

Energetics of the biosphere

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Heterotrophic organisms live on accumulated plant and animal biomass. By harvesting the output of a land area that exceeds their coverage of the Earth's surface they attain consumption rates (per unit coverage by the organism) that exceed by several orders of magnitude the rate of production of vegetation (per unit Earth surface area). This occurs as a result of the fact that organisms move over the area they utilize due to the accumulation of production as biomass. Plants use photons, which have zero rest mass. Photons cannot be stored so that plants cannot increase their utilization of photons by moving about. For this reason, plants are stationary and the area they utilize coincides with the Earth surface area that they cover. Under natural conditions, approximately 90% of the vegetation is consumed by immobile microscopic organisms, for which the rate of consumption equals the rate of production of vegetation. As organisms become larger, their rates of consumption increase and the fraction of the production of vegetation that they consume decreases. (All vertebrates in the wild consume about 1% of the vegetation produced.) This results in a rapid increase in the area utilized as the size of the animal increases and increases the energy expended on grazing, which limits the increase in size. Man falls into the class of large organisms and under natural conditions must expend a large amount of energy on locomotion, which leads to all of his energy problems. When man learned how to combust the products of the biosphere and the fossil fuels outside the body and how to use this energy for locomotion, he became a more competitive mammal and he was able to increase his share of the total consumption in the biosphere to 25% of the vegetation produced on land by displacing the natural consumers. Such a high anthropogenic share of the total consumption in the biosphere can only be achieved through the use of nonrenewable energy resources.

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1. INTRODUCTION

Over the past decade as a result of their increasing significance to mankind discussion of ecological problems has passed beyond the narrow confines of specialists in biology. This article was conceived as a review of ecological problems in a form adapted to physicists, since the terminology and notation used in ecology is rather specialized. The translation into physical language required not only simplifications, but also conversion of many terms and traditional ecological variables. As a result, ecologists may possibly find it difficult to understand this article. However, from our point of view, such a conversion turned out to be useful. Some of the phenomena and relationships that have been considered in ecology as being

accidental turned out to be founded on established rules. Some factors that heretofore were considered as being insignificant turned out to be very important. For this reason, we hope that this article will be of interest not only to physicists, but to ecologists as well.

The biosphere occupies a thin layer on the Earth's surface. This layer is populated by all the living organisms on Earth and functions as a result of the absorption of short-wavelength solar radiation and emission of long-wavelength thermal radiation.¹⁻⁶ Living organisms in the biosphere exist as a result of the flow of chemical elements that, having participated in chemical transformations within an organism, are then eliminated from it. All substances that are eliminated from an organism are used by other organisms in the

biosphere. As a result, chemical substances circulate in the biosphere in closed cycles. This circumstance is made possible by the enormous variety of different kinds of specialization. The regulation of life processes in an organism is based on the principle of centralized control of organs that do not compete with each other. Regulation of life processes in the biosphere as a whole with a fixed influx of energy is based on the principle of free competition between the organisms that compose it, which ensures the most efficient assimilation of the input energy and results in the distribution of organisms into weakly overlapping ecological niches. Under stable conditions, the number of species in different niches attains a maximum, which is determined by the magnitude of the energy influx and by the minimum species population that ensures continued reproduction. In such a state, the energy expended on competition is at a minimum. Species that coexist in the biosphere form complete communities that are necessary in order to ensure closed circulation of biogenic substances. In the process of evolution, the communities of species change, retaining the property of completeness that ensures stability of the existence of life.

The flows of energy in the biosphere and the circulation of chemical elements are based on the photosynthesis of organic compounds out of inorganic compounds by autotrophic organisms—plants and on subsequent decomposition of the organic material so formed into primary inorganic components by heterotrophic organisms. Under the variable conditions of the environment, for any conditions that arise, there exists a species that under these conditions develops the maximum efficiency in assimilating energy. The population of this species becomes dominant. Its numbers increase and most of the energy flow passes through it. Under variable conditions, the number of species on the average is greater than the minimum that ensures continued reproduction, and, therefore, the variety of species is lower than under stable conditions with the same energy influx.¹⁻⁶ The possibility of changing the dominant species depends on mortality and fertility. The mortality of autotrophs makes it impossible in principle to form a closed circulation system for biogenic elements within an autotrophic organism and requires the existence of heterotrophs.

Mankind enters into the composition of the biosphere and most of its ecosystems as one of its species, having its own food consumption, fertility, mortality, population, ecological niches, and evolution.

2. SOLAR ENERGY FLUX IN THE ATMOSPHERE AND AT THE EARTH'S SURFACE

Most of the processes on earth occur because of the short-wavelength solar radiation (J) incident on the Earth. This radiation is transformed by the atmosphere, by the underlying surface, and by the ocean, and is reradiated into space in the form of long-wavelength thermal radiation.

Due to the large difference between the surface temperature of the Sun and that of the Earth, the incident

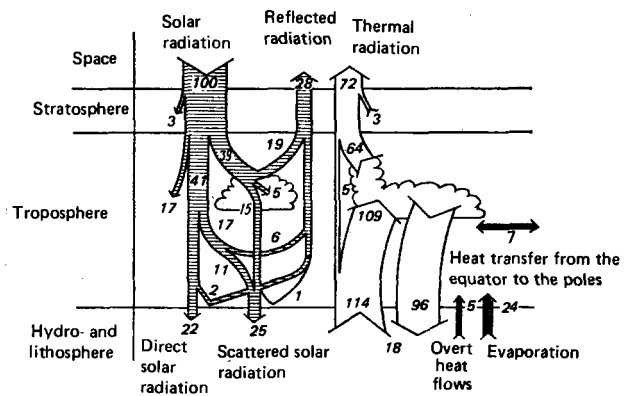


FIG. 1. Conversion of solar energy in the atmosphere and at the underlying surface (according to Rotty and Mitchell⁸).

solar radiation can be transformed on Earth into work or potential energy in reversible equilibrium processes with a transformation coefficient close to unity. The work being performed and the stored potential energy are expended on supporting nonequilibrium and irreversible processes in the atmosphere, the ocean, and the biosphere.

The total flux of solar radiation for the Earth outside the atmosphere equals

$$\pi r^2 J_S = 4\pi r^2 J_E = 1.7 \cdot 10^{17} \text{ W}, \quad (1)$$

where $J_S = 4J_E = 1,360 \text{ W/m}^2$ is the solar constant, $J_E = 340 \text{ W/m}^2$ is the average flux of radiation per unit of Earth surface area,^{1,7,11} and r is the radius of the Earth. One third (albedo) of the solar radiation is reflected back, mainly by the atmosphere (Fig. 1).^{8,9} One third of the absorption occurs in the atmosphere. The radiation that reaches the earth's surface amounts to $\pi r^2 \bar{J} = 0.8 \cdot 10^{17} \text{ W} = 6.0 \cdot 10^{20} \text{ kcal/yr}$.^{8,9} The average flux of solar energy at the Earth's surface equals

$$\bar{J} = 1.2 \cdot 10^6 \text{ kcal/m}^2 \cdot \text{yr} = 3300 \text{ kcal/m}^2 \cdot \text{deg} = 160 \text{ W/m}^2. \quad (2)$$

Table I displays the order of magnitude of the amount of solar energy distributed in the atmosphere and on the Earth's surface. The entries in the table constitute the renewable power resources of the planet. Lines 12 and 13 show the magnitude of geothermal and tidal power resources, which also constitute renewable resources and line 15 gives the present world consumption of energy which is almost entirely based on non-renewable fossil fuels.

3. UTILIZATION OF SOLAR ENERGY BY THE BIOSPHERE

Photosynthesis is an endothermic reaction synthesizing primary organic product from carbon dioxide gas and water¹⁸⁻²²:



¹⁾The maximum flux at the Earth's surface on a clear sunny day incident on a surface perpendicular to the sun's rays is $\sim 0.7J_S \sim 900 \text{ W/m}^2$. The maximum average diurnal flux in the absence of absorption in the atmosphere at the equator equals $J_S/\pi = 0.32J_S = 420 \text{ W/m}^2$; at the poles it is $J_S \sin 23.5^\circ = 0.40J_S = 540 \text{ W/m}^2$, 25% greater than at the equator.⁷

TABLE I. Distribution of solar energy.

	Power, W	
	Total	Available (allowable) ^{a)} for use
1. Total flux to Earth outside the atmosphere ^{4,8,9}	1.7 · 10 ¹⁷	
2. Absorbed by the Earth's surface ^{8,9}	8 · 10 ¹⁶	
3. Expended on evaporation ^{8,9}	4 · 10 ¹⁶	
4. Heat transfer from the equator to the poles by the atmosphere ^{8,9}	1 · 10 ¹⁶	
5. Heat transfer from the equator to the poles by the oceans ^{b),4,9}	2 · 10 ¹⁵	
6. Absorbed by land ^{8,9}	2 · 10 ¹⁶	
7. Evaporated by land (evapotranspiration) ^{8,9}	5 · 10 ¹⁵	
8. Output of photosynthesis ¹⁰	1 · 10 ¹⁴	5 · 10 ¹³ (< 10 ¹² c)
9. Gravitational power output via precipitation ^{8,11,12}	1 · 10 ¹⁴	
Hydropower of rivers (drop of flow from a height of 300 m) ¹¹⁻¹⁴	3 · 10 ¹³	3 · 10 ¹³ (~ 10 ¹²)
10. Solar radiation incident on the desert ¹⁰	6 · 10 ¹⁶	
Power of solar batteries ^{15,20}		10 ¹² (< 10 ¹¹)
11. Wind power ^{4,8,9}	2 · 10 ¹⁵	
Wind-power installations ¹³		1 · 10 ¹¹ (< 10 ¹⁰)
12. Geothermal power ¹³	3 · 10 ¹³	
13. Tidal power ^{13,14}	3 · 10 ¹¹	3 · 10 ¹¹ (3 · 10 ¹¹)
Tidal stations ^{13,14}	1 · 10 ¹³	6 · 10 ¹⁰ (6 · 10 ¹⁰)
14. Total renewable power	1.7 · 10 ¹⁷	5 · 10 ¹³ (> 10 ¹²)
15. World-wide human consumption of energy (1978) ^{24,27}	1 · 10 ¹⁷	

a) For stable existence of mankind in the present-day biosphere.

b) The observed fluctuations in the average global temperature of the Earth over a period of several decades constitute ~0.1 K, which corresponds to variations in the energy flux ~0.1%, i.e. ~10¹⁴ W (from the relation $J = \sigma T^4$, $dJ/J = 4dT/T$). It is natural to assume that the removal (for example, into the deep layers of the ocean or by melting ice), generation (by additional energy sources), or redistribution on a global scale of heat amounting to not more than the average level of the fluctuations are allowable. Then, the allowable power derivable from heating deep ocean water in the next few decades, assuming an efficiency ~1% $\leq \Delta T/T$ with $\Delta T \leq 10$ K, amounts to ~10¹² W.

c) See Section 12.

d) The available power is limited by reserves of the materials necessary for constructing solar batteries and the energy consumed in constructing the batteries and maintaining them in working order. The allowable power is limited by the allowable distribution on a global scale of the power of solar radiation.

The photosynthetically active solar radiation (PAR) has wavelengths varying from 400 to 700 nm with an intensity of 0.43J at the Earth's surface.^{18,20} The continuous canopy of multilayered vegetation absorbs on the average $J_0 = 0.8$ PAR.¹⁸ For this reason, the fraction of the solar energy β , used by plants for photosynthesis, equals

$$\beta = \frac{J_0}{J} = 0.43 \cdot 0.8 = 0.35.$$

Green plants, which absorb visible solar radiation J_0 in the biomass of photosynthesizing organs B_0 , produce organic substances P_0 , the gross primary production (Fig. 2). For each mole of CO₂ that is bound, 8 moles (einsteins) of PAR photons are absorbed and 114 kcal are stored²⁰ in the synthesized organic compounds. Assuming that the average wavelength of the absorbed photons equals 600 nm, we obtain that 8 moles of photons have an energy equal to 400 kcal.²⁰ From this, we find that the theoretical maximum for the possible efficiency of photosynthesis is given by 114/400 ≈ 0.3 .²⁰ Therefore the efficiency for transforming PAR

into the gross production of photosynthesis $\alpha_0 = P_0/J_0$ cannot exceed this value:

$$\frac{P_0}{J_0} = \alpha_0 \leq 0.3, \quad \frac{P_0}{J} = \beta \alpha_0 \leq 0.1.$$

Part of the stored solar energy is released within the plant with biomass B_1 by way of oxidation in the process of respiration R_1 of the plant and subsequent dissipation of energy in the form of heat. The remaining energy P_1 , the net primary production, is stored in the net mass added to the plant and is used by heterotrophic organisms (see Fig. 2).

The coefficient $\alpha_1 = P_1/P_0$ corresponding to the transformation of the gross production into net production averaged over the entire biosphere equals 0.5 and varies from 0.8 to 0.3 for different plants.^{1,15} This means that the energy flux passing through plants is decreased by a factor of 2. The intensity of net production P_1 by photosynthesis is limited by the condition²⁾

$$\frac{P_1}{J} = \beta \alpha_0 \alpha_1 = \eta_{ph} \leq 0.05. \quad (3)$$

Table II displays the values of the average and maximum efficiencies observed under natural conditions for gross and net production by photosynthesis per year and over short periods of time during intense daytime photosynthesis.

The observed maximum values are close to the theoretical values.^{18,20,21} Average annual values of the

²⁾At the present time, the process of photosynthesis is traced by the cycles of chemical reactions beginning with the photo-reaction and ending with the fixation of carbon dioxide. However, the complete energetics of these reactions is unclear. Only the initial photon energy and the energy that is stored in the synthesized organic compounds are well-known. The gross production of photosynthesis (P_0) is determined experimentally from the fluxes of the basic elements absorbed from the environment, excluding energy. The net production $P_1 = P_0 - R_1$. Respiration R_1 is determined by the products of the decomposition of organic compounds in the surrounding medium. The net production P_1 is measured directly. Respiration is difficult to measure because of the necessity of separating simultaneous and oppositely directed fluxes of substances absorbed by and excreted from the organism. This difference can be determined by using tracer elements (radioactive or having a different isotopic composition) and a complex sequence of light and dark time intervals.^{18,20} However, such measurements do not take into account the possibility of energy processes occurring within the photosynthesizing organs in a closed lossless cycle without the use of substances from the environment, excretion into the environment, or noticeable transport within the organism. Such transformations of energy, which can attain a power close to that of the total absorbed PAR, should be included in the metabolism of plants. As a result, due to the large difference between the temperature of the Earth T and that of the Sun T_s , the true efficiency in the use of solar energy by plants can be close to the thermodynamic limit $(T_s - T)/T_s \sim 0.95$. In this connection, we have denoted the total solar PAR in the production block B_0 (see Fig. 2) absorbed and not stored in the gross production P_0 in the same way as in the remaining blocks by the letter R_0 , keeping in mind that this energy is removed from the organism after a large part of it has possibly been used in the metabolism of the photosynthesizing organs of plants, thereby storing energy in the end products of photosynthesis.

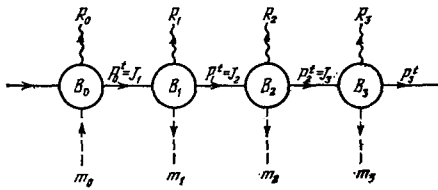


FIG. 2. Energy flux at various trophic levels. J_i —consumption, R_i —respiration, P_i^t —total output energy, B_i —biomass; $i = 0$ denotes the photosynthesizing organs of plants, $i = 1$ denotes all plants, $i = 2$ denotes herbivorous heterotrophs, and $i = 3$ denotes carnivorous heterotrophs.

efficiency of photosynthesis close to maximum values are observed for specific cultured (sugar cane, corn, sorghum^{1,20,21}) and wild (eucalyptus²⁰) plants, as well as for entire ecosystems (tropical rain forest,¹ tropical swamp,¹⁰ and marine estuaries and reefs¹⁰).

