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## Macrobenthos and Sedimentary Environments in a Malaysian Intertidal Mudflat of the Cockle Bed

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### Abstract

A quantitative survey (12 stations) of the intertidal soft bottom macroinfauna in the Selangor River estuary of the peninsular Malaysian west coast was conducted during December, 1986. A total of 56 species were collected, polychaeta being the dominant group in number of species (46.4%) and bivalve being the dominant group in density (51.1%). The Correspondence Analysis performed with the abundance data of the most abundant species rendered the ordination of three groups of stations (concordant with the Cluster Analysis performed with the abundance data of all species collected) in the Q-mode and three groups of species in the R-mode. The Group 1 stations were distributed in the middle of the area surveyed and were dominated by *Anadara granosa* and *Diogenes* sp. The Group 2 stations, in the lower part of the estuary, were predominated by four species of polychaeta, *Paraprionospio pinnata*, *Sternaspis scutata*, *Notomastus* sp. and *Nephtys* sp. The Group 3 stations were restricted to the upper part of the estuary and were dominated by one species of both the Family Lyonsiidae and the Family Ocyrodidae.

The ordination of stations by Correspondence Analysis (concordant with the Cluster Analysis) is fundamentally defined by coarse sand, medium sand, very fine sand and silt-clay percentage.

Between the three faunal groups, significant differences in sedimentological variables were detected. Group 1 was found in the habitat with a high proportion of very fine sand to silt-clay, Group 2 was found in the area containing a relatively high proportion of coarse sand and medium sand to silt-clay and Group 3 was found in the habitat with a silty substratum.

### Introduction

In peninsular Malaysia, the culture of the arcid bivalve mollusc *Anadara granosa* L., which is one commercially important marine product has a recent history. It, however, has spread rapidly throughout the mangrove areas of the west coast of peninsular Malaysia (Pathansali and Soong, 1958). Cockle is mostly cultured by sowing cockle spats transported from the areas where they occur naturally to the culture sites. The question arises then as to how to hold down the spat mortality to a minimum. Significant spat mortality in the culture sites depends on the size of the spats as well as the time taken to transport them. However, it can also be attributed to the suitability of the culture bed, as well as to predation by fish or boring gastropods (Oon, 1984). The suitability of sedimentary environments in the

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culture sites is uncertain because virtually nothing is known of the ecology of the intertidal mud flats which form the cockle habitat.

Macrobenthos and sedimentary environments in the intertidal mud flat were observed to provide background information to assess the suitability of this environment as a cockle culture bed that might sow the cockle spats.

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### Materials and Methods

This research was carried out at the Selangor River estuary on the west coast of peninsular Malaysia (Fig. 1). In December 1986, two samples of the macrobenthos were taken from each station using a Ekman-Birge grab sampler of a 225 cm<sup>2</sup> area. All organisms retained on the 1.0 mm mesh sieve were collected, sorted and counted. In order to determine size frequency, and total carbon and total nitrogen content in the sediment, a small amount of surface sediment in 2 cm obtained from the same grab samples as used in the collection of organisms was collected in a polyethylene bottle and frozen as soon as possible to prevent organic matter decomposition caused by micro-organisms. It was taken to the laboratory and after being melted and adequately prepared, total carbon and total nitrogen content were determined using a Yanagimoto C-N Corder MT 500 instrument and the size frequency of the sediment was mechanically sorted by a series of screens.

A hierarchical, agglomerative classification of the macrobenthos was carried out

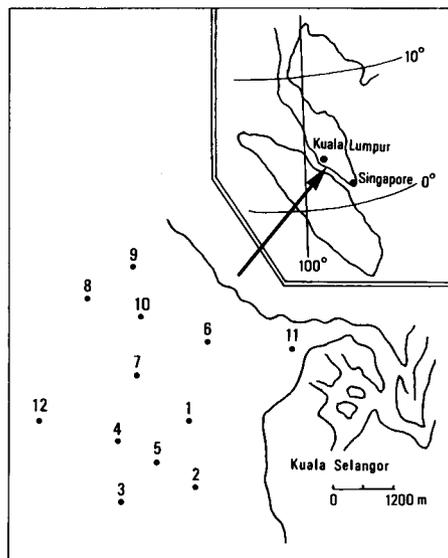


Fig. 1. Map showing the location of sampling stations at the Selangor River estuary in Malaysia.

to discern the station groupings using the Morisita similarity index (Morisita, 1959) using the a group average sorting method (Mountford, 1962) and for environmental variables, using the Euclidean distance method.

