

Temporal Variability in the Intertidal Macroinfauna in the Queule River Estuary, South-central Chile

Pedro Quijón and Eduardo Jaramillo

Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile

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The surface sediments (0–3 cm) of two intertidal areas of the Queule River estuary (c. 39°S) were sampled monthly to study the seasonal variability of the macroinfauna and its relationship with the variability of water and sediment characteristics. One of the areas had sandy sediments; the other had muddy sand. Temperature and water salinity showed a seasonal trend with the lowest values during winter months. No differences were found in the sediment temperatures between areas but the muddy sand area had higher percentages of mud, aggregates, organic matter and water, as well as higher penetrability values. All but one of the macrobenthos species occurred at both areas and the same taxa dominated both assemblages. Population abundances fluctuated seasonally with higher values during summer–autumn and higher variability at the muddy-sand area. Of the variability in the abundances of the most representative species 28–84% was accounted for by the variability in some of the physical variables. Thus, these results show that macrofaunal assemblages occupying different sedimentological facies in the intertidal zone (sand–muddy sand) do not have major differences in their patterns of seasonality, and suggest that sedimentological characteristics have a limited role in determining community structure in the areas studied.

Introduction

Estuaries are coastal habitats characterized by a high physical heterogeneity in the water column (e.g. salinity) and substrate. Sediment distribution and deposition rates show wide spatial and temporal variability related to different factors, such as degree of shelter from tidal currents and waves of small amplitude (Anderson, 1972), distance to sediment source areas and temporal variability in fluvial discharge (Peterson *et al.*, 1984). The distribution of benthic organisms capable of modifying the physical characteristics of the substrate is also variable (Meadows & Tait, 1989). The patterns of distribution and abundance of the macroinfauna are most often related to this substrate variability (Ishikawa, 1989).

Drowned river valleys or coastal plain estuaries characterize the coast of south-central Chile (35–40°S). Among these, in the Queule and Lingue River estuaries the characteristics and distribution of the sedimentary facies and macroinfaunal communities are well described (Pino & Mulsow, 1983; Rojas, 1983; Bertrán, 1984; Bravo, 1984; Jaramillo *et al.*,

1984, 1985a; Turner, 1984; Richter, 1985). The seasonal variability of subtidal macroinfaunal assemblages living in bottoms subjected to similar water salinities, but characterized by different sediment characteristics, have been studied by Jaramillo *et al.* (1985b). They showed that even though the subtidal muddy-sand sediments of the middle reach of the Queule River estuary had higher macroinfaunal abundances than estimated for sandy sediments, the assemblages of both substrates followed a similar seasonal variability, suggesting that sediment characteristics were not primarily involved in the temporal variability of the macroinfauna.

In contrast to the more extensively studied subtidal estuarine habitats, analyses searching for physical factors controlling community structure of the more stressed intertidal estuarine habitats are rather sparse (but see Tufail *et al.*, 1989). Differences in substrate characteristics in the intertidal zone of the middle reach of the Queule River estuary provided the opportunity to test the hypothesis that macrobenthic assemblages occupying different sedimentological facies do not have differences in their temporal patterns of community structure. To test this hypothesis, we studied a sandy area close to the main flow channel of the estuary and a muddy-sand area over 13 months. The latter area had a higher content of fine particles and was located further away from the flow channel.

Materials and methods

Study zone

The Queule River estuary (39°24'S, 73°13'W) is located in the southern part of Bahía Queule, south-central Chile (Figure 1). The average and maximum depths are close to 3 and 12 m respectively, while the minimum and maximum widths are approximately 50 and 440 m respectively. The tides are semi-diurnal with maximum tidal differences of 1.5 m. The two intertidal areas studied were in a flat (*c.* 10 ha) located in the middle reach of the estuary (approximately 1500 m from the mouth). The origin and granulometry of this flat were studied by Pino and Mulsow (1983) and Turner (1984).

Sampling and analytical procedures

Water salinity and temperature were monitored monthly in the adjacent shallow waters (approximately 0.5 m) of the study zone (Figure 1). Water samples were collected with a Ruttner bottle during high and low tides. Water salinity was determined with a Hydrobios MC5 salinometer, while water temperature was measured with a mercury thermometer accurate to 0.1 °C. Three replicates of sediment were collected monthly (May 1988–May 1989) in each area by inserting plastic cylinders (7 cm id.) to a depth of 3 cm. Sediment aliquots were collected from these samples with a plastic cylinder (1.7 cm id.) for analyses of texture, water and organic matter content.

