshwater environments (De Grave et al., 2008). Another explanation of the distribution is that this prawn was found in western zones, which are marginal areas. These regions, aquatic environments of the "Pre-cordillera de los Andes" mountains, were not affected by the most recent marine transgressions. Hence, palaemonid species could be displaced by seawater and subsequently re-colonized the central and southern zones of the La Plata Basin when sea retraction occurred. The species that were registered in the eastern zones of the basin, e.g., some species of *Macrobrachium*, *Pseudopalaemon* Sollaud, 1911, and *Palaemon* Weber, 1795, did not have similar pressures from the sea. Other colonization processes could have occurred recently by some Amazon species, but these colonizations have been limited by climatic factors (mainly temperature), which have fixed the southern distribution. This assumption coincides in part with that of some studies, which indicated the history of freshwater prawns in the La Plata basin (Boschi, 1981; Morrone and Lopretto, 1994). According to these observations, in the La Plata basin, there could be endemic prawn fauna and other species that have more recently colonized this hydrosystem.
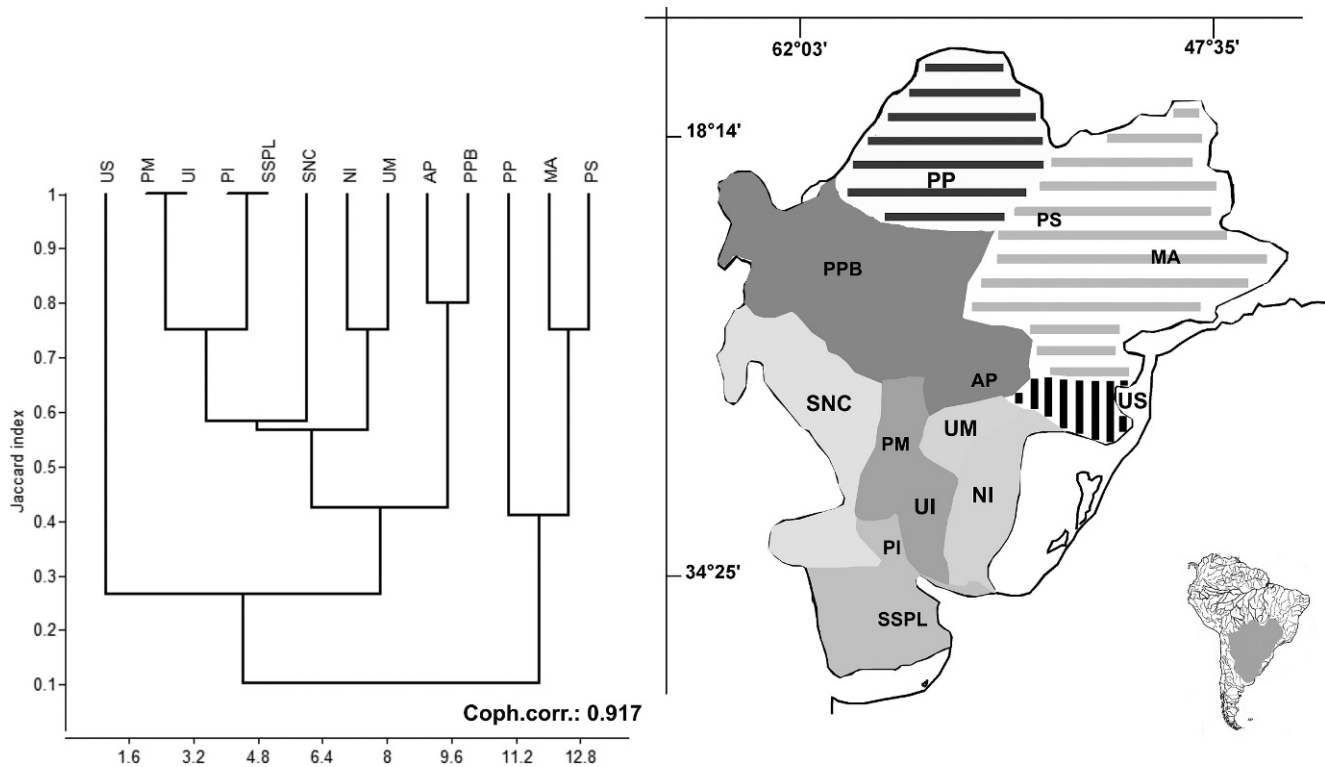
Fig. 4.   Dendrogram of faunistic similarity of prawn species (Sergestidae and Palaemonidae) using the Jaccard index. UPGMA arrangement was used and co-phenetic coefficient was indicated. Map showing the association zones.

