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DISTRIBUTION OF MARINE BENTHIC AMPHIPODS OFF PHUKET ISLAND, WITH EMPHASIS ON TIN MINING AND A MODEL OF SPECIES-INDIVIDUAL RELATIONSHIPS

by

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ABSTRACT

Grain size distribution of sediments, species composition, distribution and density of 30 species of amphipods were studied along the west coast of Phuket Island, the Andaman Sea, southern Thailand. Bimonthly bottom samples were obtained during one year with a 0.1 m^2 Smith McIntyre grab at 15 stations, ranging in depth from 10-30 m.

A modification of traditional sieving and searching procedures yielded 2-3 times higher densities of amphipods per unit area. Contrary to previous findings, amphipods were prominent members of the offshore benthic communities.

The distribution of the amphipods is discussed in relation to concentrations of silt-clay, heterogeneity of sediments, and other groups of benthos at the 15 stations. It is concluded that amphipods are good indicator organisms with respect to silt-clay conditions of the sea bed.

A model is proposed for the relationship between total density of species and total density of individuals per station. The model is based on a truncate normal curve distribution and divided into four areas of amphipod occurrence termed inadequate, suboptimal, acceptable, and optimal. Lines of demarcation of these four areas is based on a division of the density of individuals into geometric classes.

I. INTRODUCTION

A number of studies have been conducted on marine amphipods of the Indian Ocean, basically from a taxonomic point of view (Barnard, 1935, 1940; Chilton 1921, 1925; Giles 1885, 1887, 1888, 1890; Gravely 1927; Nayar 1950, 1959, 1965; Panikkar & Aiyar 1937, 1939; Pillai 1957; Rabindranath 1971, 1972; Sivaprakasam 1966, 1967, 1968, 1969, 1970; Stebbing 1887, 1904, 1907, 1908; Tattersall 1912, 1922; Walker 1904, 1905, 1909). In Thai coastal waters little attention has been paid to marine benthic amphipods and only pelagic amphipods (Order Hyperiidae) have been reported from the Gulf of Thailand and the South China Sea (Sudara 1972, 1975). Therefore,

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systematic knowledge of the amphipods of Thailand is very limited. Generally, benthic amphipods form an important component of small crustaceans found in littoral sea beds and they are frequently found in quantities in stomachs of predatory, benthos-feeding fish (Nakata 1959, 1965; Price & Hylleberg 1982).

The purpose of the present study is to describe the number of species, and the distribution and density of individuals of benthic amphipods in relation to environmental factors, especially the effects of offshore tin mining on amphipods. The structure of plant and animal communities, in terms of species and individuals in the communities, has been of ecological interest for many years (Driscoll & Swanson 1973) and it is clear that in no community are all species equally abundant. The distribution of species abundance is a significant aspect of the structure of a community. In consequence, we have included a discussion of a model relating densities of species and individuals to the abiotic environment and biotic characteristics. The model provides a feeling for the relationship between the relative abundance of species and other aspects of the structure of amphipod assemblages, such as diversity, dominance, and impact of severe environmental disturbance.

II. MATERIALS AND METHODS

The present study was carried out along an approximately 40 km long stretch of the west coast of Phuket Island, the Andaman Sea, Thailand. Fifteen stations ranging in depth from 10 to 30 m were sampled off four bays, viz. the open bays of the Airport, Bang Tao, and Kamala, in addition to the sheltered bay of Patong (Fig. 1). The offshore tin mining took place in Bang Tao Bay. The dredges were normally in operation during November to April, that is the period of the north-east monsoon. Reference is given to Hylleberg *et al.* (in press) for details about dredging activities in Bang Tao Bay.

A benthic study programme was launched in cooperation between the National Environment Board (NEB) and Phuket Marine Biological Center (PMBC) in order to study the effects of offshore tin mining on macro-benthic communities during 1980-1983. The material examined in this paper is based on the first year of collection April 1980 to February 1981. Bimonthly sampling was done using a 0.1 m^2 Smith McIntyre grab except that sampling in August was postponed to September due to rough sea conditions. Three samples were taken at each station at each cruise. The grab samples were sieved through 1 mm mesh size. During the first four cruises animals were picked by hand from the sieves. During the last two cruises, the sieving residue, containing small suspended animals, was filtered through a 0.5 mm mesh screen. The organisms were fixed in 10% formalin. Amphipods were sorted in the laboratory, preserved in 70% ethyl alcohol, and identified. Sediment samples were taken at random from the surface of each grab sample in order to determine particle size distribution (Hylleberg *et al.*, in press).

Unless otherwise stated, data on abundance of individuals has been divided into geometric classes according to Preston (1948). The intervals are denoted arabic numbers, i.e., 1-2 individuals = I, 2-4 ind. = II, etc. If a species is represented by, e.g., 2 specimens interval I is credited with half a species and interval II with the other half. When all individuals are assigned to geometric classes the number of species per interval is counted. This is the ordinate of the graph and the abscissa is a scale of increasing commonness.

III. RESULTS

Occurrence of amphipods in the study area

From 270 samples each 0.1 m^2, a total of 962 amphipods were collected and identified. At least 30 species from 11 families were found. With few exceptions the amphipods could be referred to species as shown in Table 1. The family Ampeliscidae dominated at all stations,

