

Spatial Distribution of the Infaunal Benthos of Hong Kong

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ABSTRACT: Five replicate Smith-McIntyre grab samples were collected at 200 stations around Hong Kong. In a total of 1,000 samples, there were 10,142 specimens belonging to 139 animal species; mean density was 101.4 individuals m⁻², mean wet weight 35.2 g m⁻². Agglomerative hierarchical classification was used to delineate 5 station groups; these were related to environmental parameters by multiple discriminant analysis. Four station groups were separated along a salinity gradient extending from the Pearl River estuary in the west to more oceanic waters in the east. The 5th group was associated with coarser sediments in scoured tidal channels; it had the lowest diversity value and the highest numbers and biomass. The other 4 groups were highly diverse, biologically accommodated communities, despite the fact that Hong Kong has an annual temperature range from 15 to 30 °C, and bottom salinity may fall to 6.3‰ S in western waters when the Pearl River is in spate in summer. It is argued that biological interactions, involving keystone species, may have a controlling influence on community structure and diversity, and must be taken into account when infaunal communities are compared. In 4 of the station groups, low biomass may be partially accounted for by the preponderance of silt, a difficult sediment to colonise. Communities could be named after the 3 most dominant species in each group, but there seemed to be little purpose in doing so because fidelity was low. Although central Hong Kong receives very large quantities of untreated sewage, the effects of this were not evident in the benthos and this is attributed to dispersion by strong tidal currents.

INTRODUCTION

In shallow tropical seas, recent studies of the infaunal benthos have yielded results that conform to the 'stability-time hypothesis' of Sanders (1968, 1969). In stable environments, a diverse 'biologically accommodated community' may evolve as biological interactions become more complex, but this process is prevented by periodic physiological stress in 'physically controlled communities' exposed to large seasonal fluctuations in environmental factors. For example, Stephenson et al. (1970) described diverse and ill-defined communities from Moreton Bay, Australia, but Stephenson and Williams (1971) found low diversities in Sek Harbour, Papua New Guinea, which they attributed to the likely effect of seasonal rainfall and estuarine inflow. Wade (1972) found a highly diverse community in a stable environment at Kingston Har-

bour, Jamaica, in which dominance by a few species was greatly reduced, but Rosenberg (1975) reported lower diversities in a community exposed to a temperature range of 19 to 30 °C and high turbidity, at Biscayne Bay, Florida (USA).

Two problems arise from the above conclusion. First, the 'stability-time hypothesis' has been criticised and amended by subsequent workers. Thus, Dayton and Hessler (1972) presented evidence that intense predation can maintain high diversities, while Huston (1979) has argued that diversity reflects the interaction of population growth rates and frequency of disturbance, with maximum diversity occurring when disturbance is just frequent enough to prevent competitive interactions between expanding populations. Second, the data base for tropical benthos is small. Previous workers have all commented on the paucity of data from tropical and subtropical waters, and Wade (1972) drew particular attention to the need for a better understanding of the effects of fluctuations in salinity and dissolved oxygen.

The present paper evaluates a survey of the infaunal

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benthos of the coastal waters of Hong Kong, a subtropical area that presents interesting variations in salinity, dissolved oxygen and temperature. Hong Kong lies on the eastern shore of the Pearl River, which drains an area of about 4.4×10^5 km² in southern China and flows in spate during the summer, when rainfall is high (Williamson, 1970). In consequence, almost isohaline conditions prevail throughout Hong Kong waters in winter, with mean bottom salinities of about 32‰ S, but in summer there are 3 generalised regions. These are a western estuarine region, a central mixing region, and an eastern, more oceanic region, in which minimum bottom salinities are 6.3, 17.1 and 25.8‰ S respectively (Watts, 1973; Morton and Wu, 1975). Reduced dissolved oxygen values occur in Victoria Harbour, in the central mixing region, which receives about 280×10^6 tonnes yr⁻¹ of untreated sewage from 3.4 million people. There is a pronounced oxygen sag through the Harbour but, because tidal currents are strong, dissolved oxygen values rarely fall below 50 % saturation in unenclosed waters (Oakley and Cripps, 1972). Although Hong Kong lies within the tropics, the interaction of monsoon winds and ocean currents causes a seasonal variation in sea temperature, from about 15°C in winter to 30°C in summer (Watts, 1973; Morton and Wu, 1975).

MATERIALS AND METHODS

Field Sampling

Five replicate 0.1 m² Smith-McIntyre grab samples were collected at each of 200 stations around Hong Kong (Fig. 1) in July, August, September and November 1976 and January 1977. Positions were fixed by radar and depths by echo-sounder. Of the 200 stations, 26 were visited at regular 2 month intervals

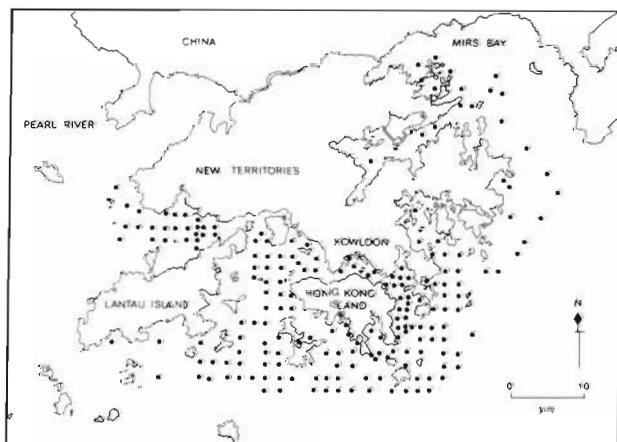


Fig. 1. Map of Hong Kong, showing sampling locations and place names mentioned in text

