Similarity principles for the biology of pelagic animals

(biomass/respiration/fractals/oxygen absorption)

G. I. BARENBLATT AND A. S. MONIN

P. P. Shirshov Institute of Oceanology, U.S.S.R. Academy of Sciences, Moscow, U.S.S.R.

ABSTRACT   A similarity principle is formulated according to which the statistical pattern of the pelagic population is identical in all scales sufficiently large in comparison with the molecular one. From this principle, a power law is obtained analytically for the pelagic animal biomass distribution over the animal sizes. A hypothesis is presented according to which, under fixed external conditions, the oxygen exchange intensity of an animal is governed only by its mass and density and by the specific absorbing capacity of the animal's respiratory organ. From this hypothesis a power law is obtained by the method of dimensional analysis for the exchange intensity mass dependence. The known empirical values of the exponent of this power law are interpreted as an indication that the oxygen-absorbing organs of the animals can be represented as so-called fractal surfaces. In conclusion the biological principle of the decrease in specific exchange intensity with increase in animal mass is discussed.

We consider in the present paper the power laws established empirically by biologists for the animal biomass distribution of the poikilothermic pelagic animals over their sizes:

$$F = dB/dW = \text{Const } W^{-\alpha} \qquad [1]$$

in which $W \approx \rho\ell^3$ is the mass of the animal, ρ is the animal's body density, ℓ is a characteristic size of the animal, and α is a dimensionless constant; and for the mass dependence of the animal exchange intensity R (oxygen mass absorbed by an animal per unit time):

$$R = AW^k \qquad [2]$$

in which A and k are constants. The biologists were interested for a long time (see ref. 1 for a review) in understanding whether the power laws such as Eqs. 1 and 2 are only convenient approximations of the empirical data or reveal some deep general laws of nature.

It is shown in the present paper that these laws can be deduced in a precise mathematical way from certain simply formulated general principles. Similarity methods and dimensional analysis are used for these considerations. These methods were used earlier in other biological problems (see, for instance, refs. 2 and 3). We use them here, however, in a completely different aspect.

BIOMASS DISTRIBUTION OVER THE RANGE OF ANIMAL WEIGHTS

The power law of biomass distribution over the animal weights (4, 5) is proved to be valid in a wide range of weights: from 10^{-6} g to 10^8 g. We suppose that this law can be considered as one of the manifestations of the following general principle of pelagial biology: the statistical pattern of the pelagial population is identical in all scales that are large in comparison with molecular ones. This exclusion of molecular scales is necessary for the following reasons. The molecular processes can be of great significance in the nutrition of the smallest organisms. Due to the existence of a united trophic chain, these molecular processes can influence the total biomass, $\int F dW$, but not the contribution to it of sufficiently large animals, $F dW$. A direct confirmation of this principle for the benthos can be found in ref. 6.

According to the similarity principle just formulated, there exists no distinguished weight scale W_0 in the whole range of not-too-small animal masses W. Consequently, for two arbitrary masses from the similarity range, W_1 and W_2, the ratio $F(W_2)/F(W_1)$ can depend on the ratio W_2/W_1 only. If such a distinguished mass scale W_0 were to exist, then the ratio $F(W_2)/F(W_1)$ should depend on the location of the masses W_1 and W_2 with respect to the distinguished mass scale—i.e., should depend on an additional argument W_1/W_0. Consequently, for three arbitrary masses W_1, W_2, W_3 from the similarity range, the relationships are valid:

$$\frac{F(W_2)}{F(W_1)} = \varphi\left(\frac{W_2}{W_1}\right),$$

$$\frac{F(W_3)}{F(W_1)} = \varphi\left(\frac{W_3}{W_1}\right), \qquad [3]$$

$$\frac{F(W_3)}{F(W_2)} = \varphi\left(\frac{W_3}{W_2}\right),$$

in which φ is the same function for all three relationships. Dividing the second relationship 3 by the first one, we obtain in the left-hand side $F(W_3)/F(W_2)$; equating the right-hand sides of the relationship obtained and of the third relationship 3, we obtain a functional equation for the function φ:

