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Seasonal Vertical Distribution of the Intertidal Macroinfauna in an Estuary of South-central Chile

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Seasonal sampling of sediments (May 1988–May 1989), carried out at two intertidal areas of the Queule River Estuary, was used to analyse the vertical distribution of the macroinfauna and sedimentological characteristics. In all seasons, the substratum characteristics of both areas showed small differences between 0 and 12 cm depth. The macroinfauna of both areas showed a clear stratification with the highest abundances at the superficial layer of sediment (0–3 cm). No spatial partitioning among the species was evident. It was concluded that the substratum characteristics were not a primary factor in determining the stratification of the macroinfauna. However, some physical factors may well limit the burrowing capabilities of the species (e.g. the discontinuity between the oxidized and reduced sediments), as well as biological factors such as body size (particularly that of the juveniles) and responses against epibenthic predation by burrowing to deeper sediments. Some of these factors would probably better explain the vertical distribution of the intertidal macroinfauna in the Queule River Estuary. © 1996 Academic Press Limited

Introduction

Several sediment characteristics limit the vertical distribution of the macroinfauna. Factors such as compactness (Meadows & Tait, 1989), water content and texture of sediments (Johnson, 1977; Rhoads & Young, 1970) change significantly with substratum depth. For example, Rhoads and Young (1970) found differences of up to three orders of magnitude between the water content of superficial *vs.* deeper sediments (5 cm depth) on the muddy substratum at Buzzard's Bay, U.S.A. These variations are not independent of bioturbation produced by burrowing organisms in the substratum (Brenchley, 1981; Brey, 1991; Posey *et al.*, 1991). These organisms can deepen the oxidized layer of the sediments (Hines *et al.*, 1990) and mix their nutrient content (Posey, 1986; Rice *et al.*, 1986). In turn, these organisms affect the vertical distribution of other infaunal organisms (e.g. Reise, 1983).

Biological interactions have been also implicated in the vertical stratification shown by the macroinfauna. Zwarts (1986) and Haddon *et al.* (1987), amongst others, have identified escape strategies by burrowing activity of infaunal organisms (bivalves) against

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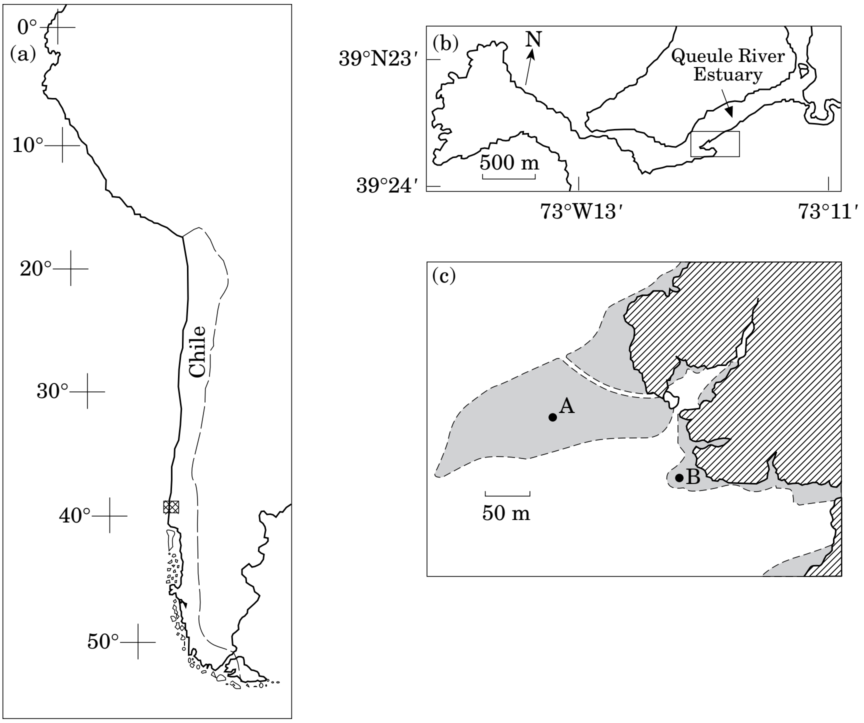

Figure 1. (a) Outline of Chile. The general location of Queule River Estuary is indicated by the black square. (b) Outline of Queule River Estuary. The location of the study zone at the middle reach of the Estuary is indicated by the box. (c) Outline of the study zone with the locations of Areas A (sand) and B (muddy-sand). Stippled area, tidal flats; hatched area, salt marsh; – – –, low tide level.

epibenthic predators. Peterson (1977), Whitlatch (1980) and Grant (1981), have reported vertical partitioning in muddy and sandy habitats, suggesting that separation reduces potential competition.

