Review

Scaling and power-laws in ecological systems

Pablo A. Marquet[1,2,*], Renato A. Quiñones[3], Sebastian Abades[1], Fabio Labra[1], Marcelo Tognelli[1], Matias Arim[1] and Marcelo Rivadeneira[1]

[1]*Center for Advanced Studies in Ecology and Biodiversity (CASEB) and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, casilla 114-D, Santiago, Chile,* [2]*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA* and [3]*Centro de Investigación Oceanográfica en el Pacífico Sur-Oriental (COPAS) y departamento de Ocenografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile*

*Author for correspondence (e-mail: pmarquet@bio.puc.cl)

Summary

Scaling relationships (where body size features as the independent variable) and power-law distributions are commonly reported in ecological systems. In this review we analyze scaling relationships related to energy acquisition and transformation and power-laws related to fluctuations in numbers. Our aim is to show how individual level attributes can help to explain and predict patterns at the level of populations that can propagate at upper levels of organization. We review similar relationships also appearing in the analysis of aquatic ecosystems (i.e. the biomass spectra) in the context of ecological invariant relationships (i.e. independent of size) such as the 'energetic equivalence rule' and the 'linear biomass hypothesis'. We also discuss some power-law distributions emerging in the analysis of numbers and fluctuations in ecological attributes as they point to regularities that are yet to be integrated with traditional scaling relationships and which we foresee as an exciting area of future research.

Key words: scaling, power-law, metabolism, complexity.

Introduction

Living entities are embedded in and constituted by, networks at any level of organization, from cells to ecosystems (e.g. Ulanowicz, 1986; Pahl-Wostl, 1995; Strogatz, 2001; Barabási and Oltvai, 2004). The structure and dynamics of these networks emerge as a result of the processes whereby energy, materials and information are acquired, stored, distributed and transformed. Biological networks typically consist of a large number of non-identical elements whose interaction are usually localized, although their effects are not and whose emergence, maintenance and dynamics represent a challenge to understanding let alone prediction (e.g. Weng et al., 1999; Levin, 1998, 1999, 2002). Biological networks represent the most complex physical system in the universe and yet, as most complex systems they can be described by simple relationships (West, 1999; Brown et al., 2000). These relationships are of the form

$$Y = \beta x^{\alpha} , \qquad (1)$$

where Y is some response or dependent variable, x represents an independent or explanatory variable, β is a normalization constant and α is the scaling exponent. Depending on the value of the exponent these relationships are called allometric ($\alpha \neq 1$) or isometric ($\alpha = 1$). The functional form of the relationship in

Equation 1 is also called a power-law relationship, where some quantity can be expressed as some power of another. Power-laws are ubiquitous in physical and social systems where they most commonly arise as probability or frequency distributions, of the form $f(x) = \beta x^{\alpha}$, different from the usual exponential or Gaussian distributions. For example power-law distributions describe phenomena such as the frequency of earthquakes of different magnitudes (the Gutenberg-Richter law), the distribution of income among individuals (Pareto's law) and the rank-frequency distribution of words in natural languages and city sizes (Zipf's law). Power-laws are well-known to biologists in the form of bivariate relationships of power-law type, called scaling relationships (e.g. Peters, 1983; Niklas, 1994; Wiesenfeld, 2001; Brown and West, 2000; Brown et al., 2002; Chave and Levin, 2003) by which molecular, physiological, ecological and life history attributes relate to some attribute of organisms raised to a power as in Equation 1. Although the history of the term scaling in biology probably has deep roots in time, its use has been associated with relationship where the independent variable is the size of an organism (Calder, 1983, 1984; Peters, 1983; Schmidt-Nielsen, 1984). For the sake of consistency we will retain the use of scaling as related to relationships involving body size and will

differentiate them from power-law distributions as defined above.

This special issue is devoted to explore the consequences of organismal size as affecting biological processes. Most of the papers in this special issue have addressed scaling relationships where the response variable is an individual level attribute, such as metabolic rate, life span and running speed, and where the independent variable is body size. However, as pointed out above, scaling relationships are common at higher levels of organizations as well, such as at the level of populations, communities and ecosystems, and they are usually an allometric function of body size (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Bonner, 1988; Brown, 1995). This fact underscores the importance of body size at all levels of organization, and opens the way for synthesis and integration across levels. In fact, it has been a pressing challenge for ecologists and evolutionary biologists to develop a conceptual and quantitative framework bringing together disciplines traditionally viewed as distinct, such as physiology, ecology, biogeography and macroevolution (e.g. Brown and Maurer, 1987, 1989; Ricklefs, 1987; Brown, 1995, 1999; Marquet and Taper, 1998) and much of this quest for a synthetic framework has been based on empirical statistical patterns relating body size with physiological, ecological and evolutionary traits (e.g. Lawton, 1990; Blackburn et al., 1993a; Brown et al., 1993; Brown, 1995). In what follows we review some of this relationships as they emerge at the population, community and ecosystem levels, and emphasize their connections as well as future developments.

Our main focus in this review paper will be scaling relationships were body size features as the independent variable, however we will restrict ourselves to scaling relationships related to energy acquisition and transformation primarily at the level of populations. Our aim will be to show how individual level attributes can help to explain and predict patterns at the level of populations, communities and ecosystems. In addition, we will also discuss power-law distributions emerging in the analysis of numbers and fluctuations in ecological attributes as they point to regularities that are yet to be integrated with traditional scaling relationships, and that we foresee as an exciting area of future research. However, before delving into the main theme of our paper we will make a brief detour to introduce some general concepts associated with scaling and power-law relationships that will be used throughout the paper.

Why bother with scaling and power-law relationships?

There are two notions or characteristics associated with power-law relationships that stand out because of their theoretical and empirical importance. (1) Power-laws, as well as scaling relationships as used here, are scale-invariant (e.g. Sornette, 2000; Stanley et al., 2000; Gisiger, 2001), that is, they display invariance under scale change. This can be seen if we consider a scale transformation in x such that $x \rightarrow \lambda x$ then $f(x)=\beta x^\alpha \rightarrow \beta\lambda^\alpha x^\alpha=\lambda^\alpha f(x)$, thus a change in the scale of the independent variable preserves the functional form of the original relationship. Scale invariance describes phenomena that are not associated with a particular or characteristic scale and are also known as scale-free or true on all scales, that is they posses the same statistical properties at any scale. In practical terms, this means that the same principles or processes are at work no matter what the scale of analysis (Milne, 1998). This property makes scaling and power-law relationships very well suited for the study of ecological systems, which show variability at different temporal, spatial and organizational scales such that there is no single 'correct scale' for their analysis (Levin, 1992). (2) The notion of universality. This concept was introduced into physics in association with critical phenomena (e.g. Biney et al., 1992) to describe the state and dynamics of systems as they approach a phase transition (such as water turning into ice or the onset of magnetization when temperature is changed or the transition between dynamical regimes through bifucartions in deterministic dynamical systems). Near phase transitions, systems are said to become critical and relevant quantities to describe their state (e.g. magnitude of fluctuations, correlation length) behave as power-law relationships with critical exponents (e.g. Maris and Kadanoff, 1978; Solé et al., 1996; Milne, 1998; Stanley et al., 2000; Gisiger, 2001). Interestingly, it has been shown that systems that are completely different away from a critical point, show similar critical exponents near a phase transition (e.g. Biney et al., 1992). These non-arbitrary exponents are said to be universal and define disjoint classes (universality classes) into which different physical systems can be classified. A system can arrive to a critical state through changes in a variable external to it (e.g. temperature), but also as a result of its own internal dynamics, in which case we speak of self-organized criticality a concept introduced by Bak et al. (1987, 1988). During the past decade or so, several empirical and theoretical investigations have suggested that biological systems in general, and ecological systems in particular, seem to operate near a critical state, which results in the ubiquity of power-law behavior in several descriptors of their dynamics (e.g. Miramontes 1995; Bak, 1996; Keitt and Marquet, 1996; Rhodes et al., 1997; Ferrier and Cazelles, 1999; Solé et al., 1999, 2002; Gisiger, 2001; Roy et al., 2003; Pascual and Guichard, 2005) and might even belong to the same universality class as other complex systems such as economic systems (Stanley et al., 2000). Thus the analysis of power-law and scaling relationships can help us to identify general principles that apply across a wide range of scales and levels of organizations, revealing the existence of universal principles within the seemingly idiosyncratic nature of ecological systems. However, it should be borne in mind that power-laws might emerge as a consequence of several processes not necessarily related to critical points and phase transitions (Brock, 1999; Sornette, 2000; Mitzenmacher, 2001; Allen et al., 2001) such that the claim that ecological systems are maintained near a critical state is still an open question.

Scaling in ecology

Life on earth has diversified in form and function to occupy virtually all kinds of environments forming spatially and temporally diffuse associations of organisms, or ecological systems, wherein energy acquisition, allocation and transformation is carried out through complex webs of interacting species. To understand the structure and dynamics of these complex ecological systems, two major approaches have predominated among ecologists. On the one hand, experimental microscopic approaches have emphasized the highly variable and idiosyncratic nature of communities with regard to the relative importance of specific biotic interactions (e.g. competition, predation, mutualism) and their effect on local coexisting populations (Diamond and Case, 1986; May, 1986; Lawton, 1999). Two representative quotations from major figures in the field of ecology can help as to clarify this point further. May (1986, p. 1116) in his MacArthur Award address wrote: *'Ecology is a science of contingent generalizations, where future trends depend (much more than in the physical sciences) on past history and on the environmental and biological setting.'* A view that is also sponsored by Diamond and Case (1986) in an edited volume that is appreciated as representing the last synthesis in community ecology, in their own words (Diamond and Case, 1986; p.x): *'The answers to general ecological questions are rarely universal laws, like those of physics. Instead, the answers are conditional statements such as: for a community of species with properties A_1 and A_2 in habitat B and latitude C, limiting factors X_2 and X_5 are likely to predominate.'*

On the other hand, macroscopic non-experimental approaches have emphasized the existence of statistical patterns in the structure of communities that seemingly reflect the operation of general principles or natural laws and emerge as scaling relationships with similar or related exponents (West et al., 1997). These regularities underlie two recent research programs in ecology, the first is macroecology (Brown and Maurer, 1989; Brown, 1995; Gaston and Blackburn, 2000; Marquet, 2002a; Storch and Gaston, 2004) and the second is the 'metabolic theory of ecology' (Brown et al., 2004). The change in the conceptualization of ecological systems entailed by this latter approach, as opposed to the idiosyncratic view expressed by Diamond and Case (1986) and May (1986), is apparent in the following excerpt (Brown et al., 2003; p. 411): *'...Our own recent research is based on the premise that the general statistical patterns of macroecology… are emergent phenomena of complex ecological systems that do indeed reflect the operation of universal law-like mechanisms.'*

Much of the connections between individual, population, community and ecosystem level scaling relationships has been exceptionally synthesized in Brown et al. (2004) in the context of the metabolic theory of ecology, which attempts to explain material and energetic fluxes, in ecological systems, from first principles of thermodynamics, chemical reaction kinetics and fractal-like biological structures and which is expressed in a 'master equation' relating metabolism to body size and temperature (Gillooly et al., 2001; Brown et al., 2004). In the following we will revisit some of the relationships that are at the core of Brown et al. (2004), but with an emphasis in the connections between individual and population level scaling relationships and predominantly on the scaling of population number and fluctuations, to show how these can help us to explain and predict relationships emerging at other levels of organization and at different scales in time and space.

