

## Community Structure of the Subtidal Macroinfauna in an Estuarine Mussel Bed in Southern Chile

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With 8 figures and 1 table

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**Abstract.** The mussels *Choromytilus chorus* and *Mytilus chilensis* are the most distinctive bivalves of the subtidal soft bottoms of Queule River estuary, southern Chile (ca. 40°S). In some artificially farmed areas of this estuary, the semi-buried mussels reach densities as high as 250–300 adult indiv. m<sup>-2</sup>. We carried out seasonal (1983) and fortnightly samplings (August 1984 to December 1985) to compare abiotic and biotic characteristics (*i. e.*, macroinfaunal community structure) on bottom areas with and without mussels. Biodeposition within the mussel bed area did not result in organic enrichment of the sediments, a situation which is discussed in relation to the breakdown of mussel biodeposits. During most of this study, organic matter (%) was higher in the sediments of this area versus that without mussels. While the sediments of the mussel and control area were dominated by the same macroinfauna (*i. e.*, polychaetes), that of the mussel area generally had lower abundances, number of species, and diversity indices. Several explanations are presented to account for diminished abundance and diversity values here. These include insufficient substrate for settling larvae, space limitation, and negative effects of sediment characteristics.

### Problem

Burrowing bivalves are widespread in marine, estuarine, and lacustrine soft-bottom environments (RHOADS & YOUNG, 1970; NIXON *et al.*, 1971; SEED, 1976; LEVINTON, 1977; TUNNICLIFFE & RISK, 1977; MCCALL *et al.*, 1979, 1982, 1986; ANDERSON & MAYER, 1984; SALZWEDEL *et al.*, 1985; COMMITO & BONCAVAGE, 1989; DITTMANN, 1990). Because of their size, abundance and sediment reworking, they may significantly affect physical and chemical properties of sediments, including grain size, water content, shear strength, and diffusion rates of some solutes in the interstitial space (LEVINTON, 1977; MCCALL *et al.*, 1979, 1982, 1986). Their protruding shells increase habitat heterogeneity (DITTMANN, 1990) and may also affect physical properties of sediments by perturbing water flow near the sediment – water interface as has been shown by the effect of protruding animal tubes on sediment stability (ECKMAN *et al.*, 1981; NOWELL *et al.*, 1981; RHOADS & BOYER, 1982). In turn, such physical heterogeneity may

provide the conditions for the growth of bacteria (cf., MILLS, 1967; ECKMAN, 1985), infaunal recruitment (e. g., ECKMAN, 1983), and refuge from predation to benthic organisms (e. g., WOODIN, 1978, 1981).

The mussels *Choromytilus chorus* (MOLINA) and *Mytilus chilensis* (HUPE) are the most distinctive bivalves of the subtidal bottoms of the Queule River estuary, southern Chile. In some artificially farmed areas of this estuary, the semi-buried mussels reach densities as high as 250–300 adult indiv. · m<sup>-2</sup>. Thus, space may be a limiting factor for infaunal organisms living here compared with areas lacking such densely packed bivalves. The soft substratum in these mussel beds can also be expected to have different physical and chemical characteristics than bare areas due to a higher content of mussel biodeposits. Therefore, these contrasting microhabitats are likely to accommodate differently structured infaunal communities. Accordingly, the objective of the present study was to investigate the influence of mussel abundance on the community structure of the macroinfauna at the subtidal soft bottoms located in the middle reach of the Queule River estuary.

## Material and Methods

### 1. Study site

The Queule River estuary (39° 24' S, 73° 13' W) is located in the southern part of Bahía de Queule (Fig. 1). It belongs to the drowned river valley or coastal plain estuary category (after PRITCHARD, 1967) with a sandy bar at its mouth. The maximum depth is approximately 12 m, while that of the main study sites is about 4 m. The tides are semidiurnal with tide differences close to 1.5 m. Water temperature follows a typical seasonal pattern, with the lowest values (10–11 °C) registered from early winter (June) to early spring (September) and summer highs of nearly 20 °C (unpublished data). The salinity follows a pattern similar to that of water temperature, i. e., the lowest values (0.5–2.0‰) occurred during June through September, the period with the highest rainfall. These

