ISSN 0001-4370, Oceanology, 2006, Vol. 46, No. 4, pp. 483–491. © Pleiades Publishing, Inc., 2006.
Original Russian Text © A.A. Udalov, T.A. Britaev, N.T.H. Than, 2006, published in Okeanologiya, 2006, Vol. 46, No. 4, pp. 518–526.

MARINE BIOLOGY

# Features of the Soft-Bottom Subtidal Macrobenthos in Nha Trang Bay (Vietnam, South China Sea)

**A. A. Udalov[a], T. A. Britaev[b], and N. T. H. Than[c]**

[a] Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia
[b] Severtsov Institute for the Problems of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia
[c] Joint Russian–Vietnamese Technical and Scientific Tropical Center, Nha Trang, Vietnam

Received October 7, 2005

**Abstract**—General characteristics of macrobenthos of the muddy sediments of the subtidal (19–24 m) zone in Nha Trang Bay (South Vietnam) were described based on the survey performed in April–May 2002. The mean abundance of organisms was 637 ind/m$^2$ and the mean biomass was 2.3 g/m$^2$. Sixty-seven macrobenthic species were found during the study. The main structural features of the macrobenthos were high species diversity, low species recurrence, and high evenness of the species structure with the absence of clearly manifested dominants. The number of species encountered regularly increased with the increase in the total area sampled from 210 to 5000 cm$^2$, though the relation did not reach saturation. The similarities and differences between the macrobenthos structures in Nha Trang Bay and those in some tropical and boreal soft-bottom communities are discussed.

**DOI:** 10.1134/S0001437006040059

## INTRODUCTION

Though the concept of the existence of latitudinal differences in the structure of marine bottom communities is widespread [26, 38], there is a dissenting point of view. In particular, Thorson [43] showed that, though the epifauna in tropical regions is richer, the level of infaunal diversity in different climatic zones is similar. This conclusion is drawn in some other studies [27, 50]. Most of the theories and generalizations concerning the structure and functioning of benthic communities are based on studies of communities of temperate latitudes and subtropical zones of Europe and North America. In other regions, including tropical and equatorial, the studies are episodical, except for the areas of coral reefs and mangroves [9].

A great number of publications devoted to the soft-bottom benthos of the tropical zone are related to the coasts of India and adjacent islands [10, 21, 32, 33]. These studies assessed, for the most part, quantitative parameters such as density and biomass of different groups of benthos, while no information on the species or structural characteristics of the communities was presented. Sufficiently complete descriptions of benthos with species lists and analysis of the main parameters (diversity, identification and description of the communities, distribution, and dynamics) are known for Costa Rica [31, 46, 47], the coast of Kenya (Gazi Bay) [40], northeastern Australia [17, 18], and Tahiti [23, 24]. For the coasts Southeast Asia, one may note the descriptions of selected communities of the muddy intertidal zone off the continental part of Malaysia [13] and Pukhet Island, Thailand [34], of the intertidal area off Hong Kong [42], and at six stations located from the intertidal zone to a depth of 30 m off Java Island [50].

Systematic studies of the fauna of Vietnam started in 1924 with the opening of the Kaude Marine Biological Station (Nha Trang Bay) and, later, of the Oceanographic Institute of Indochina. In 1937, Serene [41] published the first, though far from complete, list of invertebrate species of Indochina. More complete species lists with faunistic remarks were published by Dawydoff [15]. In the 1950s–1960s, this region (especially its northern part – Hainan Island and the Gulf of Tongking) was actively studied by Soviet, Chinese, and Vietnamese scientists from the faunistic and biogeographic points of view [3–5]. Nevertheless, only recently have data on the structure of the benthic communities off the Vietnamese coasts started to appear [2, 6, 44]. In order to fill this gap, in 2002, a joint Vietnamese–Russian program for studying the spatial distribution and monitoring the benthic communities in Nha Trang Bay was initiated. To date, four surveys have been performed of the spatial distribution of benthos in the intertidal zone of Nha Trang Bay at depths down to 40 m.

The main purpose of this publication is to describe the primary structural characteristics of the soft-bottom macrobenthos in the intertidal zone of Nha Trang Bay according to the data of the pioneering survey performed in the spring of 2002 and to analyze the data obtained in terms of the existing concepts of the latitudinal gradient of diversity of soft-bottom communities.