Crayfish

Crayfish are found in the eastern zone of the La Plata Basin, with effective separation between the northern (MA) and southern (NI) zones (Fig. 5). The MA and US zones have the highest species richness values and are characterized by rivers and streams with rock bottoms and subtropical climates (Fig. 3). The UM and UI zones had the lowest species richness values; the only species present were *Parastacus saffordi* Faxon, 1898 and *P. pilimanus* (von Martens, 1869).

The monophyletic group could be given in the genus *Parastacus*, then of vicariance and/or dispersal (Schull et al., 2005; Crandall and Buhay, 2008) that were provoked by several marine transgressions in South America during the end of the Tertiary and the beginning of the Quaternary. In agreement with the effects provoked by extreme geoclimatic events during this period, other species are found in the mountain region of Patagonia (southern Argentina and Chile), currently with no relationship to the La Plata Basin (Ortmann, 1902). The crayfish distribution in both zones (eastern La Plata Basin and Patagonia) could have been modeled by marine water permanence during the transgressions that occurred from the Cretacic period to the Middle Paleogen period (Crandall and Buhay, 2008; Breinholt et al., 2009). The divergence time between *P. brasiliensis* von Martens, 1869 and *Samastacus spinifrons* (Philippi, 1882) was estimated to be 78 m. y. a. (Breinholt et al., 2009), when a great transgression occurred in South America that separated the western and eastern areas of the southern continent (Lundberg et al., 1998); during this period, vicariant events occurred. Moreover, the low dispersion capacity together with scavenger habits, cave life, potential competitors, and predators could restrict the recolonization of this group throughout the La Plata Basin. The range distributions of some crayfish from Australia and North America contrast with the observations of South American species, which are more aggressive and therefore have greater invasion capacities (Hobbs, 1988).

Pseudo-Crabs

The distribution pattern of Aeglidae could be separated into three zones according to Jaccard index of similarity and their cluster: eastern, central and northwestern (Fig. 6). A high species abundance was found in the MA, US, PPB, and NI zones (Fig. 6). Furthermore, the zones with the highest similarity values and lowest species richness values were PM, PI, UM, and UI, due to the presence of only two species among them (*A. uruguayana* Schmitt, 1942 and *A. platensis* Schmitt, 1942). Furthermore, these zones have some affinities with the UM and NI zones in the eastern region and the SSPL zone in the western region, due to the presence of one species with a wide distribution, *A. uruguayana*. No species of anomura crabs were registered in the PP zone.

For an explanation of this distribution, it is necessary to go back to the formation of aquatic environments in South America and the marine influences during the Haumurian era of the Upper Cretaceous Maastrichtian (approximately 70 m. y. a.) (Feldmann, 1986). Taking consideration of the great changes in South American geography, some studies have reported that this family could have entered through the
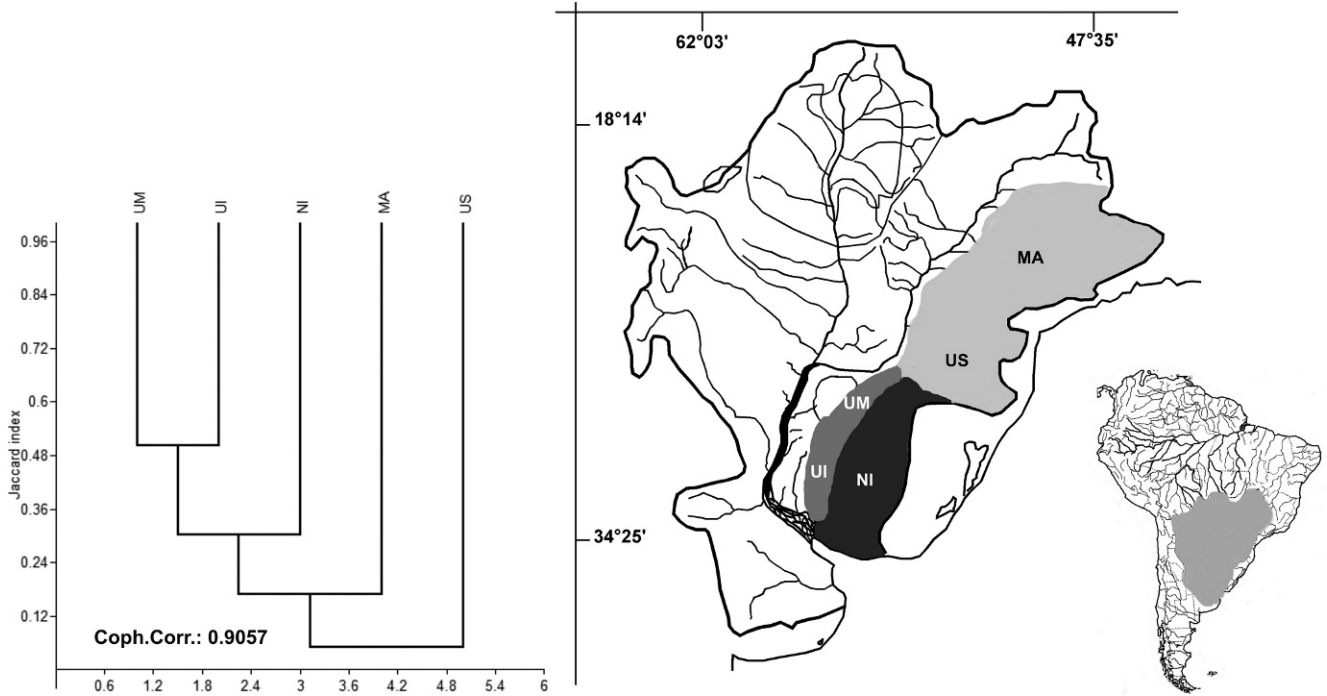
Fig. 5.   Dendrogram of faunistic similarity of crayfish species (Parastacidae) using the Jaccard index. UPGMA arrangement was used and co-phenetic coefficient was indicated. Map showing the association zones.

