

## Seasonal and interannual variability in population abundances of the intertidal macroinfauna of Queule river estuary, south-central Chile

Variabilidad estacional e interanual en las abundancias poblacionales de la macroinfauna intermareal del estuario del río Queule, centro-sur de Chile

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### ABSTRACT

Sediment samples were monthly collected at Queule river estuary (ca. 39° S), south-central Chile, from October 1990 to April 1992, and from September 1995 to November 1997 to study temporal variability in population abundances of the macroinfauna inhabiting sandy and muddy-sand intertidal substrates. Sandy sediments had higher percentages of sand particles and lower percentages of mud particles, biogenic aggregates and total organic matter than muddy-sand sediments. The same macroinfaunal species were found at both sites. That macroinfauna was dominated by polychaetes: the spionid *Prionospio (Minuspio) patagonica* Augener 1923, the capitellid *Capitella* sp. and the nereid *Perinereis gualpensis* Jeldes 1963. Other common organisms were the amphipod *Paracorophium hartmannorum* Andres 1975 and the small bivalve *Kingiella chilena* Soot-Ryen 1959. The highest abundances of the total macroinfauna usually occurred during summer months (January-February). The most abundant species was *P. (M.) patagonica* (up to 130-140,000 ind m<sup>-2</sup> in the muddy-sand sediments). During some months, this species had significantly higher abundances at the muddy-sand sediments. A similar trend is that shown by *P. hartmannorum*; i.e., significantly higher abundances at the muddy-sand sediments (up to 75,000 ind m<sup>-2</sup>). During many months, the population abundances of *Capitella* sp. and *K. chilena* were significantly higher at the sandy site. The highest population abundances of *Capitella* sp. were close to 37,800 ind m<sup>-2</sup> (February 1991 and February 1996), while the maximum values for *K. chilena* ranged from 13,000 to 14,000 ind m<sup>-2</sup> (February 1991 and November 1995, respectively). The population abundances of *P. gualpensis* (with the exception of the period October 1995-January 1996) were similar at both sites. Interannual comparisons of macroinfaunal abundances carried out for the sandy site showed no significant differences among years for the total macroinfauna and for all the species, but *P. gualpensis*. No significant differences among years were found for the total macroinfauna, *P. (M.) patagonica*, *P. gualpensis* and *P. hartmannorum* at the muddy-sand site. On the other hand, the abundances of *Capitella* sp. and *K. chilena* differed significantly among years. Significant differences among months within annual periods were found for the total macroinfauna and species population abundances at the sandy and muddy-sand sites. The temporal variability of the macroinfauna did not have any significant relationship with the temporal variability in sediment characteristics.

**Key words:** macroinfaunal population abundances, estuarine intertidal flats, south central Chile.

### RESUMEN

Durante octubre de 1990 a abril de 1992 y entre septiembre de 1995 a noviembre de 1997 se recolectaron muestras mensuales de sedimento en el estuario del río Queule (ca. 39° S), centro sur de Chile, con el objetivo de estudiar la variabilidad temporal en las abundancias poblacionales de la macroinfauna que habita los sustratos arenosos y areno-fangosos del intermareal. Los sedimentos arenosos tuvieron mayores porcentajes de partículas de arena y porcentajes más bajos de partículas de fango, agregados biogénicos y materia orgánica total en relación a los sedimentos areno-fangosos. Se encontraron las mismas especies de macroinfauna en ambos sitios. La macroinfauna total estuvo dominada por poliquetos: *Prionospio (Minuspio) patagonica* Augener 1923, *Capitella* sp. y *Perinereis gualpensis* Jeldes 1963. Otros organismos comunes fueron el anfípodo *Paracorophium hartmannorum* Andres 1975 y el pequeño bivalvo *Kingiella chilena* Soot-Ryen 1959. Las abundancias más altas de la macroinfauna total ocurrieron usualmente durante los meses de verano (enero-febrero). La especie más abundante fue *P. (M.) patagonica* (hasta 130-140.000 ind m<sup>-2</sup> en los sedimentos areno-fangosos). Durante algunos meses, esta especie tuvo abundancias significativamente más altas en esos sedimentos. Tendencia similar es la mostrada por *P. hartmannorum*; i.e., abundancias significativamente más altas en los sedimentos areno-fangosos (hasta 75.000 ind m<sup>-2</sup>). Durante muchos meses las abundancias poblacionales de *Capitella* sp. y *K. chilena* fueron significativamente más altas en el sitio arenoso. Las abundancias más altas de *Capitella* sp. estuvieron próximas a 37.800 ind m<sup>-2</sup> (febrero de 1991 y febrero de 1996), mientras que los valores máximos para *K. chilena* estuvieron en el rango de 13.000-14.000 ind m<sup>-2</sup> (febrero de 1991 y noviembre de 1995, respectivamente). Las abundancias poblacionales de *P. gualpensis* (con la excepción del período octubre de 1995 a enero 1996) fueron similares en ambos sitios. Comparaciones interanuales de las abundancias de la macroinfauna del

sitio arenoso no mostraron diferencias para la macroinfauna total y todas las especies con excepción de *P. gualpensis*. No se encontraron diferencias interanuales significativas para la macroinfauna total y las abundancias de *P. (M.) patagonica*, *P. gualpensis* y *P. hartmannorum* en el sitio areno-fangoso. Por otra parte, las abundancias de *Capitella* sp. y *K. chilensis* mostraron diferencias significativas entre años. Se encontraron diferencias significativas entre meses dentro del mismo período anual, tanto para la macroinfauna total como para las abundancias específicas en el sitio arenoso y areno-fangoso. La variabilidad temporal de la macroinfauna no tuvo ninguna relación significativa con la variabilidad temporal de las características del sedimento.

**Palabras clave:** abundancias poblacionales de la macroinfauna, planicies estuariales intermareales, centro-sur de Chile.

## INTRODUCTION

Microtidal estuaries (1-2 m of tidal range) are well represented along the coast of south central Chile (ca. 35-41° S, Pino 1994<sup>1</sup>). Most of them can be classified as plain river estuaries, with ages of about 6,000 years (Pino 1994<sup>1</sup>). The majority of these estuaries get waters from the coastal range, and just a few of them originate in rivers which drain water from lakes located in the foothill of Andean mountains (Campos & Moreno 1985). According to water movement, most of these estuaries can be classified as partially mixed (Pino 1994<sup>1</sup>). Water currents and tectonic movement (Pino 1995) have created extensive intertidal flats with sandy and muddy-sand sediments as the most representative substrates. The highest content of organic matter is associated to that muddy-sand sediments (Pino & Mulsow 1983, Bertrán 1984, 1989, Turner 1984, Jaramillo et al. 1985b, Pino 1994<sup>1</sup>).