Individual and population level scaling

The most basic property of a population is the number of individuals it contains. Furthermore, since both the turnover as well as the maintenance of each individual requires resources available in the environment, everything else being equal, the maximum number of individuals that a species can achieve in a given area (or maximum density N) will be proportional to the ratio between rate of resource supply per unit area of the environment ($\dot{R}$) and the average per individual rate of resource use ($\dot{B}$). This can be written as:

$$N \propto \dot{R}/\dot{B} . \tag{2}$$

Since environmental resources are used by individuals to sustain their metabolism (or the complex set of chemical reactions that allow the organisms to sustain its living) the rate of resources used by an individual can be assimilated to its metabolic rate, which is well known to scale with body size (M) as:

$$\dot{B} = C_0 M^b , \tag{3}$$

where the scaling exponent b has been shown to be 3/4 both on empirical and theoretical grounds (West et al., 1997, 1999; Savage et al., 2004a) although the issue is still contentious (Dodds et al., 2001). Assuming b=3/4 leads to:

$$N = C_1 M^{-3/4} , \tag{4}$$

where C_1 contains both the effects of variability in resource supply rates as well as other sources of variability (C_0) affecting body size and density (i.e. $C_1 = C_0/\dot{R}$). Compilation studies based on the analysis of published data for closely related species worldwide (e.g. Damuth, 1981, 1987, 1991) typically report that the slope of the relationship between density and body mass approximate –3/4. Although this relationship seems to be stronger in mammals than in other taxa, such as birds (Bini et al., 2001; Dobson et al., 2003), and might be affected by the scale of analysis, level of data aggregation, type of environment, latitude, taxa, trophic position, census area and method of statistical analysis (see reviews in Cotgrave, 1993; Cyr, 2000; Gaston and Blackburn, 2000; Silva et al., 2001), recent analysis of this relationship underscores the empirical generality of the –3/4 scaling exponent as well as its strong theoretical support (Li, 2002; Belgrano et al., 2002, Brown et al., 2004). Furthermore, as shown by Marquet et al. (1990), this relationship holds in local communities when a wide spectrum of taxonomic groups are included (see also Cyr et al., 1997; Schmid et al., 2000; Cohen

et al., 2003; Mulder et al., 2005; but see Dugan et al., 1995; Navarrete and Menge, 1997), although the exponent is closer to –1 (which is expected when analyzing species in more than one trophic level, see discussion below) and is maintained in the face of perturbations affecting changes in the abundance and identity of species (Fig. 1, see also de Boer and Prins, 2002; Cohen et al., 2003). The existence of temporal invariance in this relationship further testifies to its importance in understanding ecological dynamics (Marquet, 2000).

Although most studies do not usually try to disentangle the effect of both $\dot{R}$ and C_0 (but see discussion below), Equation 4 is widely accepted as an accurate description of the relationship between maximum density and body size, although most of the time it is not explicitly realized that energetic limitation through average per individual rate of resource use ($\dot{B}$) should be stronger in the boundary of maximum density at carrying capacity (i.e. it is a boundary condition) and when resource supply is constant and bounded within similar levels among species (Enquist et al., 1998; Brown et al., 2004; Savage et al., 2004b). As discussed below, when this is not the case deviations are expected. A case in point is the scaling of secondary consumers. Since energy available to secondary consumers (i.e. those feeding on other animals) is less than that available to primary consumers (Lindeman, 1942), it is expected that they will reach lower densities than similar sized herbivores (Marquet, 2002b; Ernest et al., 2003; Brown et al., 2004) as was first described by Mohr (1940). However, what has puzzled ecologists for a long time is that its allometric

exponent is considerably smaller (i.e. steeper slopes in the range –1.0 to –0.8, see Fig. 2) than –3/4. Explanations for this discrepancy have been elusive and usually based on presumed systematic (allometric) variation in prey biomass and productivity with predator body mass (Peters and Raelson, 1984). However, Carbone and Gittleman (2002) solved this problem by showing that the relationship between population density and size in mammalian carnivores is constrained by metabolic rate and also by variability in their resource base (prey species) such that the –3/4 power law only emerges if the local productivity of prey species, experienced by a carnivore population, is taken into account. Thus, the answer to the anomalous scaling of mammalian secondary consumers is found in local resource availability.

The fact that resources ($\dot{R}$) are distributed in space allow us to calculate how much space or area would an individual require or its home range (H). This can be calculated as the inverse of Equation 2, assuming that individuals use just the sufficient area to sustain their energy demands ($\dot{B}$) (McNab, 1963) and that resources are homogeneously distributed in space. Furthermore, if we assume that Equations 3 and 4 hold then it is expected that

$$H = N^{-1} \propto \dot{B}/\dot{R} \propto M^{3/4} . \qquad (5)$$

However, there are two important considerations to make regarding this relationship: (1) empirical analysis of home range scaling in mammals shows that the exponent is larger than 3/4 and (2) it is non-monotonic, showing a change in slope
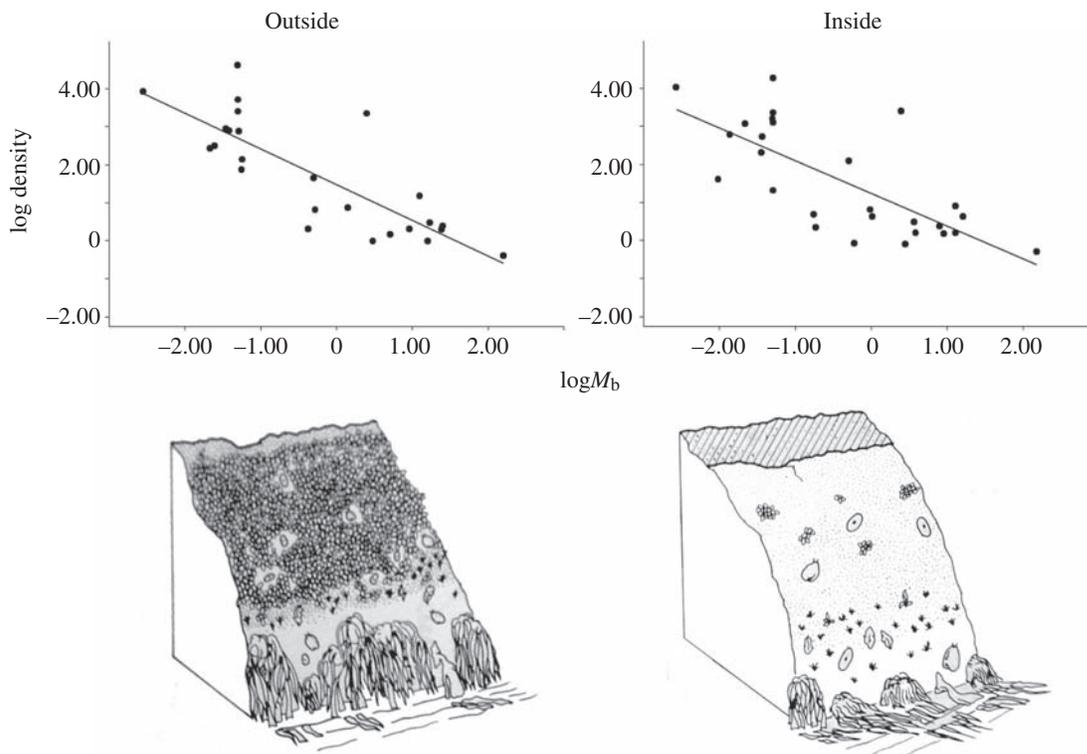

Fig. 1. Population density scaling for intertidal invertebrates found in a protected (inside) and unprotected (outside) site in central Chile. The presence (outside) or absence (inside) of human exploitation is associated with strong changes in community composition and dominance as shown below each graph (after Durán and Castilla, 1989 and Marquet et al., 1990). Density (individuals m^{-2}); body mass (M_b) (g).
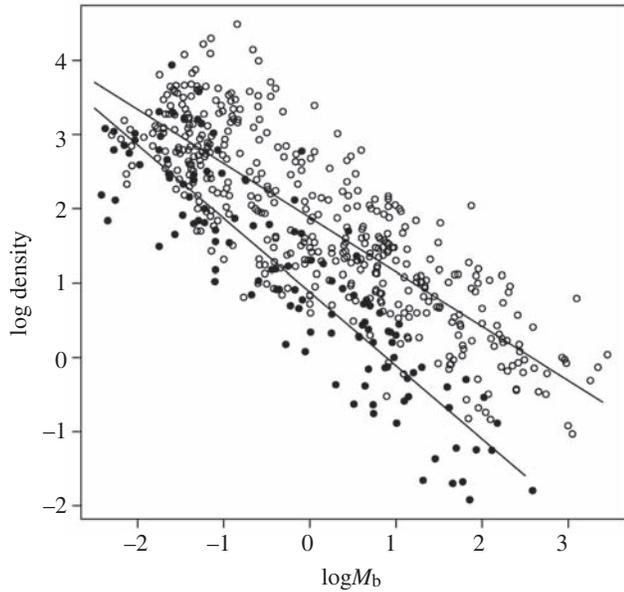
Fig. 2. Population density scaling for primary (open symbols) and secondary (filled symbol) consumer species of mammals. The slope of the relationships is –0.73 (not different from –3/4) for primary consumers and –0.99 (not different from –1) for secondary consumers (data from Damuth, 1993). Density (individuals km^{-2}); M_b (kg).

at a threshold body size M_T (around 100 g in mammals) (Marquet and Taper, 1998; Kelt and Van Vuren, 1999, 2001). The first anomaly was recently explained by Jetz et al. (2004) by noticing that the realized home range of an individual might be smaller than that assumed by Equation 5 due to intraspecific overlap in space use as a consequence of intrusions from foraging conspecific neighbors, which would reduce the supply of resources and hence the area exclusively used by an individual (but see Haskell et al., 2002). With regard to the non-monotonicity issue, it has been hypothesized that it reflects energetic constraints upon small-sized organisms that lead to trophic specialization on energetically rich but widely dispersed resources (Brown and Maurer, 1987; Brown et al., 1993; Marquet and Taper, 1998; Kelt and Van Vuren, 1999) and this could also explain the observed departures from Equation 4 for small species (see Silva and Downing, 1995; Marquet et al., 1995; Siemann et al., 1996; Armbruster et al., 2002; McClain, 2004). Available estimates for the scaling exponent of H below M_T range between –1.81 to –2.4 (Marquet and Taper, 1998; Kelt and van Vuren, 2001). These considerations imply that for mammals:

$$H \propto M^{1.0} \text{ for } M>M_T \tag{6}$$

$$H \propto M^{-(1.81–2.4)} \text{ for } M<M_T . \tag{7}$$

On extreme body sizes, extinction and minimum viable populations

Marquet and Taper (1998) first realized that Equations 6 and 7 allow us to predict the maximum and minimum body size

able to persist in a landmass of a given area. Their argument starts by estimating the minimum area of a landmass required for persistence (A_m) as:

$$A_m \propto N_m \times H , \tag{8}$$

where N_m is the minimum number of individuals required to avoid extinction in the absence of immigration (see also McNab, 1994). Thus if N_m is equal to 500 (individuals) and H is equal to 0.1 (km^2 per individual), then the minimum area required for the persistence of this species (A_m) would be 50 km^2. Substituting Equations 6 and 7 into Equation 8 we arrive at:

$$A_m \propto N_m \times M^{1.0} \text{ for } M>M_T \tag{9}$$

$$A_m \propto N_m \times M^{-(1.81–2.4)} \text{ for } M<M_T . \tag{10}$$

Equations 9 and 10 set the boundary for persistence and apply to the largest and smallest species able to persist in a given landmass in the face of extinction. Although the scaling of N_m is not known it can be estimated by estimating the exponents associated with A_m *vs* M. Marquet and Taper (1998) tested for these relationships using data on mammals found in land bridge islands, mountaintops and continents, whose actual species compositions are mainly the result of a selective extinction process associated with relaxation phenomena (e.g. Diamond, 1984a,b).