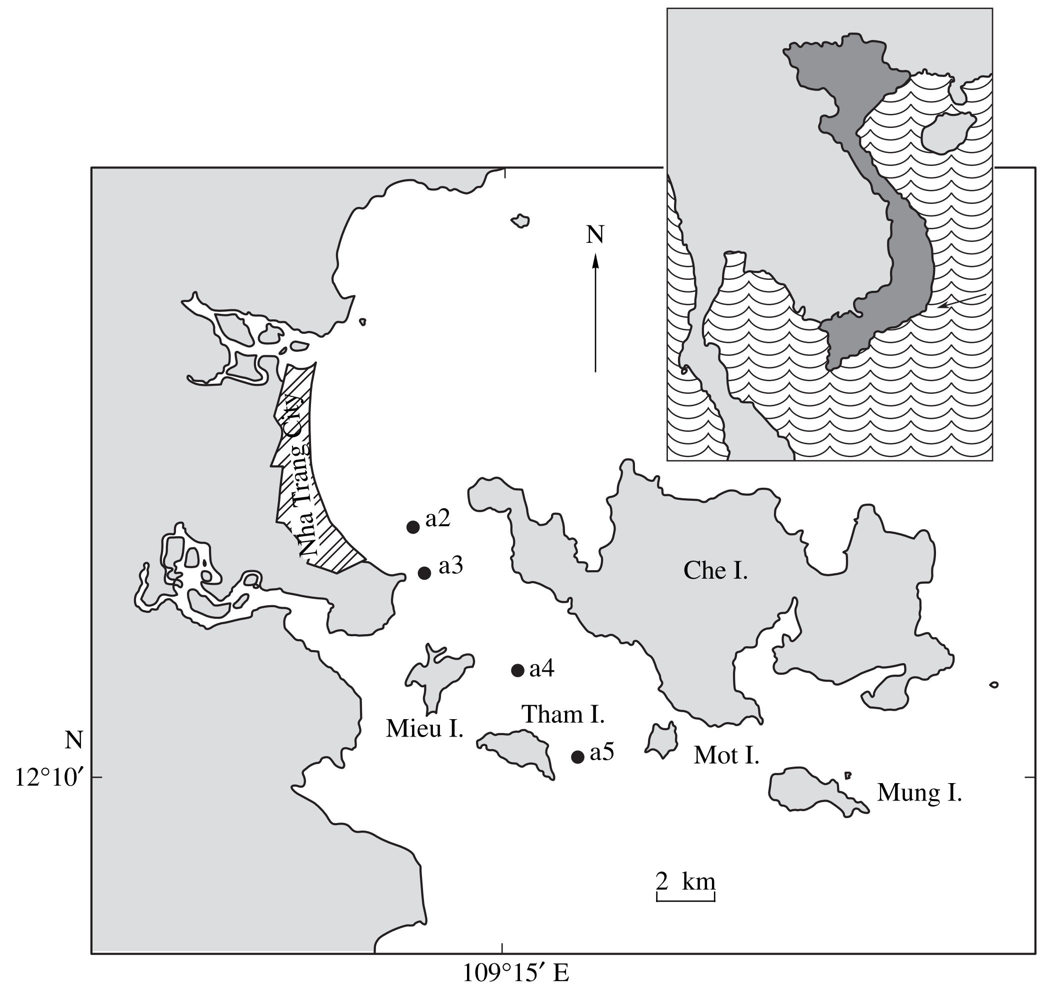


**Fig. 1.** Map of the region studied; a2–a5—sampling stations.

## MATERIALS AND METHODS

The survey was performed in the spring of 2002 (April–May). Four stations were occupied, located in the upper sublittoral zone over a section directed southeastward from the Kai River mouth between Chemical, Mieu, and Tham islands (Fig. 1). All the stations were located on muddy sediments in the depth range from 19 to 24 m, in the zone of the Kai River outflow. Therefore, at all the stations, the proportion of fine silty fraction (<10 μm) in the sediment was very high, ranging from 75 to 95%. The data on the station coordinates and abiotic parameters are listed in the table.

Macrobenthos sampling was performed from a vessel with a light spring grab sampler with a sampling area of 0.021 $m^2$. At each of the stations, five or six grab samples were collected. The sediment was washed through a sieve with a mesh size of 0.5 mm. All the organisms were fixed with a 4% formalin solution; subsequently, at the laboratory, the animals were grouped with respect to taxa, weighed, washed with fresh water, and put in 70% alcohol for further identifications. Thus, the biomass is presented in wet weight units; in so doing, mollusks were weighed together with their shells, since nondestroyed individuals were required for subsequent taxonomic determinations.

Since the tropical benthic fauna have been poorly studied to date, we faced a problem common to most of the ecological studies conducted in this region [18, 50]. In all the groups, only genera were reliably identified, while species were distinguished on a conventional basis, except for mass species of mollusks and polychaets. Therefore, in this paper, we do not present species lists. At present, taxonomic examination of selected groups is in progress.

In order to estimate the diversity, we calculated Margalef indexes of species richness, Shannon diversity indexes, and indexes of evenness ($H/H_{max}$) using the abundances of individuals. When determining the dependences of the species number on the sample number for all the range considered (from 210 to 5000 $cm^2$), in order to eliminate the influence of the summing order, we calculated mean values of the numbers of the species encountered and the standard deviations for 30 random combinations of samples [1].

Characteristics of the stations

| Station | Coordinates | Sea depth, m | Characteristics of the sediments | | |
|---|---|---|---|---|---|
| | | | mean particle diameter, μm | percentage of silty fraction (<50 μm) | organic matter content, % |
| a2 | 12° 13′ 30.4″ N<br>109° 13′ 29.6″ E | 24 | 42.4 | 75 | 0.84 |
| a3 | 12° 12′ 40.2″ N<br>109° 13′ 41.1″ E | 20.1 | 5.9 | 97 | 1.53 |
| a4 | 12° 11′ 25.4″ N<br>109° 15′ 05.7″ E | 19.6 | 10 | 95 | 1.06 |
| a5 | 12° 10′ 24″ N<br>109° 15′ 42″ E | 21.8 | 7.7 | 95 | 0.93 |

## RESULTS

### *Macrobenthos Abundance*

The abundance and biomass of the macrobenthic organisms at the stations in the muddy subtidal zone of Nha Trang Bay in the spring of 2002 was extremely low. Their density varied from 343 (station a2) to 856 (station a5) ind/m$^2$ (at a mean value of 637 ind/m$^2$), and the biomass ranged from 1.8 to 2.9 g/m$^2$ (at a mean value of 2.3 g/m$^2$). No reliable differences were revealed in these parameters between the stations. In particular, this is related to the extremely high microspatial heterogeneity in the macrobenthos distribution. The differences between the grab samples within the same stations were significantly greater than the differences between the stations. For example, the coefficient of variation (CV) of biomass between the stations was 25%, while the CV between the samples at a single station varied from 39 to 72%. A similar pattern was observed in the individual densities.