La Plata Basin (Schmitt, 1942; Ringuelet, 1949; Feldmann, 1986). While other studies have mentioned the Chilean region, related to the Pacific Ocean, as a potential zone in faunal incorporation (Ortmann, 1902; Feldmann, 1986;

Pérez-Losada et al., 2004). Certainly, the fossils found, like those of *Aegla* in Mexico, could be due to the arrival of ancestors in those regions through the connection between the Atlantic Ocean and the Caribbean Sea during the middle
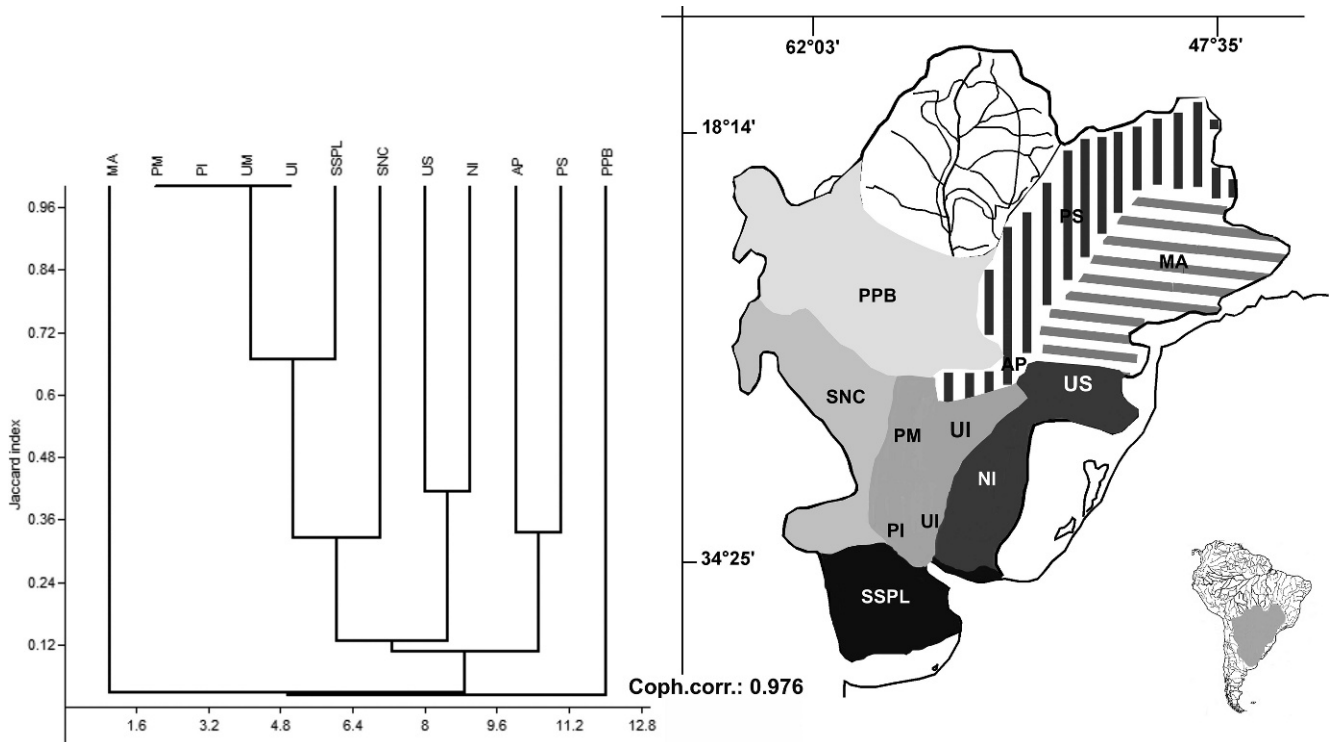