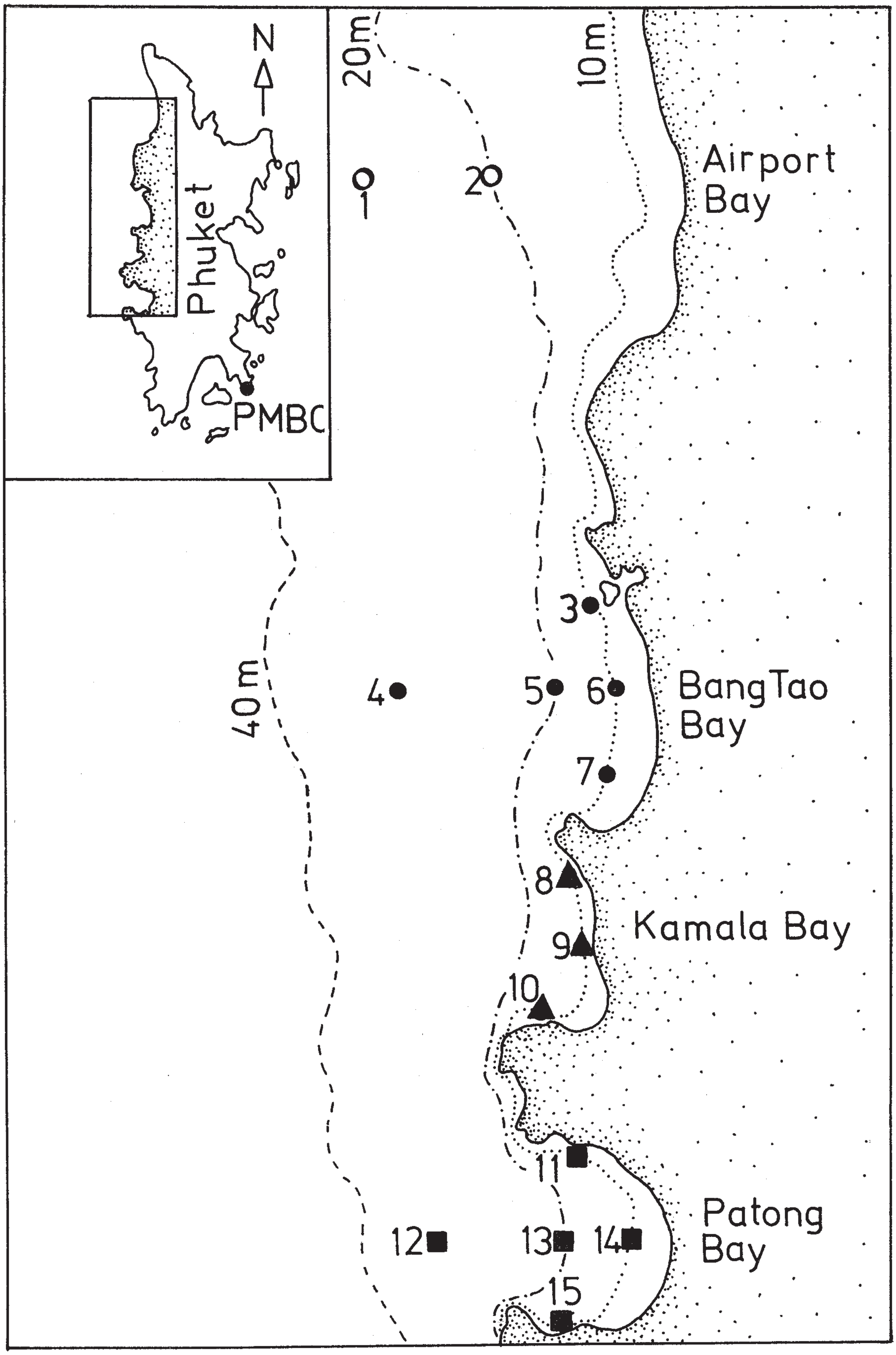

Fig. 1. Study area on the west coast of Phuket Island showing the stations sampled between 10 and 30 m depth.

Table 1. Species list and number of amphipods found during investigated period (April 1980-February 1981).

No.	Species	Station 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
	AMPELISCIDAE																
1	*Ampelisca brevicornis*	18	-	2	16	1	1	7	-	2	15	2	5	4	12	10	95
2	*A. cyclops*	27	-	-	1	-	-	-	3	14	6	4	29	7	20	4	115
3	*A. misakiensis*	9	-	-	-	1	-	-	10	1	16	-	7	3	3	5	55
4	*A. tridens*	-	-	-	-	-	-	-	-	-	2	-	-	-	-	3	5
5	*A. zamboangae*	18	-	-	1	-	-	-	-	1	3	3	9	3	13	1	52
6	*Byblis sp.*	1	29	5	1	12	1	11	-	-	13	-	3	27	2	21	126
	AORIDAE																
7	*Lembos sp.*	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2
	COROPHIIDAE																
8	*Grandidierella gilesi*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	GAMMARIDAE																
9	*Eriopisa chilkensis*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
10	*Eriopisella sechellensis*	6	2	1	-	-	1	1	-	3	1	97	73	1	48	5	239
11	*Elasmopus sp.*	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	4
12	*Maera sp.*	-	1	-	-	-	-	-	-	-	1	-	-	1	1	7	11
13	*Megaluropus agilis*	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	3
	HAUSTORIIDAE																
14	*Platyischnopus herdmani*	-	1	-	-	-	-	-	-	-	-	4	-	-	-	-	5
15	*Urothoe platydactyla*	-	-	-	-	-	-	-	3	19	2	5	-	-	30	20	97
16	*U. spinidigitus*	-	-	-	-	-	-	-	-	1	5	-	-	-	-	4	10
	ISAEIDAE																
17	*Cheiriphotis megacheles*	-	1	-	1	1	-	1	-	-	-	-	-	-	1	-	5
18	*Gammaropsis afer*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
19	*G. atlanticus*	-	13	-	-	2	-	1	-	-	10	-	4	22	-	3	55
20	*Photis longicaudata*	-	3	-	-	1	-	1	1	-	7	1	-	5	-	2	21
	LEUCOTHOIDAE																
21	*Leucothoe furina*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	LILJEBORGIIDAE																
22	*Idunella janisae*	-	1	-	1	1	-	-	-	-	-	4	-	4	-	-	11
23	*I. serra*	1	-	-	1	-	-	-	-	-	-	-	7	2	8	-	19
24	*Idunella sp.*	1	-	-	-	-	-	-	2	-	-	-	-	3	-	-	6
	LYSIANASSIDAE																
25	*Lysianassid*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	OEDICEROTIDAE																
26	*Periculodes longimanus*	-	2	-	-	-	-	-	1	-	5	-	-	2	1	1	12
	PHOXOCEPHALIDAE																
27	*Harpiniopsis sp.*	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2
28	*Mandibulophoxus uncirostratus*	-	2	-	-	-	-	-	1	-	3	2	-	1	-	1	10
29	*Paraphoxus rostrata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	6	7
30	Unidentified	-	3	1	-	-	-	-	-	-	-	-	3	1	-	-	8
	Total	82	65	9	22	19	3	24	22	41	89	123	140	87	140	96	962

making up 47% of all individuals. Next followed the family Gammaridae, accounting for 27% of the collected individuals. Gammarids, especially the species *Eriopisella sechellensis* (Chevreux 1901), were quantitatively dominant at depths of 10 m (Fig. 2).

Three families contained from 4-10% of the individuals while seven families contained from