Polychaets dominate at all the stations in terms of abundance (from 30 to 43%, at a mean value of 38%). The second are bivalve mollusks, crustaceans, and sipunculides. All the stations differ not only in the contributions of these groups but also in the order of their domination (Fig. 2a). A similar situation is observed when the biomasses are assessed (Fig. 2b). Here, the main contribution is also provided by polychaets, crustaceans, and bivalve mollusks.

### *Species Richness and Diversity*

A total of 67 species of macrobenthos were encountered during the spring survey of 2002. Of these, 36 species (54%) were encountered at a single station, 19 species (28%) were common to two stations, 6 species were observed at three stations, and only 6 species were encountered at each of the four stations. In our samples, about a half of the species (31 species) were represented by a single specimen each; only 5 species were represented by 15 specimens or more (Fig. 3). Thus, the recurrence of the bulk of the species is extremely low. This allows us to suggest that, in the course of future studies, the number of species may significantly increase.

This inference is also confirmed by the dependence of the number of the species encountered on the number of the samples considered (sample volume). Within the entire range examined (its upper boundary corresponds to 23 grab samples with a total area of 5000 cm$^2$), this dependence follows a power law with an exponent equal to 0.59 and an approximation accuracy of 0.99; it

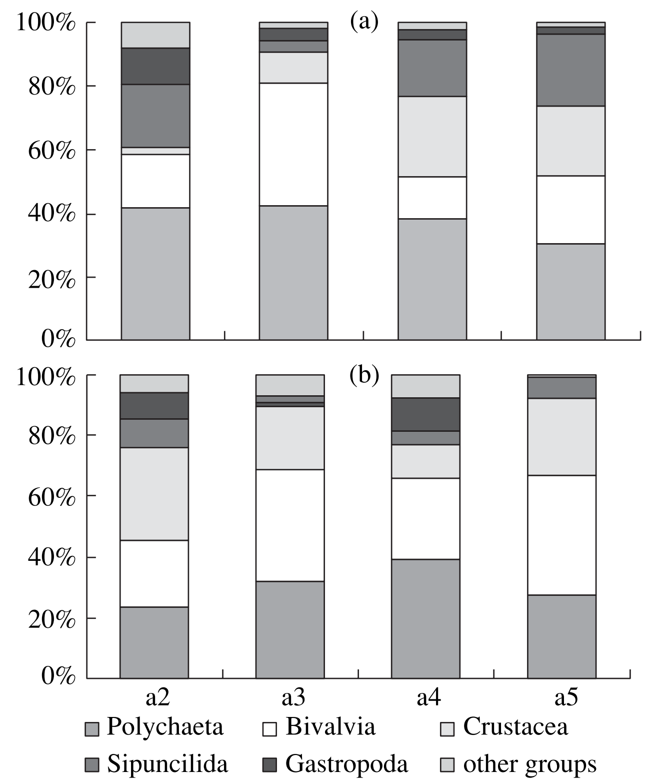


**Fig. 2.** Percentages of main taxonomic groups of macrobenthos in the total (a) abundance and (b) biomass on the stations.

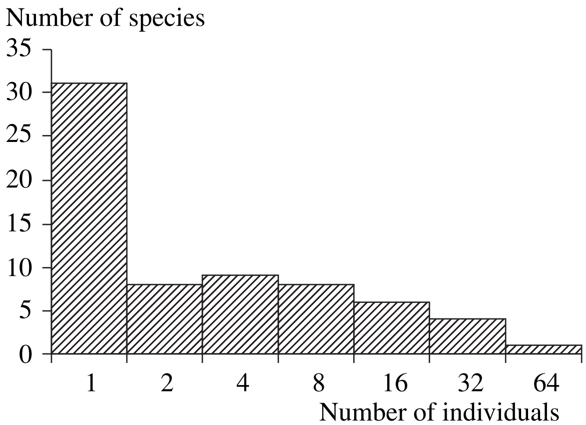


**Fig. 3.** Species recurrence frequency at all the stations in 23 grab samples.

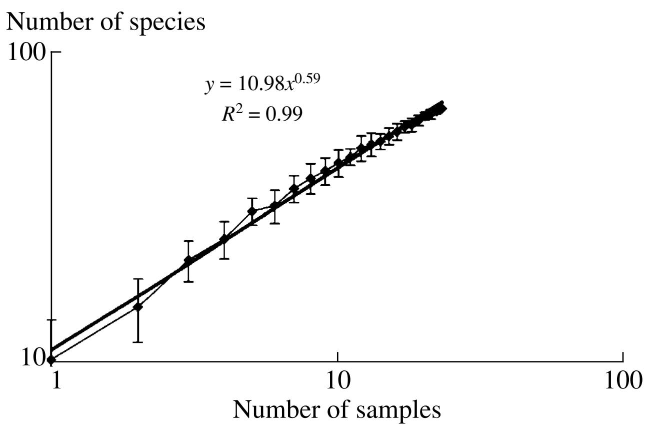


**Fig. 4.** Dependence of the number of species encountered on the sample volume (number of samples).

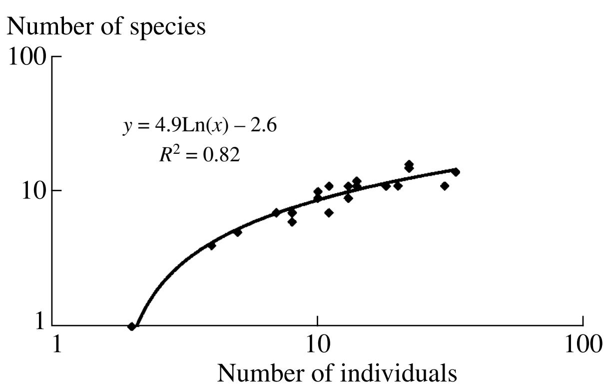


**Fig. 5.** Dependence of the number of species on the number of organisms in a grab sample for the subtidal zone of Nha Trang Bay.

features no signs of saturation (Fig. 4), which points to the incompleteness of the description of the species composition.