As seen in Fig. 3A, as the size of the largest mammal species within an insular fauna increases so does the landmass area required for persistence. Furthermore, as the size of the smallest species decreases the area of the landmass where it is found also increases. These patterns were found to be highly significant within archipelagoes, across continental landmasses and when all cases are analyzed jointly in one general regression. A similar pattern has been reported for snakes by Boback and Guyer (2003, see Fig. 3B). Since the estimated exponents for mammals reported by Marquet and Taper (1998) did not differ from the expected ones it is possible to conclude that

$$N_m \propto M^0 \tag{11}$$

or, in other words, the minimum number of individuals required to avoid stochastic extinction is invariant i.e. independent of body size.

A similar analysis carried out by Burness et al. (2001) using mammals, birds and reptile species found in oceanic islands and continents during the last 65,000 years, confirmed our predictions for the maximum size of species and show that part of the variability in these scaling relationships can be explained by diet and thermoregulatory physiology. Furthermore, the patterns shown in Fig. 3, suggest the existence of an evolutionary advantage for medium sized species linked to reduced extinction probability, and is consistent with macroevolutionary and microevolutionary changes in mammalian body size (see Brown et al., 1993; Alroy, 1998; Schmidt and Jensen, 2003), although the mechanistic basis of these changes are not yet fully comprehended.

Fig. 4. Power-law relationship relating number of species and body size in South American mammals.
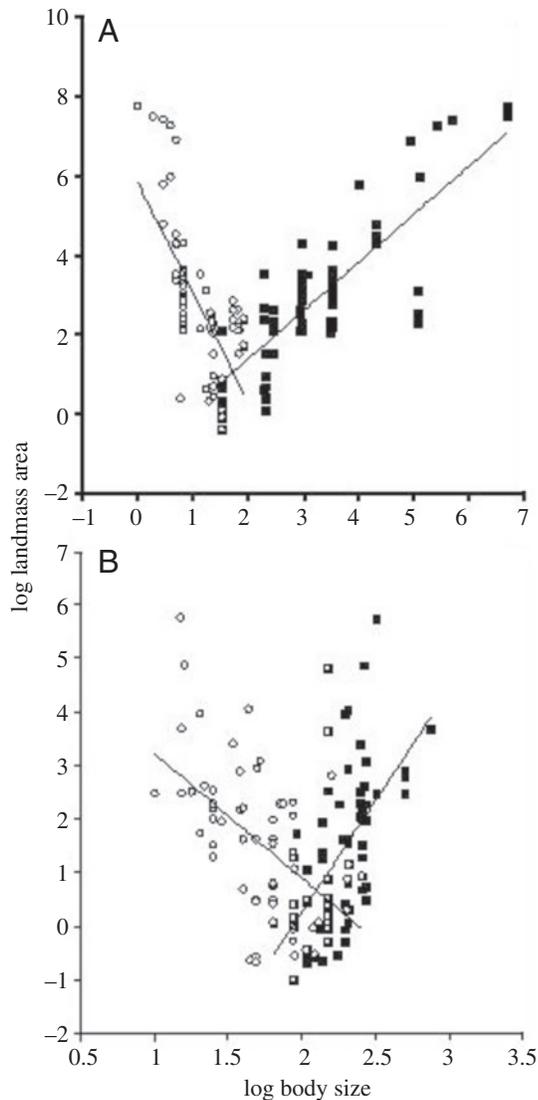
Fig. 3. Relationship landmass area and maximum (filled symbol) and minimum (open symbol) body sizes of mammalian (A, after Marquet and Taper 1998; land mass area, km^2; body size, g) and snake (B, data from Boback and Guyer 2003; land mass area, km^2; body size, cm) species inhabiting them.

If Equation 11 is correct, the further away a species is from N_m the better its chances to persist. In macroevolutionary time scales, this implies that small-sized species will tend to survive longer and likely accumulate by resisting extinction, thus implying that the number of species should decrease with body size. If this is correct in a given area, such as the South American continent, the number of species (S) of a given size (M) should be characterized by a power-law with a scaling exponent close to the one characterizing density (N) and body size i.e.:

$$S(M) \propto M^{-3/4} . \qquad (12)$$

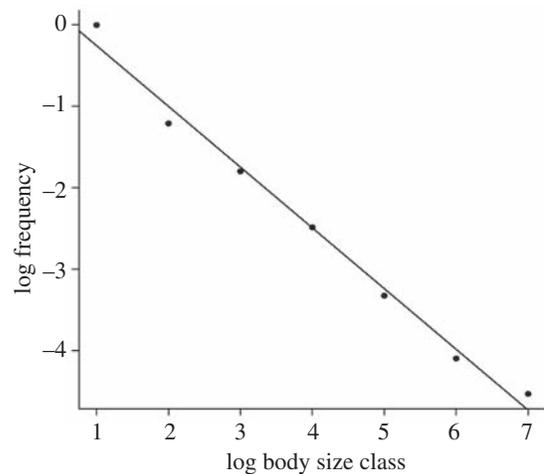A preliminary test of this idea is presented in Fig. 4 where we plot the size frequency distribution of the number of species of mammals in South America (Marquet and Cofre, 1999) using exponentially increasing size classes. As predicted the exponent is not different from the expected –3/4 (P.A.M. and S.A., unpublished).

To derive the patterns in extreme body size, minimum population size and size frequency distributions just discussed, we assumed that habitat and food resources are either homogeneously distributed in space or clumped for species below a threshold size, but did not specify any particular spatial pattern. While this could be a reasonable assumption at large spatial scales, at finer scales (i.e. at the level of landscapes), the spatial distribution of resources (which is usually fractal and can be described by a power-law) can affect the distribution, abundance and interaction of species (e.g. Milne et al., 1992) and affect community patterns (Ritchie and Olff, 1999; Schmid, 2000).

Ecological invariants

As noted by West (1999), one of the most intriguing consequences of biological scaling laws is the emergence of invariant quantities. These are seen, for example, in association with longevity (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Because lifespan increases like $M^{1/4}$, it follows that most rates (such as heart-rate and specific metabolic rate), which decrease as $M^{-1/4}$, give rise to relationships that are size invariant (i.e. they scale as M^0) at the scale of a lifetime. So, for example, the number of heartbeats in a lifetime is the same for all mammals and so is the total energy needed to support a given mass of an organism during its lifetime. And they are also common in life history theory (Charnov, 1993) but associated with the timing of life history events. However, at present it is not known if these fundamental symmetries in living entities are just a by-product of fundamental scaling laws or have a deeper ecological and evolutionary meaning. Several invariant relationships associated with the density scaling relationship shown in Equation 4 have been postulated for

ecological systems. These are seen in: (1) the total energy used by a population or population energy use scaling; (2) the distribution of biomass in ecosystems; and (3) the minimum size of populations. Since we have already elaborated on (3), in this section we will devote our attention to (1) and (2).

The first invariant relationship has been dubbed the 'energetic equivalence rule' (Nee et al., 1991). Its derivation follows. Because metabolic rate (*B*) scales with body mass raised to the 3/4 power, the existence of the same scaling exponent for *N* has been taken as evidence that the abundance of species is limited by energetic requirements (Damuth, 1981, 1991). Similarly, the total energy used by a species' population per unit area (EU) can be assessed by multiplying the average energy used by an individual times the density of individuals. Thus, by multiplying Equations 3 and 4 one gets:

$$EU = B \times N \propto M^{3/4} \times M^{-3/4} \propto M^0 \qquad (13)$$

such that the energy used by different species should be roughly equal and independent of body mass. This pattern was first pointed out by Damuth (1981), although not exempt from criticism (e.g. Marquet et al., 1995; Taper and Marquet, 1996) as it depends on the exact value of the scaling exponents associated with *B* and *N* and has yet to be mechanistically understood (Damuth, 1998, but see Charnov et al., 2001) especially for mobile organisms that utilize a broad spectrum of resources and inhabit different ecosystems around the world (Marquet et al., 1995; Brown et al., 2004). For tree-dominated communities, this relationship has been shown to hold at local, regional and worldwide scales (Enquist and Niklas, 2001; see also Enquist et al., 1998 for plant species in general, see Fig. 5) and have been hypothesized to emerge from the allometric rules that influence the behavior of individual plant species (Niklas and Enquist, 2001) competing for space and limiting resources. Similarly it has been recently documented in local parasite communities of fishes (George-Nascimento et al., 2004).

The second ecological invariant is that related to biomass distribution in ecosystems. Unlike previous invariants, this one is associated with work conducted mostly in aquatic ecosystems. In brief, this invariant was proposed by Sheldon et al. (1972) who, by doing what they called a size spectra (see below), concluded that there is a *'tendency for roughly similar amounts of particulate materials to occur in logarithmically equal size ranges...'* (Sheldon et al., 1972: p. 336). This relationship can be expressed as a power-law of the form:

$$Z(s) \propto s^0 , \qquad (14)$$

where *Z*(*s*) stands for the number or biomass of particles of size or volume (*s*). It is usual practice to work with the normalized biomass spectra (see below), thus after normalizing we arrive at:

$$Z(s) \propto s^{-1} . \qquad (15)$$

Because the equal biomass invariant, when normalized, implies a linear proportional decrease in biomass across size classes it has been dubbed 'the linear biomass hypothesis' (Sheldon et al., 1986). This relationship has been shown to be a well-known pattern in pelagic ecosystems (Sheldon et al., 1972, 1977; Rodriguez, 1994; Rinaldo et al., 2002; Quiñones et al., 2003). It should be noted that although this relationship is different from the one depicted in Equation 4, for this does not rely on distinguishing species (i.e. it is ataxonomic), they are related (Rinaldo et al., 2002). As shown by these authors, the linear biomass hypothesis implies that the scaling exponent of the relationship between number of individuals and average size should be –1 instead of the observed –3/4. Brown and Gillooly (2003) hypothesized that an exponent of –1 is expected when analyzing species in more than one trophic level, as is the case in marine ecosystems and in size-structured food webs in general. The –3/4 exponent and, hence, the energetic equivalence rule, is expected in situations where all species use the same source of energy (i.e. within trophic levels). However, the same relationships for size-structured food webs need to account for energy transfer efficiency as well as body mass differences between trophic levels. In this case the prediction is an exponent of –1. A formal test of this hypothesis using a marine food web has shown that it accurately predicts observed patterns (Jennings and Mackinson, 2003) thus narrowing the gap between two research traditions (marine *vs* terrestrial), both of which have appreciated the value of scaling approaches (e.g. Platt, 1985; Cyr and Pace, 1993; Brown et al., 2004). Notice that this result implies that both invariant relationships are not independent, such that the existence of invariance in energy use within trophic levels entails the existence of biomass invariance across them. To our knowledge the only terrestrial biomass spectra so far reported is that carried out by Enquist and Niklas (2001) for tree-dominated communities using a worldwide data set of 227 plots of 0.1 ha assembled by the late Alwyn Gentry. These authors show, as expected, that the number of individuals in logarithmic size classes decreases as $M^{-3/4}$ implying that population energy use is invariant.