from November 1975 to January 1977, and analysis of the data showed that although seasonal changes occurred, they may be discounted in the present work (Shin, 1977). The grab was weighted with 54 kg of lead and was completely filled at most stations; on harder bottoms it was assumed that an area of 0.1 m² was sampled although the grab did not dig to its full depth. Samples were gently sieved on a screen of mesh size 0.40 ± 0.02 mm and preserved in 5 % borax-buffered formalin. A sixth grab sample was collected at each station for particle size and organic content determinations, and sub-samples were later analysed for trace metal content by Yim (Phillips and Yim, 1981). Samples for organic content determination were frozen at -20°C until analysed, except that those collected in the final cruise (January, 1977) were lost in a freezer failure.

Laboratory Analysis

Faunal samples were sorted under a low-power microscope and animals were identified to species and counted, using the following authorities: Polychaetes: Fauvel (1923, 1927); Imajima and Hartman (1964); Day (1967); Gallardo (1967); Fauchald (1967, 1977); Molluscs: Kira (1965); Habe (1968); Crustaceans: Sakai (1965); Banner and Banner (1966); Echinoderms: Clark and Rowe (1971); Fishes: Institute of Zoology, Academia Sinica (1962).

Biomass was determined as g m⁻² preserved wet weight, for selected stations only, because many specimens were set aside for taxonomic confirmation. Particle-size analysis was carried out by the sedimentation technique of Bouyoucos (1951), and sediment organic content was estimated as the loss in weight of sediment, dried at 100°C to constant weight, after combustion at 500°C for 8 h.

Data Processing

Species diversity H' and evenness J were calculated for pooled data from each set of 5 replicates, using the formulae:

$$H' = - \sum_{i=1}^s (N_i/N) \log_2 (N_i/N) \quad (\text{Shannon and Weaver, 1963})$$

$$J = H'/\log_2 s \quad (\text{Pielou, 1966})$$

where s = total number of species; N = total number of individuals; N_i = number of individuals of the i th species.

The relationship between sampling stations was determined using agglomerative, hierarchical classifi-

cation (Clifford and Stephenson, 1975). The 5 replicate faunal samples at each station were pooled and species which occurred only at one station were excluded. The remaining data were logarithmically transformed ($\ln [x + 1]$) before being subjected to classification using the Bray-Curtis similarity index (Bray and Curtis, 1957) and the group-average sorting method (Clifford and Stephenson, 1975).

The grouping of stations that resulted from the normal classification method, as described above, was assessed by the pseudo- F test (Williams and Stephenson, 1973). The calculated F value was listed for frequently occurring species (total > 50 individuals from all stations) in order of the magnitude of their contribution to the different station (site) groups. For each species, mean abundance in each station group was also listed. Dominant species were defined by rank-score analysis (Fager, 1957). A 5-point system was used in which 5 points were assigned to the most abundant species in a given sample, 4 points to the next, and so on. The scores from all the stations within a particular site group were summed and listed as a 'biological index' (BI).

Multiple discriminant analysis (Davies, 1971; Shin, 1982) was carried out to correlate the station group separation with 4 environmental variables: sediment particle size distribution (expressed as $\arcsin \sqrt{\% \text{ silt-clay}}$), organic content ($\arcsin \sqrt{\%}$), depth and mean bottom salinity. The last variable was not determined during the survey, because of seasonal changes, and a relevant data set was obtained from Public Works Department, Hong Kong Government (1979) for 38 stations, and from Dr. M.T.L. Chiu (pers. comm.) for 12 stations. This covered the period January 1975–June 1976, i.e. the period of 18 mo immediately preceding the survey, and it was assumed that at each benthos station, mean bottom salinity was the same as at the nearest salinity station. A similar assumption was made for the missing values for organic content.

RESULTS

Sediments

Particle-size distribution is summarised in Fig. 2, as % silt-clay. Fine sediments, >90% silt-clay, were found at most stations; coarser sediments, <80% silt-clay, mainly in scoured tidal channels between Lantau Island and the New Territories, and around the eastern coast of Hong Kong Island. Intermediate values, 80 to 90% silt-clay, were recorded mainly between Lantau and Hong Kong Islands, in an area of intermediate tidal flow.

Organic content distribution is shown in Fig. 3; sta-

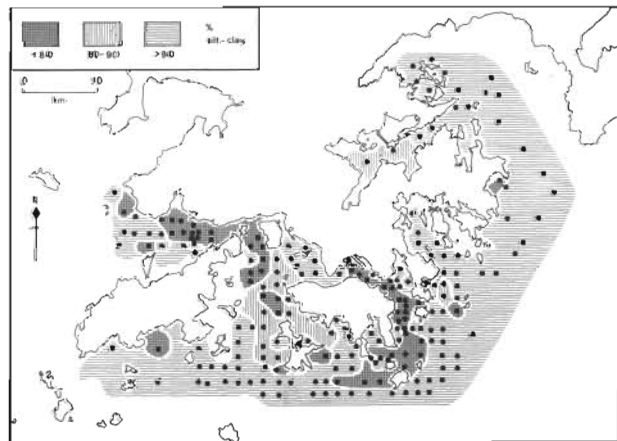


Fig. 2. Distribution of % silt-clay in sediments

tions visited in the final cruise (Jan 1977) are omitted because the samples were lost. There was no clear pattern in organic content distribution, but it is noteworthy that there was no evidence of consistently

