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Distribution of Large Benthic Gastropods in the Uruguayan Continental Shelf and Río de la Plata Estuary

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ABSTRACT

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We analyzed the distribution and ecology of large gastropods inhabiting the continental shelf of Uruguay and the Río de la Plata estuary, in depths ranging from 4 to 62 m. Seven species belonging to Tonnidae, Ranellidae, Muricidae, Nassariidae, and Volutidae were collected. While the seven species recorded in this study have been previously reported for the Uruguayan coast, here we provide the first detailed description of its habitat preferences in terms of depth, salinity, and sea bottom temperatures. Clustering analysis of stations based on biological data (presence/absence of species) indicated a spatial segregation of the large gastropods assemblages in three areas: estuarine, low specific richness, dominated by *Rapana venosa*; inshore (10 to 36 m), high richness, codominated by *Zidona dufresnei* and *Pachycymbiola brasiliana*; and offshore (21 to 62 m), intermediate richness, characterized by *Z. dufresnei.* Mean values for environmental parameters showed significant differences among clusters of stations. Direct developers were more ubiquitous than planktotrophic developers. On the other hand, the exotic planktotrophic species *R. venosa* dominated the estuarine area. This pattern is not coincident with predictions based on life history traits, such as dispersal capabilities; this suggests that generalizations in this respect are complicated and scale and species dependent.

ADDITIONAL INDEX WORDS: Cymatium, Tonna, Buccinanops, Rapana, *Volutidae, Uruguay.*

INTRODUCTION

The distribution of benthic invertebrates over a range of temporal and spatial scales is the result of both historical events and ecological processes. The interlocking roles of life history types and strategies and adaptive tolerances to a number of factors, including water temperature, salinity, depth, and the nature of the seabed, are key variables associated with the observed distribution patterns.

Gastropods life history traits, such as type of development, may have significant effects on species distribution. In most marine habitats, planktotrophic developers with long-living veliger larvae are widely dispersed by currents, thus enhancing those species dispersal capabilities. In contrast, direct and lecithotrophic developers with short-living larvae have relatively low dispersal capabilities (Mileikovsky, 1971; Morgan, 1995; Poulin *et al.,* 2001; Thorson, 1950). On the other hand, Gallardo and Penchaszadeh (2001) proposed that the prevalence of soft-bottom sediments in the southwestern Atlantic favors direct developers. However, while there is a good theoretical basis dealing with the latitudinal and bathymetric distribution of the relative frequency of hatching modes in marine prosobranch gastropods (namely Thorson's rule), similar predictions are lacking when considering small or mesoscale environmental gradients.

There is a dearth of current knowledge about the ecological factors that govern the distribution of benthic shelf organisms off Uruguay. Particularly, and despite the ecological and current or potential socio-economic importance (Fabiano *et al.,* 2000; Giménez and Penchaszadeh, 2003; Masello, 2000; Riestra and Fabiano, 2000; Riestra *et al.,* 2000), data on large gastropods are poor. Most existing references are of small-scale scope, and are preliminary or imprecise. At present, Olivier and V. Scarabino (1972) and Kaiser (1977) are the only published works that relate the distribution of some large gastropods from the Uruguayan shelf with depth, temperature, and salinity, while Milstein *et al.* (1976) did the same in relation with depth and sediment features.

The Uruguayan shelf is characterized by a singular hydrographic system composed of water masses of contrasting thermohaline characteristics, *e.g.,* sub-Antarctic waters (SAW; Sverdrup *et al.,* 1942; Thomsen, 1962), tropical waters (Emilsson, 1961; Thomsen, 1962), subtropical waters (Emilsson, 1961; Thomsen, 1962), and coastal waters (CW), which are defined by salinities (S) < 33.2 (Guerrero and Piola, 1997) and, off Uruguay, are mainly a mixture of SAW and waters from the Río de la Plata estuary. The Río de la Plata flows into the Atlantic Ocean with an average discharge of

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22,000 m^3 s^{-1} (Framiñan and Brown 1996; Guerrero *et al.,* 1997a), and the study area is dominated by CW as a consequence of low depths (<50 m) and the proximity of the coast. River discharge and wind control the saline and turbidity front location in the estuary (Nagy *et al.,* 1987). The occurrence of these water masses over the shelf determines a complex horizontal and vertical structure with a high degree of seasonal and interannual variation that affects the biological productivity and the dynamics of the shelf ecosystem (Lima *et al.,* 1996).