Turner (1984), Jaramillo *et al.* (1984) and Bertrán (1989) have identified tidal and vertical gradients in the texture and quality of sediments in intertidal estuarine flats of South-central Chile. However, those findings are the results of snapshot studies in which the eventual effect of seasonality has not been accounted for. Otherwise, this heterogeneity suggests that the intertidal zone is affected by different hydrodynamic regimes, which can explain in part the distribution of the macroinfauna (Quijón & Jaramillo, 1993). This study provides seasonal data for the vertical distribution of substratum characteristics and the abundance of macroinfaunal species. The authors sampled in sandy and muddy-sand intertidal areas, seeking to characterize a complete range of variability in the vertical distribution of the sediment and species.

Material and methods

Study area

The tidal flats located in the middle reach of the Queule River Estuary (39°41′S, 73°13′W. Figure 1) cover an approximate area of 10 ha. The maximum elevation of the flats is about 40–50 cm above low tide level.

Sampling and data analysis

During May 1988–May 1989, sediment samples were collected seasonally from sandy ($n=3$) and muddy-sand ($n=3$) substrata; Areas A and B, respectively (Figure 1). The samples for sedimentological and faunistic analysis were collected by using plastic cylinders (1·7 and 7·5 cm diameter, respectively) buried to a depth of 12 cm. The samples were divided into four strata, each of 3 cm. The compactness of the sediment was measured at 0,3,6,9 and 12 cm depth in the bottom. Compactness was measured as penetrability, by dropping a 18·6-g metal rod (15 cm long, 0·6 cm diameter) down a 70 cm tube and reading the depth of penetration. Compactness values reported here are the averages of the readings in the top and lower limits of each strata.

The water and organic matter contents of the sediments were determined as the loss in weight following drying in an oven (80 °C, 72 h) and after combustion (550 °C, 4 h). Textural analyses were carried out to determine percentages of gravel (particles >2000 μ), and aggregates (63–2000 μ) and mud (<63 μ) (Anderson *et al.*, 1981). The samples for the faunistic analyses were sieved with a 0·5-mm mesh and the residue was preserved in 10% formaldehyde to laboratory sorting.

One way analysis of variance (Sokal & Rohlf, 1969) was used for comparisons of sedimentological characteristics and macroinfaunal abundances among areas and sediment strata. Percentage data were transformed by the expression arc sin (n) and the abundance values by $\log_{10}(n+1)$. If the analyses of variance indicated significant differences ($P<0{\cdot}05$) among means, these were compared using the *a posteriori* Tukey-Kramer multiple comparison test (see Stoline, 1981). When the values did not show a normal distribution, non-parametric analyses (Kruskal–Wallis ANOVA) (Sokal & Rohlf, 1969) were used.

Results

The substratum

All the sediment characteristics were significantly different between areas ($P<0{\cdot}05$). The stratified analysis of these characteristics in the sandy area (Figures 2 and 3) generally showed little change between 0 and 12 cm depth ($P>0{\cdot}05$). A similar situation was observed in the muddy-sand area in most of the estimates of water and organic matter contents ($P>0{\cdot}05$). However, the largest variations in penetrability, mud content and some of the water contents were observed in this area. During May 1988 and February 1989, for example, the surface penetrability of the muddy-sand area was more than twice as high as the estimate in the third and fourth strata, respectively. Likewise, in Autumn 1988, the mud content was three times higher at the surface than in the fourth stratum of the sediment ($P<0{\cdot}05$, Figures 2 and 3). The temporal variability in the sediment properties and in the stratification of these characteristics was minimal (Figures 2 and 3).

