CHAPTER ONE

The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems

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Introduction

Body size is the single most important axis of biodiversity. Organisms range in body size over about 22 orders of magnitude, from tiny bacteria such as *Mycoplasma* weighing 10^{-13} g to giant *Sequoia* trees weighing 10^9 g. Such size variation is a pervasive feature of aquatic ecosystems, where the size spectrum spans at least 20 orders of magnitude, from the smallest free-living bacteria at about 10^{-12} g to the great whales at about 10^8 g (e.g., Sheldon *et al.*, 1972; Kerr & Dickie, 2001). Nearly all characteristics of organisms, from their structure and function at molecular, cellular and whole-organism levels to ecological and evolutionary dynamics, are correlated with body size (e.g., Peters, 1983; McMahon & Bonner, 1983; Calder, 1984; Schmidt-Nielsen, 1984). These relationships are almost always well described by allometric equations, power functions of the form:

$$Y = Y_0 M^b \tag{1.1}$$

where Y is a measure of some attribute, Y_0 is a normalization constant, M is body mass, and b is a scaling exponent (Thompson, 1917; Huxley, 1932). A longstanding puzzle has been why empirically estimated values of b are typically close to multiples of 1/4: 3/4 for whole-organism metabolic rates (Savage *et al.*, 2004a) and rates of biomass production (Ernest *et al.* 2003), −1/4 for mass-specific metabolic rates and most other biological rates such as the turnover of cellular constituents (Gillooly *et al.*, 2005a), population growth rates (Savage *et al.*, 2004b) and rates of molecular evolution (Gillooly *et al.*, 2005b), and 1/4 for biological times such as cell cycle time, lifespan and generation time (Gillooly *et al.*, 2001, 2002).

Recent theoretical advances in biological scaling and metabolism represent tremendous progress in solving this puzzle. The pervasive quarter-power

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exponents are due to the fractal-like design of the networks and surfaces that supply energy and materials used by cells in biological metabolism (West *et al.*, 1997, 1999). One additional advance has strengthened and extended this theoretical foundation. The well documented exponential effect of temperature on metabolic rate can be incorporated by adding a Boltzmann–Arrhenius factor, $e^{-E/kT}$, to Eq. (1.1). Whole organism metabolic rate or production, P, can then be expressed as:

$$P = P_0 M^{3/4} e^{-E/kT} \tag{1.2}$$

where E is the activation energy, k is Boltzmann's constant (8.62×10^{-5} eV/K), and T is absolute temperature in degrees Kelvin (Gillooly *et al.*, 2001, 2002). Therefore, mass-specific metabolic rate, B, and most other rates can be expressed as:

$$B = P/M = B_0 M^{-1/4} e^{-E/kT} \tag{1.3}$$

where B_0 is another normalization constant. The addition of temperature to this model proved critical to the development of a metabolic theory of ecology (MTE) (Brown *et al.*, 2004). MTE incorporates these fundamental effects of body size and temperature on individual metabolic rate to explain patterns and processes at different levels of biological organization: from the life histories of individuals, to the structure and dynamics of populations and communities, to the fluxes and pools of energy and materials in ecosystems. Brown *et al.* (2004) began to develop MTE in some detail, made many testable predictions, and evaluated some of these predictions, using data compiled from the literature for a wide variety of ecological phenomena, taxonomic and functional groups of organisms, and types of ecosystems.

Here we apply the metabolic theory of ecology to focus on some important correlates and consequences of body size in marine and freshwater ecosystems. In so doing, we build on a rich tradition that extends back over a century. Many of the most eminent aquatic ecologists have contributed. Several themes have been pursued. With respect to population dynamics and species interactions, this includes work from Gause (1934), Hutchinson (1959), Brooks and Dodson (1965), Paine (1974), Leibold and Wilbur (1992) and Morin (1995, 1999). With respect to distributions of biomass, abundance and energy use across species, this includes work from Sheldon and Parsons (1967), Sheldon *et al.* (1972, 1977), Cyr and Peters (1996) and Kerr and Dickie (2001). With respect to food webs, this includes work from Lindeman (1942), Odum (1956), Hutchinson (1959), Carpenter and Kitchell (1988), Sprules and Bowerman (1988) and Cohen *et al.* (2003). Finally, with respect to nutrient relations and ecological stochiometry, this includes work from Redfield (1958), Schindler (1974), Wetzel (1984) and, more recently, Sterner and Elser (2002). Many of these themes have been addressed by the contributors to this volume.