In this area, volutid species are a major component of molluscan assemblages and typical direct developers, with both attached and unattached egg capsules containing embryos feeding on yolk (Penchaszadeh *et al.*, 1999). Direct development is also displayed by the nassariid genus *Buccinanops* (Penchaszadeh, 1971, 1973). The capsules, which remain attached to the adults, contain nurse eggs on which embryos feed. In contrast, *Tonna galea, Cymatium parthenopeum,* and *Rapana venosa* exhibit veliger larvae with planktotrophic development (Mann and Harding, 2003; Scheltema, 1966, 1971).

The aim of this study is to analyze the spatial distribution of these large gastropods (*i.e.,* >5 cm adult size) and its assemblages at the inner Uruguayan continental shelf and the outer half of the Río de la Plata estuary. Large-scale distribution patterns of seven large gastropod species belonging to Tonnidae, Ranellidae, Muricidae, Nassariidae, and Volutidae are examined. Finally, life-history traits and abiotic factors are related to the observed distribution patterns. Conclusions are made on the basis of a good knowledge of previously published information on the species here treated, and factors leading to eventual misidentifications or poor autoecological discussion, which may lead to inconsistent results, are avoided. Southwestern Atlantic benthic ecology studies seem to be affected by both problems, partially due to poor taxonomical knowledge/expertise, and to a bias in considering the whole community, neglecting species biology and ecology. In this context, a brief synthesis on the current knowledge of the species considered herein is presented (focused on bathymetric distribution), since much available data are dispersed and in obscure sources, even for the countries where it was produced. Special consideration on the status of the collected material (living or empty shell) was given.

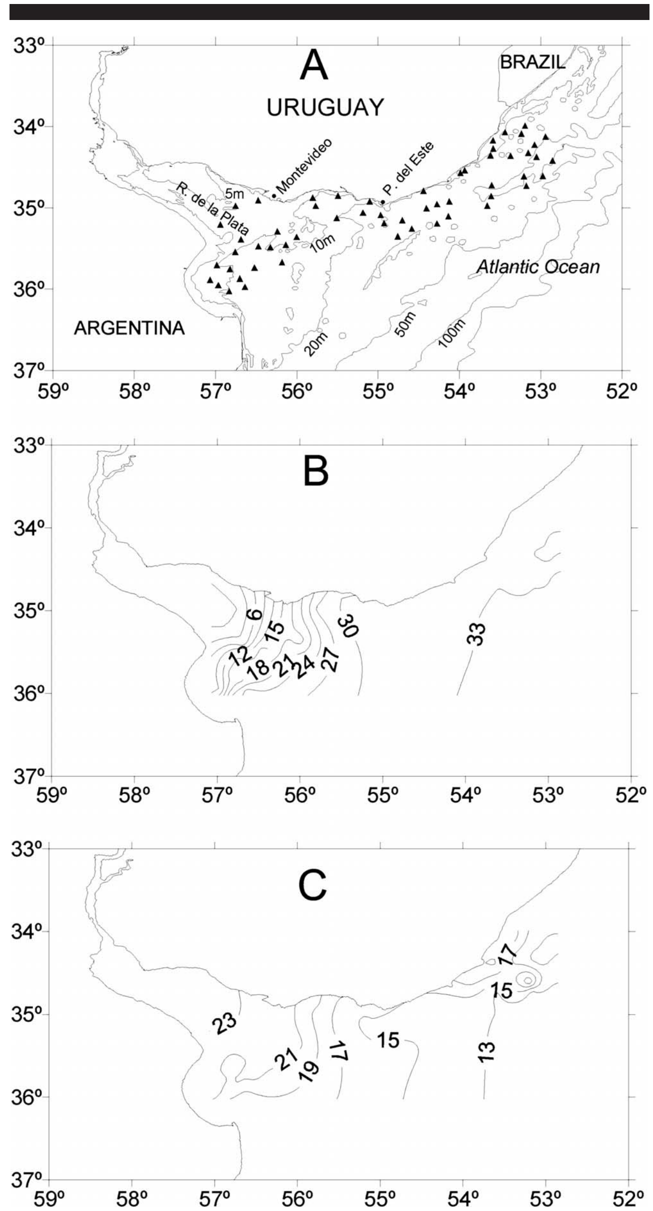

Figure 1. Study area with sampling locations and isolines of depth (A), horizontal sea bottom salinities (psu) (B), and sea bottom temperatures (°C) (C).