Most of the faunistic studies carried out on that intertidal estuarine flats deal primarily with the benthic macroinfauna, which is numerically dominated by polychaetes (Jaramillo et al. 1985a, Quijón & Jaramillo 1993). The community structure of the intertidal estuarine macroinfauna has been mainly analyzed in relation to physical factors, such as water salinity gradients and substrate characteristics (Bertrán 1984, 1989, Turner 1984, Jaramillo et al. 1985b, Donoso 1991, Quijón & Jaramillo 1993, 1996). As found in other estuarine temperate areas (e.g., McLusky 1971), finer sediments and richer in organic matter content support the highest macroinfaunal abundances and biomasses, while that sandy bottoms located closer to the estuarine mouths support higher species richness (e.g., Bertrán 1984, Jaramillo et al. 1985b).

There are no studies on the temporal variability of the estuarine intertidal macroinfauna of south-

central Chile. Thus, the main objective of this study was to characterize the intertidal macroinfauna of Queule river estuary in relation to sediment characteristics and temporal variability. Results from this study will provide a baseline data for future studies aimed for example, to examine the role of anthropogenic use of this estuary on the benthic macroinfauna.

## MATERIAL AND METHODS

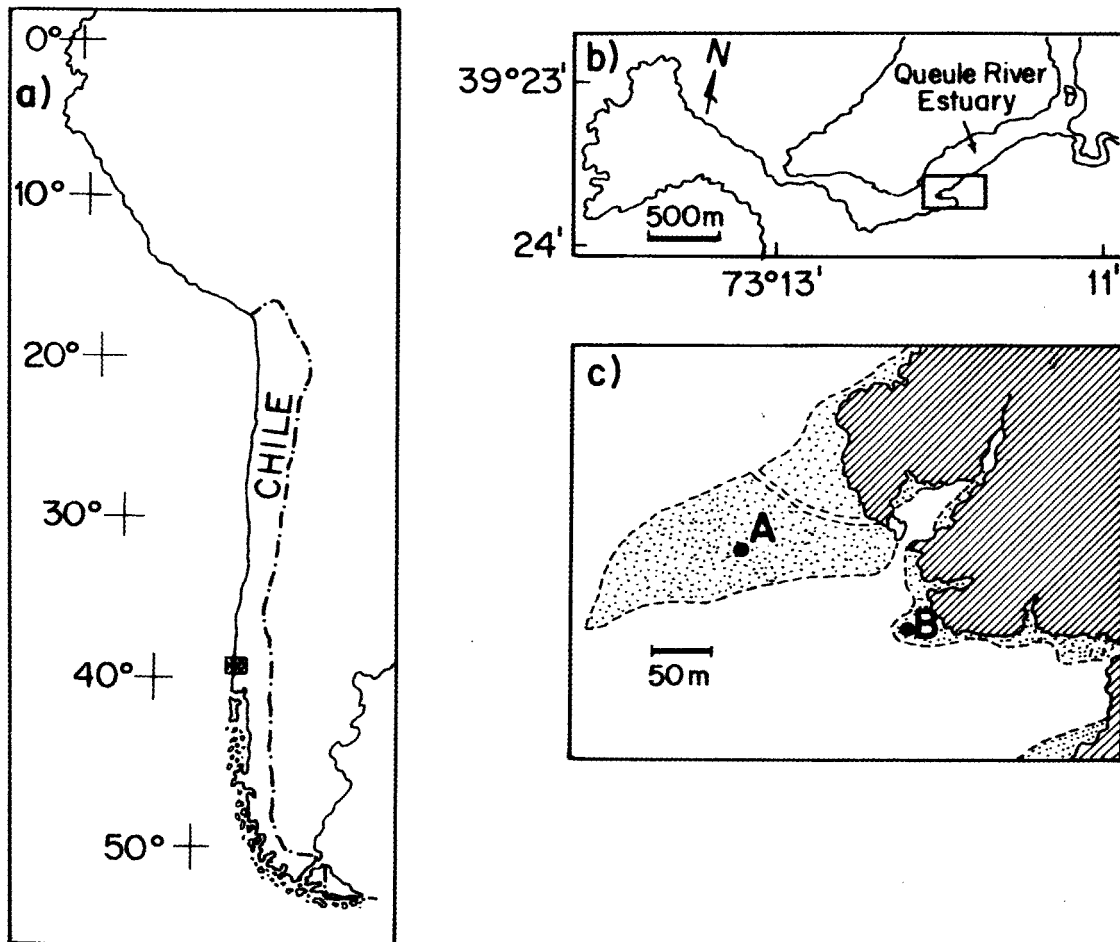
### *The study area*

Queule river estuary is located in south central Chile (39° 24' S, 73° 13' W, Fig. 1). The intertidal flat studied is located in the middle reach of the estuary, about 1,500 m from the mouth. It is roughly triangular with an approximate surface of 10 ha. The two study sites were located at the sandy and muddy-sand areas of the flat. The tides are semi-diurnal with maximum tidal differences of 1.5 m. The highest salinities (25-29 ppm) in the adjacent waters to the flat occur during the high waters of summer and autumn months (February-May), while the lowest values (1-7 ppm) have been measured during the low tides of winter months (July-early September) (Quijón & Jaramillo 1993).

### *Sampling procedures and analyses*

Monthly sediment samples were randomly collected at each site (n = 5 replicates) during two periods: October 1990 to April 1992, and September 1995 to November 1997. A plastic tube, 75 mm in diameter, was buried to a depth of 30 mm to collect the samples. Samples were sieved through a 250 µm mesh sieve and the residue preserved in 10 % formalin for later sorting and counting of the macroinfauna in the laboratory. Only repeatedly recorded species during the whole study were considered for further analyses. Monthly samples were also collected for textural analyses carried out to analyze the proportion of sand (63-1,000 µm), mud (< 63 µm) and biogenic

<sup>1</sup> PINO M (1994) Geomorfología, sedimentología y dinámica de la circulación en estuarios micromareales del centro sur de Chile. Resumen XIV Jornadas de Ciencias del Mar, Puerto Montt, Chile: 106 - 107.



*Fig. 1:* (a) Map of the Chilean coast. The location of Queule river estuary is indicated by the square close to 40° S. (b) outline of Queule river estuary. The location of the study area at the middle reach of the estuary is indicated by the box; (c) location of the sandy (A) and muddy-sand sites (B). Shaded area indicates tidal flats, hatched area indicates salt marshes, and dotted line marks the low tide level.