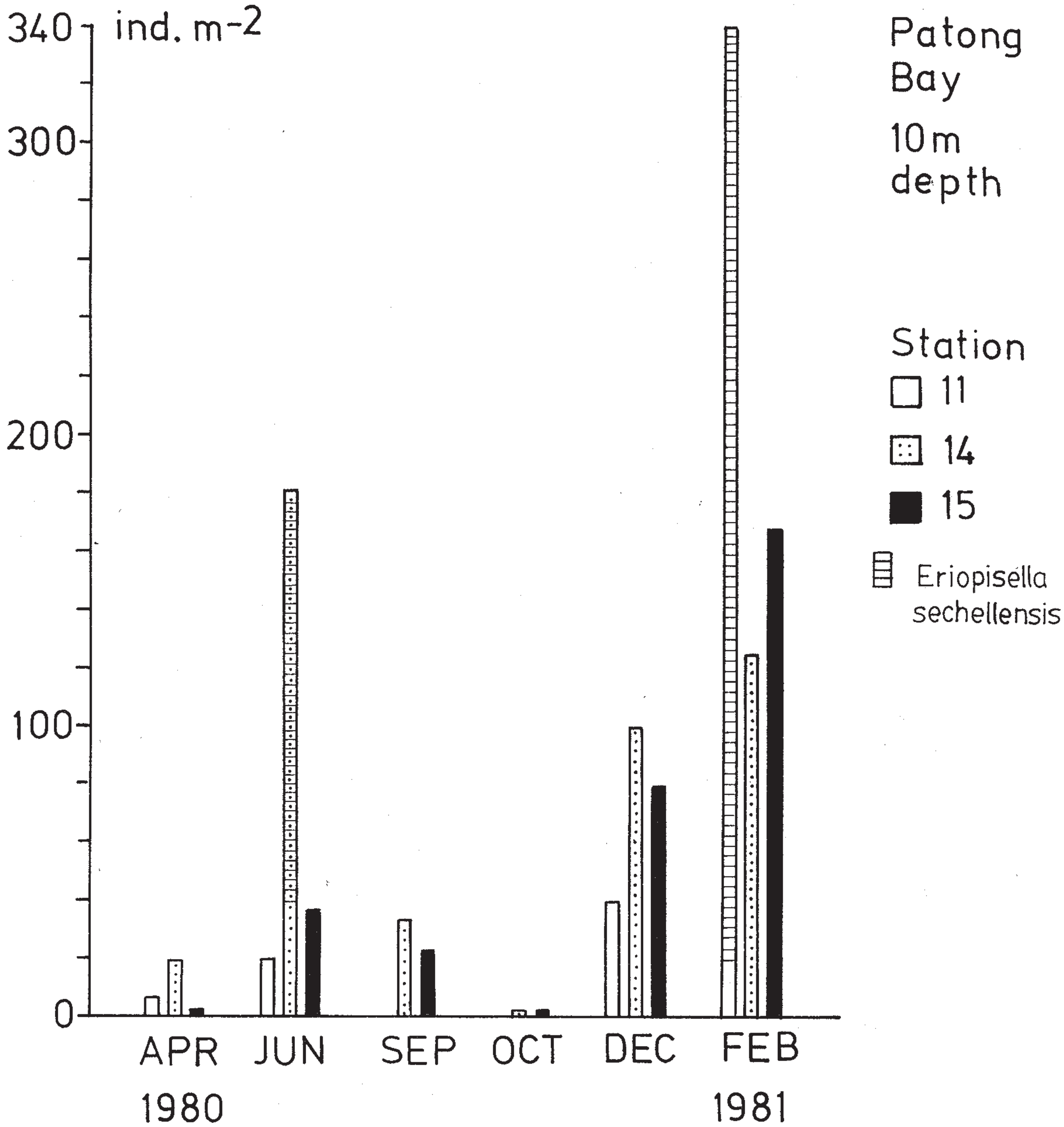

Fig. 2. Number of individuals of amphipods per square meter in Patong Bay. The three stations 11, 14, and 15 are located in the northern, central, and southern part respectively.

0.1-2% of the specimens; in other words, the amphipods conform with the general pattern of species occurrence, there being a few common species and many rare species (Fig. 3). This pattern is well known from all biotopes, although particularly conspicuous in tropical marine areas.

Fig. 4 shows that commonness in terms of individuals is positively correlated with frequency of encounter as exampled by *Ampelisca brevicornis*, *Byblis* sp., and *Eriopisella sechellensis* (sp. no. 1,6 and 10 respectively, Table 1). These species reached the highest total individual densities and were collected from more than 75% of the stations.

Overall density of amphipods

The density of species of amphipods in relation to the number of individuals collected at each cruise is shown in Fig. 5. This graph indicates seasonal variation in occurrence since the first four cruises took place during the SW monsoon and the last two cruises during the NE monsoon.

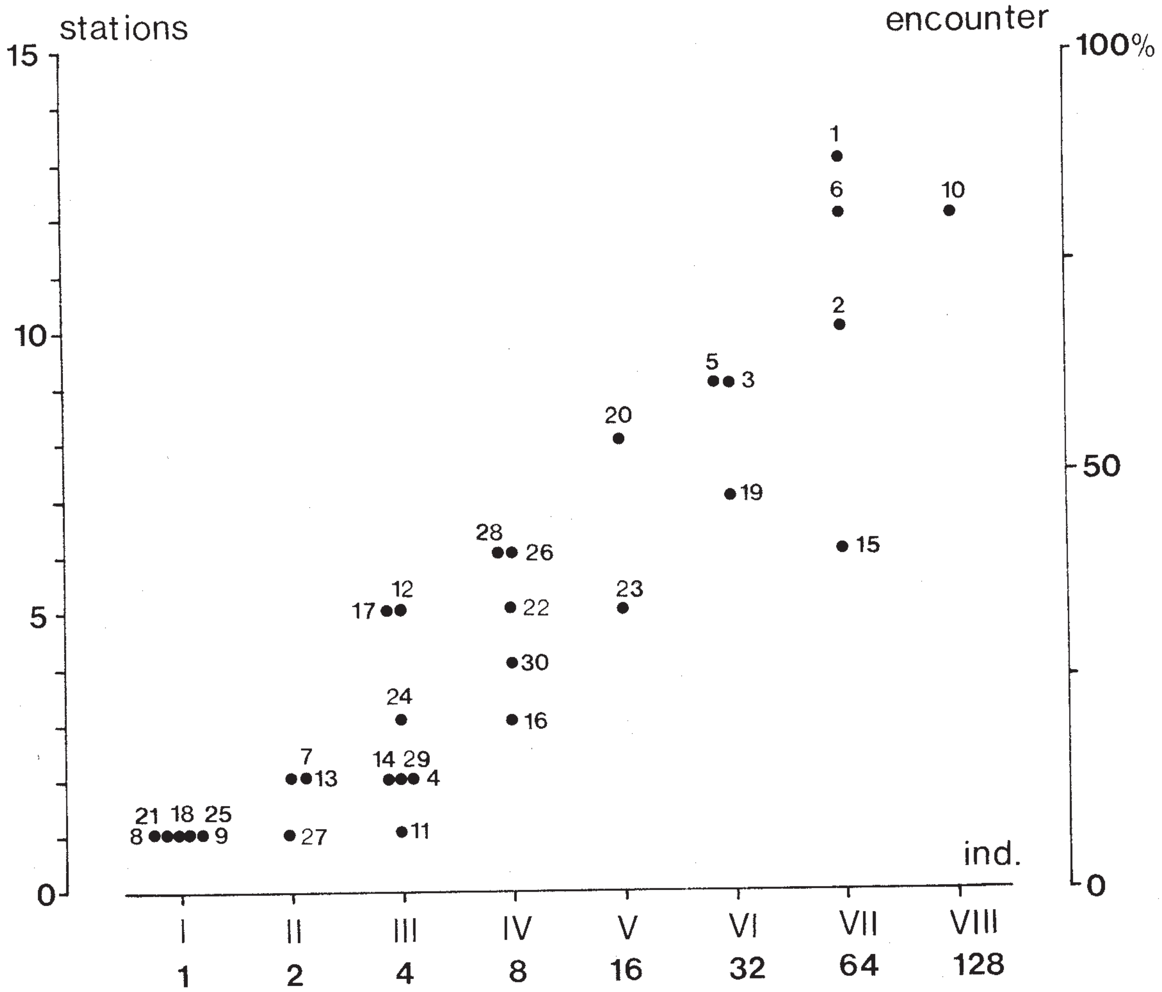

Fig. 3. The number of amphipod species per geometric class as a function of the number of individuals per geometric class. Values are calculated for taxa encountered at each station, cf. Table 1. Overall plot of the 15 stations.