The macroinfauna

The total macroinfaunal abundances were higher in the muddy-sand area (295–563 ind. 38·5 cm^{-2}) than in the sandy area (242–284 ind. 38·5 cm^{-2}). The highest abundances were always observed in the surface sediments (0–3 cm depth), with values of up to 259 and 520 ind. 38·5 cm^{-2}, in the sandy and muddy-sand areas, respectively (Figure 4). These values include up to 65·2% of the specimens collected in the sandy sediments and 98·2% of those collected in the muddy-sand sediments. Throughout the entire study

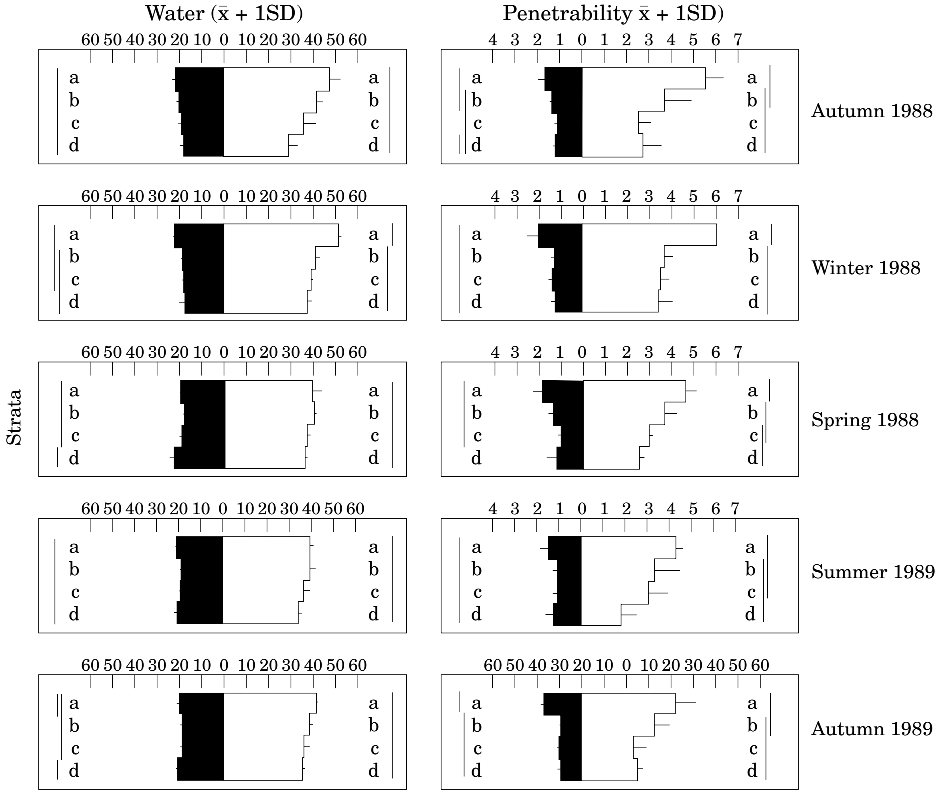

Figure 2. Vertical distribution of the water content (%) and penetrability (cm) in the sandy (solid) and muddy-sand (open) areas. Vertical lines link strata with similar characteristics ($P>0\cdot05$). These strata were: a, 0–3 cm; b, 3–6 cm; c, 6–9 cm; d, 9–12 cm.

period, abundance below 3 cm was proportionately higher in the sandy substratum ($P<0\cdot05$). This abundance varied with time, with the highest percentage of specimens below 3 cm during the winter (25·7–34·8% in the sandy area), and the lowest during the summer (2·2–11·6% in the muddy-sand area).

The numerically dominant species were the polychaetes *Prionospio* (*Minuspio*) *patagonica* Augener and *Capitella capitata* Fauvel. These species, as well as the worm *Perinereis gualpensis* Jeldes, the ostracod *Cyprideis beaconensis* Leroy, the amphipod *Paracorophium hartmannorum* Andrés and the bivalve *Kingiella chilenica* Soot Ryen, were collected in both areas. The polychaete *Boccardia polybranchia* (Haswell) was collected only in sandy sediments.

