

# Macroinfaunal Assemblages Associated With Mussel and Clam Beds in an Estuary of Southern Chile

PEDRO QUIJÓN<sup>1</sup>  
EDUARDO JARAMILLO  
*Instituto de Zoología*  
*Universidad Austral de Chile*  
Valdivia  
Chile

MARIO PINO  
*Instituto de Geociencias*  
*Universidad Austral de Chile*  
Valdivia  
Chile

**ABSTRACT:** Samples were collected from September 1990 to February 1992, at three subtidal sites of the middle reaches of the Queule River estuary, southern Chile, to analyze the spatial and temporal variability of the macroinfauna inhabiting substrata with different abundances of bivalves. In addition, water and sediment samples were obtained to study the relationships between the temporal variability in macroinfaunal abundances, physical factors, and chlorophyll *a* content. Temperature, salinity, and chlorophyll *a* showed a rather strong seasonal variability but slight between-site differences. Sediment characteristics and bivalve abundances, by contrast, exhibited little temporal variability but large differences between sites. The macroinfauna was primarily represented by polychaetes, *Prionospio (Minuspio) patagonica* being dominant in the three areas. Most dominant species showed similar trends of temporal variability, with maximum abundances recorded during spring and fall. The appearance of recruits was restricted to the summer with little difference among sites. Multiple regression analyses showed that the temporal variability of macroinfaunal adults and recruits, was primarily associated with variability in salinity and water temperature, respectively. Spatial variability of these organisms was also explained by variations in these factors, together with those of sediment texture and organic matter content. No evidence of interactions (significant relationships) was found between the abundances of bivalves and those of the macroinfauna, nor among macroinfaunal organisms.

## Introduction

The dynamics of soft-bottom benthic assemblages have been related to the seasonal variability of physical factors such as salinity and temperature (Holland et al. 1987; Beukema 1990), food availability (Roman and Tenore 1978; Beukema and Cadée 1986), natural or anthropogenic disturbances (Souza 1979; Dethier 1984; Levin 1984), reproductive events and species interactions (Gray 1974; Peterson 1979; Wilson 1991). In estuarine habitats, natural or man-induced circulation patterns and spatial heterogeneity of the sediments (Pethick 1984; Nichols et al. 1986; Sha and de Boer 1991) introduce other variable habitat factors.

Bivalve culture activities are common anthropogenic disturbances in estuaries. Through their burrowing and feeding activities, bivalves may modify

the nutritive value (Risk and Moffat 1977; Reise 1983), stability, and textural composition of the sediments (Rhoads and Young 1970; Haven and Morales-Alamo 1972), thereby playing an important role in the organization of macroinfaunal assemblages (Posey 1990). Negative interactions among suspension-feeding bivalves (e.g., mussels) and macroinfaunal assemblages (mediated by consumption and/or burial of larvae and biogenic modification of the sediments) have been documented for a wide variety of taxa (Rhoads and Young 1970; Woodin 1976; Posey 1987; Dittman 1990; André and Rosenberg 1991).

Studies of the subtidal benthos of the Queule River estuary (southern Chile) have shown a negative relationship between the abundances of mussels and that of the macroinfauna living among them: differences of up to 1 to 4 orders of magnitude, in areas with and without bivalves, respec-

<sup>1</sup> Corresponding author.

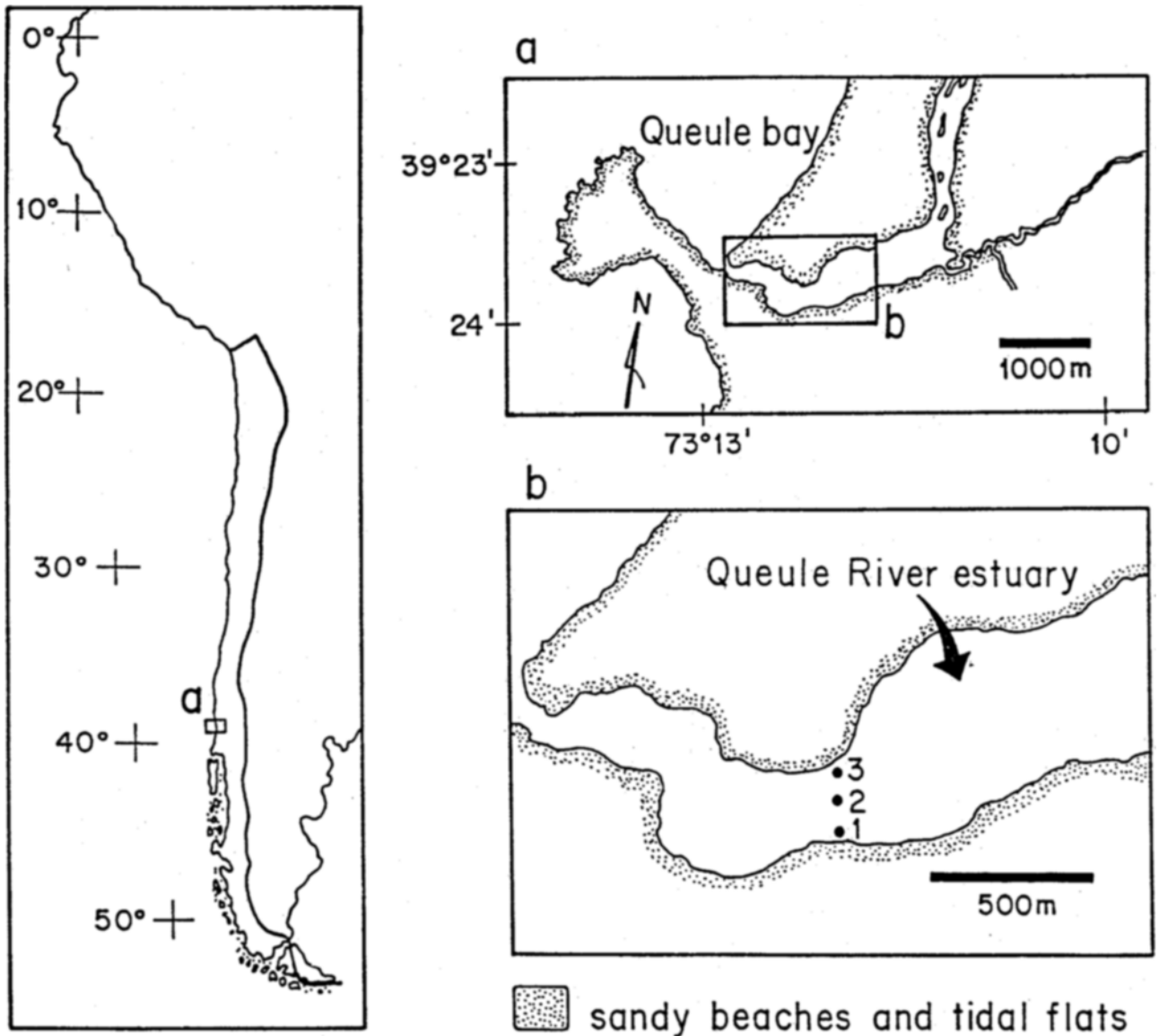


Fig. 1. Map of the Chilean coast showing the location of the Queule River estuary (a) and the study area (b). Points 1, 2, and 3 indicate the approximate location of sampling sites.

