Does developmental mode influence distribution patterns of megabenthic gastropods from the Uruguayan shelf?

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SUMMARY: We analyzed the effect of development mode (direct vs. pelagic development) on the spatial structure of a megabenthic gastropod assemblage at a regional scale. The research was carried out along the bathymetric, saline and thermal gradients generated by the interaction between the shelf topography, the freshwater discharge of Río de la Plata and the presence of oceanic water masses. Direct developers dominated in terms of number of species in the entire area and when the inner and outer shelves were considered separately. Species with pelagic development were not observed to be ecologically successful (i.e. have higher abundances) on the inner shelf, which suggests that high environmental variability may not necessarily favour this strategy. No patterns were found in the relative abundance of species in each developmental mode between the inner (i.e. <50 m) and outer shelves. However, richness patterns of the two groups were differentially affected by environmental conditions. Species richness for direct developers was affected by mean annual temperature, bathymetry and longitude while pelagic developers showed evident trends in relation to temperature range and latitude. Further studies are necessary to derive general predictions concerning the relative advantages of each developmental type in relation to these gradients in ecological time scales and local or regional spatial scales.

Keywords: pelagic development, direct development, gastropods, *Adelomelon, Zidona, Fusitriton, Cymatium,* Thorson's rule.

RESUMEN: ¿EL MODO DE DESARROLLO AFECTA LOS PATRONES DE DISTRIBUCIÓN DE LOS GASTERÓPODOS MEGABENTÓNICOS DE LA PLATAFORMA CONTINENTAL URUGUAYA? – Se analizó el efecto del modo de desarrollo (directo vs. pelágico) en la estructura espacial de una asociación de gasterópodos megabentónicos a una escala regional. Esto se hizo a lo largo de los gradientes batimétricos, salinos y de temperatura generados por la interacción entre la topografía de la plataforma, la descarga del Río de la Plata y la presencia de masas de agua oceánicas. La riqueza de especies con desarrollo directo fue mayor, tanto a lo largo de toda el área como al considerar separadamente la plataforma interna y externa. El éxito ecológico (i.e. mayores abundancias) de especies con desarrollo pelágico en la plataforma interna no fue verificado, sugiriendo que una alta variabilidad ambiental no necesariamente puede favorecer a esta estrategia. No se encontraron patrones en la abundancia relativa entre las especies con diferentes modos de desarrollo entre la plataforma interna (i.e. <50 m) y externa. Sin embargo, los patrones de riqueza de especies de ambos grupos fueron afectados en forma diferencial por las condiciones ambientales. La riqueza de especies con desarrollo directo fue afectada por la temperatura anual promedio, la batimetría y la longitud, mientras que la riqueza de especies con desarrollo pelágico exhibió patrones evidentes en relación con el rango de temperatura y la latitud. Se insiste en la necesidad de futuros estudios para derivar predicciones generales en relación con las ventajas relativas de cada modo de desarrollo en relación con gradientes ambientales, en escalas de tiempo ecológicas y escalas espaciales locales o regionales.

Palabras clave: desarrollo pelágico, desarrollo directo, gasterópodos, *Adelomelon, Zidona, Fusitriton, Cymatium,* regla de Thorson.

INTRODUCTION

Developmental modes in marine invertebrates may be classified according to the place of development and trophic mode. In this vein, this scheme recognizes three main categories, namely a free swimming (i.e. pelagic) feeding larvae (planktotrophic development), a pelagic non-feeding larvae (lecithotrophic development) and complete intracapsular development (direct development) without a pelagic phase (see e.g. Thorson, 1950; Mileikovsky, 1971; Havenhand, 2001). However, the feeding status of pelagic larvae is often unknown, and as a consequence developmental type is often mentioned in the bibliography as pelagic or direct.