All the species, with the exception of the deposit-feeder *B. polybranchia*, had highest abundances between 0 and 3 cm depth ($P<0\cdot05$, Figures 5 and 6). However, during various periods of the year, the tube-builder *P.* (*M.*) *patagonica*, the deposit-feeder *C. capitata* and the omnivorous *P. gualpensis* reached depths greater than 3 cm. The occurrence was only significant (i.e. in similar abundances to those in the surface layer) in the sediments of the sandy area. *Cyprideis beaconensis, P. hartmannorum* and *K. chilenica* did not reach depths greater than 3 cm, or did so in minimal densities, with

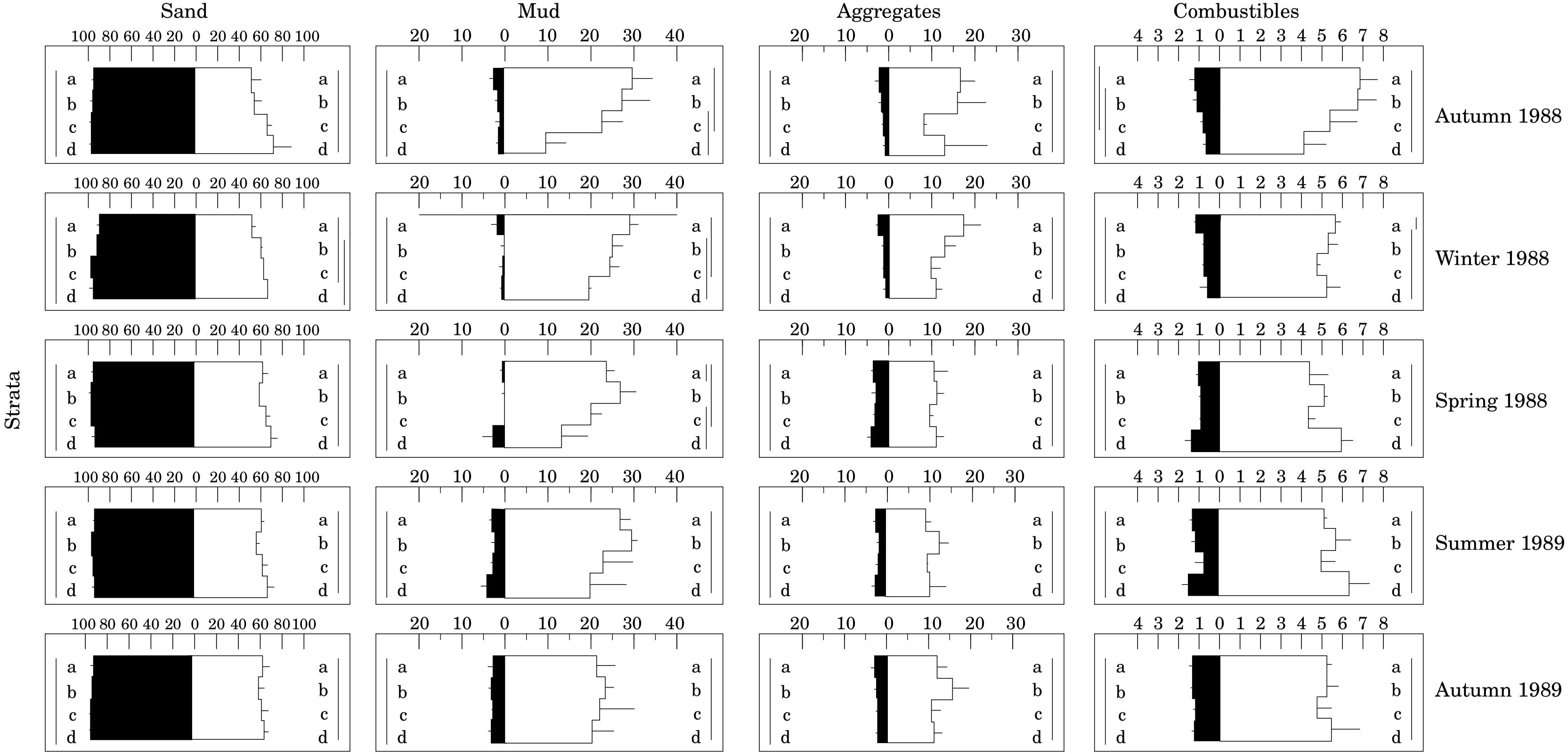

Figure 3. Vertical distribution of textural characteristics and organic matter content [weight (%), x̄+1 SD] in the sandy (solid) and muddy-sand (open) areas. Vertical lines link strata with similar characteristics ($P>0\cdot05$). These strata were: a, 0–3 cm; b, 3–6 cm; c, 6–9 cm; d, 9–12 cm.

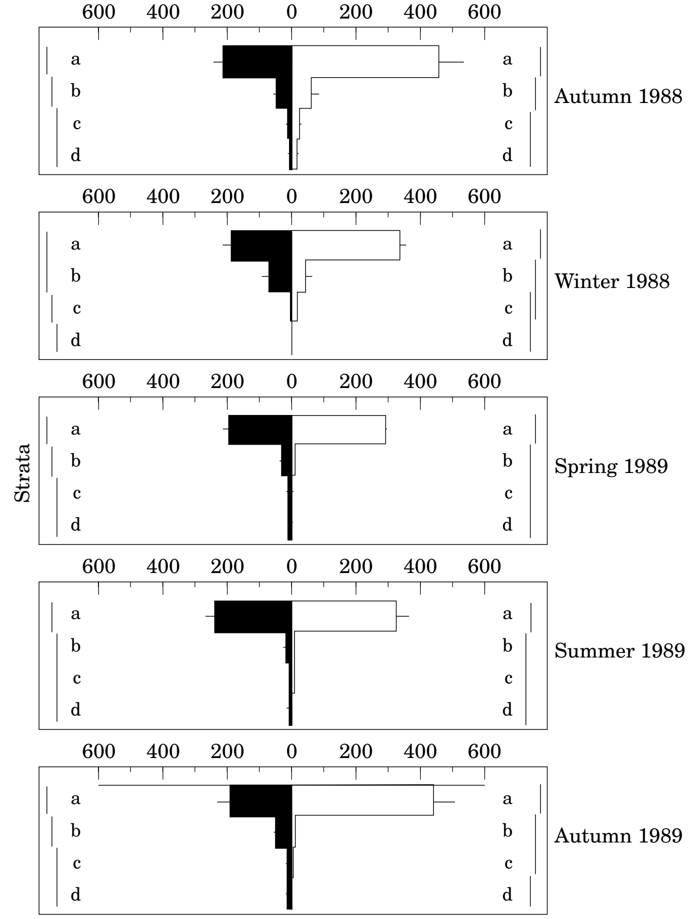

Figure 4. Vertical distribution of total density per 38·5 cm^2 ($\bar{x}$+1 SD) of the macroinfauna in the sandy (solid) and muddy-sand (open) areas. Vertical lines link strata with similar characteristics (P>0·05). These strata were: a, 0–3 cm; b, 3–6 cm; c, 6–9 cm; d, 9–12 cm.

the exception of the suspension-feeder *K. chilenica* in Autumn 1988. *Boccardia polybranchia* showed similar abundances between 0 and 12 cm depth (P>0·05) throughout the study period (Figure 5). Comparing the sandy and muddy-sand areas, no differences in patterns of vertical distribution of populations of a particular species were found.

Discussion

The patterns of vertical distribution of the macroinfauna were similar in areas that can be considered extremes within the range of sedimentological characteristics at the intertidal of Queule River Estuary. Such results suggest that, at the sampling scale used, the relationship between substratum type and this aspect of community structure is barely relevant. When the stratification of the infauna was analysed in relation to characteristics of each area, some degree of co-variability was found in the muddy-sand

