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NOTE

Zonations and organismic assemblages: comments on the comprehensive review by Pérès (1982)

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ABSTRACT: This Note considers critically the comprehensive review by Professor J.-M. Pérès, published in the treatise 'Marine Ecology', edited by Professor O. Kinne and published by Wiley & Sons. The review contains a considerable amount of scientific information and also serves as a reference book on many questions of marine ecology. It is of great importance to marine scientists. However, some of the general concepts presented are not in line with internationally accepted patterns and are incorrect in terms of recent ideas about zonations and ecosystems. The author of this 'Note' claims that in regard to vertical and horizontal zonations the most significant factors are not the degree of illumination and primary production at different depths and latitudes, but physicochemical conditions, within the same regions and water masses and their layers, which determine origin, vertical and horizontal distribution and often abundance in ecosystems composed of different genotypes (species). For the terms used it is proposed to apply the principle of priority. For assessing the regular structure of natural ecoystems featuring quantitative predominance of a few genotypes over many others on a logarithmic scale, the term 'biocoenosis' introduced by Möbius, should be used.

In the treatise 'Marine Ecology' (ed. by O. Kinne, publ. by Wiley & Sons), the first part of Volume V ('Ocean Management') is devoted to reviewing our present knowledge on zonations and organismic assemblages. Authored by the famous French hydrobiologist Professor J. M. Pérès, the presentation of this topic still poses many problems and, in my opinion, shortcomings. In the introduction to Part 1 of Volume V, Professor Kinne states, and rightly so, that 'there is great need for developing a precise, internationally standardized, analytical instrumentarium and for achieving basic conceptual agreement' (p. 1).

In my opinion, the zonations introduced by Pérès (Chapter 2) for the pelagial and benthal are not in line with internationally widely accepted patterns and are not correct in terms of modern concepts of biocycles and ecosystems. In the Kuril-Kamchatka Trench, Pérès distinguishes 5 vertical zones of the pelagial: epipelagial zone (0/15 to 20 or 50/120 m, depending on light penetration); mesopelagial zone (oligotrophic layer with a lower boundary of about 200 to 300 m); infrapelagic zone (lower boundary near 600 to 700 m); bathypelagic zone (lower boundary of about 2000 to 2500 m); abyssopelagic zone (down to 6000 to 6500 m).

In the Mediterranean Sea and in the Atlantic and Indian Oceans vertical zonations are based mainly on the degree of illumination at different depths, separating phytal and aphytal. In the phytal system Pérès distinguishes 4 vertical zones: supralittoral zone (higher level of wave beating); midlittoral zone (tidal zone); infralittoral zone (from 0 m to the maximal depth of penetration of sea grasses and photophilic algae, usually at 20 to 120 m); circalittoral zone (down to the maximal depth consistent with the survival of photoautotrophic multicellular algae, usually about 150 to 250 m). The aphytal system is divided into 3 vertical zones: the bathyal zone (below the circalittoral zone, to a depth often about 3000 to 3500 m or at the isotherm of 4 °C); abyssal zone (at 3000 to 3500 m and 6500 to 7000 m); hadal zone (trenches deeper than 6000 to 7000 m). A brief account is given of vertical changes in biomass and abundance. It is significant, however, that light limits development, growth and production mainly in plants, but not in animals. At a given depth, the degree of illumination varies strongly in different seas and even in different parts of the same water body; consequently, it is difficult to compare vertical zones even inside the same landscape-geographical aquatoria. On the other hand, light does not determine speciation and geographical distribution of organisms. Primary production is a function of the quantitative ability of some species, but not (in most cases) of species composition. Therefore, light does not appear to provide the best criterion for vertical zonations.

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The oldest, the 'bathymetrical criterion' reflects distribution of organisms in different parts of the sea bottom. Using this criterion, 9 vertical zones can be distinguished: supralittoral (zone of wave breaching at high water, this is identical with Pérès uppermost zone); littoral (i.e. the tidal zone = Pérès' midlittoral); sublittoral (*s. l.* Lorenz 1863, continental and island shelves, average depth 200 m = infralittoral + circalittoral of Pérès'); pseudobathyal (Andriashev 1974, depression on shelves with depths of more than 200 to 300 m, e.g. depths of the White Sea); bathyal (Appellof 1912, continental slope with average depths of 200 to 2000 m); pseudoabyssal (Derjugin 1915, Andriashev 1974, the depression on the bathyal below 2000 m, not connected with the sea floor, depths 2000 to 5000 m, e.g. the depths of the North Polar Ocean); abyssal (Forbes & Hanley 1853, ocean floors with depths from 2000 to 7000 m); thalassobathyal (Andriashev 1974, ocean floor with bathyal depths separated from continental slope, e.g. middle oceanic ridges); ultraabyssal (Zenkevitch et al. 1954, = hadal zone of Pérès, comprising trenches deeper than 7000 m).

