Spatial patterns of soft-sediment benthic diversity in subtropical Hong Kong waters

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ABSTRACT: It has long been assumed that, just as on land, a decline in diversity from the tropics to the poles is a feature of the marine environment, yet little is known about patterns of diversity in tropical/subtropical areas. Soft-sediment macrobenthos data from the entire Hong Kong waters (22° N, 113–114° E) were used to examine faunal patterns in a subtropical area. Grab samples were taken from a depth range of 5 to 47 m at 101 sites on a spatial sampling scale of 1100 km². A total of 386 species belonging to 12 phyla was recorded in 50.5 m² of sediment collected from the 1100 km² sampling area. Species richness (alpha diversity) of the samples was low (mean 35 species) but highly variable (10 to 78 species). Relationships between community structure and environmental variables were weak. The number of rare species was high: 38 % of the species were represented by 1 or 2 individuals, 45 % were restricted to 1 or 2 sites, and no species spanned the whole sampling area. Polychaetes displayed the highest species richness, followed by molluscs and crustaceans. Molluscs were more restricted in their distribution than the other dominant groups, whereas polychaetes had the highest proportion of widespread species. Beta diversity, measured as Whittaker's β_W and Bray-Curtis similarity, was high. Beta diversity varied among the dominant groups and was highest for molluscs, followed by crustaceans and polychaetes. The faunal patterns changed with spatial scale. The study shows that patterns of diversity depend considerably on which element of biodiversity is measured.

KEY WORDS: Soft-sediment communities · Marine biodiversity · Alpha diversity · Beta diversity · Rarity · Scale

INTRODUCTION

In recent years there has been an upsurge of interest in whether or not there are declines in diversity from the tropics to the poles in the marine domain, comparable to that seen for many animals and plants in terrestrial systems (Pianka 1966, Huston 1994, Rosenzweig 1995, Gaston 1996). It is commonly reported that species diversity in marine systems tends to increase with decreasing latitude (e.g. Levinton 2001, Nybakken 2001). The first published study of latitudinal gradients in marine species richness was that of Thorson (1957), who reported a pronounced decline in the species richness of hard-substratum epifauna towards arctic areas, while the number of soft-sediment infaunal species was roughly the same in tropical, temperate and arctic areas. Later, similar latitudinal clines in

marine species' richness were reported for shallow-water bryozoans (Clarke & Lidgard 2000), gastropods (Roy et al. 1998) and bivalve molluscs (Crame 2000, Roy et al. 2000), in deep-sea benthos (Poore & Wilson 1993, Rex et al. 1993), and for pelagic taxa (e.g. Angel 1997, Pierrot-Bults 1997). However, for shallow-water marine fauna the data are equivocal, with studies of nematodes (Boucher & Lambshead 1995) and macrofauna (Kendall & Aschan 1993) providing no support for a latitudinal cline. Thus, it is not yet clear to what extent such clines are the general rule in the sea (Clarke 1992, Clarke & Crame 1997).

The Indo-Pacific has been reported to be the world's most diverse shallow-water marine area (e.g. Stehli & Wells 1971, Kohn 1983, Veron 1995, Crame 2000, Bellwood & Hughes 2001, Morton & Blackmore 2001). However, few published surveys of tropical benthic

communities have demonstrated very large numbers of species (Longhurst & Pauly 1987). Most of the tropical/subtropical benthic communities have not been well studied, and there are as yet few published studies for these areas.

Comparative studies of diversity are problematic due to the use of different sampling gears, varied sampling effort, analyses at different spatial scales, use of different measures of biodiversity, as well as varied patterns between taxonomic groups (Clarke 1992, Gee & Warwick 1996). Patterns of latitudinal gradients in diversity may depend considerably on what element of 'biodiversity' is measured (see e.g. Clarke & Lidgard 2000).

Whittaker (1960) pioneered the partitioning of species diversity into alpha (α), beta (β), and gamma (γ) components to characterise different aspects of diversity. The scales describing alpha and gamma diversity vary among authors, but gamma diversity usually refers to the overall number of species within a defined geographic area resulting from merging a number of alpha samples taken at a smaller spatial scale. Most marine surveys have been carried out on small spatial scales, and there are few specific studies of diversity at different spatial scales for the marine environment (for notable exceptions see Clarke & Lidgard 2000, Ellingsen 2001, Izsak & Price 2001, Ellingsen & Gray 2002).

In contrast to alpha and gamma, beta diversity is not a spatial scale of diversity. Although there have been a number of studies of alpha diversity in marine systems, investigations of beta diversity have been few (Gray 2000). Beta diversity can be measured in many different ways (see Koleff et al. 2003, Magurran 2004 for an overview), but Whittaker's (1960, 1972) simple statistic (β_W, i.e. the proportion by which a given area is richer than the average of samples within it) is one of the most frequently used measures (Wilson & Shmida 1984). Beta diversity may also be based on differences in faunal composition between sites or areas, measured as (for example) the Bray-Curtis similarity index (Bray & Curtis 1957). Such measures take the identities of the species into account, in contrast to the β_W measure. As yet there are few investigations of the relationship between alpha, beta and gamma diversity, either within limited geographical areas (see Ellingsen & Gray 2002) or over latitude at larger spatial scales (but see study by Clarke & Lidgard 2000).

The 2 most popular criteria used for devising conservation strategies are species richness and rarity (Prendergast et al. 1993). Rare species can simply be regarded as those having low abundance and/or small range size (Gaston 1994). In ecological data sets most species are represented by a small number of individuals, most individuals belong to a few abundant species, and most species have a restricted range size (Gaston 1994). Furthermore, species with restricted range and which occur in few habitats are usually the most vulnerable to environmental change (Thomas & Mallorie 1985). It is therefore important to take rare species into account when measuring biodiversity and planning conservation areas. However, the proportion of rare species in a given area may vary as a function of sampling intensity (see Gaston & Blackburn 2000) and also spatial scale and geographical location.