In terms of the species number, polychaets dominate (25 species), then follow mollusks (17 species, of which 10 bivalves), crustaceans (14 species), and sipunculides (5 species).

The mean number of species encountered at a station is 30.5. The mean number of species in a sample (in a grab sampler) equals 9.43. The number of species in a sample is clearly and reliably related to the number of individuals (Fig. 5). At station a2, the species richness estimated by the Margafef index was somewhat lower than at the rest of the stations (4.06 versus 4.55–4.76). The species diversity (Shannon index) does not indicate any differences between the stations and lies in the range 4.06–4.44 (with respect to abundance). The evenness of the species structure ($H/H_{max}$) at different stations almost does not vary and is extremely high (0.88 on average), which suggests virtually equal contributions of all the species to the abundance and biomass of the community and the absence of evident domination.

The character of domination in both abundance and biomass at all the stations is similar. A comparison between the cumulative curves of abundance and biomass with the ABC technique [49] shows the existence of a relatively sustainable community, since the cumulative curve of biomass runs significantly higher than the cumulative abundances; this means that, at all the stations, relatively large forms dominate (Fig. 6).

The high diversity and the absence of a dominating group of species, by which communities are usually characterized, results in a low mean similarity between stations (Pianki index equal to 0.151 ± 0.135); one can hardly distinguish groups of similar stations. Actually, at each of the stations, one observes a random sampling of the total pool of species inhabiting this region. The differences occurring between samples taken at the same station are as significant as the differences between samples taken from different stations.

## DISCUSSION

Among the ecological features that distinguish tropical macrobenthic communities, the main ones are high species diversity [9, 25, 30] and low density of organisms [17, 34, 50]. Meanwhile, it is very difficult to estimate the actual values of these parameters, first of all, because of the differences in the approaches to this problem (mostly related to the scale on which diversity is estimated) and of the method for organism counting.

The density of macrobenthos in the muddy subtidal zone of Nha Trang Bay is rather low and comprises 343–856 ind/m$^2$ (at a mean value of 637 ind/m$^2$). Close values were registered in Southeast Asia in the tidal and subtidal zones off Java Island (330–739 ind/m$^2$ [50]), and on muddy subtidal sediments off Northeast Australia (621 ind/m$^2$ [18] and 158 ind/m$^2$ [17]), Malaysia, and Thailand (52–494 ind/m$^2$ [13, 22, 39]). The macrobenthos density on sandy sediments is greater than on silts (3785 ind/m$^2$ off Northeast Australia [18], 5614 ind/m$^2$ off Singapore [48]), in contrast to temperate latitudes, where an opposite pattern is often observed [11].

It is interesting that the hypothesis that "the abundance of macrobenthos in the tropical zone is lower than at temperate latitudes" is often illustrated by data precisely from this region (Indo-West Pacific [3–5]). For example, Warwick and Ruswahyuni [50] showed that, in the Javan transect, the macrobenthos abundance is lower than that off the coasts of England. Reise [34] used three sites from Malaysia, Thailand, and Northeast Australia, also characterized by low densities, as the reference points for the tropical zone. Meanwhile, the macrobenthos densities registered in tropical America and Africa are significantly greater. The abundance of macrobenthos in the subtidal zone of Gazi Bay, Kenya (265–6025 ind/m$^2$ at a mean value of 1933 ind/m$^2$ [40]) is quite comparable with the reference points of Warwick and Ruswahyuni [50] from the coasts of England, although in the former case, a coarser sieve was used (1–2 mm versus 0.5 mm), and the macrobenthos density in the subtidal zone off Costa Rica (3787–41 086 ind/m$^2$ at a mean value of 13827 ind/m$^2$ [46]) is significantly higher. Thus, in order to answer the question of the existence of latitudinal or regional regularities in the distributions of macrobenthos densities, more data are required, and they must be gathered with more uniform methods than at present.

One of the important aspects of the structure of tropical benthic communities is the high proportion of mesobenthos at a low macrobenthos density [9, 17, 18]. This kind of situation is observed in Nha Trang Bay as well. For example, according to our unpublished data, during the survey of 2004, when meso- and macrobenthos were counted together, the mean density of individuals comprised 3325 ind/m$^2$, while its maximum value reached 13 950 ind/m$^2$. The proportion of macrobenthos proper did not exceed 20% of the total abundance. A similar pattern was noted on the littoral beaches of Northeast Australia, where mesobenthos density was reported to be 15 840 ind/m$^2$, while the density of macrobenthos was 158 ind/m$^2$ [17, 18]. Therefore, it is natural that the mesh size of the sieve that is used for organism extraction (in different studies, it ranged from 250 μm to 2 mm) is especially important for the estimates of the densities of tropical benthos. Moreover, since small organisms of mesobenthos may or may not be included into the assessment, the estimates of the diversity, species richness, and proportions between the main taxonomic groups also strongly depend on the sieve mesh size.