In a later analysis of the same data set Enquist et al. (2002) introduces a related invariant by showing that total biomass [i.e. total standing above ground dry
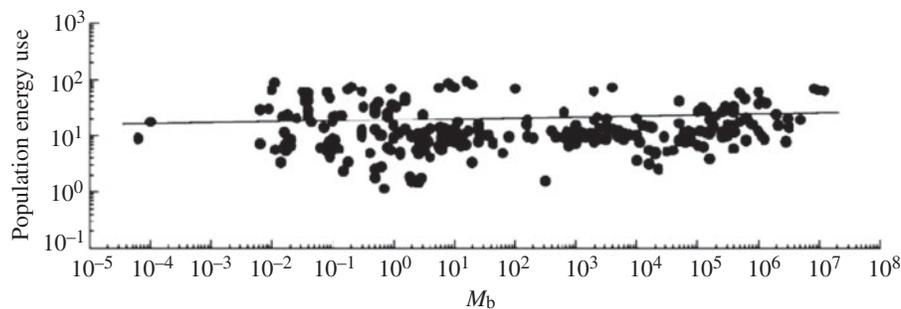

Fig. 5. Constant population energy use in plant species (after Enquist et al., 1998). Population energy use (xylem flux in $l\, m^{-2}\, d^{-1}$); M_b (g).

biomass (M_{tot}) per 0.1 ha plot] is invariant with respect to number of species (S) (i.e. $M_{tot} \propto S^0$) implying that an increase in species richness within communities results in a finer division of biomass instead of an increase in total biomass. Notice that this invariant, as well as the 'energetic equivalence rule', entail the existence of an ecological zero-sum dynamic (Van Valen, 1980) consistent with recent symmetric models of community assembly (Hubbell, 2001). However, it remains to be seen if the biomass invariant described by Enquist et al. (2002) applies to taxa other than trees and how it changes when more than one trophic level is analyzed.

Ecological scaling and biomass size spectra

The study of the distribution of biomass by size in the pelagic systems has been a significant step in the search for generalizations in aquatic ecology. Regularities in the size structure of pelagic communities have been observed in offshore systems (e.g. Sheldon et al., 1972; Beers et al., 1982; Platt et al., 1984; Rodriguez and Mullin, 1986a,b; Witek and Krajewska-Soltys, 1989; Quiñones et al., 2003) and lakes (e.g. Sprules et al., 1983, 1991; Sprules and Knoechel, 1984; Sprules and Munawar, 1986; Echevarría et al., 1990; Ahrens and Peters, 1991; Gaedke, 1993). In coastal pelagic ecosystems the biomass size distribution does not present patterns as regular as those observed in oligotrophic systems but biomass is not randomly distributed across body size (e.g. Jimenez et al., 1987, 1989; Rodriguez et al., 1987). A regular pattern in the biomass size distribution has also been found in salt marshes (Quintana et al., 2002) and benthic communities (e.g. Schwinghamer, 1981; Warwick 1984; Schwinghamer, 1985; Saiz-Salinas and Ramos, 1999; Quiroga et al., 2005).

On the other hand, aquatic food webs are strongly size-structured with larger predators eating smaller prey (Sheldon et al., 1972; Dickie et al., 1987). Many species grow in mass by five orders of magnitude; cannibalism, cross-predation and transient predator–prey relationships are common (Cushing, 1975; Kerr and Dickie, 2001). However, mean body mass of species is only weakly correlated with body mass in the whole food web (Fry and Quiñones, 1994; France et al., 1998; Jennings et al., 2001, 2002). These observations provide compelling reasons to adopt size-based rather than species-based analyses of food web structure in pelagic ecosystems (Jennings and Mackinson, 2003).

In the study of biomass size distribution of pelagic communities, the most common representation used has been the construction of biomass size spectra. In this formulation every individual in the system is assigned to one of a series of size classes represented on a logarithmic scale conforming to an un-normalized spectrum (Fig. 6). The high degree of aggregation of such an ataxonomic approach reduces the complexity of the system to a manageable level. Platt and Denman (1977, 1978) indicated that a normalization procedure was required to represent and cross-compare biomass size distributions adequately, because the width of the size classes varies significantly through the size spectra. In brief, the

normalization procedure consists of taking the variable of interest $Z(s)$ (i.e. usually biomass or numerical abundance) in the size class characterized by the weight or volume (s) and dividing it by the width of the size class, Δs. Thus the normalized version of the variable z (i.e. $Z(s)$; see Fig. 7) is equal to:

$$Z(s) = z(s)/\Delta s . \qquad (16)$$

A detailed analysis about constructing normalized (NBS) and un-normalized size spectra can be found in Blanco et al. (1994; 1998).

On the other hand, Vidondo et al. (1997) have argued in favor of using the Pareto type II distribution, which is widely used in many disciplines to describe size distributions, for representing and modeling size spectra. To apply such an approach adequately, each particle should contribute one point to the Pareto plot and, therefore, all the information contained in the observations is used. The Pareto approximation is ideal for automatic sizing instruments, such as flow cytometers and electronic or laser particle counters. Although in theory it is possible to estimate the parameters of the underlying Pareto distribution from the NBS-spectra, this procedure is not recommended from a statistical standpoint (Vidondo et al., 1997). It is important to note that, in systems that are far from equilibrium, there may be size distributions that cannot be appropriately described by the Pareto nor the normalized biomass-size-spectrum model, such as multimodal distributions (Gasol et al., 1991; Havlicek and Carpenter, 2001).

The size-spectrum approach is rooted in the well-accepted concepts of the pyramids of biomass and numbers (Cousins, 1980, 1985; Platt, 1985) and research in this field can be traced back to the first half of the century (e.g. Elton, 1927; Ghilarov, 1944). However, it is the work of Sheldon et al. (1972, 1973) that provided new impetus to the field by publishing a set of particle-size spectra from oceanic areas (for a historical
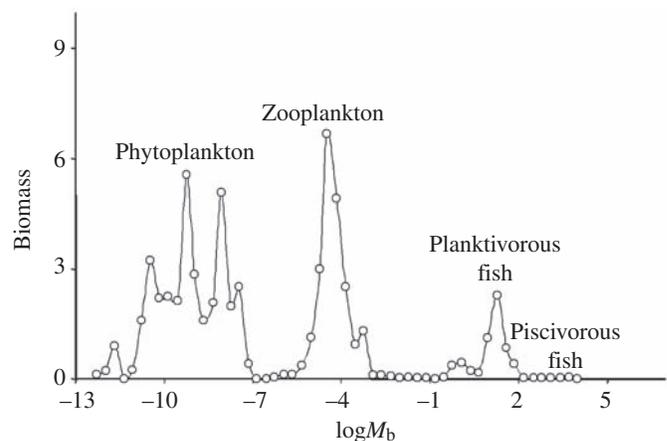

Fig. 6. Example of a unnormalized biomass size spectrum from Sprules et al. (1991) and compiled from their sampling of Lake Michigan, showing the component trophic groups. (After Thiebaux and Dickie, 1993.) Biomass (g m^{-2}); M_b (g).
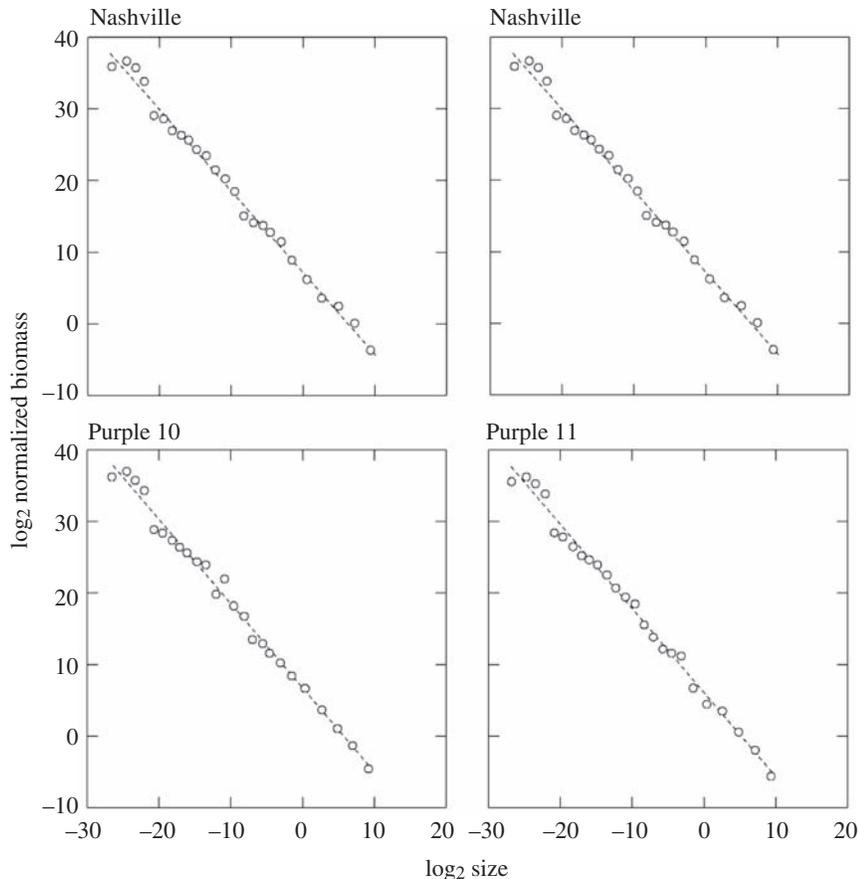
Northwest Atlantic, Quiñones et al., 2003) support the Platt and Denman's model. It is important to note that in Platt and Denman's model the exponent (–0.22) represents a balance between catabolism and anabolism and, consequently, from a scaling standpoint it is coherent with the recently proposed 'metabolic theory of ecology' (Brown et al., 2004).

Linearity, smoothness and continuity in biomass size spectra

Evidence to date shows that oligotrophic ecosystems close to a steady state present more or less linear normalized biomass size spectra (log–log scale). The slope of the NBS-spectrum of oceanic pelagic systems seems to be close to –1 or –1.2 depending on whether biomass is expressed as volume or carbon, respectively (Rodriguez and Mullin, 1986b; Quiñones et al., 2003). By contrast, ecosystems far from the steady state may present non-linear normalized biomass spectra and under extreme conditions the biomass-size spectra can present discontinuities (Quiñones, 1994). Havlicek and Carpenter (2001) show that size distributions in lake communities have multiple lump and gap regions within each functional group of phytoplankton, zooplankton and fish. Simulations showed the gaps could not be explained by incomplete censuses of species or by systematic underestimation of intraspecific size variation. Nevertheless lakes that differed widely in nutrient status, trophic structure, species diversity and area had similar size distributions. A detailed analysis of the discontinuities in the marine biomass spectra of close to steady state systems has not been conducted to date.