Human activities, directly or indirectly, are almost certainly one important cause of changes in marine biodiversity, especially in coastal areas. The present rate of habitat degradation in marine ecosystems is alarming (Gray 1997, Snelgrove et al. 1997). It is therefore important to improve our understanding of biodiversity in marine systems, and the conservation of marine biodiversity is of critical importance.

The present study examined subtidal soft-sediment macrobenthos data from subtropical Hong Kong waters (22° N, 113–114° E). The first survey of Hong Kong's territorial waters was by Shin & Thompson (1982), who recorded 139 species from as many as 200 sites (101 m^2). The main objectives of the present study were to (1) examine species richness and beta diversity at different spatial scales in a subtropical area, and (2) investigate the spatial distributions of species within the sampling area.

MATERIALS AND METHODS

Study area. Hong Kong is situated on the southern coast of China, and consists of Hong Kong Island, Kowloon Peninsula, the New Territories, and about 230 surrounding islands in a sea area of 1847 km^2 (Morton & Blackmore 2001). The hydrography of this subtropical area (22° N, 113–114° E) is complex and varies seasonally. The heavy rainfall associated with monsoon conditions (prevailing from May to September) dilutes the seawater. The western waters of Hong Kong are heavily affected by input from the Pearl River, particularly during summer when the rainfall is high (Morton & Wu 1975). There is therefore a decreasing trend in salinity from west to the east. The waters of Hong Kong have been divided into 3 zones, estuarine in the west and oceanic in the east, with a transition zone between (see Morton & Blackmore 2001 and references therein), corresponding to the western, middle and eastern intermediate scale areas in the present study (see Fig. 1). During summer, the South China Sea Current, which has moderate salinities and variable temperatures, also affects the coastal waters. In winter, this is replaced by the Kuroshio Current (high salinities and tempera-

tures) or the East China Sea Current (reduced salinities and temperatures) (Morton & Wu 1975, Morton & Blackmore 2001).

Human impact through pollution, trawling and dredging in Hong Kong waters is serious (Morton 1996). Factors contributing to the pollution of Hong Kong include dense population, rapid industrialisation and former lack of control over the release of agricultural and industrial effluents (Morton & Blackmore 2001).

Sampling and data analyses. The data were collected in June and July 2001, in subtropical Hong Kong waters. Sampling locations were established in the form of a 4 × 4 km grid system, and a total of 120 sites were sampled. The fieldwork was carried out on board the EGS (Asia) Limited's Class III survey vessel, and a differential Global Positioning System was used. The samples were taken with a 0.1 m^2 van Veen grab. At each site, 5 replicate samples for analysis of macrobenthos were taken, the samples were sieved on a 0.5 mm sieve, and the retained fauna were fixed in 5% borax-buffered formalin and stained with 1% Rose Bengal for later sorting and identification. Sorting was carried out at the City University of Hong Kong, and the animals were identified to the lowest practical taxonomic level at the Third Institute of Oceanography in Xiamen, China. At each site, 1 additional grab was collected for analysis of total organic matter (TOM), sediment median grain size (Mdφ), sorting (σ_I), kurtosis (K_G), and skewness (Sk_I), which

was carried out at the City University of Hong Kong. Additional details of sampling and analyses are given in Shin et al. (2003).

Deep Bay (close to the Pearl River estuary), Tolo Harbour and Tolo Channel (north east), and Victoria Harbour are influenced by freshwater discharge (Morton & Wu 1975), the periodic occurrence of hypoxia (Wu 1982), and sewage discharge (Thompson & Shin 1983), respectively. In order to study patterns of biodiversity in this subtropical area and not focus on disturbance, 7 sites from Deep Bay, 9 sites from the Tolo areas, and 3 sites from Victoria Harbour were therefore excluded from the analyses. These sites were identified using univariate and multivariate analyses of faunal data (results are not given here). The resulting 101 sites (Fig. 1) were used in the following data analyses if not stated otherwise. However, this data set clearly does not represent a pristine subtropical area. Total sampling coverage spanned a spatial scale of 1100 km^2, and water depth at the 101 sites ranged from 5 to 47 m. The sediment in the study area was dominated by silt, but there was considerable variation in sediment characteristics among sites (Mdφ range 0.9 to 6.4; TOM range 1.9 to 9.8%, Table 1).

