Many ecologically important empirical laws governing physiological rates can be derived from a small set of assumptions. The body size of an organism, the density of tissue and the caloric content of tissue comprise a fundamental set of dimensional quantities. Dimensional arguments can account for a wide variety of ecophysiological observations such as the difference between the size dependence of respiration in terrestrial and aquatic organisms and the independence of net growth efficiency on body size.

Recent developments in two areas of physiology suggest that much of the apparent complexity in physiological data can be expressed in terms of a small set of simple principles. One body of evidence is the empirical constancy of certain derived ecophysiological quantities such as net growth efficiency. The other is the robustness in natural populations of the allometric form established in the laboratory for the size dependence of a wide variety of physiological rates. We wish to show that these empirical findings imply a simple but general pattern of organization underlying the life processes of organisms.

Because of the expense and difficulty of conducting ecological studies on field populations, indirect methods have been sought to estimate population production from more easily measured quantities such as respiration (Engelmann, 1966; MacNeill & Lawton, 1970; Banse, 1979). The relative magnitudes of production $P$ and respiration $R$ for a given individual or population combine to yield a value of the production efficiency $E = P/(R + P)$, a quantity of central importance in food chain calculations (Slobodkin, 1966). Based on an examination of published data from 235 species of animals, Humphreys (1979) recently concluded that production efficiency is independent both of organism size and of the absolute magnitude of production. In other words, within groups of animals of a given type, production efficiency is constant (Conrad, 1977; May 1979); also the energetic cost of producing one unit of tissue is the same for rapidly-growing organisms as for slowly-growing ones (Banse & Mosher, 1980).
size independence is found in the production to respiration \((P/R)\) ratio for phytoplankton (Banse, 1976). In the context of our discussion, the remarkable feature of these physiological ratios is that they are dimensionless quantities.

The dependence of physiological rates, such as respiration, on organism size is well-established (Kleiber, 1947; Hemmingsen, 1960; Stahl, 1962; Wilkie, 1977). New reports confirm this result and extend it to cover ecological rates (Fenchel, 1974, 1980; Ikeda, 1977; Blueweiss et al., 1978; Cammen, 1980; Huntley, 1980; Tuomi, 1980). In every case it is found that the size dependence of a rate process can be expressed in allometric form, i.e. as a simple power law. This has been seized on as one of the few manifestations of a universal law in biology (Peters, 1978; Cousins, 1980); it has been exploited as the basis of a mathematical model of the pelagic marine food chain (Platt & Denman, 1977, 1978; Silvert & Platt, 1978, 1980), and as a vehicle for speculation on the trophic dynamics of dinosaurs (Farlow, 1976).

If it is true that the magnitudes of physiological variables can be described as allometric functions of body-size alone, some interesting implications follow. In particular, we can apply the basic theorem of dimensional analysis (Bridgeman, 1931) that all natural laws can be expressed as relationships between dimensionless quantities. Since physiological variables involve three distinct dimensions, namely mass, length and time, it follows that physiological laws must involve three independent dimensional quantities (three quantities \(A, B, \text{ and } C\) are dimensionally independent if \(A^aB^bC^c\) is dimensionless only when \(a = b = c = 0\); since we find that just one of these (the mass of the organism) can account for much of the variability in the physiological rates, the other two may be taken as universal physiological constants. An analogous argument in special relativity is that because two independent dimensions (length and time) are involved, there must be a universal constant (the velocity of light) to relate them. For physiological problems there are two basic quantities which play such a fundamental role in the physiological processes of living organisms that it seems essential to include them in any realistic model, no matter how simple; these are the energetic content and the density of living tissue.

The caloric content of tissue is approximately 4000 J/kg. Since 1 J = 1 kg m^2/sec^2, this constant can be written as \(C = 4000 \, \text{m}^2/\text{sec}^2\), and in dimensional notation \([C] = L^2T^{-2}\). The density of tissue on the other hand may be defined in two ways, as mass density or as weight density. From the viewpoint of how an organism functions, the relative importance of these two quantities depends on its environment. For aquatic animals, particularly those which swim, the energetic expenditure is closely related
to the inertia of the water which they displace as they move, which is
determined by the mass density of water. For a terrestrial organism the
effects of gravity are much more important, and the weight of the organism,
which depends on the weight density of tissue, is a crucial physiological
quantity. The mass density of water is \( D = 1000 \text{ kg/m}^3 \), so \([D] = ML^{-3}\).
The weight density of tissue is approximately 10 000 N/m^3, and it has
dimensions \([W] = ML^{-2}T^{-2}\).

For aquatic organisms we assume that all physiological quantities depend
to first order on only the mass \( m \) and the dimensional constants, \( C \) and
\( D \), while for terrestrial organisms we assume that the two fundamental
constants are \( C \) and \( W \). It follows from dimensional analysis that the
exponents in the allometric laws relating physiological quantities are
uniquely determined by the dimensions of the fundamental constants, and
thus these exponents can be derived from basic assumptions about the
physiological principles governing the structure and function of living
organisms.

