

 Ecological Reviews

Body Size: The Structure and Function of Aquatic Ecosystems



Edited by
**Alan Hildrew, Dave Raffaelli
and Ronni Edmonds-Brown**

CAMBRIDGE

www.cambridge.org/9780521861724

This page intentionally left blank

Body Size: The Structure and Function of Aquatic Ecosystems

Ecologists have long struggled to predict features of ecological systems, such as the numbers and diversity of organisms. The wide range of body sizes in ecological communities, from tiny microbes to large animals and plants, is emerging as the key to prediction. Based on the relationship of body size with key biological rates and with the physical world experienced by aquatic organisms, we may be able to understand patterns of abundance and diversity, biogeography, interactions in food webs and the impact of fishing, adding up to a potential 'periodic table' for ecology. Remarkable progress on the unravelling, describing and modelling of aquatic food webs, revealing the fundamental role of body size, makes a book emphasizing marine and freshwater ecosystems particularly apt. Here, the importance of body size is examined at a range of scales, yielding broad perspectives that will be of interest to professional ecologists, from students to senior researchers.

ALAN G. HILDREW is Professor of Ecology in the School of Biological and Chemical Sciences at Queen Mary, University of London.

DAVID G. RAFFAELLI is Professor of Environmental Science at the University of York.

RONNI EDMONDS-BROWN is a Senior Lecturer in Environmental Sciences at the University of Hertfordshire.

Body Size

The Structure and Function of Aquatic Ecosystems

Edited by

ALAN G. HILDREW

School of Biological and Chemical Sciences, Queen Mary, University of London, UK

DAVID G. RAFFAELLI

Environment Department, University of York, UK

RONNI EDMONDS-BROWN

Division of Geography and Environmental Sciences, University of Hertfordshire, UK



CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press

The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org

Information on this title: www.cambridge.org/9780521861724

© British Ecological Society 2007

This publication is in copyright. Subject to statutory exception and to the provision of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published in print format 2007

ISBN-13 978-0-511-29508-9 eBook (EBL)

ISBN-10 0-511-29508-1 eBook (EBL)

ISBN-13 978-0-521-86172-4 hardback

ISBN-10 0-521-86172-1 hardback

ISBN-13 978-0-521-67967-1 paperback

ISBN-10 0-521-67967-2 paperback

Cambridge University Press has no responsibility for the persistence or accuracy of urls for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Contents

<i>List of contributors</i>	page vii
<i>Preface</i>	ix
1 The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems <i>James H. Brown, Andrew P. Allen and James F. Gillooly</i>	1
2 Body size and suspension feeding <i>Stuart Humphries</i>	16
3 Life histories and body size <i>David Atkinson and Andrew G. Hirst</i>	33
4 Relationship between biomass turnover and body size for stream communities <i>Alexander D. Huryn and Arthur C. Benke</i>	55
5 Body size in streams: macroinvertebrate community size composition along natural and human-induced environmental gradients <i>Colin R. Townsend and Ross M. Thompson</i>	77
6 Body size and predatory interactions in freshwaters: scaling from individuals to communities <i>Guy Woodward and Philip Warren</i>	98
7 Body size and trophic cascades in lakes <i>J. Iwan Jones and Erik Jeppesen</i>	118
8 Body size and scale invariance: multifractals in invertebrate communities <i>Peter E. Schmid and Jenny M. Schmid-Araya</i>	140
9 Body size and biogeography <i>B.J. Finlay and G. F. Esteban</i>	167
10 By wind, wings or water: body size, dispersal and range size in aquatic invertebrates <i>Simon D. Rundle, David T. Bilton and Andrew Foggo</i>	186

11	Body size and diversity in marine systems <i>Richard M. Warwick</i>	210
12	Interplay between individual growth and population feedbacks shapes body-size distributions <i>Lennart Persson and André M. De Roos</i>	225
13	The consequences of body size in model microbial ecosystems <i>Owen L. Petchey, Zachary T. Long and Peter J. Morin</i>	245
14	Body size, exploitation and conservation of marine organisms <i>Simon Jennings and John D. Reynolds</i>	266
15	How body size mediates the role of animals in nutrient cycling in aquatic ecosystems <i>Robert O. Hall, Jr., Benjamin J. Koch, Michael C. Marshall, Brad W. Taylor and Lusha M. Tronstad</i>	286
16	Body sizes in food chains of animal predators and parasites <i>Joel E. Cohen</i>	306
17	Body size in aquatic ecology: important, but not the whole story <i>Alan G. Hildrew, David G. Raffaelli and Ronni Edmonds-Brown</i>	326
	<i>Index</i>	335

Contributors

Andrew P. Allen National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93101, USA.