Fig. 6.   Dendrogram of faunistic similarity of freshwater pseudo-crabs species (Aeglidae) using the Jaccard index. UPGMA arrangement was used and co-phenetic coefficient was indicated. Map showing the association zones.
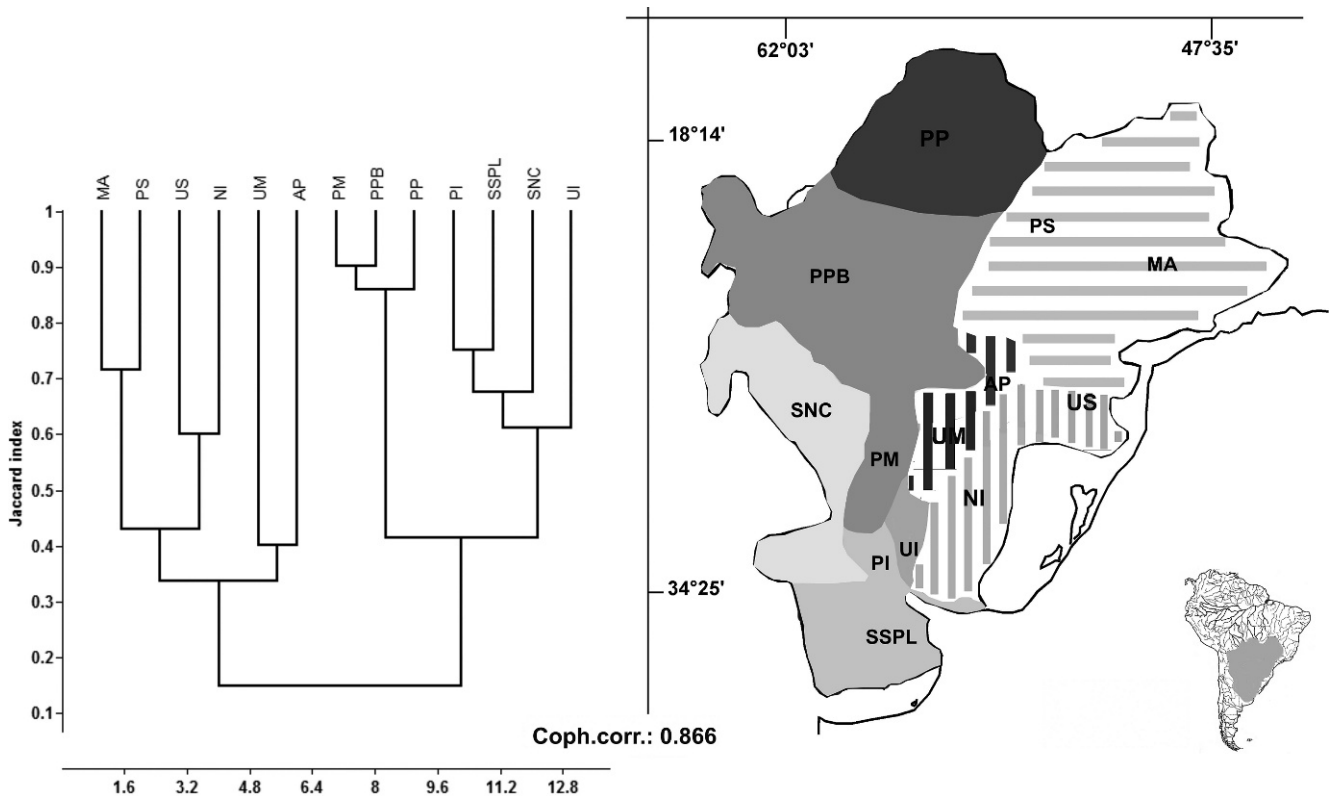
Fig. 7.   Dendrogram of faunistic similarity of freshwater crabs species (Trichodactylidae) using the Jaccard index. UPGMA arrangement was used and co-phenetic coefficient was indicated. Map showing the association zones.

and late Miocene epoch. Later, due to modifications in the land geography provoked by marine transgressions, these anomuran crabs could have moved (a dispersion event) or been restricted (a vicariant event) to zones corresponding to the highland margins of the La Plata basin. This margin area was reflected by the greatest species richness values in the zones that were not influenced by the sea (mainly the formation of the Paranaense Sea) (MA, US, AP, PS, SNC, and PPB) (Fig. 3). In the case of aeglids, is important to consider that there will be continued descriptions of new species and expansions in the distribution of known species (Bond-Buckup et al., 2010).