The abundance data of the 8 species occurring with frequency more than 1% in total number of individuals (Table 1) were subjected to Correspondence Analysis. This analysis was carried out to group and analyze trends in the distribution of stations (Q-mode) or of species (R-mode). In the Q-mode, the individuals are species and the variables are stations. This mode delineates groups of stations which have a similar quantitative species composition. This means that the members of a group should have similar numerical variations across individuals. In the R-mode the data matrix is transposed, and the individuals are now stations and the variables are species. This mode renders grouping of species which may be regarded as more or less associated due to their quantitative distribution throughout the stations (i.e. members of a group should have similar numerical variation across the stations).

In the case of environmental variables, the same method mentioned above was used, and species are now abiotic variables (e.g., total carbon, total nitrogen and size frequency in sediment) and individuals of species are now sedimentological percentage values.

In most benthic invertebrates, showing a general trend to aggregation, a log transformation was performed :

$$X = \log(\text{count} + 1)$$

(Elliot, 1971). Of the environment variables, those expressed as percentages were transformed by

$$X = \arctan \sqrt{P/(100-P)},$$

as recommended by Snedecor and Cochran (1967).

## Results

### *The macrobenthos*

The abundance of each species discovered at each station of 500 cm<sup>2</sup> is given in Table 1. Fifty-four species were obtained from the 12 stations sampled, which were composed of 26 species of polychaetes, 10 species of decapods, 7 species of both bivalves and gastropods, and 4 species of miscellaneous groups. In terms of frequency it is clear that the common frequent forms (>60% of frequency) are four species of polychaetes, *Nephtys* sp., *Paraprionospio pinnata*, *Sternaspis scutata* and *Notomastus* sp. and one species of bivalve, *Anadara granosa*, especially *P. pinnata* and *Notomastus* sp. were found in all the grab samples collected except for in two stations. In terms of abundance there are some changes in the most important species. The common dominant forms are two species of bivalves, *A. granosa* and ugly clam (Lyonsiidae), and one species of sand crab (Ocypodidae). It is clear that the common frequent polychaetes appear slightly aggregated, but the most important species in terms of abundance appear highly aggregated.

Table 1. Number of individuals at each station, total number of individuals (F<sub>1</sub>) and frequency at 12 stations (F<sub>2</sub>) of occurring species.

