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Marine biological diversity: patterns, processes and modern methodology

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Summary. Terminology and main components of biodiversity have been discussed. Species richness and taxonomic diversity of terrestrial, freshwater and marine organisms are compared. About 1.5 million of terrestrial species and only 325 000 species of water organisms have been described up-date. Despite more than 200 years of intensive researches biologists have described only about 280 000 marine species including about 180 000 marine invertebrates. Of the 33 phyla of Metazoa listed, 31 phyla are found in the sea, 13 of which are exclusively marine. Only 17 phyla are found in the fresh water and 11 phyla are found in terrestrial environments. Representatives of 4 parasitic phyla of Metazoa are found in the sea and only 2 phyla are represented in fresh-water and terrestrial hosts. Only two phyla, the fresh water Micrognathozoa, and the terrestrial Onychophora, are non-marine endemics. Diversity of the deep-sea macrobenthos and meiofauna are argued. Approximately 20-30 million undescribed macrobenthic species and about 20-30 million of meiobenthic species, including more than 10 millions of marine nematodes, are suggested, mainly in the deep-sea, based on modern extrapolations. Hypothesis to explain high benthic species diversity in the deep-sea sediments are summarized. New initiatives and methodology of marine researches are discussed.

Key words: biodiversity, deep-sea, macrobenthos, meiofauna, species richness.

The term "biodiversity" may be defined as all hereditary based variations at all levels of biological organization - from the genes diversity within a single local population and populations diversity within the species to the species diversity within a local community, and to the diversity of these communities within the various global ecosystems. Biodiversity therefore includes all variability in the natural world, at all scales in time and space. The neologism "biological diversity" was firstly used to emphasize the presence of a great number of species of plants and animals (Lovejoy, 1980). Later, the term "species richness" (or "species ability") was introduced to calculate the number of species (see Fiedler & Jain, 1992) and currently this is only one of the numerous components of the biological diversity (see Kasyanov, 2002). The term "species evenness" is also used to measure of the relative abundance of species in the area (see Moore, 2001).

About six main levels, or components, of the biodiversity may be designated: (1) species, or micro-taxonomical, (2) phylogenetic, or macro-taxonomical, (3) morphological, (4) ecological, (5) genetic, and (6) biochemical diversity. Modern understanding of the biodiversity also takes into account the geo-historical aspect - the great and unique biodiversity of the geological past of the globe.

Species diversity refers to the number and relative abundance of species in a community, and sometimes used as a synonym of species richness (alpha diversity) that is an absolute number of species in different taxonomic groups living in a given area, giving equal weight to all resident species. Phylogenetic, or macro-taxonomical, diversity is typically presented in terms of a total number of taxonomic groups (super-species level) and their relationships within the hierarchic system (phylema) of monophyletic taxa (Kussakin, 1995).

Morphological diversity includes not only structural and functional diversity of cells, tissues and organs, but also refers to a variety of living-form types, or biomorphs, the main structural units of ecosystems (see Chernov, 1991). Hierarchic sorting of this variety of biomorphs, or ecomorphs, includes the construction of the another hierarchic system, called ecomorphema (see Kussakin, 1995).

Ecological level of biodiversity refers to the diversity of habitats and accompanying ecological processes that maintain ecosystem. Ecological diversity also includes the study of populations, species, super-species groups and ecomorphs as the structural and functional elements of ecosystems of different hierarchic levels (Schulze & Mooney, 1994). The term "functional diversity" is also used as an important component of ecological diversity that influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspects of ecosystem functioning (see Tilman, 2001).

Genetic diversity includes molecular hereditary differences within and between populations. Heritable genetic variations arise in individuals by gene and chromosome mutations, and with sexual reproduction it can be spread through the population by recombination. This diversity allows the species to adapt and evolve in response to changing environments and natural selection pressure. This diversity also includes molecular diversity at the DNA and protein level, variety in number and structure of chromosomes, mutation mechanisms etc.

Biochemical diversity is based on a great number of the secondary chemicals which vary greatly from species to species. Secondary metabolites provide defense mechanisms, act as stimulators and attractants for reproduction, provide a tolerance to the environments (see Stonik, 1999).