True Crabs

The distributions of two groups of trichodactylids were observed according to the Jaccard similarity index (Fig. 7), corresponding to the eastern and northern and central and western zones. The eastern region was found to be inhabited by a lower diversity of crabs (mainly *Tricho-dactylus* spp.) (Morrone and Lopretto, 2001). The MA, PS, AP, US, UM, and NI zones (eastern zones of the La Plata Basin) were grouped by the presence of several species of *Trichodactylus* and *Goyazana castelnaui* (Milne Edwards, 1853) (Fig. 7, Appendix). The northern, central, and western zones were characterized by the species of *Dilocarcinus* Milne Edwards, 1853, *Sylviocarcinus* Milne Edwards, 1853, and *Zilchiopsis* Bott, 1969. However, some crabs are widely distributed in the La Plata system (*T. borellianus* Nobili, 1896 and *D. pagei* Stimpson, 1861).

The headlands of the Paraguay and Pilcomayo rivers (PP and PPB) are similar to the PM zone, indicating a possible species corridor from the Amazon Basin, e.g., *D. sep-temdentatus* (Herbst, 1783), *S. pictus* Milne-Edwards H., 1853, and *Z. oronensis* (Pretzmann, 1968) (Collins et al., 2002, 2009). This basin could be thought of as a center of radiation toward several freshwater systems in South America, but it does not reach the opposite side of the Andes mountain chain. These crabs characterize lowland rivers (Rodriguez, 1981).

Trichodactylidae, similar to other freshwater crabs, has an ancestral marine group that could have colonized the margins of the tropical area of the southern Tethys Sea during the Cretaceous period (Yeo et al., 2008). Moreover, invasions of trichodactylid ancestors into the rivers of South America could have occurred in the post-Gondwanan period, during or after the rise of the Andes Mountains and the separation of Africa (Yeo et al., 2008; Cumberlidge and Ng, 2009).

Several southern zones of the basin, namely the SSPL, PI, and UI zones, had similar species present and were characterized by low species richness values. The low temperatures of these zones (5-10°C) might not permit the establishment of populations of tropical and sub-tropical freshwater species. The highest species richness values were observed in the PPB and PP zones (Fig. 3).

General Considerations

Two major clades were identified according to the PAE analysis of all decapod species registered in the La Plata
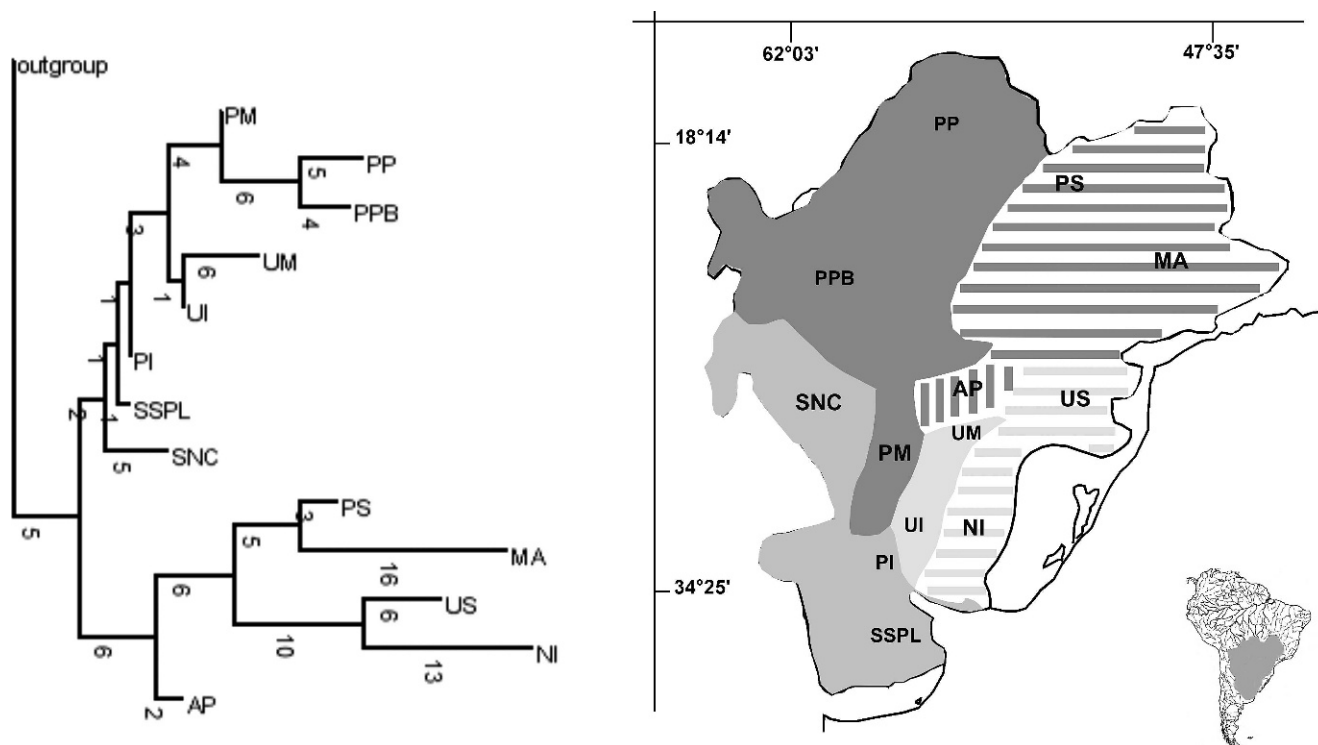
Fig. 8. Parsimony analysis of endemicity (PAE) of freshwater decapods (prawns, crayfish, pseudo-crabs, and crabs) at La Plata Basin using branch and bound algorithm with the Wagner optimization. Tree evaluated: 10081648; tree length: 111; Ensemble Cl: 0.6216. Branch lengths are shown in numbers. Map showing the association zones.