tively (Jaramillo et al. 1992). However, the trapping of larvae and/or recruits by established bivalves (e.g., through byssus threads), could have significantly affected these results. Thus, in areas of this estuary affected by a steady increase in mussel aquaculture, eventual effects of bivalves on the sediment and the structure of its macroinfauna are still poorly understood.

The objective of this study was to analyze the temporal response of the macroinfauna to the presence and effects of different densities and composition of mussels and clams, in three subtidal benthic areas in the middle reaches of the Queule River estuary. In this way, hypotheses con-

cerning such factors as adult-larval interactions (Woodin 1976), density dependent relationships with regard to space and food (Olafsson 1986; Peterson and Black 1987) and habitat heterogeneity could be evaluated by correlative methods.

**Study Area**

The Queule River estuary (south-central Chile, 39°24'S, 73°13'W; Fig. 1a) is characterized by a semidiurnal tidal regime, with a maximum range of 1.5 m (Pino and Mulsow 1983). Three sampling stations were chosen in the middle reaches of the estuary (distance between stations ca. 35 m; Fig. 1b). The bottom was occupied by artificial beds of

the mytilid bivalves *Choromytilus chorus* Molina and *Mytilus chilensis* Hupé and natural beds of the clam *Mulinia edulis* King (Jaramillo et al. 1992). The water depth at each station was close to 4 m during high tide and was affected by similar current characteristics (Pino personal communication).

### Materials and Methods

From September 1990 to February 1992, water samples ( $n = 3$ ) were collected monthly from bottom waters, (i.e., about 30 cm above the sediment surface) using a Rüttner bottle. The water samples were used to estimate salinity, temperature, and chlorophyll *a* values (high and low tide conditions) at each of the three stations. Sediment samples ( $n = 4$ ) for sedimentological and faunistic analyses were collected using PVC cylinders (10.5 cm in diameter) inserted to a depth of 15 cm. After sampling, the sediment samples were kept in the dark (12 h) at room temperature to allow decantation and subsequent draining of the supernatant water. Later, subsamples of sediments were collected with a plastic cylinder (1.7 cm in diameter) to a depth of 3 cm for particle size, chlorophyll *a*, and organic matter content analyses.

Samples for faunistic analyses were sieved with 0.5-mm mesh and the residue was preserved in 10% formalin. Separate subsamples of 30.5 cm<sup>2</sup> were collected and sieved with 0.25-mm mesh to estimate the abundance of juveniles. These included individuals smaller than 4 mm in the case of *Prionospio (Minuspio) patagonica* Augener and *Polydora* sp., 5 mm in the case of *Perinereis gualpensis* Jeldes, and 3 mm in the case of *Capitella* sp. and *Paracorophium hartmannorum* Andrés.

Water and sediment samples for chlorophyll *a* estimation were kept in 90% acetone for 24 h to extract pigments; they were then centrifuged at 3,500 rpm for 15 min. The absorbance of the supernatant was measured at 750 nm and 665 nm with and without acidification of HCl 0.1 N (Strickland and Parsons 1972). The organic matter content of the sediments (total combustibles) was determined as the loss in weight of dried samples (80°C, 72 h) after combustion (550°C, 4 h). Granulometric analyses were carried out to determine the percentages of gravel (>2,000  $\mu$ ), sand-aggregates (63–2,000  $\mu$ ), and mud (<63  $\mu$ ) (Folk 1980; Anderson et al. 1981).

One-way analyses of variance (Sokal and Rohlf 1969) were used for comparisons of sedimentological characteristics and macroinfaunal abundances among areas. Percentage data were arc sin ( $n$ ) transformed, and the abundance values were  $\log_{10}(n + 1)$  transformed. If analyses of variance indicated significant differences among means, these were compared using the a posteriori Tukey-Kra-

mer multiple comparison test (in Stoline 1981). When the data did not show normal distributions, a nonparametric analysis (Kruskall-Wallis ANOVA; Sokal and Rohlf 1969) was used.

The variability in monthly mean abundances of macroinfauna ( $n = 56$ ) was analyzed using multiple stepwise regression analyses with the forward selection technique (Hair et al. 1979). Independent variables were the environmental factors (approach A) and the environmental factors plus the abundances of recruits and coexisting species (approach B). In addition, analyses including the abundance of bivalves as independent variables ( $n = 39$ ), were carried out with data from September 1990 to September 1992.

## Results

### WATER COLUMN AND SEDIMENTS

Figure 2 shows the temporal variation of temperature, salinity, and chlorophyll *a* in the bottom waters of the three study sites (mean values for high and low tide conditions). The three variables showed a clear seasonal trend, with minimum values obtained during winter (down to 9.1°C, 12.1 g l<sup>-1</sup> and 0.1 mg l<sup>-1</sup>, respectively) and maximum values during the warmest months (up to 19.3°C, 30.3 g l<sup>-1</sup> and 28.5 mg l<sup>-1</sup>, respectively). In general, the maximum values of chlorophyll *a* measured in the water were followed by the highest values observed in the sediments (up to 52.9  $\mu$ g g<sup>-1</sup> of dry sediment weight) (cf. Figs. 2 and 3). These variables showed slight and less persistent differences among stations. However, the range of variability in chlorophyll *a* in the water was much higher than that measured in the sediments (Figs. 2 and 3).

Organic matter content had rather small temporal variability, showing clear differences among sites. During most of this study, the estimated values for site 1 (up to 6.9%) were significantly higher ( $p < 0.05$ ) than those obtained for sites 2 and 3, as shown in Fig. 3. The textural characteristics of the substratum also showed a trend of small temporal variability (Fig. 4). For most of the study, the gravel and sand contents of site 1 were significantly different from those measured at sites 2 and 3. The gravel fraction primarily comprised mica schist and a minor proportion of shell fragments originating from mytilids and barnacles (*Elminius kingii* Gray). Mud and aggregates showed similar trends over time. The substratum at site 1 was gravelly muddy-sand, and muddy-sand at sites 2 and 3.