Faunal groups not properly sampled by the methods used, such as nematodes, bryozoans and fishes as well as juveniles, were not included in the data analyses. Likewise, unidentified species were exclu-
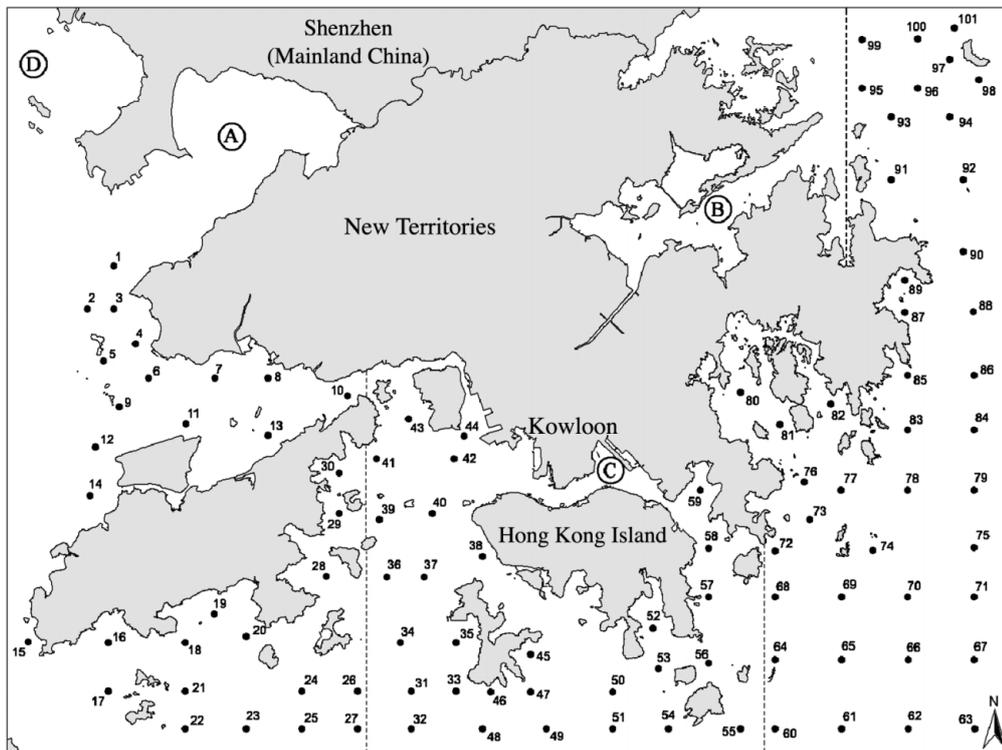

Fig. 1. Geographic position of 101 sampling sites in subtropical Hong Kong waters. Area is divided into 3 intermediate scale areas: western, middle and eastern. A: Deep Bay; B: Tolo Harbour and Tolo Channel; C: Victoria Harbour; D: Pearl River estuary

Table 1. Summary of depth and sediment characteristics for 3 intermediate-scale areas and total sampling area. W: western area; M: middle area; E: eastern area (cf. Fig. 1). Mdφ: median grain size; TOM: total organic matter (%); CV: coefficient of variation (standard deviation/mean) multiplied by 100%

Area	No. of sites	Depth (m) Range	CV	Mdφ Range	CV	TOM (%) Range	CV
W	30	5–32.5	50.4	0.9–6.2	32.0	2.7–7.8	27.9
M	29	9–47	43.7	0.9–6.4	27.5	1.9–9.0	25.0
E	42	15–35	23.5	1.9–6.4	21.4	1.9–9.8	31.9
Total	101	5–47	43.9	0.9–6.4	26.7	1.9–9.8	30.0

ded if they could be mistaken for an identified species. In this investigation, alpha diversity was designated sample species richness (SR_S, see Gray 2000), i.e. number of species in a sample. In soft-sediment studies a single grab, covering only 0.1 m², is known to sample only a small fraction of the species at a site because of small-scale spatial variation. Data analyses were therefore done on species abundance data pooled over 5 replicate grabs from each site (0.5 m²), which was designated a 'sample'. The total sampling area was divided into 3 intermediate scale areas: western (370 km²), middle (290 km²) and eastern (430 km²), based on prior knowledge of the hydrography of the area (e.g. Morton & Wu 1975, Morton & Blackmore 2001). In some data analyses, the sum of 4 adjacent sites (i.e. 2 m²) from a spatial scale of about 16 km² was used as the smallest scale, which was designated a 'small area'. Gamma diversity was equated with species richness in the total sampling area (50.5 m² sediment from 1100 km²). A species restricted to a single site was termed 'unique', a species occurring at exactly 2 sites only, 'duplicate', a species represented by a single individual, 'singleton', and species represented by only 2 individuals, 'doubleton' following Colwell & Coddington (1994),

using EstimateS software (R. K. Colwell, see http://viceroy.eeb.uconn.edu/estimates). As univariate measures of diversity, species richness (S) and the reciprocal of the Simpson index of diversity (1/SI) were used (see e.g. Magurran 2004). Average taxonomic distinctness for presence/absence information (Δ^+, Clarke & Warwick 1998) was calculated as $\Delta^+ = [\Sigma\Sigma_{i<j}\, \omega_{ij}]\,/\,[m(m-1)/2]$, where m is the number of species and ω_{ij} is the weight (path length) given to the taxonomic relationship between Species i and j; Δ^+ is the average path length between any 2 randomly chosen species in the data set. Equal step lengths were used between each taxonomic level (species, genera, family, order, class and phylum). Ordination by non-metric multidimensional scaling (MDS) based on the Bray-Curtis similarity matrix (e.g. Kruskal & Wish 1978, Clarke & Green 1988) was used to provide a graphical presentation of how faunal similarity changes in the sampling area. We used 2 measures of beta diversity. First, Whittaker's (1960, 1972) original beta diversity measure, $\beta_W = (\gamma/\bar{\alpha}) - 1$, where γ is the total number of species resulting from merging a number of individual samples and $\bar{\alpha}$ is the average number of species per individual sample. Second, the Bray-Curtis similarity between all pairwise combinations of sites (from the similarity matrix) was used as a measure of beta diversity. The relationships between faunal patterns, using the Bray-Curtis similarity matrix, and different subsets of environmental variables (matrices computed using normalised Euclidean distance) were examined using the Bio-Env procedure (Clarke & Ainsworth 1993). For the above analyses, the Primer package (Clarke & Warwick 1994) was used.