These distinct developmental strategies affect the distribution patterns of benthic animals across a variety of temporal and spatial scales (Hansen, 1980; Emlet, 1995; Heads, 2005). At a macro-scale, the traditional paradigm claims that polar and deep sea environments are unsuitable for pelagic larvae (see review of the ideas in Pearse and Lockhart, 2004). This apparent macro-evolutionary developmental trend was explained by Thorson (1950) based on ecological mechanisms (i.e. restricted food availability for planktotrophic larvae in colder waters) that lead to environment-dependent selective pressures (see Laptikhovsky, 2006), and was named Thorson's rule. A similar phenomenon (an inverse relationship between egg size and water temperature) was described by Rass (1935, 1986) for marine fishes, who hypothesized that at lower temperatures species-specific egg size tended to increase due to temperature effects on the stages of oogenesis. Another key factor is the disturbance regime, which is invoked to explain either the relative rarity of species with planktonic larvae at polar regions (Palma et al., 2006; Potthoff et al., 2006) or the ecological dominance of broadcasters within Antarctic shallow water invertebrates (Poulin et al., 2002). While the latter phenomenon may be the result of processes operating at ecological timescales that are associated with the advantage of having pelagic larvae under highly disturbed conditions, the former may represent the outcome of species-level selection that occurs over geological and evolutionary time scales (Poulin et al., 2002). This highlights the need to account explicitly for the temporal and spatial scales of the phenomenon under study.

While there are predictions on the relative frequency of pelagic vs. direct developers along latitudinal and bathymetric gradients at a macro-scale (e.g. Mileikovsky, 1971), the effect of developmental trends on assemblage structure at regional or local scales has been much less studied. In the Uruguayan shelf area, there is a conspicuous depth-related temperature gradient from warm shallow waters to the deep, cold, Subantarctic waters (SAW) over the shelf (Sverdrup et al., 1942; Emilsson, 1961; Thomsen, 1962; Guerrero et al., 1997a). In addition, the inner shelf is affected by warm Sub-Tropical waters (STW) and the fluvial discharge of the Río de la Plata, that flows into the Atlantic Ocean with an average discharge of 22.000 $m^3.s^{-1}$ and originates a strong, large-scale salinity gradient (Framiñan and Brown, 1996; Guerrero et al., 1997b). On the shelf, STW mixes with the colder and relatively fresher SAW between the 100-200 m isobath. This convergence defines a frontal zone at depths greater than 50 m (Ortega and Martínez, 2007). A previous analysis determined that there are two major biologically distinct gastropod assemblages in the area: a) an assemblage associated with the area influenced by the freshwater discharge of Río de la Plata and the shallow waters of the inner shelf; and b) an assemblage associated with the marine zone on the outer shelf, which includes Magellanic (Subantarctic) and Subtropical faunas (Carranza et al., 2008a).

Thus, on the Uruguayan shelf, spatial heterogeneity due to the combined effects of depth, salinity and temperature may affect the relative abundances and species richness within each group. Since environmental factors, such as low salinity and low but stable temperatures are important selective agents against planktotrophy (see Poulin et al., 2002), species with pelagic development should be underrepresented in low salinity areas and on the less disturbed outer shelf. If pelagic larvae are favoured under highly disturbed conditions, some ecological dominance of planktotrophy is expected on the inner shelf. Conversely, if poor nutritional conditions for the pelagic larvae favour non-pelagic development in cold water where food is usually scarce, the outer shelf should be dominated by direct developers (Fig. 1). It follows then that richness patterns of the two groups may be differentially affected by environmental conditions. In this context, this paper aims to analyze the relative species abundance within each developmental mode between the inner (i.e. <50 m) and outer shelves and to examine if there are differences in the degree to which present-day conditions (i.e. geographic areas, physical factors) affect the
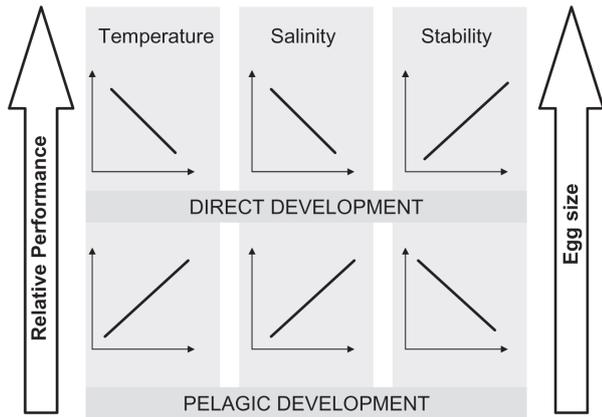
FIG. 1. – Conceptual framework showing the relationship between the relative performance of species that exhibit contrasting developmental modes and environmental variables. Different kinds of species traits are associated with the modelled responses, e.g. while physiological traits can be related to responses to salinity and temperature, dispersal capability and life span can be associated with responses to environmental stability.

spatial distribution of species in each developmental mode.