### THE BIVALVES

The mytilids *Choromytilus chorus* and *Mytilus chilensis* and the clam *Mulinia edulis* were the most abundant and persistent bivalves of the study sites (up to 22 individuals 625 cm<sup>-2</sup>, 8 individuals 625

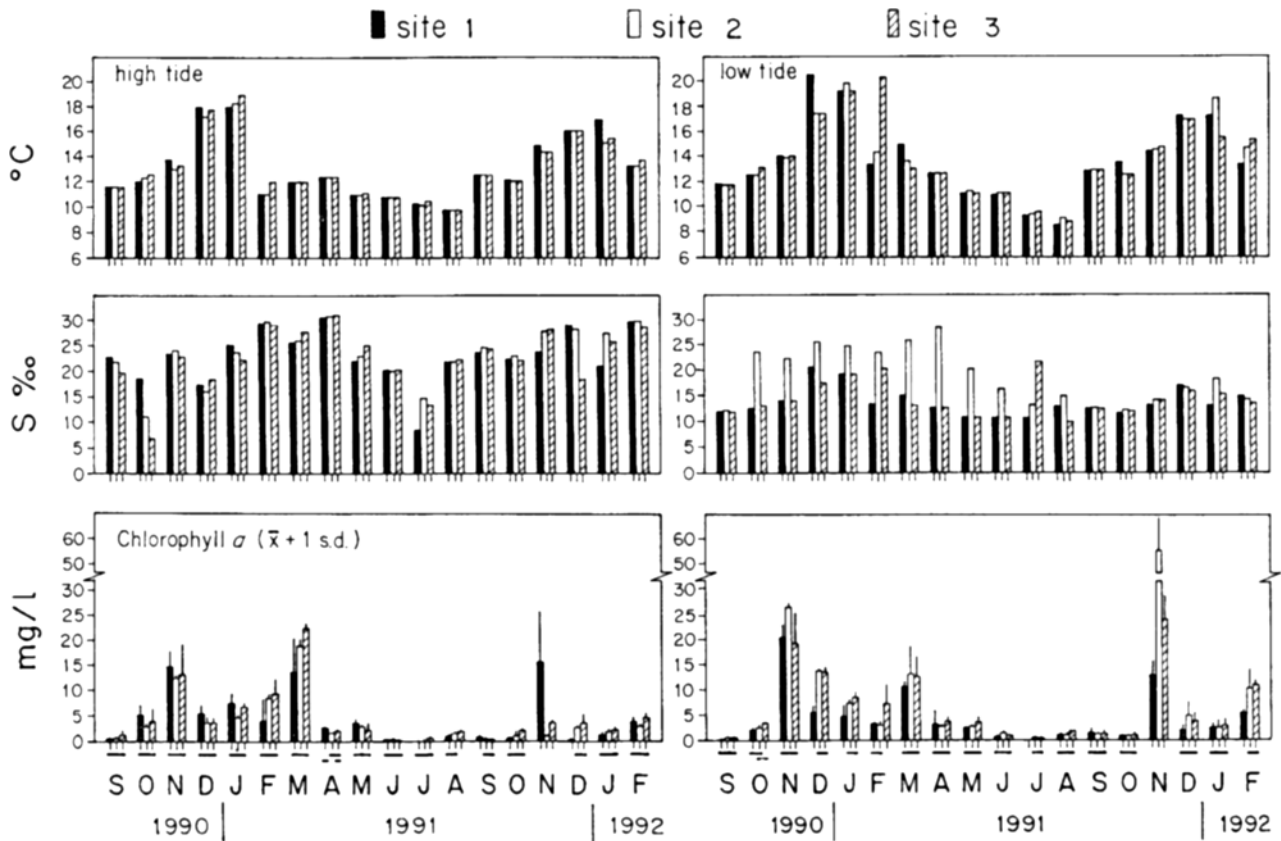


Fig. 2. Temperature, salinity, and chlorophyll *a* content in the bottom waters (ca. 30 cm above the sediment-water interface) of sites 1, 2, and 3 (high and low tide data are presented). Line below common bars (in the case of chlorophyll *a* content) indicate no significant difference among them ( $p > 0.05$ ).

$\text{cm}^{-2}$  and 6 individuals  $625 \text{ cm}^{-2}$ , respectively) (Fig. 5). *Ch. chorus* was the dominant bivalve in the sediments of sites 1 and 2, where maximum mean abundances were recorded during January and March 1991, respectively. *M. chilensis* and *M. edulis* were primarily collected from the sediments of sites 1 and 3, respectively, with maximum mean abundances recorded during May and June 1991. The maximum abundances of the three species taken together occurred at sites 1 and 2 (up to 19 individuals  $625 \text{ cm}^{-2}$  and 24 individuals  $625 \text{ cm}^{-2}$ ;  $p > 0.05$ ). These abundances differed significantly ( $p < 0.05$ ) from those estimated for site 3 (up to 6 individuals  $625 \text{ cm}^{-2}$ ) (Fig. 5). Analyses of bivalve shell size, carried out to characterize the population structure of each species, showed rather small spatial and temporal differences. Shell length ranges were: *Ch. chorus*, 17.8–119.7 mm; *M. chilensis*, 17.8–97.3 mm; and, *M. edulis*, 5.2–84.9 mm.

#### THE MACROINFAUNA

Twenty-four taxa were collected and identified to either species or genus level, with the Polychaeta being the most diverse taxon (16 taxa). Figure 6

shows the temporal dynamics of the numerically dominant species: the polychaetes *P. (M.) patagonica*, *Polydora* sp., *Perinereis gualpensis*, and *Capitella* sp., and the amphipod *Paracorophium hartmannorum*. The abundances of *Polydora* sp., *P. gualpensis*, *Capitella* sp., and *P. hartmannorum* showed seasonal variability, with minimum values recorded in winter and maximum values during the months of autumn and spring (up to 125 individuals  $86.5 \text{ cm}^{-2}$ , 26 individuals  $86.5 \text{ cm}^{-2}$ , 23 individuals  $86.5 \text{ cm}^{-2}$  and 35 ind.  $86.5 \text{ cm}^{-2}$ , respectively).