Table 2. Species richness (SR_S: sample species richness [alpha diversity]; $SR_{\bar{S}}$: mean sample species richness; SR_T: total species richness), number of individuals (N), and proportion of 'rare' species. Pol: polychaetes; Mol: molluscs; Cru: crustaceans. W: western area; M: middle area; E: eastern area. Total (sa): 18 × 4 sites from total sampling area; sa: small area (i.e. sum of 4 sites); *: small areas used. Uniques: species restricted to single site; Duplicates: species occurring at 2 sites only; Singletons: species represented by single individual; Doubletons: species represented by 2 individuals. CI: 95% confidence intervals

| Area	Taxa	No. of sites	SR_S Range	$SR_{\bar{S}} \pm$ CI	SR_T	N	Uniques (%)	Duplicates (%)	Singletons (%)	Doubletons (%)
Total	All	101	10–78	35.1 ± 2.9	386	16334	32.9	12.4	27.7	9.8
	Pol	101	7–53	23.0 ± 2.0	198	12359	26.8	11.6	22.2	7.6
	Mol	87	0–9	2.5 ± 0.4	65	916	44.6	10.8	40.0	10.8
	Cru	96	0–14	4.9 ± 0.6	58	1210	37.9	10.3	32.8	6.9
W	All	30	10–73	35.0 ± 6.7	242	7424	38.0	17.8	26.9	16.5
M	All	29	15–78	36.4 ± 5.6	223	4618	39.5	16.6	32.7	11.7
E	All	42	13–63	34.3 ± 3.9	269	4292	35.7	17.5	29.4	12.6
Total (sa)	All	18 sa	48–138*	81.1 ±11.7*	337	11058	38.0*	14.5*	29.1*	10.4*
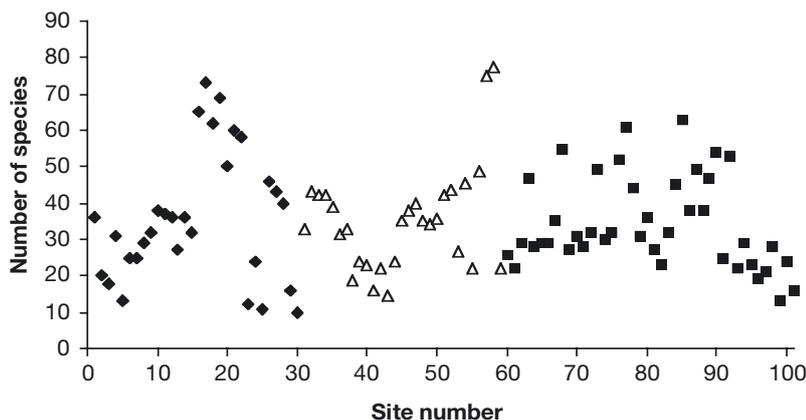
Fig. 2. Species richness of samples (*SR*$_S$, alpha diversity). (◆) western area; (△) middle area; (■) eastern area (cf. Fig. 1)

Table 3. Pairwise Spearman rank correlations (R$_S$) between alpha diversity (*SR*$_S$, sample species richness), the reciprocal of Simpson's index (1/SI) and environmental variables, with significant (p < 0.01) coefficients in **boldface** (n for all correlations = 101). Mdφ: median grain size; *Sk*$_I$: skewness; σ$_I$: sorting; *K*$_G$: kurtosis; TOM: total organic matter (%)

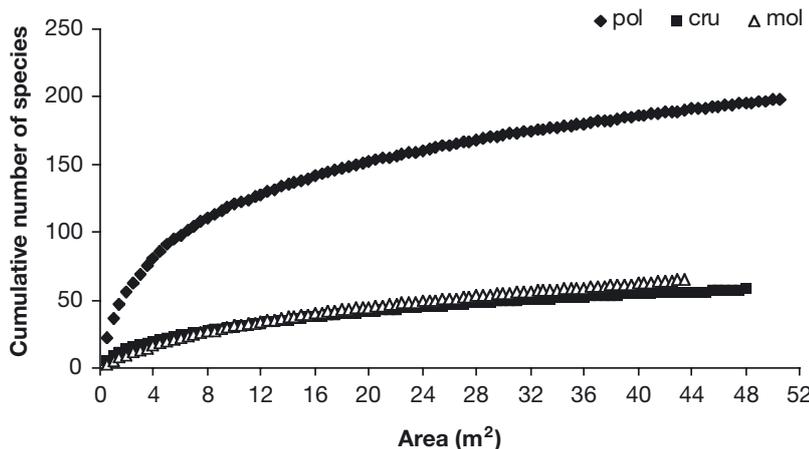|	Depth	TOM	Mdφ	σ$_I$	*Sk*$_I$	*K*$_G$	Latitude	Longitude	*SR*$_S$
Depth (m)									
TOM	0.09								
Mdφ	**0.26**	**0.64**							
σ$_I$	−0.21	**−0.29**	**−0.71**						
Sk$_I$	0.19	**−0.42**	**−0.30**	−0.15					
K$_G$	**−0.40**	−0.18	**−0.35**	0.15	**−0.37**				
Latitude	−0.23	0.12	−0.02	−0.03	−0.01	0.10			
Longitude	**0.64**	0.21	**0.29**	**−0.32**	0.09	**−0.32**	0.21		
SR$_S$	0.04	**−0.49**	**−0.37**	0.11	**0.29**	0.11	**−0.27**	0.01	
1/SI	**0.31**	0.06	0.11	−0.13	0.02	−0.08	−0.06	**0.56**	**0.33**

Fig. 3. Species accumulation rates of 3 dominant taxonomic groups for total area. Means of 50 estimates based on 50 randomisations of sample accumulation order (without replacement). pol: polychaetes; cru: crustaceans; mol: molluscs