Species	Stations												F <sub>1</sub>	(%)	F <sub>2</sub>	(%)
	1	2	3	4	5	6	7	8	9	10	11	12				
<i>Pelagobia longicirrata</i>	—	—	—	1	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Eteone</i> sp.	—	—	—	—	1	1	—	—	—	—	—	—	2	0.3	2	16.7
<i>Phyllodoce</i> p.	—	—	—	—	—	—	—	—	1	—	—	—	1	0.2	1	8.3
<i>Sigambra ocellata?</i>	—	—	1	—	—	—	1	—	—	1	—	—	3	0.5	3	25.0
<i>Dendronereis arborifera</i>	—	1	—	—	—	—	—	1	1	2	—	—	5	0.8	4	33.3
<i>Nephtys</i> sp.	—	—	2	2	2	1	—	—	2	1	—	1	11	1.8	7	58.3
<i>Glycinde</i> sp.	1	—	—	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Glycera alba</i>	—	—	—	—	—	—	—	—	—	2	—	—	2	0.3	1	8.3
<i>Glycera</i> sp. A	—	—	1	—	—	1	—	—	1	—	—	—	3	0.5	3	25.0
<i>Glycera</i> sp. B	—	—	—	2	—	1	—	—	—	—	—	—	3	0.5	2	16.7
<i>Lumbrineris</i> sp. A	—	—	1	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Lumbrineris</i> sp. B	—	—	—	—	—	—	—	—	—	2	—	—	2	0.3	1	8.3
<i>Lumbrineris</i> sp. C	—	—	—	—	—	—	—	—	—	—	3	2	5	0.3	2	16.7
<i>Haploscoloplos</i> sp.	—	—	1	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Paraprionospio pinnata</i>	2	7	3	4	5	1	—	—	2	1	2	2	29	4.7	10	83.3
<i>Spio</i> sp.	—	—	—	1	—	—	—	—	—	—	—	—	1	0.2	1	8.33
<i>Magelona</i> sp.	1	—	—	—	—	—	—	—	—	1	—	—	2	0.3	2	16.7
<i>Poecilochaetus</i> sp.	—	—	—	1	—	—	—	—	—	—	—	2	3	0.5	2	16.7
<i>Spiochaetopterus costarum</i>	—	—	—	—	—	—	—	—	—	1	—	—	1	0.2	1	8.3
<i>Armandia</i> sp.	—	—	—	—	—	—	—	2	1	3	—	—	6	1.0	3	25.0
<i>Sternaspis scutata</i>	—	—	—	—	13	1	—	—	1	6	3	4	31	5.1	7	58.3
<i>Notomastus</i> sp.	1	3	2	1	3	1	3	—	1	4	—	1	20	3.3	10	83.3
Capitellidae A	—	—	—	1	—	—	—	—	—	1	—	—	2	0.3	2	16.7
Capitellidae B	—	—	—	—	—	1	—	—	—	1	—	—	2	0.3	2	16.7
Cirratulidae	—	—	—	—	—	—	—	—	—	—	—	2	2	0.3	1	8.3
Sabellidae ( <i>Chone</i> sp. ?)	—	—	—	—	—	1	—	—	—	—	—	—	1	0.2	1	8.3
<i>Anadra granosa</i>	18	—	2	23	86	—	6	5	1	—	—	—	141	23.0	7	58.3
Lyonsiidae	1	—	—	—	—	115	—	—	42	6	—	2	166	27.1	5	41.7
<i>Tellina incerta</i>	—	—	—	1	—	—	—	—	—	—	—	—	1	0.2	1	8.3
Tellinidae ( <i>Macoma</i> sp. ?)	—	—	—	—	—	—	—	—	1	—	—	—	1	0.2	1	8.3
<i>Theora opalina</i>	—	—	1	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Solen</i> sp.	—	—	—	—	—	—	—	—	1	—	—	—	1	0.2	1	8.3
Bivalvia A	—	—	—	—	—	—	1	—	—	—	—	—	1	0.2	1	8.3
<i>Plicarcularia</i> sp.	—	—	1	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Siphonalia</i> sp.	—	—	2	—	—	—	—	—	—	—	—	—	2	0.3	1	8.3
<i>Nassarius</i> sp.	1	—	—	—	—	—	1	—	—	—	—	—	2	0.3	2	16.7
<i>Zierhiana</i> sp.	1	—	—	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Zeuxis</i> sp.	—	—	—	—	—	4	—	—	—	—	—	—	4	0.7	1	8.3
Cerithiidae	—	—	—	—	—	—	—	—	1	—	—	—	1	0.2	1	8.3
<i>Mitrella</i> sp.	—	—	—	—	—	—	—	—	—	—	—	1	1	0.2	1	8.3
Ampellicidae	1	3	—	—	—	—	—	—	—	—	—	—	4	0.7	2	16.7
Gammaridae	—	—	—	—	—	—	—	—	—	1	—	—	1	0.2	1	8.3
Panaeidae	1	—	—	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
Palaemonidae	—	—	—	—	—	—	—	—	—	3	1	—	4	0.7	2	16.7
Hippolytidae	—	—	—	—	1	—	—	—	—	—	—	—	1	0.2	1	8.3
<i>Macrophthalmus</i> sp.	—	4	—	—	—	—	—	—	—	—	—	—	4	0.7	1	8.3
<i>Charybdis</i> sp.	—	—	1	—	—	—	—	—	—	—	—	—	1	0.2	1	8.3
Ocypodidae	—	—	—	1	1	65	—	3	19	20	—	—	109	17.8	6	50.0
Unidentified Decapoda A	—	1	—	2	—	1	—	—	—	—	—	—	4	0.7	3	25.0
Unidentified Decapoda B	—	—	—	—	—	—	—	—	1	—	—	—	1	0.2	1	8.3
Unidentified Decapoda C	—	—	—	—	—	—	—	—	—	4	—	—	4	0.7	1	8.3
<i>Diogenes</i> sp.	4	—	—	—	2	—	—	—	1	—	—	—	9	1.5	4	33.3
Ophiuroidea	—	—	—	—	—	—	—	—	2	—	1	—	3	0.5	2	16.7
Nemertinea	—	—	—	—	—	—	—	—	—	1	1	—	2	0.3	2	16.7
Number of individuals	32	19	23	40	115	195	11	15	75	57	13	18	613			
Number of species	11	6	14	12	10	14	4	7	14	17	6	10	54			