Textural analyses were carried out to determine percentages of coarse particles (> 1000 µm), sand (63–1000 µm), mud (< 63 µm) and aggregates (Anderson *et al.*, 1981). Water content of sediment samples was estimated as the loss in weight of wet sediment after drying (80 °C for 72 h). The percentage of organic matter was determined as the loss in weight of dried samples after combustion (550 °C, 4 h). Sediment temperatures were measured with a mercury thermometer accurate to 0.1 °C (three readings). Temperatures were read at the surface (approximately 3 mm depth) and at a depth of 3 cm; the values reported here are the averages of these two readings. The penetrability of the sediments was measured by dropping an 18.6 g metal rod (15 cm long, 0.6 cm in diameter) down a 70 cm tube (three replicates) and reading the depth of penetration.

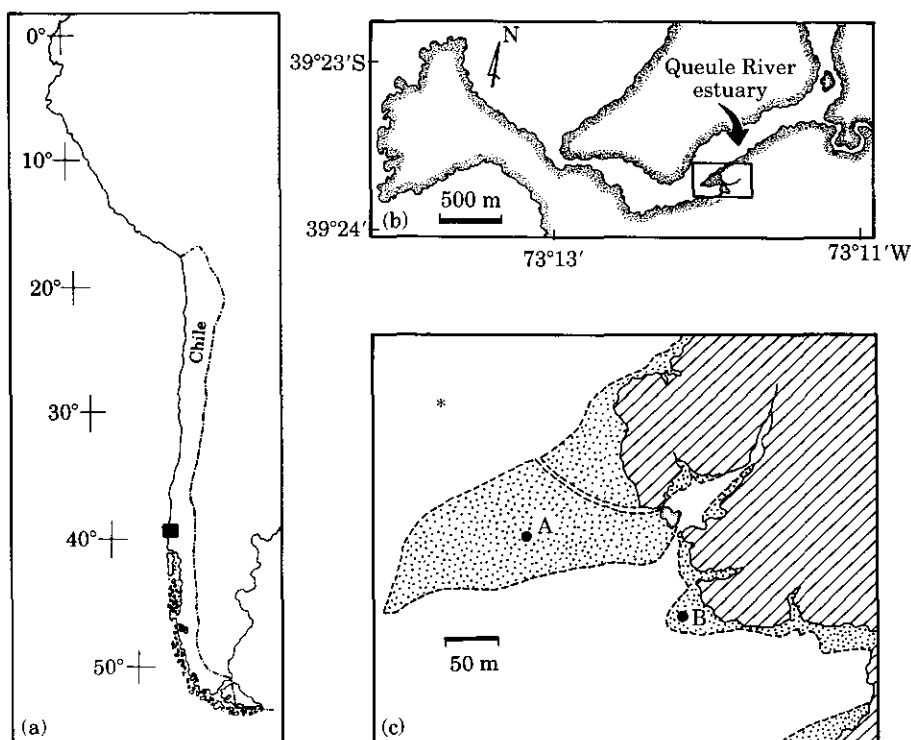


Figure 1. (a) Outline of Chile. The general location of the Queule River estuary is indicated by the black square. (b) Outline of the Queule River estuary. The location of the study zone at the middle reach of the estuary is indicated by the box. (c) Outline of the study zone with the locations of areas A and B. *, Approximate location of the water-sampling station; ▨, salt marsh; ▩, tidal flats; (---), low tide level.

Sediment samples for faunal analyses were sieved through a 0.5 mm mesh sieve and the residue preserved in 10% formaldehyde for sorting in the laboratory. One-way analysis of variance (Sokal & Rohlf, 1969) was used for comparison of sedimentological and macroinfaunal characteristics between areas. Sediment data (i.e. percentages) were analysed as angular transformations, while macroinfaunal abundances were transformed by $\log_{10}(n+1)$. When transformations failed to support the assumptions of parametric analyses, a non-parametric ANOVA (Kruskal–Wallis) was used (Sokal & Rohlf, 1969). The variability in the monthly mean abundances of the macroinfauna was analysed with multiple regression analyses by two approaches: approach A tested the relationships among the abundances and physical characteristics of water and sediments; approach B tested the relationships among these abundances and that of physical characteristics and mean abundances of coexisting species. Temperature and salinity water values from high and low tides were previously averaged. The forward selection technique was used in the multiple regression analysis (Hair *et al.*, 1979).