MATERIAL AND METHODS

Data gathering

Data of occurrence for large gastropods (>5 cm of adult size) were compiled from research surveys, commercial fishing and unpublished and published documents. The data consisted in the presence/absence of each species in particular points. These were obtained from 5 surveys carried out onboard R/V "Aldebaran" and from 2 cruises undertaken onboard commercial fishing vessels (Carranza, 2006; Carranza *et al.*, 2008a, 2008b). The fishing gear used in the research vessel consisted of an Engel type bottom trawl net with a 24 m horizontal opening and a 100 mm stretched mesh in the codends. Data was standardized for a tow time of 30 min. Mean operational depth was recorded for all stations, and when possible, salinity and temperature were also registered. In the commercial trawlers, the gear used was quite similar, but the duration of the tows was, in general, more that 2 hrs. In both cases, the exact location of the stations was determined by a Global Positioning System (GPS). Large gastropods species were identified *in situ*. Voucher material for each one has been deposited at the Museo Nacional de Historia Natural y Antropología (Montevideo). We also gathered additional information from published data that included the complete list of species caught during other trawl surveys and the exact geographic location of the operation (based on data provided in: Olivier and Scarabino, 1972; Kaiser, 1977; Quintero, 1986). All these records added to a total of 18 species sampled at 399 sites between 4 and 800 m depth (Fig. 2). The sampling errors (e.g. underestimation of smaller sizes/species due to mesh size) associated with fishing gear used in the surveys have not been evaluated for large gastropods, but it is considered here to be potentially relevant. Therefore, abundanc-
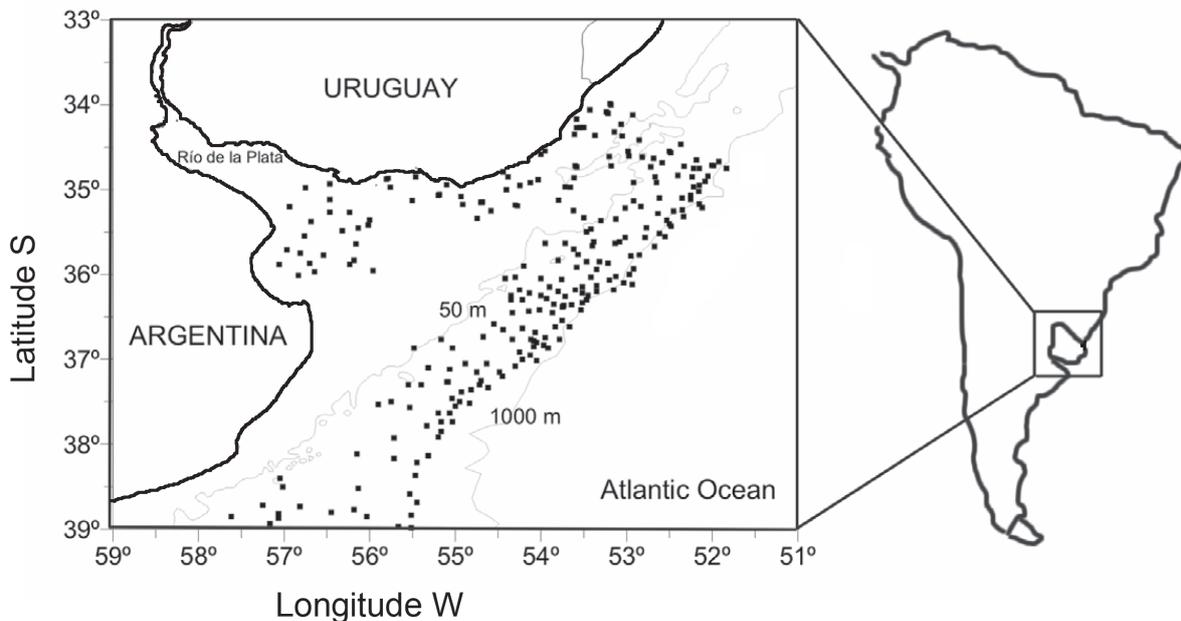

FIG. 2. – Study area showing the location of the sampling sites.

es were not considered in the analysis, although we used species frequency of occurrence as a surrogate for this variable. This measure provides a reasonable estimation of regional abundance and has been well correlated with local individual abundance (Gaston, 2003; Rivadeneira, 2005).