4. EXPENDITURE OF SOLAR ENERGY ON TRANSPIRATION

Transpiration, evaporation from the surfaces of leaves, participates in the metabolism of a plant, providing for the uptake and distribution of nutritive substances and water from the soil with the aid of capillary menisci in the leaves and osmotic pressure in the cells. The energy involved in the uptake of sap constitutes, however, not more than one one-thousandth of the energy required for transpiration of the same quantity of water, the main function of which is to cool the leaf to an optimum temperature.

It has been established experimentally that for all plants on land the average annual net production P_1 is proportional to the amount of transpiration.¹ The ratio of this quantity to the growth increment expressed in terms of dry mass (d. m.) is called the coefficient of transpiration:

$$k_d = a_r \rho E / P_{1d} = \frac{k_d a_r \rho E}{P_1}, \quad (4)$$

where a_r is the fraction of the total evaporation ρE from unit surface area that constitutes transpiration and K_d is the caloric value of the dry organic mass. The net primary production P_1 is expressed in W, while the rate of evaporation E is expressed in m/s (or in mm/yr). For many wild and agricultural crops, $k_d = 500$,^{1,22} i. e., in order to synthesize 1 t of dry organic plant matter, 500 t of water are required. For comparison: factory production of 1 t of organic matter requires 3,500–5,000 t of water.²³

TABLE II. The efficiency of photosynthesis (in %) for gross P_0/J and net ($P_1/J = \eta_{ph}$) primary production with respect to the total flux of solar energy (J).

Efficiency in using solar energy	Annual average for the entire Earth ^{1,4,10}	Observed annual maximum for individual species ^{1,10,20}	Observed diurnal maximum for individual species ²¹	Theoretical maximum
P_0/J	0.2	2.5	6.9 ^{a)}	10
P_1/J	0.1	1.4	4.6	6.6 ^{b)}

^{a)}The values were computed assuming that respiration equals $(1/3)P_0$.

TABLE III. The Earth's biosphere (dry mass).

Ecosystems	Plants							Consumers						
	$S, 10^6$ ha	d_0	$\mathcal{B}, 10^8$ ton	$\mathcal{P}, 10^8$ ton/yr	$B, \text{ton/ha}$	$P, \text{ton/ha, yr}$	τ, yr	$\beta_2^k, \%$	$\mathcal{B}_2, 10^7$ ton	$\mathcal{P}_2, 10^7$ ton/yr	$B_2^k, \text{kg/ha}$	$P_2^k, \text{t/ha, yr}$	$\tau_2^k, \%$	$\alpha_2^k, \%$
Forest	57	8	1700	84	300	14	21	5	70	47	120	1.5	10	
Savannah, steppes	24	4	70	20	24	8	3	10	30	38	125	0.8	15	
Plowed field	14	4	10	10	7	7	1	1	1	1	7	1	10	
Swamps, marches	2	7	30	6	160	30	5	10	2	3	100	0.7	10	
Lakes, rivers	2	2	0.05	1	0.2	5	0.05	10	1	1	50	1	10	
Deserts, tundras	50	0.7	20	2	4	0.4	10	5	1	1	2	1	10	
All continents	150	4.4	1800	120	120	8	15	7 (1)	100 (1)	90 (9)	70 (4)	1 (0.2)	11	
Open ocean	332	0.6	1	40	0.03	1	0.03	42	80	250	24	0.3	15	
Coastal waters	27	2	0.3	10	0.1	4	0.03	30	16	43	60	0.4	14	
Estuaries, reefs	2	8	2.6	4	14	20	0.7	15	3	8	150	0.4	13	
All oceans	360	0.8	4	50	0.1	1.4	0.08	40 (1)	100 (10)	300 (10)	30 (3)	0.3 (1)	15	
Entire Earth	510	1.7	1800	170	30	3	11	17 (1)	200 (10)	400 (20)	40 (2)	0.5 (0.4)	14	

Note. S denotes the surface area, $d_0 = \sum_i d_0^i$ is the leaf index (sum over all species of plants), d_0^i is the ratio of the photosynthesizing surface area of the plant to the area of the Earth's surface per plant (i. e. up to the nearest plants of the same species); the leaf index for aquatic ecosystems is estimated by the authors (see Sec. 9); \mathcal{B} and \mathcal{P} denote the total mass and production of live organisms, $B = \mathcal{B}/S$ and $P = \mathcal{P}/S$ denote the biomass and productivity (per unit area), $\tau = \mathcal{B}/\mathcal{P}$ is the biomass turn-over time, β_2^k is the fraction of the primary production consumed by wild consumers, $\alpha_2^k = \mathcal{P}_2/\mathcal{P}_1\beta_2^k$ is the efficiency with which the production of vegetation is transformed into animal production. The table is constructed according to the data in Ref. 10. The data enclosed in parenthesis concerns vertebrate animals in the wild.

The average value of k_d for mature plant information in any part of the biosphere equals 400 ,²⁴ ($k_i = a_r E / V_1 = k_d K_i / K_d \sim 100$). The total production on land can be estimated with the help of (4) using well-known values for the average evaporation $E = 500$ mm/yr ($5 \cdot 10^3$ t/ha · yr),^{11,12} the land area S (Table III), and the average value of \bar{a}_r . For the land areas that have been transformed by man, constituting $2S/3$, we have $a_r \approx 0.4$,²² while for the untouched areas $a_r = 0.9$.¹⁰ As a result, we have $\bar{a}_r = (2/3) \cdot 0.4 + (1/3) \cdot 0.9 = 0.55$. From this, we obtain for the net production on land

$$\mathcal{P}_1 = SP_1 = \mathcal{K}_d \frac{\bar{a}_r \bar{E} S}{k_d} = 6 \cdot 10^{13} \text{ W}, \quad \mathcal{K}_d = 4.5 \text{ kcal/yr}. \quad (5)$$

This value is close to the total production on land obtained by direct measurements (see Table III). The fraction of the solar energy expended on transpiration by plants (η_T) is given by

$$\eta_T = \frac{a_r L_w \rho E}{J}, \quad (6)$$

where $L_w = 0.6$ kcal/yr is the latent heat of evaporation of water. According to the ratio (4), η_{ph} is uniquely related to η_T :

$$\eta_{ph} = \frac{P_1}{J} = \frac{\mathcal{K}_d \eta_T}{L_w k_d} = \frac{7.6}{k_d} \eta_T. \quad (7)$$

In natural plant communities with $E = \bar{E}$ and $a_r = 0.9$, we obtain $\eta_T = 0.25$ and $\eta_{ph} = 5 \cdot 10^{-3}$. Thus, plants use up to 25% of the solar energy, up to 60% of all renewable water resources on land, and, to a significant degree, determine the climatic conditions on land.

5. TROPHIC ORGANIZATION OF THE BIOSPHERE

The flow of energy in the biosphere can be understood on the basis of sequential trophic layers (see Fig. 2).¹

The trophic levels of producers, the green plants, are described in Sec. 3. The net primary plant production P_1 is used by consumers (in the live form) and reducers (in the dead form), which constitute the next trophic level³⁾ with biomass B_2 . The organic matter that they absorb J_2 is expended by way of respiration R_2 on vital processes, and the output of transformed organic matter P_2 constitutes food for the upper trophic levels.⁶

The energy flow per unit Earth surface area for an individual, a population or a species i for a given trophic level n , forming a continuous cover or discretely distributed over the Earth's surface, are denoted by the usual capital Latin letters.⁴⁾ We will denote the total input (consumed) power as J_n^i , the power expended on respiration by R_n^i , and the total output power by P_n^i . These quantities are related by the conditions

$$J_n^i = R_n^i + P_n^i, \quad P_n^i = P_n^i + P_n^{ti}, \quad (8)$$

where P_n^{ti} consists of newly synthesized organic matter (production) P_n^i and the unassimilated part of the input organic matter (excreta) P_n^{oi} . Energy flows through the biomass of the organisms B_n^i , per unit Earth surface area. In order to describe completely the individuals, populations or species i in a given trophic level n , it is also necessary to know from which part of the Earth's surface the input energy flux is collected. We will define this quantity

$$d_n^i = \frac{s_n^i}{S_n^i}, \quad (9)$$

the coverage index of the organism, as the product of the density of organisms (per unit Earth surface area for the habitat) $1/S_n^i$ and the area (on the Earth's surface) covered by the live organism s_n^i , where S_n^i is the territory per single organism. For monocultures that cover the Earth's surface in a single continuous layer of organisms $d_n^i = 1$. If "organisms" are defined as individual photosynthesizing parts of plants, then $d_0 = \sum_i d_0^i$ will coincide with the leaf index.^{5), 10, 18} Specifying the coverage index makes it unnecessary to specify the number of organisms. The set of independent variables J_n^i , P_n^{ti} , P_n^i , B_n^i , and d_n^i adequately characterizes the energy relationships in the ecology of the species n, i .

The outgoing energy fluxes $P^t = P + P^e$ can be given with the help of the assimilation coefficients η and the

efficiency for transforming energy α

$$J - P^e = \eta J, \quad \frac{P}{J} = \alpha, \quad \alpha^e = \frac{P^e}{J} = 1 - \eta, \quad (10)$$

where ηJ is the assimilated part of the input energy flux (metabolism). For most of the organisms in the biosphere, the assimilation coefficient $\eta \sim 0.8$ and depends on the nutritional substances, decreasing in many cases to 0.4–0.3.⁶ The efficiency with which energy in food is transformed into production $\alpha \sim 0.1$ and is a small parameter,¹ but for unicellular organisms and bacteria α in some cases attains magnitudes of 0.3–0.4.^{8, 19} The coefficient $\alpha^e = 1 - \eta \sim 0.2$ characterizes the transformation of input energy into excreta, which serve as food for reducers.

In the stationary state, when the biomass in all the trophic levels of the ecosystem or in the biosphere as a whole does not change, the total outgoing energy flux for each trophic level must be completely consumed by the next trophic level:

$$\sum_i P_n^i = P_{n+1} = \sum_i J_{n+1}^i. \quad (11)$$

For what follows, it is convenient to introduce the fraction β_n^i of the overall consumption J_n that represents the species consumption J_n^i at a given trophic level n :

$$\beta_n^i = \frac{J_n^i}{J_n}; \quad \sum_i \beta_n^i = 1. \quad (12)$$

The presence of the small parameter $\alpha_n \sim 0.1$ or $\alpha_n^e \sim 0.2$ results in the fact that the energy flux in all chains decreases approximately by a factor of 10 on passing through each trophic level, forming an "ecological pyramid" with the producers (green plants) at the base, herbivores at the second stage of the pyramid, predators at the third stage, and so on. The smallness of α_n and α_n^e permits assigning each species to a definite trophic level according to the primary nutritional component. Indeed, if a species, for example, must feed equally intensively on both plant and animal food, the quantity of which in the ecosystem is ten times less than plant food, then its population will be determined by the amount of animal food and will coincide with the population of predators. For this reason, such a state for a species, if its population strives toward the maximum possible level, is unstable: it is advantageous for the species either to reject plant food and to switch completely to animal food, conserving the population, or, to increase the population by decreasing the consumption of animal food and switching to the herbivo-

⁶⁾In the ecological literature, reducers are usually not separated into trophic levels.^{1, 6} The presence of a small parameter $\alpha_n^e \sim 0.2$ allows for a clear separation of at least two trophic levels of reducers: $n=2$ and $n=3$. Reducers with $n=2$ feed largely on dead plant matter because $\alpha_f = 0$ and use a large part ($\beta_n^e \sim 0.9$) of the energy flux at the trophic level with $n=2$. Their production constitutes a large part of the matter consumed by consumers with $n=3$. Reducers with $n=3$ consume mostly the wastes of consumers and the bodies of dead reducers with $n=2$. The wastes of the next trophic level with $n=3$ are also consumed by reducers with $n=3$, but they constitute only a tenth of their ration. The separation of reducers into trophic levels allows writing Equation (11).

³⁾In ecology, reducers usually do not associate with consumers. However, for purposes of simplification, such an association is admissible.

⁴⁾We will use appropriate capital, italicized Latin letters in order to denote variables referring to individuals, populations, eco-systems, and the biosphere as a whole.

⁵⁾The coverage index referring to an assemblage of different organisms equals the sum of their coverage indices. The leaf index is the ratio of the photosynthesizing surface area of a plant and the Earth surface area that it covers.

rous trophic level. However, omnivorous animals, (for example, bears) can exist at a population level of predators that feed equally on animals and those parts of plants that constitute, as also does animal food, a tenth of the plant production (fruits, seeds, and so on). It is natural to place these animals in the trophic level of predators.

As the energy in organic substances is utilized, these substances are simultaneously decomposed into inorganic substances. The latter are removed into the environment and are once again used by producers for building up organic matter. This process is shown in Fig. 2 by the dashed lines, which represent the mass of the removed inorganic components (m_n). In order for the biosphere to exist in a stable state, the following relationship, which ensures that the circulation cycle of each chemical element is closed, must be satisfied:

$$m_0 = \sum_{n=1}^{n_{\max}} m_n,$$

where m_0 is the mass of the chemical elements used by producers for building up the organic production.

Living organisms have a fixed structure with strictly defined ratios for the elements of which they consist. Therefore, a deficiency of one of the elements will limit the synthesis of all the live organic matter (Liebig's law).

6. CONSUMPTION AND PRODUCTION OF BIOMASS IN THE BIOSPHERE

The primary product of photosynthesis has a caloric value of 4.2 kcal/g of dry weight. The primary production consists of carbohydrates (4.2 kcal/g), proteins (5 kcal/g), and fats (9.3 kcal/g) and has a total caloric value for the dry biomass (\bar{K}_d) of 4.5 kcal/g. The entire subsequent flow of energy in the biosphere occurs via multi-stage consumption, assimilation, and oxidation of these organic substances. In order to convert the live (B_l) and dry (B_d) biomass into energy units (B) the following coefficients^{7,1,10} are used:

$$B = K_d B_d = K_l B_l, \quad \bar{K}_d = 4.5 \text{ kcal/g} = 6.0 \cdot 10^2 \text{ W} \cdot \text{yr/t}, \quad (13)$$

$$\bar{K}_l = 1 \text{ kcal/yr} = 150 \text{ W} \cdot \text{yr/t}, \quad 1 \text{ W} \cdot \text{yr} = 8.8 \text{ kWh}.$$

Table III shows the biomass and the production for the most important components of the biosphere (up to the year 1900) according to the data in Ref. 10. All the numbers deviate by not more than 30 to 50%, and on the average by 10 to 20%, from the data obtained by other researchers in many studies using different methods.^{1,10,25,26-31} For this reason, these deviations may be considered to be the errors in the cited quantities. The data enclosed in parentheses on the graph for consumers correspond to herbivorous vertebrates in the wild. The consumption by vertebrates on land is estimated from the data in Refs. 19, 32-42 and their biomass and production are computed according to the

⁷⁾The value of \bar{K}_l used corresponds to a water content of 80% in the organism. For animals, K_l depends on a variable fat content and in many cases attains 2 kcal/yr.¹

formulas in Secs. 7 and 8 of this article. The production of vertebrates in the ocean is taken as equal to 10 times the present-day world fish catch,²² their biomass is taken as equal to the annual production ($\tau_2 = 1 \text{ yr}$),²² and their consumption is taken as being a factor of $\alpha_2^{-1} = 10$ greater than the production.²²

As can be seen from Table III, in a stable biosphere on land, consumers on the average consume only $\beta_2^{\text{g}} = 7\%$ of the production (nowhere greater than 10%), and the remaining energy flow from the net primary production moves along the chain of reducers that consume 93% of the dead production on land. In the ocean, due to the fact that the dead remains sink to the bottom, a significantly larger energy flow passes through the consumer chain ($\beta_2^{\text{g}} = 40\%$).

