limited and surface molecules have insufficient time to form complementary alignments on opposing membranes, the steric force was always observed. Consequently, these observed molecular rearrangements can be directly correlated to the lateral mobility of the receptor and the resulting increase in intermembrane adhesion, demonstrating the importance of surface mobility in the strength of cell adhesion.

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A Mass Transfer Explanation of Metabolic Scaling Relations in Some Aquatic Invertebrates and Algae

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Chemical engineering theory can be used in accounting for the broad range of metabolic scaling exponents found in some aquatic invertebrates and algae. Delivery of metabolically important compounds to these organisms occurs by diffusion through a boundary layer. Dimensionless relations (Sherwood-Reynolds number functions) demonstrate the degree to which water motion and organism size affect mass transfer, and ultimately, metabolic rate. Derivation of mass exponents in the range 0.31 to 1.25 for simple geometries such as plates, spheres, and cylinders directly follows from knowledge of the Sherwood-Reynolds number relations. The range of exponents predicted is that found by allometric studies of metabolic rate in these organisms.

THE RELATION BETWEEN BODY SIZE and metabolic rate in organisms is a subject of great interest to physiologists and ecologists because many organisms increase in size by one to several orders of magnitude during ontogeny, and life on Earth spans 19 orders of magnitude in mass (*1*). The relation between organism mass (M) and metabolic rate (R) is nonlinear and usually described by a power-law function: $R = aM^b$, where a is termed the mass coefficient and b the mass exponent (*2*). The nature of the allometric relation between metabolic rate and body size in homeotherms has been intensively examined (*3*). Many explanations for the clustering of interspecific mass exponents around a value of 0.75 (Kleiber's Rule) have been offered (*4*) although there is disagreement as to whether the data support the 3/4 power law or a mass exponent statistically indistinguishable from 0.67 (*5*). The situation for some aquatic invertebrates and algae is less well examined or understood. Mass exponents range from 0.47 to 1.28, with no obvious clustering around 0.75 or 0.67 [Table 1; (*6*)]. These empirical observations provoke the question of why there is such large variation in mass exponent in these taxa.

Many lower aquatic organisms have been shown to be sensitive to the rate of fluid mixing near their exchange surfaces (*7*). Such organisms are usually oxyconformers that lack mechanisms for active ventilation of exchange surfaces. They are dependent on diffusion through a boundary layer (*8*) for uptake of metabolically important compounds such as oxygen, and in the case of photosynthetic organisms or symbiotic associations, bicarbonate ion–carbon dioxide. A particularly powerful means of examining flow effects on metabolic rate is to make both the fluid convection and metabolic rate dimensionless by use of the Reynolds number and the Sherwood number (*9*). The Reynolds number ($\mathrm{Re} = \rho UW/\mu$) expresses the ratio of inertial forces to viscous forces that govern fluid motion around an organism, where ρ is fluid density [dimensions: mass (M) length $(L)^{-3}$], μ is dynamic viscosity [mass (M) length $(L)^{-1}$ time $(T)^{-1}$], W is organism characteristic dimension (L), and U is flow speed ($L\ T^{-1}$). The Sherwood number ($\mathrm{Sh} = h_{\mathrm{m}}W/D$) is a dimensionless index of metabolism; it is the ratio of mass transfer assisted by fluid motion to that which would occur if diffusion through a still layer of fluid was the only mechanism of transport to the organism, where h_{m} is the mass transfer coefficient ($L\ T^{-1}$), and D is the diffusion coefficient of the dissolved species [$L^2\ T^{-1}$; (*10*)].

Plots of Sh (ordinate) − Re (abscissa) yield information on the degree to which water motion affects mass transfer (*11*). The relation is often expressed as a power law ($\mathrm{Sh} = c\mathrm{Re}^d$). Flow-size exponents ($d$) range from 0.5, for mass transfer through a laminar boundary layer, to greater than 0.8, for transfer through a turbulent boundary layer (*11*). This mode of analysis has been infrequently applied to aquatic organisms, but flow exponents consistent with both laminar and turbulent boundary layer transfer have been observed for cnidarians (*9*). Because organism size affects Re, and Re affects metabolic rate (disguised as Sh), it is possible to examine the consequences of size in aquatic organisms where this sort of physicochemical regulation of metabolic rate obtains (Fig. 1).