MATERIAL AND METHODS

Data of occurrence and abundance of large gastropods (>5 cm of adult size) were obtained from one cruise made during spring 2002 onboard R/V *Aldebaran* (Dirección Nacional de Recursos Acuáticos, Uruguay) in the inner Uruguayan continental shelf and the outer half of the Río de la Plata estuary between latitudes 33°58′ S and 36°12′ S and longitudes between 56°50′ W and 53°11′ W. The sampling design was established for white croacker (*Micropogonias furnieri*) stock assessment. Some 55 stations were randomly allocated based on the main biological features of that species, between the 5 and 50 m isobath (Figure 1A). In each station, 30′ tows were performed with a Engel-type bottom trawl net with a 24 m horizontal opening and a 100 mm stretched mesh in the cod ends. At each station, a conductivity, temperature, and depth (CTD) cast (using an SBE-19 water column profiler, Sea-Bird Electronics) profiled the water column for temperature and conductivity from the surface to the bottom. Depth of stations was also measured. Species were determined onboard, and their presence and number of individuals were registered. Voucher material for each one is deposited at the Museo Nacional de Historia Natural y Antropología (Montevideo).

Habitat preferences for individual species were described in terms of the mean value, range, and standard deviation for all the measured enviromental parameters. Frequencies

Table 1. *Species collected, systematic position, type of development, and frequency of occurrence as number of occurrences/total stations. Mean (±SD) and ranges of the environmental parameters measured are shown for each species.*

Species	Family	Type of Development	Frequency of Occurrence	Depth (m) Range	Depth (m) Mean (±SD)	Salinity (psu) Range	Salinity (psu) Mean (±SD)	Temperature (°C) Range	Temperature (°C) Mean (±SD)
Cymatium parthenopeum	Ranellidae	Planktotrophic	0.04	25–27	26.0 ± 1.41	31.53–31.64	31.58 ± 0.08	14.61–14.88	14.73 ± 0.17
Tonna galea	Tonnidae	Planktotrophic	0.16	21–62	35.44 ± 12.60	31.62–33.30	32.59 ± 0.72	12.39–14.98	13.54 ± 0.98
Rapana venosa	Muricidae	Planktotrophic	0.16	4–12	9.00 ± 2.17	12.39–14.98	19.94 ± 4.54	18.12–22.04	20.43 ± 1.54
Adelomelon beckii	Volutidae	Direct	0.09	28–52	42.4 ± 9.61	32.38–33.19	32.91 ± 0.35	12.39–13.99	13.04 ± 0.75
Pachycymbiola brasiliana	Volutidae	Direct	0.29	9–36	18.12 ± 7.40	16.34–32.27	29.99 ± 3.78	14.17–21.56	16.50 ± 2.17
Zidona dufresnei	Volutidae	Direct	0.36	10–62	27.8 ± 13.6	25.29–33.30	31.75 ± 1.81	12.53–19.64	14.78 ± 1.82
Buccinanops cochlidium	Nassariidae	Direct	0.22	10–36	23.0 ± 9.30	30.23–33.28	31.71 ± 0.73	13.21–16.46	14.98 ± 1.00

of occurrence (as total occurrences divided by number of stations) were calculated for all species in order to assess the ecological implications of variation among species with contrasting reproductive strategies. The sampling errors (*e.g.,* underestimation of smaller sizes/species due to mesh size) associated with the fishing gear used in this study have not been evaluated for large gastropods, but it is considered to be potentially relevant. Therefore, abundances were not considered in the analysis, although some informative data are provided.

Multivariate methods were used to determine the between-habitat (β) diversity. Stations were grouped based on similarity in species composition using presence/absence data. The similarity matrix was constructed using the Jaccard index and mean average group linking method. Differences in mean values of the environmental variables among clusters due to data heterocedasticity were analyzed by means of a nonparametric analysis of variance (ANOVA) test (Kruskal-Wallis ANOVA by Ranks).

RESULTS

The minimum value of bottom salinity occurred at the inner section of the Río de la Plata estuary and increased toward the ocean in the NE direction, with a maximum of 33.3 psu. Temperature showed an inverse pattern: the maximum was recorded at the inner section the Río de la Plata estuary (23 °C), whereas the NE deeper oceanic region showed the minimum temperature (12 °C). High temperatures (17–18 °C) were also recorded near the coast in the NE of the study region (Figures 1B and 1C).