The absence of a developed concept of mesobenthos causes additional confusion in the description of the structure of tropical communities. At present, the lower size limit of mesobenthos is either assumed to be related to the sieve with a mesh diameter of 0.25 mm, while the upper mesobenthos boundary coincides with the lower limit of macrobenthos (the organisms that remain over a sieve with a mesh size of 0.5 mm [17] or 1 mm [35]), or is conventionally specified by the researcher (1 μg of wet weight [7]). Moreover, since the major part of mesobenthos is composed of larvae and juveniles, with their growth, they begin to be trapped by a sieve with a greater mesh size (0.5 mm) and enter the group which is referred to as macrobenthos by most scientists. The high abundance of mesobenthos results in strongly different (by a few orders of magnitude) estimates of the macrobenthos density depending on the sieve used (0.5, 1, or 2 mm).

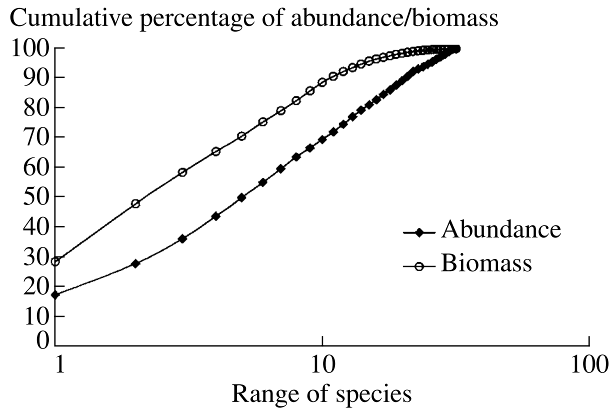


**Fig. 6.** Cumulative curves of the abundance and biomass (ABC technique) for the macrobenthos of Nha Trang Bay.

As noted by many authors, probably the most important difference between tropical macrobenthos and its counterparts from other latitudinal zones lies in its significantly higher diversity [14, 26, 36–38]. Usually, only one component of diversity is considered, namely, the species richness of benthos or its individual taxonomic groups. This estimate is performed with the use of a series of statistical procedures [1, 26] based on the total species number registered during the study under consideration. However, this kind of estimate should be used with great caution, because, in this case, each value combines information on different numbers of communities studied in different detail (different total sampling areas and individual densities). Therefore, one cannot judge whether the species richness is related to the community diversity or to the diversity within these communities.

The assessment of the degrees of diversity in terms of the hierarchical model [26, 53] allows one to rank to a certain extent the data obtained. For example, the average species richness in a sample (point or sample diversity) for the soft-bottom tropical benthos is lower than that for the communities of temperate latitudes. According to the data of selected publications in which detailed information is presented, as well as according

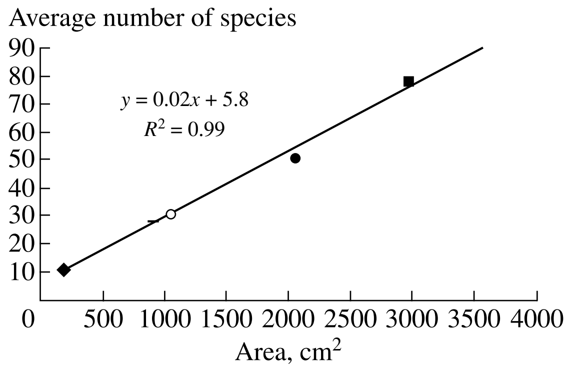


**Fig. 7.** Changes in the species number with the changes in the total area sampled for tropical soft-bottom macrobenthic communities: silty littoral zone and mangroves of Cape Northwest, Northwest Australia [51]; silty littoral zone of the Howton estuary, Northeast Australia [18]; silty sublittoral zone of Nha Trang Bay (this study); littoral zone off Phuket Island, Thailand [34]; and silty littoral zone of Nicoya Bay, Costa Rica [46] (ordered with respect to the increase in the area studied).

to our data, in the tropical zone, the number of species per sample varies from 5 to 9 (for sample areas of 100–200 cm$^2$) [17, 18, 34]; in temperate latitudes, the respective value ranges from 9 to 30 species for sampling areas from 80 to 300 cm$^2$ [8, 29, 34]. This seems to be related to the fact that, at this level, species richness mostly depends on the sample volume (individual density and area considered) (Fig. 5).

With the increase in the area considered (increase in sample number), the behavior of the "species–area" dependence for a series of tropical macrobenthic infaunal communities examined in this respect features a constant continuous growth in the species number with the increase in the number of samples. The species number does not reach a plateau for areas up to 2050 cm$^2$ in the littoral zone of Phuket Island, Thailand [34], up to 5000 cm$^2$ in Nha Trang Bay (Fig. 4), and even up to 15 000 cm$^2$ (Northeast Australian) [17], while in temperate and Arctic latitudes, an area of 500–900 cm$^2$ is sufficient for a full description of the species composition. This was shown for the littoral zone of the North Sea off Konigshaven, for the Chilean coasts [34], and for the subtidal zone of Kongsfjord, Spitzbergen [29]. Therefore, all the data obtained on the species richness of tropical benthos reflect the thoroughness of the study rather than the actual diversity of the community (local or α-diversity). This is illustrated by Fig. 7, which shows the change in the species number of a series of tropical benthic communities on muddy sediments with the increase in the total area sampled. One can see that, in the range up to 3000 cm$^2$, a linear growth is observed in the species number with increasing area; meanwhile, the accuracy of the approximation is very high ($R^2 = 0.99$), though one could expect a greater scattering of the results since the data were taken from different sources). A certain idea of the number of samples that could provide information on the actual species richness of tropical communities is presented in the paper by Vargas [46], who described the species composition of benthos over a homogeneous littoral floor 500 m$^2$ in area. The further increase in the number of samples from 168 to 700 (which corresponded to an area increase from 3000 to 12 400 cm$^2$) provided only a 15% growth in the species number (from 78 to 92), which allows one to regard the description of the species composition in this area as virtually full. Thus, one may suggest that, in tropical zones, low values of point or sample diversity are commonly observed, while the values of α-diversity (and, therefore, the regional γ- and ε-diversities) are significantly greater as compared to temperate and Arctic latitudes.