I made theoretical predictions of metabolic scaling for organisms possessing some simple geometries of uptake surface (flat plate, sphere, and cylinder) subject to assumptions of laminar or turbulent flow in the organismic boundary layer (Table 2). These geometries were chosen because many aquatic invertebrates and algae have similar shapes. Solving the simultaneous equations $\mathrm{Re} = \rho/UW/\mu$, $\mathrm{Sh} = c\mathrm{Re}^d$, and $\mathrm{Sh} = h_{\mathrm{m}}W/D$, for h_{m} (*12*) gives

$$h_{\mathrm{m}} = \frac{c\,D\,W^{d-1}\,\rho^d\,U^d}{\mu^d} \qquad (1)$$

Substituting for h_{m} in the generalized flux (metabolic) equation (*11*) and simplifying

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the result gives the mass exponent (b) relating biomass (M) to metabolic rate [R (*13*)]. The characteristic dimension, W, was taken to be equal to the height normal to the substrate, diameter, and length of right cylindrical, spherical, and plate-like organisms, respectively. Biomass (M) was assumed proportional to biovolume (*14*). For all geometries, flow-size scaling exponents (d) were assumed equal to 0.5 for laminar flow and 0.8 for turbulent flow. In addition, for turbulent flow, a third calculation was made assuming that the organism projected a substantial depth into a logarithmic benthic boundary layer (*15*).

Note that laminar flow results in smaller values for the mass exponent compared to turbulent flow, except for plate-like geometries. The greatest mass exponent is obtained for organisms assumed large enough to project appreciably in the substrate's logarithmic boundary layer. Organism shape and flow regime thus have a direct effect on the value of mass exponents obtained. It is intriguing that the range of mass exponents presented in Table 1 encompasses the range predicted by this chemical engineering approach (Table 2). At present, data necessary for a direct test of the theory exist only for two species of cnidarians. For *Alcyonium siderium*, an octocoral, the predicted value of the mass exponent is 0.69 based on data in (*7*); the observed value is 0.88 (Table 1). For the sea anemone, *Metridium senile*, the predicted value is 0.73 to 1.02 based on data in (*7*); the observed range is similar (Table 1).

Almost all mass exponents in the literature for aquatic invertebrates and algae were calculated from experiments where the degree of water motion was not quantified, and thus it is difficult to make specific assessments about how well this theory predicts mass exponents for a specific taxon. However, these results signify that given the physicochemical limitations of extracting metabolites from moving water, one should not expect mass exponents for these organisms to cluster around a specific value. The Sh/Re relations can be readily calculated if the degree of water motion in a metabolic chamber is quantified along with the absolute metabolite concentration and organism size (*10*). Dimensional analysis of mass transfer to aquatic invertebrates and algae provides a powerful alternative to traditional allometric methods in

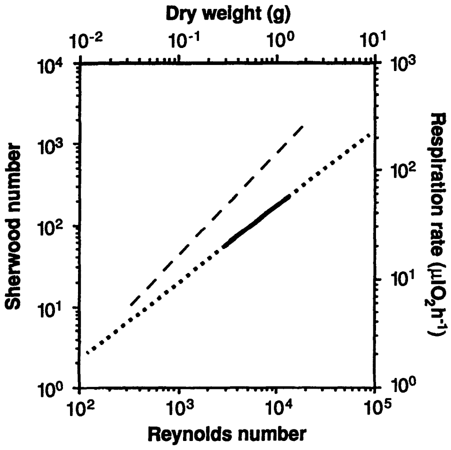

Fig. 1. Two means of examining metabolic scaling relations in aquatic invertebrates and algae. Data shown are for the octocoral, *Alcyonium siderium* [see Sebens in (*6*) and Patterson and Sebens in (*7*)]. The more traditional method plots body size (upper abscissa) against metabolic rate (right-hand ordinate). The slope of the dashed line is the mass exponent b. Another method that yields a more general analysis of the effects of both size and flow on metabolic rate is given by the Sherwood number as a function of the Reynolds number. The slope of dotted and solid line is the flow-size exponent d. The solid (dotted) portion indicates the limit of experimental (predicted) data, respectively.

Table 1. Mass exponents for some aquatic invertebrates and algae: r, respiration rate; p, photosynthetic rate; g, growth rate; and i, ingestion rate. If no specific name is given, data are for a pooled interspecific assemblage.

