Metabolic Characteristics and Total Surface Area of Living Matter of the Ocean: A Comparison of Size Spectra

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A comparison of the size spectra (i.e., the distribution of the total value of each characteristic by size class) of production and destruction indicates that they are closely correlated with the metabolically active surface areas of groups of o organisms than with their biomass and abundance. The analysis is based on published data of Sorokin for organisms measuring from 10^{-7} to 10^1 m for all oceans . over the course of the year. The results are considerably dependent on the description of the size and trophic structure of picoplankton (organisms smaller than 1 µm), which can be refined by comparing the viewpoints of phytoplankton specialists and microbiologists.

A condition essential to the existence of any organism is the exchange of metabolites with the surroundings via the surface that separates them (5). Vernadskiy regarded the individual and aggregate surface area of all living matter or of all vegetation as one of the most important characteristics of the biosphere, expressing its "film—like" nature. This Idea was not immediately appreciated. Most of the data describing living organisms of the earth are formulated in terms of biomass (a) or abundance (N). Given the huge size range of organisms (10^{-8} to 10^{1} m), the evaluation of their role in the aggregate metabolism of a community will differ considerably depending on whether abundance, biomass or surface area is compared. As noted by Odum [9, p.109), the use of biomass figures results in overstatement of the role of large organisms, whereas the use of abundance figures overstates the rote of the small organisms. In the simplest case (assuming a spherical body shape) we obtain

 $W_t = \rho - \pi D^3/6$ (1) N = B/ W_t = 6 B D⁻³/(\rho \pi) (2),

where W_t is the body weight, D is the "effective diameter" determined from body weight, and p is the specific gravity ~ 1 g cm⁻³. A possible intermediate case between B D⁰ and B D⁻³ is the total surface area of a group of organisms

| $S_{ts} = N S_t = 6 B D^{-1}$, | (3) |
|---------------------------------|-----|
| Where $S_t = \pi D^2$ | (4 |

is the individual surface area. The allometric relationships between various metabolic characteristics and body weight currently obtained for a variety of organisms have the form a W_t^b . The exponent b is generally from 0.6 to 0.83 [5, 15], indicating a closer correlation with $S_t (b \sim 0.67)$ than with $W_t (b \sim 1)$.

Current biooceanographic data not only confirms Vernadskiy's suggestion that the dispersed state and the surface area of living matter play an important role, but also allow it to be illustrated numerically for many groups of organisms. Let us compare the most general functional characteristics of the main groups of the ocean organisms, i.e ,.production and respiration with their quantitative measures, N, B, and S.

<u>Sources of the data and calculation methods.</u> Our analysis makes use of the data of Sorokin [18]. We used the total annual figures for the oceans as a whole, which enabled us to eliminate the effects of seasonal and geographical variability, spatial and temporal variability, vertical stratification, and migration of organisms. The data for the individual groups of organisms were assigned to the size scale by means of the classification table of Sieburth et al. [17]. For benthos, which is not included in this table, we use the size range 0.1-10 cm. The plant group was divided in two: phytoplankton (1—100 μ m) and phytobenthos (microphytobenthos and macrophytes, 100 μ m to 10 cm ~ 1 μ g to 1 kg of live weight.

The biomass was divided equally between them, and production was divided in 20:1 proportions (13, 20]. In this way we constructed (Fig. 1) size spectra (SS) that indicated the percentage distribution of the total value of any characteristic (total biomass, total body surface areas, production, destruction) over the sire classes i.e., equal on the logarithmic scale ranges of variation of the sizes of the organisms [15, 16].

Unfortunately, Sorokin does not present data on the virioplankton (Sieburth's "femtoplankton" [17] which has recently been attracting much interest. Thus, the left edges of all size spectra are truncated (the assumed shape of the curve is shown by a dashed line in Fig. 1a).

The breakdown resulted in seven size classes, each representing an increase of an order of magnitude in the parameter in question ($D_{i+1} = 10 D_i$). When one group of organisms described by Sorokin represented several size classes, it was subdivided in equal fractions. We then summed for each (i-th) size class the 'contributions' of the various groups (e.g., macroplankton, benthos and nekton in the 1-10 cm class) and normalized the resultant

figure (X_i): e.g_ X_{i%} = X_i 100% / X_{Σ}, where X_{Σ} is the total value of the characteristic in question (biomass, destruction, and so on) for all living matter of the oceans. For biomass, assuming 1 kcal = 1 g live weight = 1 cm³, we used Eqs. (2) and (3) to calculate the abundance and total surface area of living organisms.