While considering the macrobenthos community structure in Nha Trang Bay, attention is drawn to the low species recurrence. Thirty-nine species (58%) of the 67 species registered in Nha Trang Bay were encountered once or twice. Similar situations were reported for six islands of the Great Barrier Reef [25], and for littoral beaches of Northeast Australia [17]. In these studies, from 47 to 57% of the species were encountered as one or two specimens. Another aspect of the diversity characteristic of the macrobenthos of the bay is represented by the extremely high values of evenness of the species structure and the absence of dominating species.

Therefore, the problem of the existence of boundaries of tropical benthic communities emerges. In the communities of temperate or Arctic zones, one can rather easily distinguish groups of selected dominating species, which are observed from one station to another [1, 29, 34, 35], as well as the common set of subdominants and accompanying species; together, they determine the appearance of the community. Moreover, judging from the behavior of the "species number–area" curves, one can usually recognize the spatial scales of the existence of local communities, which are characterized by a relatively homogeneous species composition. Meanwhile, in this case, we, first, cannot distinguish a set of dominants common for several stations and, second, the rate of increment of rarely encountered species is so great that there is no saturation of the "species–samples" curve and the probability of encountering an individual of an already registered species is lower than the probability of encountering a new species. Thus, it remains unclear whether any community, in the classical sense of this term, exists in the bay at all.

One more parameter related to the species richness concerns the proportions of the species number of principal taxonomic groups—polychaets, mollusks, and crustaceans. Reise [34] posed a suggestion on the smaller number of polychaet species and on the greater role of mollusks and crustaceans in the soft-bottom communities of tropical macrobenthos as compared to their analogs from temperate latitudes. For temperate latitudes, Reise cites a value of the ratio of the species numbers of mollusks and crustaceans to that of polychaets (M + C)/P equal to 1–1.3, while in the tropical zone, this ratio grows up to 3.45–8.22 [34]. Probably, these high values are related to the methods used by the authors; in all of the publications referred to [30, 39, 51], either hand-operated collection of organisms was applied, when mollusks have evident advantages, or (or in addition), a large sieve (with a mesh size of 1–2 mm) was used, which resulted in an undercounting of small polychaets. With the techniques accepted at present (sieve with a mesh size of 0.5 mm), the (M + C)/P ratio for the tropical macrobenthos is lower and close to the value obtained in this study (1.24 for Nha Trang Bay). The corresponding values were reported to be 0.73–1.89 in the littoral zone of Northeast Australian [17, 18]; 1.2 off Punta Morales, Costa Rica [47]; and 1.44 in the littoral zone off Phuket Island, Thailand [34]. These values are somewhat greater than those obtained for the communities of temperate and Arctic latitudes: 0.97 for the subtidal zone off Devon, England [28]; 0.52–1.06 off Silt Island, the North Sea [11, 34]; and 0.24–0.82 off Spitzbergen [29, 52]; these values, in turn, are lower than the values listed by Reise [34]. Based on these data referring to different types of communities, one can suggest that selected latitudinal tendencies may actually be present. Usually, in tropical communities, the species richness of mollusks and crustaceans is the greatest, while in the communities of higher latitudes, polychaets dominate. Meanwhile, it is interesting that this feature refers only to the Northern Hemisphere. The (M + C)/P ratio values for the macrobenthic communities off the Tasmanian coasts and in Victoria Bay (38–44° S) comprises 2.44–1.73, which is greater than most of the tropical values [19, 20]. An extremely high proportion of mollusks and crustaceans as compared to polychaets ((M + C)/P = 3.39) is also reported for the Antarctic fauna on the whole [16]; though the scale of the assessment is not comparable to those of the above-mentioned regions, this fact allows one to suppose a more complicated latitudinal dependence of the proportions of different taxonomic groups in soft-bottom macrobenthic communities related to the historical aspects of the formation of the diversity of individual groups rather than to ecological reasons [12, 36, 37, 45].

## ACKNOWLEDGMENTS

The authors are grateful to V.K. Nezdolii and N.V. Doan for their support in the studies; to O.V. Savinkin, I.N. Marin, A.V. Rzhavskii, A.V. Chesunov, A.E. Zhadan, N.Z. Toan, Ch.V. Bang, N.A. Chervyakova, T.N. Antokhina, and V.V. Murina for help in the sample collection and organism identification; and to A.I. Azovskii and V.O. Mokievskii for valuable remarks and discussion. This study was supported by the Russian Foundation for Basic Research, project nos. 03-04-48018, 04-05-64734, and 04-05-64176.