MTE provides a conceptual framework for understanding the diverse effects of body size in aquatic ecosystems (see also Peters, 1983; Cyr & Pace, 1993; Cyr, 2000; Kerr & Dickie, 2001; Gillooly *et al.*, 2002; Brown & Gillooly, 2003; Brown *et al.*, 2004; Allen *et al.*, 2005; Gillooly *et al.*, 2006). MTE is based on well-established fundamental principles of physics, chemistry and biology, makes explicit, testable, quantitative predictions, and synthesizes the roles of individual organisms in populations, communities and ecosystems. The literature on body size and metabolism in general, and on aquatic ecosystems in particular, is too vast to summarize here. The references cited above and below are just a few of the relevant publications, but they will give the interested reader a place to start.

Background

For what follows, we will assume that Eqs. (1.2) and (1.3) capture the fundamental effects of body size and temperature on metabolic rate. As the examples below will show, these equations do not account for all observed variation. They do, however, usually account for a substantial portion of the variation within and across species, taxonomic and functional groups, and in ecosystems where body size varies by orders of magnitude. Moreover, fitting Eq. (1.2) or (1.3) to data generates precise quantitative predictions that can be used as a point of departure to evaluate the many factors that may contribute to the residual variation. These include experimental and measurement error, phylogenetic and environmental constraints, influences of stoichiometry, and the effects of acclimation, acclimatization and adaptation. Since we present Eqs. (1.2) and (1.3) as assumptions, it is important to state that MTE and the underlying models for the scaling of metabolic rate and other processes with body size and temperature have received both enthusiastic support and severe criticism. We will not cite or review these issues and references here, but simply state that we are confident that most substantive criticisms have been or will be answered, and that the theory is fundamentally sound.

This volume and this chapter are on the effects of body size on the structure and dynamics of aquatic ecosystems. Metabolic rate, and other rate processes controlled by metabolic rate, are strongly affected by both body size and temperature. We can 'correct' for variation due to environmental or body temperature by taking logarithms of both sides of Eq. (1.3) and rearranging terms to give:

$$\ln(Be^{E/kT}) = (-1/4)\ln(M) + \ln(B_0) \tag{1.4}$$

where k is Boltzmann's constant ($= 8.62 \times 10^{-5}$ eV/K) and E is the average activation of metabolic reactions (~0.65 eV; see Brown *et al.*, 2004). Equation (1.4) shows that, after correcting for temperature, $\ln(Be^{E/kT})$ is predicted to be a linear function of $\ln(M)$ with a slope of $-1/4$. Other allometric scaling relations can be similarly analyzed using equations that have different values for the normalization constants and sometimes for the exponents, e.g. 3/4 for whole-organism metabolic rate (Eq. (1.2)). In aquatic ecosystems, it is reasonable to assume that the body temperature of an ectotherm is equal to water temperature. Thus, coexisting species of prokaryotes, phytoplankton, protists, zooplankton, other invertebrates and fish can usually be assumed to have the same body temperature. Additionally, since daily and seasonal variations in water temperatures are relatively modest, it is often reasonable to take some average value. Correction for variation in temperature is particularly important when comparing locations or seasons that differ substantially in water temperature, and when comparing ectotherms and endotherms, which differ substantially in body temperature. In this chapter we have followed these procedures, and corrected for temperature variation when appropriate.

Individual level: metabolic rate, production and life-history traits

We begin at the level of the individual organism. The first question is whether metabolic rate varies with body size as predicted by Eqs. (1.2) and (1.3). In Fig. 1.1, we present temperature-corrected data for whole-organism metabolic rates of aquatic unicellular eukaryotes, invertebrates and fish. Note that the predicted slopes of these relationships are close to 3/4. It is apparent that the observed values cluster around and do not differ significantly from these slopes. These data confirm a large literature on the body-size dependence of metabolic rates in a wide variety of aquatic organisms, from unicellular algae and protists to invertebrates and fish (e.g., Hemmingsen, 1960; Fenchel & Finlay, 1983). Note also that there is considerable variation around these relationships. It may appear to be random scatter, but further analysis would probably suggest that much of it is due to some combination of experimental error, differences in techniques, evolutionary constraints related to phylogenetic relationships,