$$\varphi(y)/\varphi(x) = \varphi(y/x). \qquad [4]$$

We denote here $x = W_2/W_1$, $y = W_3/W_1$. Differentiation of both sides of Eq. 4 with respect to y and then setting $y = x$, we obtain for the function φ a simple differential equation:

$$\varphi'(x)/\varphi(x) = -\alpha/x; \; \alpha = -\varphi'(1). \qquad [5]$$

Integrating Eq. 5 and using the obvious condition $\varphi(1) = 1$, we obtain $\varphi(x) = x^\alpha$. After substitution of the last expression for the function φ into the first relationship 3 we obtain denoting W_2 simply by W:

$$F(W) = [F(W_1)W_1^\alpha]W^{-\alpha} = \text{Const } W^{-\alpha}. \qquad [6]$$

Thus, power law 1 is deduced analytically from the above formulated similarity principle. Note that the empirical data show that the constant α is close to unity. Therefore, we obtain the expression $B \approx \ln(W/W_0)$ for the total biomass in which W_0 is a characteristic mass scale governed by the phenomena outside the similarity range—for instance, by the nutrition processes of the smallest organisms. So, a direct application of the similarity principle to the total biomass cannot lead to a constructive result.

EXCHANGE INTENSITY

Let us turn now to the property of one of the basic biological processes: the exchange intensity R. Each animal possesses a respiratory organ that absorbs the oxygen (although the available information concerning these organs is surprisingly scanty for many pelagic animals). At first sight (as we shall see later, the situation is in fact much more complicated) the oxygen-absorbing part of the organ could be approximated by a line (if, for instance, the organ has many whiskers), by a surface, or by a volume (containing, like a kidney, many small absorbing balls surrounded by pores). The organ can be characterized by some specific absorbing capacity β_n—i.e., at first sight, correspondingly, by the absorbing capacity of a unit length ($n = 1$), unit area ($n = 2$), or unit volume ($n = 3$). Specific absorbing capacity can depend, of course, on the external conditions: temperature and composition of the ambient water (oxygen saturation, pH, salinity, etc.), time of day, and movement speed of the animal.

Our basic hypothesis is the following: under fixed external conditions, the exchange intensity R is governed only by specific absorbing capacity β_n, the animal body mass W, and its density.

Let us apply dimensional analysis to the problem under consideration. The dimensions $[R]$ of the exchange intensity are the dimensions of the oxygen mass $[m_{O_2}]$ divided by the time dimensions T:

$$[R] = [m_{O_2}]\, T^{-1}. \qquad [7]$$

Furthermore, as we showed previously, the dimensions of specific absorbing capacity are

$$[\beta_n] = [R]\, L^{-n}, \qquad [8]$$

in which L are the length dimensions. Indeed, if, for instance, the oxygen is absorbed by a surface, then the specific absorbing capacity is the absorbing capacity of the unit area, etc. Furthermore, the body mass dimensions are $[W] = M$ and density dimensions are $[\rho] = ML^{-3}$ where M are the mass dimensions. Therefore, the quantity $(W/\rho)^{1/3}$ has the length dimensions, so from Eq. 8 the quantity $\beta_n(W/\rho)^{n/3}$ has the dimensions of R. Thus, the quantity

$$\Pi = R/\beta_n(W/\rho)^{n/3} \qquad [9]$$

is dimensionless. Being dimensionless, the quantity Π remains invariant under the variation of basic measurement units. Let us note now that the units of measurement of β_n, W, and ρ are independent. Therefore, changing each one of these quantities arbitrarily by changing its measurement unit can leave the two other governing parameters invariant. Because Π remains invariant also, it appears that Π does not depend on β_n or on W and ρ. Thus, the quantity Π is constant, so we obtain

$$R = \text{Const}\, \beta_n\, \rho^{-n/3} W^{n/3}. \qquad [10]$$

Denoting $A = \text{Const}\, \beta_n\, \rho^{-n/3}$, $k = n/3$ we reduce relationship 10 to the form of Eq. 2. Thus, relationship 2 is obtained analytically from the basic hypothesis formulated above.