Data analysis

Prior to the analysis, the species were classified as pelagic developers (PD) or direct developers (DD) mainly according to information provided in Gallardo and Penchaszadeh (2001). Developmental trends along the environmental gradients (namely depth, temperature and salinity) were assessed using the complete list of large gastropods (i.e. 18 species), whereas the analysis of frequency of occurrence was restricted to only 16 species sampled with comparable methodologies.

To this end, we considered the inner continental shelf, with depths ranging from 4 to 50 m, and the outer continental shelf and slope, comprising depths between 50 and 800 m, separately. This split was made on the basis of observations that showed that 50% of inner shelf species disappear at or near this isobath (Capítoli and Bemvenuti, 2004) and because, in this way, the shelf is divided into two zones of comparable area. Species frequency of occurrence was measured as the site occupancy, i.e. the proportion of total trawls with effective presence of a species. This was carried out for each sector separately and also for the total data (both sectors together). This approach allowed us to test for the statistical

significance of the differences in frequency of occurrence between the two developmental modes by means of a Mann-Whitney U-Test for independent samples, using the frequencies as the dependent variable and hatching mode as a grouping variable.

A different approach was also used for analyzing the impact of the continuous environmental gradients in the species richness patterns within each group. Presence/absence data for gastropod species were binned in quadrats of 0.5° latitude x 0.5° longitude to match the spatial scale of oceanographic data. An environmental matrix was then constructed using oceanographic data provided by Guerrero *et al.* (1997b) gathered over 30 years. This matrix included means and ranges for annual seabed salinities and temperatures. We characterized the quadrats' bathymetry using the minimum and maximum depths sampled within each quadrat. Sediment features were not included due to the lack of available data at an appropriate spatial scale. However, the study area is dominated by a homogeneous soft bottom, with an increase in mean grain size towards the continental shelf and slope, and presents little consolidated substrata (Correia *et al.*, 1996).

For each quadrat, the total number of species within each developmental mode was obtained. The relationships between the number of species with pelagic and direct development at the quadrat scale and geographical and environmental variables were modelled with a Generalized Additive Model (GAM) (Hastie and Tibshirani, 1990) using a Poisson error model. The GAM approach was chosen due to the nonlinear nature of most relationships. Three

TABLE 1. – Large gastropod species, family, bathymetric range (m) observed at the study area, hatching mode and maximum adult size reported. *Species included in the analysis of frequency of occurrence.

Family	Species	Bathymetric range (m)	Hatching Mode	Maximum adult shell size
Fissurellidae	*Fissurellidea megatrema* d'Orbigny, 1839*	35 to 101	Pelagic	32 mm
Tonnidae	*Tonna galea* (Linnaeus, 1758)*	24 to 143	Pelagic	190 mm
Ranellidae	*Ranella olearium* (Linnaeus, 1758)	150 to 300	Pelagic	220 mm
Ranellidae	*Fusitriton magellanicus* (Röding, 1798)*	100 to 850	Pelagic	115 mm
Ranellidae	*Cymatium parthenopeum* (Salis Marschlins, 1793)*	28 to 50	Pelagic	180 mm
Muricidae	*Chicoreus beauii* (Fischer and Bernardi, 1857)	140 to 500	Pelagic	121 mm
Muricidae	*Trophon acanthodes* Watson, 1882*	90 to 229	Direct	110 mm
Muricidae	*Rapana venosa* (Valenciennes, 1846)*	0 to 18	Pelagic	161 mm
Muricidae	*Stramonita haemastoma* (Linnaeus,1767)	0 to 50	Pelagic	100 mm
Buccinullidae	*Americominella duartei* Klappenbach and Ureta 1972*	145 to 800	Direct	90 mm
Nassaridae	*Buccinanops cochlidium* (Dillwyn, 1817)*	12 to 50	Direct	91 mm
Volutidae	*Adelomelon ancilla* (Solander in Lightfoot, 1786)*	55 to 800	Direct	220 mm
Volutidae	*Adelomelon beckii* (Broderip, 1836)*	24.24 to 100	Direct	492 mm
Volutidae	*Adelomelon riosi* Clench and Turner, 1964*	300 to 650	Direct	375 mm
Volutidae	*Provocator corderoi* Carcelles, 1947*	137 to 400	Direct	79 mm
Volutidae	*Odontocymbiola magellanica* (Gmelin, 1791)*	58 to 230	Direct	195 mm
Volutidae	*Pachycymbiola brasiliana* (Lamarck, 1811)*	12 to 50	Direct	200 mm
Volutidae	*Zidona dufresnei* (Donovan, 1823)*	13 to 115	Direct	270 mm