Dickie et al. (1987) analyzed the distribution of specific production by size in ecosystems. They identified two kinds of slopes in the relationship between log-specific production and log body size (Fig. 8). First, a unique primary slope reflecting the size dependence of metabolism. This primary slope is uniform, low and negative (approximately –0.18). Second, a collection of secondary slopes, which represent an ecological scaling of production related to rapid changes of log annual-specific-production with log body size within groups of organisms with similar production efficiencies. These secondary slopes are steeper than the primary slope. Boudreau et al. (1991) have pointed out that such ecological scaling would produce dome-like patterns in the biomass size spectra. In fact, dome-

perspective see Platt, 1985). Sheldon et al. (1972), based on his field observations, proposed the 'linear biomass hypothesis', which states that in the pelagic system there is roughly the same biomass at all size classes. The regularities in pelagic size structure observed by Sheldon et al. (1972, 1973) and the fact that most aspects of energy and material flow of an organism are size dependent (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984) led to the development of theoretical models to explain and quantify the regularities (e.g. Kerr, 1974; Sheldon et al., 1977; Platt and Denman, 1977, 1978; Silvert and Platt, 1978, 1980; Borgmann, 1982, 1983, 1987; Dickie et al., 1987; Boudreau and Dickie, 1989; Boudreau et al., 1991). The first theoretical models about the size structure of the pelagic ecosystem were proposed by Kerr (1974), Sheldon et al. (1977) and Platt and Denman (1977, 1978). Whereas the two first models were based on the trophic-level concept, the last stands on the consideration of a continuous flow of energy from small to large organisms. Kerr and Sheldon's models propose that biomass is constant when organisms are organized in logarithmic size classes. On the other side, Platt and Denman's model predicts a slight decrease of biomass with organism size with a slope of –0.22 and proposes an allometric structure for the pelagic ecosystem (Platt and Denman, 1977, 1978). Until now the most comprehensive biomass size spectra constructed in close to steady state systems (i.e. North pacific Central Gyre, Rodriguez and Mullin, 1986b; oligotrophic areas of the
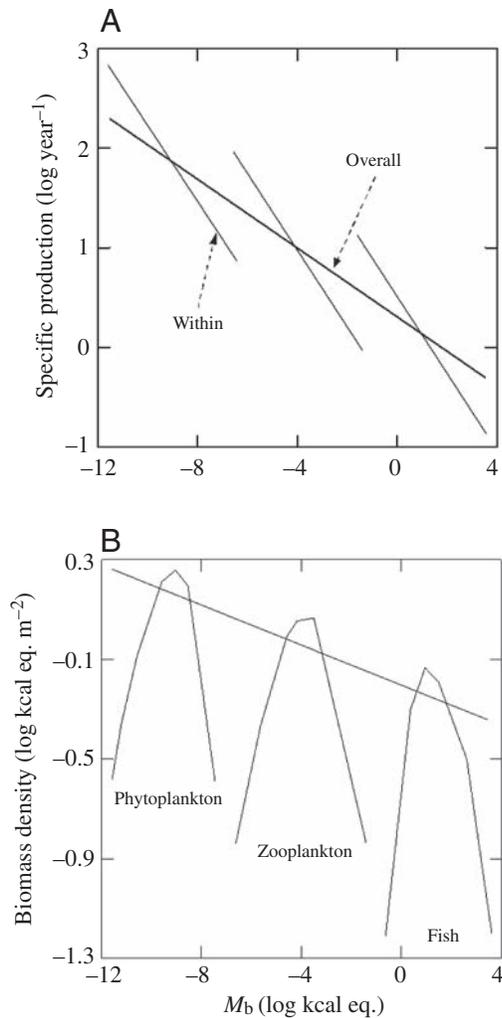
Fig. 8. Schematic representation of the equivalent body-size spectra of: (A) specific production, expressed as log P/B by trophic positional grouping. (B) Biomass density of a given enviroment. (After Boudreau et al., 1991.) Biomass (M_b) is expressed as energy equivalents of body mass.

like patterns have been observed in several ecosystems (e.g. Sprules and Munawar, 1986; Sprules et al., 1988; Rodriguez et al., 1990; Sprules et al., 1991). However, oligotrophic oceanic systems present NBS-spectra that can be properly described by a straight line (e.g. Rodriguez and Mullin, 1986a; Witek and Krajewska-Soltys, 1989; Quiñones et al., 2003). In fact, in addition to linearity, perhaps the second most-characteristic feature of the size structure of plankton in the oligotrophic ocean seems to be the similarity between primary and secondary scales. The linearity of the NBS-spectra in oligotrophic oceanic waters suggests the dominance of the metabolic scaling over the ecological scaling in these areas. It is interesting to note that the primary slope of the normalized biomass spectra seems to be strongly related to the slope of the normalized metabolic spectra as shown empirically by Quiñones (1992) and Quiñones et al. (1994) in planktonic communities from the North Atlantic and Mediterranean Sea, respectively.

The complete absence or scarcity of conspicuous dome-like patterns in the biomass size distribution in some pelagic ecosystems can also be explained in trophodynamic terms by several hypotheses that are not mutually exclusive. First, if the food web in a particular system is unstructured (*sensu* Isaacs, 1972, 1973) the domes, if any, will tend to be minor. Second, the dome-like patterns will also be less conspicuous in systems with a more-structured food web but where there is a large range of prey/predator body-size ratios (Thiebaux and Dickie, 1993). Indeed, the assumption of a constant prey/predator ratio for the pelagic ecosystem is erroneous as shown by Longhurst (1989, 1991). Third, if the trophic positions (i.e. groups of organisms having a common production efficiency, Boudreau and Dickie, 1992) are not sufficiently characterized by different size ranges, the domes will not be conspicuous in the biomass size spectra. Evidently, not all observed dome-like patterns are produced by the secondary scaling described by Dickie et al. (1987). In fact, dome-like patterns may result from mere methodological artifacts (García et al., 1994). In addition, some observed dome-like patterns in pelagic systems could be the by-product of the propagation of a peak of biomass or energy (Silvert and Platt, 1978, 1980; Han and Straskraba, 2001) through the size spectrum. Waves of energy changing the shape of the biomass spectrum have been observed both in coastal (Rodríguez et al., 1987; Jiménez et al., 1989) and oceanic waters (Rodríguez and Mullin, 1986a).

Environmental variables determining and/or affecting biomass size spectra

Sprules and Munawar (1986) proposed a relationship between the numerical value of the slope of the NBS-spectra and the trophic state of a pelagic ecosystem. Eutrophic ecosystems would present more positive slopes than oligotrophic ecosystems. However, due to both methodological difficulties and to the lack of sufficient data this hypothesis is still far from being validated.

It is known that several size-dependent processes can alter community size structure. Size-selective predation can be a primary organizing force in some communities (Brooks and Dodson, 1965; Hall et al., 1976; Vanni, 1986) and the size structure of the grazers can influence the size structure of the phytoplankton community (Carpenter and Kitchell, 1984; Bergquist et al., 1985). In fact, Rassouldagan and Sheldon (1986) and Sheldon et al. (1986) have experimentally shown that predation can play a major role in structuring size spectra.

Abiotic forcing has also the potential to modify biomass size distribution. For instance, Havens (1992) demonstrated that acidification could change the parameters of freshwater plankton size spectra and Samuelsson et al. (2002) show that nutrient enrichment in mesocosms resulted in higher biomass and changed plankton size structure.

In relation to benthic size spectra, the physical characteristics of the sediment (Schwinghamer, 1981; Drgas et al., 1998; Duplisea, 2000), the gradient of organic matter (Schwinghamer, 1985), the life-history strategies of dominant taxa (Warwick, 1984) and oxygen levels (Quiroga et al., 2005)

are thought to constrain the size spectrum of faunal species. However, the spectra seem to be quite conservative. For instance, Rafaelli et al. (2000) imposed size-specific perturbations (enrichment and predation) on marine sediment assemblages. Perturbations significantly affected the densities and relative abundance of the main invertebrate taxa and these effects were consistent with the known effects of enrichment and predation. However, there was little evidence of significant treatment effects on the overall benthic biomass or abundance size spectrum, supporting the contention that the spectrum is conservative and is probably constrained by habitat architecture.

The applications of biomass size spectra

Since the late 1970s, the NBS approach has found application in several fields, such as fisheries research and pollution studies. In fisheries, the NBS approach has been applied to predict fish production from phytoplankton standing stock (Moloney and Field, 1985) and from primary and zooplankton production (Sheldon et al., 1977; Borgmann, 1982, 1983; Borgmann et al., 1984). The NBS approach has formed the basis of models to estimate fish mortality rates (Peterson and Wrobleski, 1984) and to analyze multispecies fisheries (e.g. Pope et al., 1988; Murawski and Idoine, 1989; Duplisea and Kerr, 1995, 2000). Also, models to estimate production of multispecific fisheries based on size structure and the allometric relation of the production to biomass ratio have been developed (Dickie et al., 1987; Boudreau and Dickie, 1989, 1992). Recently, there is a growing interest in generating sound ecological indicators to support an ecosystem approach to fisheries as stated in the International Symposium on Quantitative Ecosystem Indicators for Fisheries Management (March–April 2004, UNESCO, France). Thus, size-based indicators have become one of the main avenues of research (e.g. Bianchi et al., 2000; Rice, 2000; Zwanenburg, 2000). In pollution studies, the NBS approach has been used to model the flow of contaminants up the food web (Thomann, 1979, 1981; Griesbach et al., 1982; Borgmann and Whittle, 1983; Vezina, 1986).

The metabolic spectra

It has become evident that to understand the dynamic of the pelagic ecosystem it is necessary to allocate more efforts in the empirical study of community processes, such as respiration and production, from an allometric point of view (Quiñones, 1994). The distribution of biomass by size, despite its linkage to the energetics of the system, is essentially a measure of ecosystem structure. The simultaneous study of size structure and processes, such as respiration, should permit a better understanding of the relationship between structure and function in the ecosystem. The only metabolic spectra to date are those described for the Northwest Atlantic (Quiñones et al., 1991; Quiñones, 1992) and for the Alboran Sea (Quiñones et al., 1994). These spectra covering from bacteria to zooplankton show that respiration in the pelagic system diminishes as a

power function of body size at the community level of organization, with a slope close to –1.2 (normalized metabolic spectra). Further research in this field is crucial to connect the metabolic theory of ecology (Brown et al., 2004) adequately with size-spectrum theory in the pelagic ecosystem.

Some ecological power-laws related to population abundance and fluctuation

As with scaling relationships associated with body size, power-laws are ubiquitous in ecological systems, for example in the size and duration of epidemic events (Rhodes and Anderson, 1996; Rhodes et al., 1997), in patterns of abundance, distribution and richness (e.g. Frontier, 1985; Banavar et al., 1999; Harte et al., 1999, 2001) and in food web attributes (e.g. Brose et al., 2004; Garlaschelli et al., 2003). In the following paragraphs we will present some power-laws associated with population dynamics, which highlight phenomena also seen in the context of scaling relationships (such as zero-sum dynamics) and relationships that can be categorized in terms of body size.