(a) Mapa de la costa chilena. El cuadrado próximo a 40° S indica la localización del estuario del río Queule; (b) estuario del río Queule. El rectángulo indica la localización del área de estudio en la parte media del estuario, (c) localización del sitio arenoso (A) y del arenofangoso (B). El área sombreada indica planicies intermareales, el área achurada indica marismas, y la línea segmentada señala el nivel de marea baja.

aggregates (Anderson et al. 1981). The content of organic matter was determined as the loss in weight of dried samples after combustion (during 4 h at 550 °C).

Monthly comparisons of sediment characteristics and macrofaunal abundances between sites were carried out with the use of analysis of variance (ANOVA). Assumptions of normality and homocedasticity were tested with the Kolmogorov-Smirnov's and Bartlett's tests, respectively (Sokal & Rohlf 1995). These tests revealed some significant departures from that basic assumptions; thus, the sediment data (percentages) were arcsin transformed while abundance data were transformed to log (n + 1).

Sedimentological and biological relationships were examined using non-metric multidimensional scaling (MDS). MDS was based upon a similarity matrix calculated with the Bray Curtis similarity coefficient after double root transformation of data as run by the PRIMER (Plymouth Routines in Multivariate Ecological Research) program (Carr 1997). MDS was used to graphically display two-dimensional ordination plots of the inter-relationships between sites based on the sediment characteristics and mean abundance of the major taxa found at each site. Thus, the closer the points through these plots the more similar they were. The usefulness of the MDS analyses (i.e., display of relationships between sites) was

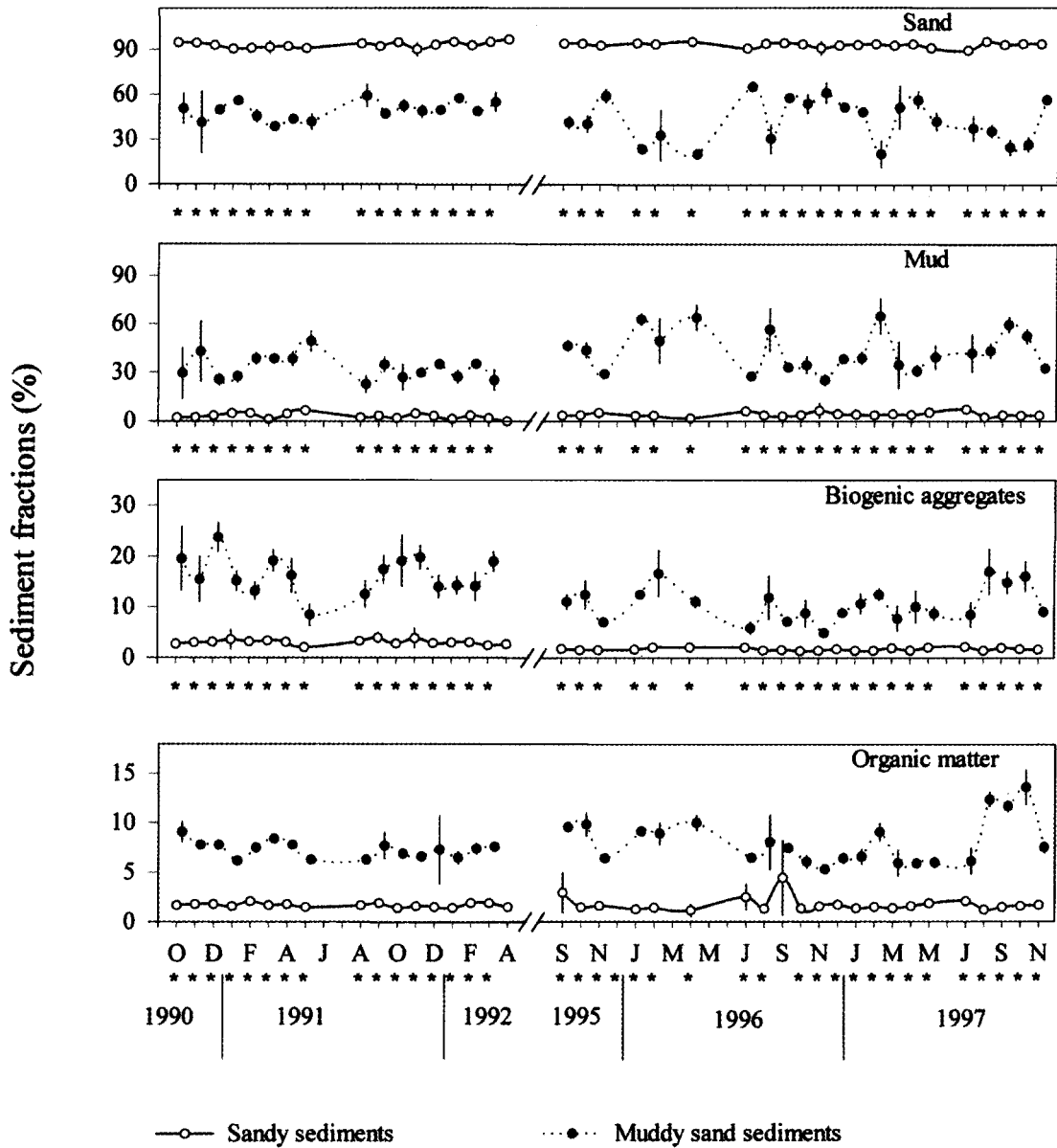


Fig. 2: Temporal variability in sediment characteristics at the sandy and muddy-sand sites. Asterisks indicate statistically significant differences between means ( $P < 0.05$ ) after using ANOVA.

Variabilidad temporal en las características sedimentológicas en el sitio arenoso y arenofangoso. Los asteriscos indican diferencias estadísticamente significativas entre medias ( $P < 0,05$ ) luego de usar ANOVA.

evaluated with the stress statistics: values smaller than 0.1 indicate that the depiction of relationships is good, while stress values over 0.2 indicate a poor depiction (Clarke 1993). The matching of macrofaunal abundances and sediment data was analyzed with the program BIOENV included in the PRIMER package. Basically, this program search for the best single variable or combination of variables that best explain the grouping of samples belonging to a site (Clarke & Warwick 1994).

Temporal comparisons of sediment characteristics and macrofaunal abundances were made among spring-summer months (October to March) of the periods 1990-1991, 1991-1992, 1995-1996, and 1996-1997. Such comparisons were carried out with the use of nested ANOVA (on data transformed as mentioned earlier), and with annual period, month, and replicate as factors (Sokal & Rohlf 1995). A similar comparison for autumn-winter months was not carried out as these months were not sampled enough. Probability levels lower

than 0.05 were regarded as statistically significant.