At sites 2 and 3, *P. (M.) patagonica* showed temporal trends similar to those shown by the other species. However, the dynamics of this species in site 1 were more complex, involving strong variability in abundance, without any clear relationship to the patterns previously described. In addition, the peak abundances of *P. (M.) patagonica* in this site (up to 216 individuals  $86.5 \text{ cm}^{-2}$ ), were higher ( $p < 0.05$ ) than those recorded from sites 2 and 3. The abundances of *Polydora* sp. and *P. gualpensis*, were significantly higher ( $p < 0.05$ ) in sites 1 and 2, respectively, while *P. hartmannorum* did not show

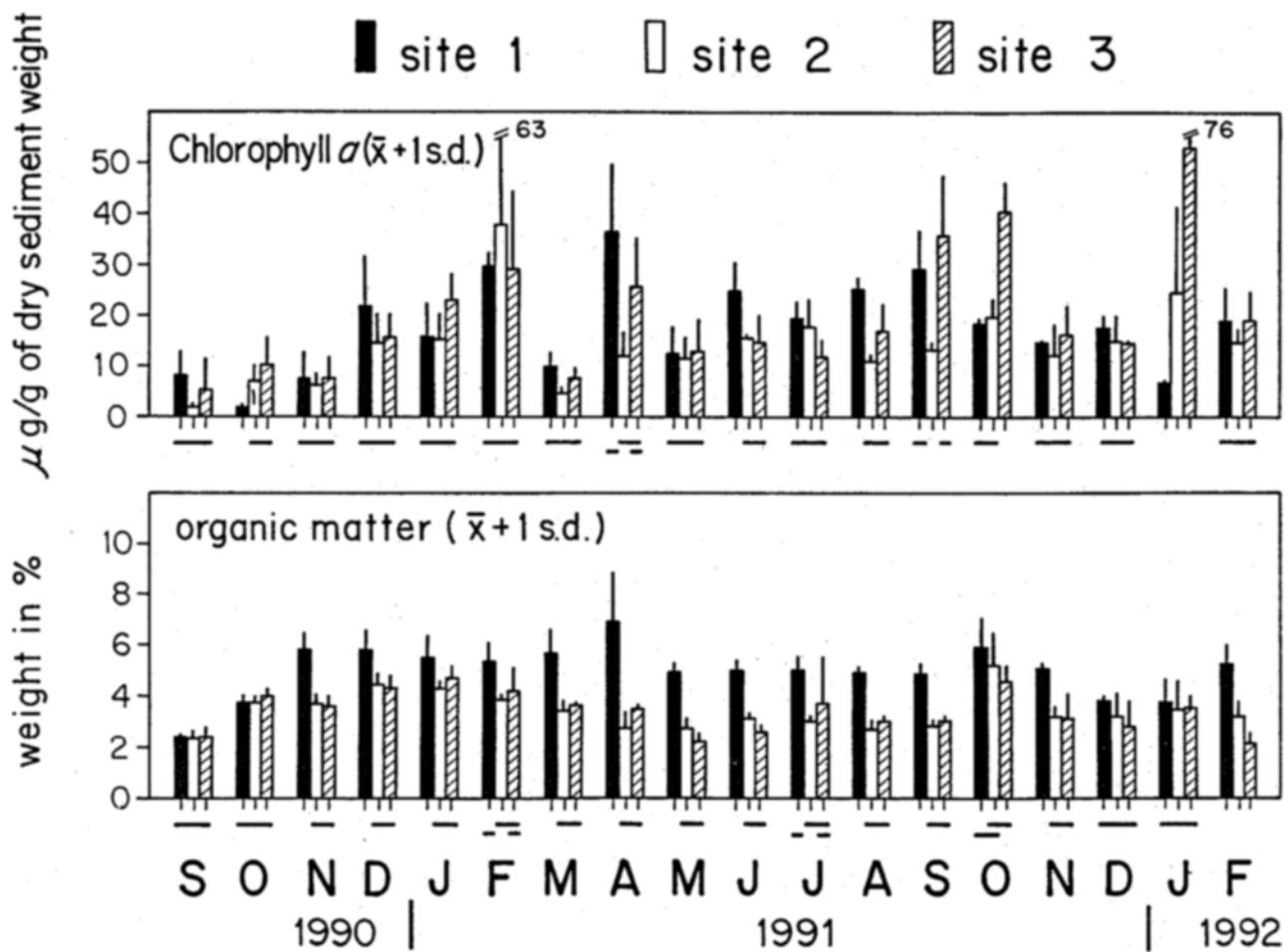


Fig. 3. Chlorophyll *a* and organic matter content in the sediments of sites 1, 2, and 3. Line below common bars indicate no significant difference among them ( $p > 0.05$ ).

significant differences between sites over long periods of time ( $p > 0.05$ ) (Fig. 6).

Figure 7 shows the temporal variability in the abundances of recruits at the three sites studied. In general, the appearance of recruits was synchronized and restricted to brief periods of time in the summer months, reaching similar abundances at the three sites. Highest abundances of *P. (M.) patagonica*, *Polydora* sp., *P. gualpensis*, *Capitella* sp., and *P. hartmannorum* were 215 individuals  $86.5 \text{ cm}^{-2}$ , 46 individuals  $86.5 \text{ cm}^{-2}$ , 59 individuals  $86.5 \text{ cm}^{-2}$ , 195 individuals  $86.5 \text{ cm}^{-2}$ , and 78 individuals  $86.5 \text{ cm}^{-2}$ , respectively. In general the peak abundances of recruits of *Polydora* sp. and *P. gualpensis*, coincided with the peak abundances of adult conspecifics. *P. (M.) patagonica*, *Capitella* sp., and *P. hartmannorum* did not show such coincidences, although 1 to 3 months time lags were occasionally observed between the abundance peaks of adults and recruits. Finally, examination of the external surfaces of the

mytilids (byssus threads) did not show the presence of recruits or adults.

Multiple regression analyses showed low values of multiple  $R^2$  (up to 25%). Salinity was the factor most frequently associated with species variability, but some textural variables (such as gravel content) were also incorporated into the model (two cases). The incorporation into the model of the abundances of co-existing species and that of recruits (approach B), resulted in increased values of  $R^2$  up to 45% (Table 1). The variation in total abundance of the macroinfauna was accounted for primarily (98%) by the variability of the five species included in the model. Negative relationships between species were not detected and, in general, there were no associations between the variability of a species and that of their recruits.