Fig. 1. Size spectra of living matter in the oceans. Curves are numbered according the table. a) Based on raw data of [18, p. 590]; b) microplankton alone, data of [19]; 8) chlorophyll (μ g m⁻³); 9) ATP ((μ g m⁻³); 10) organic carbon ((mg m⁻³). C) Resultant plots: 17) change in SS #14 resulting from the change in description of the trophic structure of picoplankton. Bac. – bacteria, Phy. – phytoplankton, Vir. - virioplankton, mic. – microzooplankton, mes. - mesozooplankton, mac. - macrozooplankton, MPB -microphytobenthos, MP - macrophytes, ben. - zoobenthos, nec. – nekton.

Naturally, the real, complex, dissected form of organisms is highly non-spherical and the surface area through which metabolic exchange with the surroundings takes place (the outer surface, i.e., branches, leaves and roots, in the case of plants, and primarily inner surfaces i.e., lungs, gills, and the gastrointestinal trace - GIT - in animals) are considerably greater than those determined from Eq. (4). We therefore introduce the concept of "metabolic surface area" ($S_{tm} = S_{lungs} + S_{GIT} + S_{skin}$) or the "surface area ratio" () and the "summary metabolic surface area" of a biota or any of its components: $S_{tms} = SUM S_{tmi} N_i = SUM KSS_i S_{ti} N_i$. The coefficient KSS was determined in the allometric form. For the Man, the metabolic data give Stm = 300 m2, Wt = 70 kg; For bacteria, substituting KSS = 1, D = 1 um, we obtain $KSS \sim W_t^{0.14}$. Thus, $KSS \sim aW_t^{b}$, where $b \sim 0.667 + 0.14 \sim 0.807$, in a good agreement with the estimates of b in other equivalent equations: 0.82 for the gill area of marine fish [2]; and 0.78 obtained by us (a separate publication, in preparation) from data of the Laboratory of Ecological Metabolism of our Institute (S for marine macrophytes) supplemented by published data (viruses bacteria, unicellular algae, leaf surface of terrestrial higher plants). The values of KSS used here are shown from the Table.

| Table | 1. | Size | Spectra | of | Living | Matter | of the | Ocean |
|-------|----|------|---------|----|--------|--------|--------|-------|
| | | | | | | | | |

| Spectru | Param | | | | | | | | |
|---------|-------|--------|---------|-----------|---------|----------|--------|--------|---------|
| m N | eter | | Size cl | ass, left | boundar | y, log D | , um | | |
| | | -1 | 0 | 1 | 2 | 3 | 4 | 5 | Total |
| 1 | В | 1.40 | 0.75 | 1.35 | 4.25 | 7.75 | 8.00 | 3.00 | 26.50 |
| | | 5.28 | 2.83 | 5.09 | 16.04 | 29.25 | 30.19 | 11.32 | |
| 2 | Log N | 28.93 | 25.66 | 22.91 | 20.41 | 17.67 | 14.68 | 11.26 | 28.93 |
| | | 99.95 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | |
| 3 | P | 210.00 | 366.00 | 426.00 | 35.00 | 36.05 | 5.65 | 0.90 | 1079.60 |
| | | 19.45 | 33.90 | 39.46 | 3.24 | 3.34 | 0.52 | 0.08 | |
| 4 | R | 490.00 | 0.00 | 40.00 | 28.00 | 30.45 | 17.10 | 3.35 | 608.90 |
| | | 80.47 | 0.00 | 6.57 | 4.60 | 5.00 | 2.81 | 0.55 | |
| 5 | S-ts | 26.56 | 1.42 | 0.26 | 0.08 | 0.02 | 0.00 | 0.00 | 28.33 |
| | | 93.74 | 5.01 | 0.90 | 0.29 | 0.05 | 0.01 | 0.00 | |
| 6 | S-tms | 26.56 | 3.73 | 1.77 | 1.47 | 0.72 | 0.25 | 0.00 | 34.51 |
| | | 76.96 | 10.82 | 5.13 | 4.27 | 2.08 | 0.73 | 0.00 | |
| 7 | ' Km | 1.00 | 2.63 | 6.92 | 18.20 | 47.86 | 125.89 | 331.13 | 533.63 |
| | | 0.19 | 0.49 | 1.30 | 3.41 | 8.97 | 23.59 | 62.05 | |
| 14 | - P1 | 439.40 | 219.20 | 73.40 | 14.00 | 14.00 | 0.00 | 0.00 | 760.00 |
| | | 57.82 | 28.84 | 9.66 | 1.84 | 1.84 | 0.00 | 0.00 | |
| 15 | Pk | 649.40 | 219.20 | 133.40 | 35.00 | 36.05 | 5.65 | 0.90 | 1079.60 |
| | | 60.15 | 20.30 | 12.36 | 3.24 | 3.34 | 0.52 | 0.08 | |