David Atkinson Population and Evolutionary Biology Research Group, School of Biological Sciences, The University of Liverpool, Biosciences Building, Crown Street, Liverpool L69 7ZB, UK.

Arthur C. Benke Aquatic Biology Program, Box 870206, Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487-0206, USA.

David T. Bilton Marine Biology and Ecology Research Centre, University of Plymouth, Plymouth PL4 8AA, UK.

James H. Brown Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

Joel E. Cohen Laboratory of Populations, Rockefeller and Columbia Universities, 1230 York Avenue, Box 20, New York, NY 10021-6399, USA.

André M. De Roos Institute of Biodiversity and Ecosystems, University of Amsterdam, P.O.B. 94084, NL-1090 GB Amsterdam, the Netherlands.

Ronni Edmonds-Brown Division of Geography and Environmental Sciences, University of Hertfordshire, College Lane, Hatfield AL10 9AB, UK.

G. F. Esteban School of Biological and Chemical Sciences, Queen Mary, University of London, East Stoke, Wareham Dorset BH20 6BB, UK.

B. J. Finlay School of Biological and Chemical Sciences, Queen Mary, University of London, East Stoke, Wareham Dorset BH20 6BB, UK.

Andrew Foggo Marine Biology and Ecology Research Centre, University of Plymouth, Plymouth PL4 8AA, UK.

James F. Gillooly Department of Zoology, University of Florida, Gainesville, FL 32607, USA.

Robert O. Hall, Jr. Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

Alan G. Hildrew School of Biological and Chemical Sciences, Queen Mary, University of London, London E1 4NS, UK.

Andrew G. Hirst British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

Stuart Humphries Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

Alexander D. Huryn Aquatic Biology Program, Box 870206, Department of

Biological Sciences, University of Alabama, Tuscaloosa, AL 35487-0206, USA.

Simon Jennings Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, NR33 0HT, UK.

Erik Jeppesen Department of Freshwater Ecology, National Environmental Research Institute, Denmark and Department of Plant Biology, University of Aarhus, Ole Worms Allé, Aarhus, Denmark.

J. Iwan Jones Centre for Ecology and Hydrology Dorset, Dorchester DT2 8ZD, UK.

Benjamin J. Koch Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

Zachary T. Long Institute of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell Street, Morehead City, NC 28557 and Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062.

Michael C. Marshall Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

Peter J. Morin Department of Ecology, Evolution & Natural Resources, 14 College Farm Rd., Cook College, Rutgers University, New Brunswick, NJ 08901, USA.

Lennart Persson Department of Ecology and Environmental Science, Umeå University, S-901 87 Umeå, Sweden.

Owen L. Petchey Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 1SA, UK.

David G. Raffaelli Environment Department, University of York, Heslington, York YO10 SDD, UK.

John D. Reynolds Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada.

Simon D. Rundle Marine Biology and Ecology Research Centre, University of Plymouth, Plymouth PL4 8AA, UK.

Peter E. Schmid School of Biological and Chemical Sciences, Queen Mary, University of London, London E1 4NS, UK and Institute of Freshwater Ecology, University of Vienna, 1090 Wien, Althanstrasse 14, Austria.

Jenny M. Schmid-Araya School of Biological and Chemical Sciences, Queen Mary, University of London, London E1 4NS, UK.

Brad W. Taylor Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

Ross M. Thompson School of Biological Sciences, Building 18, Monash University, Victoria 3800, Australia.

Colin R. Townsend Department of Zoology, University of Otago, 340 Great King Street, Dunedin 9054, New Zealand.

Lusha M. Tronstad Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

Philip Warren Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

Richard M. Warwick Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, UK.

Guy Woodward School of Biological and Chemical Sciences, Queen Mary, University of London, London E1 4NS, UK.