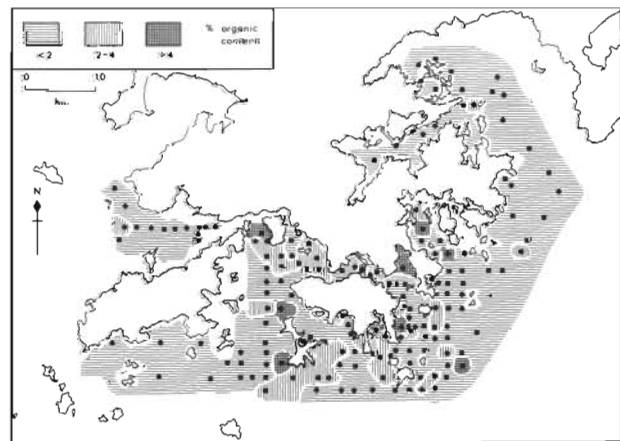


Fig. 3. Distribution of % organic carbon in sediments

high values in Victoria Harbour, which separates Hong Kong Island from Kowloon and receives much untreated sewage.

Fauna

In a total of 1,000 grab samples, there were 10,142 specimens belonging to 139 species. Five station groups were delineated from the classification results at the 0.24 Bray-Curtis similarity level (Fig. 4), and the principal environmental and biological features of each group are summarised in Table 1. The spatial distribution of the 5 station groups is shown in Fig. 5, and a complete list of species and the total numbers collected is given in the Appendix.

The principal environmental characteristics of the 5

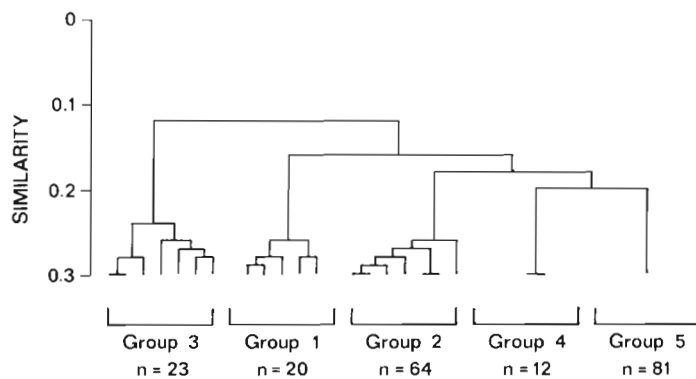


Fig. 4. Dendrogram showing the grouping of stations using hierarchical agglomerative classification. For clarity, the vertical axis is truncated at the 0.30 Bray-Curtis similarity level, and the number of stations in each of the five groups is indicated

groups are as follows: Group 1 comprised 20 stations in western Hong Kong, with the lowest mean bottom salinity (30.1‰ S) and the shallowest mean depth (13.6 m), and a silt content of 74.0%. Group 2 comprised 64 stations in west-central Hong Kong, with high mean organic content (2.24%) and a mean silt content of 77.2%. Group 3 comprised 23 stations found

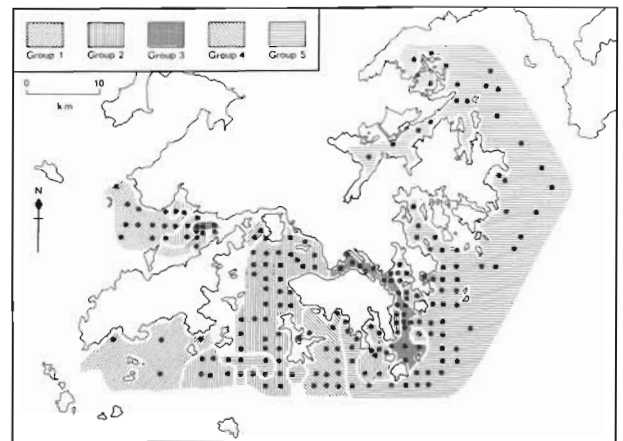


Fig. 5. Distribution of the 5 station groups

in scoured tidal channels 4, in the west between Lantau Island and the New Territories, and 19 extending from the middle of Victoria Harbour to the south-east of Hong Kong Island, where the deepest station was located in 70 m of water. Mean silt content was 44.0% and sand content was 43.3%. Group 4 comprised 12 stations in a compact group south of Hong Kong Island, with the highest mean bottom salinity (32.8‰ S) and

Table 1. Principal environmental and biological characteristics of the 5 station groups, as mean values for each group and for all stations; bracketed figures denote number of stations in sub-samples