About 2 million species names are used by taxonomists. If the mean level of synonymy is considered about 20%, in reality approximately 1.6-1.8 million species are known (Stork, 1999).

Based on the modern calculations (see Reaka-Kudla, 1997), about 1.870 million species have been described up date. There are approximately 1.450 million currently described species of terrestrial organisms, about 100 000 symbiotic organisms, and only about 320 000-325 000 described species of aquatic organisms. Most of terrestrial species are insects (950 000), plants (270 000) and fungi (70 000). Of the aquatic species, about 280 000 are estimated to be marine, and only 40 000-45 000 described species inhabit freshwater environments. Of the marine species, about 180 000 species are represented by invertebrates.

Contrary, the sea is much richer in having of major taxa of animals than the land. Of the 33 phyla of multicellular animals (Metazoa) listed by the author, 31 occur in the marine habitat of which 13 are exclusively marine. Representatives of 17 phyla are found in freshwater environments and only 11 phyla inhabit terrestrial habitats. The only two phyla - Micrognathozoa and Onychophora are thought to be freshwater and terrestrial endemics correspondently. Nevertheless, the Onychophora, now purely terrestrial, have had marine ancestors in the Cambrian (Paleoscolecida). Minute Micrognathozoa within the superphylum Gnathifera share many gomologous characters with the exclusively marine Gnathostomulida and Rotifera, and the phylum also appears to be started in the sea. Of the four phyla of parasites (Dicyemataria, Orthonectida, Acanthocephala, Pentastomida), all of them occur in the sea, while representatives of only two last phyla are known from the freshwater and terrestrial hosts.

The great differences in the macro-taxonomic diversity in the sea and on the land may be explained by the Cambrian "explosion of biodiversity", a period of about 25 million years during the Cambrian, when the diversity of multicellular life greatly increased in a relatively short time. Most of Metazoan phyla first appeared about 600-560 million years ago in the Cambrian ocean and it was about 150 million years before they started to invade the land. The Cambrian explosion of the biological diversity is realized in an appearance of the great number of new body plans, structural elements, functional and biochemical adaptations etc.

How to explain a remarkable difference in the species richness on the land and in the sea? Only about 15% of all recorded animal and plant species live in the sea. Now 51% of all know species are insects, 14% are green plants and only 9.5% of all species are marine invertebrates. Does this ratio truly reflects a real number of marine and terrestrial species on the globe?

How many species are there totally? Current estimates of the total number of species run from 10-20 (Stork, 1997) up to 100 million (Lovejoy, 1997), i.e. only from 1-2% to, more optimistically, about 10% of the real biodiversity have been described. Entomologists estimate the species richness of insects about 30-50 million, mainly in the rain forest (see Erwin, 1997) and, thus we have named only about 3-5% of global species of insects (Erwin, 2001). These calculations are based on a high degree of the endemism of tropical arthropods, great variety of rain forest trees (50 000 species) and a novel method of estimating, sketched out by Erwin.

The "moderate" experts estimate the global species richness about 12.5 million (Hammond, 1992; Stork, 1993). In these estimates, the number of marine species is also thought to be much less than on the land. For example, the ratio of terrestrial to marine is estimated nearly 60:1 (Briggs, 1994) while the same ratio only for multicellular species is about 10:1 (Williamson, 1999).

Despite more than 200 years of intensive investigations of the ocean, marine biologists have described only 36 000 species of algae, 40 000 species of marine protozoans, 180 000 species of invertebrates, 15 000 species of marine chordates (mainly fishes), 9 000 species of marine viruses and bacteria (Fig. 1). Where in the ocean we can find a highest species richness?

Oceanic pelagic systems do not show high taxonomic richness. Of the 31 phyla of Metazoa that are present in the sea, only 14 are represented in the pelagic systems, moreover there is not a single phylum endemic to them. Species diversity of bacteria (65% of all primary production in the ocean) is suggested only about 500 000 species. Total phytoplankton in the ocean is represented only by 4 500 species and comprise only 9-11% of all algal species. As it is expected the number of phytoplankton species will grow up several times only. Zooplankton is represented only by about 2 200 species of pelagic copepods (from the total 7 500), 400 species of pelagic misids (from the total 970), 86 species of euphausiids (see Pierrot-Bults, 1999). The marine phylum with the highest species richness, Mollusca (more than 100 000), is represented only by 250 and 400 pelagic species of pteropods and cephalopods respectively.