Power-laws in population growth rates

Standard ecological wisdom asserts that population size is expected to follow a lognormal distribution, given that it is the product of a multiplicative renewal process (e.g. Lawton, 1989; Blackburn et al., 1993b; Halley and Inchausti, 2002). Furthermore, several single species population models give rise to normal or lognormal population abundance distributions (e.g. Keeling, 2000). If population abundance follows a lognormal distribution, it is expected that the ratio of successive abundances $N(t+1)/N(t)$ also has a lognormal distribution and, hence, the logarithm of such a ratio $\dot{r}=\ln[N(t+1)/N(t)]$, should show a normal or Gaussian distribution. In other words, under an expectation of lognormal population abundances, population growth rates should exhibit a Gaussian probability distribution. Interestingly, as shown by Keitt and Stanley (1998), the growth rates in an avian ensemble over a large geographical scale in North America are not distributed following a Gaussian distribution, but rather follow a power-law with a characteristic tent shape (Fig. 9A), which is well described by an exponential or log-Laplace distribution (Keitt and Stanley, 1998; Keitt et al., 2002). Furthermore, the same tent-shaped power-law form is also observed when examining the conditional probability density distributions of growth rates $\dot{r}_s$ given an initial abundance class $p(\dot{r}_s|N)$, defined by grouping observations into bins or categories of initial total abundance (Fig. 9B). The width of the distribution, as measured by the standard deviation of the growth rates, widens as the initial population abundance decreases (Fig. 9B). It is remarkable that when the scaled growth rate $\dot{r}_{scal}=[\dot{r}_s-\langle\dot{r}_s\rangle]/\sigma$ and the scaled probability density $p_{scal}=\sigma p(\dot{r}_s|N)$ are calculated for these conditional probability distributions (Fig. 9C), all the data from the different bins collapse onto the same universal power-law curve $p_{scal}\equiv e^{(-|r\ scal|)}$. This non-trivial rescaling suggests that in spite of differences in body size, life history

and ecology, all the species under study fall along a single power-law relationship, which suggests that they share a common universal probability density distribution of growth rates. This powerful statement is further strengthened by the fact that this universal distribution is a power-law.

The presence of scaling and universality in population growth rates has strong implications for understanding population dynamics in general. In physical systems, scaling is often found in the presence of 'cooperative' behavior. In inanimate systems, such as ferromagnets near a critical temperature point, scaling relationships arise because each particle interacts directly with a few neighboring particles and, as these neighboring particles interact with their neighbors, interactions can 'propagate' long distances, thus resulting in

power-law distributions (Stanley et al., 2000). Similar results have been observed for the probability distributions of growth rates of companies, universities and countries' gross national product, all of which have been observed to rescale to the same exponential probability density function $f(x)=e^{(-|x|)}$ (Stanley et al., 1996; Canning et al., 1998; Plerou et al., 1999). In physics, such universal and scaling behavior is interpreted as evidence that the physical dimensions of the phenomenon predominate in setting the observed dynamical patterns. This strongly suggests that there may indeed exist universal principles that underlie the growth dynamics of complex adaptive systems that are involved in the acquisition, transformation and storage of information, materials and/or energy.

In the case of ecological communities, the scaling in population growth or fluctuation can be brought about either by the spatial dimension of spatial population structure, or more importantly, by the physical dimension of energy and material flows. In the first case, it can be argued that interactions in ecological systems may propagate through spatial metapopulational dynamics, with local patches being saved from extinction by immigration from nearby populations. Thus, rescue-effects (Brown and Kodric-Brown, 1977) may couple large systems. On the other hand, species present in an ecosystem interact directly with some (but not necessarily all) species, which may in turn interact with a second set of species, so that interactions can 'propagate' through time and space from the individual to the population, community and ecosystems and finally to the biosphere scale. The fundamental connectivity of the living makes the existence of power-laws plausible.

The relationship between energy and material flows and the emergence of observed power-laws in ecological systems can be further highlighted by an important implication which has not been emphasized by previous authors. In addition to its tent-shaped form and the observed rescaling features, the observed distribution of growth rates is highly symmetrical about $\dot{r}_s=0$ in all cases considered. This implies that exactly as
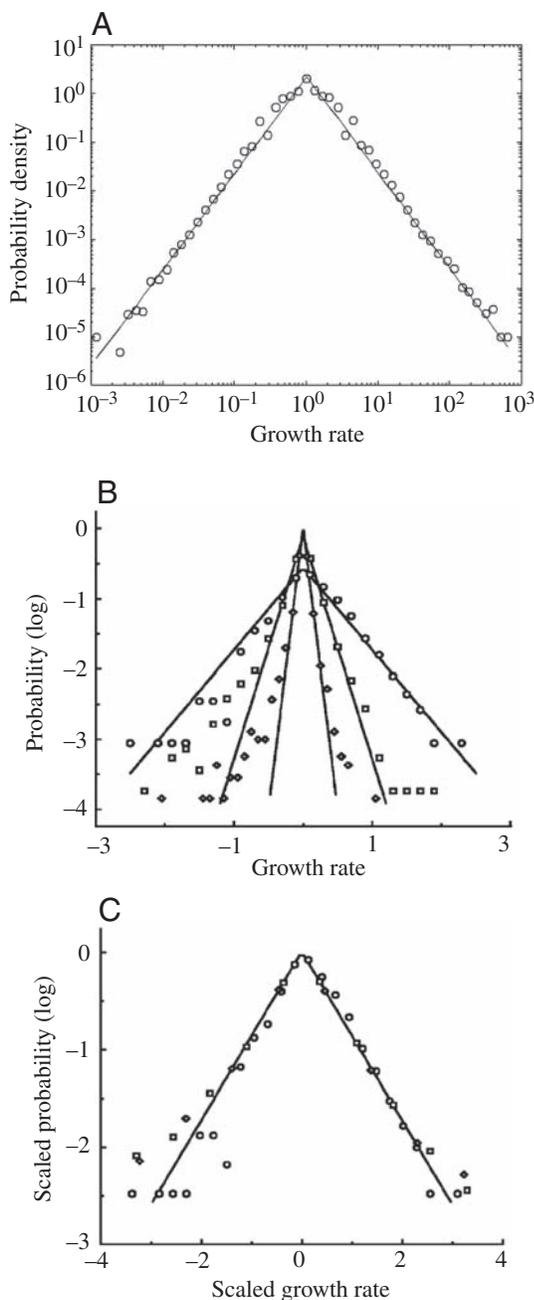
Fig. 9. Scaling of population growth rates in the BBS data set. (A) Distribution of population growth rates $\dot{r}_s \equiv \log[N(t+1)/N(t)]$ across all species in the data set. The growth rate $\dot{r}_s$ is calculated by log transforming the ratio of species abundances in successive years. Abundances are taken as the total number of individuals of a particular species counted within each survey route. (After Keitt and Stanley, 1998.) (B) Probability density $p(\dot{r}_s|N)$ of the growth rate $\dot{r}_s$ for all bird species in the BBS database for different initial population size classes. The distribution represents all annual growth rates observed in the 31 year period 1966–1996. Data are shown for three different bins of initial sizes (circles, $10^0<N(t)<10^1$; squares, $10^1<N(t)<10^{2.4}$; diamonds, $10^{2.4}<N(t)<,10^{3.8}$). The solid lines are exponential fits to the empirical data close to the peak. (C) Scaled probability density $p_{scal} \equiv \sigma p(\dot{r}_s|N)$ as a function of the scaled growth rate $\dot{r}_{s\ scal} \equiv [\dot{r}_s-<\dot{r}_s>]/\sigma$ for all species and years in the survey. The values were re-scaled using the measured values of $<\dot{r}_s>$ and σ. Notice that all the data collapse upon the universal curve $p_{scal} \equiv e^{(-|r\ scal|)}$. (After Keitt et al., 2002.)

many species are increasing in abundance as are decreasing over the 31-year period studied, be it over the whole ensemble, or when grouping by initial abundance bins. Thus, these species undergo a zero sum dynamic in population size, with demographic gains and losses by all the species balancing over the study period. This is not obvious, nor is it expected from previous theoretical explanations for the emergence of scaling laws in physical systems. The idea of zero-sum dynamics in communities has also been supported by studies of the pattern of biomass distribution between species of different communities of extant and fossil plants across different biogeographic provinces (Asia, Africa, Europe, South and North America; Enquist et al., 2002). The idea of the existence of zero-sum dynamics in systems under energy limitation can be dated back to the 'red queen hypothesis', which predicts that any change in the control of trophic energy by a species is balanced by a net equal and opposite change in the amount of trophic energy controlled by all the other species in the community with which that species interacts (Van Valen, 1976, 1977; Stenseth, 1979). In this formulation, trophic energy, defined as an individual's control of a constant amount of the energy available to a group of related species that compete for it, is a proxy for fitness. This implies that energy use by the species in a community is a zero-sum game (Hubbell, 1997, 2001; Bell, 2000), with a balance in the energy gained and lost by all the interacting species. In this regard, the red queen hypothesis emphasizes that under a scenario of limiting resources zero-sum dynamics must necessarily operate, as an expression of the first law of thermodynamics (Van Valen, 1976, 1977; also see open discussion in Van Valen, 1980). As we already mentioned, the existence of an 'energetic equivalence rule' within local communities implies that species follow a zero-sum dynamic in energy use. That zero-sum dynamics seem to hold for demographic changes, total biomass and population energy use may seem paradoxical. Indeed, it is one of the research questions left open by these various scaling and power-law relationships.

It is important to note that these results have not been exempt from criticism in the literature, and we close this section by mentioning and discussing the main points made against the existence of power-laws in the distribution of population growth rates. It has been argued that the tent-shaped distribution of population growth rates may be the end product of a mixture of lognormal distributions in population size (Allen et al., 2001). This phenomenological explanation, however, does not account for the symmetrical nature of the distribution, nor does it provide a mechanism that accounts for its form and location. Another possible explanation of these results is that the distribution of growth rates in the community arises from a mixture of Gaussian population growth rate distributions for each of the species with different variances (Amaral et al., 1998). This would require nevertheless, that all the distributions of growth rates be centered with mean zero, so that all species must be regulated around an equilibrium point and, hence, does not take into account the fact that in the observed data some species show marked trends in abundance.

Thus, species increases have to be balanced by decreases in other species.

Scaling of population fluctuations

Power-laws in population fluctuations are well known and have been the focus of an increasing number of contributions in recent years, as a consequence of the availability of long time series in population dynamics, such as the Breeding Bird Survey (BBS) and the Global Population Dynamics Database (GPDD). Time series analyses of population fluctuations have shown that the size of fluctuations (n) decrease, on average, as the inverse of the frequency (f) with which they occur or as '1/f noise' or 'pink noise' (e.g. Halley, 1996; Miramontes and Rohani, 1998; Inchausti and Halley, 2001; Storch et al., 2002; see review in Halley and Inchausti, 2004) such that the distribution of fluctuations sizes is described by a power-law of the form $D(n) \sim n^{-\alpha}$, with α close to 1, as expected under self-organized criticality (Bak et al., 1987). In addition to 1/f noise, one of ecology's most interesting patterns regarding population variablity is Taylor's power-law (Taylor, 1961). It has been observed that for many species, the variance in population abundance $\sigma^2(N)$ is related to the mean of population abundance $<N>$ by a power law with a fractional exponent: $\sigma^2(N) \propto <N>^{\gamma}$ (Taylor, 1961; Taylor and Woiwod, 1980; Anderson et al., 1982; Hanski and Tiainen, 1989; Boag et al., 1992; Keitt and Stanley, 1998). For the vast majority of species, the power-law scaling parameter, γ is found to lie between one and two, with many species lying close to the extremes (Anderson et al., 1982). This scaling relationship has been described for a wide range of taxa, both for spatial and temporal scaling. The majority of the studies focusing on population variability have emphasized species differences and seek to find ways to classify these differences among species, with due consideration given to the methodological biases and caveats inherent to such comparisons (e.g. McArdle et al., 1990). Scaling studies take a different approach. Instead of focusing on differences among species in a comparative frame, these studies seek to separate general patterns or 'laws' that are invariant across taxonomic groups from general rules that may explain deviations from these laws and which may eventually be linked to the species biology or ecology.