The biomass of dead organic matter on land (mainly soil humus) constitutes $2 \cdot 10^{12} \text{ g}$ (excluding coal, oil, and gas) and coincides with the amount of live biomass.²⁵ The amount of dead organic matter stored in the ocean, $4 \cdot 10^{12} \text{ t}$, is twice as great as on land. The overall biomass of live and dead organic matter on Earth equals $8 \cdot 10^{12} \text{ t}$ of dry weight or $4 \cdot 10^{12} \text{ t}$ of carbon and in order of magnitude coincides with the stored amounts of coal, $7 \cdot 10^{12} \text{ t}$ of carbon (the stored amounts of oil and gas is $1.3 \cdot 10^{11} \text{ t}$).^{2,14} Combustion of all this organic matter ($\sim 10^{13} \text{ t}$ of carbon) will bind only 2% of the atmospheric oxygen, of which there is approximately 10^{15} t in the atmosphere. The stored amount of organic matter dispersed in sedimentary rock is of the order of $(5-9) \cdot 10^{15} \text{ t}$ (Refs. 2 and 31) and is sufficient to bind all atmospheric oxygen. This confirms the biogenic origin of atmospheric oxygen, part of which has been expended on oxidation of volcanic eruptions.³¹

7. LIMITS ON THE SIZES OF ORGANISMS

Due to the uniformity of the distribution of solar energy, on the average, all ecological variables expressed per unit surface area are independent of the horizontal dimensions of organisms. For this reason, it is possible to express the sizes of organisms as a function of only the height l , which can be determined knowing the mass of the organism M and the area which it covers s . The density of organisms equals the density of water within several percent, and therefore⁸⁾

$$M = \rho l s, \quad \mathcal{E} = K_l M, \quad \bar{K}_l \rho \approx 150 \text{ W} \cdot \text{yr/m}^3, \quad (14)$$

where s is the coverage of the organism on the Earth's surface, l is the effective height, \mathcal{E} is the energy content of the organism,¹³ and $K_l \rho$ is the specific caloric value of the live mass per unit volume. For mobile organisms that have a compact shape $s \sim l^2$ and all dimensions have the same order of magnitude so that the size can be determined from the mass: $l = (M/\rho)^{1/3}$.

The consumption frequency ν (the specific consump-

⁸⁾Heterotrophic consumption is determined mainly at the second trophic level of herbivores. For this reason, in this and the following sections, for simplicity, the index for the trophic level $n=2$ and the species index i , which is retained only when necessary, are omitted.

tion capacity of the organism per unit energy contained in the organism) is connected in the following manner with the consumption of the entire organism j , with the consumption of the organism per unit coverage j , and with the consumption rate v :

$$j = \frac{v}{s}, \quad v = \frac{j}{\rho} = \frac{v}{l}, \quad v = \frac{j}{K_I \rho}; \quad (15)$$

ν has the dimensions of frequency and determines how much energy, expressed in multiples of the energy content of the organism, the organism utilizes per unit time, while v is the consumption rate, which has the dimensions of speed and determines the rate at which the consumed organic material enters the organism per unit of Earth surface area which it covers (or through the average cross section of the organism for mobile animals). For example, for man $\nu \sim 10 \text{ yr}^{-1}$, $v \sim 4 \text{ m/yr}$. In a similar manner, it is possible to introduce the rate of total heterotrophic consumption

$$V_1 = \frac{\sum_i j^i}{K_I \rho} = \frac{P_1}{K_I \rho}, \quad (16)$$

equal to the rate at which all types of vegetation are added per unit Earth surface area. This rate, in contrast to the consumption rate of an organism, will be denoted by a capital letter.

For animals, the consumption rate of an organism depends weakly on size and is one of the basic characteristics of the organism. For a fixed consumption rate v , the consumption frequency ν decreases with an increase in size l (15).

Vital processes can proceed only within certain limits for the magnitudes of ν , ranging from ν_{min} to ν_{max} . Below ν_{min} , the inflow of energy is insufficient to maintain life and above ν_{max} the rates of chemical reactions are not high enough to process all the incoming energy. Since the essential biochemical organization of all live cells is the same, the order of magnitude of the quantities ν_{min} and ν_{max} is approximately equal for all live matter^{1,6,21,22,32-36}.

$$10^{-1} \text{ yr}^{-1} \sim \nu_{\text{min}} \leq \nu \leq \nu_{\text{max}} \sim 10^4 \text{ yr}^{-1}. \quad (17)$$

Equation (15) and the inequality (17) permit the determination of the limits to the sizes of different groups of live organisms, if their consumption rate v is known.

The average consumption rates for bacteria, fungi, simplest unicellular and multicellular plants are $v = 10^{-3} \text{ m/yr}$,^{18,35,36} from which we obtain the limits for the sizes of bacteria, fungi, and plants: $10^{-7} \text{ m} \leq l \leq 10^2 \text{ m}$. The limits obtained correspond to those observed for bacteria, fungi and algae, but seem to contradict the observations for higher plants. As follows from Table III, the average biomass of the continuous forest cover ($d_1 \geq 1$) constitutes $B_d \sim 300 \text{ t/ha}$ of dry matter, i. e., $B_l \sim 1000 \text{ t/ha} = 0.1 \text{ t/m}^2$ of live mass, which corresponds to a layer height of $L_1 \sim 10^{-1} \text{ m}$. However, most ($\sim 90\%$)^{10,25} of the biomass of a forest consists of cellulose in the trunks and branches that is devoid of consumption fluxes so that we obtain, for the layer of metabolically-active organic matter in a forest, a thickness $l_1 \leq 1 \text{ cm}$. This corresponds to the limits presented above.

The horizontal dimensions of fungi and plants are not limited, and for this reason, the absence of competition between different parts of a single plant or fungus and the possibility for concentration of energy flows in individual organs (such as plant shoots and the reproductive organs in fungi), up to rates that are tens and hundreds of times greater than the average ($\bar{\nu} \sim 10^{-3} \text{ m/yr}$), resulting from an insignificant decrease in the energy flows in the working organs (roots, leaves, mycelia) often leads to greater competitiveness for organisms with greater horizontal dimensions compared to a group of independent organisms that occupy the same surface.

The consuming plant layer can be increased only by increasing the efficiency of photosynthesis, which, during the process of competitive evolution of plants, attained the maximum possible global level hundreds of millions of years ago. The minimum thickness of the plant layer, which leads to complete absorption of visible light and to the normal amount of photosynthesis, is of the order of $L_{\text{min}} \sim 3 \cdot 10^{-7} \text{ m}$.¹ A further decrease in the layer thickness leads to increasing transparency of photosynthesis decreases, which leads to a decrease in the rate at which new matter is added to the net primary production. When there is a deficiency of biogenic material, it is possible to build up a biomass of plant (and heterotrophic) layers with an overall thickness $L \sim 10^{-6} \text{ m}$, capable of ensuring normal photosynthesis and closed circulation of biogenic material, for which $\sim 1 \text{ g/m}^2 = 10 \text{ kg/ha}$ of live organic matter is required. A forest with a layer thickness $L_1 \sim 10^{-1} \text{ m}$ requires 10^5 times more biogenic material for building up its biomass than the minimum plant layer. Thus, the presence of forests attests to the lack of any limitations due to biogenic material (but the absence of forests does not mean a deficiency in biogenic material; it only indicates a lack of moisture).

Animals can increase their consumption rate by perfecting methods of assimilation, which allows them to increase their dimensions and their competitiveness in the competition for food resources. The appearance of the digestion and circulation systems, active respiration, and so on permitted increasing the consumption rate of multicellular animals. Poikilothermal ("cold-blooded") multicellular animals have average consumption rates $v \sim 3 \cdot 10^{-1} \text{ m/yr}$.^{34,38} The limits on their dimensions are $3 \cdot 10^{-5} \leq l \leq 3 \text{ m}$. This range is completely occupied by live organisms ranging from insect eggs to the whale shark and the giant reptiles.^{35,38} Homoiothermal ("warm-blooded") animals (mammals and birds) have attained the greatest possible biological consumption rates $v \sim 10 \text{ m/yr}$. For these animals, $j \sim 10^3 \text{ W/m}^2$ is of the order of the solar constant; for bacteria, fungi and plants $j \sim 0.1 \text{ W/m}^2$, while for poikilothermal animals $j \sim 30 \text{ W/m}^2$. This increase is attained at the expense of an increase in the body temperature approaching the limits at which proteins are decomposed.³² The allowable dimensions of warm-blooded animals turn out to be the largest in the biosphere: $10^{-3} \leq l \leq 10^2 \text{ m}$. In reality, warm-blooded animals occupy a lower range from 10^{-2} m (humming birds and shrews) to 6 m (the whale). The limits of this range

are determined by the impossibility of maintaining a stable thermal equilibrium outside these limits.⁴⁰

Thus, changing the consumption frequencies ν by 5 orders of magnitude from 10^{-1} yr^{-1} to 10^4 yr^{-1} and the consumption rates v by 4 orders of magnitude from 10^{-3} m/yr to 10 m/yr gives the possibility for building up organisms with dimensions l ranging over 9 orders of magnitude from 10^{-7} to 10^2 m . The size distribution of animals that had at any time existed on Earth encompasses a range of l from 10^{-7} to 6 m .

8. DEPENDENCE OF ENERGY CONSUMPTION ON THE DIMENSIONS OF ORGANISMS

The height of organisms l (14), the consumption rate per unit coverage on the Earth's surface v (15), the consumption fraction β (12), and the two coefficients η and α (10), the assimilation and ecological efficiencies, respectively, form five independent variables that that are uniquely related to the variables used in ecological studies: J, P, P^e, B, d (8), (9). The biomass B (in energy units) and the coverage index d are related in the the following manner to $v, \beta,$ and l (15), (16), (13):

$$B = \frac{\beta P_1}{v}, \quad d = \frac{B l}{P_1} = \frac{\beta l^2}{v}, \quad (18)$$

where the species index i and the number of the trophic level $n=2$ are omitted, while P_1 is the total consumption equal to the total production of plants.

Summation of the consumption by all species of a given size l allows for the determination of the distribution of energy consumption by organisms of different sizes at any trophic level, which is important for understanding the relationships between the population of organisms of different sizes and evaluation of their role in the biosphere.

The distribution of energy consumption as a function of l varies over a characteristic range of dimensions of the order of the sizes of organisms that it describes, i. e., over a range $\Delta l \sim 10^{-6} \text{ m}$ for unicellular and $\Delta l \sim 1 \text{ m}$ for large animals. For this reason, the distribution density can be given a meaning for the relative range $d l/l$ and depends on $x = \ln(l/l_0)$.⁹⁾ We will define the consumption distribution density as a function of size as follows:

$$\beta(z) = 2.3l \frac{1}{\Delta l} \sum_i^{l+\Delta l} \beta^i, \quad \int \beta(z) dz = 1, \quad z = \log \frac{l}{l_0} = 0.43x, \quad (19)$$

where $(1/\Delta l) \sum_i^{l+\Delta l} \beta^i$ is the fraction of the consumption for a unit size interval $d l$, which has the dimensions of inverse length; $\beta(z)$, which includes the phase volume l , is, just as β^i (12), dimensionless. This allows a transition from the linear scale for l to the logarithmic scale, which is usually used in the ecological lit-

⁹⁾In general, the dependence on size has the form $v(x), \beta(x) = (l/l_0)^b a(x) = e^{bx} a(x)$, where the function $a(x)$ varies more slowly than the exponent. At the present time, experimental data allow only the indices b for $\beta(x)$ and $v(x)$ to be determined; the function $a(x)$ is approximated by average constant values,^{32,34,39} as a result of which the equations for the functions take on the form $aM^{b/3}$, familiar in the ecological literature.

erature.

In Fig. 3a, the dashed line shows the behavior of the distribution $\beta(z)$, which was valid up to the beginning of the present century.¹⁰ The continuous line represents the present-day distribution, in which the fraction of the anthropogenic consumption (humans and domestic animals) in the range $-0.4 \leq z \leq -0.2$, $\Delta z = 0.3$ constitutes 25 to 30% of the consumption by heterotrophs on land. It is analyzed in detail at the end of the article. The histogram is constructed from empirical data on the consumption by reducers and by consumers on land (see Table III, Refs. 19, 33, 40-42).

As can be seen from Table III, 90% of the consumption by heterotrophs on land is accounted for by reducers (bacteria and fungi), which decompose the dead biomass of plants and which range in size from 10^{-6} m to 10^{-4} m . About 10% of the consumption by heterotrophs is accounted for by arthropodous consumers (mainly insects), which eat live plants, worms in soil, and other matter. They range in size from 10^{-4} m to 10^{-2} m . Vertebrates consume approximately 1% of the net primary production of plants on land.⁴⁰⁻⁴² These animals do not play a noticeable role in the distribution of energy flows in the biosphere, but their action is used by the biosphere for fine tuning the system.

In the ocean, a significantly greater energy flux flows through the consumers that eat live phytoplankton. Most of these consumers consist of small zooplankton. The consumption by vertebrates (fish), as on land, constitutes approximately 1%. For this reason, the distribution of heterotrophic consumption $\beta(z)$ in the ocean has the same form as on land, even though it results from a different ratio of consumers and reducers.

The distribution (see Fig. 3a) is one of the fundamental dynamic characteristics of the biosphere as a system. The factors that give rise to this distribution are as yet not completely understood.

The distribution of the consumption of energy by plants as a function of their dimensions has its own characteristics, determined by the conditions under which solar energy, water, and biogenic nutritive substances are absorbed. The distribution differs significantly on land and in aquatic ecosystems. On land, the maximum consumption occurs for the largest plants: trees. In the ocean, the greater part of the consumption of solar energy is accounted for by small unicellular algae.

Taking into account the normalization (19), the histogram in Fig. 3a can be approximated by a function of the form

$$\beta(z) = 1.16 \cdot 10^{-z/2} = 1.16 \sqrt{\frac{l_0}{l}} \quad (l_0 = 1 \mu\text{m}, z = \log \frac{l}{l_0}) \quad (20)$$

for the beginning of the century and $\beta(z) = 0.8 \cdot 10^{-z/2}$ (including the anthropogenic peak) at the present time. The distribution (20) corresponds to a drop in the consumption by an order of magnitude with an increase in the dimensions l by 2 orders of magnitude.