basin. The eastern zone was clearly separated from the western-central zones (Fig. 8). Moreover, in the last zone, three sub-areas were recognized, one of them being strongly influenced by Amazonian fauna to achieve the highest species richness values (Fig. 3); the others were impoverished in terms of species, probably due to climatic factors. The decapod distribution was different from the proposed distribution of freshwater fishes (Lopez et al., 2008). This difference was possibly due to differences in habitat, evolutionary distance between groups relative to the freshwater environments conquered, and movement capacities. The MA, NI, US, AP, PP, and PPB zones have the highest numbers of species among the studied zones (Fig. 3). These zones have not been completely disturbed by important marine transgressions during the recent Quaternary period (Fig. 1); in addition, they are influenced by other basins, such as the Amazon basin. On the other hand, the MA and US zones might have received species from areas that were affected by advancing seas. Previously, the PP and PPB zones have been affected by the Paranaense Sea; after this advancement, however, the seawater retreated to the lowlands, and some Amazonian decapods have colonized the La Plata basin. Furthermore, some species have also migrated more recently (Pettovello, 1996; Collins, 2000; Collins et al., 2002, 2009). Connections between the La Plata and Amazon basins occur through the Izozog swamp (PPB) (Parapeti and Grande rivers), the headwaters of the Paraguay River (PP) (Aguapehy, Jaburu, Cuiabá), and the tributaries of the Amazon River (Guapore, Alegre, Manso) during periods of flooding and/or intense rain (Iriondo and Paira, 2007). The

movements of these decapods include those that walk across the land, such as Trichodactylidae (Fernandez and Collins, 2000). In the western region, the PPB zone has higher species richness values, due to the presence of aeglids in the headwaters of the Pilcomayo and Bermejo Rivers (Bond-Buckup and Buckup, 1994). In the MA, NI, and US zones, high diversity values (approximately 42% and 35%, respectively, of the total species counts) are favored by optimal abiotic and biotic conditions (temperature, dissolved oxygen, trophic offer, refuge availability, and habitat diversity). Moreover, these zones are considered to be endemic for freshwater fishes that have not been affected by Quaternary marine transgressions (Lundberg et al., 1998). The zones that have been recently affected by the sea (PI, SSPL, UI, and SNC) showed the lowest species numbers (less than 20%), while the PM zone was strongly influenced by the superior zones (PPB, PP, and PS), showing medium species richness values (25%).

There is clear evidence that South American aquatic fauna were affected by diverse geo-climatic events, particularly the rise of the Andes mountains during the Tertiary (Miocene), marine transgressions, and land elevations on the eastern side of the continent. At some points, these events resulted in increased water discharge toward the Amazon River and Magdalena-Orinoco Rivers to the north, Paraguay, Pilcomayo, and Bermejo Rivers to the south, and flooded lowland, leading to favorable environments for decapod populations. Furthermore, the Parana River has an important relationship with the present basin, as the Serra Geral basalt effusion occurred in the later Cretaceous (Potter, 1997).