It is interesting to note that, should Taylor's power-law hold for temporal variation in abundance and if the temporal mean abundance follows a negative relationship with body size, the scale invariance in both power-law relationships makes it possible to derive the scaling in population variability as a function of body size and it can be expected that $\sigma^2(N) \propto (<M>^{\nu})^{\gamma} \propto <M>^{\nu\gamma}$. Thus, as ν is expected to be $-3/4$ and γ is usually between 1 and 2, hence population variability should show a negative scaling relationship with body mass, taking values between $-3/4$ and $-3/2$. Although this relationship has not been tested explicitly in the literature, the work by Keitt et al. (2002) provides evidence that such a negative scaling may hold for North American birds when studied at the population level. These authors show that the standard deviation $\sigma(\dot{r}_s)$ of

population growth rates in North American birds is strongly related to the average total population size. The relationship follows a power law $\sigma(\dot{r}_s) \propto <N>^{\beta}$, for over four orders of magnitude in $<N>$, the total population abundance averaged across all 31 years studied. Using major axis regression with bootstrap precision estimates, Keitt et al. (2002) find $\beta=0.36\pm0.02$, so that Taylor's exponent (here replicated across species) is found to be $\gamma=2(1-\beta)=1.28\pm0.04$. Again, under the assumption that there exists a negative relationship between average abundance in time and body size: $<N> \propto <M>^{\nu}$, with $\nu=-3/4$, it can be seen that the temporal variance in population abundance should scale approximately as $M^{-1.0}$ (the observed value is -0.96 ± 0.03). On the other hand, the standard deviation in population growth rate should scale as $\sigma(\dot{r}_s) \propto <M>^{\beta\nu}$, which predicts then that fluctuations in growth rates should show a $M^{-1/4}$ scaling (the observed value is -0.27 ± 0.05), as do other temporal phenomena in ecology and biology (Calder, 1983; West et al., 1999). It certainly would be interesting to test whether these predictions hold to empirical scrutiny for the species studied by Keitt and collaborators (Keitt and Stanley, 1998; Keitt et al., 2002) as well as for other taxa and at other spatial scales of study.

Scaling and conservation biology

As mentioned in previous sections, scaling and power-laws point out to the action of universal or law-like phenomena that allow the study of ecological systems even in the absence of detailed knowledge on demography and dynamics. In this context, the application of scaling relationships to conservation biology should be widespread provided the pressing need to slow down the extinction crisis and the lack of detailed demographic information for the majority of endangered species (Calder, 2000; but see Simberloff, 2004). However, despite their generality, the use of scaling relationships in conservation biology has been scant and most of the attention has been given to the power-law relating number of species and area (e.g. Rosenzweig, 1995; Brooks et al., 1997, 1999). One recent exception is the development of the software RAMAS Ecorisk (Hajagos and Ferson, 2001) that uses scaling relationships in combination with traditional population analysis to assess species extinction risk. In this section, we review some applications of body size scaling to predict species' traits that might be useful in conservation biology. We provide some examples of allometric scaling relationships that deal with vulnerability to extinction, minimum viable population size, minimum area requirements, habitat fragmentation and invasion success by non-indigenous species.

When it comes to risk of extinction, not all species are equal. Understanding what factors predispose a species to become endangered and extinct is one of the major challenges for conservation biologists. In addition to external factors, such as habitat loss, over-exploitation, introduced species and chains of extinction, several intrinsic traits have been implicated in the extinction process of species (Fisher et al., 2003). Among them are population density, population variability,

reproductive output, trophic position, geographic range and dispersal ability (Pimm et al., 1988; Gaston and Blackburn, 1995, 1996; Lawton, 1995; Bennett and Owens, 1997; Cardillo and Bromham, 2001). However, many of these traits correlate well with body size. Therefore, body size has been used as a surrogate for other life history or ecological traits that influence vulnerability to extinction (e.g. Johst and Brandl, 1997; McKinney, 1997; Cofré and Marquet, 1999; Dulvy and Reynolds, 2002).

One of the first modeling approaches to link body size with population persistence over time in mammals was developed by Belovsky (1987). Based on a population model by Goodman (1987), he estimated the population reproductive growth rate and population maximum size (taken from the literature) as a function of body mass, and calculated minimum viable population size and minimum area requirements for mammals. As a surrogate for variability in population parameters, he employed environmental variability. Using datasets of mammals in mountaintops in the Great Basin desert and the Southern Rocky mountains of North America, he found a close agreement between the predictions from the model and the observed persistence time. As expected, smaller species required higher minimum viable population sizes than larger species to persist over a certain period of time. However, the predicted minimum area required to sustain a given maximum population size varied depending on the species' feeding ecology (with larger areas required for carnivores than for herbivores) and its environment (with larger areas needed for tropical than for temperate species). The model is somewhat simple in that it assumes that there is a single isolated population and that all individuals experience the same environmental variability. In reality, it is more likely that species are patchily distributed, perhaps forming a metapopulation, in which each population experiences different levels of environmental variability. Despite its shortcomings, this model represented a first approximation of the population sizes and habitat area required for sustaining mammal populations over some period of time and, therefore, a relatively useful tool for managing endangered species and the design of wildlife preserves.

Besides the use of body size to estimate parameters in population models, as in the example above, scaling of body size has been directly related to minimal viable population densities (MVPD) of mammals (Silva and Downing, 1994). Silva and Downing (1994) compiled data on MVPD for 143 species of mammals and performed correlations against body size. They found that minimum density of mammal species decreases as body size increases, supporting the predictions of empirical models based on average density. Correlations between body size and MVPD were negative within taxonomic groups, habitat types and climatic zones. This finding has implications for estimating minimum habitat area required to sustain minimum viable population densities of a species of a given body mass. However, as discussed previously there empirical evidence related to the scaling of body mass extremes that support the invariance of MVPD (Marquet and

Taper, 1998). According to the authors, the mechanism underlying this pattern is the result of body size related biases in extinction probabilities, with medium-sized species (of about 100 g in mammals) being less prone to extinction. This argument is based on the idea that medium-sized species attain higher population densities (Marquet et al., 1995; Silva and Downing, 1995) and have lower population variability (Pimm, 1992) than both smaller and larger species; two factors of crucial importance in minimizing the risk of extinction of species. Marquet and Taper (1998) provided empirical evidence for the validity of this relationship when extended from the evolutionary scale to the ecological scale (Schmidt and Jensen, 2003). At the ecological scale, the implication of this pattern is relevant for dealing with habitat fragmentation since it is the result of processes related to the way body size affects the number of individuals that a particular species can pack in a given area (Marquet and Taper, 1998). Thus, in fragmented habitats where the distance between patches prevents migration and rescue-effects (Brown and Kodric-Brown, 1977), it is expected that medium-sized species would fare better than both smaller and larger species. In the long run, species with extreme body sizes may become extinct. Therefore, one could predict what species are more vulnerable to extinction after habitat fragmentation occurs.

A long-standing goal for ecologists has been to predict which species will become invasive when introduced to a new environment. Several life-history traits have been hypothesized to be important at different stages of the invasion process (transport, introduction, establishment and spread; Sakai et al., 2001). Some of these traits are the ones related to faster population growth (e.g. fecundity, clutch size, incubation time). The idea behind this concept is that most introduced populations start off small and are, therefore, more vulnerable to extinction. Consequently, species with higher rates of population growth should have higher probabilities of surviving and establishing and, thus, escape the risks of extinction from being a small founding population (Pimm et al., 1988). However, because population growth is very difficult to measure, most studies use body size as a surrogate, since both traits are known to be inversely correlated (Duncan et al., 2003). If growth rate is indeed important in determining invasion success, the expectation would then be that smaller species are more successful at invading new environments than large species. Hence, body size has been implicated in the invasion success and subsequent spread of non-indigenous species (Cassey, 2001).

The findings of empirical studies regarding body size and invasion success are ambiguous. For introduced birds in Australia, it was found that large body size is associated with introduction success, whereas, among the introduced species, small-bodied species attained larger geographical ranges (Duncan et al., 2001). A similar pattern was found for introduced mammals in Australia, with the exception that body size was not significantly associated with introduction success (Forsyth et al., 2004). Small species were also found to have large geographic ranges in introduced birds to New Zealand

(Duncan et al., 1999). Additionally, the relationship between body size and introduction success seems to vary depending on the taxonomic rank considered. Cassey (2001) found that global introduction success of land bird species is negatively correlated across species, families and higher family nodes. However, he found that, within taxa, successfully established species had large body size. An important characteristic of these studies is that they had information on non-indigenous species that were both successful and that failed to establish in the new environment. Other studies that correlated body size with invasion success of only successfully established species are those for marine bivalves introduced in the northeast Pacific coast (Roy et al., 2002) and insects into Britain (Lawton and Brown, 1986). Roy et al. (2002) found that large-bodied species of marine bivalves were more likely to be successful invaders. They argue that this may be due to fundamental differences in life histories between vertebrates and marine invertebrates. In contrast to birds and mammals, fecundity and body size are positively related in marine bivalves. In the other study, Lawton and Brown (1986) found that the probability of establishment of different orders of non-indigenous insects introduced into Britain was negatively correlated with body size. However, when they included other successfully introduced groups in the analysis (e.g. mammals, fish, birds, molluscs), the relationship between probability of establishment and body size became positive. As mentioned above, the results are ambiguous and do not generalize across taxa, or even among different stages of the invasion process when the same taxon is considered. Hence, the application of scaling relationships to predict invasion success is not straightforward.

Concluding remarks

We have attempted to show how body size scaling relationships and power-laws provide a fresh perspective to tackle ecological complexity, from individuals to ecosystems. However, their use can be improved and refined. One of those refinements has recently been articulated by Brown at al. (2004) who first provide a quantitative theory (the metabolic theory of ecology) able to explain and predict scaling relationships and exponents based on first principles associated with fundamental processes of energy acquisition and transformation as affected by size, metabolism and temperature.