Let us now examine how the distribution is filled in

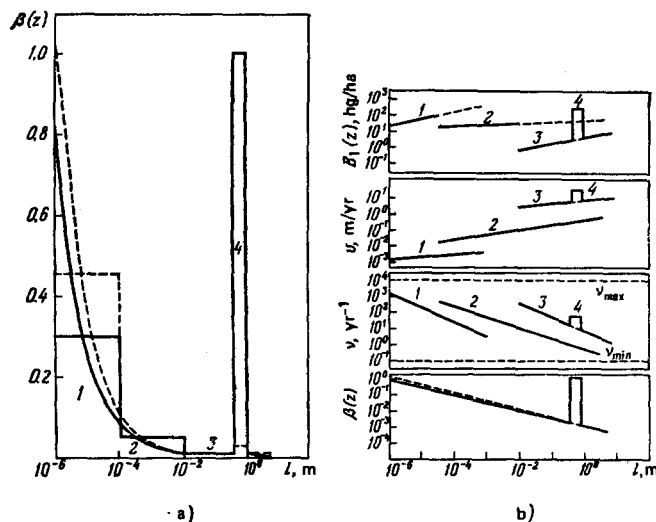


FIG. 3. Distribution showing the utilization of land by heterotrophic organisms as a function of the sizes of the organisms. The logarithm of the size of an organism $z = \log(l/l_0)$, where $l_0 = 1\text{m}$, $l = M/\rho_s$, s is the coverage of the organism on the Earth's surface, M is the mass of the live organism, $\rho \approx 1\text{t/m}^3$ is the density of the live organism taken as equal to the density of water, is plotted along the horizontal axis. The consumption fraction $\beta(z)$ per unit relative size dz is plotted along the vertical axis in Fig. 3a. The areas marked off in the histogram are as follows: 1—bacteria, fungi-saprophages (mold); 2—worms, mollusks, and arthropoda; 3—wild vertebrates; 4—total anthropogenic consumption by humans and domestic animals. The continuous line denotes the present-day distribution and the broken line denotes the distribution at the beginning of the present century. In Fig. 3b, the following quantities are shown plotted on a logarithmic scale along the vertical axis (from bottom to top): consumption fraction $\beta(z)$, consumption frequency $\nu(z)$, consumption rate $v(z) = l\nu(z)$, and the biomass density for organisms $B_1(z)$ per unit relative size dz ; 1—bacteria, fungi, simplest animals, 2—poikilothermal ("cold-blooded") animals, and 3—mammals.

by different groups of organisms. Figure 3b shows how the distribution $\beta(z)$ (shown in the lower graph using a logarithmic scale with the normalization condition becoming less obvious) is filled in by organisms that have different consumption rates and dimensions. The consumption frequencies $\nu(z)$ for bacteria, fungi and the simplest animals (graph 1), cold-blooded animals (graph 2), and warm-blooded animals (graph 3) are taken from experimental data.^{10,32,34,39} The functions $v(z)$ and $B(z)$ are constructed from the functions $\beta(z)$ and $\nu(z)$ using the relations (18) and (19) with $\bar{P}_1 = 0.5\text{ W/m}^2$. The consumption rates $v(z)$ depend weakly on dimensions ($v \sim l^{0.2}$)^{32,34,39} for each of the subdivisions

¹⁰The rates v and the frequencies ν , corresponding to the metabolism of a living organism, which is taken as equal to the basal metabolism (at rest at 20°C) for groups 1 and 2 and to twice the basal metabolism for group 3, are shown in Fig. 3, b. The lines v and ν for group 2, in reality, are divided into a series of closely lying lines with lesser slopes. The peaks 4 are obtained from the data on the total anthropogenic consumption of the products of the biosphere (excluding fossil fuels), the human biomass, and the biomass of domestic animals (see Section 11).

1–3. For this reason, assuming that the distribution $\beta(z)$ (20) holds over the entire range of sizes z , we obtain for the biomass in the energy expression $B(z)$, expressed per unit Earth surface area, a function of the form

$$B(z) = P_1 \frac{l\beta(z)}{v(z)} \sim \frac{\sqrt{l}}{v(z)} \sim l^{0.5}, \quad (21)$$

where P_1 is the net primary production of vegetation. The function (21) indicates that the total biomass of organisms for each of the groups 1–3 is determined by the largest organisms, while the consumption is determined by the smallest organisms. The dimensions in each of the groups (1, 2, 3) overlap by 1 to 2 orders of magnitude, but with the appearance of a new group the consumption of the previous group ceases to play a definitive role in the overall consumption, in spite of the fact that the biomass of this group can continue to increase. This justifies the choice of intervals in the histogram shown in Fig. 3a. The distribution $\beta(z)$ retains its shape and if a new group appears, the biomass of the previous group begins to increase more slowly than indicated by equation (21) or even decreases (dashed line), i. e., if the consumption of the preceding group in the overlap region decreases more rapidly than in Eq. (20).

The biomass density $B(z)$ is the product of the average biomass of species by the number of species per unit relative size interval dz . The latter quantity, as a rule, does not increase with increasing size.^{1,6} Apparently, the average biomass of mammalian species is constant over a wide range of sizes ($B_1^i \approx 200\text{ g/ha}$).⁴⁰ Therefore, in the mammalian range, $B(z)$ probably does not increase with an increase in size l , and for this reason, $\beta(z)$ in the range of mammalian sizes decreases with an increase in l more rapidly than according to Eq. (20).

9. IMMOBILE AND MOBILE ORGANISMS

The question arises as to why, in spite of the long period of time over which they have existed, primitive unicellular organisms did not yield to more highly perfected multicellular organisms and continue to form the foundation for the bioenergetics of the Earth. In order to answer this question, it is necessary to analyze the nature of consumption by mobile organisms, which turns out to be essentially different from the nature of consumption by immobile bacteria and fungi.³⁹

The flow of net primary production of plants is relatively uniformly distributed over the entire Earth with an average production P_1 and production rate $V_1 = P_1/K_t$, (see Table III) given by

$$\bar{P}_1 = 0.14\text{ W/m}^2, \quad \bar{P}_1 \text{ land} = 0.5\text{ W/m}^2, \quad P_{1\text{max}} = 5\bar{P}_1 \text{ land}, \quad (22)$$

$$\bar{V}_1 = 10^{-3}\text{ m/yr}, \quad \bar{V}_1 \text{ land} = 3 \cdot 10^{-3}\text{ m/yr}, \quad V_{1\text{max}} = 1.5 \cdot 10^{-2}\text{ m/yr},$$

where $P_{1\text{max}}$ is the average annual value of the production in the most productive parts of the earth, while V_1 is the increment to the biomass of plants over the course of a year per unit Earth surface area. In the stationary case and in the absence of any accumulation of organic matter, the consumption must occur at rates equal to the rate of production. The consumption rates

of bacteria and fungi are of the same order of magnitude as the production rates of plants averaged over the Earth \bar{V}_1 (22). For this reason, these organisms, which cover the Earth's surface with a continuous layer having a coverage index $d \geq 1$ [see (10), (18)], are capable of processing the entire production of plants while in the immobile state. Immobile organisms are considered here as organisms that do not have to move in order to survive, since their consumption does not exceed the primary production of a surface area equal to their coverage of the Earth's surface ($d \geq 1$) (these organisms also can move under the influence of external forces as well as independently). Mobile organisms are here considered as organisms that must move in order to survive, since their consumption is always greater than the primary production of a surface area equal to their coverage of the Earth's surface ($d < 1$) (these organisms can also be stationary, if they are located in a flow or create the flow).

Warm-blooded animals, for example, have consumption rates that are four orders of magnitude greater than the average production rate of plants (22). In order for such animals to provide for their food, consuming the entire production ($\beta^i = 1$), it is necessary for them to forage for the plant production in a territory that is 10^4 times greater than their coverage of the Earth's surface, i. e., the coverage index of such animals is $d \leq 10^{-4}$. We refer to species for which the consumption areas of individuals are contiguous as massive. The density of individuals of massive species in a consumption territory coincides with their density per unit Earth surface area in their habitat. Rare species have average individual densities per unit Earth surface area in their habitat that is much less than their densities in a consumption territory; their role in the energy flux is secondary and we neglect it here for simplicity.

The strategy of mobile animals is possible only due to the fact that plants accumulate their production as biomass. Mammals, for example, in using the entire primary production must eat within one hour the biomass of plants that has accumulated over the course of one year. If the production did not accumulate, mobility would be useless and consumption rates could not exceed the rate at which new production is added. Such a situation exists for plants that use the nonaccumulating production of the Sun, i. e., photons with zero rest mass. Plants cannot increase the absorption of photons above the fixed solar energy flux as a result of mobility, and for this reason, plants are immobile.

Phytoplankton in the ocean and in fresh water reservoirs are often equipped with a means for moving about (flagella, variability of buoyancy) and have a coverage index that is similar to that of mobile organisms, $d < 1$. This is related to the limitations placed on the flows of biogenic matter (CO_2 , O_2 , phosphorous, nitrogen, and so on) that are necessary for photosynthesis, respiration, and body building.⁴³ In order to ensure normal photosynthesis, it is necessary to collect flows of biogenic matter from a surface area that exceeds the coverage of algae on the water surface area. The pre-

sence of consumption areas for phytoplankton organisms leads to an unavoidable loss of photons and to a decrease in photosynthesis per unit water area, in spite of the normal amount of photosynthesis taking place per unit surface area of the organism. The average density of primary production in the ocean is 8 times less than the average density of primary production on land (see Table III). From here, we find that the average coverage index of marine phytoplankton (assuming that the average production density is proportional to the leaf index²¹) is $d_0 \sim 0.6$ ($0.13 < d_0 < 1$).

The emergence of feeding on accumulated biomass (and not on the increments) made it possible for the consumption rates to increase to magnitudes that greatly exceed the growth rate of plants. This led to the appearance of large organisms. The high consumption rates of large animals, which make their high mobility possible, require feeding on high-calorie, concentrated food. Large animals cannot provide for their energy needs by feeding on dead plant matter, detritus or excreta and consume more calorific and concentrated live plant and animal organic matter or the carcasses of other animals.^{32,68} For this reason, in contrast to immobile reducers, such as bacteria and fungi that decompose dead plant matter without horizontal transport of biogenic material and not harming plants in any way, large mobile consumers destroy the live biomass of plants and concentrate biogenic materials in their excreta, thereby increasing the nonuniformity in the distribution of biogenic materials on the Earth's surface. The main danger that is related to the action of mobile consumers on their food source consists of the possibility of consuming the entire biomass of plants and causing them to become extinct. A balance is achieved by the differential feeding of consumers and the development of protective mechanisms by plants. As a result, it turns out that for a given animal only an insignificant part of the net primary production of plants is edible. For an average biomass of a mammalian species $B_i^i = 210$ g/ha (Ref. 40) and animal size $l \approx 10$ cm, the coverage index $d^i = B_i^i / \rho l \approx 2 \cdot 10^{-7}$ and, therefore, the animal uses about $\beta^i = d^i v / \bar{V}_1 \text{ land} \sim 0.1\%$ of the net primary production. The smallness of the fraction of the production consumed by large animals is maintained also by the rigid structure of the higher trophic levels. The population of herbivorous animals is greatly limited and stabilized by predators, which consume them in quantities comparable to the size of their incremental growth. The reducers' share of the consumption of the production of herbivorous animals is less. For this reason, the entire complex organization of trophic interrelationships of large animals can be viewed as a single system, adjusted (in order to avoid disturbing the functioning of plants) to a low fraction β of consumption of vegetation.

In the size range of unicellular heterotrophs $v \sim \bar{V}_1$. Then, it follows from (18) that for them $d \sim \beta$. But, with an increase in size, β decreases and, therefore, d also decreases. For this reason, with an increase in the size of unicellular heterotrophs, mobility becomes necessary fairly rapidly. However, the main contribution to the utilization by heterotrophs of land

$[\bar{V}_1 \text{ km} \cdot \text{d}^{-1} \sim 3\bar{V} \text{ (22)}]$ is made by the smallest immobile heterotrophs. Thus, the greater part of the energy flows in the animate world passes through immobile organisms without horizontal transport of biogenic materials.

10. ENERGETICS OF MOBILE ANIMALS

Large animals that do not play a definitive role in the functioning of the biosphere play a basic role in human consumption. Man himself belongs to the class of large mammals. For this reason, it is necessary to examine in greater detail the nature of the bioenergetics of large animals.

Mobile animals assure their mobility by energy consumed as a result of mobility. As the size of an animal increases, the energy expended on mobility increases, while the fraction of the consumption by the animal β and, therefore, its coverage index d , must decrease, as follows from Fig. 3 and (18). For this reason, starting with some definite size, animals cannot forage over an ever-increasing territory, necessary for collecting food (because the index d is inversely proportional to the territory used). The territory ceases to increase, while the consumption fraction β (the load on the territory) increases. This undermines the food resources and must stop further increase in the sizes of animals.³⁹

Depending on the body size l and the speed of motion, the basic force resisting motion will either be friction against the Earth's surface or friction against air for

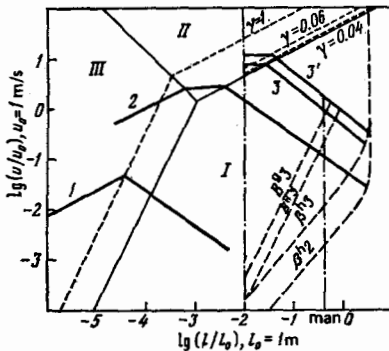


FIG. 4. Regions of allowable locomotion speeds for animals of various sizes. I-III—regions corresponding to various types of resistance to motion: overcoming the force of gravity (I), overcoming air resistance at a Reynolds number $Re \gg 100$ (II) and at $Re \ll 100$ (III). The fine lines bound these regions for $\gamma = 0.04$; drag forces coincide in pairs along these lines. The broken lines denote the boundaries of regions I, II, and III for different values of the coefficient of friction γ . The heavy lines indicate changes in the speed of motion as a function of the dimensions of the body with natural power output: simplest (1), poikilothermal ("cold-blooded") (2), homiothermal ("warm-blooded") (3) animals, and homiothermal animals with a doubled power capacity (3'). The broken lines show the minimum speeds required for moving over the territory being utilized: B^b3 for foragers and B^h3 for herbivorous mammals with constant mass per unit territory ($B = \text{const}$); β^h3 for herbivorous mammals and β^h2 for herbivorous reptiles with a constant consumption fraction ($\beta = 10^{-3}$). The dot-and-dash lines indicate the minimum sizes of warm-blooded animals and the size of human beings.

different values of the Reynolds number (Re).⁴⁴ As a result, there are three ranges for body sizes and speeds (Fig. 4). In region III (not occupied by large animals), the main force is Stokes' drag force in air, which is proportional to ul . In region II, the basic force is air resistance, which is proportional to u^2l^2 . This is the region of flight. In region I, the basic force is friction against the surface of the Earth D , which is proportional to the body weight: $D = \gamma W = \gamma g \rho l^3$, where γ is the coefficient of friction. The coefficient γ determines what fraction of the body weight is the force applied by the animal to overcome D , including the lift force and acceleration of extremities, swinging of the center of gravity, and so on. The minimum known value of $\gamma = 0.04$ is attained, for example, by horses³²; for walking by man, $\gamma = 0.06$.³³ Small animals do not always have a minimum value of γ , while large animals usually have minimum values as a rule. The lines drawn in Fig. 4 correspond to the power per unit coverage j developed by the simplest (line 1, $\gamma = 1$), poikilothermal (cold-blooded) (line 2, $\gamma = 0.04$), and homiothermal (warm-blooded) (line 3, $\gamma = 0.04$) animals with a vital power equal to twice the basic power (at rest)³⁴ and the line 3' corresponds to homiothermal animals with vital power equal to four times the basic power with $\gamma = 0.06$.¹¹⁾

Figure 4 also contains lines that correspond to the minimum speeds that are necessary for mammals to forage in the territory that they use. With a regeneration time of τ_1 for the consumed vegetation, which is distributed uniformly along the surface, the minimum speed of motion for an herbivore using a territory S in the stationary state equals

$$u = \frac{S}{l_{\text{eff}} \tau_1}, \quad l_{\text{eff}} \geq l, \quad (23)$$

where l_{eff} is the linear dimension of the area that the animal can use for food without moving about. Equation (23) can be rewritten in terms of the basic variables:

$$u = \frac{lv}{L_1 \beta} \left(\frac{l}{l_{\text{eff}}} \right), \quad (24)$$

$L_1 = V_1 \tau_1$ is the thickness of the layer of the vegetational biomass, V_1 is the rate of growth of vegetation, and v is the total consumption rate of the animal. The formula for u (24) is obvious because the time $\beta L_1/v$ for eating the fraction β of the vegetation over an area corresponding to the cross section of the organism equals to the time l/u for the organism to move over a distance equal to its own linear body dimensions with $l_{\text{eff}} = l$. The dashed lines in Fig. 4 correspond to (24). The lines B^b3 and B^h3 are drawn for constant biomass

¹¹⁾ The total power $j = j_0 + j_w$, where j_0 is the basic power (in the standardized rest state). The working power j_w is transformed into motive power with an efficiency $\sim 20\%$.³² Long-term existence usually is attained for $j_w \sim j_0$. Over short time intervals, an animal is capable of developing $j_w \sim 20j_0$ (with oxygen balance) and $j_w \sim 100j_0$ (with an oxygen debt). A human has a basic power of about 80 W, a subsistence power of about 140 W, and develops a power of up to 2 kW in long-distance running and up to 8–10 kW in sprinting.³²

of mammalian animals and consumption fractions β [see (18)] satisfying a distribution of the type of Fig. 3a [$u = l^2/L\tau_1$, $L = B_1/\rho$, $\tau_1 \sim 1$ yr (18), (22)] B^h3 is drawn for herbivorous animals with $B_1^h = 210$ g/ha (Ref. 40), B^3 is drawn for foragers of dispersed food with $B_1^3 = (1/3)B_1^h = 70$ g/ha (intermediate value between the biomass of herbivorous B_1^h and predatory $B_1^p \sim 0.1B_1^h$ mammals)⁴⁰; the lines β^h3 and β^h2 are drawn for constant $\beta = 10^{-3}$, β^h3 for mammals, and β^h2 for reptiles. The vertical (straight slope) part of the lines β^h3 and β^h2 corresponds to regions in which the total expenditure of energy on motion is much greater (much less) than the expenditure of energy in the rest state, $L_1 = V_1\tau_1 \sim 3$ mm, $\tau_1 \sim 1$ yr (22).