Multiple regression analysis including the abundances of bivalves ( $n = 39$ , September 1990 to September 1992) showed similar results to those de-

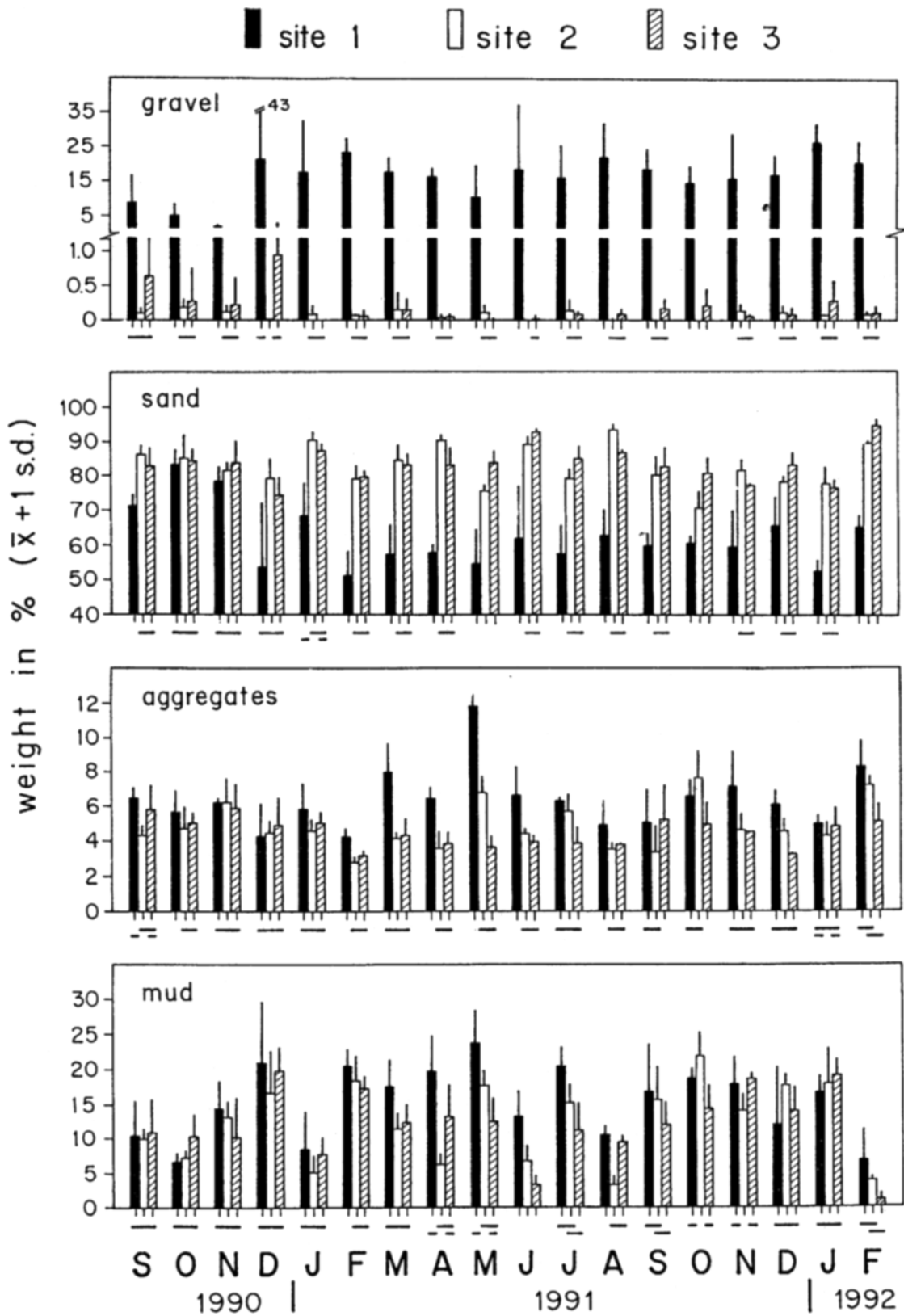


Fig. 4. Gravel, sand, aggregates and mud content in the sediments of sites 1, 2, and 3. Line below common bars indicate no significant difference among them ( $p > 0.05$ ).