	Group					All groups
	1	2	3	4	5	
<i>No. of stations:</i>	20	64	23	12	81	200
Environmental parameters						
Depth (m)	13.6	17.1	19.1	20.6	23.0	19.5
Bottom salinity (‰ S)	30.1	31.5	31.4	32.8	32.6	31.9
Percent gravel (> 2 mm)	2.1	0.7	8.9	0	0	1.5
Percent sand (0.062–2 mm)	19.4	17.7	43.3	4.7	6.2	15.4
Percent silt (2–62 μm)	74.0	77.2	44.0	90.8	88.7	78.5
Percent clay (< 2 μm)	4.6	4.5	3.9	4.5	5.1	4.7
Organic content (%)	1.62	2.24	1.66	1.85	1.90	1.91
	(15)	(34)	(22)	(8)	(81)	(160)
Biological parameters						
No. individuals m ⁻²	107.1	96.0	182.6	54.8	88.2	101.4
No. species 0.5 m ⁻²	17.2	18.8	17.5	16.2	19.2	18.5
Species diversity <i>H'</i> (mean)	3.55	3.70	3.19	3.51	3.84	3.67
(pooled)	4.85	5.39	3.41	4.27	5.31	5.43
Evenness <i>J</i> (mean)	0.88	0.88	0.80	0.89	0.91	0.88
(pooled)	0.80	0.78	0.60	0.79	0.83	0.76
Percent polychaetes	82.5	80.4	48.3	78.7	72.5	71.2
Percent molluscs	1.7	3.1	45.3	3.7	5.2	12.4
Percent crustaceans	3.7	8.4	4.1	13.1	9.5	7.6
Percent echinoderms	5.2	3.3	0	0.6	5.9	3.7
Percent other groups	6.8	4.8	2.2	3.9	6.9	5.2
Formalin wet weight (g m ⁻²)	23.9	20.2	155.2	12.7	22.5	35.2
	(7)	(17)	(9)	(5)	(50)	(88)

the greatest silt content (90.8%). Group 5 comprised 81 stations mainly in eastern Hong Kong, with the greatest mean depth (23.0 m), a mean silt content of 88.7% and a mean salinity of 32.6‰ S. The differences in salinity are underemphasized by the use of mean values, including isohaline winter conditions, but this makes the most effective use of the available data set.

Biologically, mean no. individuals m^{-2} were similar in Groups 1, 2 and 5 (88.2–107.1), higher in Group 3 (182.6) and lower in Group 4 (54.8). Mean no. species $0.5 m^{-2}$ was similar in all groups, from 16.2 to 19.2. Mean species diversity H' varied from 3.19 in Group 3 to 3.84 in Group 5, but mean sample size was only 50.7 specimens. Sanders (1968) has shown that diversity H' is affected by sample size when there are < 200 individuals, and diversity was therefore re-calculated using pooled data for each group. Substantially higher values were obtained, from 3.41 in Group 3 to 5.39 in Group 2, and it may be assumed that the pooled values are the correct ones. Evenness J was treated in the same way, and pooled values varied from 0.60 in Group 3 to 0.83 in Group 5. Polychaetes were the most abundant animals in all groups, comprising 72.5 to 82.5% of the total no. in Groups 1, 2, 4 and 5 but only 48.3% in Group 3, where molluscs comprised 45.3% of the total. Formalin wet weights varied from 12.7 $g m^{-2}$ in Group 4 to 155.2 $g m^{-2}$ in Group 3.

In the pseudo- F test, only 8 species possessed significant F values (Table 2), and only *Tapes philippinarum* was confined to a single station group, Group 3. Of the remaining species, 2 were found in 3 groups, 2 were found in 4 groups, and 3 were found in all 5 groups. This indicates that fidelity, the extent to which species are confined to a particular group, was generally low.

The relative importance of the most abundant species is summarised in Table 3, in which species are ranked by numbers. In Groups 1, 2, 4 and 5, the 5 most abundant species comprised only 37.3 to 54.5% of the total numbers but in Group 3 a single species, *Tapes philippinarum*, comprised 45.2% of the total, and the 5

most abundant species comprised 70.5%. Species were also ranked by the biological index, determined in rank-score analysis, which gives an estimate of constancy of occurrence within a group. This varied from group to group and some species that were ranked highly by abundance were less important when ranked by biological index. This was most obvious in Group 3, where *Tapes philippinarum* was found at only 26.1% of the stations, or 6 out of 23.

In the multiple discriminant analysis, discriminant functions (DF) I and II contributed 97.01% of the total separation among groups at $P < 0.001$ (Table 4). A high positive value along DF I is due mainly to high salinity (coefficient 0.998) and, to a lesser degree, to % silt-clay (coefficient 0.549). Along DF II, negative values are associated with high % silt-clay (coefficient -0.816), but salinity is also important (coefficient 0.992). Station group centroids are plotted in Fig. 6. The centroid of Group 3 is well separated from those of the remaining groups, mainly on the DF II axis, while the centroids of Groups 1, 2, 4 and 5 form a series mainly on the DF I axis. Thus, these 4 groups appear to lie on a transect running west-east from the Pearl River estuary to more oceanic waters, and are separated mainly by changes in mean bottom salinity (which may be regarded as a general index of estuarine conditions). Group 3 is separated from the others because it lives in coarser sediments, in scoured tidal channels.

DISCUSSION

Comparison with Other Tropical and Subtropical Areas

The Hong Kong infauna is characterised by high diversities, low numbers of individuals and low biomass; in this, it resembles biologically accommodated communities found in stable environments. For example, Longhurst (1958, 1959) described similar communities in shallow (0 to 20 m) silty sediments on

Table 2. Results of the pseudo- F test with all species in which > 50 animals were collected; ***, **, * = significant at $P < 0.001$, 0.01, 0.05; - = absent

Species	F value (4194 d.f.)	Mean no. ind. m^{-2} in groups 1 to 5				
		1	2	3	4	5
<i>Tapes philippinarum</i>	12.00***	-	-	82.6	-	-
<i>Sternaspis scutata</i>	4.44**	3.4	1.4	1.7	11.2	3.7
<i>Terebellides stroemi</i>	3.68**	3.0	1.2	6.5	0.3	4.5
<i>Glycinde</i> sp.	3.24*	1.1	1.0	3.4	-	1.2
<i>Sthenolepis yhleni</i>	3.11*	0.2	0.5	-	-	1.8
<i>Aglaophamus lyrochaeta</i>	3.05*	5.7	12.9	6.4	2.5	9.5
<i>Marphysa stragulum</i>	2.59*	3.3	4.5	17.0	-	0.7
<i>Paraprionospio pinnata</i>	2.54*	11.0	8.0	-	-	0.4