The dot-and-dash vertical lines correspond to the minimum sizes of mammals and birds and to human dimensions. It is evident that for the smallest dimensions the range of attainable speeds is greater than for the largest dimensions. Since, for existence, the speed indicated by broken lines is sufficient, it is evident that small animals have excess energy for activity. Animals with a body size close to 1 m can exist only in the range of high speeds and large expenditures of energy on motion. The larger animals in general cannot exist in the range of constant biomass density and constant consumption distribution, corresponding to that shown in Fig. 3a. Large animals unavoidably must increase their consumption fraction (in comparison with that required according to Fig. 3a), which increases the load on the vegetation. For this reason, large animals, in spite of the fact that an insignificant energy flux flows through them in the biosphere, exert a strong influence on the ecosystems. It is well-known that large animals determine the appearance of certain ecosystems, for example savannas.⁴⁵

Predators feed on the production of herbivorous animals, which is $\alpha^{-1} \sim 10$ times less than the consumption of the latter. For this reason, the territory used by predators is ten times greater than the territory of herbivorous animals of the same size.⁴⁰ At first glance, the permissible sizes of predators decrease in comparison with herbivorous animals in correspondence with Fig. 4. However, this is not so because the production of animals per unit of their surface area (αv) can be hundreds and thousands of times greater than the primary production on the same surface area (V_1). For this reason, a predator that feeds on game (or herds) comparable in size with its own dimensions can forage over a territory with l_{eff} (23) of the order of the distances between individual game animals (or herds) equal to the linear dimensions of the territory of the latter. This significantly decreases the speeds of motion necessary for predators (24), relaxing the limitations on their sizes.¹²⁾ A successful choice of food ob-

¹²⁾In the ocean, phytoplankton is distributed in a photic layer of thickness $H \sim 30$ m. The rate at which any mammal must move when feeding on phytoplankton in the open ocean with $l < H$ and $\beta \sim 10^{-2}$ would equal $u = Hv/L_1\beta = 360$ km/h, $v \sim 10$ m/yr, $L_1 \sim 10^{-5}$ m (see Table III). For this reason, feeding on phytoplankton is possible for $v \leq 0.1$ m/yr (which is of the order to magnitude of v for crablike organisms and smaller than v for fish).

jects allows a predator to live with a relative excess of energy and food due to the energy expended on motion by its prey, which perform the work of concentrating production.³⁹

11. FRACTION OF THE ENERGY FLOW IN THE BIOSPHERE USED BY MAN

In spite of all his special characteristics, man is still one of the species in the biosphere. According to his consumption, he is a mobile consumer, a large mammal, that retains the physiological features of his predecessors. The contemporary ecology of man can be better understood if we examine how it has changed over the course of the evolution of man.

A. Evolution of man's ecological niches

Man first evolved occupying the niche of a forager, a species with a wide spectrum of plants and animal products consumed as food. The animal food in the diet of a primitive forager corresponded to the smallness of the coefficient of ecological efficiency for transforming plant production into animal production, $\alpha_2 \sim 0.1$, and consisted of about one tenth of the overall consumption. The organism of a forager is adapted to the availability of an appropriate fraction of animal production and as a result does not have the capability to synthesize independently certain irreplaceable amino acids and fatty acids, which he obtains from animal food. Consumption of one tenth of the food in the form animal production became a necessity, which modern man also encounters.

Most of man's consumption consisted of plant production, mostly fruit, roots, and buds, which constitute a small fraction of the net primary production. The territory of the forager is of an intermediate size between the territory of a predator and that of an herbivorous mammal. Man (with a body mass of 60 kg) has a coverage index (5), (21) $d^2 \sim 1 \cdot 10^{-8}$, which corresponds to a territory $S^c \sim 500$ ha/person.⁴⁰ As is evident from Fig. 4, the size of a man is close to the upper limit for foragers. Man must expend more energy on motion than a four-legged animal with the same mass,³¹ and for this reason, the human forager is forced to exist in the high working power range with a narrow range of allowable speeds of motion (see Fig. 4). This required great activity. If the area of the territory suitable for the life of a primitive forager equals $1 \cdot 10^9$ ha (of the order of the surface area occupied in our day by cultivated fields), then the primitive population of the Earth constituted $N_t \sim 2 \cdot 10^6$ individuals. Under such conditions, man's ancestors existed for $2 \cdot 10^6$ years.^{45,46}

The possibility of using fire for heating and cooking food was discovered about $4 \cdot 10^5$ years ago.⁶ Combustion of organic matter outside the organism in quantities such that the caloric value of the matter combusted was twice as great as the caloric value of the food consumed⁴⁷ tripled the effective rate at which a man consumed organic production in comparison with mammals having an equal body mass. This allowed man, first of all, to move far to the north, and second, to

broaden the spectrum of the food he consumed, which now included plant products that could not be consumed before cooking. Fire, together with shelter and clothing, decreased the expenditure of biological energy on temperature control, but it did not free man from expending biological energy on motion. Specialization in hunting led to the fact that for hunting tribes these expenditures increased due to the increase in the territory required by the hunter. This specialization became possible due to the fact that the use of tools that could strike an animal at a distance and traps, as well as symbiosis with the dog, allowed man to compete successfully with large predators. Rapid progress in perfecting hunting equipment often led to over-hunting of game, especially as man assimilated new territories, where animals did not have time to adapt to him.⁴⁵ This undermined the hunting base, decreased the population of hunting tribes, and forced dispersal to new territories. The Earth's overall population increased at this time only as a result of the assimilation of new territories that were not suitable for life based on foraging, but the average population density remained constant or even decreased.

The discovery of animal husbandry and farming by individual peoples once again altered man's ecological niche in a fundamental way. Agriculture allowed man to broaden significantly the spectrum of plant matter he consumed as food at the second trophic level by including in his diet previously inedible production of new plants as a result of cooking by fire. Not all plants were edible by man, even after cooking. Of the edible plants, only an insignificant part of their production, mainly seeds, could be used as food. As a rule, these are plants that do not build up a large mass in the wild. Man learned to displace all plants that were unsuitable for food and to cultivate monocultures of edible plants by specially working the earth. At the same time, the harvest of edible production from a unit area β^a increased by a factor of 50 to 100, as a result of which the area required for life decreased to a few hectares per person. The main characteristic of plowed fields consists of the fact that man consumes such a fraction of the biomass of the production of a plowed field that the production can no longer sustain itself naturally. Man is forced to assume the functions of reproduction annually or once in several years (for crops involving many years), working, fertilizing, and sowing the arable land.

However, man could not completely cross over to the second trophic level. As a result of his physiology, inherited from that of a forager, he must have a prescribed minimum of animal protein, which the forager obtained in adequate quantities in his territory. The farmer could not acquire the required number of animal proteins by hunting in an area reduced in size by a factor of 100. Very often, the farmer settled near rivers, lakes, and bays, and obtained the required animal proteins by catching fish. But, farming over large territories could emerge only together with animal husbandry. The essence of primitive animal husbandry consists of the domestication of animals for which man provides an existence in pastures without

competition with wild animals. At first, man used natural formations such as river flood plains, savannas, and steppes for raising cattle, and then gradually increased these lands by clearing forests. In contrast to natural lands, man-made fields and pastures require annual working (cultivation, sowing and so on), without which they are overgrown with plant species that are unsuitable for cattle. Man eliminates all predators on the fields and pastures, thereby becoming the only consumer of the domestic livestock. However, in contrast to plowed fields, meadows and pastures retain their ability to self-regenerate, if an allowable fraction of the biomass that grows on them is removed. Since the production of livestock is ten times less than its consumption, in order to obtain a tenth of his food in the form of animal production man must have a livestock biomass of the order of the biomass of people and the area of the meadows and pastures must be comparable to the area of the cultivated fields. This relationship is observed over the entire period of the existence of farming.

The motive energy, which the forager and the hunter expended on searching for food over great distances, is expended by the farmer on working a small plot of land. In order to increase production, man began to use the excess energy of domesticated animals and trained them to work in the fields as working livestock. The peasant always existed at the marginal edge of his energy requirements with very little free time. However, the farm provides man with a more stable consumption base than hunting. Farming provided a clear advantage only in those parts of the Earth that had a temperate climate, where life based on foraging was impossible because the production of vegetation ceased during the winter months.

Having increased the fraction of the consumed production (β^a) and feeding, as every mobile consumer, on the biomass of plants and animals, man constantly encounters the problem of a poor crop, over-grazing, and over-hunting. The biochemical cycles of elements on agricultural lands, especially on pastures, turn out to be seriously disrupted, and as a result, after a certain amount of time the productivity of the land drops and man must move on to new lands, leaving the cultivated lands to the natural ecosystems that restore the normal circulation of substances over a certain period of time (slash-and-burn agriculture). In some locations that have a natural influx of nutritive substances (the deltas of large rivers) or large quantities of stored nutritive substances (chernozem), it is possible to farm the land for a long period of time without a decline in its fertility. Stable civilizations arose in such locations (the Nile, Tigris, and Euphrates deltas, and the Yangtze and Indus River basins). Without such conditions, civilizations invariably declined (for example, the civilizations in Central America).

Farming, marking man's transition to a lower trophic level, made possible the assimilation of much larger new territories in the temperate and northern zones and an increase in Earth's population by approximately a factor of 20 compared to the foraging level.²²

The necessity for periodically changing the worked land led to fluctuations in the population level and to stiff competition for land suitable for grazing and cultivating.

B. The ecology of modern man

Mankind, both with respect to body structure and nutrition and way of life, is one of the most diversified species on earth. Populations with different ecological niches have always existed simultaneously on this planet. Even now, in spite of the global development of means of information, transportation and trade, foragers, hunting peoples, primitive farmers and cattle raisers, as well as industrial-urban and industrial-agricultural countries exist on Earth.

The scientific-technical revolution (STR), which began about 200 years ago, brought about a fundamental change in man's life. The ecological significance of STR consists of the discovery of the possibility of using nonbiological energy sources for working agricultural lands and transporting people as well as food. Almost all territories that are suitable for the existence of man possessing additional energy were assimilated over a short period of time. With unlimited land resources or a fixed population, the use of additional energy would allow man to increase the area of the territory on which food was grown, to decrease the consumption fraction β^a per unit area, and to decrease to optimum values the pressure on the products being consumed. At the same time, there would be a decrease in the load on man's biological power, which he could use for other activities that are unrelated to the production of food. Man attained a surplus of power and a potential abundance of food resources.

However, the STR also permits increasing the consumption fraction β^a per unit area, which leads to an increase in the population density. Niches with a high population density and with equal energy expenditures per individual unavoidably displace niches with a lower density. For this reason, the increase in the per capita expenditure of energy led to a global increase in the population density and a rapid increase in the overall population of the Earth. From the time that agriculture and animal husbandry were discovered to the beginning of STR, the population of the Earth grew slowly and increased by a factor of 20 in 10^4 years.⁴⁶ Over the two hundred years of additional energy input, the productivity of cultivated lands $J^a = \beta^a P_1$ increased by a factor of 3 [mainly due to an increase in the consumption fraction β^a with constant net primary production P_1 (Refs. 1, 22, 46)] and the area of the worked lands doubled in size. This led to an increase in the population level, which at present amounts to $4.5 \cdot 10^9$ people, by approximately a factor of 5.⁴⁶ As a result, it became impossible for people to exist on the newly assimilated territories as well as on the traditionally occupied territories without additional energy expenditures. The present-day energy consumption of mankind, which constitutes 10^{13} W (2.5 kW/person),^{2,17} is based on non-renewable fossil fuel resources (coal, oil, and gas)^{2,14} and exceeds by approximately an order

of magnitude the power sustained by renewable energy sources (see Table I). In developed countries, this power is distributed in the following manner¹⁷: approximately equal power (30%) is expended on (1) heating buildings and other forms of temperature control, (2) heavy industry, (3) transport; approximately 10% is used for producing, preparing, and distributing food (including farming and the agricultural industry), and other forms of consumption of the products of the biosphere (removal of wood, catching fish, and so on), of which the direct expenditure of useful power on cultivated fields constitutes several percent. The expenditures of useful power on the cultivated fields in the world on the average constitutes one-half^{1,25,44} the caloric value of the edible crop, equal to $9 \cdot 10^{11}$ W.^{13,10} With a technological efficiency of ~25%, the total power tapped in the fields has an order of magnitude of $1.8 \cdot 10^{12}$ W. The power in the agricultural industry, including the production of fertilizers and individual food preparation, is twice as great as the expenditures of useful power on fields⁴⁷ and has an efficiency of energy utilization of the order of 80%.¹⁷ (The removal of wood absorbs approximately one-tenth of the caloric value of the harvested forest, equal to $2 \cdot 10^{12}$ W.^{10,22} The power expended on fisheries in the ocean is close to the caloric value of the fish caught, equal to 10^{10} W.)¹⁰ As a result, the overall energy expenditures on consuming the products of the biosphere constitute $\sim 3 \cdot 10^{12}$ W, i. e., 30% of the overall energy consumption. The consumption of nonrenewable fossil fuel resources gave mankind the possibility to increase its share of the consumption of the plant production in the biosphere.

The part of the primary production used by man (indirectly or through the domestic animals) constitutes in the overall flow of energy in the biosphere the anthropogenic channel, which now includes the production of cultivated lands, meadows, pastures, exploited forests, and the ocean.

Let us examine the flow of production that enters into this channel.