However, in our opinion the most acceptable pattern is vertical zonation on the basis of the position of water masses and their layers. The term 'water masses' implies temperature-salinity specific characteristics (Defant 1929), composing 'Hydrobiocomplexes' with organisms connected with them by origin. Temperature and temperature-salinity combinations are most significant for determining rates of biological activity, growth, reproduction and distribution of organisms; to a high degree they determine vertical and horizontal organismic distributions (Orton 1920, Runnström 1927, 1929, Hutchins 1947, Kinne 1970, and others).

According to this criterion of vertical zonation, 9 vertical zones can be distinguished (Fig. 1): (1) supralittoral and (2) littoral zones (Forbes & Hanley 1853); (3) adlittoral zone (Golikov 1980, from 0 to 5 to 10 m, at the depth of wave action, high turbidity and daily change of temperature in temperate waters, this is the upper layer of surface water masses); (4) circumlittoral or laminarian zone (Forbes & Hanley 1853, from 5/10 to 25/27 m, at the lower border of this zone spring and autumn thermoclines are located in temperate waters, this is the middle layer of surface water masses); (5) median or coralline zone (Forbes & Hanley 1853, from 25/27 to 55/70 m, lower layer of summer heating in temperature waters, this is the lowest layer of surface water masses); (6) inframedian zone (Forbes & Hanley 1853 = elittoral zone of Kjellmann 1877, from 55/70 to 120/180 m, layer of winter cooling, this is the upper layer of intermediate water masses); (7) bathyal zone (Appellöf 1912, upper part from 120/180 to 600/800 m, middle layer of intermediate water masses, lower part from 600/800 m to 1200/2000 m, lower layer of intermediate water masses); (8) abyssal zone (Forbes & Hanley 1853, from 1200/2000 to 5000 m; deep water masses); (9) ultra-abyssal zone (Zenkevitch et al. 1954,

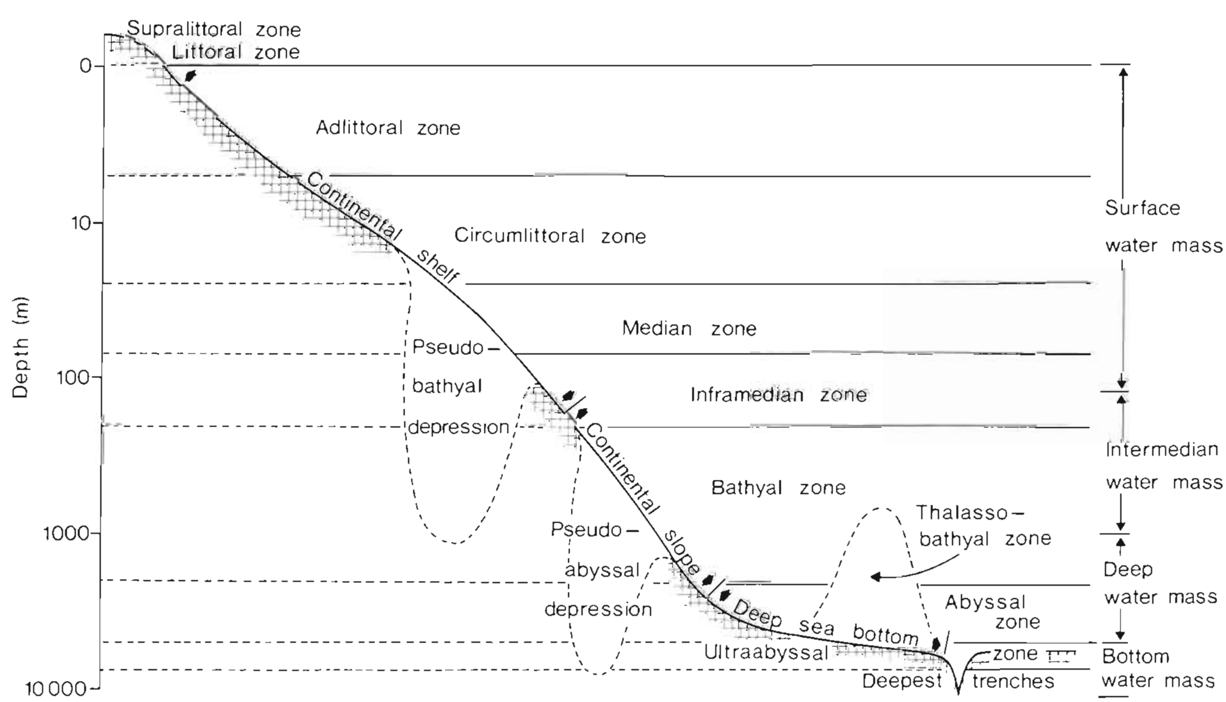

Fig. 1. Main vertical zones of the marine environment

deeper than 5000 m, sometimes at bottom water masses, e.g. waters antarctic by origin in the northern part of the Pacific Ocean). This vertical zonation corresponds well to the vertical distribution of life, the components of which differ by origin at different depths.