## RESULTS

### *The sediments*

As expected, the sediments of the sandy site had significantly ( $P < 0.05$ ) higher percentages of sand particles (63-2,000  $\mu\text{m}$ ), and significantly lower percentages of mud particles ( $< 63 \mu\text{m}$ ), biogenic aggregates and total organic matter. Thus, sand particles were close to 90 % at the sandy site, and most of the time below 70 % at the muddy-sand site (Fig. 2). Percentages of mud particles were lower than 5 % at the sandy site, and about 30-60 % at the muddy-sand site. Biogenic aggregates were represented by less than 5 % at the sandy site and by a percentage varying from 5 to 25 % at the muddy-sand site. A seasonal trend of higher concentrations of these aggregates was found during spring-summer months at the muddy-sand site (Fig. 2). Total organic matter content was lower than 5 % at the sandy site,

while at the muddy-sand sediments it varied between 5 and 10 % (Fig. 2). During all the study period, the percentages of sand, mud, and biogenic aggregates were significantly different between sites (Fig. 2). The total organic matter content was significantly different between sites during all the study period, but September 1996 (Fig. 2). Differences in sediment characteristics at both sites are depicted by means of MDS in Fig. 3. Sediment samples collected from the sandy site are separated from that collected at the muddy-sand site. Interannual comparisons of sediment characteristics carried out at both sites showed no significant differences among years. Significant differences among months within annual periods were found in the percentages of sand and mud particles, biogenic aggregates and total organic matter at the sandy and muddy-sand sediments (Table 1 and 2).

### *The macroinfauna*

The macroinfaunal assemblage of the intertidal of Queule river estuary was dominated by poly-

TABLE 1

Result of the nested analyses of variance carried out to test for differences among years in sediment characteristics of the sandy site (see Material and Methods)

Resultados de los análisis de varianza anidados llevados a cabo para evaluar las diferencias entre años en las características sedimentológicas en el sitio arenoso (ver Materiales y Métodos)

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-ratio	P-value
Percentage of sand particles					
Among groups (annual periods)	3	68.8	22.9	2.8	0.06
Among subgroups within groups (among months within annual periods)	22	180.0	8.2	19.6	0.00
Within subgroups (error among replicates collected at each month)	103	43.1	0.4		
Total	128	291.9			
Percentage of mud particles					
Among groups (annual periods)	3	68.4	22.8	1.9	0.16
Among subgroups within groups (among months within annual periods)	22	266.9	12.1	3.7	0.00
Within subgroups (error among replicates collected at each month)	103	334.1	3.2		
Total	128	669.4			
Percentage of biogenic aggregates					
Among groups (annual periods)	3	2.5	0.8	1.8	0.18
Among subgroups within groups (among months within annual periods)	22	10.0	0.5	27.5	0.00
Within subgroups (error among replicates collected at each month)	103	1.7	0.0		
Total	128	14.2			
Percentage of organic matter					
Among groups (annual periods)	3	84.0	28.0	3.1	0.05
Among subgroups within groups (among months within annual periods)	22	199.0	9.0	4.5	0.00
Within subgroups (error among replicates collected at each month)	103	207.2	2.0		
Total	128	490.2			

TABLE 2

Result of the nested analyses of variance carried out to test for differences among years in sediment characteristics of the muddy-sand site (see Material and Methods)

Resultados de los análisis de varianza anidados llevados a cabo para evaluar las diferencias entre años en las características sedimentológicas en el sitio areno-fangoso (ver Materiales y Métodos)

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-ratio	P-value
Percentage of sand particles					
Among groups (annual periods)	3	613.4	204.5	2.8	0.07
Among subgroups within groups (among months within annual periods)	21	1,560.0	74.3	9.5	0.00
Within subgroups (error among replicates collected at each month)	98	762.9	7.8		
Total	122	2,936.3			
Percentage of mud particles					
Among groups (annual periods)	3	4,380.6	1,460.2	2.6	0.08
Among subgroups within groups (among months within annual periods)	21	11,647.7	554.7	9.8	0.00
Within subgroups (error among replicates collected at each month)	98	5,542.4	56.6		
Total	122	21,570.7			
Percentage of biogenic aggregates					
Among groups (annual periods)	3	92.5	30.8	2.6	0.08
Among subgroups within groups (among months within annual periods)	21	250.0	11.9	2.4	0.00
Within subgroups (error among replicates collected at each month)	98	500.0	5.1		
Total	122	842.5			
Percentage of organic matter					
Among groups (annual periods)	3	3,977.7	1,325.9	2.2	0.12
Among subgroups within groups (among months within annual periods)	21	12,749.6	607.1	10.5	0.00
Within subgroups (error among replicates collected at each month)	98	5,672.7	57.9		
Total	122	22,400.0			

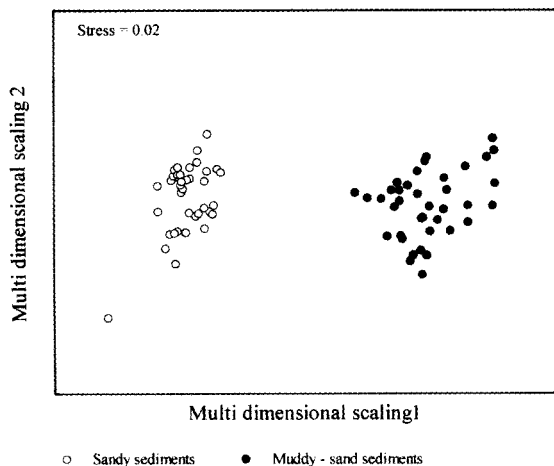


Fig. 3: Multidimensional scaling (MDS) plot of the sedimentological characteristics at the sandy (white circles) and muddy-sand (black circles) sites. Each point represents a sediment sample collected as explained in Material and Methods.

Gráfico de escalamiento multidimensional (MDS) de las características sedimentológicas en el sitio arenoso (círculos blancos) y areno-fangoso (círculos negros). Cada punto representa una muestra de sedimento recolectada tal como explicado en Materiales y Métodos.

chaetes: the spionid *Prionospio (Minuspio) patagonica* Augener 1923, the capitellid *Capitella* sp. and the nereid *Perinereis gualpensis* Jeldes 1963. Other common organism were the amphipod *Paracorophium hartmannorum* Andres 1975 and the small bivalve *Kingiella chilena* Soot-Ryen 1959. Other species with sporadic presence on the flat were the polychaete *Boccardia polybranchia* (Haswell 1885), and the amphipod *Cheus* sp. Thurston. Due to the low abundances of the last two species, they were excluded from further analyses.