Table 3. Assessment of species dominance in the 5 station groups, showing cumulative % by no., rank by no., rank by biological index (BI) and % of stations occupied for the 5 most abundant species in each station group

Species	% by no.	Cumulative % by no.	Rank by no.	Rank by BI	% of stations occupied
Group 1					
<i>Tharyx</i> sp.	12.0	12.0	1	1	80.0
<i>Paraprionospio pinnata</i>	10.3	22.3	2	5	45.0
<i>Prionospio ehlersi</i>	8.3	30.6	3	7	40.0
<i>Lumbrineris shiinoi</i>	7.8	38.4	4	3	75.0
<i>Nephtys</i> sp.	7.2	45.6	5	2	60.0
Group 2					
<i>Aglaophamus lyrochaeta</i>	13.5	13.5	1	1	95.3
<i>Nephtys</i> sp.	8.8	22.3	2	2	79.7
<i>Paraprionospio pinnata</i>	8.4	30.7	3	3	42.2
<i>Tharyx</i> sp.	6.0	36.7	4	4	45.3
<i>Marphysa stragulum</i>	4.7	41.4	5	6	35.9
Group 3					
<i>Tapes philippinarum</i>	45.2	45.2	1	4	26.1
<i>Marphysa stragulum</i>	9.3	54.5	2	1	73.9
<i>Tharyx</i> sp.	8.4	62.9	3	2	65.2
<i>Nephtys</i> sp.	4.1	67.0	4	3	69.6
<i>Terebellides stroemi</i>	3.5	70.5	5	7	52.2
Group 4					
<i>Sternaspis scutata</i>	20.4	20.4	1	1	91.7
<i>Mediomastus californiensis</i>	19.4	39.8	2	2	75.0
<i>Ophiudromus pugettensis</i>	5.8	45.6	3	3	41.7
<i>Aglaophamus lyrochaeta</i>	4.6	50.2	4	5	33.3
<i>Alpheus</i> sp. A	4.3	54.5	5	6	50.0
Group 5					
<i>Nephtys</i> sp.	11.9	11.9	1	4	95.1
<i>Aglaophamus lyrochaeta</i>	10.8	22.7	2	3	96.3
<i>Ophiura kinbergi</i>	5.3	28.0	3	1	55.6
<i>Terebellides stroemi</i>	5.1	33.1	4	2	58.0
<i>Sternaspis scutata</i>	4.2	37.3	5	5	60.5

the West African shelf, with about 80 individuals m^{-2} , a biomass of 7 to 15 $g m^{-2}$, and 11 to 17 species $0.5 m^{-2}$ sample. In Kingston Harbour, Jamaica, Wade (1972) found a community with 240 individuals m^{-2} , a live biomass of 24.6 $g m^{-2}$, a total of 153 species and diversity H' values (calculated from Wade's tabulated data) ranging from 3.60 to 5.07.

Physically, however, Hong Kong waters appear to be an unstable environment that resembles some tropical and subtropical areas which have lower species diversity, higher numbers of individuals and higher biomass. For example, the annual temperature range spans 15–30°C; this is a larger range than was implicated in reduced diversity on the temperate continental shelf (Sanders, 1968), in Biscayne Bay, Florida (Rosenberg, 1975), and probably off Ghana also (Buchanan, 1958). In western Hong Kong, bottom salinity may vary from 6.3 to 32‰ S, and this range is comparable with those associated with low-diversity, physically controlled communities in Indian estuaries

(Desai and Kutty, 1967; Sanders, 1968), in West African estuaries (Longhurst, 1958, 1959) and in Sek Harbour, Papua New Guinea (Stephenson and Williams, 1971). Reduced dissolved oxygen values are probably less important because they rarely fall below 50% saturation in Hong Kong, while values of only 5% saturation have been implicated in reduced diversities on the Indian continental shelf (Sanders, 1968).

Thus, the present results are not in accord with the stability-time hypothesis, because highly diverse communities occurred in a subtropical, highly seasonal climate, and diversity values did not change across a marked salinity gradient. Diversity was slightly lower in Group 1 than in Group 2, but did not show any further increase with increasing salinity, and the lowest diversity value was found in Group 3 where it probably reflects changes in sediment type, as discussed below. It may be that the results could be explained in terms of Huston's (1979) model of species diversity, which includes predation along with other

Table 4. Results of discriminant analysis of environmental conditions among the 5 site groups: discriminant functions III and IV are omitted because they account for < 3% of separation: ***, $P < 0.001$

Discriminant function	I	II
Percent of separation	74.06	22.95
Cumulative percent of separation	74.06	97.01
Test of significance		
Chi-squared value	148.43***	59.06***
Degrees of freedom	7	5
Variables and standardized discriminant function coefficients		
Salinity	0.998	0.992
% silt-clay	0.549	-0.816
% organic content	-0.021	-0.097
Depth	0.005	-0.009

sources of disturbance (Gray, 1981), but this cannot be ascertained until data on predation and growth rates become available.