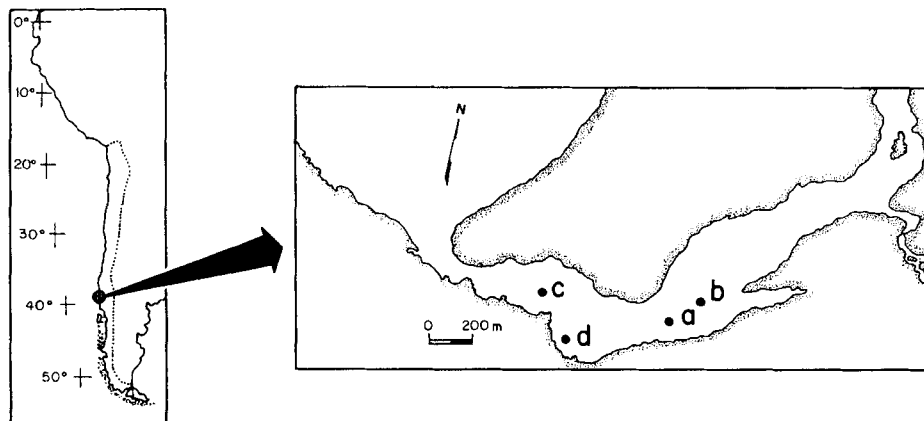


Fig. 1. Queule River estuary. Location of the mussel (station a) and control area (station b) in the middle reach of the estuary. Stations c and d were also examined (water current profiles) for comparative purposes.

low salinities are primarily registered at the surface waters and during low tide. Salinities of up to 28.5‰ have been registered at the bottom waters of the study site (unpublished data).

The investigated mussel site had an approximate area of 25,000 m<sup>2</sup> (200 × 125 m) and was located at the middle reach of the estuary (station a in Fig. 1). It was represented by numerous semi-infaunal mussels and by a bouchôt system (5 × 60 m) in which trays filled mostly with *Choromytilus chorus* were suspended about 1 m above the bottom. During this study, the number of mussels in this system was about 100,000. The semi-infaunal *Choromytilus chorus* and *Mytilus chilensis* had a mean density of approximately 200 and 70 indiv. · m<sup>-2</sup>, respectively. Shell length in *Choromytilus chorus* was 8–112 mm (mode: 83 mm) and 8–94 mm in *Mytilus chilensis* (mode: 77 mm). A control area without mussels, neither semi-infaunal nor artificially farmed (station b in Fig. 1), but similar in depth to the mussel farming area, was located about 200 m away. There was no major source of water pollution at the sites surrounding either area.

## 2. Sampling and analytical procedures

Five replicates of sediments for macroinfaunal analyses were seasonally collected by SCUBA divers at the mussel and control area during 1983. A fortnightly sampling was carried out during most of the period August 1984 – December 1985. Replicate sediment samples were collected among clusters of mussels with plastic cylinders (2 cm in diameter) inserted to a depth of 3 cm. The replicates were randomly collected about 1 m from one another. Due to the small sample size, no large macroinfauna – mussels and the clam *Mulinia edulis* (KING) – was collected. The epibenthic crab *Hemigrapsus crenulatus* (MILNE EDWARDS), a common mussel bed inhabitant, was also absent from the samples. The sediment was sieved through a 500 µm mesh net, preserved in 10 % formaldehyde, and sorted for abundance, species richness, and diversity figures. The latter index was calculated by using the SHANNON Index as quoted by BROWER & ZAR (1977).

Three replicates of sediments for determination of total combustibles were seasonally obtained by SCUBA divers at the mussel and control area during 1983. This sampling schedule also followed a fortnightly schedule during most of the period August 1984 – December 1985 (five replicates during the fortnightly sampling). A plastic cylinder was used as above. The percentage of combustibles was determined as the loss in weight of dried samples (60 °C, 96 h) after combustion (550 °C, 6 h). During 1985, we also studied the textural characteristics of the sediments at the mussel and control area. Five replicates of sediments were collected fortnightly with the same methodology as indicated for the determinations of combustibles. Textural analyses were carried out to determine percentages of gravel, sand, mud and aggregates (ANDERSON *et al.*, 1981). These values, together with the community parameters, were compared by using a non-parametric analysis of variance (KRUSKAL-WALLIS test; SOKAL & ROHLF, 1969), as some of our data did not satisfy the assumptions of ANOVA.

The effect of tides on the deposition and resuspension of mussel biodeposits was indirectly measured through determinations of percentages of combustibles at the near fluid, fecal-rich surface of the sediment/water interface during flood and ebb tides. We assumed that most of this material was represented by mussel biodeposits. Five replicates were collected by SCUBA during April and September, 1987 (spring tides). The sampling device was a sled-like sampler calibrated to sample 8 cm<sup>2</sup> (0.5 cm deep) of the sediment/water interface.

The disintegration of mussel biodeposits as a function of transport distance was determined in a circular flume. The flume had a 33 cm outside diameter and consisted of two concentric water channels. The outer channel was 9.5 cm wide. Water flow was generated by a circulating pump connected to a rheostat for water current control. Mussel biodeposits were used immediately after production and placed in the outer channel. Water velocity was increased steadily to the current level measured in the field. The length of experimental biodeposits was measured after 30, 60, and 90 m of transport. The changes in biodeposit size were used as rates of disintegration.