Note: Spectrum numbers: 1) biomass, B, 10^{15} kcal; 2) logarithm of abundance (N), individuals; 3, 4) production, P, and respiration, R, 10^{15} kcal/yr; 5, 6) total surface area of organisms (S_{ts}) and total metabolic surface area (S_{tms}), 10^{15} m²; 7) surface ratio (KSS); 14, 15) primary production (P₁, production of all groups with allowance for distribution of primary production (Pk), 10^{15} kcal/yr.

*Class number is the logarithm of its lower boundary (Dm, um), where D is the effective diameter, $\sim W^{1/3}$. Numerator for each curve gives absolute values, denominator gives the percentage distribution. **Size spectra Nos., see explanation in the text and in the captions to Fig. 1.

<u>Results</u> The, above procedure was used to obtain the size spectra (SS) for several characteristics (biomass, abundance, production, destruction, total and aggregate surface area; see Table) of living matter of the oceans (SS Nos. 1-6). For clarity and convenience of analysis, some of them are also shown in Fig. 1a. As can be seen from the Table and from Fig. 1a, the size spectra for production (P), descruction.(R) and aggregated surface area (S_{tms}) are qualitatively similar but differ considerably from the biomass size spectrum. The preponderance (~90%) of the cumulative quantities (P, R, S_{tms}) is contributed by organisms smaller than 100 um, primarily phytoplankton and bacterioplankton. But the data on these groups of organisms are undergoing a major reevaluation [6, 14, 19] in connection with the problem of the "primary production deficit" [13].

Recent research results [6, 14. 19] make it possible to refine the distributions of several parameters (Fig. lb), including primary production, in this area of the size spectrum. It is divided between the 0.1, 1 and 10 um classes (the left boundaries of the classes are given) in the approximate proportions 60:30:10 (SS No. 14) rather than 0:50:50 as was used in calculating the plots of Fig. 1a. The size spectra for production (SS Nos. 14 and 15) based on these proportions are presented in the Table and in Fig. 1c.

Because the synthesis of organic matter is associated with catabolic processes (photorespiration and dark respiration of autotrophs), the leftward shift of a considerable proportion of the primary production should produce a similar change in the destruction plot. But this change will be considerably dependent on the way in which the raw data are interpreted.

Discussion. The main result of this investigation is an agreement between the characteristics of the metabolically active surface area (we emphasize again that this is not only external surface) of the biota and its main functional characteristics (i.e., respiration and production) that is in general quite satisfactory for the oceans as a whole. This agreement is particularly valuable because other methods of comparing these characteristics show considerable divergence. As examples of such divergence, we note the problem of the primary production deficit and the poor correlation between the functional characteristics (P, R) and the customary structural characteristics (B, N) of various groups (trophic, topical, taxonomic) of organisms.

We achieve this agreement by representing the totality of organisms in a specific form, i.e. the size spectrum. This form is not new: It has already been used in numerous theoretical and experimental studies in ecology and hydrobiology [2, 4, 11, 15, 16, 19], including analyses of production and destruction processes [11]. Size and body weight are formal, quantitative features that are extremely important in biological terms and are

closely associated with the biological characteristics of organisms [3-5, 12, 15] and in addition are convenient for mathematical manipulation [2, 7, 11, 12, 15] and for automatic data collection [16].