From the 55 stations surveyed, 17 stations lacked large gastropods. Seven species were collected in the remaining 38 stations (Table 1, Figure 2A–G). The highest total number of specimens (716 individuals) was shown by *Pachycymbiola brasiliana,* which occurred at 16 stations and also displayed the maximum number of individuals in a single sample (225 individuals). *Zidona dufresnei* was found at 20 stations, whereas the largest South American volutid, *Adelomelon beckii,* occurred as single individuals at five stations. The nassariid *Buccinanops cochlidium* was found at 12 stations. Presence of *T. galea* was registered at nine stations, ranging between 1 and 113 individuals. *C. parthenopeum* occurred only at two stations. Finally, the alien species *R. venosa* was found at nine stations, with a maximum of 50 individuals.

In terms of frequency of occurrence, direct developers dominated over planktotrophic species when considering the whole area. Habitat preferences for the collected species, in terms of range, mean values, and standard deviations of environmental parameters are shown in Table 1. Cluster analysis showed two major groups with 4.77% similarity. In addition, within one of these major groups, two subgroups showing 12.30% similarity were discriminated (Figures 3A and 3B).

Group 1 (estuarine) is composed of 12 stations characterized by a mean depth of 11.75 ± 5.77 m, ranging from 4 to 26 m, mean bottom salinity of 22.63 ± 6.21 psu (range 14.93–31.29 psu), and bottom temperature ranging from 15.25 to 22.05 °C (19.65 ± 2.08 °C). Faunal composition of this group includes *R. venosa* (9 occurrences, 75% of stations), *P. brasiliana* (5 occurrences, 41.67% of stations), and a single occurrence of *Z. dufresnei* (8.33%).

Group 2 (12 stations, offshore) bathymetric distributions ranged from 21 to 62 m (37.916 ± 11.88 m), had a mean bottom salinity of 32.85 ± 0.43 psu (range 33.30–32.07 psu), and bottom temperatures ranging from 12.39 to 14.39 (13.25 ± 0.74 °C). Presence of *Z. dufresnei* (8 stations, 66.67%), *T. galea* (6 stations, 50%), and *A. beckii* (5 presences, 41.67 %) characterized this group of stations. *B. cochlidium* also occurred rarely (one presence, 8.33%).

Group 3 (14 stations, inshore areas) showed a mean bottom temperature of 15.41 ± 1.49 °C, salinities ranging from 29.54 to 32.26 psu (31.32 ± 0.79 psu), and a bathymetric distribution from 10 to 36 m (20 ± 7.9 m). All species except *R. venosa* and *A. beckii* were present in this group. *P. brasiliana* (11 stations, 78.57%) and *Z. dufresnei* (11 stations, 78.57 %) were the most frequent species, followed by *B. cochlidium* (10 stations, 71.43%), *T. galea* (3 stations, 21.43%), and *C. parthenopeum* (2 stations, 14.28%).

Salinity (Kruskal-Wallis test: $H_{(2,N=38)=30.80}$; $p < 0.0001$), depth (Kruskal-Wallis test: $H_{(2,N=38)=\ 18.57}$; $p < 0.0001$), and temperature (Kruskal-Wallis test: $H_{(2,N=38)=29.78}$; $p < 0.0001$) showed statistically significant differences between groups of stations.

DISCUSSION

We found a spatial segregation of large gastropods assemblages in three areas: estuarine low specific richness, dominated by *R. venosa,* inshore high specific richness, codomi-