Results

Physical characteristics

Figure 2 shows the temporal variability of water salinity and temperature in the adjacent shallow waters of the study zone. The highest salinity values (25–29 g l⁻¹) were measured

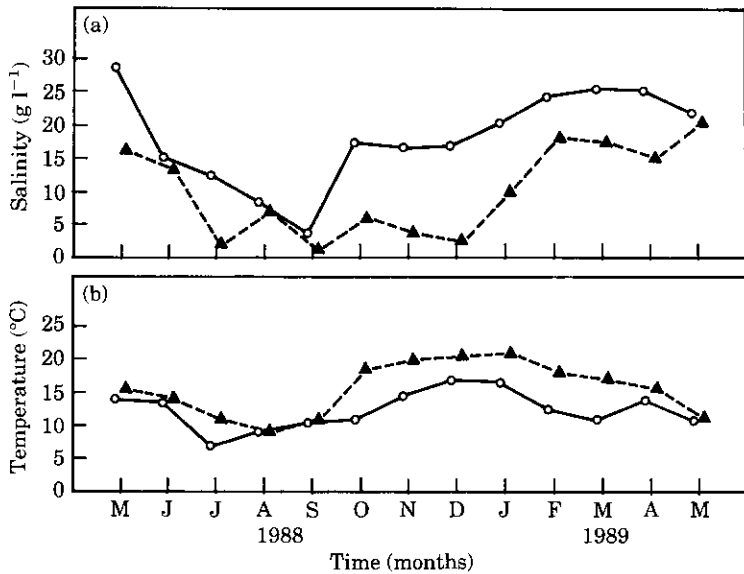


Figure 2. Seasonal variability of (a) salinity and (b) temperature in the shallow waters adjacent to the study zone at high (—○—) and low (—▲—) tides.

during the high tides of summer and autumn months (February–May), while the lowest ($1\text{--}7\text{ g l}^{-1}$) occurred during the low tides of the winter period (July–early September; Figure 2). The highest temperatures ($20\text{--}21\text{ }^{\circ}\text{C}$) were registered during the spring–summer period (November–January), while the lowest ($7\text{--}10\text{ }^{\circ}\text{C}$) were during winter (July–August). The highest temperature values were typically measured during low tides (Figure 2).

The sediments of area B had significantly higher percentages of mud ($15\text{--}35\%$), aggregates ($10\text{--}20\%$) and organic matter ($4\text{--}8\%$) than the sediments of area A (Figure 3). The seasonal variability of sediment temperature was similar at the sandy and muddy-sand areas (Figure 4). The minimum mean values were close to $10\text{ }^{\circ}\text{C}$ (July–September), while the maximum were $19\text{--}24\text{ }^{\circ}\text{C}$ (October–February). The muddy-sand sediments of area B had significantly higher ($P < 0.05$) water content ($40\text{--}50\%$) and penetrability ($4\text{--}7\text{ cm}$) than the sandy sediments of area A. All the physical variables (with exception of sediment temperature) showed little seasonal variability in area A, while in the sediments of area B variability was higher (Figures 3 and 4).

The macroinfauna

Seven species were collected: the polychaetes *Prionospio (Minuspio) patagonica* Augener, *Capitella capitata* Fauvel, *Perinereis gualpensis* Jeldes, and *Boccardia polybranchia* (Haswell), the ostracod *Cyprideis beaconensis* Leroy, the bivalve *Kingiella chilensis* Soot Ryen and the amphipod *Paracorophium hartmannorum* Andrés. Throughout most of the study period, the sandy sediments of area A had seven species, decreasing to six in September (absence of *B. polybranchia*) and November–January (absence of *Paracorophium hartmannorum*), and to five in October when *B. polybranchia* and *P. hartmannorum* were absent simultaneously (cf. Figures 5 and 6). With the exception of the period October–January (absence of *P. hartmannorum*) the muddy-sand sediments of area B had six species. The maximum values of macroinfaunal abundances occurred in the muddy-sand sediments of area B during autumn months (May–June) when values as high as $470\text{--}477$