### Community types

A dendrogram made by classifying stations using values of the Morisita similarity index is presented in Fig. 2. When this dendrogram is arbitrarily truncated at a faunal similarity level of 0.3, a well defined distribution pattern of three groups appears. In Group 1 there are five stations located in the middle of the area sampled. Four stations in Group 2 are found from near the mouth of the Selangor River estuary to in the lower part of the estuary. Group 3 included three stations shows a distinct distribution in the upper part of the estuary (Fig. 2).

In order to search for relationships in species composition between these groups, Correspondence Analysis was applied. The first two vectors of Correspondence Analysis have eigenvalues representing 68.3% of total variance (I: 43.9%, II: 24.4%). In the Q-mode, Group 1, Group 2 and Group 3 stations are established (Fig. 3). In Group 1 there are 5 stations (Sts 1, 4, 5, 7 and 8) which correspond to stations of Group 1 in the dendrogram (Fig. 2). Group 2 includes four stations (Sts 2, 3, 11 and 12) and Group 3 includes three stations (Sts 6, 9 and 10) which correspond to Group 2 and Group 3 respectively represented in Fig. 2. In the R-mode for 8 species, Group 1, Group 2 and Group 3 are established (Fig. 3). In Group 1 there are two species (*A. granosa* and *Diogenes* sp.) and in Group 2, four species (*Notomastus* sp., *P. pinnata*, *S. scutata* and *Nephtys* sp.). In Group 3 ugly clam (Lyonsiidae) and sand crab (Ocypodidae) were found. In addition, in this analysis the situation of each group in the Q-mode corresponds to that of each group

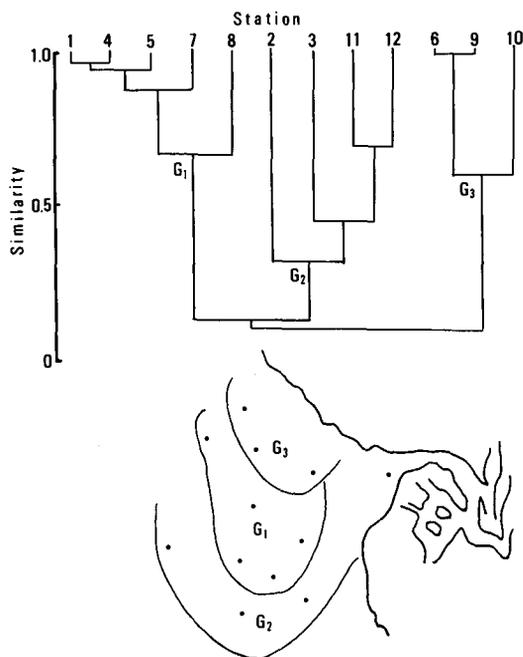


Fig. 2. Dendrogram produced by group average method with Morisita similarity index (upper) and spatial distribution of three groups of the stations (bottom).