RESULTS

Species richness and taxonomic distinctness

Alpha diversity or sample species richness (*SR*$_S$) at 101 sites in the subtidal Hong Kong territorial waters (1100 km^2) was low (mean sample species richness, $\overline{SR_S}$ = 35, Table 2) but highly variable, ranging from 10 to 78 species (Fig. 2). A Spearman rank-correlation analysis (Table 3) of measured environmental variables showed that no variables were highly correlated; median grain size and sorting was highest related (R$_S$ = −0.71). Sample species richness (*SR*$_S$) showed the highest relationship to total organic matter (R$_S$ = −0.49), while the reciprocal of Simpson's index (1/SI) was most highly correlated with longitude (R$_S$ = 0.56, Table 3). Most of the relationships between the univariate measures of diversity and measured environmental variables were either weak or not significant (Table 3). Differences in *SR*$_S$ between the western, middle and eastern intermediate-scale areas (290 to 430 km^2, see Fig. 1) were low (range 34 to 36 species, Table 2). The number of species at the scale of the small areas (i.e. 4 adjacent sites pooled) varied between 48 and 138 species, and mean species richness at this scale (81 species) was higher than *SR*$_S$ (Table 2).

A total of 386 species recorded from 101 sites belonged to 12 phyla. Polychaetes (198 species) constituted 51% of the total number of species, whereas molluscs (65 species) and crustaceans (58 species) comprised 17 and 15%, respectively. The species accumulation rates for the dominant groups showed little sign of approaching asymptotic values, although the slope of the curves for the molluscs and crustaceans was less steep than that for the polychaetes (Fig. 3). The total number of species at the scale of the intermediate area (range 223 to 269 species, Table 3) was lower than at the scale of the entire area. However, the species accumulation rates were almost equal for the 3 intermediate areas and the total sampling

Table 4. Average taxonomic distinctness (Δ⁺) for dominant taxo-
nomic groups. For molluscs and crustaceans only sites with more
than 1 species were included. CI: 95% confidence intervals

Taxonomic group	No. of sites	Δ^+ Range	Δ^+ Mean ± CI
Polychaeta	101	57.8–64.6	62.1 ± 0.3
Mollusca	63	33.3–83.3	60.2 ± 3.0
Crustacea	88	44.4–66.7	55.1 ± 1.0
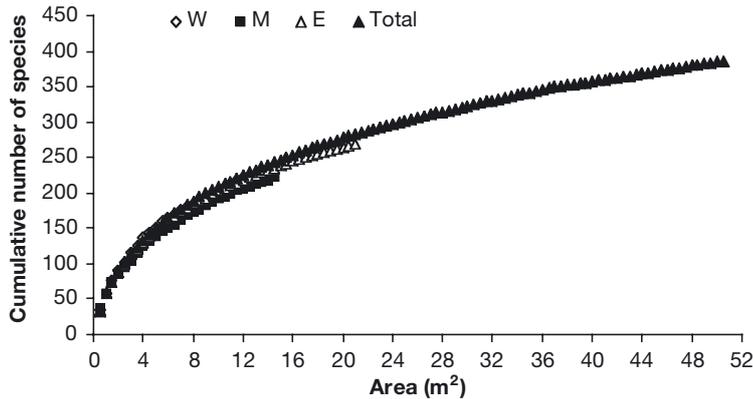
Fig. 4. Species accumulation rates of total number of species for 3 inter-
mediate-scale areas and total area (cf. Fig. 1). Means of 50 estimates based
on 50 randomisations of sample accumulation order (without replace-
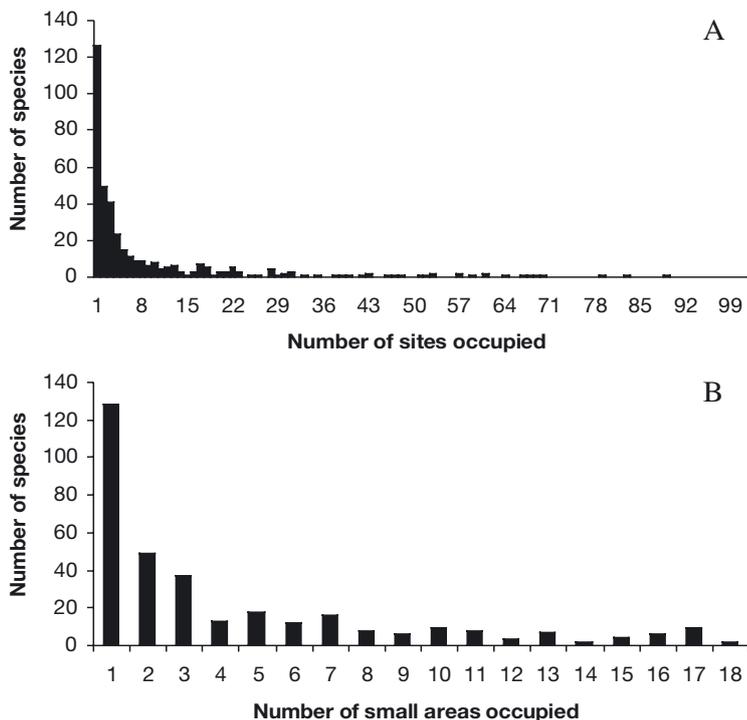ment). W: western area; M: middle area; E: eastern area

Fig. 5. Species range sizes. (A) Number of sites occupied by a species out
of total of 101 sites; (B) number of small areas (i.e. sum of 4 sites) occupied
by a species out of total of 18 small areas

area, and neither stabilised towards asymp-
totic values (Fig. 4).