Diversity may also be affected by biological structuring of the community. In Hong Kong, Wu and Richards (1981) studied the less-mobile epifauna at 3 stations along the northern coast of Lantau Island (Fig. 1) and found a marked inverse correlation between salinity and diversity. They attributed this to the effect of salinity fluctuations on community structure but, in view of the present results, this conclusion has been re-examined. Wu and Richards' low diversity community was dominated by *Turritella terebra* and it resembled a community found off Ghana by Buchanan (1958), dominated by *T. annulata* and associated with a stiff sandy silt: the animals seemed unable to burrow into coarser sediments. Live and dead shells of *T. annulata*

covered the bottom to an extent that probably inhibited the establishment of other species, resulting in low diversity. In this way, it is possible to interpret Wu and Richards' results in terms of a biological interaction, the establishment of an 'inhibiting' or 'monopolising' species, that is in turn dependent upon particle-size distribution rather than the salinity regime.

Further evidence that biological interactions are important may be taken from a comparison of the Hong Kong benthos with that of Biscayne Bay, Florida. The major difference is that in Biscayne Bay in 1957-59, diversity was low and, although total abundance was also low at 166 individuals m^{-2} , the community was dominated by the amphiid brittlestars *Amphioplus coniotodes* and *Ophionephthys limicola* (Singletary and Moore, 1974). In temperate waters, amphiid brittlestars play a unique role in structuring the community, because other species can only settle and survive while the amphiuroids are spawning and feeding has ceased (Thorson, 1955). Singletary and Moore found no evidence that this was happening in the Biscayne Bay community, but it is still reasonable to suppose that tropical communities dominated by amphiuroids have a different structure from those that are not. Evidence to support this may be taken from the work of Rosenberg (1975), who resurveyed part of Biscayne Bay in 1974 and compared his results with those collected in 1957-59. He found that *A. coniotodes* and *O. limicola* were reduced or absent, species diversity had apparently increased, and the number of polychaete species had increased from 15 to about 27, i. e. with a marked decline in amphiid domination, the community had become more like that found in Hong Kong.

The amphiid brittlestars and *Turritella* spp. may be described as keystone species that control the structure of their community (Paine, 1969), and other examples of soft bottom keystone species may be found among the organisms that bind or rework sediments (Rhoads, 1974). It seems likely that almost all soft-bottom benthos communities are structured by biological interactions involving keystone species (Peterson, 1977). For the interpretation of diversity patterns comparisons should only be made within similar habitats (Sanders, 1968), and it seems from recent work that biological structure must be considered as a part of the habitat for this purpose. The structure of, e. g. an amphiid dominated community, is probably fundamentally different from that of a community in which amphiuroids are unimportant, and there may be little to learn from a comparison of their species diversity values. This is not an original observation: e. g. Gray (1974) distinguished between primary diversity, shown by keystone species, and secondary diversity, shown by dependent species, and Eagle (1975) argued that

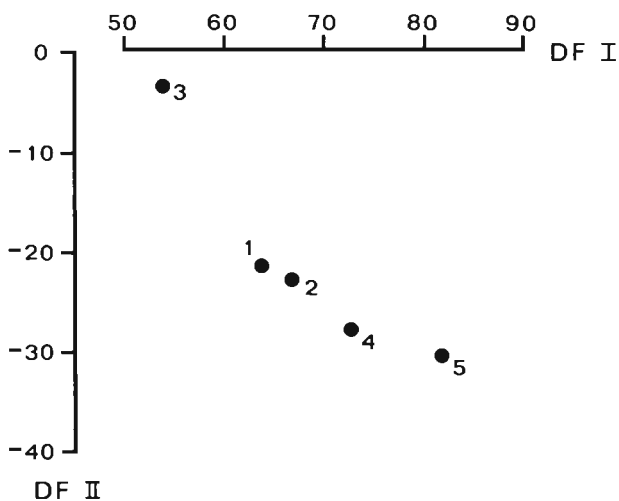


Fig. 6. Station plot of the results of the multiple discriminant analysis, showing the centroids of Groups 1 to 5

the stability-time hypothesis should be modified to take account of amensalism (the inhibition of one population by another). Nevertheless, it should be more widely appreciated that differences in biological structure impose limitations on comparisons of species diversity.

Influence of Sediment Type

Diversity was markedly lower in Group 3 than in the other groups, and numbers and biomass were higher. These differences may follow from the general observation that silt (Groups 1, 2, 4, 5) can be a difficult sediment to colonise and coarser sediments (Group 3) are able to support more life (Sanders, 1958; Gray, 1974; Parker, 1975). This is relevant to the low numbers and biomass found in some tropical communities: Wade (1972) argued that high reproduction and turnover rates were the most important factors regulating biomass, but it is likely that the particular problems of colonising silt also contribute. Buchanan (1958) did find large numbers of animals in a tropical silt with an organic content > 1%. These were large *Thalassema* sp., *Cucumaria* sp. and *Schizaster* sp. that swallow large quantities of sediment. *Thalassema sabinum* and *Schizaster lacunosus* were occasionally found in the present survey, especially in Mirs Bay (Fig. 1), and the biomass of the Hong Kong infauna would be greatly increased if they were more abundant. In the absence of these large animals, it is likely that bioturbation is low in Hong Kong sediments.