## REFERENCES

1. A. I. Azovskii, *Extended Abstract of Doctoral Candidate Dissertation in Biology* (Moscow State Univ., Moscow, 2003) [in Russian].
2. T. A. Britaev, Yu. N. Sbikin, Chyong Shi Ki, and Chan Viet Ngan, "Benthos of the Be River Estuary," in *Fishes in the Vietnam Coastal Waters*, Ed. by D. S. Pavlov and Yu. N. Sbikin (Nauka, Moscow, 1991), pp. 77–88 [in Russian].
3. E. F. Gur'yanova, "Marine Zoological Expedition to Hainan Island," Vestn. Akad. Nauk SSSR, No. 3, 89–92 (1959).
4. E. F. Gur'yanova, "Vietnamese Scientific–Exploration Expedition," Vestn. Akad. Nauk SSSR, No. 2, 95–96 (1962).
5. E. F. Gur'yanova, "Fauna of the Gulf of Tonkin and Its Dwelling Conditions," in *Fauna of the Gulf of Tonkin and Conditions of Its Existence* (Issledovaniya Fauny Morei, Vol. 10 (18)) (Moscow, 1972), pp. 22–146 [in Russian].
6. V. I. Lukin, V. I. Fadeev, S. A. Rostomov, and Chung. Van, "Soft-Bottom Macrobenthic Communities of the Nyafu Lagoon," in *Biology of the Coastal Waters of Vietnama* (DVO AN SSSR, Vladivostok, 1988), pp. 87–110 [in Russian].
7. A. A. Udalov and I. V. Burkovskii, "The Role of Mesobenthos in the Size Structure of an Intertidal Ecosystem," Okeanologiya **42** (4), 527–536 (2002) [Oceanology **42** (4), 502–511 (2002)].
8. A. A. Udalov, I. V. Burkovskii, V. O. Mokievskii, et al., "Changes in the General Characteristics of Micro-, Meio-, and Macrobenthos along the Salinity Gradient in the White Sea Estuary," Okeanologiya **44** (4), 549–560 (2004) [Oceanology **44** (4), 514–525 (2004)].
9. D. M. Alongi, "Ecology of Tropical Soft-Bottom Benthos: A Review with Emphasis on Emerging Concepts," Rev. Biol. Tropical **37**, 85–100 (1989).
10. Z. A. Ansari, "Benthic Macro- and Meiofauna of Seagrass (*Thalassia hemprichii*) Bed at Minicoy, Lakshadweep," Indian J. Mar. Sci. **13**, 126–127 (1984).
11. W. Armonies and M. Hellwig-Armonies, "Synoptic Patterns of Meiofaunal and Macrofaunal Abundances and Specific Composition in Littoral Sediments," Helgolander Meeresunters **41**, 83–111 (1987).
12. W. E. Arntz and J.-M. Gili, "A Case for Tolerance in Marine Ecology: Let Us Not Put Out the Baby with the Bathwater," Scientia Marina **65**, 283–299 (2001).
13. M. J. Broom, "Structure and Seasonality in a Malaysian Mudflat Community," Est. Coast. Shelf Sci. **15**, 135–150 (1982).
14. N. Coleman, A. S. H. Gason, and G. S. B. Poore, "High Species Richness in the Shallow Marine Waters of South-East Australia," Mar. Ecol. Prog. Ser. **154**, 17–26 (1997).

15. C. Dawydoff, "Contribution a l'Etude des Invertebres de la Faune Marine Benthiques de l'Indochine," Bull. Biol. France et Belgique **37**, 1–158 (1952).

16. C. De Broyer, J. H. Hecq, and S. Vanhove, "Life under the Ice: Biodiversity of the Southern Ocean," in *The Belgica Expedition Centennial: Perspectives on Antarctic Science and History (Proceedings of the Belgica Centennial Symposium, 14-16 May 1998)*, Ed. by H. Decleir and C. De .Broyer (Brussels University Press, Brussels, 2001), pp. 271–286.

17. S. Dittmann, "Benthos Structure on Tropical Tidal Flats of Australia," Helgolander Meeresunters **49**, 539–551 (1995).

18. S. Dittmann, "Zonation of Benthic Communities in a Tropical Tidal Flat of North-East Australia," J. Sea Res. **43**, 33–51 (2000).

19. G. J. Edgar and N. S. Barrett, "Benthic Macrofauna in Tasmanian Estuaries: Scales of Distribution and Relationships with Environmental Variables," J. Exp. Mar. Biol. Ecol. **270**, 1–24 (2002).

20. G. J. Edgar, G. Watson, L. S. Hammond, and C. Shaw, "Comparisons of Species Richness, Size Structure, and Production of Benthos in Vegetated and Unvegetated Habitats in Western Port, Victoria," J. Exp. Mar. Biol. Ecol. **176**, 201–226 (1994).

21. S. A. Fernando, S. A. Khan, and R. Kasinathan, "Observations on the Distribution of Benthic Fauna in Vellar Estuary, Porto Novo," Mahasagar **16**, 341–348 (1983).

22. D. W. Frith, R. Tantanasiriwong, and O. Bhatia, "Zonation of Macrofauna on a Mangrove Shore, Phuket Island," Phuket Mar. Biol. Cent. Res. Bull. **10**, 1–37 (1976).

23. P. Frouin, "Effects of Anthropogenic Disturbances of Tropical Soft-Bottom Benthic Communities," Mar. Ecol. Prog. Ser. **194**, 39–53 (2000).

24. P. Frouin and P. Hutchings, "Macrobenthic Communities in a Tropical Lagoon (Tahiti, French Polynesia, Central Pacific)," Coral Reefs **19**, 277–285 (2001).

25. P. E. Gibbs, "Macrofauna of the Intertidal Sand Flats on Low Wooded Islands, Northern Great Barrier Reef," Phil. Trans. Royal Soc. London, Ser. B, **284**, 81–97 (1978).

26. J. S. Gray, "Marine Diversity: The Paradigms in Patterns of Species Richness Examined," Sci. Mar. **65**, 41–56 (2001).

27. M. A. Kendall and M. Aschan, "Latitudinal Gradients in the Structure of Macrobenthic Communities: A Comparison of Arctic, Temperate, and Tropical Sites," J. Exp. Mar. Biol. Ecol. **172**, 157–169 (1993).