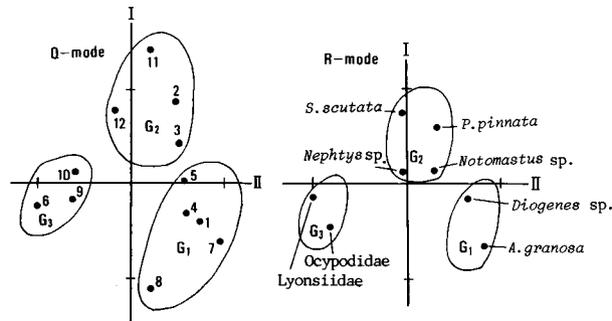


Fig. 3. Correspondence Analysis ordination of 12 stations (Q-mode) and 8 dominant species (R-mode) on components I and II. Stations are numbered 1 to 12.

in the R-mode. The Group 1 stations in the Q-mode are, therefore, also included in Group 1 in the R-mode, the Group 2 stations in the Q-mode, to Group 2 in the R-mode and the Group 3 stations in the Q-mode, to Group 3 in the R-mode.

The three macrobenthos groups and their geographic distributions (Fig. 2) can be summarized as follows:

1) Group 1 (*Anadara* type community). This is principally predominated by *A. granosa*. The other common species is *Diogenes* sp. The number of species is comparatively small (average no. = 8.8). This group was found in the middle of the area surveyed.

2) Group 2 (*Paraprionospio-Sternaspis* type community). In terms of abundance, there was no important species, but the common fauna which make a notable contribution include *P. pinnata*, *S. scutata*, *Notomastus* sp. and *Nephtys* sp. The number of species is similar to Group 1 (average no. = 9). The stations in this group are distributed from near the mouth of the Selangor River estuary to the lower part of the area sampled.

3) Group 3 (Lyonsiidae-Ocypodidae type community). In this group the number of species is larger than the number in the other two groups (average no. = 15) but in terms of abundance this group is principally predominated by two species, ugly clam (Lyonsiidae) and sand crab (Ocypodidae). This community shows a distinct distribution in the upper nearshore of the area investigated.

#### The bottom

Total carbon values of the sediment surface (0-2 cm) in the investigated area vary from 0.98 to 1.66% of total dry weight, with a mean of 1.32%. The higher carbon values are present off the mouth of the Selangor River estuary but the greater part of the investigated area is characterized by carbon values ranging between 1.4 and 1.0% (Fig. 4a). The distribution of total nitrogen in the sediments closely resembles the distribution of carbon (Fig. 4b). A large part of the investigated area had nitrogen values which do not exceed 0.12%. Values in excess of 0.12% are found at three stations off the estuary, recording a maximum of 0.15% at St 12.

The distribution of the percentage silt-clay fraction (< 63  $\mu$ m) in the sediments differs markedly from that of the other elements discussed (Fig. 4c). Values of high silt-clay content (> 50%) were found in the upper part of the estuary with lower



Fig. 4. Spatial distributions of total carbon (%) (a), total nitrogen (%) (b) and silt-clay (%) (c) content in the surface sediment.

carbon and nitrogen contents. Silt-clay contents ranging between 50 to 40% were present off the estuary with comparatively high values of the other elements and the lower side of the estuary had silt-clay values which do not exceed 40% with variable amounts of the other elements.

A dendrogram made by classifying stations produced by the Euclidean distance method is presented in Fig. 5. When this dendrogram is arbitrarily truncated at a sedimentary dissimilarity level of 130, a well defined distribution pattern with three groups appears. The stations included in the three groups and their distributions correspond to those of the three faunal groups (Fig. 2 and Fig. 3).

There was no significant difference between carbon values and nitrogen values in stations included in the three groups ( $P > 0.05$ ). Only size frequency data was, therefore, used for Correspondence Analysis to search the sedimentary characteristics between those groups discussed. The first two vectors of the Correspondence

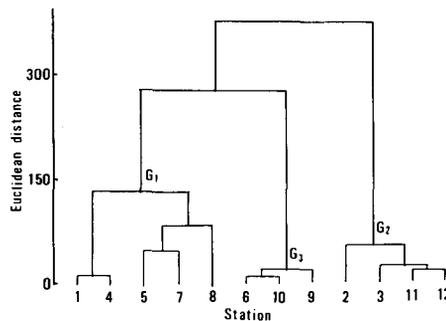


Fig. 5. Dendrogram of the Euclidean distance of sedimentological variables obtained by group average method.