Community Characteristics and Dominant Species

Wade (1972) named the benthic community of Kings-ton Harbour a *Lumbrineris* sp.-*Alpheus cristulifrons*-*Diplodonta punctata* community, but he pointed out that these 3 species occupied only 17.9% of the total numbers. If further communities were described in which dominance was lower, it might be necessary to incorporate even more names, thus making the procedure very cumbersome. In the present results, dominance is higher than in Wade's data and it is possible to name communities from the 3 most dominant species in each group, as measured by the biological index. This gives the following names, with the proportion of total numbers given in brackets. Group 1: *Tharyx* sp.-*Nephtys* sp.-*Lumbrineris shiinoi* (27.0%); Group 2: *Aglaophamus lyrochaeta*-*Nephtys* sp.-*Paraprionospio pinnata* (30.7%); Group 3: *Marphysa stragulum*-*Tharyx* sp.-*Nephtys* sp. (21.8%); Group 4: *Sternaspis scutata*-*Mediomastus californiensis*-*Ophiodromus pugettensis* (45.6%); Group 5: *Ophiura kinbergi*-*Terebellides stroemi*-*Aglaophamus lyrochaeta* (21.1%).

While it is obviously possible to name each group in this way, it seems doubtful whether any useful purpose is achieved by doing so. The main problem is not so much in species dominance as in low fidelity. Thus, *Nephtys* sp. occurs in 3 of the names listed above, while *Tharyx* sp. and *Aglaophamus lyrochaeta* occur twice. Low fidelity is also apparent if Table 2 is examined and compared with a similar table in Shin (1982). Several species in the above lists of names did not have significant values in the pseudo-*F* test, and only 8 species gave significant results at $P < 0.05$. By contrast, Shin carried out the same type of survey in the temperate waters of Galway Bay and found highly significant ($P < 0.001$) *F* values in 37 species. From this, it appears that the present groups are formed of intergrading populations responding to a local gradient in environmental conditions, and conforming to the concept of continua of distribution (Mills, 1969): there seems to be no reason to expect them to recur elsewhere.

Seasonal Changes

In an extended survey of this kind, there is an obvious danger that seasonal changes will confound the interpretation of data (Frankenberg and Leiper, 1977). For this reason, the survey was carried out at the same time as bimonthly sampling described by Shin (1977) and the new stations were sampled during cruises to Shin's 26 stations. This meant that sampling locations were evenly distributed among different areas on each cruise, except that eastern waters were not visited on the final cruise in January 1977. From an examination of Shin's seasonal data it appears that seasonal changes may be discounted in the present study, but this is partly because the most variable period is from February to May, when samples were not collected.

Effects of Sewage Pollution

A prime reason for undertaking this survey was to assess the effects of sewage pollution on Hong Kong benthos. Victoria Harbour receives about 280×10^6 tonnes yr^{-1} of untreated sewage from 3.4 million people and is thought to be severely impacted (Morton, 1976). It is interesting, therefore, that the present results show no evidence of pollution affecting the benthos, and spatial distribution can be accounted for in terms of salinity changes and sediment distribution. The Harbour is in fact occupied by Group 2 in its wider, western reaches, and by Group 3 in its narrower, eastern channel (Fig. 5).

This conclusion was checked by calculating log-

normal distributions of individuals per species for pooled data in each group, as described by Gray and Mirza (1979). Short steep lines, spanning 5 to 8 geometric classes, were obtained for each group, indicating an absence of pollution-induced changes.

There are abiotic areas in Victoria Harbour, especially in typhoon shelters where enclosed waters receive large local inputs of sewage, but the present results indicate that the ecological effects of pollution are minimal in the central parts of the Harbour. This may be attributed to the effects of strong tidal flushing, which maintains dissolved oxygen values at a minimum of about 50 % saturation.

Appendix

List of species, arranged by families, with total number of individuals collected