separate hypotheses were tested: a) species richness within each developmental type can be described with geographic variables only (latitude, longitude and bathymetry); b) it can be described with environmental variables (salinity, temperature); and c) both types of variables are needed to best explain the observed patterns. Differences in the models that best describe species richness patterns can be related to group-specific selective pressures. All analyses were performed using STATISTICA V6.0.

RESULTS

The assembled data consisted of information on 18 large gastropod species, all previously reported for the study area. The taxonomic information, bathymetric ranges, hatching mode and maximum adult size of the studied species is summarized in Table 1. Our results indicated that, in terms of number of species, direct development (10 species) dominated among the megabenthic gastropods on the entire Uruguayan shelf. This pattern is also observed on the outer shelf (8 direct vs. 5 pelagic species), whereas on the inner shelf species richness is very similar between both strategies (6 direct vs. 5 pelagic species).

Frequency of occurrence

Frequency of occurrence was similar between direct and pelagic developers across the whole area and on the outer shelf (Fig. 3A). However, a slightly higher frequency was found for direct developers on the inner shelf, but no statistically significant differences were found when the frequencies between pelagic and direct developers were compared in the entire area (Mann-Whitney U Test; $z = 0.16$, $p > 0.05$) or within the inner ($z = 1.73$, $p > 0.05$) or outer shelf alone ($z = -0.41$, $p > 0.05$) (Fig. 3A). Among the direct developers, two species (*P. brasiliana* and *B. cochlidium*) were present exclusively in the inner shelf (0-50 m) areas and 6 species (*Americominella duartei*, *A. ancilla*, *O. magellanica*, *P. corderoi*, *A. riosi* and *T. acanthodes*) were found in both areas, but all species occurred more frequently in the shallower stations. Among the pelagic developers, *Cymatium parthenopeum* and the exotic *R. venosa* only occurred in shallow waters, whereas *F. magellanicus* was exclusive to the deeper stations. Two species occurred in both areas: *F. megatrema* showed a pref-
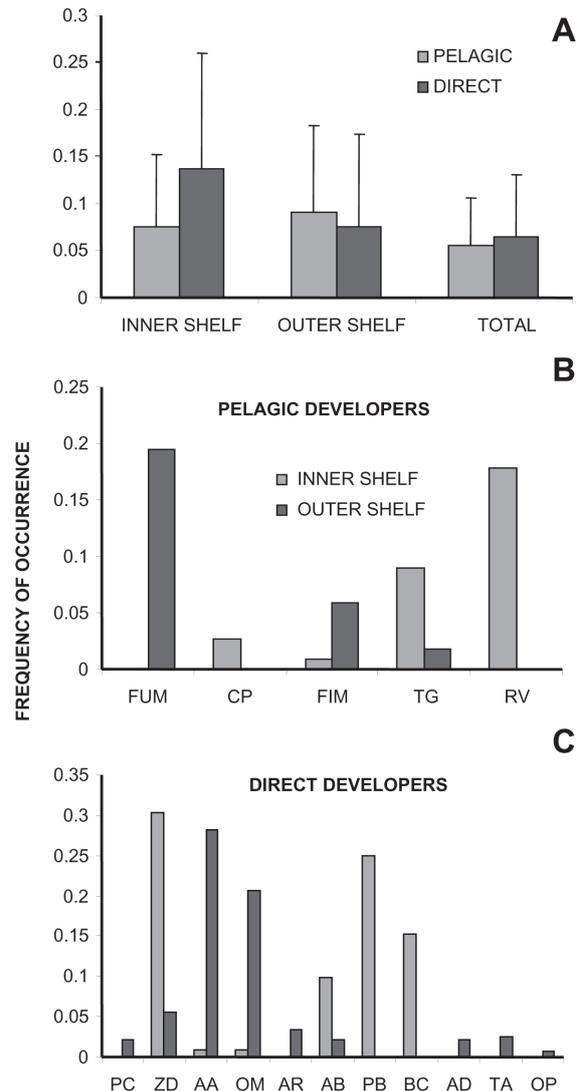