Mussel biodeposit disintegration was analyzed in relation to estuary current characteristics. Current profiles were measured at surface, middle, and bottom waters of the mussel area during summer (January 1987) and winter conditions (June 1987) and during different tidal stages. For comparative purposes, we also measured current profiles during flood and ebb tides at two other stations (November 1987). The first was located at the main channel of the estuary (station c in Fig. 1), the second at a protected cove with a mussel culture (station d in Fig. 1). All these studies were carried out during spring tides.

## Results

### 1. The sediment

Sand and silt-clay particles (*i. e.*, mud) dominated the sediments at the mussel and control area (Fig. 2). Larger particles dominated at the former area, with gravel percentages ranging from 0.6–28.0‰. The gravel-sized particles primarily consisted of broken shells of mussels and barnacles (*Elminius kingii* GRAY). Generally, the percentage of aggregates (*i. e.*, fecal pellets, small polychaete tubes) was higher at the control area, with apparent peaks during spring months. No clear trend was observed in the temporal variability of gravel, sand, silt-clay,

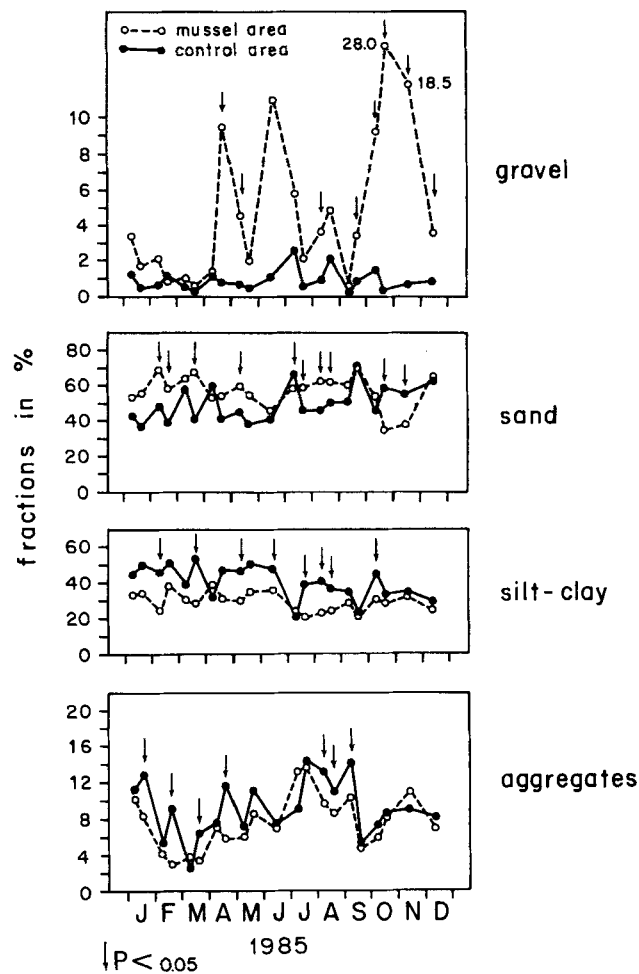


Fig. 2. Temporal variability in the mean percentages of gravel (> 0 phi), sand (> 4 phi), silt-clay (< 4 phi), and aggregates in the sediments of the mussel and control area. Significant differences ( $P < 0.05$ ) between means are indicated by arrows.

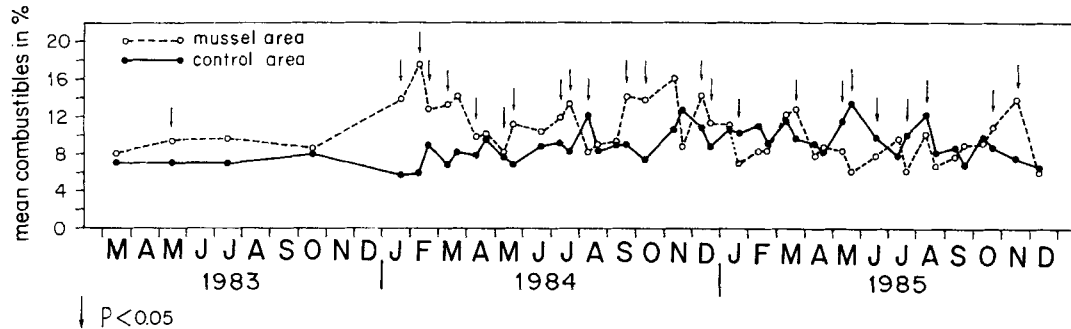


Fig. 3. Temporal variability in the mean values of total combustibles (*i. e.*, organic matter) in the sediments of the mussel and control area. Significant differences ( $P < 0.05$ ) between means are indicated by arrows.