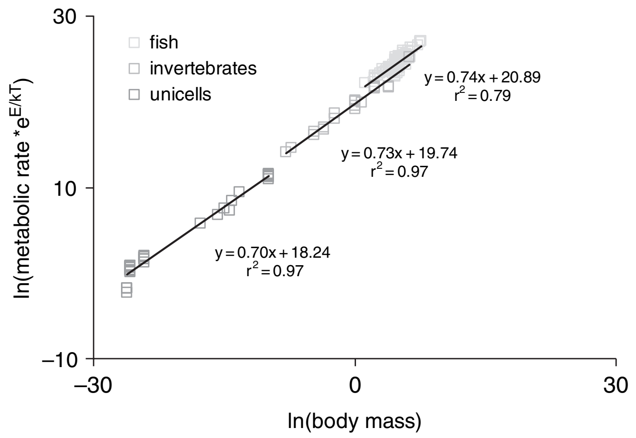

Figure 1.1 The relationship between temperature-corrected metabolic rate, measured in watts, and the natural logarithm of body mass, measured in grams. Metabolic rate is temperature corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Gillooly *et al.* (2001).

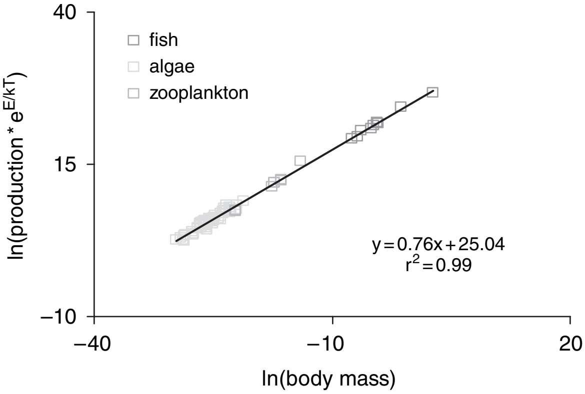

Figure 1.2 The relationship between temperature-corrected biomass production rate, measured in grams per individual per year, and the natural logarithm of body mass, measured in grams. Metabolic rate is temperature corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Ernest *et al.* (2003).

body plan, stoichiometry, as well as acclimatization, acclimation and adaptation to different environmental conditions.

The metabolism of an individual organism reflects the energy and material transformations that are used for both the maintenance of existing structure and the production of new biomass. Within taxonomic and functional groups, organisms allocate a relatively constant fraction of metabolism to production (Ernest *et al.*, 2003). In endotherms, this is typically less than 10%, but in ectotherms it tends to be of the order of 50%. Consequently, rates of whole-organism biomass production are predicted to scale according to Eq. (1.2), with an allometric exponent of 3/4, the same as whole-organism metabolic rate. Figure 1.2 shows that the temperature-corrected rates of production for algae, zooplankton and fish cluster closely around a common allometric scaling relation with an exponent of 0.76, almost identical to the theoretically predicted value of 3/4. This implies that the relative allocation of energy and materials to biomass production is indeed similar across most organisms.

It follows from the above discussion and Eq. (1.3) that the mass-specific rate of ontogenetic growth and development should scale as $M^{-1/4}$, and therefore that developmental time should scale as $M^{1/4}$. In Fig. 1.3, we present two examples, rates of ontogenetic development of zooplankton eggs in the laboratory (panel A) and fish eggs in the field (panel B) (Gillooly *et al.*, 2002). This is a nice model system, because the mass of the egg indicates not only the size of the hatchling, but also the quantity of resources stored in the egg and expended in metabolism during the course of development. Note that the data for fish eggs in the field give an exponent, −0.22, very close to the predicted −1/4, but there is considerable unexplained variation. This is hardly surprising, giving the inherent difficulties in measuring both development time and temperature under field conditions. The data for development rate of freshwater zooplankton eggs measured under controlled conditions in the laboratory give an allometric exponent, −0.26, essentially identical to the predicted −1/4. The regression explains 84% of the observed

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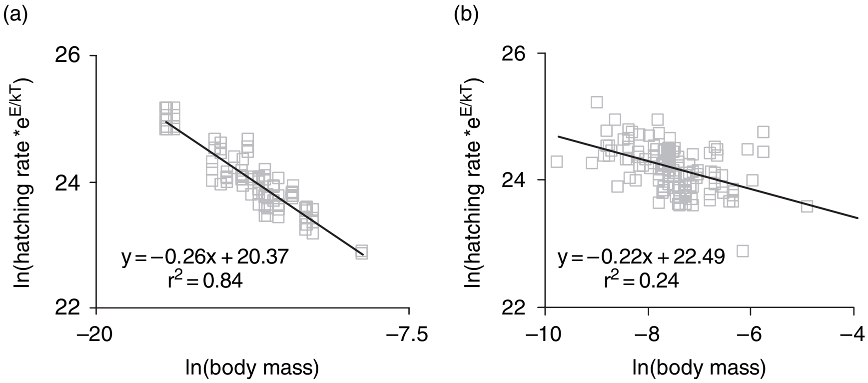