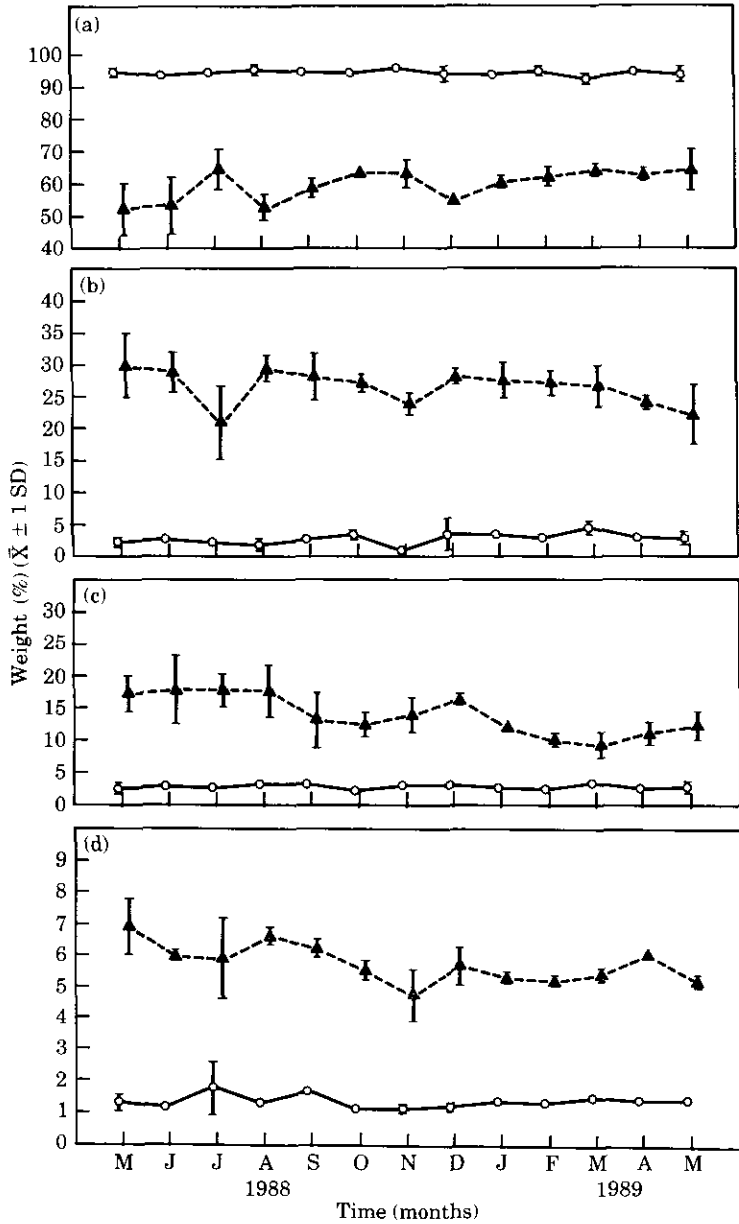


Figure 3. Seasonal variability of the textural characteristics: (a) sand, (b) mud, (c) aggregates and (d) organic matter content in the sandy ($\text{---}\circ\text{---}$) and muddy-sand ($\text{---}\blacktriangle\text{---}$) areas. The means of all variables were significantly different at $P=0.05$ in the monthly between-areas comparisons.

individuals 38.5 cm^{-2} were recorded. At the sandy sediments of area A the maximum abundance values occurred during the summer months (January–March) when values as high as 227–237 individuals 38.5 cm^{-2} were estimated. Thus, the macroinfaunal abundances at the muddy-sand sediments of area B were nearly twice those of area A; the maximum abundances at each area were out of phase by 2–3 months.

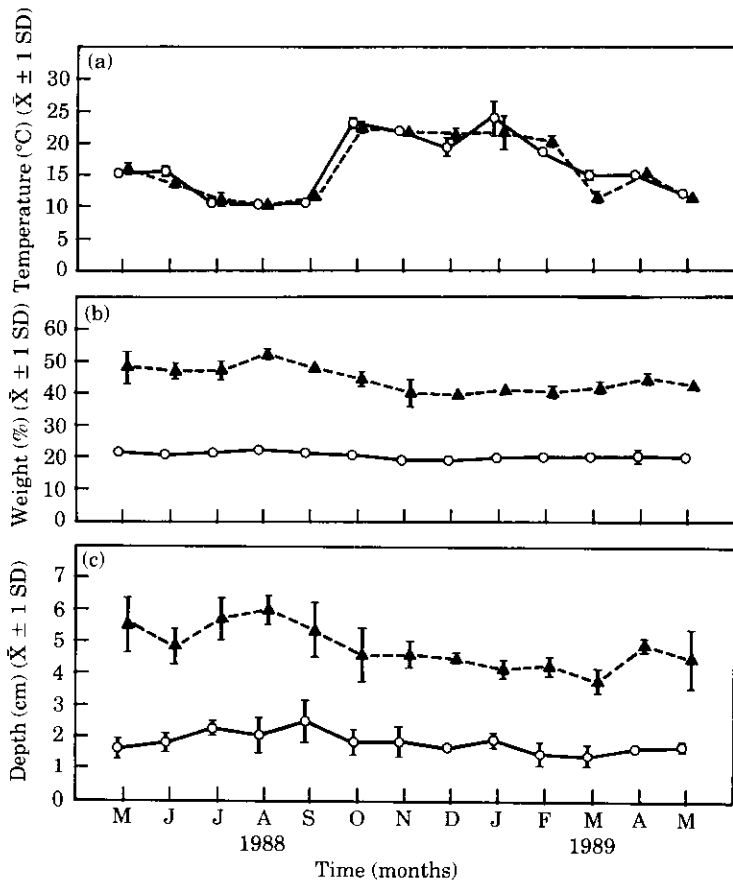


Figure 4. Seasonal variability of (a) temperature, (b) water content and (c) penetrability of the sediments in the sandy (—○—) and muddy-sand (—▲—) areas. The means of water content and penetrability were significantly different at $P=0.05$ in the monthly between-areas comparisons.