Over 90% of all marine species are benthic (bottom-living). From the total numbers of described species of marine creatures, one can calculate that about 80% of all known marine species occur in the coastal zones (Reaka-Kudla, 1997). Shallow-water benthos is rather well described. For example, in the coastal areas of the Russian Far East seas about 30% of flatworms and nemerteans, 40% of cnidarians, 80% of bryozoans, echinoderms, tunicates and more than 90 of decapod crustaceans are thought to be known. But it is not the same with deep-water benthic creatures.

There has been a common misperception that the deep-sea is species poor because of inhospitable food-limited environments and very stable habitat. But within last few decades, quantitative samples have revealed that sediments in the deep sea are teeming with a rich diversity of various invertebrates (see Snelgrove & Grassle, 2001). Based on a modern calculations, the projected number of species for benthic marine invertebrates is estimated to 20-30 million species, most of them are deep-water species (Fig. 2).

There are numerous data that indicate a much greater diversity of species in the deep-sea than previously thought. The most extensively sampled area of the deep sea is the western North Atlantic. For example, from depth of between 1500 m and 2100 m alongside a transect of 176 km off the east coast of North America a total about 800 of macrobenthic invertebrates and 91 000 individuals were collected at 14 stations from a total area sampled of 21 m^2 (Grassle & Maciolek, 1992). Of these, 480 species, or 58%, had not been recorded before. Just one box-corer (30x30 cm) at 2100 m depth contained 135 species of macrobenthic invertebrates, thus showing a remarkably high species density. These samples were also characterized by a high macro-taxonomic diversity. About 12 phyla of Metazoa were represented by polychaetes, mollusks, crustaceans, cnidarians, nemerteans, priapulids, sipunculans, echiurans, bryozoans, brachiopods, echinoderms, hemichordates. About 90% of these species were represented by less than 1% of collected specimens and 28% of all species were collected only that ones, thus showing a high level of the "deep-water endemism".

This is generalized to one new species per km^2 for an oceanic area at 1 500-2 000 m depth. It is scaled these estimates of the total number of macrobenthic species to 10 million for an oceanic area deeper than 1 000 m (Grassle & Maciolek, 1992). Similar results were obtained for several multi-km transects from New England to South Caroline in the west Atlantic (see Rex *et al.*, 1999); at Britain coast in the eastern Atlantic (see Snelgrove, 2001); at Australian coast in the South-West Pacific (see Poore & Wilson, 1993). Data from the Pacific suggests that only 1 in 20 species has been described (Snelgrove & Grassle, 2001). On the average, at most known deep-water samples more than 50% of species were designated as the new for science.

The diversity varies parabolically with depth, being low at the continental shelf, increasing to a maximum at mid-bathyal depth and declining in the abyssal plain. All groups analysed exhibit essentially the same pattern with depth, though peak diversity varies between 2 000 and 3 000 m.

There are a few hypothesis to explain the high species diversity in the deep-sea (Sanders, 1968; Dayton & Hessler, 1972; Connel, 1978). (1) Environmental conditions in the deep sea appeared to be so constant that niche fragmentation has occurred on a lavish scale with a large number of highly specialized species being able to co-exist in these physically undemanding and resource-poor conditions (Sanders, 1968). At the low sedimentation rates, biologically generated habitat heterogeneity, such as mounds and burrows (bioturbations by large burrowers) is more persistent and contribute more to niche diversification in the deep sea than in more energetic shallow- water sediments. The granulometric heterogeneity of deep-sea sediments is also very important for species diversity. (2) High diversity of small-sized species is also maintained by large benthic "croppers" (holothurians, isopods etc.). This predatory disturbance decreases their prey populations so that prey species are less able to displace other small species through competition for food resources (Dayton & Hessler, 1972). (3) The "intermediate disturbance hypothesis" (Connel, 1978) predicts that highest species richness occurs at intermediate levels or frequencies of disturbance. These ecological disturbances are that created by mechanical forces, extreme physico-chemical conditions, living burrowers (bioturbators), consumers, and pathogens. Only few species are able to tolerate very intense and severe disturbance regimes. At the opposite, if disturbances are weak or infrequent the competitive exclusion occurs and a few species are able to compete successfully.