Table 1. Percentage of total combustibles (*i. e.*, organic matter) in the near fluid, fecal-rich surface (*i. e.*, 0.5 cm) of the sediments at the mussel and control area. The values are means  $\pm$  1 standard deviation. Means marked with asterisks were not significantly different ( $P > 0.05$ ) in the tidal period comparisons. No significant inter-station differences were detected, either at flood or ebb tides. Statistical comparisons carried out with one-way analysis of variance.

	autumn (April, 1987)		spring (September, 1987)	
	flood tide	ebb tide	flood tide	ebb tide
mussel area	10.00 (1.24)	8.00 (0.84)	8.87* (1.59)	7.20* (0.88)
control area	8.90* (0.60)	9.42* (0.78)	6.62 (0.95)	8.41 (0.81)

and silt-clay sized particles. During 1983 and most of 1984, the percentage of combustibles (*i. e.*, organic matter) was significantly higher in the mussel area sediments, with values as high as 16–18% (Fig. 3). During most of 1985, the sediments of both areas had a similar percentage of combustibles. This content at the mussel area decreased significantly ( $P < 0.05$ ) through time ( $r = -0.496$  in the regression analysis between percentage of combustibles and cumulative number of months). No significant changes were found in the control area ( $r = 0.248$ ).

Table 1 shows that no significant differences were found between the content of combustibles at the near fluid, fecal-rich surface of the mussel and control areas, either during the flood or ebb tides of April and September 1987. During April, the sediment-water interface of the mussel area had a higher content during the flood tide compared with the ebb tide. During the September ebb tide, the percentage of combustibles at the near fluid, fecal-rich surface of the control area was higher than during the flood tide.