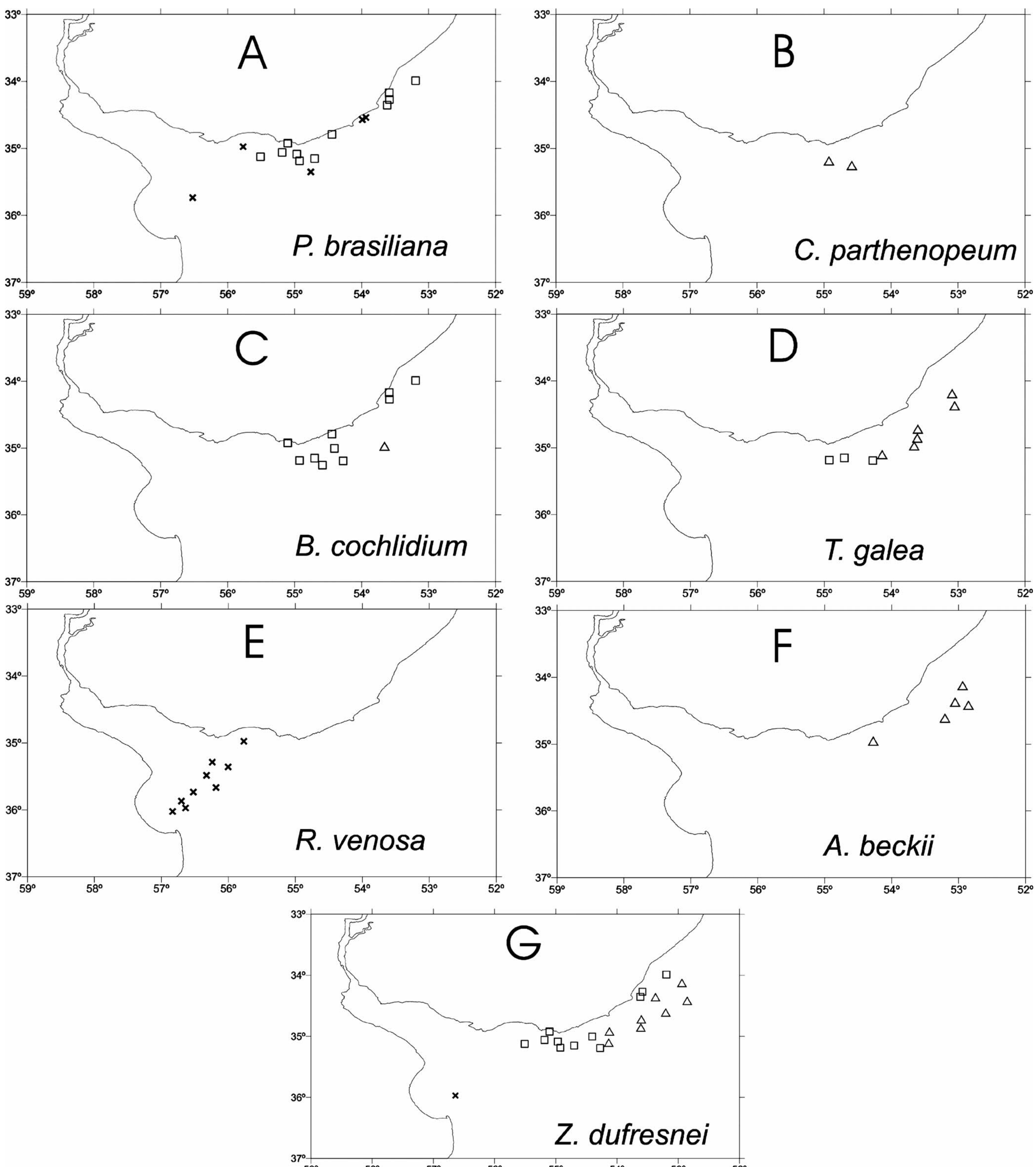

Figure 2. Distribution of species in the study area: (A) *P. brasiliana*; (B) *C. parthenopeum*; (C) *B. cochlidium*; (D) *T. galea*; (E) *R. venosa*; (F) *A. beckii*; and (G) *Z. dufresnei.* Symbols are as in Figure 3.