Like pseudo-crabs and crayfish (more than for crabs and shrimp), a large number of fish species are placed in the endemic category (Ribeiro, 2006). Those are species with habitats in rivers and streams, and their lifestyles involve burrowing along riverbanks and fields or under stones. The range of *Aegla* is similar to that of parastacids, suggesting a similar colonization route, indicating that their ranges overlap and resulted in a strong competitive force (Riek, 1972). In addition, climatic successions include cool and warm periods from the Paleocene to the Neocene, which determined the pulses of expansion and retraction in faunal distributions. These pulses were also manifested in vertebrate fauna (Ortiz-Jaureguizar et al., 2006). During the middle and late Miocene epoch, other marine transgressions occurred in South America that affect the Parana-Paraguay axis and skirted the Andes mountains to connect the Amazon, Orinoco, and Magdalena basins (Lundberg et al., 1998). The effective connection between the Caribbean Sea and South Atlantic oceans could permit species exchanges through the Paranean Sea and Tethys Waterspout (Donato et al., 2003). Subsequently, the isolation of the peripheral drainage of the southern, western, and northern Parana, Amazon, and Orinoco basins could provoke local allopatric divergence in widespread species, such as that observed for sub-tropical fishes (Ribeiro, 2006), showing a vicariant pattern. Geological processes prompted the occurrence of vicariant events in freshwater fauna, including decapods. Moreover, other aquatic crustaceans have peculiar distributions, such as the case of the bathynellaceans, where species are present in the northeastern and southwestern sides of South America (Schram, 2008). This distribution disruption could be attributed to marine ingressions in South America during the Quaternary period, similar to the effects on freshwater decapods in the southern part of the continent.

CONCLUSION

The actual situation of decapod species at the La Plata Basin is different from that of other basins; the highest species richness values occur in the mouths of rivers (high-order zone) (Vannotte et al., 1980). We have observed that, in the La Plata Basin, this high species richness happens in low-order rivers, mainly in the eastern and northern zones, which correspond to the basin margins. We assume that these habitats were molded by geo-climatic history, where the apparition of the Andes mountain chain, marine transgression, and the geomorphologic history of the basin have allowed the present distribution of decapod fauna.

Finally, we observe three situations in the studied system, according to the evidence presented in this study:

1) Species for which colonization precedes marine ingressions. When these events occur, these species moved to higher areas, at the edges of the system.
2) Estuarial species that could arrive with seawater; when the sea retracted, these species could begin the process of adaptation to fresh water.
3) Species that recolonized (situation 1) or colonized areas that were previously invaded by the sea, while other decapods colonized more recently from the Amazon basin.

These could be an explanatory model for understanding the distribution of other groups of freshwater aquatic organisms, and it is the first step that evaluates the distributions to determine susceptible areas to justify a conservation efforts.

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Appendix.   Presence (1) - absence (0) of decapod species registered in each definite area of Rio de la Plata systems. Paraná Superior (PS), Alto Paraná (AP), Paraná Medio (PM), Paraná Inferior (PI), Mata Atlántica (MA), Uruguay Superior (US), Uruguay Medio (UM), Uruguay Inferior (UI), Negro-Ibicuí (NI), Paraguay-Pantanal (PP), Paraguay-Pilcomayo-Bermejo (PPB), Salado Norte-Carcarañá (SNC) and Salado Sur-Río de La Plata (SSLP).

Species	Species/Area												
	PS	AP	PM	PI	PP	PPB	MA	US	UM	UI	NI	SNC	SSLP
Acetes paraguayensis	0	0	1	1	1	1	0	0	0	0	0	0	1
Palaemonetes argentinus	0	1	1	1	1	1	0	1	1	1	1	1	1
P. ivonicus	1	0	0	0	1	0	0	0	0	0	0	0	0
Macrobrachium borellii	0	1	1	1	1	1	0	0	1	1	1	1	1
M. amazonicum	1	1	0	0	1	1	1	0	0	0	0	0	0
M. jelskii	1	1	0	0	1	1	1	1	0	0	0	0	0
M. brasiliense	1	0	0	0	1	0	1	0	0	0	0	0	0
M. ferreirai	1	0	0	0	0	0	0	0	0	0	0	0	0
M. iheringi	1	0	0	0	1	0	1	0	0	0	0	0	0
M. natereri	1	0	0	0	0	0	0	1	0	0	0	0	0
Pseudopalaemon bouvieri	1	0	1	0	0	0	1	0	1	1	1	0	0
P. pandaliformis	1	0	0	0	0	0	1	1	0	0	1	0	0

Appendix. Continued.