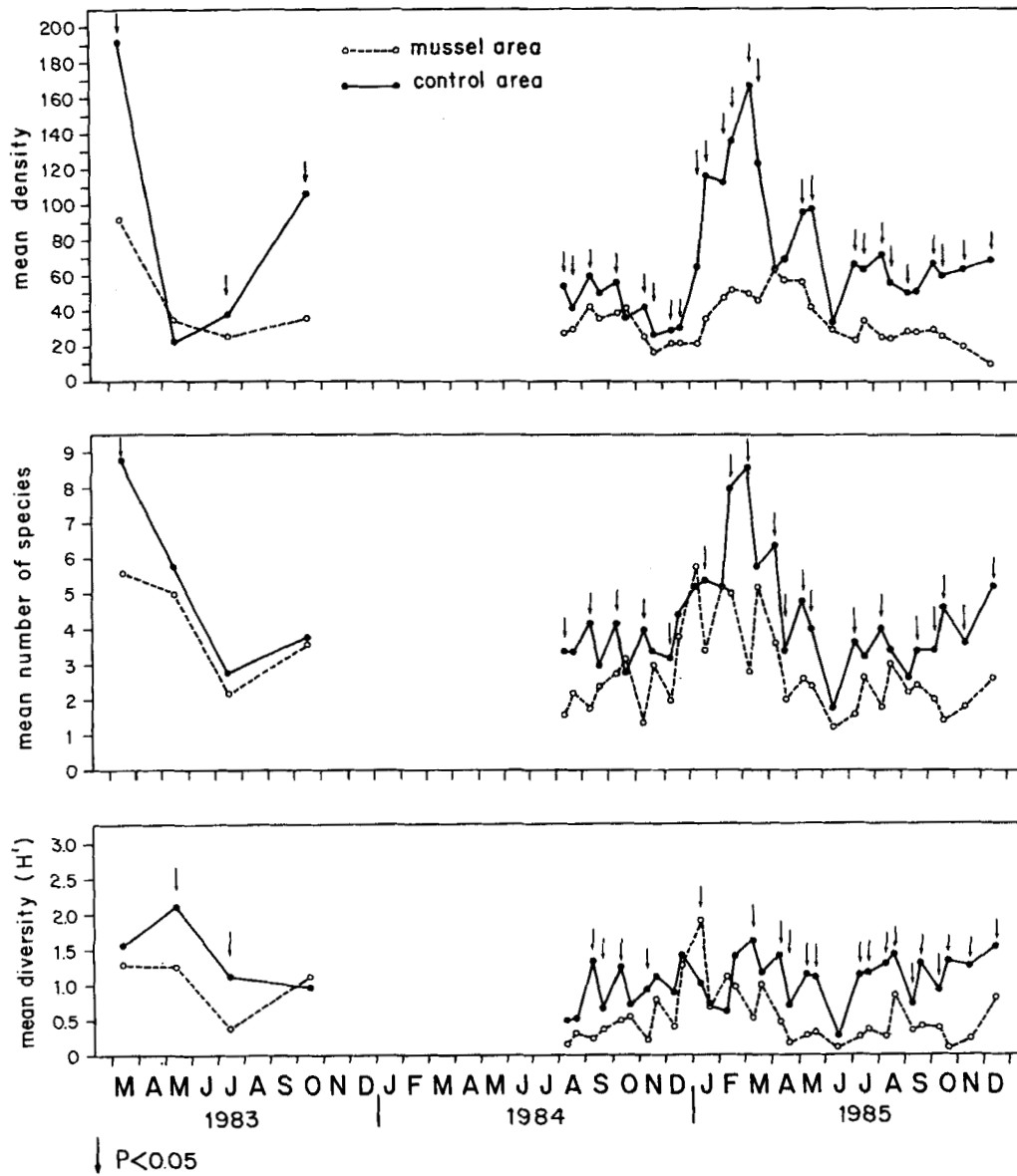


Fig. 4. Temporal variability in the mean densities, mean number of species, and mean diversities in the sediments of the mussel and control area. Significant differences ( $P < 0.05$ ) between means are indicated by arrows.

Fig. 5. Temporal variability in the abundance of the most abundant macroinfaunal species in the sediments of the mussel and control area. Significant differences ( $P < 0.05$ ) between means are indicated by arrows. The asterisks indicate samplings in which no statistical analyses were carried out because no animals were collected at one of the areas.



## 2. The macroinfauna

Twelve taxa were collected during this study. The most abundant species were the spionid polychaetes *Minuspio chilensis* HARTMANN-SCHRODER and *Polydora* sp., followed by one capitellid worm, one nereid polychaete (*Perinereis gualpensis*, JELDES), and one amphipod (*Paracorophium hartmannorum*, ANDRÉS). The other taxa collected were two polychaetes of the families *Orbiniidae* and *Glyceridae*, the amphipod *Cheus* sp., the ostracod *Cyprideis beaconnensis* LEROY, and juveniles of the bivalves *Mulinia edulis* (KING) and *Tagelus dombeii* (LAMARCK).

Figure 4 shows the temporal variability of the macroinfauna in the mussel and control area. During most of the study, the sediments of the control area had higher mean macroinfaunal abundances (up to 167–192 indiv. · 15.9 cm<sup>-2</sup>), mean number of species (8.6–8.8 spp. · 15.9 cm<sup>-2</sup>), and mean diversity values ( $H'$ : 1.6 – 2.1 · 15.9 cm<sup>-2</sup>) than those of the mussel area. In general, the highest values were recorded during summer months (January–March), especially with regard to abundance and number of species (Fig. 4).

Figure 5 shows the temporal variability of the most abundant taxa at both areas. *Minuspio chilensis*, *Perinereis gualpensis*, *Paracorophium hartmannorum*, and the capitellid species were collected during most of this study, while *Polydora* sp. was mostly restricted to the summer – autumn seasons of 1983 and 1984–1985. Generally, the abundances of these species were significantly higher in the control area, with peaks of abundance during the summer – autumn months.

## 3. Disintegration of mussel biodeposits

Fresh experimental fecal pellets of adult *Choromytilus chorus* (shell length ca. 80 mm) had a mean length of 7.82 mm (s. d. 1.72 mm, n = 15), while that of adult *Mytilus chilensis* (shell length ca. 70 mm) averaged 8.32 mm (s. d. 1.97 mm, n = 15). No significant differences were found between the mean lengths of both pellets (one way ANOVA,  $P > 0.05$ ). Most of the experimental biodeposits decreased 50 % after 30 m of bed load transport in the circular flume (Fig. 6). After 90 m, all but one pellet had a length equal to or less than 50 % of their initial length. Thus, the biodeposits of both mussels had a similar resistance to experimental disintegration conditions.