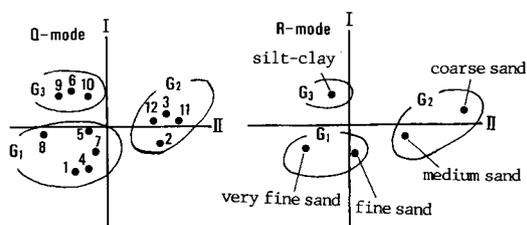


Fig. 6. Correspondence Analysis ordination of 12 stations (Q-mode) and particle size fractions (R-mode) on component I and II.

Analysis have eigenvalues representing 92.2% of total variance (I: 68.9%, II: 23.3%). In the Q-mode and the R-mode (Fig. 6), all three groups are established and stations included in each group in the Q-mode correspond to those of each group in the dendrogram (Fig. 5). In addition, corresponding groups in the two modes are situated in similar locations on vectors I and II in each mode. Three station groups differ significantly in size frequency values (Table 2). Group 1 stations (Sts 1, 4, 5, 7 and 8) in the Q-mode contain, therefore, a high proportion of very fine sand. Group 2 consists of four stations (Sts 2, 3, 11 and 12) containing a relatively high proportion of coarse sand and medium sand, in particular the mean coarse sand content in Group 2 is five times higher than that in the other groups and Group 3

Table 2. Particle size fractions with standard deviations (S.d) of means ( $\bar{x}$ ) at three group stations.

Bottom	G <sub>1</sub> $\bar{x}$ (S.d)	G <sub>2</sub> $\bar{x}$ (S.d)	G <sub>3</sub> $\bar{x}$ (S.d)
coarse sand (%)**	1.0(0.5)	5.3(1.2)	0.8(0.3)
medium sand (%)**	9.7(7.5)	16.0(1.2)	6.7(1.5)
fine sand (%)	15.7(5.4)	16.2(3.1)	10.8(0.1)
very fine sand (%)**	33.9(3.2)	15.4(1.0)	21.7(1.9)
silt-clay (%)*	39.8(6.1)	42.4(4.0)	60.1(1.2)

difference significant \* P<0.05, \*\* P<0.01

Table 3. Three type communities with important macrobenthos species and sediment particle size fractions.

	G <sub>1</sub>	G <sub>2</sub>	G <sub>3</sub>
Community type	<i>Anadara</i> community	<i>Parapionospio-Sternaspis</i> community	Lyonsiidae-Ocypodidae community
Species	<i>A. granosa</i> <i>Diogenes</i> sp.	<i>P. pinnata</i> <i>S. scutata</i> <i>Nephtys</i> sp. <i>Notomastus</i> sp.	one species of the Family Lyonsiidae one species of the Family Ocypodidae
Sediment	very fine sand to silt-clay	coarse sand and medium sand to silt-clay	mainly silt-clay

includes three stations (Sts 6, 9 and 10) with a silty substratum (>60% of silty-clay fraction).

### Discussion

The intertidal mudflats which border much of the west coast of the peninsular Malaysia cover an area of at least 40,000 ha. They constitute one of the major coastal systems of Malaysia and form a natural habitat base for at least one commercially important marine product, cockle, the arcid bivalve mollusc *Anadara granosa* (Broom, 1982). It is also possible that these mudflats could be an important sowing area for cockle spats although this is uncertain because virtually nothing is known of the ecology of these mudflats.

Broom (1982) carried out a survey initially to assess community composition and the functional roles of the dominant species in two intertidal areas of a Malaysian mudflat. One of them was adjacent (3°20'N, 101°14'E) to the present study area, the estuarine mudflats at the mouth of the Selangor River dominated by the natural population of *A. granosa*.