Prionospio (Minuspio) patagonica, *Capitella capitata*, *Perinereis gualpensis* and *Cyprideis beaonensis* had higher abundances at the muddy-sand area (Figures 5 and 6). Throughout most of the study period, only the abundances of *Capitella capitata* and *Cyprideis beaonensis* were significantly different ($P < 0.05$) between areas. *Boccardia polybranchia* was absent in the sediments of area B and *K. chilensis* was more abundant at the sandy sediments, whereas *Paracorophium hartmannorum* showed similar abundances in both areas (Figures 5 and 6). *Prionospio (Minuspio) patagonica* and *Capitella capitata* were the most abundant taxa in the sediments of both areas. The former species reached mean abundances as high as 198 and 134 individuals 38.5 cm^{-2} in the muddy-sand and sand sediments respectively, whereas the highest mean abundances estimated for *C. capitata* were 180 and 51 individuals 38.5 cm^{-2} (areas B and A, respectively) (Figure 5). Most of the polychaetes had their main peaks of abundance during summer and autumn; however, the maximum abundance of *Perinereis gualpensis* in the sediments of area B occurred during spring; 2 months before the time in which the population of the sandy area peaked (Figure 5). The maximum abundances of *Cyprideis beaonensis* and *Paracorophium hartmannorum* also occurred during the summer and autumn months, while the abundance of *K. chilensis* peaked during spring (Figure 6).

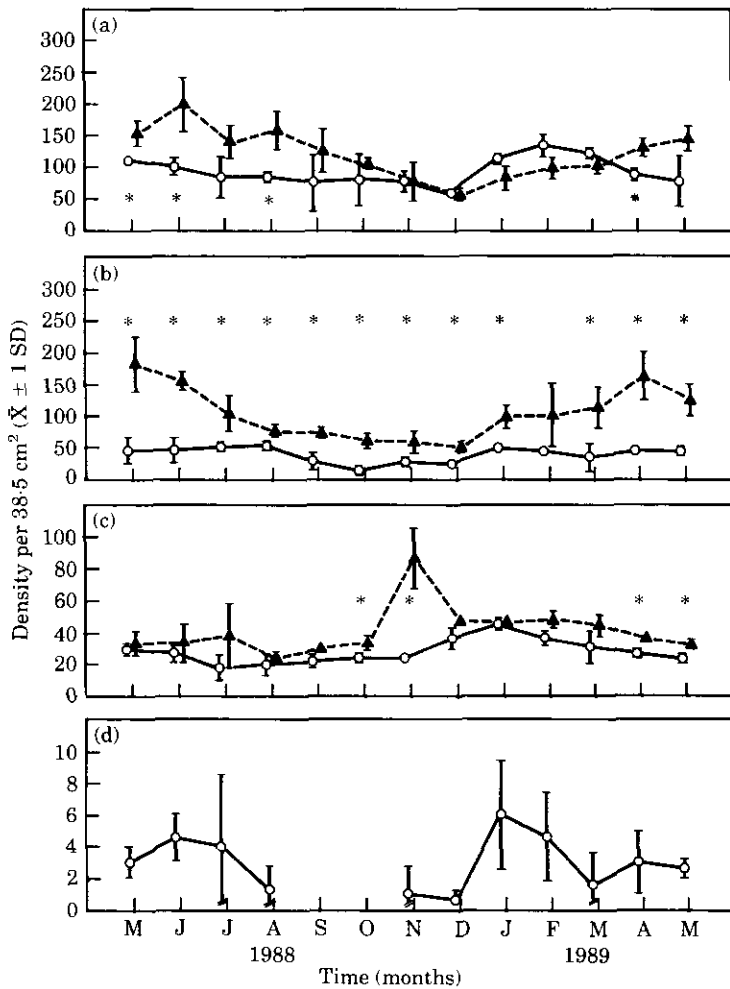


Figure 5. Seasonal variability in the abundances of (a) *Prionospio (Mimuspio) patagonica*, (b) *Capitella capitata*, (c) *Perinereis gualpensis* and (d) *Boccardia polybranchia* in the sandy (—○—) and muddy-sand (—▲—) areas. The asterisks indicate significant differences ($P < 0.05$) between means in the monthly between-areas comparisons.