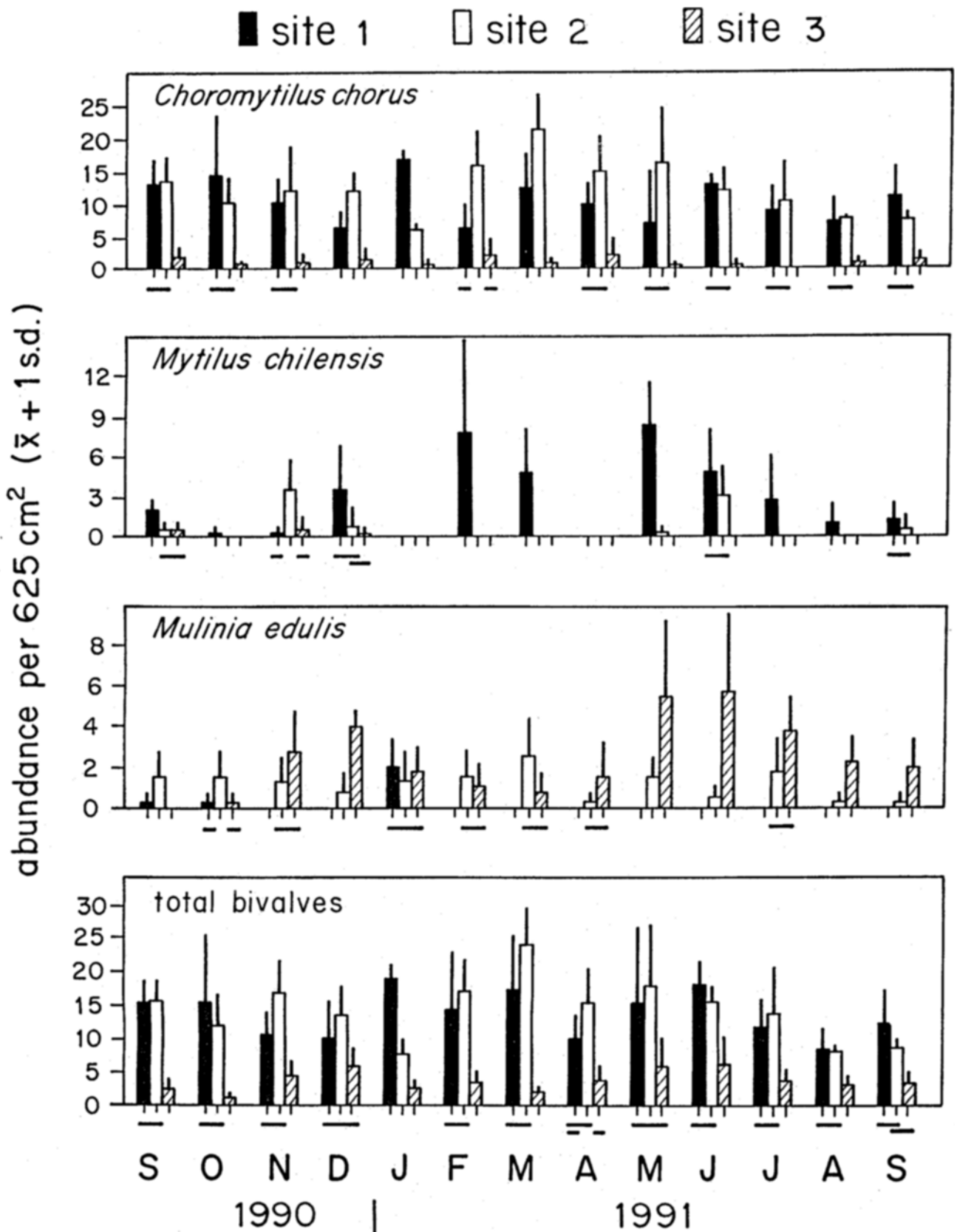


Fig. 5. Mean abundances of bivalves in the sediments of sites 1, 2, and 3. Line below common bars indicate no significant difference among them ( $p > 0.05$ ).

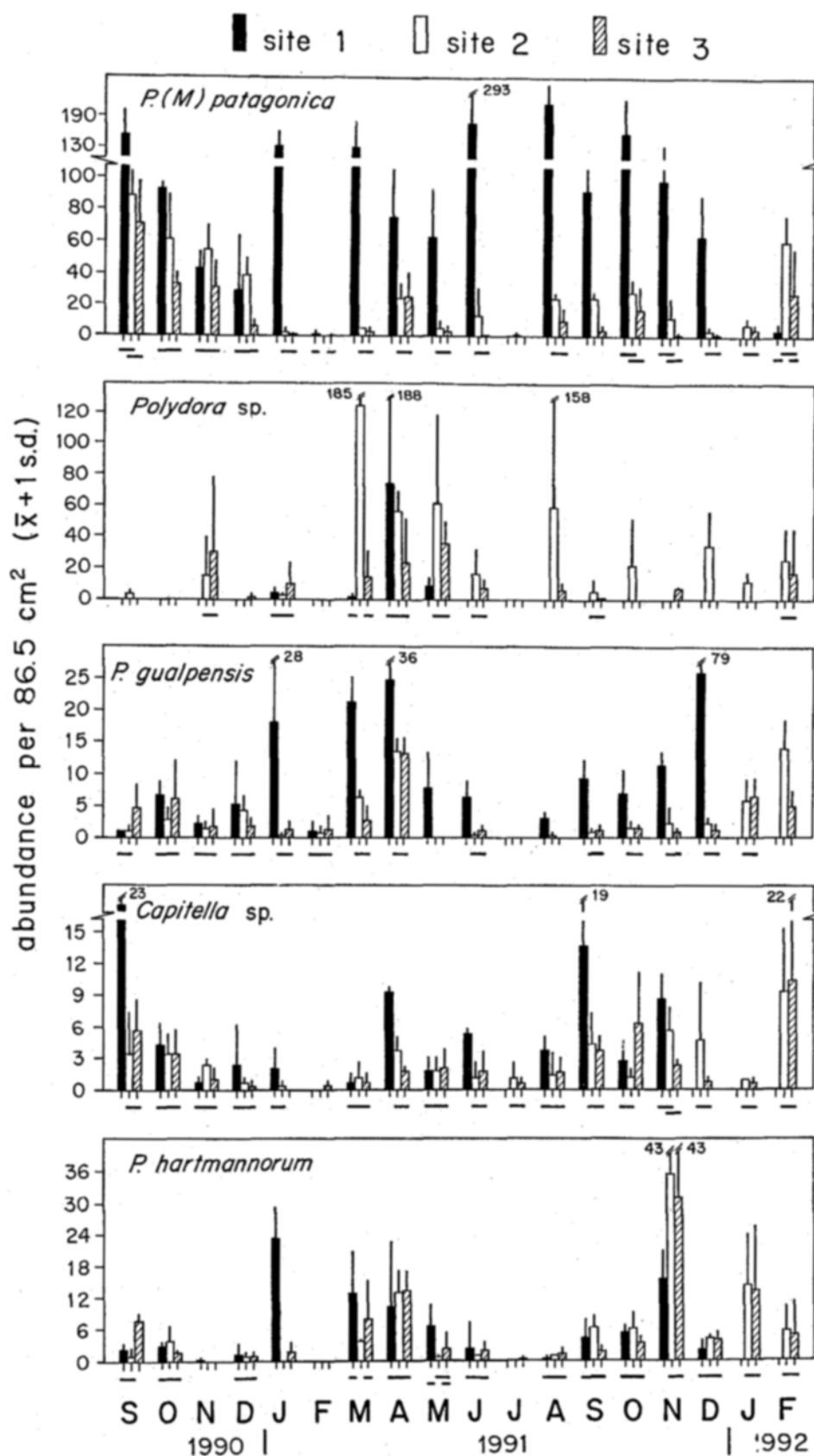


Fig. 6. Mean abundances of the macroinfauna in the sediments of sites 1, 2, and 3. Line below common bars indicate no significant difference among them ( $p > 0.05$ ).