The highest abundance of the total macroinfauna usually occurred during summer months (January-February) (Fig. 4). The most abundant species was *P. (M.) patagonica* (up to 130-140,000 ind m<sup>-2</sup> in the muddy-sand sediments). During some months, this species had significant higher abundances at the muddy-sand sediments (Fig. 4). A similar trend is that shown by *P. hartmannorum*; i.e., significantly higher abundances at the muddy-sand sediments (up to 75,000 ind m<sup>-2</sup>). During many months, the population abundances of *Capitella* sp. and *K. chilena* were significantly higher at the sandy site (Fig. 4). The highest population

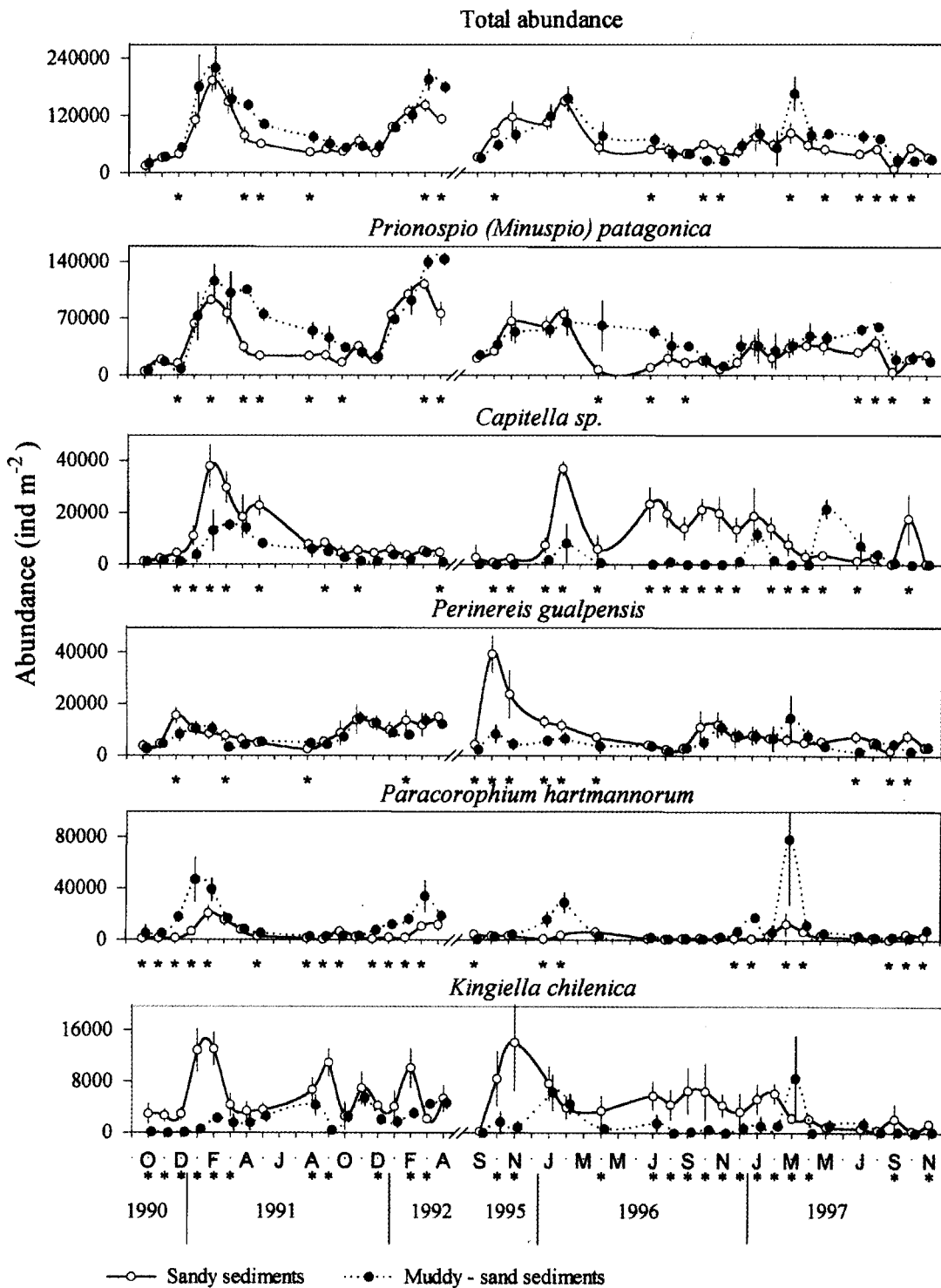


Fig. 4: Temporal variability in population abundances of the total macroinfauna and that of the most common species of the macroinfauna at the sandy and muddy-sand sites. Asterisks indicate statistically significant differences between means ( $P < 0.05$ ) after using ANOVA.

Variabilidad temporal en las abundancias poblacionales de la macroinfauna total y en las de las especies más comunes de la macroinfauna en el sitio arenoso y areno-fangoso. Los asteriscos indican diferencias estadísticamente significativas entre medias ( $P < 0,05$ ) luego de usar ANOVA.

abundance of *Capitella* sp. was close to 37,800 ind m<sup>-2</sup> (February 1991 and February 1996), while the maximum values for *K. chilensis* ranged between 13,000 and 14,000 ind m<sup>-2</sup> (February 1991 and November 1995, respectively). The abundance of *P. gualpensis* (with the exception of the period October 1995-January 1996) was similar at both sites (Fig. 4). The macrofaunal similarities between sites are depicted by means of the MDS plot, which revealed a gradient of macrofaunal abundances from sandy to muddy-sand sediments (Fig. 5).

Interannual comparisons of macrofaunal abundances carried out for the sandy site showed no significant differences among years for the total macrofauna and for all the species, but *P. gualpensis* (Table 3, Fig. 6). The use of LSD post-hoc tests showed that the abundance of this species was significantly higher during the spring-summer months of the periods 1991-1992 and of 1995-1996, as compared with that of the periods 1990-1991 and 1996-1997 (Fig. 6). No significant differences among years were found for the total macrofauna, *P. (M.) patagonica*, *P. gualpensis* and *P. hartmannorum* at the muddy-

TABLE 3

Result of the nested analyses of variance carried out to test for differences among years in macrofaunal abundances of the sandy site (see Material and Methods)

Resultados de los análisis de varianza anidados llevados a cabo para evaluar las diferencias entre años en la abundancia de la macrofauna en el sitio arenoso (ver Materiales y Métodos)