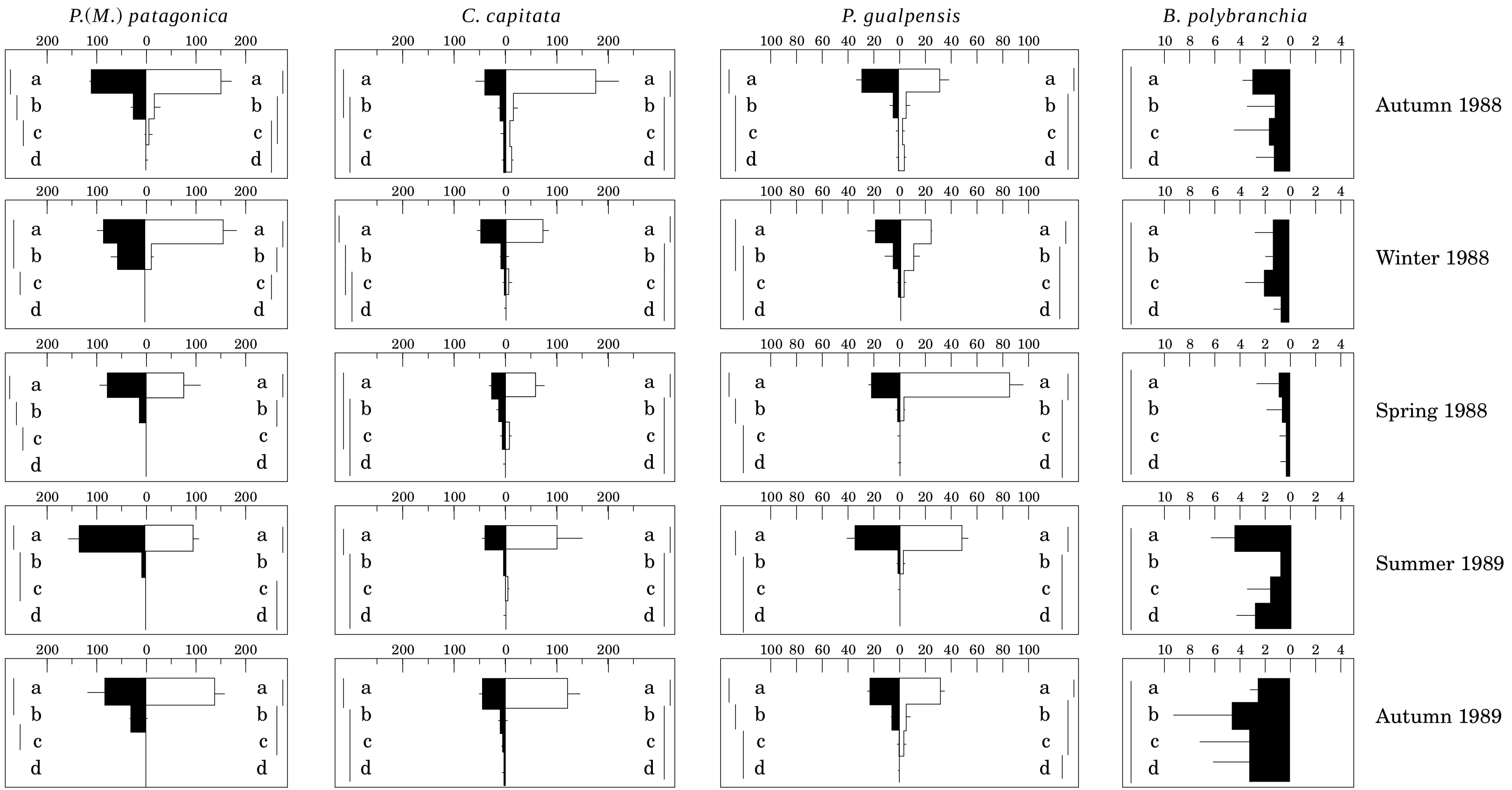

Figure 5. Vertical distribution of the population abundances [density per 38·5 cm^2 ($\bar{x}$+1 SD)] of *Prionospio (Minuspio) patagonica, Capitella capitata, Perinereis gualpensis* and *Boccardia polybranchia* in the sandy (solid) and muddy-sand (open) areas. Vertical lines link strata with similar characteristics (P>0·05). These strata were: a, 0–3 cm; b, 3–6 cm; c, 6–9 cm; d, 9–12 cm.