## 4. Current velocities

Figure 7 shows that in the mussel area the highest current velocities (up to 35 cm · sec<sup>-1</sup>) occurred during the ebb tide period for both sampling periods. In general, current velocities decreased from surface to bottom waters. Inter-site comparisons showed the lowest velocities at the most protected site (station d), the highest (up to 60 cm · sec<sup>-1</sup>) at the main channel of the estuary (station c)

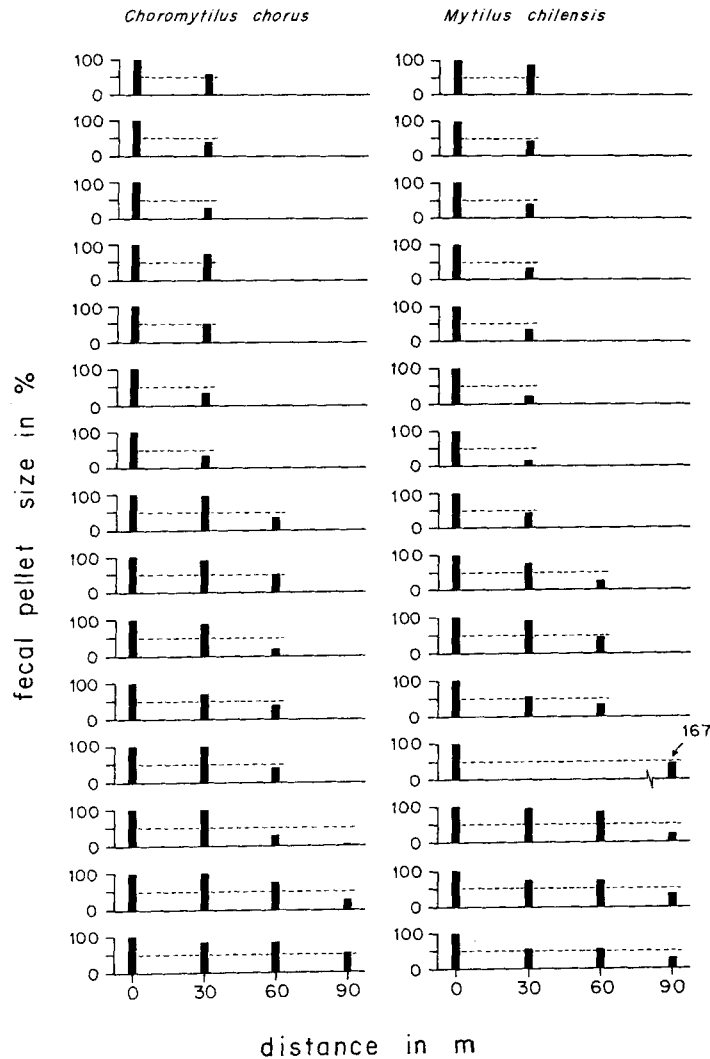


Fig. 6. Disintegration of biodeposits of *Choromytilus chorus* and *Mytilus chilensis* in relation to distance moved in the experimental chamber. Broken lines of each graph represents a 50% decrease in size (*i. e.*, disintegration) compared with that measured at the beginning of each trial (100%).

(Fig. 8). During the flood tide, the current velocity increased from surface to bottom waters at the three compared stations. During ebb tide each station behaved differently: no water movement was detected at station d, current velocity decreased from surface to bottom waters at station c, while it decreased from surface to middle waters and then increased from that depth to the bottom at station a (the mussel area) (Fig. 8).

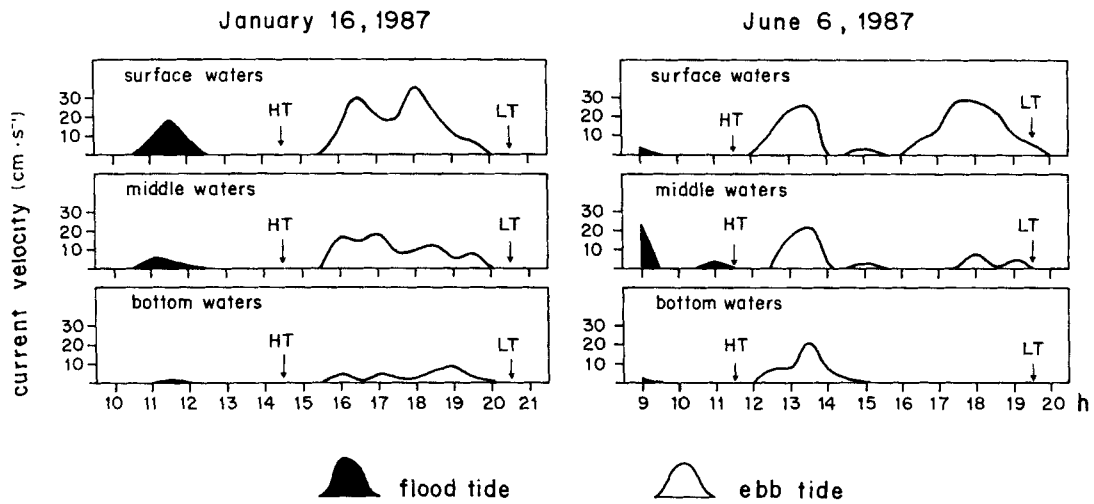


Fig. 7. Current velocities at the surface, middle (ca. 1 m), and bottom waters (ca. 3 m) of the mussel area during summer and winter conditions.