FIG. 3. – Proportion of stations occupied (frequency of occurrence) by the pelagic and direct developing gastropods analyzed here. A: Mean frequencies (+/- standard deviation) of occurrence for species within each development type discriminated by area (inner shelf, depth<50m and outer shelf, depth >50m); B: Observed frequencies for direct developers compared in the two areas; C: Observed frequencies for pelagic developers compared in the two areas. Species abbreviations: AA=*Adelomelon ancilla*; AB=*Adelomelon beckii*; AR=*Adelomelon riosi*; PC=*Provocator corderoi*; OM=*Odontocymbiola magellanica*; OP=*Odontocymvbiola pescalia*; PB=*Pachycymbiola brasiliana*; ZD=*Zidona dufresnei*; BC=*Buccinannops cochlidium*; AD=*Americominella duartei*; CP=*Cymatium parthenopeum*; FIM=*Fissurellidea megatrema*; FUM=*Fusitriton magellanicus*; RV=*Rapana venosa*; TA=*Trophon acanthodes*; TG=*Tonna galea*.

erence for deeper areas, whereas *T. galea* showed the inverse pattern (Figs. 3B and 3C).

Environmental trends

For the direct developers, the GAM explained between 58.88 and 77.15% of the deviance in quadrat

TABLE 2. – GAM models fitted to species richness for direct and pelagic developers, species richness and geographic conditions only (bathymetry=Z, longitude and latitude: geographic model), environmental conditions only (MEANS= mean annual bottom salinity; MEANT= mean annual bottom temperature; RS= salinity range; RT= temperature range; environmental model) and a mixed model (including both types of variables), Poisson error model.