Preface

More than ten years ago, two of us (AGH and DGR) were lucky enough to edit a previous symposium of the British Ecological Society (BES) – *Aquatic Ecology: Scale, Pattern and Process* (Giller, Hildrew & Raffaelli, 1994). In the Introduction to that volume, we pointed out that the BES had not devoted a single previous symposium to aquatic ecosystems. Evidently we did not change the culture, since the *Body Size* symposium held at the University of Hertfordshire in September 2005 was only the second! *Aquatic Ecology: Scale, Pattern and Process* had two objectives: (i) to explore how the scale of approach affected the patterns that were detected and the processes that appeared to be important, and (ii) to compare freshwater and marine ecosystems. In *Body Size: The Structure and Function of Aquatic Ecosystems*, both those questions of scale and comparison among systems are very much still alive as continuing themes. Body size determines overwhelmingly the scale at which organisms perceive and navigate through their physical world, and the contrasts between freshwater and marine ecosystems remain evident. Body size is a species trait with implications beyond scale, however, and we believe that the present volume shows that more similarities than differences are evident among the diverse aquatic systems considered. Indeed, several authors argue here that fundamental ecological processes are revealed by comparing marine, freshwater and terrestrial systems.

In organizing this meeting, we were well aware of the increasing interest in body size from the wider ecological community over the past 30 years, as well as the technical challenge involved in exploring body-size data. Of course, the fascination with body size has a much longer history in ecology and was prominent in the writings, for example, of Alfred Wallace (1858) and Charles Elton (1927), the latter having discussed at length its relevance to trophic interactions (see review by Warren, 2005). It was R. H. Peters' (1983) elegant exposition of the physiological, environmental and ecological correlates of body size that re-ignited modern interest, however, and which led indirectly to an explosion in the macroecological literature over the past ten years (Blackburn & Gaston, 2003), to the metabolic theory of ecology (Brown *et al.*, 2004) and indeed to this present volume. All of the papers presented at the Hatfield meeting connect

with one or more of these themes and in many cases attempt to integrate aspects of body-size research that were previously treated separately. A focus on aquatic systems seemed appropriate because aquatic ecologists have historically been particularly prominent in the debate. Thus, Hardy (1924) was amongst the first to point out the significance of ontogenic (sized-based) shifts in the food webs supporting fisheries, Ryther (1969) illustrated the effects of predator and prey body sizes on food-chain length and global patterns of marine productivity, whilst Hutchinson (1959) provided a classic account of body size and species coexistence. It may well be that patterns and processes related to body size are particularly important in aquatic systems, or at least are more obvious.

We asked the author(s) of each paper to examine the importance and role of body size in the systems in which they work. Essentially the book builds from the level of the individual and a consideration of body size as a species trait (Humphries; Atkinson & Hirst; Hurn & Benke; Townsend & Thompson), through food webs and communities (Woodward & Warren; Jones & Jeppesen; Schmid & Schmid-Araya), to body-size related macroecological patterns in aquatic systems (Finlay & Esteban; Rundle, Bilton & Foggo; Warwick), to dynamics and patterns in whole communities and ecosystems (Persson & De Roos; Petchey, Long & Morin; Jennings & Reynolds; Hall *et al.*; Cohen). Jim Brown and colleagues set the scene with a 'wet' exposition of metabolic theory, and although we did not ask contributors explicitly to test these ideas several did. The meeting certainly generated an old-fashioned sense of community and of excitement in what people had to say, though it was just as apparent how fragmented the community is, as was reflected in the examples chosen to illustrate particular points and the literature cited by authors from different 'stables' and backgrounds.

We hope that this book reflects just a little of this excitement and serves as a useful synthesis of this area of ecology. Finally, we wish to thank all the contributors for their efforts and remarkable efficiency, the British Ecological Society and the Freshwater Biological Association for their support, and the local organizers at the University of Hertfordshire for all their hard work.

Alan Hildrew,
Dave Raffaelli,
Ronni Edmonds-Brown.

References

- Blackburn, T. M. & Gaston, K. J. (2003). *Macroecology: Concepts and Consequences*. Oxford: Blackwell Science.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004). Towards a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Elton, C. S. (1927). *Animal Ecology*. London: Sidgwick & Jackson Ltd.
- Giller, P. S., Hildrew, A. G. & Raffaelli, D. G. (eds.) (1994). *Aquatic Ecology: Scale, Pattern and Process*. The 34th Symposium of the British Ecological Society. Oxford: Blackwell Science.

- Hardy, A. C. (1924). The herring in relation to its animate environment. Part 1. The food and feeding habits of the herring with special reference to the east coast of England. *Fisheries Investigations Series II*, **7**(3), 1–53.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **32**, 571–581.
- Peters, R. H. (1983). *The Ecological Implications of Body Size*. New York: Cambridge University Press.
- Ryther, J. H. (1969). Photosynthesis and fish production in the sea. *Science*, **166**, 72–76.
- Wallace, A. R. (1858). On the tendency of varieties to depart indefinitely from the original type. In C. R. Darwin and A. R. Wallace: On the tendency of species to form varieties, and on the perpetuation of varieties and species by natural selection. *Journal of the Proceedings of the Linnean Society, Zoology*, 20 August 1858, **3**, 45–62.
- Warren, P. H. (2005). Wearing Elton's wellingtons: why body size still matters in food webs. In *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change*, eds. P. C. de Ruiter, V. Wolters & J. C. Moore. San Diego: Academic Press.