The most interesting aspect about the data obtained from the two surveys is the evidence of the existence of marked differences in the abundance and in the number of species, particularly in terms of the annelid polychaetes present. The numbers of species (56) and individuals (943 individuals m<sup>-2</sup>) obtained in the present study is higher than those (479 individuals m<sup>-2</sup> and 19 species) reported by Broom (1982). He pointed out that polychaetes were conspicuous by their absence, even in material passed through a 500- $\mu$ m sieve and the reason for their absence is uncertain. However, annelid polychaeta with 26 species collected in the present study area was the most important taxonomic group in the number of species. Even if some caution is paid to the difference in sampling sites and sampling time between these two surveys, the reason for their absence or existence is uncertain. While Broom (1982) reported that in terms of abundance, the important species were *A. granosa*, *Pelecypora trigona*, *Plicarcularia leptospina* and *Diogenes* sp. Apart from *A. granosa* itself, *Diogenes* sp. is the common dominant species but *Plicarcularia* sp. is very small in abundance in this study. *P. trigona* was not obtained but four species of polychaetes (*Nephtys* sp., *P. pinnata*, *S. scutata* and *Notomastus* sp.), one species of Lyonsiidae and one species of Ocypodidae are dominant species in the present study. It should be considered that these species which are often characteristic of such unpredictable environments as estuaries tend to fluctuate widely in abundance (Boesch et al., 1976). In this sense, those mentioned by Broom (1982) as dominant species could be dominant at another time of the year in the present study area.

In this study, the use of a Cluster Analysis and Correspondence Analysis has provided clear pictures of species distribution and station affinities, and of sedimentary gradient and station affinities in the Selangor River estuary. The Correspondence Analysis performed with the abundance data of the most abundant species rendered the ordination of three groups of stations (concordant with the Cluster Analysis performed with the abundance data of all species collected) in the Q-mode and three groups of species in the R-mode (Fig. 2 and Fig. 3). Similarly, Correspondence Analysis with the sedimentological variables rendered three groups in the Q-mode (concordant with the Cluster Analysis of the Euclidean distance method)

and in the R-mode respectively (Fig. 5 and Fig. 6). As the abundance data and sedimentological variables of all three groups of stations pointed out above include the same stations respectively (Fig. 2 and Fig. 3 or Fig. 5 and Fig. 6), the Group 1 stations (*Anadara* type community) in the dendrogram (Fig. 2) predominated by *A. granosa* and *Diogenes* sp. were distributed in the middle of the estuary with a high proportion of very fine sand, the Group 2 stations (*Paraprionospio-Sternaspis* type community) predominated by polychaetes (*P. pinnata*, *S. scutata*, *Nephtys* sp. and *Notomastus* sp.) were found in the lower part of the study area containing a relatively high proportion of coarse sand and medium sand. The Group 3 stations (Lyonsiidae-Ocypodidae type community) predominated by two species, ugly clam (Lyonsiidae) and sand crab (Ocypodidae) were distributed in the upper area of the estuary with a silty substratum. The relationships pointed out above between the macrobenthos divided into three faunal assemblages and sedimentary environments in the Selangor River estuary are shown in Table 3. The communities of the estuary could be conveniently described as faunal assemblages which when integrated with the environmental characteristics (Table 2) allow us to show the sedimentological characteristics of a cockle habitat. It may be said that a suitable bottom environment for a cockle habitat has a particle composition with a high proportion of very fine sand to silt-clay and without a coarse sand fraction such as the distribution area of the *Anadara* type community. If the large number of *A. granosa* as the dominant species of this community type indicates a high survival of its spats, the sedimentary environment described above may be suitable for sowing cockle spats.

Finally, in this study the trophic roles of the community's members which have some connection with bottom particle composition (Broom, 1982; Jaramillo et al., 1984; Eleftherious and Basford, 1989) were not surveyed. Furthermore important factors in the organization of a soft bottom community, for example, predation by fishes and removal of the substrate by epi- and infauna (Rhoads and Young, 1970; Virnstein, 1977; Woodin, 1981) should be examined in detail. Concurrently, it is necessary to survey seasonal variations on macrobenthos distribution and environmental conditions, in particular such unpredictable environments as estuaries in which species tend to fluctuate widely in abundance.

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