Mean average taxonomic distinctness
(Δ⁺) varied between the dominant groups
and was highest for polychaetes (62), fol-
lowed by molluscs (60) and crustaceans
(55) (Table 4). However, molluscs dis-
played the widest range of average taxo-
nomic distinctness (33 to 83), whereas Δ⁺
for polychaetes ranged from only 58 to 65.

Abundance and spatial distributions of species

The data for the total area comprised
16 334 individuals. Maximum dominance of
a single species across the entire area was
15.8% (for the polychaete *Prionospio
malmgreni*), and the tenth most dominant
species comprised 2.1% (Table 5).

Polychaete species were found at all the
101 sites, while crustaceans and molluscs
were represented at 96 and 87 sites,
respectively. No species spanned the en-
tire sampling area of 101 sites, and only
17 species (4.4%) were found at more
than 50 sites (Fig. 5A). These relatively
widespread species, dominated by poly-
chaetes (71%), were among the 31 most
abundant species. The number of rare
species, both with regard to distribution
across the sampling area and abundance,
was high (Table 2). As many as 175 spe-
cies, or 45% of the total number of spe-
cies recorded, were restricted to only 1 or
2 sites (uniques and duplicates, respec-
tively, Fig. 5A). Furthermore, 145 species
(38% of the total number of species) were
represented by only 1 or 2 individuals
(singletons and doubletons, respectively,
Table 2). Of the total number of poly-
chaetes, 38% were found at 1 or 2 sites
only, while 48% of the crustaceans and as
much as 55% of the molluscs were
uniques or duplicates (Table 2). The pro-
portion of species restricted to 1 or 2 sites
was higher at the intermediate area scale
(range 53 to 56%) than at the scale of the
total area (Table 2). The data set from 18
small areas comprised 337 species, and as
much as 53% of these species were
restricted to 1 or 2 small areas, with only
2 species found in all 18 small areas (Fig.
5B, Table 2).

Table 5. Dominance patterns of 10 most abundant species across whole sampling area. P: Polychaeta; C: Crustacea; S: Sipuncula; E: Echinodermata; N: no. of individuals

Faunal group	Species	N	Dominance (%)	Cumulative dominance (%)
P	*Prionospio malmgreni*	2578	15.78	15.78
P	*Mediomastus* sp.	1795	10.99	26.77
P	*Aglaophamus dibranchis*	869	5.32	32.09
P	*Heteromastus* sp.	754	4.62	36.71
S	*Apionsoma trichocephalus*	542	3.32	40.03
P	*Mediomastus californiensis*	377	2.31	42.34
C	*Neoxenophthalmus obscurus*	362	2.22	44.55
P	*Sigambra hanaokai*	356	2.18	46.73
P	*Tharyx* sp.	356	2.18	48.91
E	*Amphipodia obtecta*	347	2.12	51.03

Beta diversity

Whittaker's beta diversity (β_W) for all taxonomic groups pooled for the entire area was high (10.0, Table 6). β_W varied between the dominant taxonomic groups and was highest for molluscs (25.4), followed

Table 6. Whittaker's beta diversity (β_W) for all taxa pooled and for dominant taxonomic groups for intermediate scales, total area (based on sample species richness), and 18×4 sites from total area (based on small-area species richness). W: western area; M: middle area; E: eastern area; Total (sa): 18×4 sites from total sampling area

Area	All taxa	Polychaeta	Mollusca	Crustacea
W	5.9	4.6	11.0	7.2
M	5.1	4.2	14.7	5.0
E	6.8	5.5	17.6	7.6
Total	10.0	7.6	25.4	10.9
Total (sa)	3.2	2.5	6.6	3.0

Table 7. Bray-Curtis similarity (%) between all pairwise combinations of sites (or small areas). Pol: polychaetes; Mol: molluscs; Cru: crustaceans; W: western area; M: middle area; E: eastern area; Total (sa): 18×4 sites (=18 small areas) from total sampling area. n: number of pairwise combinations of sites; CI: 95% confidence intervals

Area	Taxa	n	Bray-Curtis similarity (%) Range	Mean ± CI	Occurrence of similarity = 0
Total	All	5050	0–62.9	27.6 ± 0.3	5
	Pol	5050	0–66.9	30.1 ± 0.3	6
	Mol	3741	0–100	7.3 ± 0.5	2869
	Cru	4560	0–100	27.6 ± 0.6	885
W	All	435	3.7–58.5	25.4 ± 1.1	0
M	All	406	5.8–62.9	33.8 ± 1.1	0
E	All	861	3.1–58.7	32.0 ± 0.7	0
Total (sa)	All	153	10.9–63.1	42.4 ± 1.7	0

by crustaceans (10.9), and polychaetes (7.6). β_W for all taxonomic groups pooled was lower at the intermediate-area scale (range 5.1 to 6.8) than at the scale of the total area (Table 6). At the intermediate-area scale β_W also varied between the dominant groups, and was greatest for molluscs (range 11.0 to 17.6). β_W for all taxonomic groups was only 3.2 when calculated for the small areas (Table 6).