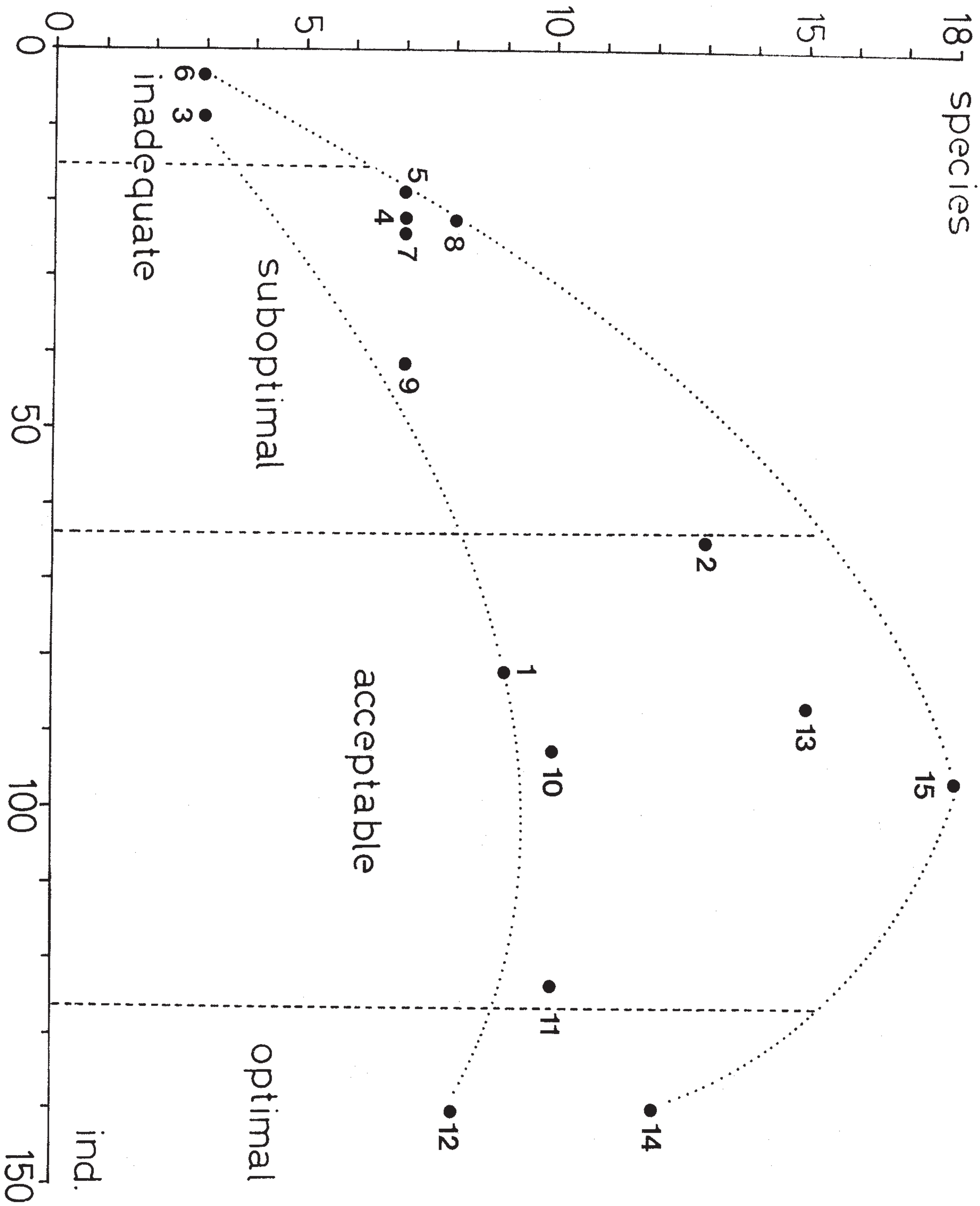

Fig. 4. The total number of stations where a given amphipod species has been encountered. Data points show the species, numbered according to Table 1, as a function of the overall density of individuals divided into classes where the starting points form a geometric series.

However, interpretation of the data is difficult because low numbers of amphipods recorded during April to October and high numbers obtained in December and February can partly be explained in terms of different sorting technique employed during the two periods. The method of handpicking individual amphipods upon encounter yielded rather low and similar numbers during

72	110	65	124	204	387	ind. cruise-1
13	14	10	16	21	24	sp. -
APR	JUN	SEP	OCT	DEC	FEB	month &
1980					1981	year of cruise

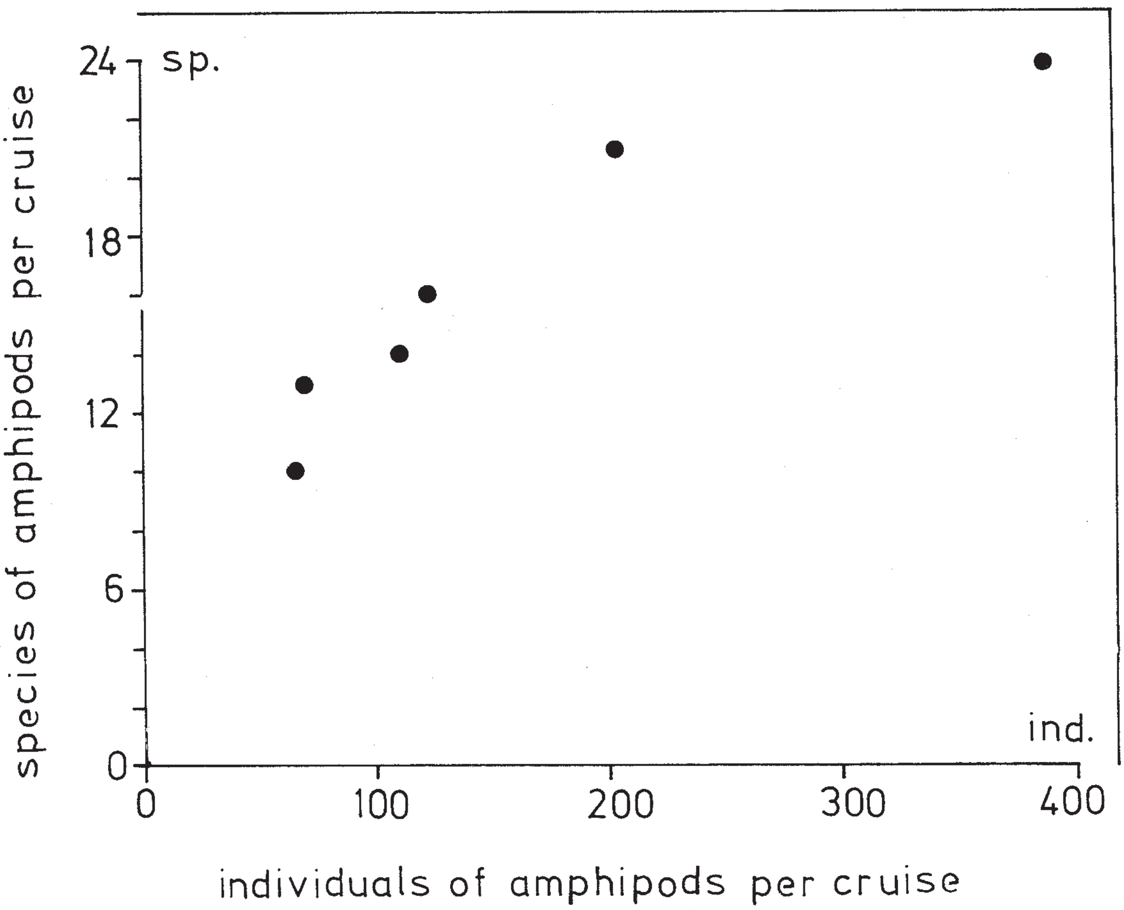

Fig. 5. Number of individuals and species of amphipods per cruise. The number of species is graphed as a function of the number of individuals for the 15 stations sampled.

the first four cruises. By improving the technique of collecting the encounter of specimens may have increased by a factor 2 to 3.

Distribution associated with depth

Generally, the abundance decreased with increasing depth. A maximum of 18 species of amphipods was obtained at 10 m depth (st. 15) while 15 and 9 species were found at 20 and 30 m depth, respectively, (st. 13 & 1). However, individual species showed much overlap with respect to distribution along the gradient of depth, although species such as *Urothoe platydactyla* and *U. spinidigitus* were only found at 10 m depths (Table 1). *Grandidierella gilesi* was only found at 30 m depth, and, at 20 m depth, st. 2 did not harbour any species of *Ampelisca.* The latter station had coarse sediment, very different from all other stations as shown in the following paragraph, Fig. 7C.