Tables 1 and 2 show the results of the multiple regression analyses performed on the monthly mean abundances of the sandy and muddy-sand areas, respectively. Temporal variability in the mean abundances of the total macroinfauna in both areas was primarily accounted for by the temporal variability of water salinity and mean abundances of some individual species. Values of r^2 in approach A indicated that 31, 28, 74 and 31% of the variability in the monthly mean abundances of *Prionospio (M.) patagonica*, *Capitella capitata*, *Perinereis gualpensis* and *Cyprideis beaonensis* respectively in the sandy area were accounted for by the variability in some of the physical variables examined (Table 1). Inclusion of the monthly mean abundances of coexisting species (approach B) resulted in an increase in r^2 only for *P. gualpensis*. The results for the muddy-sand area showed that the temporal variability of the four species was primarily accounted for by the temporal variability of the water content of the sediments and water salinity, and that the values of r^2

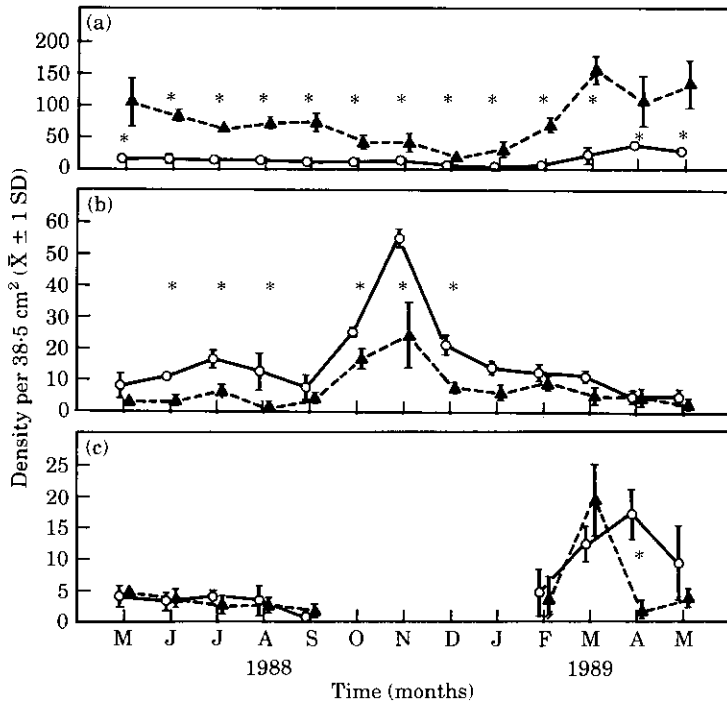


Figure 6. Seasonal variability in the abundances of (a) *Cyprideis beaçonensis*, (b) *Kingiella chilénica* and (c) *Paracorophium hartmannorum* in the sandy (—○—) and muddy-sand (—▲—) areas. The asterisks indicate significant differences ($P < 0.05$) between means in the monthly between-areas comparisons.

were higher (Table 2). Inclusion of monthly mean abundances of coexisting species (approach B) resulted in slight increases of r^2 only for *Prionospio (M.) patagonica* and *Cyprideis beaçonensis*. No inverse relationships were detected among the mean abundances of coexisting species at either area (Tables 1 and 2).

Discussion

The results of this study show that two nearby intertidal areas in the middle reach of the Queule River estuary differed significantly in textural and physical characteristics of their substrates. The differences in textural characteristics (e.g. percentages of sand and mud) may have been related to different dynamics of sediment erosion and deposition. Differences in macroinfaunal abundances (which probably result in differences in biogenic reworking of sediments) may have also been involved in the observed differences in the percentages of aggregates, water content and the values of penetrability. Several studies have shown that benthic organisms are able to modify characteristics of substrates similar to these (see Rhoads & Boyer, 1982 for a review).

Although the two areas studied differed in substrate characteristics, the composition and species ranking of the macroinfauna were similar; only differences in the magnitude of variability and some out of phase temporal variability was detected between areas. The former results suggest that the sedimentological characteristics studied have a limited role in the community structure of the intertidal macroinfauna of the Queule River estuary, an

TABLE 1. Summary of multiple regression analyses with monthly samples ($n = 13$) collected in the sandy area. The values given in this table (other than intercept values and multiple coefficient of determination) are partial regression coefficients or values of each variable in the multiple regression equation. Values in brackets correspond to partial coefficients of determination at each step of the model