For all pairwise combinations of sites in the entire sampling area, Bray-Curtis similarities ranged from 0 to 62.9%, with a mean of only 27.6% (Table 7). In the 3 intermediate-scale areas, the mean Bray-Curtis similarity was also low, ranging from 25.4% in the western area to 32.0 and 33.8% in the eastern and middle areas, respectively (Table 7). Thus, this component of beta diversity, the faunal differences between sites, was high both at the scale of the total area and at the intermediate-area scale. There was no relationship between β_W and mean Bray-Curtis similarity at the intermediate-area scale (cf. Tables 6 & 7), however only 3 values were included. The MDS-ordination, based on Bray-Curtis similarities, is shown in Fig. 6. Most of the sites in the western area were located on one side of the plot, with most of the sites in the eastern area plotted on the opposite side; the sites in the middle area were distributed on both sides on the plot. Thus, the multivariate analysis indicated that the faunal patterns changed across the area, although the stress value (0.2) was relatively high. The rank correlations between single environmental factors and the faunal patterns (Bray-Curtis similarity matrix) were weak (range of R_S 0.17 to 0.33, BIO-ENV analysis, Table 8). The subset of environmental variables which best 'explained' the faunal composition included median grain size, total organic matter, longitude and depth ($R_S = 0.5$), although the relationship was weak. The mean Bray-Curtis similarity varied between the dominant groups and was highest for polychaetes (30.1), followed by crustaceans (27.6) and molluscs (7.3, Table 7). For molluscs, the Bray-Curtis similarity between as many as 2869 pairwise combinations of sites (of a total of 3741) was zero. Likewise, the faunal pattern between 885 pairwise combinations of sites (of a total of 4560) for crustaceans was completely dissimilar, whereas only 6 similarity values (of 5050) were zero for the polychaetes. The mean Bray-Curtis similarity for all pairwise combinations of the 18 small areas (42.4%) was higher than for the

Table 8. Summary of results of Bio-Env analysis. Spearman rank correlations (R_s) between biotic and abiotic similarity matrices, with highest correlations in **boldface**. Lower correlations omitted. Biotic data square-root-transformed, abiotic data log $(1 + N)$ transformed; exception of latitude, longitude and depth. Mdφ: median grain size; Sk_I: skewness; σ_I: sorting; K_G: kurtosis; TOM: total organic matter (%)

Variable	R_S
Mdφ	**0.33**
K_G	0.31
TOM	0.30
Longitude	0.28
Sk_I	0.28
σ_I	0.22
Latitude	0.18
Depth	0.17
Max. corr.	Mdφ, TOM, longitude, depth (**0.50**)

101 sites (27.6%, Table 7). Thus, the faunal differences between sites were higher than the faunal differences between small areas.

DISCUSSION

Patterns of species richness

The present study reports the highest number of soft-sediment species ever recorded for Hong Kong waters. Shin (1998) reviewed the literature published since the 1970s and reported a total of 183 polychaetes from this area. At a larger spatial scale, Crame (2000) reported 1176 bivalve species from the East China Sea, including Hong Kong, and 1211 bivalve species from the Indonesia–Philippines region. This shows that the total number of species in this region is high. Bouchet et al. (2002) found 2738 species of marine molluscs at 42 stations on a spatial sampling scale of only 295 km² on the west coast of New Caledonia in the tropical waters of the Indo-Pacific. These findings suggest that although the total number of benthic species in the tropics/subtropics seems to be exceptionally high, there are considerable variations in large-scale species richness in these areas.

In a study of soft-sediment macrobenthos from 5 large areas (<100 × 260 km) along the Norwegian continental shelf (56 to 71° N) Ellingsen & Gray (2002) recorded 477 species from an area (25 sites, 12.5 m²) in the southern–central part (depth 93 to 356 m) and 405 species from an area (20 sites, 10 m²) in the northernmost part (160 to 365 m). The fact that the depth range in the Hong Kong waters is less than of the Norwegian shelf may be one explanation for the lower species richness in this subtropical area. However, in a study of shallow-water (11 to 51 m) benthic infauna of SE Aus-

tralia, Coleman et al. (1997) found 803 species in a total area sampled of only 10.4 m² from 50 km of coast line. This shows that species richness may also be high within a narrow depth range. However, irrespective of depth, the species lists for Hong Kong waters show that the total number of species in this area is not particularly high, especially for subtropical waters.

In accordance with the present study, Ellingsen & Gray (2002) found that sample species richness at 101 sites along the Norwegian shelf was highly variable (35 to 148 species). Thus, high variability in species richness at small spatial scales is typical for marine soft-sediments independent of latitude, and extensive sampling is therefore necessary to reflect the variability at this scale (see also Clarke & Lidgard 2000: bryozoans; Cornell & Karlson 1996: corals). Sample species richness in Hong Kong waters was lower than along the Norwegian continental shelf ($SR_{\bar{S}}$ 87, Ellingsen & Gray 2002), a finding that shows that species richness at small scales not necessarily increases with decreasing latitude. The fact that human impact through pollution, trawling and dredging in the Hong Kong waters is heavy (Morton 1996), may distort patterns of diversity. However, in many tropical regions benthic ecologists have recognised similar associations of organisms, with approximately the same diversity, as temperate benthic communities in comparable environments (Longhurst & Pauly 1987). According to Levinton (2001), the generalisation of increasing diversity with decreasing latitude applies to species lists, but not necessarily to the number of species living within a small area of e.g. 1 m². In a study of North Atlantic bryozoans, Clarke & Lidgard (2000) found strong evidence of a latitudinal cline in regional species richness, but no cline in alpha diversity.