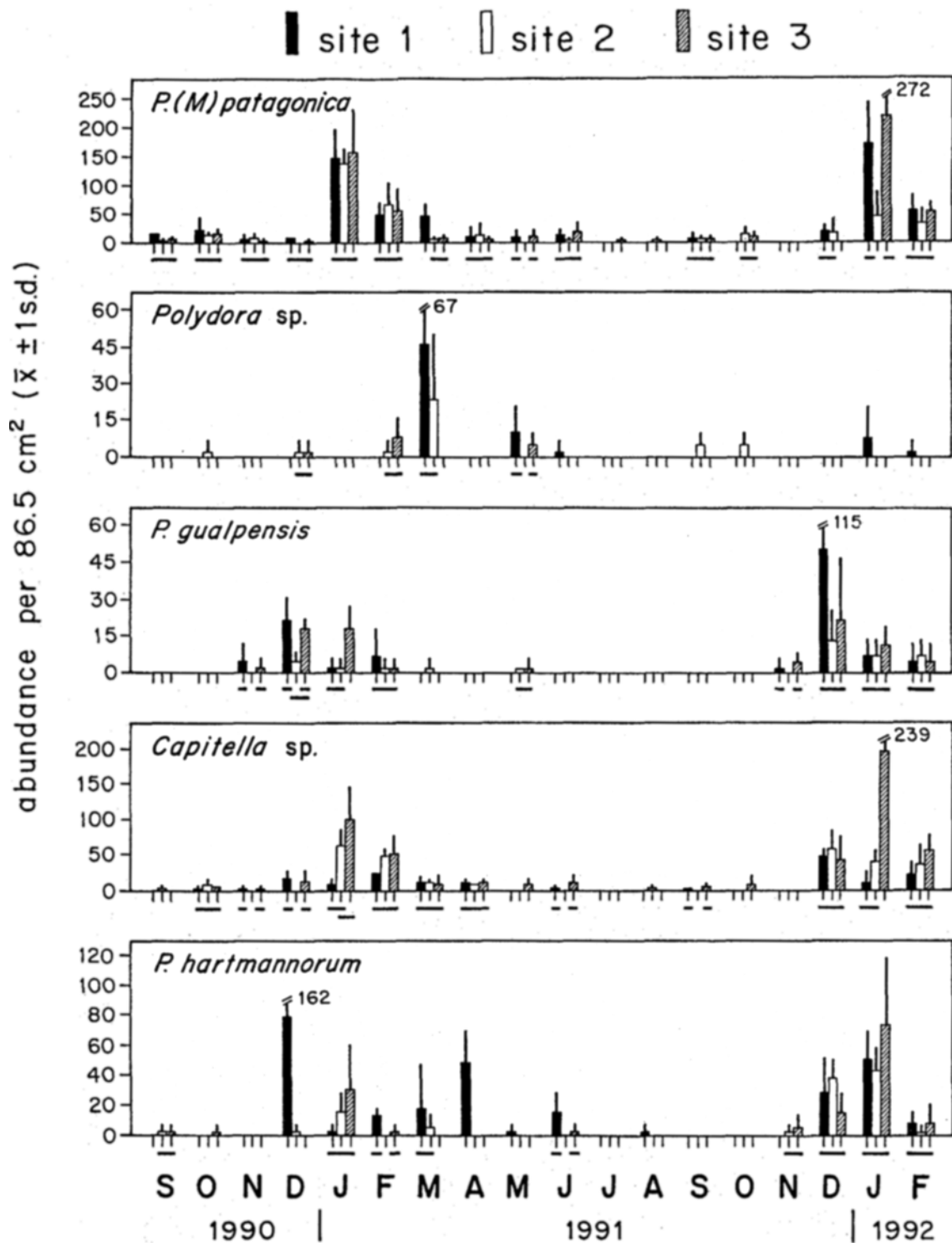


Fig. 7. Mean abundances of juveniles of the macrofauna in the sediments of sites 1, 2, and 3. Line below common bars indicate no significant difference among them ( $p > 0.05$ ).

TABLE 1. Summary of multiple regression analyses with monthly samples ( $n = 54$ ) collected at the areas 1, 2, and 3. The values given in this table (other than intercept values and multiple determination coefficient) are partial regression coefficients or values of each variable in the multiple equation. Values in brackets correspond to partial coefficients of determination at each step of the model.

	Variables	<i>Protopisio (Mimuspro) patagonica</i>	<i>Polydora</i> sp.	<i>Pemneris gualpensis</i>	<i>Capitella</i> sp.	<i>Paracorophium hartmannorum</i>	Total Abundance
Mode A	temperature						
	salinity		2.13 (0.16)	0.33 (0.18)		0.61 (0.16)	
	water chlorophyll <i>a</i>						
	sed. chlorophyll <i>a</i>						
	organic content			2.15 (0.13)			
	gravel	3.22* (0.25)**					2.71 (0.12)
	sand						
aggregates							
mud							
intercept	22.48	-31.37	-10.81		-7.63	56.34	
multiple R <sup>2</sup>	0.25	0.16	0.18		0.16	0.12	
Mode B	temperature						
	salinity		2.13 (0.16)			0.28 (0.16)	
	water chlorophyll <i>a</i>					0.49 (0.27)	
	sed. chlorophyll <i>a</i>						
	organic content			1.48 (0.40)	-1.14 (0.27)		
	gravel	2.84 (0.25)					
	sand						
	aggregates						
	mud						
	<i>P. (M.) patagonica</i>	N.C.		0.05 (0.14)	0.04 (0.19)		0.95 (0.70)
	<i>Polydora</i> sp.		N.C.	0.06 (0.45)			0.97 (0.94)
	<i>P. gualpensis</i>			N.C.		0.40 (0.20)	1.48 (0.97)
	<i>Capitella</i> sp.	5.01 (0.39)			N.C.		1.22 (0.98)
<i>P. hartmannorum</i>			0.23 (0.36)		N.C.	0.95 (0.98)	
recruits abundance							
intercept	9.03	-31.37	-6.25	5.80	0.82	3.51	
multiple R <sup>2</sup>	0.39	0.16	0.45	0.27	0.27	0.98	

N.C. = do not correspond.

\* = partial regression coefficient.

\*\* = partial determination coefficient (R<sup>2</sup>).

scribed above. In general, bivalve variability cannot itself explain the variability in infaunal abundances (Table 2). In addition, analyses carried out separately showed that the abundance of recruits was explained by water temperature and less frequently by chlorophyll *a* content (approaches A and B).

### Discussion

The results of this study suggest that hydrological conditions (primarily salinity) and some sediment characteristics have a relatively important role in the dynamics of the subtidal macroinfauna of the Queule River estuary. This conclusion does not support the predictions derived from the hypothesis of adult-larval interactions (Woodin 1976; Hines et al. 1989) or those from density-dependency relationships (e.g., Peterson and Black 1987) between suspension feeders such as bivalves and either juveniles or adults of the macroinfauna. These results are supported by the multiple regression analyses, which suggest a rather weak relationship between these biological variables.

The results agree with those reported for the same estuary by Jaramillo et al. (1985) and Quijón

and Jaramillo (1993), as well as with those of Beukema (1990) and de Vooys (1990) for coastal habitats in the northern hemisphere. Moreover, in opposition to the proposal of Bravo (1989) and other authors (e.g., Gray 1974; Bachelet 1986; Butman 1987), the recruitment pattern does not seem to be always the primary factor involved in macroinfaunal variability, since in only some cases were recruitment periods coincident with, or followed by, increases in macroinfaunal abundances.