COELENTERATES			
<i>Cerianthus</i> sp.	3	<i>Onuphis eremita</i> Audouin	48
<i>Pteroeides</i> sp.	1	<i>Marphysa stragulum</i> (Grube)	403
<i>Cavernularia obesa</i> (M. Ed. & Haime)	1	<i>Lumbrineris nagae</i> Gallardo	77
NEMERTEANS		<i>Lumbrineris shiinoi</i> Gallardo	270
Nemertean sp. A	178	<i>Drilonereis logani</i> Crossland	2
Nemertean sp. B	148	<i>Dorvillea</i> sp.	37
POLYCHAETES		<i>Scoloplos</i> sp.	5
<i>Lepidasthenia ohshimai</i> Okuda	37	<i>Cirrophorus branchiatus</i> Ehlers	3
<i>Polynoe</i> sp.	1	<i>Paraonides lyra</i> (Southern)	62
<i>Parahalosydropsis hartmanae</i> Pettibone	6	<i>Laonice cirrata</i> (Sars)	100
<i>Polydortes melanonotus</i> (Grube)	2	<i>Paraprionospio pinnata</i> (Ehlers)	382
<i>Sthenelais boa</i> (Johnston)	108	<i>Prionospio ehlersi</i> Fauvel	331
<i>Sthenolepis yhleni</i> (Malmgren)	91	<i>Spiophanes bombyx</i> (Claparede)	12
<i>Eulepethus hamifer</i> (Grube)	16	<i>Polydora</i> cf. <i>socialis</i> (Schmarda)	2
<i>Bhawania brevis</i> Gallardo	3	<i>Polydora</i> cf. <i>tentaculata</i> Blake & Kudenov	1
<i>Chloeia fusca</i> McIntosh	10	<i>Polydorella novaеgeorgiae</i> Gibbs	1
<i>Pseudeurythoe</i> sp.	6	<i>Magelona</i> sp.	96
<i>Anaitides</i> sp.	47	<i>Spiochaetopterus costarum</i> (Claparede)	2
<i>Phyllodoce</i> sp.	1	<i>Poecilochaetus</i> sp.	30
<i>Eteone siphodonta</i> (D. Chiaje)	14	<i>Chaetozone setosa</i> Malmgren	99
<i>Eteone</i> sp.	3	<i>Cirratulus</i> sp.	22
<i>Leocrates chinensis</i> Kinberg	3	<i>Cirriformis tentaculata</i> (Montagu)	21
<i>Leocrates wesenberglundae</i> Pettibone	25	<i>Tharyx</i> sp.	620
<i>Micropodarke dubia</i> (Hessle)	9	<i>Cossura coasta</i> Kitamori	153
<i>Ophiidromus pugettensis</i> (Johnson)	60	<i>Brada ferruginea</i> Gallardo	33
<i>Sigambra constricta</i> (Southern)	19	<i>Brada villosa</i> (Rathke)	16
<i>Sigambra tentaculata</i> (Treadwell)	52	<i>Pherusa</i> sp.	7
<i>Synelmis albini</i> (Langerhans)	2	<i>Ophelina acuminata</i> (Örsted)	31
<i>Syllis gracilis</i> Grube	8	<i>Sternaspis scutata</i> (Renier)	315
<i>Nereis persica</i> Fauvel	8	<i>Heteromastus similis</i> Southern	20
<i>Neanthes</i> sp.	29	<i>Mediomastus californiensis</i> Hartman	159
<i>Nectoneanthes oxypoda</i> (Marenzeller)	92	<i>Notomastus latericeus</i> Sars	122
<i>Leonnates persica</i> Wesenberg-Lund	18	<i>Axiothella</i> sp.	4
<i>Aglaophamus lyrochaeta</i> (Fauvel)	945	<i>Praxillella gracilis</i> (Sars)	35
<i>Nephtys</i> sp.	858	<i>Owenia fusiformis</i> D. Chiaje	7
<i>Micronephtys sphaerocirrata</i> (W.-Lund)	1	<i>Lagis bocki</i> (Hessle)	11
<i>Glycera chiori</i> Izuka	129	<i>Ampharete arctica</i> (Malmgren)	136
<i>Glycera decipiens</i> Marenzeller	55	<i>Auchenoplax</i> sp.	40
<i>Glycera onomichiensis</i> Izuka	16	<i>Lysippe</i> sp.	6
<i>Glycera</i> sp.	210	<i>Amaeana</i> sp.	34
<i>Goniada</i> sp.	32	<i>Lanice conchilega</i> (Pallas)	64
<i>Glycinde</i> sp.	128	<i>Terebellides stroemi</i> Sars	327
<i>Diopatra variabilis</i> Southern	27	ECHIUROIDS	
		<i>Thalassema sabinum</i> Lanchester	20
		SIPUNCULIDS	
		<i>Phascolosoma</i> sp.	4
		<i>Sipunculus nudus</i> (Linne)	1
		<i>Golfingia</i> sp.	1
		CRUSTACEANS	
		<i>Ampelisca</i> sp.	32
		Amphipod sp. A	69
		Tanaidacid sp. A	3
		<i>Alpheus</i> sp. A	178
		<i>Alpheus</i> sp. B	17
		Hippolytid sp. A	24
		<i>Solenocera sinensis</i> Yu	36
		<i>Porcellana</i> sp.	61
		<i>Arcania heptacantha</i> (de Haan)	3
		<i>Philyra</i> sp.	1
		<i>Charybdis truncata</i> (Fabricius)	13
		<i>Charybdis vadorum</i> (Alcock)	5
		<i>Portunus hastatooides</i> (Fabricius)	9
		<i>Thalamita pyrmna</i> (Herbst)	1
		<i>Ceratoplax</i> sp.	25
		<i>Eucrate alcocki</i> Serene	15
		<i>Eucrate crenata</i> de Haan	18
		<i>Macrophthalmus</i> sp.	210

- Xanthiid sp. A 23
- Oratosquilla oratoria* (de Haan) 24
- MOLLUSCS
- Turritella terebra* Reeve 6
- Mamilla simiae* (Deshayes) 2
- Sinum* sp. 2
- Distorsio cancellinus* (Roissy) 3
- Bursa rana* (Linne) 3
- Nassarius siquinjorensis* (Adams) 9
- Turricula javana* (Linne) 3
- Philine* sp. 65
- Anadara tricenica* (Nyst) 118
- Corbula* sp. 1
- Solen* sp. 3
- Vepricardium sinense* (Sowerby) 4
- Callanaitis hiraseana* Kuroda 3
- Paphia exarata* (Philippi) 3
- Paphia undulata* Born 54
- Tapes philippinarum* (Adams & Reeve) 950
- Micromactra reevesi* (Gray) 30
- Octopus aegina* Gray 2
- ECHINODERMS
- Luidia* sp. 6
- Ophiura kinbergi* Ljungman 323
- Lovenia subcarinata* (Gray) 4
- Schizaster lacunosus* (Linne) 16
- Protankyra bidentata* (Woodward & Barrett) 23
- HEMICHORDATES
- Balanoglossus* sp. 101
- FISH
- Uroconger lepturus* (Richardson) 8
- Moringua macrochir* (Bleeker) 7
- Apogon quadrifasciatus* (Cuv. & Val.) 2
- Platycephalus indicus* (Jordan & Hubb) 3
- Oxyurichthys papuensis* (Cuv. & Val.) 3
- Oxyurichthys tentacularis* (Cuv. & Val.) 2
- Parachaeturichthys polynema* (Bleeker) 2
- Trypauchen vagina* (Bloch & Schneider) 40
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