The actual calculation of dimensional equations is straightforward and
is described in many textbooks; the classic reference is Bridgeman (1931).
A number of examples are worked out in detail in Günther's (1975)
important paper on biological similarity, so only a brief description will be
given here. The essential result of dimensional analysis in the present
context is that given three independent dimensional quantities \( A, B, \) and
\( C \), any physiological quantity \( Q \) can be expressed in the form
\[
Q = fA^a B^b C^c
\]
where \( f, a, b, \) and \( c \) are dimensionless numbers and the three exponents \( a, b, \) and \( c \) are uniquely determined by dimensional considerations alone. The
actual values are determined by balancing the powers of each of the
fundamental dimensions of mass, length, and time appearing on each side
of the equation. For example, respiration has units J/sec and dimensions
\([R] = ML^2T^{-3}\). For aquatic animals respiration depends on the mass \( m \),
the caloric content of tissue \( C \), and the mass density of water \( D \). Balancing
the dimensions leads to an equation of the form
\[
ML^2T^{-3} = (M)^a (L^2T^{-2})^b (ML^{-3})^c
\]
and equating the powers of each dimension gives
\[
M: 1 = a + c
L: 2 = 2b - 3c
T: -3 = -2b
\]
which has the unique solution $a = \frac{2}{3}$, $b = \frac{2}{3}$, and $c = \frac{1}{3}$. Thus for aquatic organisms the theory predicts that respiration should vary as the $\frac{2}{3}$ power of body size. For terrestrial animals we replace the mass density of water, $D$, by the weight density of tissue, $W$, to obtain

$$ML^2T^{-3} = (M)^a(L^2T^{-2})^b(ML^{-2}T^{-2})^c$$

so that we get

$$M: 1 = a + c$$
$$L: 2 = 2b - 2c$$
$$T: -3 = -2b - 2c$$

with the unique solution $a = \frac{3}{4}$, $b = \frac{5}{4}$, $c = \frac{1}{4}$. Thus we find a slightly higher power of body mass for terrestrial organisms, reflecting the fact that gravity imposes an additional metabolic cost on land animals and plants. This is consistent with much of the research that has been carried out, and Economos (1979) has recently noted that among mammals the exponent appears to be $\frac{3}{4}$ for terrestrial species but falls to $\frac{5}{4}$ for marine mammals.

Physiological rates are commonly expressed in units of sec$^{-1}$ (e.g. mortality rates), or as specific rates in units of J kg$^{-1}$ sec$^{-1}$ (e.g. specific respiration). Dimensional analysis shows that the mass dependence for either type of quantity must be allometric with exponent $-\frac{1}{3}$ for aquatic and $-\frac{1}{4}$ for terrestrial organisms. This result is consistent with the available empirical evidence. Fenchel (1974) obtains a universal exponent of $-0.28$, but gives no confidence interval on the estimate; a more detailed and recent analysis by Banse & Mosher (1980) points to a value of $-0.37$, and the value $-0.33$ falls well within their interval estimate.

We do not insist that organism mass itself is necessarily the fundamental scale for ecophysiological processes. The possibility remains open that some correlate of organism mass, such as mass of carbon, surface area (Harding, 1977) or total caloric content is the true absolute scale. If this is the case, the allometric dependence is still preserved, but with a smaller residual variance (Derome, 1977). The justification for using the mass itself from among these covariates is that it is the only independent variable for which we have sufficient data to make a general survey.

Two potential complications deserve comment. One is that the allometric laws are usually established at a particular point in the organism's life history, such as the age $T$ and size $M$ at first maturity (Banse & Mosher, 1980); what then can we say about the organism at other ages and sizes? Any function $f(m, t)$ of the dimensional variables $m$ and $t$ can be written as a function $F(m/M, t/T)$ of the dimensionless variables $m/M$ and $t/T$. Thus the allometric laws should be valid at any point in the life cycle, and
relationships established by integrating or averaging over the life cycle, or part of the life cycle, should be equivalent to those established for instantaneous rates. However, to the extent that profound differences in life history strategies are involved, the residual variance can be expected to increase, and it is not surprising that Banse & Mosher (1980) find their best fits by concentrating on one stage of the life cycle.

The second complication is that two different kinds of data exist: those dealing with individual organisms and those dealing with effects integrated over populations of animals. In the case of the latter, natality has to be considered as a component of growth and there is a mortality term that does not occur in the former: once an individual organism is dead, the growth efficiency no longer has meaning. A corollary of the foregoing is that dimensional consistency requires that specific mortality rates scale in the same way as specific growth rates, with the result that properties of individuals must scale in the same way as the corresponding properties of the populations of which they are a part. The same point can be perceived as a direct consequence of the continuity equation for populations in equilibrium (Banse & Mosher, 1980).

Even with these complications out of the way, one cannot, of course, ignore the values of biological insight in applying the general arguments developed in this paper. For example, Cammen (1980) has recently published a study of ingestion rates of invertebrates as a function of size. The ingestion rate may be expressed in terms of mass (kg sec\(^{-1}\)) or of energy (J sec\(^{-1}\)); both should be given by allometric laws having the same size dependence according to the arguments presented here. However, the different size classes which he studied consumed prey of quite different organic content, so that it would be impossible for both allometric laws to hold at the same time. He found that the specific energy intake was very well described by an allometric law (with an exponent of \(-0.26\)), but the rate of mass ingestion was erratic.

Against the background we have sketched here, the conclusion of Humphreys (1979) that production efficiency is independent of body size follows as a natural and inevitable consequence of dimensional considerations. Similarly, if our arguments are valid, Banse's (1979) failure to find any evidence for a size dependence of net growth efficiency may be taken as supporting evidence for a fundamental similarity between living organisms as revealed by the constancy of these dimensionless ratios.

REFERENCES


HEMMINGSEN, A. M. (1960). *Reports of the Steno Memorial Hospital, Copenhagen 9 (Part 2)*, p. 110.