The exchange intensity mass dependence power law 2 was established empirically for the warm-blooded animals in the last century [see the review by Wienberg (1)]. It was obtained in 1950s for crustaceans with $k \approx 0.75$ and also for fishes with average $k \approx 0.8$. The empirical data for various cold-blooded pelagic animals were summarized by Hemmingsen (7) for a huge mass range from 10^{-6} g to 10^8 g. From the average of all data, Hemmingsen obtained the power law of the form of Eq. 2 with $k \approx 0.75$. As Wienberg stressed in his review (1), the exponents of the power law show some difference for various animal species. So, according to Wienberg (8) $k \approx 0.7$ for cyprinodont fishes,

$k \approx 0.75$ for Salmonidae, $k \approx 0.8$ for Cyprinidae and Acipenserida, and $k \approx 0.85$ for carp. According to a review in the paper by Musaeva and Shushkina (9) in the western part of the Pacific, for instance, at 28–30°C, $k \approx 0.35$ for ctenophores, $k \approx 0.5$ for medusas, $k \approx 0.7$ for calanoids and pteropods, $k \approx 0.8$ for chaetognaths, $k \approx 0.85$ for euphausiids, $k \approx 0.95$ for siphonophores, and k is about unity for hyperiids. It should be noted however that the values of k presented are to be considered as preliminary ones only; the study of the interspecies variability of the exponent values requires more detailed investigations with possible data reduction to uniform conditions and good statistics.

FRACTALITY OF THE RESPIRATORY ORGANS

It is essential that the measured values of the exponent k be mainly within the range between $k = 2/3$ (absorption by a surface) and $k = 1$ (absorption in a volume), so that the dimension n of the respiratory organ $n = 3k$, appears to be (cf. the formula 10) not an integer number. It appears to be mainly >2 but <3 (for instance, $n = 2.4$ for Acipenseridae). This fact can be considered as established reliably, independently of the usual natural scatter of the experimental data. We interpret this fact in the following way: the oxygen-absorbing organs of the animals can be approximated by fractal surface with fractal (*Hausdorf*) dimension $n = 3k > 2$.

Remember that fractals are defined (10) as surfaces that are continuous but have very broken form. For them the total areas S_η of all faces of the polyhedrons inscribed into them—for instance, composed from equilateral triangles with the side length η—do not tend to a finite limit at $\eta \to 0$—i.e., at unbounded decrease of face areas. In fact S_η tend to infinity according to a power law

$$S_\eta \sim \sigma \eta^{2-3k},\ N\eta^{3k} \to \sigma. \qquad [11]$$

Here N is the number of the inscribed polyhedron faces and σ is, to within a constant factor, the so-called *Hausdorf* measure of the fractal surface. In other words, the areas of these geometric objects are infinite and the volumes are equal to zero; however, they possess a finite peculiar intermediate characteristic, the *Hausdorf* measure, having the dimension of length to a noninteger degree. Such objects were studied intensively by the mathematicians of the end of the last century and the beginning of the present one. The majority of scientists found them to be mathematical monsters having no applications to real problems of natural sciences. In fact, this is not so. The revival of interest in such objects, and especially the recognition of their importance in applications, is due to the work of B. B. Mandelbrot and especially to a remarkable monograph-essay (10). The very term "fractal" was proposed by Mandelbrot. Because the surface of the respiration organ is a fractal one, the specific absorbing capacity of this organ β_n is to be related not to its area, which is infinite, but to its *Hausdorf* measure. Therefore, the noninteger power of length appears in the dimensions of β_n:

$$[\beta_n] = [R]\, L^{-3k}.$$

We observed here in living organisms the transition from usual two-dimensional surfaces to fractal ones with the *Hausdorf* dimensions $n = 3k > 2$. We think that it can be considered as revealing a general tendency of biological systems to accommodate the membranes of maximal area within minimal volumes; apparently, this tendency reaches to molecular levels. These considerations are in agreement with the results of area measurements (rather than *Hausdorf* measures) of fish branchia, available, for instance, in Klyashtorin's book (11). The

branchia of teleost fishes consist of branchial arcs. From each of these arcs, coupled gill filaments come off, contracting to their ends and possessing multiple transverse secondary plates (having thickness 10–15 μm and height 150–200 μm). These plates are covered by a dense network of capillary vessels. The dependence of branchial area σ on the fish mass is described also by a power relationship

$$\sigma = \alpha W^x$$

analogous to Eq. 2. For sea fishes x is about 0.82 on the average (for *Micropterus dolomien*, $x \approx 0.78$; for tuna $x = 0.85$–0.90). The fact that x exceeds 2/3 can be considered as an indication of the approximation of branchia by fractal surfaces.

If rather rare values of the exponent k in the law 2 falling within the range $1/3 < k < 2/3$ can be considered as reliable ones for some animal species, it can be interpreted as an indication of the fact that for these animals the oxygen-absorbing organs are approximated by fractal lines rather than fractal surfaces with the dimension $n = 3k$ within the range $1 < n < 2$. It means that the total length L_η of the broken lines with the size lengths η inscribed into these continuous curves tend, at $\eta \to 0$, to infinity according to a power law $L_\eta \sim \lambda \eta^{1-n}$ (so that $N\eta^n \to \lambda$, where N is the number of the sides of the broken line and λ is the *Hausdorf* measure of the fractal line). The known form of the copepods with their multiple hair-like whiskers covering all articulations resembles such a possibility.

ON THE PRINCIPLE OF THE DECREASE IN SPECIFIC EXCHANGE INTENSITY WITH INCREASE IN ANIMAL MASS

By specific exchange intensity we understand, as usual, the exchange intensity of an animal per unit of its mass: $I = R/W$. According to Eq. 10 we have

$$I = \text{Const } \beta_n \rho^{-n/3} W^{(n-3)/3}. \qquad [13]$$

Because the values of n are always <3 (the oxygen absorption cannot be more than volume related) it follows from the last relationship that the specific exchange intensity of an animal is decreasing as its mass grows. This general principle is well known to biologists [an impressive discussion of this principle can be found in Wienberg's review (1)]. This principle is explained by one completely general reason—the geometric dimensions of the respiratory organ cannot exceed the dimensions of the animal body.

For some clarification of this important point let us consider an imaginary animal for which this principle is not valid. This animal—we called it "mamot"—is designed in the following way. Its body consists of a very dense film, like the body of the flatfish; however, its respiratory organ is usually branchia situated on the sides of the animal. The width of a growing animal, as well as its branchia, increases but the thickness of its film-body does not change. It is obvious that obtaining the relationships of type 10 for the mamots we have to introduce into the consideration the surface density ρ_s instead of the usual volume density ρ; the dimensions of surface density are $[\rho_s] = ML^{-2}$. Repeating the same arguments as earlier, we obtain in this case

$$R = \text{Const } \beta_n \left(\frac{W}{\rho_s}\right)^{n/2},$$

$$I = \text{Const } \beta_n \rho_s^{-n/2} W^{(n-2)/2}. \qquad [14]$$

It is clear that, since $n > 2$, the specific exchange intensity is growing, not decreasing, with mamot's mass growth. The general validity of the principle of the specific exchange intensity decreasing with animal mass growth is due to the nonexistence of such mamots.

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