Vertical changes in mean biomass are well characterized and agree with recent data. Unfortunately, most papers cited by Pérès were published prior to 1970. According to recent information, the biomasses of macrophytes at 1 to 15 m depth are usually as high as 20 to 30 kg m^{-2} and may attain 100 kg m^{-2} *(Macrocystis)*.

In his section 'horizontal zonation', Pérès does not clearly separate landscape-geographical and biogeographical zonations. In landscape-geographical zonations the main factor is the distribution of biomasses of abundant species while in biogeographical zonations the qualitative composition and the taxonomic level of organisms of different origin are most significant. Pérès pays particular attention to landscape-geographical zonations. The theoretical and terminological aspects of this type of zonation have been discussed by Golikov & Scarlato (1979) and others. In terms of biogeographical zonation the World Ocean has been divided into 3 kingdoms or overregions: cold and temperate waters of the northern and of the southern hemispheres, and tropical waters. The kingdom of cold and temperate waters of the northern hemisphere is divided into 3 regions: North Pacific boreal region (age: 12 to 14 million yr); North Atlantic boreal region (age: 5 million yr); Arctic region (age: 1.8 million yr). Some authors associate the last region with the Atlantic boreal region in a united Arctic-Atlantic region.

The cold and temperate waters of the southern hemisphere are divided into 5 regions: Patagonic region; Kerguelenic region; New Zealand region; Araucanic region; Antarctic region. The tropic kingdom is divided into 4 regions: Mediterranean-Lusitanic region; South African region; Caribbean region; Indo-West Pacific region. Biogeographic regions, according to physicochemical conditions and generic and species composition in its different parts, are subdivided into subregions, provinces and smaller units. For example, in the kingdom of cold and temperate waters of the northern hemisphere (which has been most thoroughly investigated in this respect), the Pacific boreal region is subdivided into Japonic (Woodward 1851–1856), low-boreal, and Aleutic (Woodward 1851–1856) high-boreal subregions, with the border near Iturup island and the shoals of Terpenia and Aniwa bays (the southern border of the Pacific boreal regions are located near Noto and Boso peninsulas on Honshu). The northern border of the high-boreal Pacific subregion lies between southern parts of the Anadyr Bay and the Chukchi Sea, and the southern border of this subregion lies off the American continent, passing near the coasts of Washington State (USA).

The Arctic region is subdivided into Eurasian and Amerasian provinces with the border near the Novosibirskie islands and Lomonosov ridge, and the Estuary-Arctic province near the estuaries of the great Siberian rivers. The Atlantic boreal region is subdivided into 2 provinces (Forbes & Hanley 1853): the Germanic high-boreal province is separated from the Arctic region in the Barents Sea near the southern island of Novaja Zemlya and continues past Northwest Spitzbergen, near northern Iceland, South Greenland and the northern part of the Newfoundland bank, prolongated to the southern American coasts to Cape Cod; the Celtic low-boreal province has its border in the north with the Germanic province near northwestern Ireland and western Norway, and is separated from the Lusitanic province of the Mediterranean-Lusitanic subtropical region near the English Channel.

In Pérès' section 'Food: the major factor controlling vertical and horizontal in pelagial and benthal', the author concludes that distribution and fate of primary production and trophic input from land determines zonations in the distribution of organisms (the relatively recent data on the giant deep-water chemical production near the Galapagos islands and in other places are not included in his observation). A more realistic view may be that food supply often determines only biomasses and numbers of individuals in food chains, whereas zonations in organismic distributions differ in origin, qualitative composition of life and comparative abundance of different genotypes in biotopes; in most cases they depend on physico-chemical conditions at different water depths and in different geographical regions (first of all on temperature and hydrodynamic regimes).

Works of Möbius (1877), quantitative investigations of Petersen (1911, 1913) and mathematical applications of some authors (e.g. Fisher et al. 1943, Williams 1947) indicate that the organization of life in the sea and on land at the population level exhibits regularities, in which one or a few species dominate in terms of bioenergetic indices (e.g. biomass) over many others on a logarithmic scale. This is true not only for the benthal but to the same degree also for the pelagial. Sometimes not a single species, but a life form represented by several coexisting species predominates (e.g. on coral reefs and in algal mosaics). For denoting such a type of organization of life in general, in all places where different species live together, the term 'biocoenosis' (Möbius 1877) has been accepted and there seems to be no reason to change this term to the younger and less clearly defined term 'assemblage'. Discussed in the chapter are also specific characters in the structure of 'assemblages' in the benthal and pelagial, with special observations of factors acting upon the distribution and abundance of different ecological and structural subdivisions of plankton and benthos and also comparison of qualitative and quantitative methods for delimiting organismic communities.

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