The new clement, we believe, is the comparison of size spectrum series for the totality of organisms of an ecosystem, i.e., its living matter as a whole (Fig. 1a, c). The comparison reveals that metabolism (P, R) is better correlated with surface area (S_{tms}) than with the customary characteristics (B, N) in size spectra Nos. 3 and 4, 6, 1 and 2, respectively. The close correlation of production with S_{leaf} (S_{tms} for groupings of various rank) has long been known in the ecology of the higher plants and has been investigated [7] and used far forecasting crop yields. The correlation between the surface area and metabolism has been discussed at various levels of organization of living matter, including the ocean as a whole [1]. Of particular interest is the structural organization of metabolic surface area, i.e., "fractalization", the behavior of similar structures at various size scales and levels of organization, which has been studied in considerable detail in the case of marine multicellular algae [10]. The general. tendency of biological systems to place the greatest metabolic surface area in the smallest volume, which extends down to the molecular level [2. p. 243], shows up in structures typical of living material such am dendritic structures (hierarchical branching) and nest structures (hierarchical inclusion).

The fractalization of living matter increases the S/B ratio and the aggregate surface area. In the context of Vernadskiy's ideas it is significant that the individual weight and specific body surface (S/W) are indicators of the degree of dispersion of living matter whereas the shape of the SS- S_{tms} plot probably expresses types of fractalization of metabolic surface area. Fractalization complicates analysis of the correlation of surface area with metabolism (the evaluation of S_{tms} depends on the accuracy with which the hierarchically dissected surface area is approximated), but it will still be useful, making it possible to estimate the surface area by the principles of identity of structural components. The principles of similarity and the absence of a "preferred scale" are manifested in the similarity of the plots approximating the various sections of the SS—B plot [2], and thus the SS-S_{tms} plot as well. If they are also applicable when comparing the size spectra of different hierarchical levels, then mathematical methods can be used to reconstruct hard-to-measure sections of the size spectra.

It is possible that nature's use of the principles of fractal geometry is the reason that the allometric coefficient in the surface area and metabolism equations is about 0.8 [2]. The similarly of the values of *b* (0.66-0.74-0.83) in the allometric equations for various characteristics associated with metabolism (P, R, S_{tms}) [2, 5, 7, 13, 15], the concentrations of respiratory enzymes and coenzymes and RNA [15, pp. 216, 258, 268] may be of great importance in certain sections of the scale. Most interesting are the coefficients obtained through analysis of the broadest size spectra (i.e., for all living matter rather than for individual taxa): 0.789 [7], 0.75-0.80 [13], 0.73-0.75 [15], and 0.78 for S_{tms} (see above) over a range of ΔW of about 8 to 23 orders of magnitude. Because b < 1, the contribution of small organisms (or of biological structures to the production-destruction balance may be considerably greater than their contribution to biomass. For $\Delta W \sim 23$ orders of magnitude, the differences in specific metabolism can be as great as a factor of 10.000. Thus, the biomass of organisms mast be determined more accurately as their size decrease. In view of the above, it appears logical to change over from live weight, carbon, and energy content to specifically active metabolites (RNA, ATP, respiratory enzymes, chlorophyll), methods for measuring that have already been developed and incorporated into hydrobiology [14].

Overall, our analysis leads to the conclusion that it is beneficial to change over from biomass and abundance of marine organisms to aggregated metabolic surface, at the acme time representing the principal groups of living matter of the ocean as a set of size spectra (SS). A comparison of several site spectra, using the concept of "active metabolic surface area" and the usual allometric equations, will make it possible to combine data on biomass and metabolism of the main groups of ocean organisms into a single non-contradictory picture, which organically incorporates recent results on picoplankton production. In the complete size spectrum of living matter of the oceans, most of the aggregate metabolic surface, production and destruction are accounted for by the relatively little-studied picoplankton organisms (smaller than 1 um). Joint study of this part of the spectrum by phytoplankton biologists and bacteriologists will probably result in considerable revisions of the estimated balance and in our understanding of living matter in the oceans and in large ocean regions.

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