Organism	Mass exponent (b)	Reference from (*6*)
Marine phytoplankton (r)	0.92	Laws (1975)
Marine phytoplankton (g)	0.89	Laws (1975)
Acanthophora spicifera (red alga) (r)	0.83	Jokiel and Morrissey (1986)*
Acanthophora spicifera (red alga) (p)	0.94	Jokiel and Morrissey (1986)*
Protozoa (r)	0.70	Zeuthen (1953)
Protozoa (r)	0.75	Fenchel and Finlay (1983)
Pocillopora damicornis (scleractinian coral) (p)	0.84	Jokiel and Morrissey (1986)*
Pocillopora damicornis (scleractinian coral) (r)	0.99	Jokiel and Morrissey (1986)*
Fungia scutaria (scleractinian coral) (p)	0.68	Krupp (1982)*
Fungia scutaria (scleractinian coral) (r)	0.79	Krupp (1982)*
Metridium senile (sea anemone) (r)	0.77–0.86	Walsh and Somero (1981)
Metridium senile (sea anemone) (r)	0.81	Sebens (1981)
Metridium senile (sea anemone) (r)	0.82–0.94	M. Lesser
Anthopleura elegantissima (sea anemone) (r)	0.77–0.83	Shick *et al.* (1979)
Anthopleura elegantissima (sea anemone) (r)	0.54–0.57	Shick *et al.* (1979)
Alcyonium siderium (octocoral) (r)	0.88	Sebens (1987)
Mnemiopsis leidyi (ctenophore) (r)	0.96–1.28	Kremer (1978)
Platyhelminthes (flatworms) (r)	0.67–1.0	Various authors in Calow (1987)
Nematodes (roundworms) (r)	0.72	Klekowski *et al.* (1972)
Nematodes (roundworms) (r)	0.76	Banse (1982)
Polychaetes (annelid worms) (i)	0.47, 0.73	Cammen (1987)
Polychaetes (annelid worms) (r)	0.85	Cammen (1987)
Echinoids (sea urchins) (r)	0.64	Lawrence and Lane (1982)
Holothuroids (sea cucumbers) (r)	0.85	Lawrence and Lane (1982)
Holothuria forskali (sea cucumber) (r)	0.60	Astall and Jones (1991)

*Computed from data in source.

Table 2. Predicted mass exponents (b) relating body size to metabolic rate for aquatic organisms. Exponents are derived algebraically from Sherwood-Reynolds number functions for laminar and turbulent flow in the organism's boundary layer. Log layer mass exponents are those obtained in turbulent flow in a logarithmic boundary layer (*15*), when there is only a very weak size dependence for the mass transfer coefficient, h_m. For cylinders, radius is assumed proportional to height$^{(\text{radial exponent})}$. Thickening cylinders get proportionately wider as height increases (radial exponent > 1). Thinning cylinders get proportionately thinner as height increases (radial exponent < 1). No mass exponent for log layer flow was calculated for the plate because unit thickness was assumed (*14*).

Shape	Radial exponent	Flow condition	Mass exponent (b)
Sphere		Laminar	0.50
		Turbulent	0.60
		Log layer	0.67
Cylinder	0.5	Laminar	0.75
	0.5	Turbulent	0.90
	0.5	Log layer	1.00
Thinning	0.9	Laminar	0.54
	0.9	Turbulent	0.64
	0.9	Log layer	0.71
Isometric	1.0	Laminar	0.50
	1.0	Turbulent	0.60
	1.0	Log layer	0.67
	1.1	Laminar	0.47
	1.1	Turbulent	0.56
	1.1	Log layer	0.63
Thickening	2.0	Laminar	0.31
	2.0	Turbulent	0.36
	2.0	Log layer	0.40
Flat plate		Laminar	1.25
		Turbulent	1.10

investigations of the effect of size on metabolic rate.