Species	PS	AP	PM	PI	PP	PPB	MA	US	UM	UI	NI	SNC	SSLP
Parastacus laevigatus	0	0	0	0	0	0	1	0	0	0	0	0	0
P. saffordi	0	0	0	0	0	0	1	1	1	1	0	0	0
P. brasiliensis	0	0	0	0	0	0	0	0	0	0	1	0	0
P. pilimanus	0	0	0	0	0	0	1	1	1	1	1	0	0
P. varicosus	0	0	0	0	0	0	1	1	0	0	1	0	0
P. deffosus	0	0	0	0	0	0	0	0	0	0	1	0	0
Aegla uruguayana	0	0	1	1	0	1	0	0	1	1	1	1	1
A. platensis	0	0	1	1	0	0	0	1	1	1	1	1	1
A. franca	0	0	0	0	0	0	1	0	0	0	0	1	0
A. perobae	0	0	0	0	0	0	1	0	0	0	0	0	0
A. castro	0	0	0	0	0	0	1	0	0	0	0	0	0
A. parva	0	0	0	0	0	0	1	1	0	0	0	0	0
A. odebrechtii	0	0	0	0	0	0	1	1	0	0	0	0	0
A. parana	1	1	0	0	0	0	1	0	0	0	0	0	0
A. singularis	0	1	0	0	0	0	0	1	1	0	0	0	0
A. rossiana	0	0	0	0	0	0	0	1	0	0	0	0	0
A. inconspicua	0	0	0	0	0	0	0	1	0	0	0	0	0
A. jarai	0	0	0	0	0	0	1	1	0	0	0	0	0
A. spinosa	0	0	0	0	0	0	0	1	0	0	0	0	0
A. franciscana	0	0	0	0	0	0	0	1	0	0	0	0	0
A. serrana	0	0	0	0	0	0	0	1	0	0	0	0	0
A. lomgirrostri	0	0	0	0	0	0	0	0	0	0	1	0	0
A. camargoi	0	0	0	0	0	0	0	1	0	0	0	0	0
A. cavernicola	0	0	0	0	0	0	1	0	0	0	0	0	0
A. lata	0	0	0	0	0	0	1	0	0	0	0	0	0
A. leptochela	0	0	0	0	0	0	1	0	0	0	0	0	0
A. leptodactyla	0	0	0	0	0	0	0	1	0	0	0	0	0
A. ligulata	0	0	0	0	0	0	0	1	0	0	0	0	0
A. marginata	0	0	0	0	0	0	1	0	0	0	0	0	0
A. microphthlma	0	0	0	0	0	0	1	0	0	0	0	0	0
A. paulensis	0	0	0	0	0	0	1	0	0	0	0	0	0
A. plana	0	0	0	0	0	0	0	1	0	0	0	0	0
A. prado	0	0	0	0	0	0	0	0	0	0	0	0	1
A. schmitti	0	0	0	0	0	0	1	0	0	0	0	0	0
A. strinatii	0	0	0	0	0	0	1	0	0	0	0	0	0
A. septentrionalis	0	0	0	0	0	1	0	0	0	0	0	0	0
A. humahuaca	0	0	0	0	0	0	0	0	0	0	0	1	0
A. jujuyana	0	0	0	0	0	1	0	0	0	0	0	1	0
A. sanlorenzo	0	0	0	0	0	1	0	0	0	0	0	0	0
A. intercalta	0	0	0	0	0	0	0	0	0	0	0	1	0
A. ringueleti	0	0	0	0	0	0	0	0	0	0	0	1	0
Dilocarcinus pagei	1	1	1	1	1	1	0	0	0	1	0	0	1
D. septemdentatus	0	0	1	0	1	1	0	0	0	0	0	0	0
Trichodactylus borellianus	0	1	1	1	1	1	0	0	0	1	0	1	1
T. dentatus	1	0	0	0	0	0	1	0	0	0	0	0	0
T. fluviatilis	1	1	0	0	0	0	1	1	0	0	0	0	0
T. parvus	0	0	0	0	1	0	0	0	0	0	0	0	0
T. kensleyii	1	1	0	0	0	1	0	1	1	0	1	0	0
T. panoplus	0	0	1	0	0	0	1	1	1	1	1	0	0
T. petropolitanus	0	1	0	0	0	0	1	1	1	0	0	0	0
Sylviocarcinus pictus	0	0	1	0	1	1	0	0	0	0	0	0	0
S. australis	0	1	1	0	1	1	0	0	0	0	0	1	0
Goyazana castelnaui	1	0	0	0	1	1	1	0	0	0	0	0	0
Poppiana argentiniana	0	0	1	1	1	1	0	0	0	0	0	0	0
Valdivia camerani	0	0	1	0	1	1	0	0	0	0	0	0	0
Zilchiopsis oronensis	0	0	1	0	1	1	0	0	0	0	0	0	0
Z. colastinensis	0	0	1	1	0	1	0	0	0	1	0	1	1