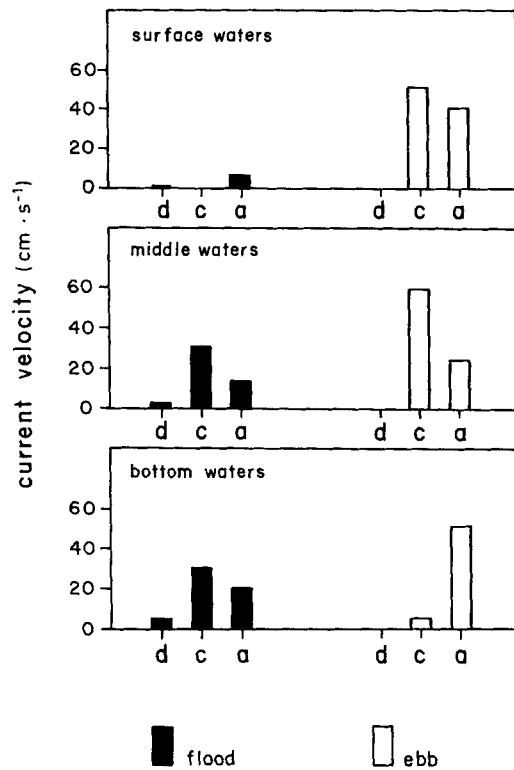


Fig. 8. Current velocities at the surface, middle (ca. 2 m), and bottom waters at different estuary sites (cf. Fig. 1) (spring conditions). Bottom waters of station a were ca. 3 m, those of station c ca. 5 m, while those of station d were approximately 3 m.

## Discussion

This study has shown significant differences in the macrofauna community structure between mussel-occupied bottoms of the middle reach of Queule River estuary and bare substratum. During most of the study period, macrofaunal abundances, number of species, and diversity indices were significantly greater on the bottoms without mussel beds. Similar results were reported by DITTMANN (1990), who contrasted the macrofauna of mussels beds and sand flats of the North Sea. The extent to which the between-habitat differences found here are directly related to the presence of mussels themselves remains to be studied. However, several explanations may be proposed to account for differences.

Biodeposit accumulation, increase in particle size (through broken shells of mussels and barnacles), and bed roughness are the most obvious evidence of the heterogeneity produced by mussels on the surrounding substrate. The results of the inter-site comparisons performed during flood and ebb tides of April and September 1987 showed no differences in the biodeposit content between the sediment / water interface of the mussel bed and the bare substratum. The water current velocities were probably strong enough to homogenize this material across a bottom field far beyond the mussel area. Moreover, the laboratory experiments showed that mussel biodeposits are easily broken upon transport over a smooth bottom such as that of the experimental chamber. An even higher rate of biodeposit disintegration might be expected under natural conditions due to the rougher bottom. Therefore, mussel biodeposits will probably not accumulate on the mussel beds here, and their role in the observed macrofaunal differences should be negligible. Conversely, mussel biodeposits may accumulate at very protected areas like station d (Fig. 1), where the current was the weakest (Fig. 8). Moreover, one can predict that areas of the estuary with the strongest water currents, *e. g.*, station c (Fig. 1), should have the lowest accumulation of biodeposits.

The results of the inter-site comparisons carried out during flood and ebb tides of April and September (*i. e.*, no significant differences in the percentages of organic matter between the mussel and control area) were different from those found in the 34 months (March 1983 – December 1985) routine sampling. In some of the latter samplings, the organic matter content in the mussel bed sediments was higher than that in the bare bottom area. The observed differences were probably attributable to sampling procedures, *i. e.*, samples for the intersite comparisons came from the top surface of the sediments, while those collected for the periodic comparisons originated from a depth of 3 cm. Thus, during the periodic study we measured not only the organic matter which is easily moved across the surface itself (like that represented by the near fluid, fecal-rich surface), but also that which is trapped between the mussel shells and byssuses. Moreover, it is also possible that during neap tide periods, when the currents are weaker, mussel biodeposits accumulate in the mussel area. If their organic content is higher than the indigenous sediment, they will increase the organic content of that substrate. If this is the case, the diminished macrofauna in the mussel area may be related to the negative effect of sediment characteristics such as low oxygen and high sulfide levels. Such characteristics,

due to organic enrichment, have been mentioned for sediments of several mussel farming areas (*e. g.*, DAHLBÄCK & GUNNARSSON, 1981; MATTSON & LINDÉN, 1983).