28. M. A. Kendall and S. Widdicombe, "Small Scale Patterns in the Structure of Macrofaunal Assemblages of Shallow Soft Sediments," J. Exp. Mar. Biol. Ecol. **237**, 127–140 (1999).

29. J. Laudien, M. Herrmann, and W. E. Arntz, "Soft-Bottom Community Structure and Diversity in Kongsfjorden (Svalbard)," Berichte zur Polar- und Meeresforschung **492**, 91–102 (2004).

30. W. Macnae and M. Kalk, "The Fauna and Flora of Sand Flats at Inhaca Island, Mozambique," J. Animal. Ecol. **31**, 93–128 (1962).

31. D. Maurer and J. A. Vargas, "Diversity of Soft-Bottom Benthos in a Tropical Estuary: Gulf of Nicoya, Costa Rica," Mar. Biol. (Berlin) **81**, 97–106 (1984).

32. A. H. Parulecar, S. A. Nair, S. N. Harkantra, and Z. A. Ansari, "Some Quantitative Studies on the Benthos off Bombay," Mahasagar **9**, 51–56 (1976).

33. H. V. Prabhu, A. C. Narayana, and R. J. Katti, "Macrobenthic Fauna in Nearshore Sediments Off Gangolli, West Coast of India," Indian J. Mar. Sci **22**, 168–171 (1993).

34. K. Reise, *Estuaries and Coasts: Spatial and Temporal Intercomparisons*, Ed. by M. Elliott and J.-P. Ducrotoy (Fredensborg: Olsen and Olsen, 1991, pp. 211–216).

35. K. Reise, E. Herre, and M. Sturm, "Biomass and Abundance of Macrofauna in Intertidal Sediments of Konigshafen in the Northern Wadden Sea," Helgolander Meeresunters **48**, 201–215 (1994).

36. K. Roy, D. Jablonski, and J. W. Valentine, "Higher Taxa in Biodiversity Studies: Patterns from Eastern Pacific Marine Mollusks," Phil. Trans. Roy. Soc. London, Ser. B, **351**, 1605–1613 (1996).

37. K. Roy, D. Jablonski, J. W. Valentine, and G. Rosenberg, "Marine Latitudinal Diversity Gradients: Tests of Causal Hypotheses," Proc. Natl. Acad. Sci. USA **95**, 3699–3702 (1998).

38. H. L. Sanders, "Marine Benthic Diversity: A Comparative Study," Amer. Nat. **102**, 243–282 (1968).

39. A. Sasekumar, "Distribution of Macrofauna on a Malayan Mangrove Shore," J. Animal. Ecol. **43**, 51–69 (1974).

40. J. Schrijvers, D. van Gansbeke, and M. Vincx, "Macrobenthic Infauna of Mangroves and Surrounding Beaches at Gazi Bay, Kenya," Hydrobiologia **306**, 53–66 (1995).

41. R. Serene, *Inventaires des invertebres marine de l'Indochine (1-er List)* Inst. Oceanogr. de l"indochine, Saigon, 1937).

42. P. K. S. Shin and G. B. Thompson, "Spatial Distribution of the Infaunal Benthos of Hong Kong," Mar. Ecol. Prog. Ser. **10**, 37–47 (1982).

43. G. Thorson, "Bottom Communities (Sublittoral or Shallow Shelf)," Geol. Soc. Amer. **67**, 461–534 (1957).

44. P. D. Trong, D. C. Thung, L. T. Thanh, et al., "Species Composition, Abundance, and Biomass Distribution of Zoobenthos in Vietnamese Waters," in *Proceedings of the SEAFDEC, Seminar on Fishery Resources in the South China Sea, Area IV: Vietnamese Waters* (SEAFDEC/TD, 1999), pp. 55–76.

45. C. Valdovinos, S. A. Navarrete, and P. A. Marquet, "Mollusk Species Diversity in the Southeastern Pacific: Why Are There More Species Towards the Pole?," Ecography **26**, 139–144 (2003).

46. J. A. Vargas, "The Benthic Community of an Intertidal Mud Flat in the Gulf of Nicoya, Costa Rica. Description

of the Community," Revista de Biologia Tropical **35**, 299–316 (1987).

47. J. A. Vargas, "Community Structure of Macrobenthos and the Results of Macropredator Exclusion on a Tropical Intertidal Mud Flat," Revista de Biologia Tropical **36**, 287–308 (1988).
48. F. C. Vohra, "Zonation on a Tropical Sandy Shore," J. Animal. Ecol. **40**, 679–709 (1971).
49. R. M. Warwick, "A New Method for Detecting Pollution Effects on Marine Macrobenthic Communities," Mar. Biol. (Berlin) **92**, 557–562 (1986).
50. R. M. Warwick and Ruswahyuni, "Comparative Study of the Structure of Some Tropical and Temperate Marine Soft-Bottom Macrobenthic Communities," Mar. Biol. (Berlin) **95**, 641–649 (1987).
51. F. E. Wells, "An Analysis of Marine Invertebrate Distributions in a Mangrove Swamp in North-Western Australia," Bull. Mar. Sci. **33**, 736–744 (1983).
52. J. M. Weslawski, M. Wlodarska-Kowalczuk, and J. Legezynska, "Occurrence of Soft Bottom Macrofauna along the Depth Gradient in High Arctic, 79° N," Polish Polar Research **24**, 73–88 (2003).
53. R. H. Whittaker, *Communities and Ecosystems* (MacMillan Press, New York, 1975).