CHAPTER ONE

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

JAMES H. BROWN

University of New Mexico, Albuquerque

ANDREW P. ALLEN

National Center for Ecological Analysis and Synthesis, Santa Barbara

JAMES F. GILLOOLY

University of Florida, Gainesville

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

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:

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

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:

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

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 stoichiometry, 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:

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

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,

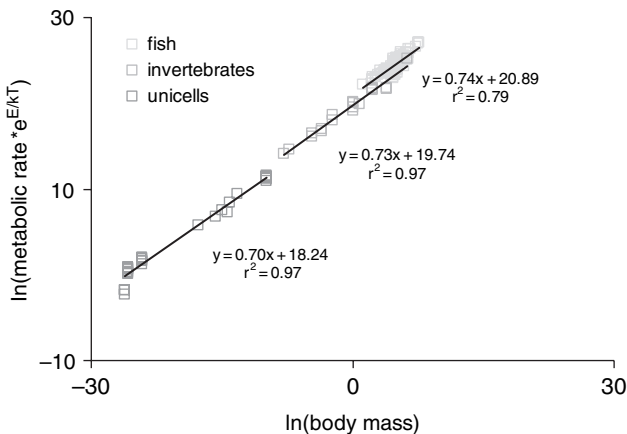


Figure 1.1 The relationship between temperature-corrected metabolic rate, measured in watts, and the natural logarithm of body mass, measured in grams. Metabolic rate is temperature corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Gillooly *et al.* (2001).

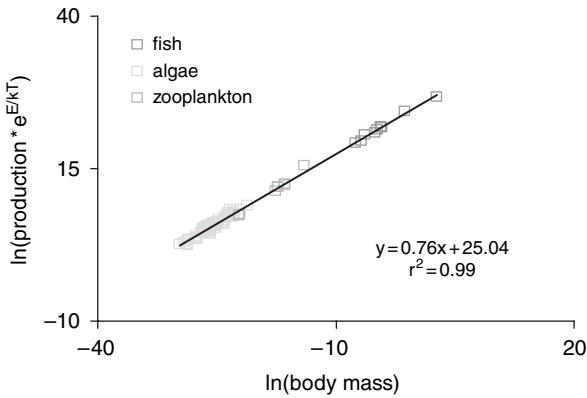


Figure 1.2 The relationship between temperature-corrected biomass production rate, measured in grams per individual per year, and the natural logarithm of body mass, measured in grams. Metabolic rate is temperature corrected using the Boltzmann factor, $e^{-E/KT}$, following Eq. (1.2). Data and analyses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

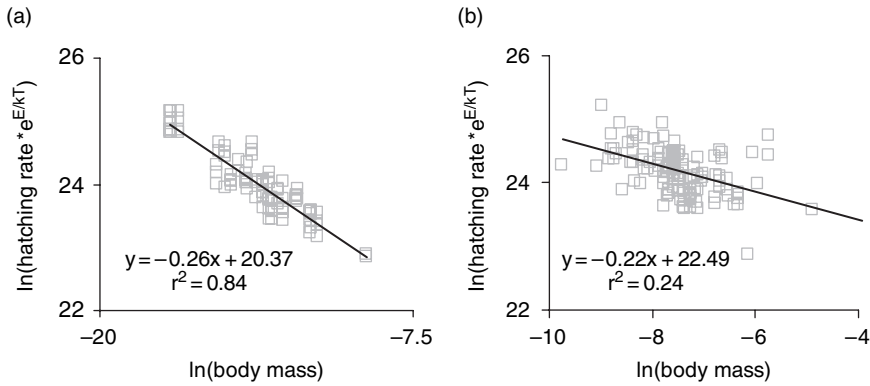


Figure 1.3 The relationship between temperature-corrected hatching rate, measured in 1/days, and the natural logarithm of body mass, measured in grams, for zooplankton eggs in the laboratory (panel A) and fishes in the field (panel B). Hatching rate is temperature-corrected using the Boltzmann factor,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