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-ratio	P-value
<b>Total macrofauna</b>					
Among groups (annual periods)	3	2.09	0.70	1.57	0.23
Among subgroups within groups (among months within annual periods)	22	9.77	0.44	29.67	0.00
Within subgroups (error among replicates collected at each month)	107	1.60	0.01		
Total	132	13.45			
<b><i>Prionospio (Minuspio) patagonica</i></b>					
Among groups (annual periods)	3	10.58	3.53	1.23	0.32
Among subgroups within groups (among months within annual periods)	22	63.23	2.87	7.71	0.00
Within subgroups (error among replicates collected at each month)	107	39.89	0.37		
Total	132	113.70			
<b><i>Capitella</i> sp.</b>					
Among groups (annual periods)	3	2.98	0.99	0.55	0.65
Among subgroups within groups (among months within annual periods)	22	39.58	1.80	6.64	0.00
Within subgroups (error among replicates collected at each month)	107	29.01	0.27		
Total	132	71.57			
<b><i>Perinereis gualpensis</i></b>					
Among groups (annual periods)	3	2.86	0.95	4.11	0.02
Among subgroups within groups (among months within annual periods)	22	5.10	0.23	9.74	0.00
Within subgroups (error among replicates collected at each month)	107	2.55	0.02		
Total	132	10.51			
<b><i>Paracorophium hartmannorum</i></b>					
Among groups (annual periods)	3	3.14	1.05	0.43	0.74
Among subgroups within groups (among months within annual periods)	22	54.16	2.46	5.23	0.00
Within subgroups (error among replicates collected at each month)	107	50.36	0.47		
Total	132	107.66			
<b><i>Kingiella chilensis</i></b>					
Among groups (annual periods)	3	0.87	0.29	0.83	0.49
Among subgroups within groups (among months within annual periods)	22	7.69	0.35	7.27	0.00
Within subgroups (error among replicates collected at each month)	107	5.15	0.05		
Total	132	13.71			



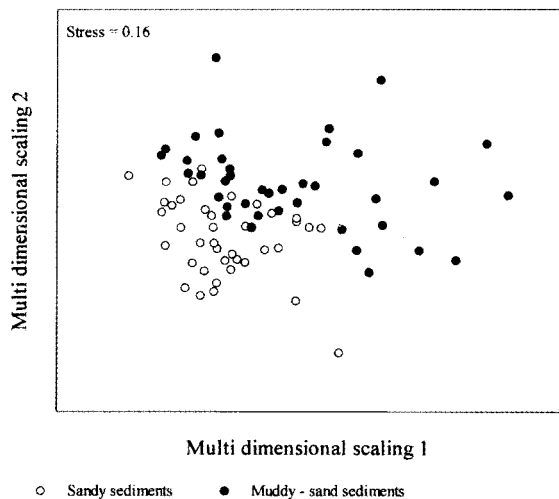


Fig. 5: Multidimensional scaling (MDS) plot of the macroinfaunal abundances (*P. (M.) patagonica*, *Capitella* sp., *P. gualpensis*, *P. hartmannorum* and *K. chilena*) at the sandy (white circles) and muddy-sand (black circles) sites. Each point represents a macroinfaunal sample collected as explained in Material and Methods.

Gráfico de escalamiento multidimensional (MDS) de las abundancias de la macrofauna (*P. (M.) patagonica*, *Capitella* sp., *P. gualpensis*, *P. hartmannorum* y *K. chilena*) en el sitio arenoso (círculos blancos) y arenofangoso (círculos negros). Cada punto representa una muestra de macrofauna recolectada tal como explicado en Materiales y Métodos.

sand site (Table 4, Fig. 6). On the other hand, the abundances of *Capitella* sp. and *K. chilena* differed significantly among years (Table 4). The use of LSD tests showed that the abundance of *Capitella* sp. was significantly higher during the spring-summer months of the period 1990-1991 as compared with that of the other spring-summer periods (Fig. 6). During the same spring-summer period (1990-1991), the abundance of *K. chilena* was significantly lower as compared with other periods. Significant differences among months within annual periods were found for the total macrofauna and species population abundances at the sandy and muddy-sand sites (Table 3 and 4). Table 5 displays the outcome of the BIO-ENV procedure included in the PRIMER package. The inclusion of either a single or a combination of environmental variables rendered no significant correlations between macroinfaunal abundances and physical variables.

## DISCUSSION

This study revealed significant differences in the sedimentary characteristics at two closed sites of the intertidal flats of the middle reach of Queule river estuary. Such differences persisted through years, a trend similar to that of subtidal soft bottoms recorded before in the same estuary (Jaramillo et al. 1985a, Quijón et al. 1996). The muddy-sand site had significantly higher concentrations of mud sized particles, biogenic aggregates and total organic combustion matter. Since biogenic aggregates are easily broken by physical disturbances such as tidal currents (Haven & Morales-Alamo 1968), the most sheltered position of the muddy-sand site may well explain the higher concentration of such aggregates, as well as a higher sedimentation rate of organic matter at that site. Our data also showed some sort of seasonal trend in biogenic aggregates, with higher percentages during the warmer months at the muddy-sand site. This trend may be related to the higher population abundance of the macroinfauna, which would result in a higher production of biogenic aggregates (Rhoads et al. 1978). Ovoid fecal pellets of *Capitella* sp. and *P. (M.) patagonica* are quite distinctive features of the study area during summer months. Also, the cohesive feature of the muddy-sand sediments may probably account for the higher concentration of biogenic aggregates due to the low erodability of such sediments (Rhoads & Boyer 1982).

Despite the notorious differences in sediment characteristics, the same macroinfaunal species were collected at both sites, suggesting that sediment type does not affect the taxonomic composition of the intertidal macroinfauna studied. The macroinfauna of the intertidal sandy and muddy-sand sediments of Queule river estuary is quite stable in terms of dominant species, a similar feature recorded for the benthic communities of the subtidal soft bottoms of the same estuary (Jaramillo et al. 1985a, Quijón et al. 1996). At both sites, the community was dominated by polychaetes which accounted for an average of 80.1 and 76.7 % of the total macroinfauna at the sandy and muddy-sand site, respectively. High dominance of polychaetes have been recorded for other estuarine coasts, such as for example intertidal areas in South America (Bertrán 1984, 1989, Donoso 1991, Ieno & Bastida 1998), North America (Maurer & Aprill 1979, Talley et al. 2000), northern Europe (Boyden & Little 1973), Nigeria (Snowden & Ekweozor 1990), and New Zealand (Read 1984).