The accumulation of organic matter associated with mussel farming has been suggested as a key factor structuring macroinfaunal communities of the underlying sediments (*e. g.*, TENORE *et al.*, 1982; MATTSON & LINDÉN, 1983). For example, the latter authors found that the replacement of the bivalve *Nucula nitidosa* SOWERBY by *Capitella capitata* (FABRICIUS) on the sea floor of a Swedish mussel farm coincided with an increase in organic matter produced by continuous mussel biodeposition. In contrast to their study, we did not detect a significant increase in the organic matter content of sediments or change in community structure (*e. g.*, changes in the rank of dominant species). Our data suggest that accumulation of mussel biodeposits is probably not an important factor influencing differences between the macroinfaunas of the mussel and control areas.

The inter-mussel sediment spots in the mussel area should act as macroinfaunal refuges against predation, *e. g.* by fishes, which apparently substantially affects the organization of the subtidal macroinfauna of this estuary (TURNER, 1988). The above argumentation would agree with the hypothesis that any structure that decreases the likelihood that a species living near or in it will die is a spatial refuge for that organism. Thus, the higher abundances and species diversities found, *e. g.*, in seagrass beds versus unvegetated sediments (THAYER *et al.*, 1975; ORTH, 1977; REISE, 1977; STONER, 1980; PETERSON *et al.*, 1984; SUMMERSON & PETERSON, 1984), in areas with *Diopatra cuprea* (BOSC) tubes versus areas without such structures (WOODIN, 1978), or at spots with fecal mounds of *Molpadia oolitica* (POURTALES) versus inter-mound areas (RHOADS & YOUNG, 1971) have been interpreted as being biological refuges against physical disturbance. Our results, however, sharply contrast with the above findings: higher abundances and diversities were found in the bare substratum and not in the mussel area with its inter-byssus and shell space. Perhaps the refuges that the mussel beds provide to predatory crabs (*Hemigrapsus crenulatus*) increase predation pressure on the macroinfauna here.

It is possible that broken shells and space limitation may affect macroinfaunal abundances in the mussel area. Large particles (mainly shell gravel) here could negatively affect normal larval settlement. Moreover, large particles, intermingled with byssal threads and mussel shells themselves, may restrict the movement of burrowing organisms and affect population abundances. This would be analogous to the situation in fiddler crabs (RINGOLD, 1979; BERTNESS & MILLER, 1984), whose abundance is (among other factors) related to the root density of salt marsh plants, or in juvenile *Carcinus maenas* (L.), whose predation impact on macroinfaunal invertebrates can be altered by eelgrass roots (REISE, 1977). Thus, macroinfauna community structure in the mussel area would be controlled by the ability of the species (specially small individuals) to burrow here. Even in those cases in which protruding mussel shells enhance larval settlement – as has been shown for physical barriers affecting the near-bed water flow (ECKMAN, 1983; PETERSON, 1986) – such structures would put a threshold on macroinfaunal abundances. An alternative hypothesis is that enhanced larval settlement actually results in high macroinfaunal abundances,

but that space limitation due to mussel shells, byssal threads, and shell gravel decreases this abundance via competition. A final explanation involves the effect of adult-larval interactions: one source of mortality for settling larvae in soft bottom habitats is consumption by suspension feeders and biogenic sediment turnover caused by burrowing forms (RHOADS & YOUNG, 1970; BRENCHLEY, 1981; WOODIN, 1983). One would therefore expect areas close to large suspension feeders or burrowing forms to have lower abundances of macrofaunal species – as in the sediments of the mussel area.

### Summary

Mussel biodeposition in a mussel bed area at the Queule River estuary did not result in organic enrichment of the sediments. This may be attributed to the high rate of biodeposit disintegration. During most of the study, the percentage of combustibles (*i. e.*, organic matter) was higher in the mussel bed sediments. This was not necessarily the effect of mussel biodeposit accumulation, since field studies (between-site comparisons during flood and ebb tides) showed no significant differences between the amount of organic matter in the near fluid, fecal-rich sediments surface (*i. e.*, 0.5 cm) of the mussel and control area. The macrofauna of both areas was dominated by the spionid *Minuspio chilensis* and one capitellid worm. The abundance of the whole macrofauna and that of the most characteristic taxa peaked during summer-autumn months. No changes were detected in the community structure of either area (*e. g.*, no changes in the rank of dominant species). The abundances, number of species, and diversity indices were generally lower in the mussel bed area. This condition may be related to negative effects of some sort of mussel-macrofauna interaction such as space reduction, adult-larval interactions, or changes in sediment characteristics.

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