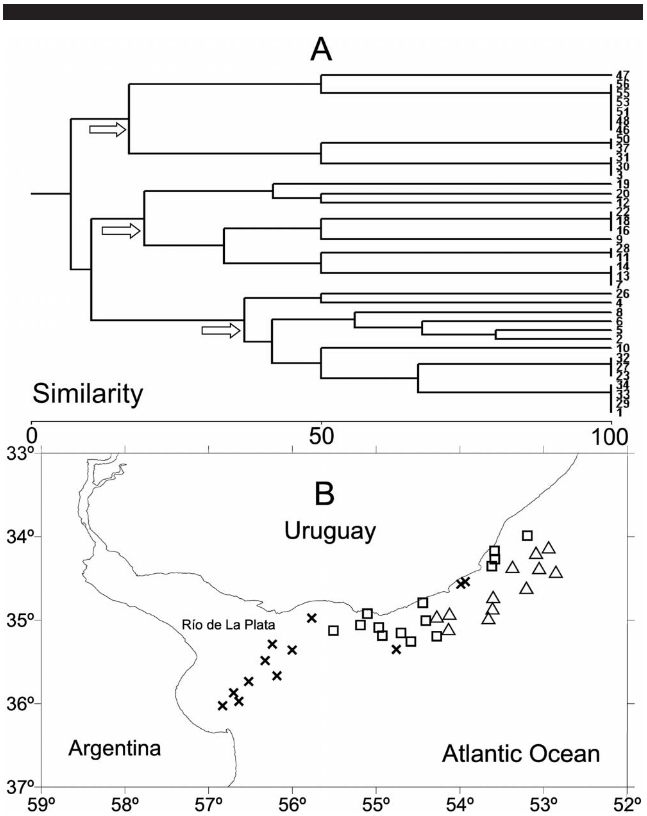

Figure 3. Dendrogram (A) and spatial arrangement of groups determined by Jaccard Cluter Análisis (JCA) (B). Arrows in the dendrogram indicates the three clusters. Group 1 = **X**; Group 2 = △; Group 3 = □.

nated by *Z. dufresnei* and *P. brasiliana,* and offshore, characterized by *Z. dufresnei.* This spatial structure reflects not only the current effects of salinity, bathymetry, and temperature but also the phylogenetic background determining (or constraining) species life-history traits and the biogeographical history of the area and taxa involved. Our results showed that, when considering the whole area, frequency of occurrence of direct developers was generally higher than planktotrophic species. In fact, with the exception of *A. beckii,* all direct developers occurred in more locations that planktotrophic species. This is not coincident with the predictions made based on life-history traits such as dispersal capabilities (MILEIKOVSKY, 1971; POULIN *et al.,* 2001). This suggests that generalizations in this respect are complicated and scale and species dependent. However, it is remarkable that the only species that successfully colonized the estuarine area is the exotic and planktotrophic *R. venosa.*

This spatial segregation is in turn coincident with well-defined oceanographic areas. While wind field, river discharge, and the Coriolis force control Río de la Plata surface salinity patterns, bottom salinity does not exhibit seasonality, because the shelf water intrusion is controlled by bathymetry (GUERRERO *et al.,* 1997a). However, sea bottom temperature at the study area is seasonally variable (GUERRERO *et al.,* 1997a), and so temperature ranges are likely to be affected by the short observation period.

Salinity ranges have not been previously reported for the volutid species found during this study. The observed assemblages showed changes along the salinity and bathymetric gradient, as found in other studies dealing with distribution of macrobenthic species (GASTON and EDDS, 1994; GIBERTO *et al.,* 2004; HOLLAND *et al.,* 1987). Stations in group 1 showed a wide range of bottom salinity. These stations were mostly associated with areas characterized by high variability in salinity. However, the inclusion of stations 3, 30, and 31, placed in this group due to the presence of *P. brasiliana,* increases the range of salinity values. In fact, this assemblage is defined by the presence of *R. venosa,* which has now been found to be successfully occupying a previously vacant ecological niche. Consequently, the large gastropods assemblage of the estuarine area was significantly less diverse than the adjacent marine areas.

R. venosa have recently colonized the Río de la Plata estuary (SCARABINO *et al.,* 1999; PASTORINO *et al.,* 2000) and are successfully breeding in (and restricted to) this area. During the cruise, large masses of ovicapsules of this species were found attached to a variety of substrata, including plastic debris and garbage. It has been proposed that salinity tolerance is the dominant factor controlling the potential dispersal (= invasion) range of the species into the estuaries of the Atlantic coast of the United States; all larval stages exhibit a 48 h tolerance to salinities as low as 15 psu with minimal mortality (MANN and HARDING 2003). In this sense, the observed salinity range (14.93 to 28.24 psu) in which *R. venosa* was collected appears to fall within the range of environmental tolerances of the early life-history stages of this invading species.