Deep-water investigations in the last couple decades have indicated that small-scale patchiness is very common, seasonal variation in phytoplankton production from the surface can be directly reflected in the material that reaches deep-sea sediments, and some deep-sea areas are even very dynamic in terms of currents and sediment movement (see Snelgrove & Grassle, 2001).

Experiments and observations on the deep-sea bed have supported the idea of small-scale patchiness and processes in maintaining species richness (Gage, 1999). These include small-scale transient biogenic structures, such as burrowers and sediment mounds; phytodetrital pulses from surface blooms and patch food supply; carcass falls; predation (see Rex *et al.*, 1999). The food supply patches are the local concentrations of phytodetrical flocs and the organic remains of zooplankton and floating algae dropping from the surface. The experiments indicated that small-scale patches can persist for 2-5 years, that is much longer than similar patches in shallow-water (see Rex *et al.*, 1999).

It has been estimated that of the 325 million of km^2 of the seafloor, that is part of the deep sea, only about 2 km^2 has been sampled for macrofauna (Snelgrove & Grassle, 2001) and only from 500 m^2 to 0.5 km^2 of the deep seafloor has yet been adequately sampled by modern quantitative corers and grabs (Gage, 1999, 2001). Thus, our current quantitative conclusions for the deep-water are based on a very limited spatial coverage. Nevertheless, it hardly could be doubted that the deep sea is the most species-rich habitat in the ocean and, probably, one of the richest on the earth.

Meiobenthos, or meiofauna, is the most poorly investigated ecological community in the sea which appears to be even more rich in species diversity than deep-water macrobenthos. Meiobenthos is a community of benthic organisms that pass through the 1 mm mesh sieves and that are retained on a 42 micron sieve (see Higgins & Thiel, 1988). Nineteen of 33 Metazoan phyla have meiofaunal representatives. Of these multicellular phyla, some are always meiofaunal in size (permanent meiofauna), whereas others are of meiofaunal size during the early time of their life history (temporary meiofauna). On the average there are about 1 million meiofaunal organisms per m^2 of sediment surface with highest abundance up to 9 million in the upper subtidal and up to 12 million per m^2 in the intertidal mud from estuarine habitats. They are worldwide in distribution from intertidal to abyssal depth. Meiofaunal creatures may be relatively numerous even in the sea ice (up to 60 000 per m^2 – Carey & Montagna, 1982), in the deep-water at 3000 m depth (up to 1.5 million) and even in the abyssal trenches at 8300 m depth (0.5 million per m^2) (see Shirayama, 1983, 1984).

The systematics of meiofauna is even less known as compared with deep-water macrobenthos. For example, a nematode study in the Arctic reported that only 4% of the 92 species found in the corer were known to science, while a study in the tropic (Venezuela Basin) could only name 1.5% of the 136 species found (see Lambshead & Shalk, 2001). In many taxa about 80-90% of species are known only from a single locality thus showing a high level of the endemism comparable with that of deep-water macrofauna (see Adrianov & Malakhov, 1999).

The projected number of meiofaunal species may be estimated to 20-30 million species including about 10 million species of marine nematodes (see Fig. 2). Marine nematodes are nearly always more abundant and species rich in individual core samples than deep-water macrofauna. Because of this, there are some extremities to estimate for total nematodes in the deep-sea up to

100 million species (see Boucher & Lambshead, 1995).