Figure 1.3 The relationship between temperature-corrected hatching rate, measured in 1/days, and the natural logarithm of body mass, measured in grams, for zooplankton eggs in the laboratory (panel A) and fishes in the field (panel B). Hatching rate is temperature-corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Gillooly *et al.* (2002).

variation in the temperature-corrected data. Interestingly, for ontogenetic growth rates of adult zooplankton, Gillooly *et al.* (2002) have shown that stoichiometry, specifically the whole-body C:P ratio, explains most of the variation that remains after accounting for the effects of body size and temperature. This supports the 'growth-rate hypothesis' and the large body of theoretical and empirical work in ecological stoichiometry (Elser *et al.*, 1996; Elser *et al.*, 2000; Sterner & Elser, 2002). The growth-rate hypothesis proposes that differences in the C:N:P ratios of organisms are due to differences in the allocation of phosphorus-rich RNA necessary for growth. For these zooplankton, living in freshwater where phosphorus may be the primary limiting nutrient, rates of metabolism and ontogenetic growth are limited by whole-body concentrations of RNA. Not only does the C:P ratio explain most of the residual variation in development rates as a function of body size in zooplankton, but it is also related to the body-size dependence of development itself. Whole-body concentrations of phosphorus-rich RNA scale inversely with body size, with an exponent of approximately −1/4 in both aquatic and terrestrial organisms (Gillooly *et al.*, 2005a). Therefore, this example shows how a quantitative prediction from metabolic theory can be used to assess the influence of other factors, such as stoichiometry, which may account for much of the remaining variation.

Since times are reciprocals of rates, metabolic theory predicts that biological times should scale with characteristic powers of 1/4. Figure 1.4 shows data for one such time, maximal lifespan, for a variety of aquatic animals ranging from zooplankton to fish. The slope of this relationship, 0.23, is very close to the theoretically predicted value of 1/4, and the fitted regression accounts for the

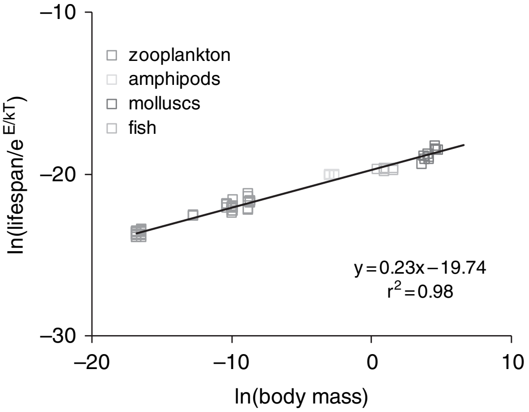

Figure 1.4 The relationship between temperature-corrected maximum lifespan, measured in days, and the natural logarithm of body mass, measured in grams, for various aquatic organisms. Lifespan is temperature-corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Gillooly *et al.* (2001).

vast majority of variation ($r^2 = 0.98$). The enormous variation in body size across these organisms masks considerable unexplained residual variation. It is well established that even closely related animals of the same body size can differ in lifespan by at least an order of magnitude. If the first-order effect of temperature had not been removed, then there would have been even more variation, with species in cold-water environments living longer than those of similar size in warmer waters.

Population and community levels: growth, mortality and abundance

There are two logical benchmarks to measure population growth rate: the maximal rate, $r_{\max}$, and the rate of turnover at steady state. Data on $r_{\max}$ for a wide variety of organisms, from unicellular eukaryotes to invertebrates and vertebrates, have been compiled and analyzed by Savage *et al.* (2004b). These data give a slope of -0.23, very close to the predicted $-1/4$. We have extracted and plotted the subset of these data for aquatic organisms, including algae, zooplankton and fish in Fig. 1.5. The slope is a bit lower, -0.20, but the confidence intervals still include the predicted value of $-1/4$. We conclude that maximal population-growth rates scale similarly to mass-specific metabolic rate and follow Eq. (1.3). This is not surprising, since metabolism fuels individual production, which in turn fuels population growth, thereby determining $r_{\max}$.