The pattern of density of individuals showed two maxima at 10 and 30 m depth at st. 12 and 8, respectively. On an average the number of individuals per m^2 were 50, 32, and 45 individuals at 10, 20, and 30 m depth, respectively. This pattern of distribution was caused by dominance of Ampeliscidae and Gammaridae at 10 and 30 m depth, Haustoridae at 10 m, and Isaeidae at 20 m depth.

Distribution associated with sediment characteristics

i) stations at 10 m depth

The offshore tin mining was carried out in Bang Tao Bay near st. 3 & 6 (Fig. 1). Operations were large scaled, involving huge dredges which, according to the type of dredge, would either dig or suck up the sea bed to about 8 m sediment depth. Processing of the ore was carried out onboard the dredges by washing on jigs and the unwanted material was discharged to the sea behind the dredges. The finer particles (silt-clay) were transported by currents and settled again on the sea bed some distance away from the dredges. Of course, the impact of sedimentation could be expected most pronounced in the vicinity of the dredges. Fig. 6 shows that amphipods conformed with this expectation. St. 3 & 6 near the dredges were impoverished in terms of species as well as individuals compared with stations at similar locations in Kamala (st. 8 & 9) and Patong Bay (st. 11 & 14), increasingly away from the dredges.

We have desisted from analysis of the statistical significance of these differences on account of the limited data and the heterogenous variances. However, with a larger material of polychaetes Hylleberg & Nateewathana (in press) showed significant impoverishment at st. 3 & 6, in addition to some seasonal effect at 20 m depth (st. 5). The latter station was impoverished during the NE monsoon when dredging occurred in the area and recovered during the SW monsoon when dredging was halted. On this background we draw the conclusion that the abundance of amphipods was reduced by offshore tin mining in Bang Tao Bay. This bay had fine grained sediments with a small median diameter and 15-20% silt-clay. The sediments of the neighbouring Kamala Bay fluctuated considerably in regard of median diameter, especially at st. 9 & 10 in the central and southern parts of the bay. The percentage of silt-clay was 10%, i.e., lower than in Bang Tao and the subsequent Patong Bay. The deeply indented Patong Bay had silt-clay concentrations similar to Bang Tao Bay, except at st. 15 where the sea bed was composed of medium sand with a small percentage of silt-clay. This station harboured the maximum number of amphipod species and the average density was 53 individuals per m^2.

By visual matching of Fig. 6 A, B & C it is obvious that occurrence of amphipods and characteristics of sediments were not correlated in a simple way. As an example reference is given to st. 7 in Bang Tao Bay and st. 14 in Patong Bay. These stations were almost identical regarding concentration of silt-clay particles, median diameter, and standard deviations of these parameters but the amphipod fauna differed considerably in terms of abundance of species as well as density

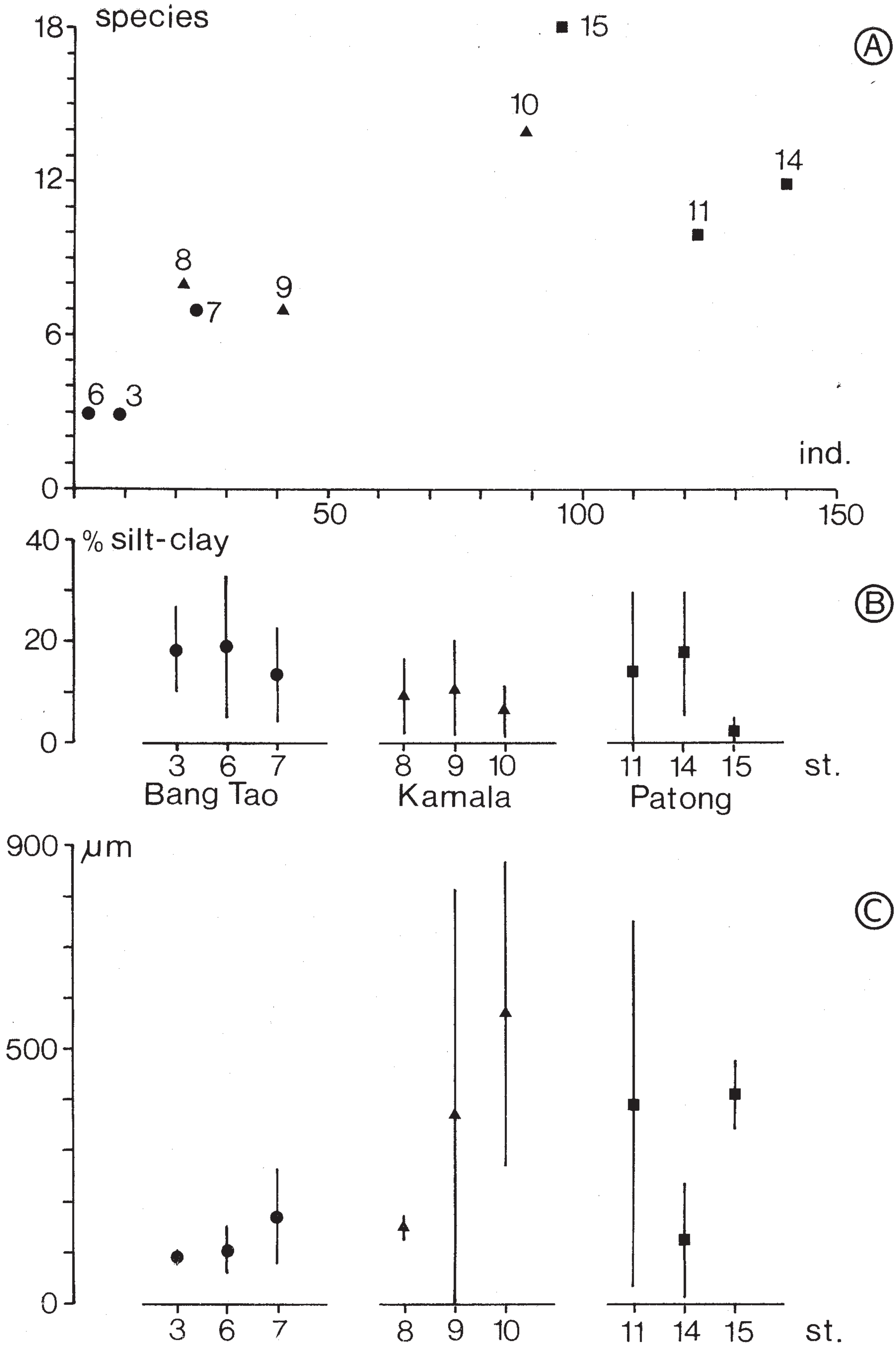

Fig. 6. (A) the total number of species as a function of total number of individuals at 9 stations at 10 m depth, cf. Fig. 1. (B) the percentage of silt-clay particles, and (C) the mean particle diameter of sediments from the same stations. Means and standard deviations are shown.

of individuals. We interpret the data in Fig. 6 to indicate some unknown between-bay differences in oceanographic conditions which were not reflected in the sediments.

We make the general conclusion that the lowest number of species, as well as density of individuals, were associated with very fine sand (63-125 µm) characteristic of the offshore tin mining area. More species were associated with fine sand (125-250 µm) and the maximum density of amphipods was encountered within this grade (77 ind. m^2 at st. 14). Medium sand (250-500 µm) was rich in species as well as individuals.