C. Cultivated lands, pastures, and the ocean

The power associated with the consumption of food by people (H) can be estimated from the population $N = 4.2 \cdot 10^9$ (Ref. 46) and the average consumption per person [$2500 \text{ kcal/day} = 120 \text{ W/person}$ (Ref. 46)], which varies under different conditions from 2000 (=100 W/person) to 3000 (=150 W/person) kcal/day. Therefore

$$H = 5.0 \cdot 10^{11} \text{ W}; 4.5 \cdot 10^{11} \text{ W} < H < 6.2 \cdot 10^{11} \text{ W}.$$

Let us now estimate the consumption of food by people together with their domestic animals. Since the biomass of domestic animals (livestock) on Earth \mathcal{B}_L is five times greater than the human biomass \mathcal{B}_H (Refs. 10, 48) their overall consumption can be estimated as

¹³⁾The expenditure of energy per unit of production consumed by man equals the caloric value of edible food, since half of the crop is fed to livestock (see below, Fig. 5).

$$HL = 6H = 3 \cdot 10^{12} \text{ W.}^{14),1}$$

The consumption of the animal production of the ocean constitutes $7 \cdot 10^7$ t/yr of live mass ($1 \cdot 10^{10}$ W), which is 10% of the consumption of animal foods by mankind and 2% of the total food consumed by people.^{1,49} This consumption, apparently, is greater than one-tenth the entire production of vertebrates in the ocean and is close to the limit of the allowable catch of fish.⁴⁹

Thus, humans obtain 87% of their food from cultivated lands, 11% from meadows and pastures,¹⁵⁾ and 2% from the ocean.

The overall consumption of the production of cultivated lands, meadows, and pastures is not limited to food consumption. While harvesting cultivated fields, man removes the entire production of plants above ground and part of the root crop, which constitutes about 50% of the net production of a cultivated field \mathcal{P}_a .^{16),10} All the production removed from a cultivated field is primarily not returned to the consumers, but processed by man himself, burned,¹⁷⁾ and stored in various forms. The edible production of a cultivated field constitutes 13% (Ref. 10) of the net primary production of such a field, equalling $1.2 \cdot 10^{10}$ t of dry matter (d.m.) per year = $6.7 \cdot 10^{12}$ W. The surface area of cultivated fields is $S_a = 1.4 \cdot 10^9$ ha.¹⁰ The production density of cultivated fields $P_a = 8$ t (d.m.)/ha · yr and coincides with the average production density on land

¹⁴⁾This estimate does not take into account the difference between the food assimilation coefficients η (Ref. 10) and the consumption frequencies ν (Ref. 15) for man and domestic animals, as well as the fact that the products of animal husbandry provide 20% of the food consumed by humans.¹⁰ In estimating HL , taking into account these facts, we obtained $HL = 2.4 \cdot 10^{12}$ W, which does not differ greatly from the rough estimate. Below, we assume $HL = 2.5 \cdot 10^{12}$ W.

¹⁵⁾The present edible harvest of cultivated land provides $9 \cdot 10^{11}$ W (Ref. 48), of which $4 \cdot 10^{11}$ W is used by humans as food and $5 \cdot 10^{11}$ W is consumed by domestic animals. The latter figure represents 40% of the energy required by domestic animals. The remaining 60% is supplied by the production of meadows and pastures, which provide 11% of the animal production out of the 18% obtained from all domestic animals. The assimilation coefficient for vegetation on pastures is one half the value for grain-fed cattle.²² From here, the consumption by cattle on meadows and pastures constitutes $1.5 \cdot 10^{12}$ W.

¹⁶⁾The production of cultivated lands shifted in the anthropogenic channel can be estimated on the basis of the amount of fertilizer added as compensation for the biogenic material removed from the soil. At the present time, the annual input of nitrogen and phosphorus fertilizers constitutes 30% of the nitrogen and phosphorus used by cultivated plants as part of the annual production.⁴⁷ This means that $0.3 \mathcal{P}_a$ is used with a displacement of biogenic material. The productivity of a cultivated field is by a factor of 2 to 3 lower without the use of fertilizer,^{1,10} so that assuming $0.2 \mathcal{P}_a$ is used without displacement of biogenic material we obtain that the over-all consumption of production of cultivated lands constitute $0.5 \cdot 0.5 \mathcal{P}_a$.

¹⁷⁾The decomposition of organic material in dumps and garbage can occur to a large extent as a result of being acted upon by bacteria and fungi, but, in this case, the displaced biogenic material does not return to the plants so that this loss must also be referred to the anthropogenic channel.

(see Table III). The total anthropogenic consumption is $0.5 \mathcal{P}_a = 3.4 \cdot 10^{12}$ W.

The (cultivated) area of meadows and pastures $S_c = 3.6 \cdot 10^9$ ha.^{10,47} The net primary production of meadows and pastures $\mathcal{P}_c \approx 1.1 \cdot 10^{10}$ t (d.m.)/yr = $6.6 \cdot 10^{12}$ W. The production density $P_c \approx 3.0$ t (d.m.)/ha · yr, which constitutes 40% of the average production density of land. The food consumption of domestic animals on meadows and pastures equals $0.2 \mathcal{P}_c$.¹⁸⁾ We estimate the total anthropogenic consumption of meadows and pastures, taking into account trampling and losses, as $0.3 \mathcal{P}_c$.¹ Therefore, the anthropogenic consumption of the production of cultivated lands, meadows, and pastures constitutes $0.5 \mathcal{P}_a + 0.3 \mathcal{P}_c \approx 0.8 \mathcal{P}_a \approx 5.2 \cdot 10^{12}$ W.

The modern farm occupies lands with the highest productivity, previously covered by forests, savannas, and steppes. As can be seen from Table III, the productivity of forests is twice as high as the average productivity of a farm. If it is assumed that the productivity of modern farm land equals the average productivity of forests, then the anthropogenic channel should also include the production that these lands provided before they were assimilated by man,¹⁹⁾ which together with the 50% consumption of present-day production constitutes $1.5 \mathcal{P}_a = 1.0 \cdot 10^{13}$ W. This is the upper limit because we do not know the true production of these lands in the past.

The production of present-day meadows and pastures is 2.7 times lower than the average production of land and 4.7 times lower than the average production of forests as a result of over-grazing. For this reason, taking into account 30% of the consumption of the production of present-day meadows and pastures, a minimum of $[2.7 - (1 - 0.3)] \mathcal{P}_c = 2 \mathcal{P}_c = 1.3 \cdot 10^{13}$ W and a maximum of $[4.7 - (1 - 0.3)] \mathcal{P}_c = 4 \mathcal{P}_c = 2.6 \cdot 10^{13}$ W should be ascribed to the anthropogenic channel. Apparently, if cultivation ceases, modern farms, meadows, and pastures are capable of restoring over a period of time the magnitude of production attained in the past. This cannot be said of most deserts, which were irreversibly destroyed by man's actions. Taking into account the lost production of deserts would further increase the potential production of the biosphere, which has been decreased as a result of man's actions.

Let us estimate the magnitude of anthropogenic consumption of forests.

D. Forests

The consumption of wood by people in 1958 constituted $1.6 \cdot 10^9$ m³/yr,²² $2.2 \cdot 10^9$ m³/yr in 1969,^{10,22} and about $3.0 \cdot 10^9$ m³/yr in 1979. Wood consumption increases at a rate of 3% per year. The 1979 figure

¹⁸⁾See footnote 13.

¹⁹⁾As far as the biosphere is concerned, it is of no significance as to what happens to the removed part of the production. It can be eaten by humans or by livestock, consumed or decomposed by reducers, without the biogenic material being returned to the vegetation, or simply not be available, as, for example, under the roofs of buildings.

exceeds the growth of wood in exploited forests²² and constitutes about one-half the growth of wood in all the remaining forests of the world. The average density of wood $\sim 0.6 \text{ t (d.m.)}/\text{m}^3$. The biomass of round timber constitutes about 60% of the biomass above ground extracted from forests.^{10,22} For $K_d = 600 \text{ W} \cdot \text{yr}/\text{t}$ the power consumption of round timber and of all the biomass extracted from forests equals $1 \cdot 10^{12} \text{ W}$ and $2 \cdot 10^{12} \text{ W}$, respectively. The growth of wood equals 10% (Ref. 22) of the net primary production of a forest. Cutting in a forest represents the harvesting of only the wood growth while the continuous plant cover is conserved. With clear cutting, the continuous plant cover is regenerated within 5 to 6 years,^{22,50} which constitutes $\sim 10\%$ of the average regeneration time of a forest $\tau_D \sim 56 \text{ years}$.²² For this reason, clear cutting with the removal of the biomass above ground constitutes the removal of approximately 30% of the net primary production of a forest, which contributes approximately $3 \cdot 10^{12} \text{ W}$ to the anthropogenic channel. This estimate represents a lower limit. Most virgin forests never achieve their original production²⁰ after the first cutting, which is especially characteristic of tropical forests which are situated on laterite soils, where most of the biogenic materials are concentrated not in the soils, but in the biomass of the forest. The decrease in the production of forest land areas is likewise related to the replacement of forests by cultivated lands, plowed fields, meadows, and pastures.

There is an important difference in the assimilation of the herbage on plains and that in a forest. Plains and cultivated lands have comparable biomass, and for this reason, the replacement of plains with cultivated lands may only involve a change in the production. The biomass of a forest is more than 40 times greater than the biomass of cultivated lands. For this reason, cutting wood out of a forest and replacing virgin forests with secondary forest, plowed fields, meadows and pastures involves a nonrenewable decrease in the biomass of the planet, 90% of which is concentrated in the biomass of forests (see Table III). Before the development of agriculture, forests covered approximately 10^{10} ha ,⁵¹ and by the beginning of this century the forest area decreased to $5.7 \cdot 10^9 \text{ ha}$ (see Table III), and in 1958, according to the inventory taken by the FAO,²² forests covered an area of $4.4 \cdot 10^9 \text{ ha}$.²² At the present time, the area covered by forests constitutes about $3 \cdot 10^9 \text{ ha}$.⁵¹ One-half ($1.46 \cdot 10^9 \text{ ha}$) of the forest remaining at the beginning of the Seventies is situated in the tropics,⁵¹ $5.6 \cdot 10^8 \text{ ha}$ constitute tropical rain forests,⁵¹ and $4 \cdot 10^8 \text{ ha}$ of tropical forests are situated along the Amazon, of which $1.6 \cdot 10^7 \text{ ha}$ is cut out every year.^{52,53}

The change of the biomass on land \mathcal{B} is determined by

$$\frac{d\mathcal{B}}{dt} = \mathcal{P} - \mathcal{Y}, \quad \mathcal{Y} = \mathcal{Y}_n + A, \quad (25)$$

where \mathcal{Y}_n and A are the natural and anthropogenic con-

sumption, and \mathcal{P} is the net primary production of land. The first decrease in the forest lands by a factor of 1.5 to 2 occurred over a period of 10^4 years, the second such decrease occurred over a period of approximately 50 to 100 years beginning at the end of the last century, which has led to a decrease in the biomass of forests by approximately 10^{12} t (d.m.) , i. e., the biomass of forests is at present decreasing at a rate $(1-2) \cdot 10^{10} \text{ t (d.m.)}/\text{yr}$. As virgin forests make the transition to a state in which the mature forest is continuously cut, the average biomass of the forest decreases by a factor of 2 assuming uniform growth (a triangle instead of a square in the temporal distribution of biomass over the course of the time it takes the forest to regenerate). For this reason, the increase in the consumption of wood in our century up to 50% of the forest growth, even with constant forest area, results in a similar estimate of the rate at which the forest biomass is decreasing. A similar value for the rate at which the forest biomass is decreasing [$8 \cdot 10^9 \text{ t}/\text{yr}$ of carbon = $1.8 \cdot 10^{10} \text{ t (d.m.)}/\text{yr}$] is obtained with the more detailed estimate given in Ref. 54.²¹ The latter figure is 5 times greater than the data on the cutting of forests and corresponds to the difference in the produced and consumed power (25), $\mathcal{P} - \mathcal{Y} = -1.1 \cdot 10^{13} \text{ W}$. This difference can arise as a result of a decrease in the production of forests or as a result of an increase in the anthropogenic or natural share of consumption. However, since in the stationary state, before intervention by man, production precisely equalled natural consumption, in every case, the difference that arises must be ascribed to the anthropogenic channel.

As experiments have shown, in greenhouses the production of terrestrial and aquatic vegetation increases with an increase in the concentration of carbon dioxide in the environment.¹⁸ Over the past 100 years, the concentration of atmospheric carbon dioxide increased by 15–20%.⁵⁴ The production on land and in the ocean could have increased by a similar amount. The production of forests at the beginning of the century constituted approximately 70% of the production of land (see Table III). The replacement of one-half of the forest area by vegetation that is half as productive over the past 100 years has led to a decrease in the production on land by $1/4 \cdot 70\% \sim 20\%$, which compensated the possible increase in the production on land as a result of the increase in the concentration of atmospheric carbon dioxide. As a result, the production on land, apparently, did not change and constitutes at present $\mathcal{P} \approx 1 \cdot 10^{11} \text{ t (d.m.)}/\text{yr} = 6 \cdot 10^{13} \text{ W}$ [Table III and Eq. (5)].

The total anthropogenic consumption $A = \mathcal{Y}_a - d\mathcal{B}/dt$, where $\mathcal{Y}_a = \mathcal{P} - \mathcal{Y}_n$ is the anthropogenic consumption of the production on land. Adding the food consumption by people and domestic animals to the consumption of round timber, we obtain $5 \cdot 10^{12} \text{ W}$, which is 8% of the production on land. The overall contribution of the present-day net primary production of cultivated lands,

²⁰We have in mind the net production of all types of plants (not only species of trees valuable for humans) and not the increment in biomass (25), which is maximum for a young forest and equals zero for a mature forest.

²¹The problem of the carbon dioxide equilibrium in the atmosphere and the ocean, which arises in connection with the decrease in the biomass of forests, is discussed in Ref. 55.

meadows, pastures, and forests to the anthropogenic channel without taking into account changes in the biomass of the biosphere constitutes $A = 0.9 \cdot 10^{13} W$ or 15% of the production on land. Taking into account the changes in the biomass of the biosphere

$$A = 1.6 \cdot 10^{13} W \quad (26)$$

which is 27% of the production on land and 17% of the production on Earth.²²⁾ As a result of cultivation by man, 65% of the production on land is excluded from the process of natural regeneration (100% of cultivated fields, meadows, and pastures, 70% of the production of forests). Taking into account the disappearing production of farmlands, meadows and pastures, a minimum of $2.7 \cdot 10^{13} W$ and a maximum of $5 \cdot 10^{13} W$ flows into the anthropogenic channel.

The consumption of the products of the biosphere ($1.6 \cdot 10^{13} W$) together with the consumption of nonrenewable fossil fuel resources ($1.0 \cdot 10^{13} W$, see Table 1) constitutes $2.6 \cdot 10^{13} W$ or 6 kW/person, which is 60 times greater than the biological consumption of food ($\sim 100 W$ /person). In developed countries, the consumption of nonrenewable fossil fuel energy resources attains 10 kW/person, while the overall energy consumption ~ 20 kW/person. Modern man expended hundreds of times more energy per capita than the primitive man-forager in order to obtain almost the same amount of food.

E. Energetics of man's ecological niches

Every method for obtaining an adequate amount of food that permits a population to exist for a long time can be viewed as an equivalent ecological niche.²³⁾

Here, an attempt is made to compare the energetics of the various niches of man on the basis of three indicators⁵⁵:

1) expenditures of useful energy on all forms of activity related to obtaining a given amount of food (harvesting food and crops, working land, hunting, raising cattle, and so on), w_{agr} ;

2) all expenditures of energy that are unavoidable for a given way of life (the biological energy of man and domestic animals; the power used by all industry; the energy for heating dwellings, preparing food, transportation, and so on) expended on the same amount of food products, w_{tot} ;

3) the ratio of these quantities, which indicates the efficiency with which energy resources are used for producing food: $\eta = w_{agr}/W_{tot}$.