Despite similarities in the taxonomic composition of the macroinfauna inhabiting the sandy and

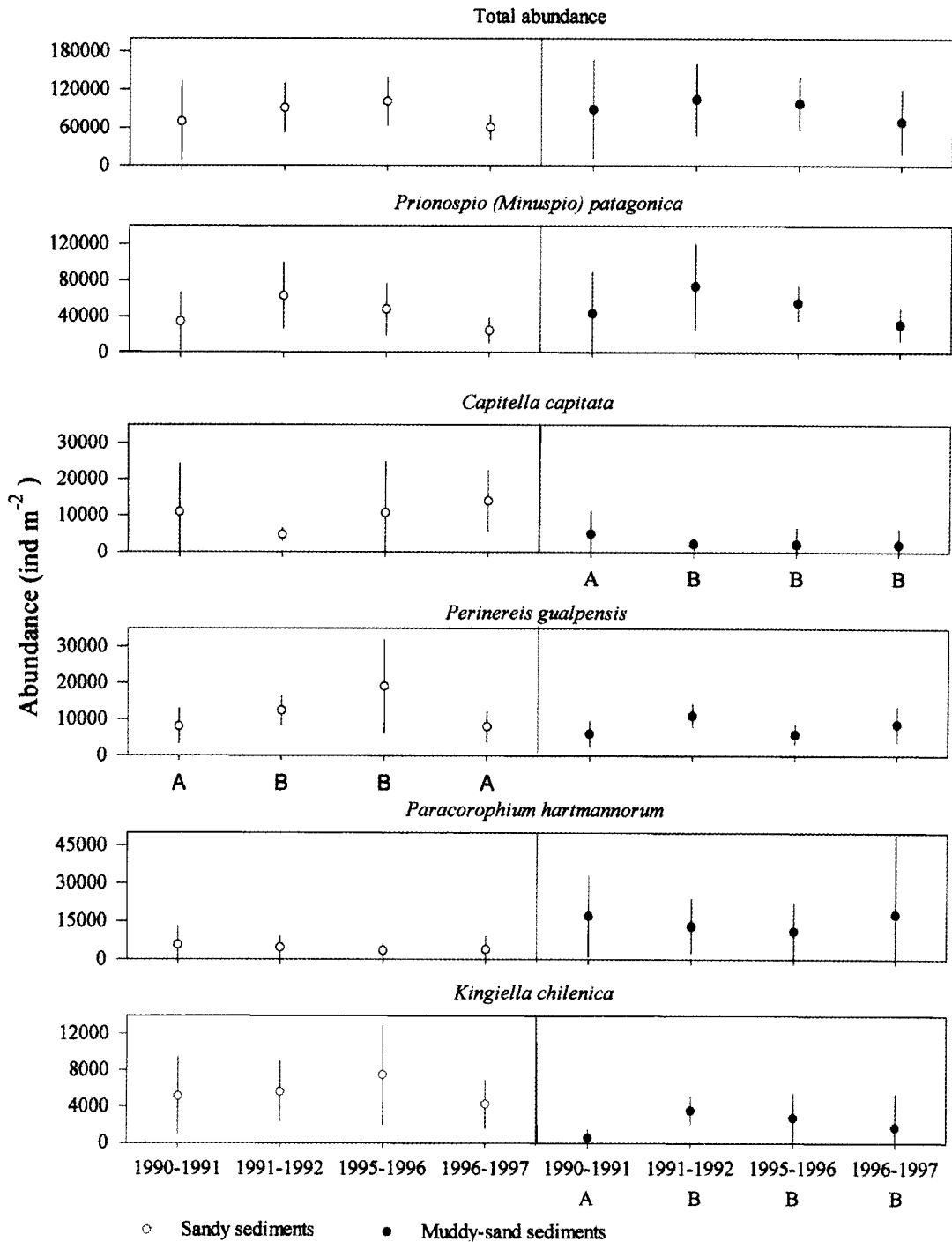


Fig. 6: Interannual variability in population abundances of the most common species of the macroinfauna at the sandy and muddy-sand sites. Analyses are based upon sets of data collected during spring-summer months (see Material and Methods). Statistically significant interannual differences in population abundances were detected for *P. gualpensis* in the sandy site, and for *Capitella* sp. and *K. chilena* in the muddy-sand site as indicated by different capital letters.

Variabilidad interanual en las abundancias poblacionales de las especies más comunes de la macroinfauna en el sitio arenoso y areno-fangoso. Análisis basados en datos recolectados durante meses de primavera-verano (ver Materiales y Métodos). Se detectaron diferencias interanuales estadísticamente significativas en las abundancias poblacionales de *P. gualpensis* en el sitio arenoso, y en las de *Capitella* sp. y *K. chilena* en el sitio areno-fangoso. Estas diferencias se indican con letras mayúsculas diferentes.

TABLE 4

Result of the nested analyses of variance carried out to test for differences among years in macroinfaunal abundances of the muddy-sand site (see Material and Methods)

Resultados de los análisis de varianza anidados llevados a cabo para evaluar las diferencias entre años en la abundancia de la macroinfauna en el sitio areno-fangoso (ver Materiales y Métodos)

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-ratio	P-value
<b>Total macroinfauna</b>					
Among groups (annual periods)	3	3.09	1.03	0.98	0.42
Among subgroups within groups (among months within annual periods)	22	23.13	1.05	3.03	0.00
Within subgroups (error among replicates collected at each month)	107	37.14	0.35		
Total	132	63.36			
<b><i>Prionospio (Minuspio) patagonica</i></b>					
Among groups (annual periods)	3	14.73	4.91	1.71	0.19
Among subgroups within groups (among months within annual periods)	22	63.24	2.87	5.16	0.00
Within subgroups (error among replicates collected at each month)	107	59.64	0.56		
Total	132	137.60			
<b><i>Capitella</i> sp.</b>					
Among groups (annual periods)	3	111.14	37.05	5.29	0.01
Among subgroups within groups (among months within annual periods)	22	154.00	7.00	12.04	0.00
Within subgroups (error among replicates collected at each month)	107	62.20	0.58		
Total	132	327.33			
<b><i>Perinereis gualpensis</i></b>					
Among groups (annual periods)	3	2.64	0.88	2.06	0.13
Among subgroups within groups (among months within annual periods)	22	9.38	0.43	1.80	0.03
Within subgroups (error among replicates collected at each month)	107	25.37	0.24		
Total	132	37.39			
<b><i>Paracorophium hartmannorum</i></b>					
Among groups (annual periods)	3	2.17	0.72	0.21	0.89
Among subgroups within groups (among months within annual periods)	22	74.28	3.38	5.09	0.00
Within subgroups (error among replicates collected at each month)	107	70.92	0.66		
Total	132	147.37			
<b><i>Kingiella chilensis</i></b>					
Among groups (annual periods)	3	96.92	32.3	4.88	0.01
Among subgroups within groups (among months within annual periods)	22	145.66	6.62	8.80	0.00
Within subgroups (error among replicates collected at each month)	107	80.49	0.75		
Total	132	323.07			

muddy-sand sediments of the intertidal of Queule river estuary, population abundance of most species differed at both substrates. While the abundance of the polychaete *P. (M.) patagonica* and the amphipod *P. hartmannorum* were usually significantly higher at the muddy-sand sediments, the polychaete *Capitella* sp. and the small bivalve *K. chilensis* were more abundant at the sandy sediments, suggesting preferences for different types of sediment. The opposite trend shown by the animal-sediment relationships of the polychaetes *P. (M.) patagonica* and *Capitella* sp. was also observed in earlier studies. In an across shore transect at Queule river estuary, Turner (1984) found that these polychaetes divided the intertidal with maximum abundances of *P. (M.)*