A between-bay comparison of the southern stations (7, 10, 15) shows that the coarsest sediment, the lowest concentration of silt-clay particles, and the highest number of species were found at these sites in each bay. The density of individuals followed a similar pattern in Bang Tao and Kamala Bay but not in Patong Bay.

ii) stations at 20 & 30 m depth

The fauna contained few species and individuals off Bang Tao Bay at st. 4 & 5 (Fig. 7 A). The sediment characteristics do not give any hints to why these stations should be impoverished compared with other stations at identical depth. The measured sediment parameters, including their standard deviations, were almost identical at st. 4, 5 & 1. With respect to granulometrics only st. 2 was significantly different from the other stations. The median diameter indicated very coarse sand and there was only a small, predictable concentration of silt-clay particles (Fig. 7 B & C).

Fig. 7 shows trends similar to those found at 10 m depths, namely that most species occurred in sediments with a large median diameter while fewer species were present in very fine, and fine sand with an average concentration of 15-20% silt-clay.

Density of amphipods relative to other invertebrates

Interactions between species can influence the composition of the fauna. For example, successful species can prevent other species from becoming established in an area. However, this so-called competitive exclusion principle is rarely documented in nature but is inferred from indirect evidence (Fenchel & Kofoed 1976; Peterson 1979). On level sea bottom exclusion of other species has been referred to as trophic group amensalism (Rhoads & Young 1970). Deposit feeding benthos was found to exclude species of suspension feeders due to reworking of sediment. However, trophic group amensalism is not a universal phenomenon and it should be noted that reworking of sediment also will affect deposit-feeders, including the dominating species responsible for the bulk of sediment reworking (Hylleberg & Riis-Vestergaard 1984). The magnitude of interspecific competition will also depend upon the density of species as well as individuals. Finally, the dominance of single taxa can take place on account of special fitness to environmental factors not tolerated by other taxa. A simple relationship between amphipods and other invertebrates should, therefore, not be expected. The relationship depicted in Fig. 8 shows that, apparently, the number of individuals of amphipods increased with increasing density of other invertebrates up to a density of about 300 individuals per m^2. Above this value the number of amphipods seemed to increase without relationship to the density of other invertebrates. However, st. 11 made an exception since this station was rich in amphipods and relatively poor in other invertebrates. The graph also emphasizes a relatively high proportion of amphipods of the total fauna at st. 12 & 14. These three stations resemble each other in terms of species-individual relationships of the amphipods as shown in Fig. 9 and discussed in the following paragraph.

IV. DISCUSSION

Occurence of amphipods in the area

In the results we have argued that differences in occurrence of amphipods between the first four and the last two cruises could be explained as a matter of sampling technique. However,

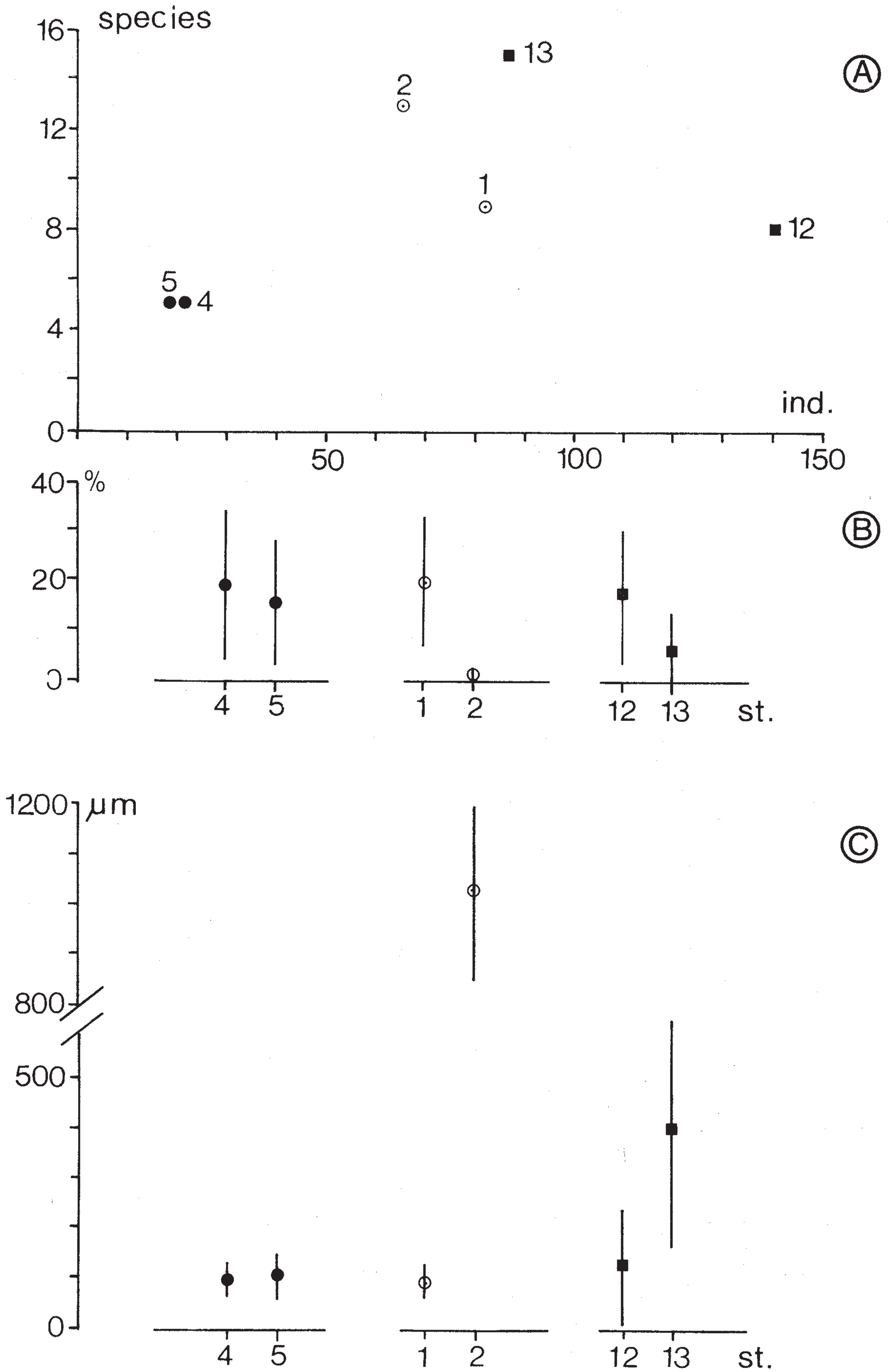

Fig. 7. (A) the total number of species as a function of the total number of individuals at 6 stations at 20 and 30 m depth, cf. Fig. 1. (B) the percentage of silt-clay particles, and (C) the mean particle diameter of sediments from the same stations. Means and standard deviations are shown.