The required amount of food is obtained from the food

²²⁾All consumption by a forest is included in the term $d\mathcal{B}/dt$. The anthropogenic part of the consumption is given by $\beta = A/\mathcal{P} = 0.23$, $\mathcal{P} = \mathcal{P} - d\mathcal{B}/dt = 7.1 \cdot 10^{13} W$.

²³⁾In animals, the characteristics that are necessary for consumption in each niche are hereditary, and for this reason, they cannot change or be adopted rapidly. In man, the sum total of characteristics, knowledge and technology is transferred via education and as a result can change and be adopted rapidly.

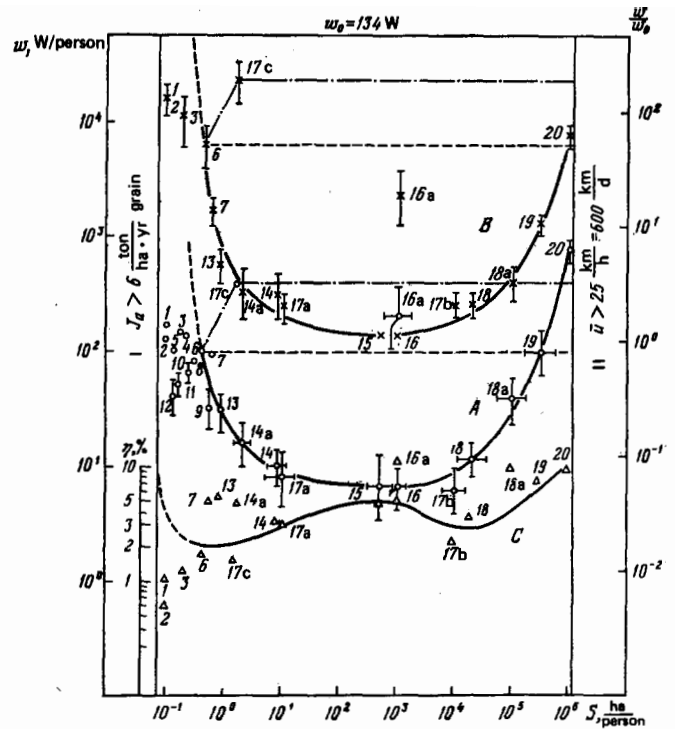


FIG. 5. Expenditure of energy and consumption area for a man with a normal diet in different niches. The vertical axis corresponds to energy consumption in W/person and the horizontal axis corresponds to consumption area in ha/person. The dots and the curve A correspond to net energy expenditure for the consumption area for all forms of activity related to gathering food for a consumption norm of 500 kg of grain per year or 280 kg of meat per year. The crosses and curve B correspond to the total energy expenditure for production of the same quantity of food (including the energy expended on food for humans and domestic animals, household heating, food preparation, industry and transportation). The triangles and curve C correspond to the ratio of the first to the second types of energy expenditures in percent (auxiliary scale on the left). Data: 1-12 denote various countries in the world for the period 1964-1968 (Ref. 13 and 14). 1—Japan, 2—England, 3—USA, 4—Israel, 5—Western Europe, 6—World average, 7—Asia and India, 8—Oceania, 9—Africa, 10—Latin America, 11—Taiwan, 12—United Arab Republic, 13—traditional agriculture,⁵⁸ 14—slash-and-burn agriculture, 14a—Tsembago tribe,¹⁷ 15—foraging, 16—fishing, 16a—modern fishing, 17—animal husbandry: a) pasture, b) primitive, c) in stalls; hunting: 18—primitive, 18a—modern hunting by Eskimos,²⁰ 19—on horseback, 20—motorized. Dashed and dot-and-dash horizontal lines indicate the average world-wide levels of energy expenditure (see text). The horizontal and vertical lines comparing the dots and crosses indicate estimates of the possible scatter in the corresponding values. The computational methods and the initial data are discussed in the appendix.

required by one man for a balanced diet (12% animal food): 500 kg/yr of calorie-equivalent grain, of which 1/2 is consumed by domestic animals, transforming it into 35 kg of animal production (in terms of calorie-equivalent grain). In the case of livestock grazing, fishing, and hunting, if no energy is expended on feeding animals, while people only consume the animal production, the given quantity of food equals 280 kg/yr in terms of calorie-equivalent grain.

The area utilized is computed as the territory from

which the amount of food products given above are obtained using a given method.

In Fig. 5, with the area used shown along the abscissa axis and the power expended for various methods of obtaining food shown along the ordinate axis,²⁴⁾ we find a definite relationship between the area used and the power expended.

The ratio $\eta = w_{agr}/w_{tot}$ is the efficiency with which energy is consumed (η^{-1} characterizes the energy availability). In the figure, the line of triangles for η in percent on the left scale, apparently, has two minima near 6 and 18 and a maximum near 15 and at the boundaries of the region. Regions I and II are forbidden: region I corresponds to an average crop yield $\bar{J}_a > 6$ t/ha · yr of grain,⁴⁷ while region II corresponds to speeds of motion $u > 25$ km/hr = 600 km/day. The dashed line shows the "profitability" of the energy input corresponding to the present world-average energy input into the production of cultivated fields.²⁵⁾ The points that lie outside the dashed (or dot-and-dash) lines correspond to an unprofitable input of energy. Niches that correspond to the points located between the dashed (or dot-and-dash) lines and the main curve are energetically profitable, but unstable: with prolonged excessive energy input the permissible norms for consumption are exceeded and as a result there is either a degradation of the surrounding environment with an accompanying drop in productivity and a transition to the right side of the curve or the productivity increases as a result of land cultivation and there is a transition to the left side of the curve. For this reason, in the case of a sufficiently prolonged constant energy input, the niches near the points at which the curves intersect a given energy input line turn out to be stable (see niche 16a).

Mankind has existed about $2 \cdot 10^6$ years in niches 15 and 16 with minimum biological energy consumption; for 10^4 years in niches 14, 17, and 18 with an energy consumption that is twice as high; for 1000 years in niche 13 with an energy consumption that is 5 times as high; and, for 100 years in niche 6 with an energy consumption that is 20 times as high.

12. CONCLUSIONS

Let us examine the changes in the basic energy parameters of the biosphere over the period of time that mankind has existed.

Figure 6 shows the change in the energy flow in W : on a logarithmic time scale for the last million years (Fig. 6a); on a linear time scale for the last 400 years

²⁴⁾See the appendix for the initial data on various niches.

²⁵⁾The dashed profitability line is valid only for noninteracting niches, when all consumption occurs within each niche. When niches interact (trade), the profitability line is raised by a factor of four (dot-dash) because the production of 280 kg of animal products with $\alpha_2^1 = 7$ is equivalent not to 500 kg of grain, but to 7×280 kg ~ 2000 kg of grain (see niche 17c)^{22,56} The dashed line and the dot-dashed line are drawn under the assumption that the productivity of a niche does not change at the initial stages of an increase in the energy input.

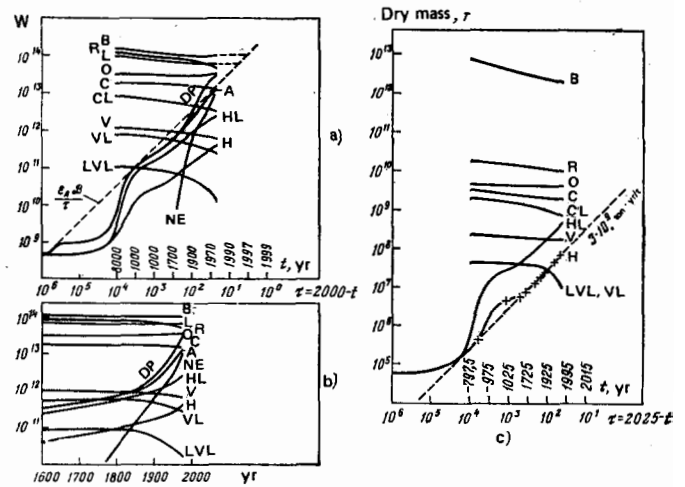


FIG. 6. Variations in the flow of energy and in mass of living organisms in the biosphere. The vertical axis in Figs. 6a and 6b indicates the energy flux in W and in Fig. 6c, the mass of living organisms in tons of dry matter. The horizontal axis in Figs. 6a and 6c indicates the time on a logarithmic scale for the last million years and in Fig. 6b, for the last 400 years on a linear scale. H denotes food for humans; HL denotes food for humans and livestock; A denotes the total human consumption in the biosphere, including HL , processing and burning of wood, straw, and trash; DP denotes the production of the assimilated part of the biosphere, involving disruption of the natural flow of energy (plowed fields, meadows, pasture, exploited forests); NE denotes consumption of non-renewable energy resources (fossil fuels) by man; B denotes the production of the biosphere: $B = L + O \approx R + C + A$, where L is the production of land, O is the production of the oceans, R is the consumption of reducers, C is the consumption of consumers; CL is the consumption by consumers on land; V is the consumption by vertebrates; VL is the consumption by wild vertebrates on land; LVL is the consumption by large vertebrates on land (with live weight exceeding 10 kg), deprived of energy flows in DP regions. The dashed line in Fig. 6a is described by the equation $A = \epsilon_A \mathcal{B} / \tau_A$, where $\epsilon_A = 0.25$, $\tau_A = t_A - t$, $t_A = 2000$ yrs, $\mathcal{B} = 1.2 \cdot 10^{15}$ $W \cdot \text{yr}$, corresponds to the mass of all living organisms in the biosphere. The same notation is used in Fig. 6c for the mass of living organisms in the biosphere, $H = N \cdot 15$ kg; the crosses for H are obtained from the data in Ref. 46; the dashed line in Fig. 6c is described by the equation $H = 3 \cdot 10^9 \text{ ton} \cdot \text{yr} / \tau_H$, where $\tau_H = 2025 - t$.

(Fig. 6b); the change in biomass expressed in tons of dry matter (Fig. 6c). Food for human consumption is $H = 100N$ W , where N is the number of people^{1,10,46}; food for humans and livestock is $HL = 5H$ from the beginning of farming,^{1,10} while A is the total anthropogenic consumption in the biosphere, including HL and the processing and burning of wood, hay, and garbage. Up to 1900, A is taken as equal to $2H + HL$ under the assumption that energy expenditures on heating and cooking food are equal to twice the caloric value of the food,^{1,47} P is the production of the assimilated part of land where the natural energy flows have been disrupted (cultivated land, meadows, pastures, exploited forests); NE denotes the human consumption of non-renewable fossil fuel energy resources (coal, oil, gas)^{2,14}; B is the net primary production of land and ocean,¹⁰ C and R denote the consumption by consumers and reducers,¹⁰ CL denotes the consumption of wild consumers on land,¹⁰ V denotes the consumption of wild

vertebrates on the Earth,^{10,42} V_L denotes the consumption of wild vertebrates on land,^{1,10,42} and LVL denotes the consumption of large, wild vertebrates on land with a live weight exceeding 10 kg.^{1,10} It is assumed that LVL do not have access to the consumption flows in the region of DP . The data on the changes in the production and biomass of the biosphere, the land, and the ocean, and in the consumption of consumers and reducers, were obtained on the basis of Refs. 10 and 26 and of the dynamics involved in the reduction of forests described in Refs. 22, 51, and 52 under the assumption that the ratios of the production of vegetation, consumption by consumers, and the biomass in different ecosystems shown in Table III remain constant.

In a stable biosphere, the time periods τ_J over which consumption can be increased to a magnitude J in comparison with the average value \bar{J} are determined by the condition [see (25)]

$$\tau_J = \varepsilon_J T_J, \quad \varepsilon_J \ll 1, \quad T_J = \frac{B}{|J - \bar{J}|} \approx \frac{B}{\bar{J}} \text{ for } J \gg \bar{J},$$

where T_J is the time required for processing the entire biomass. After a time τ_J , either the magnitude of consumption must decrease or the methods of consumption must change, which can lead to further growth, but over a shorter period of time. The dashed curve in Fig. 6a, which approximates the growth of the anthropogenic share of the energy flow in the biosphere is described by the following equation⁵⁵:

$$A = \frac{\varepsilon_A \mathcal{B}}{\tau_A}, \quad \tau_A = t_A - t, \quad \varepsilon_A = 0.25, \quad t_A = 2000 \text{ yr}, \quad (26)$$

where $\mathcal{B} = 1.2 \cdot 10^{15} \text{ W} \cdot \text{yr}$ is the mass of all living organisms in the biosphere, which is constant in the first approximation; t is the time in years; and, ε_A and t_A are parameters. The hyperbola corresponding to the growth in the human population is proportional to the food consumption H , which is described by a similar equation with $\varepsilon_H = 0.02$ and $t_H = 2025 \text{ yr}$; the parameters are computed from data of Ref. 46 (pp. 8, 44, and 498).²⁶⁾ The presence of a pole singularity in (26) means that the nature of the growth must change as the singularity is approached.²⁷⁾

From Fig. 6c, it is evident that the biomass of human beings and domestic livestock is tens of times greater than the biomass of all vertebrates on land and several times greater than the biomass of vertebrates in the ocean. The confinement of a large part of the energy flow in the biosphere to the anthropogenic channel leads to a displacement of the natural species of organisms and a redistribution of consumption in the biosphere (see Fig. 3a). The signs of environmental degradation and pollution began to appear when the total anthropogenic consumption exceeded the cumulative consumption of wild vertebrates (see Figs. 3a and

c). In order to support a stable existence for a small community of cultivated plants and domesticated animals, which does not form the complete community that is necessary for withstanding changes in environmental conditions and forming closed cycles for circulation of chemical elements, man must stabilize the external conditions by additional energy inputs and he must compensate the disruption of the closed cycles of nutritive substances by creating in the fields a flow of fertilizers obtained from concentrated natural deposits. Energy is also needed in order to maintain the biosphere in a state needed by man. This state will be constantly disrupted by microscopic species that change rapidly and that easily adapt to man-made changes in the biosphere. The pressure from these species with complete disruption of equilibrium can turn out to be equal to the productive and working power of all heterotrophs (regions I and II in Fig. 3a), i. e., 10 to 30% of their consumption or $(1-3) \cdot 10^{13} \text{ W}$. Under these conditions, over a period of time man can encounter shortfalls in energy and depletion of deposits of chemical elements that are necessary for building up the biomass of cultivated plants and industrial production.

Provided we are willing to give up the concept of closed circulation of elements and compensate for it by utilization of deposits of such elements, the laws governing the distribution of consumption in the biosphere can be ignored. In this case, starting with the law of conservation of energy, the flow of energy in the biosphere within the anthropogenic channel can be increased by a factor of 4 to 5 with a constant flow of energy through the biosphere determined by the solar constant and the energetics of existing photosynthesis. Apparently, on the basis of the available nonrenewable resources, the biospheric flow of energy in the anthropogenic channel can be increased by a factor of 1.5 to 2.⁵⁶ This will require a realizable increase in energy consumption by a factor of 2 to 3 in comparison with the present level,¹⁴ at which climatic changes do not have time to occur.²⁸⁾ Further growth in energy consumption will not lead to a noticeable increase in the anthropogenic biological energy flow⁵⁶ and is unlikely to occur. The time during which the level of anthropogenic consumption thus attained can be maintained is determined by the time for depleting the nonrenewable resources.⁶³

Energy estimates reveal the impossibility of many conceivable projects for increasing the global energy flow in the anthropogenic channel by an increase in the total energy flow in the biosphere, i. e., by a complete restructuring of the present biosphere.⁵⁵

It is possible to increase the net primary production per unit area in greenhouses via hydroponics or grow-

²⁶⁾ Only the point $t = 0$ (the beginning of the era) in Ref. 46, which lies twice as high, does not follow the hyperbolic curve (see Fig. 6).