Variable	Total macrofauna	<i>Prionospio (Mimuspio) patagonica</i>	<i>Capitella capitata</i>	<i>Perinereis gualpensis</i>	<i>Cypridites beaiconensis</i>
Approach A					
Salinity	0.01 ^a (0.47) ^b	0.01 (0.31)	—	—	—
Temperature	—	—	—	0.03 (0.63)	—
Sediment temperature	—	—	—	—	-0.04 (0.31)
Water	—	—	—	—	—
Penetrability	—	—	—	—	—
Gravel	—	—	—	—	—
Sand	—	—	—	-0.05 (0.74)	—
Mud	—	—	—	—	—
Aggregates	—	—	—	—	—
Combustibles	—	—	0.56 (0.28)	—	—
Intercept	2.16	1.83	0.82	5.82	1.71
Multiple r^2	0.47	0.31	0.28	0.74	0.31
Approach B					
Salinity	—	0.01 (0.31)	—	—	—
Temperature	—	—	—	0.03 (0.63)	—
Sediment temperature	—	—	—	—	-0.04 (0.31)
Water	—	—	—	—	—
Penetrability	-0.06 (0.89)	—	—	—	—
Gravel	—	—	—	—	—
Sand	—	—	—	-0.04 (0.82)	—
Mud	—	—	—	—	—
Aggregates	—	—	—	—	—
Combustibles	—	—	0.56 (0.28)	—	—
<i>Prionospio (Mimuspio) patagonica</i>	0.38 (0.63)	NC	NC	0.35 (0.76)	—
<i>Capitella capitata</i>	0.20 (0.81)	—	—	NC	—
<i>Perinereis gualpensis</i>	—	—	—	NC	—
<i>Cypridites beaiconensis</i>	—	—	—	—	NC
Intercept	1.33	1.83	0.82	4.06	1.71
Multiple r^2	0.89	0.31	0.28	0.82	0.31

—, Variable not entered in the model; NC, do not correspond; ^a, partial regression coefficient; ^b, partial coefficient of determination (r^2).

TABLE 2. Summary of multiple regression analyses with monthly samples ($n = 13$) collected in the muddy-sand area. The values given in this table (other than intercept values and multiple coefficient of determination) are partial regression coefficients or values of each variable in the multiple regression equation. Values in brackets correspond to partial coefficients of determination at each step of the model

Variable	<i>Prionospio (Minuspio)</i>				
	Total macrofauna	<i>patagonica</i>	<i>Capitella capitata</i>	<i>Perinereis gualpensis</i>	<i>Cyprideis beaumontis</i>
Approach A					
Salinity		0.01 (0.74)	0.03 (0.33)	—	0.02 (0.79)
Temperature		—	—	—	—
Sediment temperature		0.06 (0.54)	0.03 (0.68)	—0.03 (0.58)	—0.04 (0.50)
Water	0.01 ^a (0.67) ^b	—	—	—	—
Penetrability	—0.02 (0.33)	—	—	—	—
Gravel	—	—	—	—	—
Sand	—	—	—	—	—
Mud	—	—	—	—	—
Aggregates	—	—	—	—	—
Combustibles	—	—0.15 (0.84)	—	—	—
Intercept	2.65	0.20	0.31	2.81	2.18
Multiple r^2	0.67	0.84	0.68	0.58	0.79
Approach B					
Salinity	—	—	—	—	0.02 (0.66)
Temperature	—	—	—	—	—
Sediment temperature	—	—	—	—	—0.03 (0.82)
Water	—	0.04 (0.54)	—	—0.03 (0.58)	—
Penetrability	—	—	—	—	—
Gravel	—	—	—	—	—
Sand	—	—	—	—	—
Mud	—	—	—	—	—
Aggregates	—	—	—	—	—
Combustibles	—	—0.16 (0.93)	—	—	—
<i>Prionospio (Minuspio) patagonica</i>	—	NC	—	—	—
<i>Capitella capitata</i>	0.36 (0.95)	0.53 (0.80)	NC	—	0.53 (0.50)
<i>Perinereis gualpensis</i>	—	—	—	NC	—
<i>Cyprideis beaumontis</i>	0.28 (0.83)	—	0.49 (0.49)	—	NC
Intercept	1.31	0.07	1.08	2.81	2.18
Multiple r^2	0.95	0.93	0.49	0.58	0.82

—, Variable not entered in the model; NC, do not correspond; ^a, partial regression coefficient; ^b, partial coefficient of determination (r^2).

assertion also supported by the results of the multiple regression analyses which produced low values of r^2 . Thus, these results suggest that the structure of these intertidal assemblages is regulated by other factors; for example, physical characteristics of the water column and interstitial space (e.g. salinity), events related to recruitment (Butman, 1987), biological interactions (see reviews by Peterson, 1979; Wilson, 1990), and/or synergistic effects of these factors. Bertrán (1989) came to similar conclusions after studying the intertidal macroinfauna of the Lingue River estuary (approximately 5 km south of the Queule River estuary).