Seasonal patterns of salinity and temperature can be related to rainfall levels and the input of river discharges. The temporal variability in chlorophyll *a* in the water was probably the result of the annual variability in phytoplankton biomass occurring during the warmer months and after the accumulation of nutrients of limnetic origin during the winter (Roman and Tenore 1978; Toro 1984). The increase of this pigment in the sediments followed the periods in which the maximum values of chlorophyll *a* were recorded from the water column, suggesting high rates of particulate matter sedimentation and biodeposition in this

TABLE 2. Summary of multiple regression analyses with monthly samples ( $n = 39$ ) collected at the areas 1, 2, and 3, and including the abundance of bivalves. The values given this table (other than intercept values and multiple determination coefficient) are partial regression coefficients or values of each variable in the multiple equation. Values in brackets correspond to partial coefficients of determination at each step of the model.

Variables	<i>Prionospio (Minuspio) patagonica</i>	<i>Polydora</i> sp.	<i>Penneris gualpensis</i>	<i>Capitella</i> sp.	<i>Paracorophium hartmannorum</i>	Total Abundance
Mode A						
temperature						
salinity		2.39 (0.16)	0.41 (0.35)		0.43 (0.14)	
water chlorophyll <i>a</i>						
sed. chlorophyll <i>a</i>						
organic content			2.58 (0.26)			
gravel	-5.81* (0.33)**					-7.03 (0.23)
sand	-15.06 (0.55)					-5.30 (0.42)
aggregates						
mud	-19.56 (0.43)					-10.34 (0.32)
intercept	555.41	-34.96	-14.13		-5.11	611.75
multiple R <sup>2</sup>	0.53	0.16	0.35		0.14	0.42
Mode B						
temperature						
salinity		2.39 (0.16)	0.41 (0.35)			
water chlorophyll <i>a</i>						
sed. chlorophyll <i>a</i>						
organic content			2.24 (0.77)		-1.24 (0.69)	
gravel	-4.17 (0.33)					
sand	-4.32 (0.60)					
aggregates						
mud	-8.15 (0.54)					
<i>P. (M.) patagonica</i>	N.C.			0.04 (0.26)		0.99 (0.73)
<i>Polydora</i> sp.		N.C.	0.05 (0.80)			1.06 (0.97)
<i>P. gualpensis</i>			N.C.		0.80 (0.64)	0.82 (0.99)
<i>Capitella</i> sp.	3.84 (0.47)		0.22 (0.82)	N.C.		0.91 (0.99)
<i>P. hartmannorum</i>			0.79 (0.64)		N.C.	1.50 (0.99)
recruits						
<i>Ch. chorus</i>						
<i>M. chilensis</i>						0.16 (0.99)
<i>M. edulis</i>						
intercept	555.41	-34.96	-18.68	1.12	5.08	0.84
multiple R <sup>2</sup>	0.53	0.16	0.35	0.26	0.69	0.99

N.C. = do not correspond.

\* = partial regression coefficient.

\*\* = partial determination coefficient (R<sup>2</sup>).

area of the estuary (Rojas 1984; Jaramillo et al. 1992).

As has been recorded for coastal habitats in the northern hemisphere (see Johnson 1977), the substratum characteristics remained relatively constant throughout time. This absence of temporal variability is similar to the results obtained for other subtidal and intertidal sites of this estuary and the Lingue River estuary (Jaramillo et al. 1985; Bertrán 1989; Bravo 1989; Quijón and Jaramillo 1993). The sediments of site 1 had higher contents of gravel than those for sites 2 and 3. This fraction was primarily represented by mica schists originating from the metamorphic basement of the southern border of the estuary (Pino and Mulsow 1983). The gravel that protrudes from the substratum, together with some shells and bivalve byssus, may affect water flow near the sediment-water interface and the stability of the sediments (see reviews by Rhoads and Boyer 1982 and Paterson and Daborn 1991). Thus, a trapping effect may explain the usu-

ally higher percentages of fine particles and organic matter estimated for the sediments of site 1 (Vos et al. 1988).

As suggested by Jaramillo et al. (1993), the supply of mytilid biodeposits does not contribute to the enrichment of the estuary bed due to the low resistance of pellets subjected to strong water currents of this area of the estuary. The observed differences in macroinfaunal abundances observed between sites 1 and 2 (characterized by similar abundances of mytilids), corroborate the role suggested for the gravel-size particles and the trapping effect of, for example, organic matter as suggested earlier. Consequently, the higher abundances of macroinfauna in the sediments of site 1 may be explained by its higher organic matter content as a result of protruding material.

Other factors, such as immigration processes or differential mortality as a response to the predation caused by, for example, fish and crabs (see reviews by Peterson 1979; Reise 1985; and Wilson

1991), could not be invoked to explain differences in abundances of *P. (M.) patagonica* and *P. gualpensis* between sites 1 and 2, since both areas were similar in biogenic structure (composition and abundance of bivalves). This assertion is made in view of the weak effects the bivalves seem to have on texture and nutritive value of the sediments, as well as the absence of recruits or adults of the macroinfauna attached to byssus threads. In addition, this conclusion is supported by the results of the multiple regression analyses using data from the three sites, in which the gravel content (in addition to salinity) emerged as one of the factors significantly associated with macroinfaunal variability.

The results of this study differ from those reported by Jaramillo et al. (1992) for the same estuary; that is, in this study the highest abundances of the macroinfauna occurred in sediments with clams. The causes of this difference may be in the size of the sampling devices used for each study. Jaramillo et al. (1992) collected samples with a 2-cm diameter cylinder, which may have been underestimating the abundance of the macroinfauna. Also, we sampled a more representative site (at least 25 times larger) than that study.

In general, most of the species showed a similar pattern of temporal variability. However, in the sediments of site 1, *P. (M.) patagonica* showed a different trend. This situation may be related to localized events of sediment disturbances (sensu Thistle 1981), as a consequence of the culture of mytilids (i.e., extraction activities). Such disturbances could promote mortality and recolonization processes (Grassle and Grassle 1974) by the adult macroinfauna into the sediment patches with the biogenic fabric mechanically altered. The same kind of anthropogenic activities could explain the amount of schists observed in some sediments of site 1; this material is used in the mussel bed culture because of its role as a natural collector of bivalve spats. In conclusion, our data support the proposed role of the hydrological and sedimentological characters in determining macroinfaunal features of this and the other microtidal estuaries so far studied (Jaramillo et al. 1985; Bertrán 1989; Low 1993; Quijón and Jaramillo 1993).

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