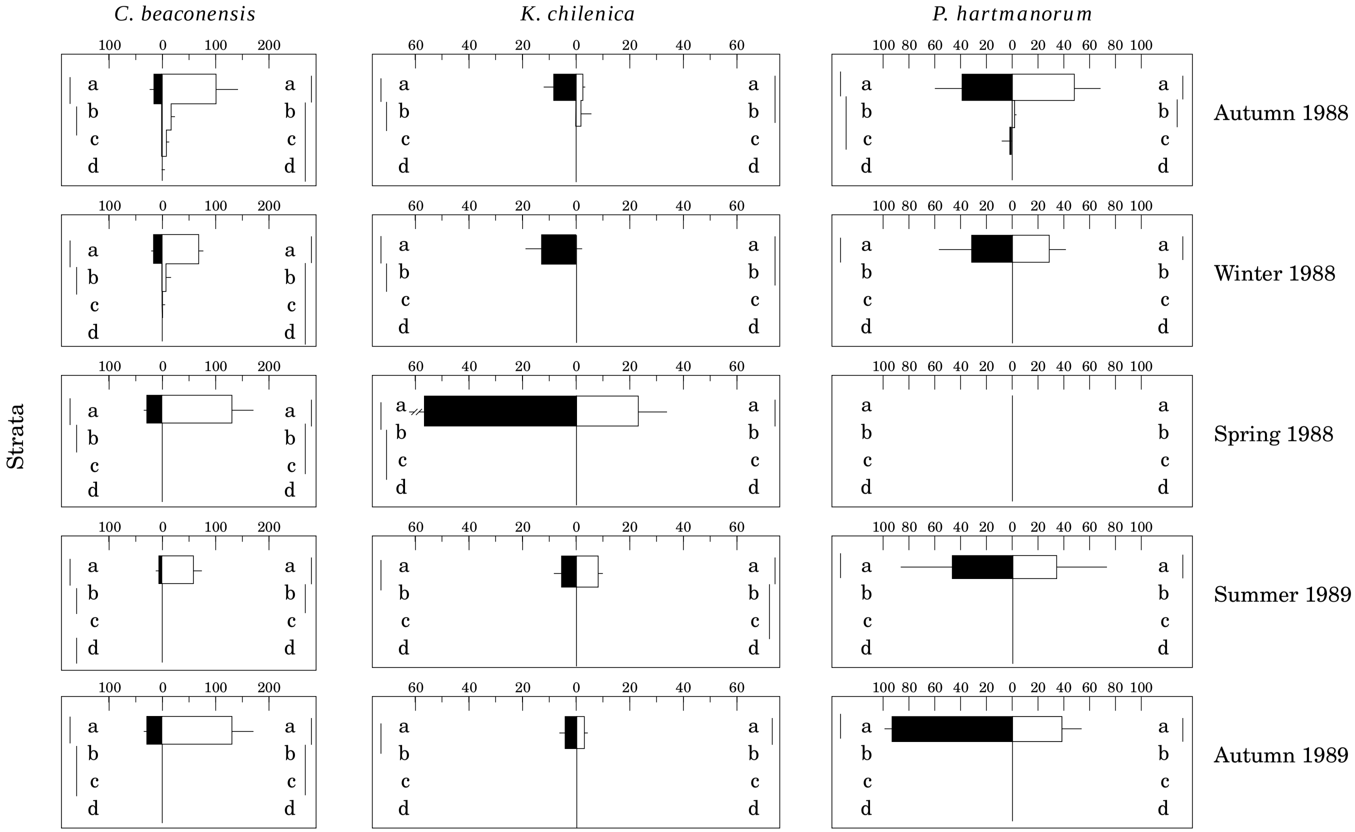

Figure 6. Vertical distribution of the population abundances of *Cyprideis beaconensis, Kingiella chilenica* and *Paracorophium hartmannorum* in the sandy (solid) and muddy-sand (open) areas. Vertical lines link strata with similar characteristics ($P>0{\cdot}05$). These strata were: a, (0–3 cm; b, 3–6 cm; c, 6–9 cm; d, 9–12 cm.

area. However, the latter was not a consistent pattern throughout the year. When the sediment column became physically homogenous, the marked stratification of the infauna was maintained.