The abundances of the intertidal macroinfauna of the muddy-sand area were higher than those estimated for the sandy area. Larger amounts of potential food for these deposit-feeder organisms, as shown by the higher amount of organic matter in the sediments, can account for the differences. In a broad spatial study of the intertidal macroinfauna of Queule and Lingue River estuaries, Donoso (1991) showed that the higher abundances of most of the species studied here occurred in those areas with the highest concentrations of organic matter.

The abundances of the macroinfauna in the muddy-sand sediments were more variable than those in the sandy sediments. This could have been related to the major variability shown by the sedimentological parameters in area B. Tufail *et al.* (1989) also observed that in a low energy intertidal environment of Scotland (muddy-sand sediments), a higher variability occurred in sedimentological parameters and abundances of the macroinfauna than that occurring in coarser sediments. However, in contrast to their results, ours show that the values of correlation between environmental parameters and abundances of the macroinfauna were higher in the muddy-sand area than those estimated for the sandy area.

The seasonal trends in the specific abundances of the macroinfauna showed that most of the species peaked during summer and autumn months. Sorting of samples revealed that the abundance peaks in both areas coincided with the main recruitment period of the macroinfauna, a relationship also observed for the subtidal bottoms of the Queule River estuary (Bravo, 1989), as well as for other estuarine areas (Holland, 1985; Bachelet, 1986). The within- and between-areas seasonal variability of the population abundances were not totally in phase. For example, the population abundances of the sandy and muddy-sand areas were significantly correlated ($P < 0.05$) in the cases of *Capitella capitata*, *K. chilensis* and *Cyprideis beaumontensis* and correlation values close to the 0.05 probability level were found for the abundance of the total macroinfauna and that of *Paracorophium hartmannorum*. Whereas no correlations were found between the abundances of *Prionospio (M.) patagonica* and *Perinereis gualpensis* in the between-areas comparisons.

All the species of the macroinfauna studied here are eaten by the benthophagous fishes of the Queule River estuary (Turner, 1988). Thus, we might suggest that the absence of adult individuals (juveniles might have been there but went through the 500 μm sieve) of *Paracorophium hartmannorum* in the sediments of both areas during the warmer months can be accounted for by predation, as it has been suggested and/or shown for estuarine areas of North America, for example by Nelson (1979) and Chester *et al.* (1983). Nelson (1979) showed that amphipods from sea-grass habitats of North Carolina were inversely correlated with the abundance of benthophagous fishes, which in inclusion experiments depleted the amphipod abundances. However, this amphipod is as heavily predated as *Prionospio (M.) patagonica*, but the latter species did not show a comparative spring-summer crash. Migration movements related to competitive interactions (Wilson, 1988; Jensen & Kristensen, 1990) and biogenic disturbance of sediments (DeWitt & Levinton, 1985; Jensen, 1985) have also been invoked to explain temporal and spatial variability in

TABLE 3. Temporal variability in the abundances (individuals 38.5 cm⁻²) of the intertidal macroinfauna at the sandy area of the middle reach of the Queule River estuary

	May 1988–May 1989	May 1984–May 1985
	Annual mean (range)	Annual mean (range)
<i>Prionospio (Minuspio) patagonica</i>	92 (59–134)	122 (36–218)
<i>Capitella capitata</i>	38 (12–51)	17 (1–50)
<i>Perinereis gualpensis</i>	27 (17–45)	28 (11–40)
<i>Boccardia polybranchia</i>	3 (0–6)	3 (0–12)
<i>Paracorophium hartmannorum</i>	5 (0–17)	9 (0–27)
<i>Kingiella chilensis</i>	15 (5–55)	17 (4–69)
<i>Cyprideis beaonensis</i>	14 (2–36)	25 (8–54)
Total macroinfauna	194 (142–235)	221 (123–376)

tidal-flat organisms. We are not aware that *Paracorophium hartmannorum* undertakes seasonal migration as shown by *Gammarus palustris* in Chesapeake Bay (Van Dolah, 1978) and *Corophium volutator* into the upper intertidal of Avenport (Bay of Fundy, Canada) over periods as short as 1 week (Wilson, 1988). Thus, the absence of *P. hartmannorum* from the sediments of both areas during the warmer months remains an enigma.

A review of data collected during 1982 by Turner (1984) along an intertidal transect covering sandy and muddy-sand sediments of the Queule River estuary, as well as unpublished data collected at the sandy area during May 1984–May 1985, indicates that *Perinereis gualpensis* and *B. polybranchia* are the most conservative taxa, while *Capitella capitata*, *Prionospio (M.) patagonica* and *Cyprideis beaonensis* are the species with the largest apparent changes in abundance (Table 3). As shown in several studies, high population variances are common for capitellid and spionid worms (Grassle & Grassle, 1974), a feature also found in the Queule River estuary.

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