The species accumulation curves did not reach asymptotic values, and thus there was no sign of having collected all species potentially present in the study area (Fig. 4). Ugland et al. (2003) developed a new method for estimating species richness for areas larger than that sampled. Using the same data set as in the present study (i.e. 386 species) they estimated as many as 2254 species for the entire Hong Kong waters. The finding in the present study that the species accumulation curves were almost equal for the 3 intermediate scale areas (Fig. 4) shows that the number of new species recorded per area of sediment sampled was relatively similar across the study area. Ellingsen & Gray (2002) found that the species accumulation curves for the 5 large areas along the Norwegian shelf differed and were related to the level of environmental variability. However, in Hong Kong waters, the level of environmental variability (Table 1) was relatively high in all 3 areas. Furthermore, the scale of the total area in Hong Kong waters is smaller than for each of the large
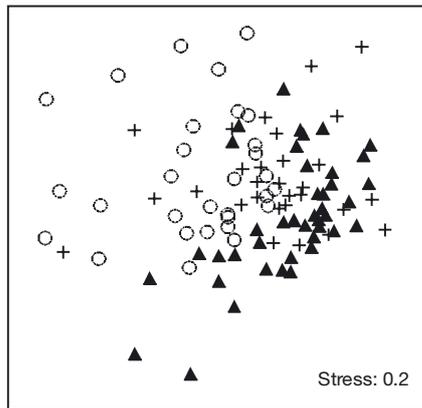
Fig. 6. Multidimensional scaling ordination for square-root-transformed macrobenthos data based on Bray-Curtis similarities. (O) western area; (+) middle area; (▲): eastern area (cf. Fig. 1)

areas along the Norwegian coast. Thus, both spatial scale and variation in environmental heterogeneity may be important factors explaining the different slopes of species accumulation curves. The locations of the sites on the MDS-plot (Fig. 6) indicate that the faunal pattern was related to hydrographical conditions in the study area. Thus, the multivariate analysis gave additional information on sample species richness and species accumulation rates.

Distributions of species and beta diversity

Comparable numbers of species with restricted ranges were found in the present study (Fig. 5A) and in 5 large areas along the Norwegian shelf (range 33 to 50%, Ellingsen & Gray 2002). The finding in this study that the proportion of rare species at the intermediate scale was higher than at the total-area scale shows that species that appear to have a restricted range may actually prove to be more widespread if the extent of the area is increased (see also Ellingsen 2001). In a study of molluscs in New Caledonia, Bouchet et al. (2002) found that rare species made up a considerable proportion of the fauna; 32% of the species were found at a single station and 20% of the species were represented by single specimens. Thus, this pattern of many rare species and only a few that are widespread occurs at different spatial scales and seems to be common for benthic communities (see also Gaston 1994). If most species are rare at a given spatial scale, then this may also have important implications for conservation strategies.

In the present study, Whittaker's beta diversity (β_W) for all taxa pooled from the entire area was higher than for each of the 5 large areas along the Norwegian shelf (range 1.7 to 4.7, Ellingsen & Gray 2002). Thus, species

richness in the total Hong Kong area was high compared to the average of the sites within it. Moreover, mean Bray-Curtis similarity for all pairwise combinations of sites also showed that beta diversity in Hong Kong waters was high, in contrast to both alpha and gamma diversity.

In the Hong Kong area, beta diversity (Tables 6 & 7) was highest for molluscs, followed by crustaceans and polychaetes, while in the 5 large areas along the Norwegian shelf crustaceans had the highest β_W values (range 2.5 to 7.7, Ellingsen & Gray 2002). Beta diversity was highest for the taxonomic group with the highest proportion of restricted-range species (Table 2), a finding also reported for the Norwegian shelf (Ellingsen 2001, 2002, Ellingsen & Gray 2002), although the ranking of the dominant taxonomic groups differed between the 2 latitudes. Ellingsen (2001) suggested that the fact that many crustaceans are mobile, and hence may be undersampled because they are able to move away from the grab, might distort the result and therefore be one reason why this group had the highest proportion of restricted-range species on the Norwegian shelf. Virtually all of Hong Kong's 1800 km^2 of seabed is perturbed by pollution, trawling, or direct and indirect dredging impact (Morton 1996). According to Morton (1996), molluscs have a greater potential to survive trawl-sampling than other taxa, and this may be one reason why molluscs had the highest proportion of rare species with regard to both distribution across the sampling area and abundance.

The present study showed that beta diversity changes with spatial scale, and that the choice of both the largest and the smallest scales in measures of beta diversity is of importance (Tables 6 & 7). According to Levin (1992) there is no single correct scale at which ecosystems can be descried. However, more care is needed in the selection of spatial scales when comparing faunal patterns between areas. The finding that β_W in subtropical Hong Kong waters was higher than that reported for the much larger scales along the Norwegian shelf (Ellingsen & Gray 2002) shows that factors other than spatial scales must also be important. Ellingsen & Gray (2002) found that beta diversity increased with increasing environmental variability, and in a study of North Atlantic bryozoans, Clarke & Lidgard (2000) found a tendency for beta diversity to be higher at lower latitudes, suggesting that this might be a result of greater heterogeneity in warmer waters. However, the measured variability in depth and sediment type (Table 1) in the present study was not higher than on the Norwegian shelf. This indicates that it is difficult to explain patterns of biodiversity, and that factors other than spatial scale, depth and sediment type (biological or non-biological) may also play important roles in determining the level of beta diversity.

CONCLUSIONS

This investigation of macrobenthos diversity in Hong Kong waters has shown that it is important to use different measures of 'biodiversity' in a given area. Alpha diversity was low, and species richness at larger spatial scales was not particularly high even though the study area is located in the subtropics. However, beta diversity was high. Although human impact on Hong Kong waters is serious and may distort patterns of diversity, this study has shown that species richness in subtropical areas is not always high and may be variable. Knowledge of biodiversity patterns at different spatial scales in subtropical/tropical areas that are not influenced by human activities is, however, needed in order to determine latitudinal gradients. The number of 'rare' species both with regard to spatial distribution and abundance was high, a patterns that seems to be common in ecological systems.

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