*patagonica* at the lower shore and *Capitella* sp. further up. Also, Donoso (1991) found at several sites of the intertidal flats of this estuary and at that of Lingue river estuary (about 6 km south of Queule) that both species presented their highest abundances at different intertidal areas. This spatial partition of the habitat and the population abundance data of this study suggest some sort of biological interactions, such as that demonstrated by Levin (1981) for spionid polychaetes inhabiting intertidal flats of California and by Jensen & Kristensen (1990) for amphipods (*Corophium* spp.) living in mudflats of the Danish Wadden Sea. The experimental test of hypotheses tempting to evaluate negative interactions between *P. (M.) patagonica* and *Capitella* sp. are indeed

TABLE 5

Results of the BIO-ENV procedure of PRIMER (see Material and Methods). The use of single or combined variables did not render any significant Spearman rank correlation between macroinfaunal abundances and sediment characteristics. The variables included in each step were those that rendered the highest rank correlation value

Resultados del procedimiento BIO-ENV del PRIMER (ver Materiales y Métodos). El uso de una sola variable o combinación de variables no resultó en rangos significativos de correlación de Spearman entre las abundancias de la macroinfauna y las características del sedimento. Las variables incluidas en cada paso fueron las que entregaron los rangos de correlación más altos

	Sandy sediment	Muddy-sand sediment
1 variable	-0.036 (organic matter)	0.039 (organic matter)
2 variable	-0.056 (organic matter + mud)	0.108 (organic matter + biogenic aggregates)
3 variable	-0.053 (organic matter + sand + mud)	0.050 (organic matter + sand + biogenic aggregates)
4 variable	-0.110 (organic matter + sand + mud + biogenic aggregates)	0.014 (organic matter + sand + mud + biogenic aggregates)

worthwhile to get deeper in the factors involved in community organization of this macroinfauna.

Most macroinfaunal communities exhibit seasonal and interannual variability in population abundances (Rachor et al. 1982, Díaz 1984, López-Jamar et al. 1986, Beukema 1989, Gaston et al. 1995, Bone & Klein 2000, McCarthy et al. 2000). Densities of the temperate intertidal soft-bottom macroinfauna peak during the spring, then decline throughout the summer, and usually have a second smaller peak during the autumn to decline again in winter (Levin 1984, Frid & James 1989, Marsh & Tenore 1990, Sarda et al. 1995). The results of this study generally agreed with such trend as the intertidal macroinfauna of Queule river estuary usually peaked during spring-summer months. However, population abundances of some species such as *P. (M.) patagonica* varied between sites. During some months, this polychaete presented similar abundances at both sites. However, subsequently higher abundance at the muddy-sand site suggests higher mortality of juveniles at the sandy site (Fig. 4). The interannual variability observed in the population abundances of some species was probably related to recruitment variability since the sediment samples were sieved through a 250 µm sieve; thus, many small animals were indeed collected. This interpretation would explain, for example, the high population abundance of the macroinfauna during some specific periods: *P. (M.) patagonica* in the muddy-sand sediments during March through April 1992, *Capitella* sp. in the sandy site during February 1991 and 1996, *P. gualpensis* in the same site during October through November 1995, and *P. hartmannorum* in the muddy-sand site during March 1997 and *K. chilénica* in the sandy site during January-February 1991 and November

1995. Thus, such higher abundances were probably the result of high recruitment pulses. Since the inspection of macroinfaunal population abundances and sediment variability did not show any significant relationship (results of the BIO-ENV procedure of PRIMER), it can be said that variability in recruitment and subsequent population abundance is apparently not related to the variability of that environmental factor. If so, it can be hypothesized that this variability is probably related to nearshore events such as wind and propagation of internal waves in the water column (Shanks & Wright 1987, Eckman 1996) that, when occurring out of the estuary, it may indeed extend their effects to the middle reaches of this estuary.

Temporal variability in population abundances of the estuarine macroinfauna has been also linked to biological interactions such as predation by fishes and birds (Virnstein 1977). According to the studies of Turner (1988), the macroinfauna of this estuary contributes significantly to the food of demersal fishes *Eleginops maclovinus* (Valenciennes) and *Cauque mauleanum* (Steindachner). The same can be said for the brown pintail duck *Anas georgica* Gmelin and the whimbrell *Numenius phaeopus* (Linné) (Velásquez 1987). Both fishes and birds were particularly abundant during late spring-summer months. Venegas (1992) showed that the experimental exclusion of predators (demersal fishes and birds) during those months resulted in increased macroinfaunal population abundances, which suggest that seasonal variability in macroinfaunal abundances may well be related to seasonal variability in population abundance of these vertebrate predators. Nonetheless, and since most of the macroinfauna of the intertidal flats of

Queule river estuary peaked at the same time of the highest abundance of predators, vertebrate predation does not control population abundances of this macroinfauna.

The results of this study emphasize the fact that basic to the understanding of inter-annual variability in population abundances of the intertidal estuarine macroinfauna, is the awareness of factors which may cause long-term changes in the estuarine environment. Contemporaneous records of water temperature, river runoff, nutrient and oxygen water concentrations, changing sea level and seasonal variability in biological interactions, should probably shed light on their importance for macroinfaunal communities, specially if for example, changes in water properties are expected to occur in the small sized estuaries of south central Chile from the continued increasing human influence around the intertidal flats (Reise 1982). That would help in making predictions on long-term variability of the intertidal estuarine macroinfauna in this area of the Chilean coast or elsewhere. In the meantime, the results of this study stands as the most complete baseline data on the population abundances of the intertidal estuarine macroinfauna of south central Chile.

#### ACKNOWLEDGMENTS

To Marcia González, Carlos González, Claudia Añazco, Sonia Fuentealba, and Cesar Cuevas for help during field and laboratory work. To FONDECYT grants 0304-90 and 1951168 for financial support. The final data analyses and manuscript writing benefited from the financial support given to E.J. and P.Q. by Proyecto Fondap O & BM (Programa Mayor No. 3).

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