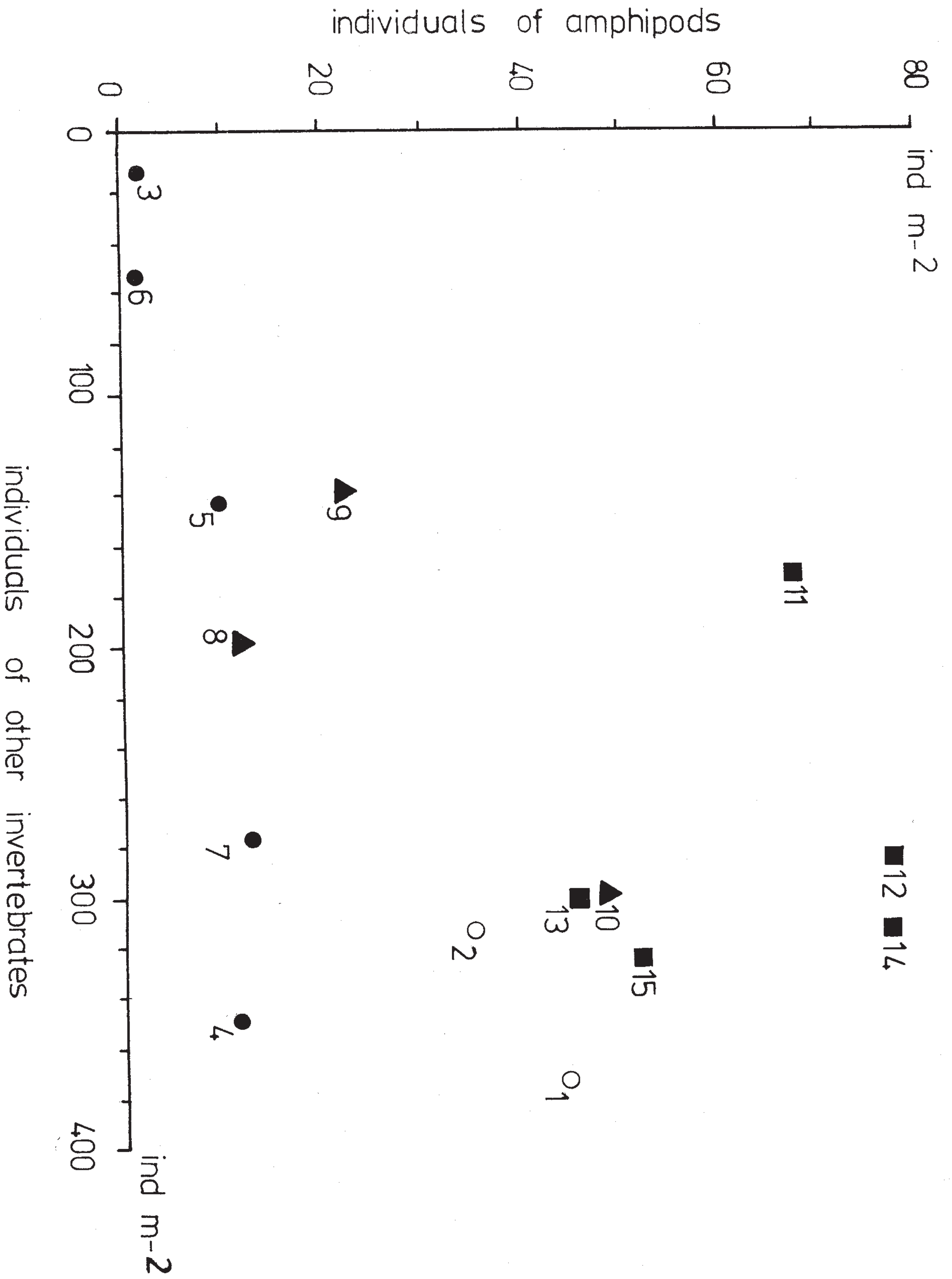

Fig. 8—Density of individuals of amphipods per square meter as a function of the density of other benthic invertebrates sampled at the 15 stations shown in Fig. 1. Mean values for six cruises are shown.

it is also possible that the low number of species in September may be related to storms in the previous month. For example, Croker & Hatfield (1980) and Grant (1980) have shown a significant washout of amphipods in intertidal and shallow water sediments. Dobbs & Vozarik (1983) found a significant increase in the number of individuals, as well as species, in the water column following a storm. This was the result of washout of infauna. Of course the effect of storms on amphipods cannot be judged completely in the present study since emphasis has not been put on the timing of sampling in relation to storms raging during most of August (Hylleberg *et al.*, in press). However, if there was an effect our data indicate a small scale and temporary effect on the number of species while density was less affected. This condition would agree with findings in Dobbs & Vozarik (1983).

Species-individual relationships

The number of species as a function of the number of individuals collected at all stations per cruise shows a relationship which has the form of a saturation curve, that is, the density of individuals increased faster than the density of species per unit area (Fig. 5). This finding agrees with Lindroth (1935) who found that high species density was usually observed in biotopes rich in individuals. It should be noted, however, that a saturation curve is only obtained when the species and individuals are pooled per cruise. If we analyse species density at individual stations we get a different picture as shown in Fig. 6 & 7. Taken together data in Fig. 6 & 7 may show a bell-shaped pattern when species density (a measure of diversity) is viewed as a function of the density of individuals (a measure of dominance). In consequence we have redrawn the data and propose the model shown in Fig. 9 to describe the structure of amphipod assemblages observed during the present study. The model depicts species-individual relationships in terms of total number of individuals per station and, as such, it is a modified version of distributional patterns proposed by Preston (1948), Driscoll & Swanson (1973), Patric (1977) and Cairns (1982). The latter discussed a model of species per geometric class as a function of the number of individuals per species and showed that the number of individuals per species were arrayed in a predictable fashion following a truncate normal curve. The relationship becomes curved because low density species are by far the most common, and high density species are few. The latter constitute the recurved part of the relationship termed optimal in Fig. 9. Before we proceed to discuss Fig. 9 the following facts should be noted.

The prime control for the distribution of the amphipods is not known in the present study area but many factors may contribute to the natural controls for a specific population. Hence, the situation may be very complex to interpret. For example, the area termed optimal in Fig. 9 may turn out to be suboptimal in terms of tolerance responses when the species have been studied in detail. Species which flourish in habitats that are suboptimal with respect to important abiotic factors are not uncommon, especially species normally found in harsh environments. Reference can be given to botanical examples such as European heather and cattails (Phleger, 1971). Yet, these shortcomings in our knowledge do not invalidate the model which emphasizes the following facts:

(1) Data points at the beginning of the rising curve represent stations poor in species as well as individuals.

(2) Stations at the top of the bell-shaped curve are rich in species at medium densities of individuals.

(3) Stations at the end of the falling curve are poor in species but rich in individuals.

Re (1). With respect to the first case the low numbers at station 3 & 6 indicate that stress conditions affect the amphipods greater than the adaptive abilities of the amphipods can handle. In the present study such stress may be caused by offshore tin mining which increased the rate of sedimentation and disturbance of the sea bed (Hylleberg *et al.*, in press). Stations 3 & 6 in Bang Tao Bay are inadequate for amphipods.

The area encompassing st. 4, 5, 7, 8 and 9 is termed suboptimal and covers the geometric classes IV-V of density of individuals. It should be noted that st. 4 & 7 harboured a rich fauna of other invertebrates (Fig. 8) but conditions were certainly suboptimal for amphipods. The deeper stations 4 & 5 off the tin dredges also seemed to