The rate of population turnover, and hence birth and death rates, should scale similarly. Figure 1.6 shows the body-mass dependence of mortality rates of fish in the field. The fitted regression has a slope of -0.24, very close to the predicted value of $-1/4$. The $-1/4$ power scaling of natural mortality may come as a surprise to many ecologists because mortality in the field is generally thought to be controlled by extrinsic environmental conditions, such as predation, food shortage or abiotic stress, rather than to intrinsic biological traits such as metabolic rate. The majority of mortality may indeed be due to predation or

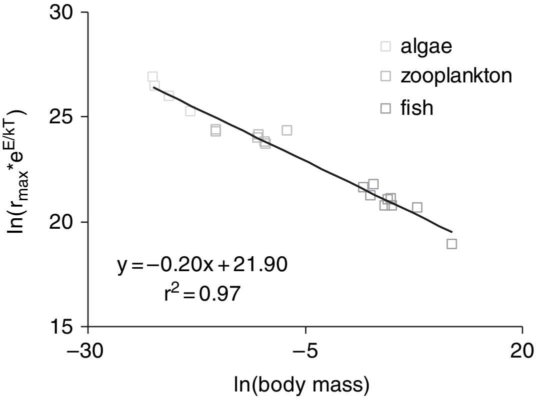

Figure 1.5 The relationship between the temperature-corrected maximum rate of population growth (i.e. r_{max}), measured in 1/days, and the natural logarithm of body mass, measured in grams, for various aquatic organisms. R_{max} is temperature-corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Savage *et al.* (2004b).

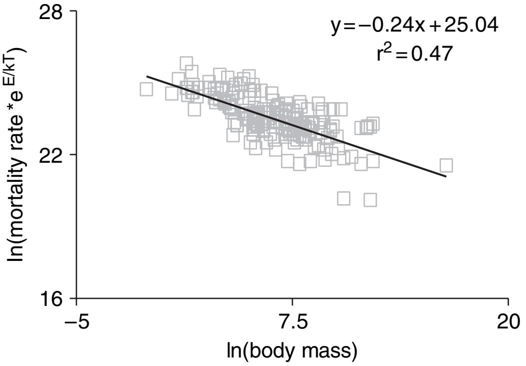

Figure 1.6 The relationship between the temperature-corrected mortality rate of marine fishes in the field, measured in 1/years, and the natural logarithm of body mass, measured in grams. Mortality rate is temperature-corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Savage *et al.* (2004b).

other extrinsic factors, but birth and death rates must match, and the rate of production must offset the rate of mortality for a population to persist. Population-turnover rate is another of those phenomena which is controlled by metabolic rate and, consequently, shows characteristic 1/4-power scaling.

Metabolic rate determines the rate of population turnover, but what about the abundances or steady-state densities of populations in the field? Based on data for mammals, Damuth (1981) showed that population density scales as $M^{-3/4}$. This is what would be expected if populations of a guild or trophic level had equal rates of resource supply, R, because the steady-state population density, N, should be proportional to the rate of resource supply divided by the resource use or field metabolic rate per individual, P, so $N \propto R/P \propto M^0/M^{3/4} \propto M^{-3/4}$. Recent compilations of data on population density as a function of mass generally support this prediction (Damuth, 1981; Belgrano *et al.*, 2002; Li, 2002; Allen *et al.*, 2002; Brown *et al.*, 2004). For example, Li (2002) showed that the densities of morphospecies of phytoplankton in the North Atlantic scaled as $M^{-0.78}$, where M is cell carbon mass. An important community-level consequence of population density or number of individuals per area, N,

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scaling as $M^{-3/4}$ and whole-organism field metabolic rate or energy use per individual, P, scaling as $M^{3/4}$, is that the rate of community energy use per unit area, E, is independent of body size: $E \propto NP \propto M^{-3/4}M^{3/4} \propto M^0$. Damuth (1981) called this the energy equivalence rule.