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8. The boundary layer is a region of fluid near a surface where a gradient in momentum (flow speed) exists because of fluid viscosity. Viscous dissipation robs momentum from a moving fluid, converting kinetic energy into heat. A concentration gradient (diffusional boundary layer) also exists near a surface surrounded by a fluid that is absorbing or releasing dissolved materials. For biologically important molecules (for example, oxygen) diffusing in water, the ratio of momentum boundary layer thickness to diffusional boundary layer thickness is about 8. For both types of boundary layers, as flow speed increases, boundary layer thickness decreases.
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10. A flux of dissolved material in a convecting fluid to an organism can be generally given by F_c (mol T^{-1}) $= h_m \Delta C A$, where ΔC is the concentration difference between the organism and the free-stream environment (mol L^{-3}), and A is surface area available for uptake (L^2). In a stagnant fluid, delivery will be by diffusion, and the flux is thus: $F_s = D \Delta C A W^{-1}$, assuming the boundary layer thickness is proportional to organism size. Sh is the dimensionless ratio, F_c/F_s.
11. F. M. White, *Heat and Mass Transfer* (Addison-Wesley, New York, 1988), pp. 270–367 and 643. These indices follow directly from a dimensional analysis of convective mass transfer using the Buckingham Pi theorem.
12. Algebraic solutions to scaling exponents for various assumptions of allometry and flow regime were explored with the use of the computer language Mathematica, running under a local kernel on an Apple Macintosh IIcx.
13. The surface area available for uptake is assumed $\propto W^2$.
14. For a sphere, $M \propto W^3$. For a cylinder, $M \propto r^2 W$, where $r \propto W^{\text{radial exponent}}$. For geometric scaling, radial exponent = 1. For a cylinder that gets proportionately thinner (thicker) as it grows, radial exponent <1 (>1), respectively. For a plate that does not get appreciably thicker as it lengthens (for example, an encrusting invertebrate or algal blade), $M \propto W^2$.
15. The relation between flow speed and height above the bottom is often logarithmic in benthic environments [P. A. Jumars and A. R. M. Nowell, *Am. Zool.* **24**, 45 (1984)]. Thus the average flow speed experienced by an organism growing up into the substrate's boundary layer will scale as the logarithm of its own characteristic dimension, W. Dimensional analysis of the Sh-Re relation now yields $h_m \propto W^{d-1} [\log(W)]^d$. This relation forces almost independent scaling between the mass transfer coefficient and size; we can thus approximate this relation as $h_m \propto W^0$. T. Daniel (personal communication) derived this effect in the context of heat transfer to intertidal organisms.
16. I thank T. Daniel, A. Heusner, P. Jokiel, C. Jordan J. Kingsolver, M. Lesser, W. S. Price, L. Sanderson, K. Sebens, V. Weis, S. Wing, and the students of the 1990 Physical Biology course, Friday Harbor Laboratories, University of Washington, for helpful discussion. P. Basser gave me the initial inspiration to explore the chemical engineering literature and technical advice concerning *Mathematica*. Supported by NSF grants OCE-87-16427 and OCE 90-16721 (GLOBEC), National Oceanic and Atmospheric Administration National Undersea Research Program Aquarius habitat mission 88-6, and Nitrox SCUBA research cruise to the Florida Keys, and a Faculty Research Award from the University of California, Davis.

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Behavioral Hypothermia and Survival of Hypoxic Protozoans *Paramecium caudatum*

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Hypoxia has been shown to elicit behavioral hypothermia in a number of different metazoan species, all with nervous systems. The protozoan, *Paramecium caudatum*, has no nervous system and was not expected to display behavioral hypothermia. However, this species was also found to select a lower temperature in a thermal gradient under hypoxic conditions. This response proved to be beneficial as survival of hypoxic paramecia was greatly increased at lower temperatures. This unicellular species may provide a useful model to investigate the cellular and molecular basis of adaptive thermoregulatory behavior.

HYPOXIA CAUSES BODY TEMPERATURE to fall in a number of different animals, from crayfish to mammals (*1*). In all the animals previously studied, thermoregulation is controlled by a nervous system. In mammals, hypoxia induces hypothermia by decreasing heat production and increasing heat loss. In ectotherms, hypoxia induces behavioral selection of a lower ambient temperature. Hypoxia-induced hypothermia is beneficial, primarily because it lowers metabolic rate, and thus O_2 need, when O_2 availability is limited. Hypothermia should enhance survival, but this has never been directly tested. The purpose of our study was to determine whether hypoxia-induced hypothermia can occur in an organism without a nervous system (for example, the protozoan *Paramecium caudatum*) and whether the response would enhance survival. Two specific hypotheses were tested: (i) Hypoxia causes paramecia to select a lower temperature in a thermal gradient. (ii) Survival of hypoxic paramecia is increased at lower temperatures.

To test the first hypothesis, selected temperature (T_s) of paramecia was determined in an aquatic thermal gradient (0.4° ± 0.6° to 34.6° ± 1.4°C) placed in a petri dish at different ambient oxygen pressures ($P\text{O}_2$) (*2*). Thermocouples were placed at each end of the gradient and ten intermediate locations for measuring gradient temperatures.

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