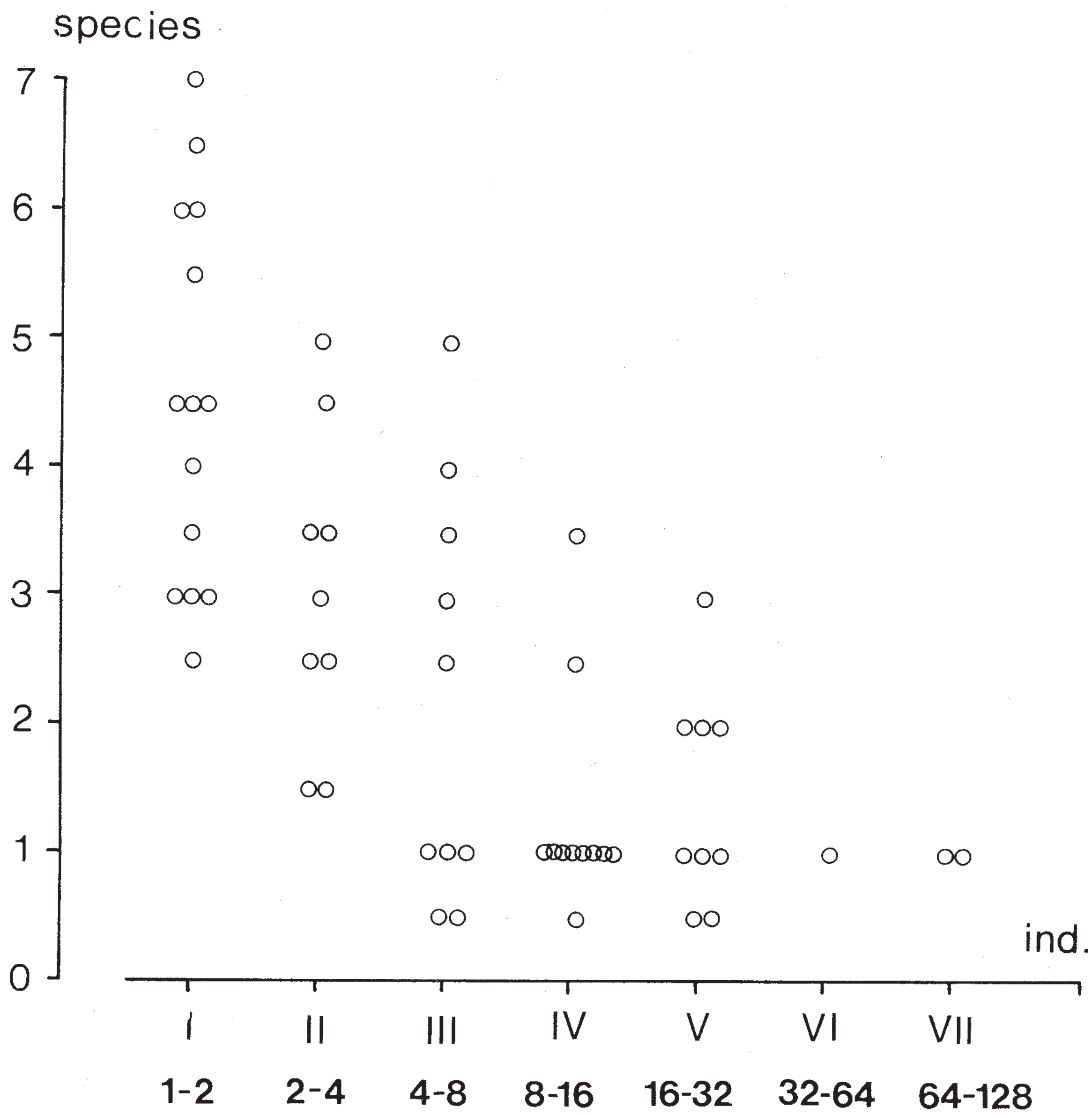

Fig. 9. Model of distribution of amphipods. The total density of species is plotted as a function of the total density of individuals at the 15 stations. Demarcation lines (based on geometric classes of individuals) and bell-shaped curves (based on higher and lower species densities) form four cases of amphipod occurrence ranging from near absence of amphipods (inadequate) to dominance (optimal for amphipods).

be affected by mining activities since the values are found in the left hand side of Fig. 9. However, according to arguments presented in the results and Fig. 8, these stations cannot be considered affected by offshore mining in general but they represent suboptimal habitats for the amphipods.

Re (2). Regarding the second case, the top of the curve is represented by st. 15 in the southern part of Patong Bay. The conditions which caused st. 15 to contain the maxinum number of species are open for discussion; we can only direct attention to some general factors. The southern sites in Kamala (st. 10), and Patong Bay (st. 15) were generally rich in benthos compared to the northern parts (Hylleberg *et al.*, in press) and they also have the best developed fringing reefs, indicating good exchange of water. Furthermore, the sea beds consisted of mixed sediments, i.e., displayed structural complexity of the bottom and structural complexity has often been considered an important determinant of biotic diversity (Kohn 1971; Gallucci & Hylleberg 1976; Kohn & Leviten 1976). However, it is also obvious that the living organisms themselves constitute a very important factor in terms of creating structural complexity. A species rich area will create more environmental heterogeneity than a species poor area. A few examples may illustrate this point. Corals can establish themselves in homogenous environments such as a slab of concrete. Once the basic material is settled the most diverse community develops on account of shapes, holes, and quality of intersticies which determine the density and composition of fauna associated with the corals. Reference can also be made to benthic polychaetes which make burrows and tubes, thereby providing habitats for a number of associates (Nielsen 1964) and affecting microbial processes (Hylleberg & Henriksen 1980). Finally, the sipunculan *Phascolion strombi* keeps gastropod shells exposed on the surface of the mud. This behaviour provides habitats for a number of epifauna associates which otherwise would be absent from the level bottom (Kristensen 1970). In other words, animals may provide habitats for other animals in a self-increasing way. In the context of Fig. 9 we note that the stations designated acceptable, i.e., acceptable for many species of amphipods, were also rich in other species of invertebrates (Fig. 8).

Re (3). The third regime, the declining part of the curve referred to as optimal in Fig. 9, contains st. 12 & 14 while st. 11 is situated at the demarcation between acceptable and optimal areas. The latter condition can be expected to occur in areas where food is abundant and a certain homogeneity of the sea bed prevail. The underlying principle is that the environmental impact, which in the present study area would be currents, are powerfull, though constrained within predictable bounds. Those species tolerating the predominantly physically controlled conditions will be limited but may obtain high densities of individuals (Slobodkin & Sanders 1969; Sanders 1969) and yield data points in the right hand area of graphs such as Fig. 9. From tough clay bottom in Scandinavian waters a so-called amphipod community has been described in a limited area at about 30 m depth (Thorson 1957). The characterizing animal *Haploops tubicola* may reach 4000 individuals m^{-2} and only few other amphipod species occur in that area. Additional evidence for right hand points can be expected in mangroves and estuaries. Such areas are often poor in species but rich in individuals since opportunistic species that are adapted to the physical stresses can exploit the habitats successfully (Tenore 1972). With reference to polychaetes the study of Rao & Sarma (1980) showed an average of 140 *Nephtys oligobranchia* m^{-2} in an Indian estuary and this was the only species of *Nephtys* found in that area. In comparison, 8 species of nephtyids were obtained in the present study area and none of these species exceeded 30 individuals m^{-2} (Hylleberg & Nateewathana, in press).

V. CONCLUSIONS

Considering the data obtained between 10 and 30 m depths we conclude that the relationship of species density as a function of individual density is complicated to interpret. The simple relationship apparent from pooled data (Fig. 5) seems to obscure important ecological information. The relationship is more likely described in terms of a bell-shaped curve. Therefore, we have proposed a model for the species-individual relationship based on a lognormal distribution where the total number of species per station is shown as a function of total density of individuals per station. The curve is divided into four areas termed inadequate (1), suboptimal (2), acceptable (3), and optimal (4) according to the combination of species and individuals encountered during the present study (1.8 m^2 sampled at each station). Lines of demarcation were drawn between the geometric classes I-III (inadequate), IV-V (suboptimal) VI (acceptable, and VII (optimal).

The terms acceptable and optimal are used in a descriptive way and do not refer to tolerances or competitive abilities of the amphipods. Since the common species also are the widespread species (Fig. 4) we suggest that the assemblages of the acceptable area (Fig. 9) contains many stenotopic species with a narrow tolerance to most environmental variables. In comparison, the optimal area of Fig. 9 mainly contains eurytopic species with broad optima for most environmental variables.

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