As it was noted for deep-water macrofauna, highest diversity and high endemism level of the meiofaunal species is also maintained by small-scale patchness and processes on the surface and inside marine sediments. Meiobenthic populations appear to be also locally isolated because of the total absence of plankton larval stages. Contrary to plankton and macrobenthos, there are no cosmopolitan species within meiofauna. High species diversity of the meiofauna could also be explained by a relatively high evolutionary rate because of the rather high metabolic rate and generation time. It is calculated that for an equivalent biomass, the meiofauna are responsible for about 5 times the total benthic metabolism of the macrofauna (Gerlach, 1971, 1978) and the metabolic rate is correlated with the rate of mutations and thus, with molecular evolution (Rand, 1994). In turn, a speed of the molecular clock is correlated with morphological evolution. In some meiofaunal taxa (harpacticoids, ostracods, nematods), one can get new generation per every 3-4 weeks and that might cause the evolutionary rate to vary considerable as compared with the most of macrobenthic species.

At the average density of 1 million specimens per m^2, meiobenthic animals are the most numerous Metazoans on the Globe. Marine nematodes (up to 9 million per m^2) are the most numerous meiofaunal invertebrates in the world ocean which are more numerous than even totally ants, termites, and beetles from terrestrial habitats.

The main problem in the study of biodiversity is that the modern rate of extinction because of ecosystem destruction exceeds the modern rate of description of new species. Currently, up-to 15 000 species have been described per year. In the last 30 years about 8700 new species have been described per year while for more than 200 years before about 4500 species have been described per year (Erwin, 1997). Even at the modern rate of descriptions we need more than 100 years just to describe next 1.5 million of species.

At the modern rate of researches we are not able to describe totally the biological diversity in the ocean. According to the new approaches and the modern strategy of biodiversity studies it is necessary to identify centers of evolutionary diversification that act as genetic sources for existing biodiversity (see Thomas, 1997). These centers are the local areas with highest biodiversity which are selected for every climatic zones and latitude ranges. International teams of taxonomists could concentrate their efforts to integrated study, inventory and monitoring of marine biodiversity in these areas. According to the strategy above the following tactics can be used to initiate biodiversity inventories in marine areas of international or particular interest and importance: (1) based on the inventory of marine biota to identified the centers of evolutionary divergence (areas of the highest species and genetic diversity) and to protect these water area; (2) within the selected water area or protected area to establish concrete zones for a long-time biological monitoring; (3) to publish primary taxonomic monographs, identification guides, keys and manuals, especially computerized; (4) to use these selected water area to study biodiversity at all other levels.

As an example, this approach was adopted by DIWPA (the International Network for Diversitas in the Western Pacific and Asia) established in 1993 to: (1) promote international collaborative research project; (2) facilitate the international citizen program; (3) promote governmental and non-governmental activities for the conservation and utilization of biodiversity; 4) create an international network of networks that already exist in each country and the research projects that focus on specific subjects or topics. (see Inoue, 1996). In the Western Pacific, that is the most species rich area of the ocean, DIWPA has selected 21 local aquatic areas in shallow coastal water from New Zealand to the Okhotsk Sea, including most latitude ranges and climatic zones. Since 2002, the comprehensive hydrobiological monitoring, including video-monitoring methods, are recommended to be used according to standardizing protocol accepted by all international participants (see Biodiversity Research Methods, 2002).

One of the northern point of these 21 areas is the Peter the Great Bay, now the only area selected by DIWPA in Russian Far East seas and the only point in the Sea of Japan. The Peter the Great Bay is characterized by the richest taxonomic diversity in the Russian waters. Currently, about 6 900 of only macrobenthic invertebrates have been described from the coastal areas of the Russian Far East, that is even more than in all Russian Arctic seas (4 800) and totally around the Europe (6 500) (see Pullen, 1999; Sirenko, 2001). About 42% of these total diversity is that of the Sea of Japan. About 2 900 species of Metazoa have been described up-date from the Sea of Japan that is more than from the Okhotsk (2 700), Bering (2 000) and Chukchi (950) Seas (see Sirenko, 1995). In the Peter the Great Bay, representatives of 52 phyla, 105 classes and 4 000