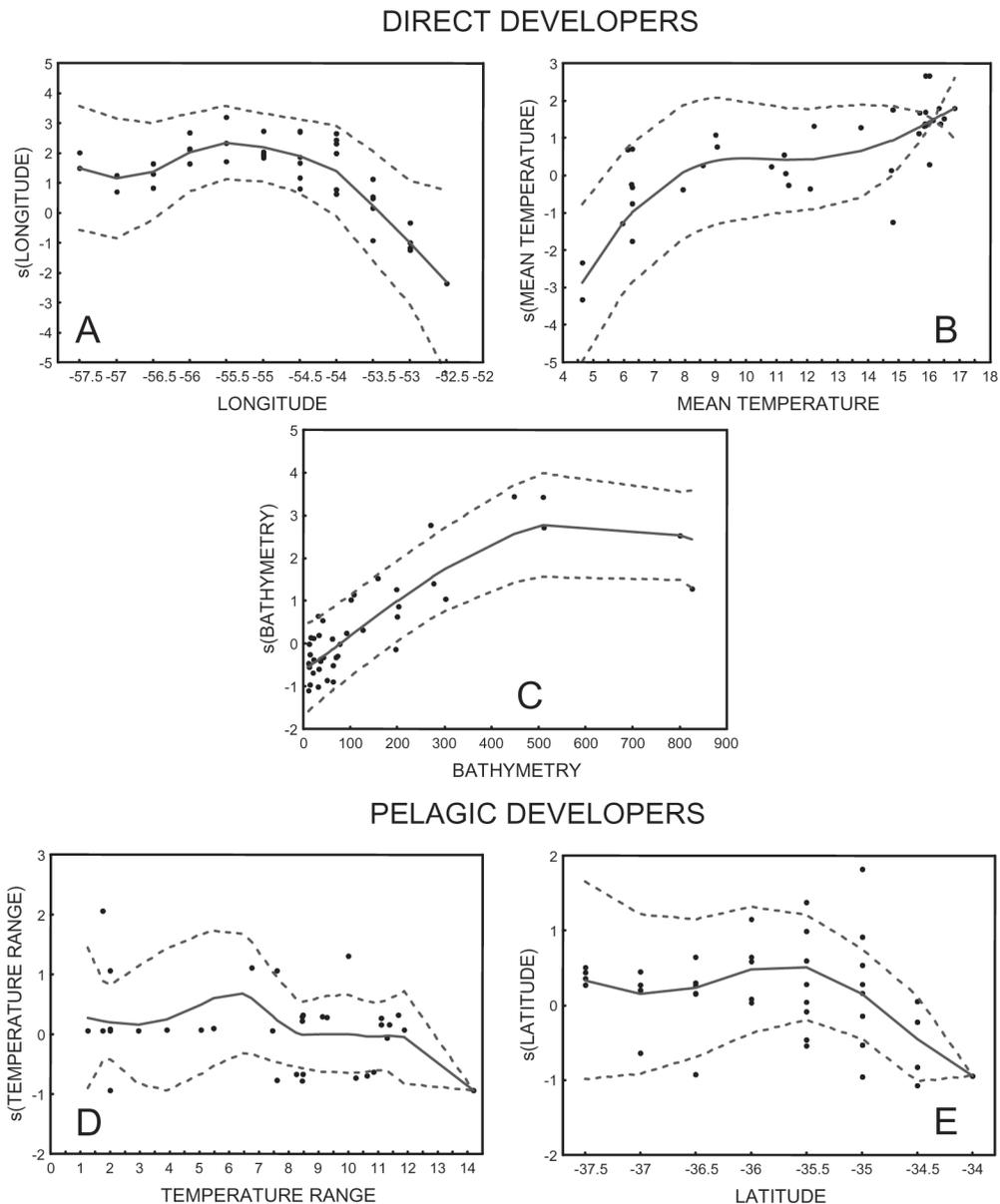|	LAT	LONG	Z	MEANS	MEANT	RS	RT	R2
DIRECT DEVELOPERS								
Mixed	0.847	**P<0.01**	**P<0.01**	0.867	**P<0.01**	0.559	0.988	77.156
Geographic	0.409	**P<0.01**	**P<0.01**					72.901
Environmental				0.808	**P<0.05**	0.375	0.992	58.885
PELAGIC DEVELOPERS								
Environmental			0.751	0.851	0.819	**P<0.01**	25.191	
Geographic	**P<0.01**	0.647	0.985					24.232
Mixed	0.555	0.965	0.935	0.885	0.955	0.767	0.822	13.657

FIG. 4. – Results of the Generalized Additive Model showing the relationship (solid line) between quadrat species richness and meaningful predictors. Dashed lines indicate the 95% confidence interval for the estimated curve.

species richness, while pseudo-R^2 for the models explaining pelagic species richness ranged from 13.66 to 25.19 (Table 2). The best model for direct developers was the mixed model, which contained both geographical and environmental variables, while the environmental and geographic models explained the same level of variation in species richness for the pelagic developers. However, in most cases not all variables considered in the analysis were significant (Table 2). Longitude, bathymetry and mean temperature entered in the best model for direct developers (Fig. 4A-C), while only temperature range and latitude entered in the model for pelagic developers (Fig. 4D and 4E, Table 2). When the effects of the other variables were removed, species richness for direct developers was highest around 55º30'W latitude, and increased linearly with depth until 500 m depth. Mean temperature also showed a positive correlation with species richness for direct developers. Species richness of pelagic developers showed a local maximum at intermediate temperature ranges (6-7ºC), and was highest around 36º to 36º30'S latitude.

DISCUSSION

The results highlighted the evolutionary success of direct developers in this area. The dominance of direct developers on the Atlantic coast of South America has been related to the prevalence of near-continuous soft-bottom habitats (Gallardo and Penchaszadeh, 2001), but the underlying ecological mechanisms have not been clearly stated.