Assemblage 2 was determined by the co-occurrence of *Z. dufresnei, T. galea,* and *A. beckii.* This group comprised stations with deeper waters and higher salinities. The dominant species of this assemblage, *Z. dufresnei,* (66.67%), was also the most ubiquitous species (36% of total stations). It was the only species common to the three large gastropods associations characterized in this paper. This species has the largest bathymetric range of the studied species in the area. It has been reported from 5 to 10 m (MILSTEIN *et al.,* 1976; NIÓN, 1979) down to 115 m (BUCKUP and THOMÉ, 1962; FABIANO *et al.,* 2000; GIMÉNEZ and PENCHASZADEH, 2003; JUANICÓ and RODRÍGUEZ-MOYANO, 1976; KAISER, 1977; RIESTRA and FABIANO, 2000; WATSON, 1886). According to the strongest influence of subtropical waters, this species has a deeper distribution off the northern portion of the Uruguayan shelf than in the Buenos Aires Province. Our results extend the temperature range (14–17 °C) reported by KAISER (1977). Its presence in the low-salinity waters of the Río de la Plata estuary seems to be circumstantial, as may be inferred by the small size (mean size = 10 cm) of the specimens collected at the estuarine area. Small sizes have been also reported by FABIANO *et al.* (2000) in the Piriápolis–Punta del Este area (around 34°55′ S and 55°05′ W, near the coast ~10 m isobath). This area is characterized by marked variations in salinity. FERRARI and PÉREZ (2002) reported ranges between 2.2 and 32.6 psu in Piriápolis and between 5.1 and 32.6 in Punta del Este during a year-round survey. Accordingly, GUERRERO *et al.* (1997b) documented mean bottom values between 2.37 and 30.97 psu for an area close to Piriápolis. This evidence suggests that the small size might be reflecting nonoptimal growing conditions, probably related to osmotic stress.

Assemblage 2 is also defined by the occurrence of *T. galea,* previously mentioned for the Uruguayan shelf for depths ranging from 35 to 150 m (CARCELLES, 1953; DOELLO-JURADO, 1938; JUANICÓ and RODRÍGUEZ-MOYANO, 1976; MATTHEWS *et al.,* 1989; SIMONE, 1995). During 2002, dense banks of this species located around 34°45′ S and 53°35′ W (65–73 m) in the Uruguayan shelf were commercially exploited and detected as reproductively active (FABIANO *et al.,* 2003; SANTANA *et al.,* 2003). In contrast, *A. beckii* was in all cases represented by single specimens, suggesting low population densities within the studied area. It occurred exclusively in deeper stations, associated with stenotherm and stenohaline conditions of the sea bottom. This bathymetric distribution agrees with previous data (JUANICÓ and RODRÍGUEZ-MOYANO, 1976; SCARABINO, 2004), where presence of this species has been reported from 30 to 70 m.

On the other hand, assemblage 3 was the most diverse (5 species) and occurred at intermediate values of depth, salinity, and temperature, in a transition zone from estuarine to oceanic conditions. This may reflect high spatial heterogeneity within this group of stations. The dominant species were *Z. dufresnei* (78.57%) and *P. brasiliana* (78.57%). The latter is the shallower Volutidae occurring in the Uruguayan coast and neighboring areas, reported previously from depths of 5–10 m down to depths of 55–70 m (BUCKUP and THOMÉ, 1962; DEMICHELI and SCARABINO, 2006; ESCOFET *et al.,* 1979; MILSTEIN *et al.,* 1976; NIÓN, 1979; RIESTRA *et al.,* 2000). *P. brasiliana* has been previously reported as widely distributed in the Atlantic coast of Uruguay both on sandy and muddy bottoms (see above references), in Buenos Aires Province, Argentina (BREMEC, 1989; PECHASZADEH and DE MAHIEU, 1976), and Rio Grande do Sul state, Brazil (GIANUCA, 1988). This species displays some tolerance to low salinities, and can live in euryhaline conditions from 16 to 32 psu. However, it is not known if it can achieve reproductive success in the lower fringe of salinity conditions. The likelihood of colonization of the estuarine area may be enhanced by the high dispersal capability of its conspicuous nonattached ovicapsule, which may be dispersed by bottom currents (see PENCHASZADEH and DE MAHIEU, 1976). This assemblage is characterized also by the occurrence of *B. cochlidium,* reported previously as living between 5 and 80 m in sandy and muddy bottoms (CARCELLES and PARODIZ, 1939; ESCOFET *et al.,* 1979; JUANICÓ and RODRÍGUEZ-MOYANO, 1976; MILSTEIN *et al.,* 1976; NIÓN, 1979; SCARABINO *et al.* 2006; WATSON, 1886), which is coincident with the depths (10 to 36 m) reported here.