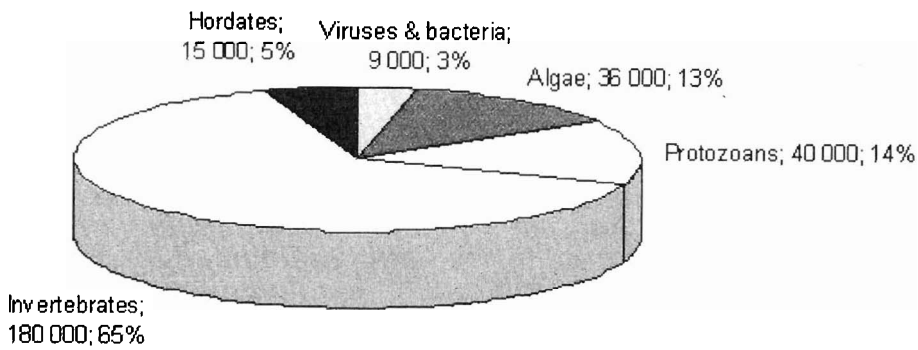

Fig. 1. Number of known species of marine organisms.

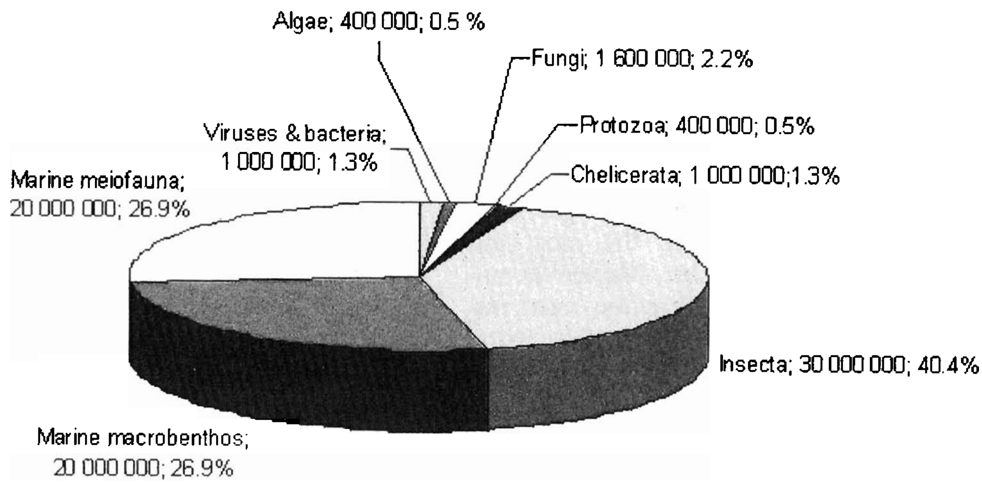

Fig. 2. Projected number of species.

species of marine creatures, including 2 600 species of Metazoa, have been described up-date (Adrianov & Kussakin, 1998). Since 2002, in this area the standardizing hydrobiological monitoring of marine biodiversity according the DIWPA protocols has also been organized.

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Адрианов А.В. Биологическое разнообразие в морских экосистемах: закономерности, динамика и современная методология.

Резюме. Обсуждаются терминология и основные составляющие биологического разнообразия. Сравнивается видовое богатство и таксономическое разнообразие наземных, пресноводных и морских организмов. К настоящему времени описано около полутора миллионов наземных организмов и лишь 325 000 водных. Несмотря на более чем двухвековую историю интенсивных исследований описано лишь около 280 000 видов обитателей моря, включая 180 000 видов морских беспозвоночных. Из 33 известных типов Metazoa 31 тип обнаружен в море, а 13 из них исключительно морские. Лишь 17 типов обнаружены в пресных водах и 11 типов в наземных экосистемах. Из типов Metazoa представленных паразитами, 4 типа обитают в море, и лишь 2 типа паразитируют в пресноводных и наземных хозяевах. Лишь два типа, пресноводные Micrognathozoa и наземные Onychophora представляют собой "не-морских" эндемиков. Обсуждается разнообразие глубоководного бентоса и мейофауны. На основе последних экстраполяций предполагается, что в океане, главным образом в его глубоководной части, существует еще около 20-30 миллионов неописанных видов макробентоса, и приблизительно такое же количество мейобентических видов, включая 10 миллионов видов неописанных морских нематод. Рассматриваются гипотезы, объясняющие высокий уровень видового разнообразия в глубоководье океанов, а также новые инициативы и методологические подходы к изучению этого разнообразия.