Although the relative contribution of pre- vs. post-settlement processes to the distribution patterns is far from understood, post-settlement processes (predation) may affect the comparatively small juveniles of pelagic developers in unfavourable habitats other than rocky bottoms. Other possible explanations for the apparent dominance of direct developers includes: 1) comparatively low abundances and subsequently low capability of species detection for pelagic developers; 2) the existence of metapopulations of species with pelagic development (*C. beauii, R. olearium*; Scarabino, 2003), with potentially high temporal variability in presence-absence patterns (further, all pelagic developers studied here present their distribution limits in this area); and 3) a sampling bias associated with the preference for hard substrata observed in most pelagic developers. Accordingly, most of the pelagic developers herein studied seem to be associated with scattered hard substrata (Scarabino, 2003) or biogenic structures like mussel beds (Juanicó and Rodríguez-Moyano, 1976). This may further lead to biases in species detection because bottom trawls (the major source of information for this study) are not performed in rocky areas due to the obvious risk of gear damage.

In general, species richness within each developmental type cannot be described with geographic variables alone, and the inclusion of both geographic and environmental variables was needed to build significant models for direct developers. The trend predicted by Thorson (an increasing number of direct developers with depth) for bathymetric patterns in species richness of direct developers was supported by our data only when the effects of other variables were removed. Species richness for direct developers increased with depth until 500 m, the rest of the gradient showed less variation in this variable. In contrast, at least in the bathymetric range (0 to 800 m) in which the observations were made, an effect of depth on the relative abundance of species with pelagic development was not detected.

Mean annual temperature also showed a positive effect on the species richness of direct developers, which contrasted with the expected inverse relationship between egg size and water temperature. The question of whether selection for larger egg size and/or non-pelagic development in the deeper, colder waters of the continental shelf and slope took place in the Atlantic temperate gastropod fauna should be further tested with additional species. However, data from Antarctic echinoderms (Pearse *et al.*, 1991), deep sea gastropods (Rex and Waren, 1982) and other invertebrates (Gage and Tyler, 1991) has challenged the validity of this pattern across different taxa, which suggests that what changes is the balance between feeding and non-feeding pelagic larvae.

The positive effect of mean annual temperature on direct developers may point out the importance of this factor in determining higher species richness at quadrat scale. In contrast, variability in temperature at this scale was shown to affect the species richness of pelagic developers, although they were unaffected by mean annual temperature. Unpredictability in environmental conditions can thus be associated with the relatively low species richness in areas that exhibit high temporal variability. It seems likely that direct development buffers the effect of a shifting environment, so that direct developers are successful in recruitment (and thus prevalent).

However, surprisingly, salinity was not found to be correlated with species richness for either of the two groups. Native direct developers tended to be distributed along the entire salinity gradient determined by the freshwater discharge of Río de la Plata, with two species (*P. brasiliana* and *B. cochlidium*) commonly occurring in the estuarine area. This can be explained by the ability of the egg capsules to protect against low-salinity (Pechenik, 1982). Conversely, a greater susceptibility to environmental stresses and mismatches between larval and juvenile physiological tolerances have been suggested as possible disadvantages for planktonic larvae (Pechenik, 1999). However, observations from the estuaries of the Atlantic coast of the United States indicated that the larval stages of *R. venosa* are capable of supporting salinities as low as 15 with minimal mortality. This has been proposed to be the dominant response that controls the potential dispersal range of the species (Mann and Harding, 2003). *R. venosa* is an exotic, invading species, that recently colonized the estuarine realm of the Río de la Plata (Scarabino *et al.*, 1999; Pastorino *et al.*, 2000; Carranza and Rodríguez, 2007; Carranza *et al.*, 2008b). Therefore, we excluded this species when the relative success of each developmental strategy was assessed along the environmental gradients.

CONCLUSIONS

Direct developers dominated in terms of number of species in the entire area and when the inner and outer shelves were considered separately. No patterns were found in frequency of occurrence for species within each developmental mode between the inner (i.e. <50 m) and outer shelves. However, richness patterns of the two groups were differentially affected by environmental conditions. Further studies are needed to derive general predictions of the relative advantages of each developmental type in relation to these gradients in ecological time scales and local or regional spatial scales. These studies should encompass the broadest possible range of gastropod taxonomic diversity to avoid phyletic constraints, and provide a clearer picture on the ecological mechanisms responsible for generating the patterns. All this evidence suggests that caution should be taken when downscaling downscalling the predictions for macro-scale spatial gradients to a regional scale.

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