Finally, though *C. parthenopeum* has one of the widest distributions among benthic molluscs (BEU, 1998), it occurred rarely during the cruise. While not considered in detailed specific accounts of Ranellidae (*e.g.,* BEU, 1998; COELHO *et al.,* 1981), this species has been recorded for the Uruguay coast through shells washed ashore (BARATTINI and URETA, 1961; FIGUEIRAS and SICARDI, 1972) and as living specimens inhabiting on or near mussel beds in 35–50 m water depth (JUANICÓ and RODRÍGUEZ-MOYANO, 1976). *C. parthenopeum* is commonly obtained in the Uruguayan Atlantic coast by coastal fishing trawlers and has been repeatedly collected during fishing surveys (SCARABINO, personal observation). Further, during the present study (station 2), a female was found attached to plastic debris while ovipositioning, which is the first record of this kind in Uruguayan waters. In contrast with *Ranella olearium* (see Scarabino, 2003), the evidence suggest that *C. parthenopeum* is reproductively established on the Uruguayan shelf, which is the southernmost southwestern Atlantic locality of its current distribution. Veliger larvae belonging to this genus display a remarkable tolerance to water temperature; they are found in waters ranging from 23 °C to as low as 13.1 °C in the Northern Hemisphere (SCHELTEMA, 1966).

CONCLUSIONS

We found a spatial segregation of the large gastropods assemblages in three areas: estuarine, low specific richness, dominated by *Rapana venosa,* inshore (10 to 36 m), high specific richness, codominated by *Zidona dufresnei* and *Pachycymbiola brasiliana,* and offshore (21 to 62 m), intermediate specific richness, characterized by *Z. dufresnei.* Direct developers were more ubiquitous than planktotrophic developers in the whole area. On the other hand, the only species that successfully colonized the estuarine area was the exotic and planktotrophic *R. venosa.* This pattern is not coincident with the predictions made based on life-history traits, such as dispersal capabilities, suggesting that generalizations in this respect are complicated and scale and species dependent. We strongly stress the need for long-term quantitative studies of the species studied here, in order to reach a better understanding of its population dynamics. This is of outmost importance given the high interannual ecosystem variability, the socio-economical relevance of the species involved, and the potential anthropogenic impacts (*i.e.,* chemical contamination, fisheries by-catch, etc.) on their populations.

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□ RESUMEN □

Se analizó la distribución y ecología de las asociaciones de grandes gasterópodos en la plataforma continental uruguaya y la zona exterior del estuario del Río de la Plata en profundidades desde 4 hasta 62 m. Se colectaron siete especies, distribuidas en 5 familias: Tonnidae, Ranellidae, Muricidae, Nassariidae y Volutidae. Aunque todas las especies han sido reportadas previamente para el área, se proporciona en este trabajo la primera descripción detallada de su hábitat en términos de profundidad, temperatura y salinidad de fondo. El análisis de agrupamiento realizado con datos biológicos (presencia/ausencia) indicó una segregación espacial de las asociaciones de grandes gasterópodos en tres áreas principales: una zona estuarina, con baja riqueza, dominada por *Rapana venosa,* una zona costera (10 a 36 m), con mayor riqueza, co-dominada por *Zidona dufresnei* y *Pachycymbiola brasiliana* y una zona exterior (21 a 62 m), con riqueza intermedia, caracterizada por *Z. dufresnei.* Los valores medios para las variables ambientales mostraron diferencias significativas entre grupos de estaciones. Las especies de desarrollo directo estuvieron presentes en un mayor número de estaciones que las de desarrollo planctotrófico al considerar toda el área de estudio. Sin embargo, una especie exótica de desarrollo, planctotrófico, *R. venosa,* dominó el área estuarina, sugiriendo que este tipo de desarrollo podría verse favorecido por las condiciones ambientales del estuario. La dominancia de las especies de desarrollo directo en términos de la extensión de su área de distribución no es coincidente con lo esperado de acuerdo a las predicciones basadas en las características de dispersión de ambos tipos de historia de vida, sugiriendo que las generalizaciones a este respecto son complicadas y dependen de la escala espacial considerada, así como de factores biogeográficos y filogenéticos. Se recomienda la realización de estudios cuantitativos a largo plazo de las especies aquí tratadas, con el fin de obtener información acerca de su dinámica poblacional. Esto será de gran relevancia dada la alta variabilidad interanual en las condiciones ambientales en esta área, la relevancia socio-económica de las especies de grandes gasterópodos y los posibles efectos de la actividad humana (*i.e.,* contaminación, captura incidental, *etc.*) sobre sus poblaciones.