The differences observed in the maximum living depth of the macroinfauna when comparing sandy and muddy-sand areas did not appear to be causally related with the parameters studied (i.e. sediment temperature, water content). One factor which could explain these differences is the location of the boundary between the oxidized and reduced layers of the sediment (Revsbech *et al.*, 1980). Thus, the larger grain size, higher porosity and higher oxygen availability could explain the higher abundance (%) of burrowing polychaetes below 3 cm in the sandy area (Risk & Yeo, 1980; Grant, 1981).

Similar physiological limitations could explain the surface distribution of *C. beaconensis, K. chilenica* and *P. hartmannorum* in the muddy-sand sediments (Hines & Comptois, 1985; Roberts *et al.*, 1989), but not in the sandy area. In this case, other factors such as feeding mode (e.g. suspension feeding in *K. chilenica*) and body size could be acting as a limiting factor on the access of these species to the deeper strata (Reading & McGrorty, 1978; Hines & Comptois, 1985).

The organic matter content includes, in some cases, organic material that is not usable by the organisms (macrophytic remains). This could explain the lack of a more significant stratification of nutrients, considering that the nutrient contribution from vegetated and limnetic areas reaches the surface of the flats first (Eisma, 1987). Thus, despite these results, it follows that the greatest quantity of food for suspension- and deposit-feeding organisms is concentrated at the sediment-surface layer. This available food can be represented as phytobenthic and bacterial biomass at the water-sediment interface (Admiraal, 1984). The lack of temporal variability in the vertical distribution of organisms also suggests the need to shift sampling effort towards the surface layer of the sediment. This contains most of the phytobenthic biomass and covers the range over which these diatom species migrate vertically (Admiraal *et al.*, 1984; Paterson, 1986).

The burrower *B. polybranchia* was not limited to the surface layers of the substrata unlike those mentioned earlier (e.g. *C. beaconensis*). Also, the abundances of this species were not concentrated in any particular layer within the sediment column. Thus, the existence of this distinct pattern is not consistent with the concept of vertical partitioning in space, as has been proposed by Peterson (1977), Peterson and Andre (1980), Croker and Hatfield (1980), Whitlatch (1980) and Grant (1981) for other macroinfaunal organisms.

As Josefson (1989) found, there is evidently a lack of spatial segregation between the other macroinfaunal species. These results differ from expectations with respect to possible negative interactions between deposit-feeders *C. capitata* and *P.* (*M.*) *patagonica*, the dominant species in this intertidal area. Turner (1984), analysing the across-intertidal distribution of these species, linked the existence of a spatial segregation in the ranges of distribution to a possible competitive interaction between them. Finally, these data do not exclude the possible existence of patterns of vertical distribution among conspecifics, for example, in the case of *B. polybranchia*.

The present results show that the highest concentrations of macroinfauna on the surface of the flats occur during the summer period. Quijón and Jaramillo (1993) and Quijón *et al.* (1996), indicate that these summer populations are composed principally of juvenile organisms, which due to their size probably have limited burrowing ability. These findings are relevant in so far as they can explain the lower abundance below 3 cm depth that was shown by most of the species at this time of year.

In the case of the polychaete *P. gualpensis*, the lower abundance of this species below 3 cm depth during the summer might also result from its interaction with the whimbrel *Numenius phaeopus* Linné (Velázquez, 1987; Venegas, 1992). This species preys preferentially on adults of *P. gualpensis*, which are located primarily below 5 cm depth in the substratum (Velázquez, 1987). Similar responses to predation have been described in other tidal flats (Peterson & Quammen, 1982; Blundon & Kennedy, 1982; Zwarts, 1986; Haddon *et al.*, 1987; Roberts *et al.*, 1989).

The size stratification shown by *P. gualpensis* would be the result of at least two partially independent biological factors (size limits and predation). This study brings these factors to light in conjunction with physical and biological factors which confuse the relationship between macroinfauna distribution and sediment characteristics. Whether this causality can be extended to other species included in the diet of epibenthic organisms is a problem that can be resolved only by experimental means.

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