²⁷⁾ For example, the relative growth rate H is bounded by the limiting biological possibilities (biotic potential)³³:
 $k_H = (dH/dt = H/\varepsilon_H \mathcal{B}) \leq 0.04 - 0.05 \text{ yr}^{-1}$ (Ref. 46).

²⁸⁾ At the present time the increased interest in global processes in the existing biosphere is due to the possible influence of the biosphere on the climate and the subsequent effect of the change in climate on man. The direct effect of a change in the biosphere on man from the point of view of energy fluxes is one to two orders of magnitude greater than via the change in climate.

ing crops on soil by increasing the irradiation of plants in comparison with the average solar radiation and by enrichment with carbon dioxide. In order to obtain the net production of the modern farm [$7 \cdot 10^{12}$ W (Ref. 48)], greenhouses would require $5 \cdot 10^{14}$ W of light energy, assuming a maximum observed annual average photosynthesis efficiency of 1.4% [see Table III and also (7)], i. e., $\sim 10^{15}$ W of primary power.

The net primary production is proportional to the amount of moisture transpired by plants (1). On the average approximately 500 parts of water (by weight) are transpired per unit growth of dry weight.^{1,24} The average evaporation from land is 500 mm/yr,¹¹ while the average evaporative capability of land with excess humidity is twice as great.¹¹ By increasing the evaporation up to the evaporative capability (in this case all land must be covered by a layer of water that does not dry out), the production of vegetation on land can be doubled. For this purpose, $7 \cdot 10^4$ km³/yr of fresh water must be added to the water currently evaporated.¹¹ The total runoff of rivers [$4 \cdot 10^4$ km³/yr (Ref. 11)] is less than the evaporation, so that the additional quantity of fresh water can be obtained only by desalinating sea water or melting ice. In order to desalinate $7 \cdot 10^4$ km³ of sea water per year, $5 \cdot 10^{15}$ W would be needed and $0.8 \cdot 10^{15}$ W would be needed to melt ice. Desalination using membranes is 20 to 30 times less energy intensive than desalination by evaporation, but it is hardly applicable for desalination on a global scale.

It is possible to decouple the anthropogenic channel from the flow of energy in the biosphere by synthetic production. Synthetic food can be produced from inedible organic material stored in the biosphere, oil and gas, or from inorganic substances by artificial synthesis, similar to the photosynthesis of green plants. Ten percent of the total production of grains is edible.^{10,22} Let us assume that it is possible to transform the production of green plants, gas or oil, into edible food with an efficiency of 1%.²⁹ Then, all of the annual production of the biosphere [10^{11} t (Ref. 10)], all of the oil [$8 \cdot 10^{10}$ t (Refs. 2, 14)], and gas [$5 \cdot 10^{10}$ t (Refs. 2, 14)] would produce a quantity of food equal to the crop

produced by all the farms in the world in the course of one year [$2 \cdot 10^9$ t (Ref. 10)]. In processing all of the biomass in the biosphere [$2 \cdot 10^{12}$ t (Refs. 10, 25)], there is enough biomass for ten years of consumption at present rates. In synthesizing edible products from inorganic substances with an efficiency equal to the maximum observed efficiency of photosynthesis [0.1% (Refs. 20 and 37)], in order to create food at a power level equivalent to the present edible crop equal to 0.1 of the net primary production of farmland, i. e., 10^{12} W (Ref. 4), energy expenditures of the order of 10^{15} W would be required.

The circulation of biogenic elements in the biosphere forms closed loops as a result of the flow of a large part of the energy through small organisms (bacteria, fungi, insects, and others) that have a small individual consumption (see Figs. 3 and 6). Vertebrates, which consume 1% of the total energy flow in the biosphere equal to 10^{14} W, can exist without disrupting the stability of the biosphere. In order to assure a stable existence for modern man, who absorbs 20% of the energy flow in the biosphere, $20 \cdot 10^{14}$ W = $2 \cdot 10^{15}$ W of additional energy will be required in order to form closed pathways for circulation of biogenic elements with the same energy use efficiency as for the biosphere. In addition to the biogenic elements, man will have to organize closed circulation of elements that are required for building up industrial production.

Energy consumption several tens of times greater than the present level [of the order of $(2-3) \cdot 10^{14}$ W] can irreversibly disrupt the stability of the Earth's climate.^{4,8}

From the ecological point of view, long-term stable existence of a highly developed industry with closed circulation of industrial elements, based on renewable energy sources with a power of 10^{12} W (Ref. 14) is possible if the share of consumption by mankind in the biosphere does not exceed the share of the consumption of all vertebrates in the preindustrial biosphere. In this case, additional energy will not be required in order to form closed circulation of biogenic elements.

APPENDIX (to Fig. 5)

Points 1-12 denote the average expenditures of energy on cultivated fields in 1964-1965 in different countries.^{56,57} Manual labor corresponding to 10 W/person is added to points 9-12; the data of Refs. 13 and 14 correspond to the lower limit of the error cited. The crosses 1-6 were computed from data on total energy consumption (including consumption of the products of the biosphere) and grain production in the entire country. The deviation of the points from the curve is related to the difference between the value of the productivity and the world-average value. The points showing the high productivity to the left of the curve are balanced by point 7, corresponding to half of the population on Earth.

²⁹For biological conversion of organic matter, as a minimum, two trophic levels are required since the production of reducers cannot be eaten by man.

Remaining data:

13—traditional agriculture (Russian, 1897) using working livestock. Computations from the data: average productivity, 0.6 t/ha · yr of grain (Refs. 56, 57); 1 horse per 4 ha of plowed field;⁵⁸ average weight of a horse, 400 kg; grain equivalent of consumption by a horse, 5 times its weight per year or 2000 kg/yr or 1000 W (Ref. 32) developed in the meadows and pasture lands; average working power of a horse, 125 W (1/8 of the consumption);³² average working power of a horse in the fields, 31 W/ha or 26 W/person (for the production of 500 kg/yr of grain); average power of manual labor in the fields 5 W/person (plowman with an average power of 10 W, feeding two people, including himself), i. e. $S=0.83$ ha/person, $w_{agr}=31$ W/person, $w_{tot}=540$ W/person (134 W/person, 200 W for fire, 210 W for the horse);

14—slash-and-burn agriculture using manual labor with an

average power $w_{agr} = 10$ W/person with a productivity of 0.6 t/ha · yr during the cultivation periods and a regenerating period equal to 10 of the cultivation periods: $S = 8.3$ ha/person, $w_{tot} = 300$ W/person (130 W for the person and 170 W for the fire used);

14a—present tropical slash-and-burn agriculture practiced by the people of Tsembaga;⁵⁹ the productivity during the periods of cultivation, 6.3 t/ha · yr of grain; regenerating time, 25 yr; $S = 2$ ha/person; ratio of the energy in the harvest to the energy expended equals 16; $w_{agr} = 15$ W/person (per 500 kg of grain), $w_{tot} = w_{tot}^{(4)} = 300$ W/person;

15—primitive foraging without the use of fire; $S = 500$ ha/person; $w_{agr} = 6.6$ W/person; $w_{tot} = 134$ W/person; the quantities are computed on the basis of $S = 3 \cdot 10^7 l^2$ (territory intermediate between that of an herbivorous mammal, $10^7 \cdot l^2$, and that of a predator, $10^8 \cdot l^2$ (Ref. 40), where l is the linear size [for man $l = 0.4$ m]) and the motive power $w_{agr} = F\bar{u}$ for moving about the territory with an average speed $u = s/l_{eff} \tau \sim 0.17$ m/s ≈ 14 km/day; it is assumed that in moving about a man forages over a strip of width $l_{eff} = 1$ m, where $\tau = 1$ yr, the time for producing the food required for one year, $F = \gamma_a mg$ is the force, proportional to the weight, $\gamma_a = 6 \cdot 10^{-2}$ (Ref. 32);

16—primitive fishing; $S = 10^3$ ha/person, computed from the average catch of $1 - 2$ kg/ha · yr of live weight;¹ the energy expenditure of the fisherman and the forager are taken as equal;

16a—present-day marine fishing; computed from data on present-day catch of $7 \cdot 10^7$ t per year of live weight from an ocean area of $3.6 \cdot 10^{10}$ ha; over-all power of world fishing fleet estimated at 1.5 times the caloric value of the fish caught.^{1, 56, 63}

17a—traditional animal husbandry using pastures, providing a consumption of 280 kg/yr person of animal production calorie-equivalent to grain with a coefficient of transformation of vegetative energy into the animal production equal to 14 (twice as great as for the transformation of grain into meat⁵⁵), with average primary productivity of pasture land, 3 t (d. m.)/ha yr (Refs. 1, 10, 32) and with the present-day world-averaging grazing standards (20% of the total primary production of pastures is consumed); $w_{agr} = 8$ W/person, determined mainly by expenditures of energy on maintaining pastures, taken as equal to 1/4 (present ratio of the expenditures of energy on pastures and on plowed fields^{1, 64}) of the average expenditures of energy on pastures in niche 13; $S = 8.4$ ha/person; $w_{tot} = 240$ W/person (60% of the production from livestock (milk) is eaten in its raw form, 40 W as food for dogs)^{1, 64};

17b—primitive animal husbandry using pastures with 0.02% of the production of pastures consumed or 1000 times less than in 17a (two times greater than the consumption by corresponding wild animals)^{60, 61}; $S = 10^4$ ha/person. As in 15, energy expenditures are determined by the movement of the herder over the pasture with $l_{eff} = 30$ m (average distance separating the sheep and the sheep herder); the herder eats 8 times his weight per year, i. e. about 10 sheep, with a reproduction time for the sheep of the order of three years. Correspondingly, the herder must own a herd of 30 head; $w_{agr} = S/l_{eff} \tau_1 = 6$ W/person ($\tau_1 \sim 1$ yr, the regenerating time of vegetation); $w_{tot} = w_{tot}^{(17a)} = 250$ W/person.

Niches 17a, b corresponding to animal husbandry in pastures are most energy self-sufficient.

17c—present-day animal husbandry in stalls using the production of pastures with a coefficient for transformation of energy in grain into animal production equal to $\alpha_2^{-1} = 7$ (Ref. 56) and consumption of 280 kg/yr · person $7 = 2000$ kg/yr · person of grain is 4 times greater than that given above in niche 6:

$$S = 4S^{(6)} = 1.6 \text{ ha/person}; w_{agr} = 4 w_{agr}^{(6)} = 400 \text{ W/person};$$

$$w_{tot} = 4 w_{tot}^{(6)} = 24 \text{ kW/person}.$$

18—hunting on foot with one dog per person; $w_{agr} = 12$ W/person; $S = 2 \cdot 10^4$ ha/person; $w_{tot} = 240$ W/person $= w_{tot}^{(16)}$. The territory is estimated by postulating existence supported by a single species of game with a normal average biomass density of 210 g/ha of live weight (~ 52 g/ha of dry weight)^{40, 60} (in Ref. 60 the territory of a hunter in Siberia is estimated as $(2 - 3) \cdot 10^4$ ha/person), a regeneration time τ of the order of 1 yr and harvesting of 25% of the production of game. The power developed by the hunter corresponds to movement over the territory with an average speed of $\bar{u} = 0.2$ m/s $= 20$ km/day (see niche 15), $l_{eff} = 30$ m, corresponding to an armed hunter making a kill at a distance of 15 m. The power involved in stalking and making a kill is taken as equal to 1/4 the motive power involved in stalking. The motive power associated with a dog equals 1/4 the motive power of a human.

18a—present-day hunting by Eskimos⁶¹ (Canada, Baffin Island). The territory is estimated from the attached map as $S = 10^5$ ha/person ($2.3 \cdot 10^6$ ha per 26 persons); $w_{agr} = 40$ W/person (30 W/person for gasoline engines, 10 W as the motive power of a man and a dog), $w_{tot} = 400$ W/person (170 W/person for gasoline, 50 W/person for kerosine or seal oil for heating a dwelling, 134 W/person for food for people, 40 W/person for dog food), the efficiency of the engines is assumed equal to 20%.⁶²

19—hunting on horseback for large animals (bison, regenerating time $\tau \sim 3$ years) with one horse per person. The motive power of a horse $w_{agr} = 100$ W $= \gamma_h m_h \bar{u}$; $\gamma_h = 0.04$ (Ref. 4), $\bar{u} = 0.63$ m/s $= 54$ km/day $= S/l_{eff} \tau$, $l_{eff} = 30$ m, $\tau = 3$ yr, $S = \bar{u} \tau l_{eff} = 3 \cdot 10^5$ ha/person, $w_{tot} = 1,300$ W/person (1000 W for the horse, 134 W for the man, 150 W for fire).

20—motorized hunting: $l_{eff} = 50$ m, $S = 10^6$ ha/person $u = 6.4$ m/s $= 550$ km/day, $\tau_1 = 1$ yr, $w_{agr} = \gamma_m m_g \bar{u} = 800$ W/person $= 1$ hp/person, $\gamma_m = 0.04$, $m = 300$ kg (weight of the machine including the person), $w_{tot} \approx 7,000$ W/person; the efficiency of the engine is 20% (Ref. 62), the power for manufacturing the engines (fraction of the total energy used by our civilization) is taken as equal to the power of the engine.¹⁷

In niches 19 and 20 existence supported by hunting is possible with game having a biomass density less than the average normal value (niche 18) by a factor of 15 and 50, respectively.

Estimate of the errors in the values of w and S for the average productivity of land (0.5 W/m²) are shown on the graph.

LIST OF BASIC DEFINITIONS AND NOTATION

B (W yr/m²)—energy density of organic mass per unit Earth surface area (1 W · yr $= 8.8$ kW · hr $= 3.15 \cdot 10^7$ J);

J (W/m²) and P (W/m²)—density of consumption and production per unit Earth surface area, P_1 —net production of vegetation (productivity);

\mathcal{B} (W · yr), \mathcal{F} (W), \mathcal{P} (W)—energy content of organic mass, consumption and production, (of an organism, ecosystem, or biosphere), respectively; $\alpha = P/J = \mathcal{P}/\mathcal{F}$ —coefficient of the ecological efficiency for transformation of energy;

B_l (t/m²) $= B/K_l$ ($B_d = B/K_d$)—density of live (dry) mass per unit Earth surface area—biomass;

K_l (K_d)—energy content per unit live (dry) mass (P_l , \mathcal{P}_l , \mathcal{B}_l and P_d , \mathcal{P}_d , \mathcal{B}_d are defined in a similar manner);

L (m) $= B/K_l \rho$ —thickness of the live biomass layer, $\rho \approx 1$ t/m³;

V (m/yr) $= P/K_l \rho$ —rate at which live biomass layer is added;

τ (yr) $= L/V = B/P = \mathcal{B}/\mathcal{P}$ —turnover time for biomass;

l (m) $= M/\rho s$ —height of an organism, $M(t)$ —live mass of an organism, s (m²)—Earth surface area covered by a live organism;

$d = L/l = s/S$ —coverage index of an organism;

$S = sl/L$ —territory per organism;

$v(\text{yr}^{-1}) = \mathcal{F}/\mathcal{B} = J/B = 1/\alpha\tau$ —consumption frequency of an organism;

$v(\text{m}/\text{yr}) = lv$ —consumption rate of an organism;

$j(\text{W}/\text{m}^2) = K_1pv = \mathcal{F}/s = J/d$ —consumption density of an organism per unit Earth surface area that it covers;

Autotrophs—organisms that synthesize organic matter out of inorganic matter;

Heterotrophs—organisms that feed on organic matter and are incapable of synthesizing organic matter out of inorganic matter;

Consumers—heterotrophs that feed on live organic matter;

Metabolism—rate at which consumed energy is assimilated;

Reducers—heterotrophs that feed on dead organic matter;

Excreta—the part of the food that is not assimilated by consumers.

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