If the abundance and energy use of populations scale predictably with body size, these relationships are of potentially great interest to ecologists. However, care should be taken in making and testing these predictions of MTE for several reasons. First, the assumption of equal rates of resource supply is difficult to evaluate. It is likely that species in different guilds, functional groups and trophic levels will have quite different resource availability. This could even be true for members of the same guild or trophic level. Second, resource supply sets only an upper bound on population density. Predation, competition and other limiting factors may cause the steady-state density to be well below this limiting bound. Third, the above two factors can cause considerable variation, as much as several orders of magnitude, in the observed densities of species populations in the field. Fourth, data are often plotted with each point representing a species, but in organisms with indeterminate growth and consequently wide variation in body size, it may be difficult to estimate the average body mass and abundance of a species. If the organisms really do use the same resources, it is more logical to estimate the upper bound by summing the numbers of individuals of all species in a body-size interval. Ackerman *et al.* (2004) performed such an analysis for all of the fish coexisting at a site on the Great Barrier Reef, and found the predicted $M^{-3/4}$ scaling – except for the smallest size classes, which probably share food resources with invertebrates. We conclude that metabolic rate powerfully constrains the abundance of organisms in species populations, functional or trophic groups, and body-size categories, but, again, care should be exercised in making and testing predictions based on metabolic theory.

Ecosystem level: flux and storage of energy and materials

Through their metabolism, organisms contribute to the flows of energy and elements in ecosystems. These flows include not only the quantitatively dominant components of the carbon cycle, but also those involving critical limiting nutrients, such as phosphorus or nitrogen, that together with carbon, comprise the 'Redfield Ratio'. Metabolic theory provides a conceptual basis for predicting, measuring and understanding the roles of different kinds of organisms in the flux and storage of elements in ecosystems. The total biomass per unit area, W, is simply the sum of the body mass of all individuals. For organisms of similar size, it can be estimated by taking the product of the population, N, and the body mass, M. Similarly, the store of each element in living biomass per unit area, S, is:

$$S = \sum_{0}^{i} [X_i]N_iM_i \tag{1.5}$$

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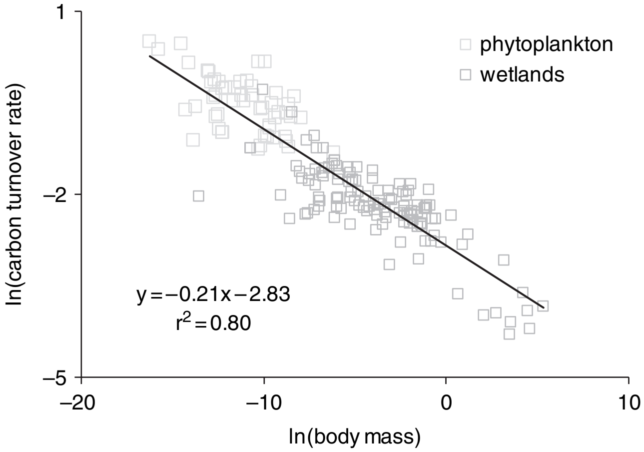

Figure 1.7 The relationship between carbon turnover rate, measured as 1/days, and the natural logarithm of average plant mass, measured in grams. Data have not been temperature-corrected because environmental temperatures were not reported. Analyses from Brown *et al.* (2004) and Allen *et al.* (2005).

where X is the whole-body concentration of substance X, and the subscript i denotes a species, developmental stage or body-size class, functional or trophic group, which should be analysed separately for accurate accounting. To a first approximation, the turnover rate of these materials is proportional to mass-specific metabolic rate, B, so the rate of flux, F, is

$$F = \sum_{0}^{i} [Y_i] N_i B_i \tag{1.6}$$

where Y is an element-specific constant required because turnover rates vary widely for different kinds of organisms, depending in part on the form in which they are stored (e.g. structural carbon in plants, and calcium and phosphorus in the shells of molluscs and the bones of vertebrates). Knowing Y, it is also then possible to use the general mass and temperature dependence of metabolic rate to estimate the turnover rate of a particular element.

We illustrate the potential applications of this framework with two examples. First, we show the relationship between the rate of carbon turnover and plant size for freshwater and marine ecosystems, where the primary producers are predominantly phytoplankton, and for wetlands, where the primary producers are predominantly herbaceous plants (Fig. 1.7). These data have not been temperature corrected due to difficulties in estimating the relevant temperatures in these ecosystems, so temperature probably accounts for substantial residual variation. Nevertheless, the regression has a slope of −0.21, close to the predicted value of −1/4, fits the data well for both phytoplankton in open waters and herbaceous plants in wetlands, and accounts for about 80% of the observed variation. Furthermore, Allen *et al.* (2005) show that this same relationship can be extended to include terrestrial ecosystems, where the dominant plants vary in size from herbs in grasslands to trees in forests.