Scaling relationships rest heavily on individual level phenomena, which by aggregation enable us to predict whole system patterns, processes and rates (e.g. Enquist et al., 2003). It is striking how strong the fit between predicted and observed patterns usually is, considering that most data on individuals and species populations come from different places around the world, with different biogeographic histories, disturbance regimes and productivities. It might seem striking that scaling relationships, which are usually free of ecological context (Marquet, 2002b; Marquet et al., 2004) can be so powerful. However, this is to some extent expected given that they

usually focus on 'bulk properties' of ecological systems that are less affected by local ecological idiosyncrasies. Scaling relationships are mostly concerned with central tendencies in ecological phenomena, which predicts how the average individual, population and ecosystem should behave and be structured. Although many would say that the interesting biology is in the scatter and that such a thing as an average ecological system does not exist, but just different realizations of them, it is important to recognize that unless we have a mechanistic theory that provides us with an expected baseline, we would not be able to identify any deviation worth explaining in the first place. In this sense, both approaches are interesting and complementary. And this is probably one of the most important attributes of the theory outlined by Brown et al. (2004) for it can provide fruitful insights and testable predictions to advance our understanding of the structure of ecological systems at disparate scales in time and space and organization, dressing with a quantitative theory the discipline of macroecology, that to a large degree has been mostly an empirical endeavor focused on the description of patterns and in the accumulation of alternative hypothesis for them (see Marquet et al., 2003 for a discussion of distribution of abundance patterns). However, further development and testing of this approach will require the collection of more and better data on the richness, density, biomass and metabolic activity of species within local ecosystems. We need standardized data on biodiversity, which will allow for rigorous tests of the predictions at a local scale. This might be a daunting task, but to advance in our understanding we need comprehensive and complete analyses of ecological systems. However, there are important methodological concerns to be aware of, which are outlined below.

The problem of aggregation

Recent work on scaling relationships has pointed out to the effect of data aggregation in the estimation of scaling relationships in ecology (Torres et al., 2001; Savage, 2004c; Cohen et al., 2005). This is an important methodological point that should be borne in mind when working with scaling relationships in general. Its mathematical base is in what is known as Jensen's inequality, which establishes that '*the expected value of a function is not (in general) equal to a function of the expected value*' and is also known as the 'fallacy of averages' (Welsh et al., 1988; Medel et al., 1995; Savage, 2004c) and 'transmutation' (O'Neill, 1979; King et al., 1991) such that it is problematic to construct scaling relationships based on average quantities, such as body mass or metabolic rate, for it can lead to bias due to their inherent nonlinearity.

The problem of causality

The usual convention in allometric studies has been to use body size as the independent variable, however there is no way to prove this causal relationship logically, for body size and physiological, ecological and evolutionary traits do not evolve in isolation, but affect each other through complex interactions.

In fact, plant ecologists have traditionally treated the size of individuals as if they were determined by population density (i.e. the 'thinning law') and the same is observed in the analysis of size-structured food webs (Cohen et al., 2003; Mulder et al., 2005). Although this might seem mostly a philosophical problem it has important implications when working with scaling relationships, for causality specifies the way error propagates in deriving scaling relationships from known ones (Taper and Marquet, 1996).

The ubiquity and simplicity of scaling relationships and power-laws in ecological systems might be deceptive when compared with the complexity of the systems that they attempt to describe. Unless their theoretical foundations and underlying mechanisms are worked out to a sufficient detail to be able to predict new and, so far unknown, relationships there is the danger for this field to become adrift in a sea of empiricism devoid of theory and with little explanatory power and generality. Recent theoretical developments, such as the metabolic theory of ecology (Brown et al., 2004) hold great hope in this direction, however there is still ample ground for synthesis and theory refinement. In particular, experimental approaches with either model organisms or simple ecosystems, have been little explored in the context of scaling and power-law relationships and could prove to be particularly fruitful to gain a deeper understanding of their generating mechanisms and implications. The way ahead is certainly challenging.

References

Ahrens, M. A. and Peters, R. H. (1991). Patterns and limitations in limnoplankton size spectra. *Can. J. Fish. Aquat. Sci.* **48**, 1967-1978.

Allen, A. P., Li, B. and Charnov, E. L. (2001). Population fluctuations, power laws and mixtures of lognormal distributions. *Ecol. Lett.* **4**, 1-3.

Alroy, J. (1998). Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**, 731-734.

Amaral, L. A. N., Buldyrev, S. V., Havlin, S., Salinger, M. A. and Stanley, H. E. (1998). Power law scaling for a system of interacting units with complex internal structure. *Phys. Rev. Lett.* **80**, 1385-1388.

Anderson, R. M., Gordon, D. M., Crawley, M. J. and Hassell, M. P. (1982). Variability in the abundance of animal and plant species, *Nature* **296**, 245-248.

Armbruster, P., Hutchinson, R. A. and Cotgrave, P. (2002). Factors influencing community structure in a South American tank bromeliad fauna. *Oikos* **96**, 225-234.

Bak, P. (1996) *How Nature Works. The Science of Self-Organized Criticality.* New York: Springer-Verlag.

Bak, P., Tang, C. and Wiesenfeld, K. (1987). Self-organized criticality: an explanation of 1/f noise. *Phys. Rev. Lett.* **59**, 381-384.

Bak, P., Tang, C. and Wiesenfeld, K. (1988). Self-organized criticality. *Phys. Rev. A* **38**, 364-374.

Banavar, J. R., Green, J. L., Harte, J. and Maritan, A. (1999). Finite size scaling in ecology. *Phys. Rev. Lett.* **83**, 4212-4214.

Barabási, A.-L. and Oltvai, Z. N. (2004). Network biology: understanding the cells's functional organization. *Nat. Rev. Genetics* **5**, 101-113.

Beers, J. R., Reid, F. M. H. and Stewart, G. L. (1982). Seasonal abundance of the microplankton population in the North Pacific Central Gyre. *Deep-Sea Res.* **29**, 217-245.

Belgrano, A., Allen, A. P., Enquist, B. J. and Gillooly, J. F. (2002). Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecol. Lett.* **5**, 611-613.

Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.* **155**, 606-617.

Belovsky, G. (1987). Extinction models and mammalian persistence. In *Viable Populations for Conservation* (ed. M. E. Soulé), pp. 35-57. Cambridge: Cambridge University Press.

Bennett, P. M. and Owens, I. P. F. (1997). Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. Roy. Soc. Lond. B* **264**, 401-408.

Bergquist, A. M., Carpenter, S. R. and Latino, J. C. (1985). Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnol. Oceanogr.* **30**, 1037-1045.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Payá, I., Sainsbury, K., Sanchez, F. et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* **57**, 558-571.

Bini, L. M., Coelho, A. S. and Diniz-Filho, J. A. F. (2001). Is the relationship between population density and bodysize consistent across independent studies? A meta-analytical approach. *Rev. Bras. Biol.* **61**, 1-6.

Binney, J. J., Dowrick, N. J., Fisher, A. J. and Newman, M. E. J. (1992). *The Theory of Critical Phenomena*. Oxford: Oxford University Press.

Blackburn, T. M., Brown, V. K., Doube, B. M., Greenwood, J. J. D., Lawton, J. H. and Stork, N. E. (1993a). The relationship between abundance and body size in natural animal assemblages. *J. Anim. Ecol.* **62**, 519-528.

Blackburn T. M., Lawton, J. H. and Pimm, S. L. (1993b). Non-metabolic explanations for the relationship between body size and animal abundance. *J. Anim. Ecol.* **62**, 694-702.

Blanco, J. M., Echeverría, F. and García, C. (1994). Dealing with size spectra: some conceptual and mathematical problems. *Scientia Marina* **58**, 17-29.

Blanco, J. M., Quiñones, R. A., Guerrero, F. and Rodriguez, J. (1998). The use of biomass spectra and allometric relations to estimate respiration of planktonic communities. *J. Plankton Res.* **20**, 887-900.

Boag, B., Hackett, C. A. and Topham, P. B. (1992). The use of Taylor power law to describe the aggregated distribution of gastrointestinal nematodes of sheep. *Int. J. Parasitol.* **22**, 267-270.

Boback, S. M. and Guyer, C. (2003). Empirical evidence for an optimal body size in snakes. *Evolution* **57**, 345-351.

Bonner, J. T. (1988). *The Evolution of Complexity*. Princeton, NJ: Princeton University Press.

Borgmann, U. (1982). Particle-size conversion efficiency and total animal production in pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* **39**, 669-674.

Borgmann, U. (1983). Effect of somatic growth and reproduction on biomass transfer up pelagic food web as calculated from particle-size-conversion efficiency. *Can. J. Fish. Aquat. Sci.* **40**, 2010-2018.

Borgmann, U. (1987). Models on the shape of and biomass flow up, the biomass size-spectrum. *Can. J. Fish. Aquat. Sci.* **44**, 136-140.

Borgmann, U. and Whittle, D. M. (1983). Particle-size-conversion efficiency and contaminant concentrations in Lake Ontario biota. *Can. J. Fish. Aquat. Sci.* **40**, 328-336.

Borgmann, U., Shear, H. and Moore, J. (1984). Zooplankton and potential fish production in Lake Ontario. *Can. J. Fish. Aquat. Sci.* **41**, 1303-1309.

Boudreau, P. R. and Dickie, L. M. (1989). Biological model of fisheries production based on physiological and ecological scalings of nbody size. *Can. J. Fish. Aquat. Sci.* **46**, 614-623.

Boudreau, P. R. and Dickie, L. M. (1992). Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. Aquat. Sci.* **49**, 1528-1538.

Boudreau, P. R., Dickie, L. M. and Kerr, S. (1991). Body-size spectra of production and biomass as system-level indicators of ecological dynamics. *J. Theor. Biol.* **152**, 329-339.

Brock, W. A. (1999). Scaling in economics: a reader's guide. *Indus. Corp. Change* **8**, 409-446.

Brooks, J. L. and Dodson, S. I. (1965). Predation, body size and composition of plankton. *Science* **150**, 28-35.

Brooks, T. M., Pimm, S. L. and Collar, N. J. (1997). Deforestation predicts the number of threatened birds in insular southeast Asia. *Conserv. Biol.* **11**, 382-384.

Brooks, T. M., Pimm, S. L. and Oyugi, J. O. (1999). Time lag between deforestation and extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140-1150.

Brose, U., Ostling, A., Harrison, K. and Martinez, N. D. (2004). Unified spatial scaling of species and their trophic interactions. *Nature* **428**, 167-171.

Brown, J. H. (1995). *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, J. H. (1999). Macroecology: progress and prospect. *Oikos*, **87**, 3-14.

Brown, J. H. and Gillooly, J. F. (2003). Ecological food webs: high quality data facilitate theoretical unification. *Proc. Natl. Acad. Sci. USA* **100**, 1467-1468.

Brown, J. H. and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445-449.

Brown, J. H. and Maurer, B. A. (1987). Evolution of species assemblages: effects of energetics constraints and species dynamics on the diversification of the North American avifauna. *Am. Nat.* **130**, 1-17.

Brown, J. H. and Maurer, B. A. (1989). Macroecology: the division of food and space among species on continents. *Science* **243**, 1145-1150.

Brown, J. H. and West, G. B. (2000). *Scaling in Biology*. New York: Oxford University Press.

Brown, J. H., Marquet, P. A. and Taper, M. (1993). The evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573-584.

Brown, J. H., West, G. B. and Enquist, B. J. (2000). Scaling in biology: process, causes and consequences. In *Scaling in Biology* (ed. J. H. Brown and G. B. West), pp. 1-24. New York: Oxford University Press.

Brown, J. H., Gupta, V. K., Li, B.-L., Milne, B. T., Restrepo, C. and West, G. B. (2002). The fractal nature of nature: power laws, ecological complexity and biodiversity. *Phil. Trans. R. Soc. Lond. B* **357**, 619-626.

Brown, J. H., Gillooly, J. F., West, G. B. and Savage, V. M. (2003). The next step in macroecology: from general empirical patterns to universal ecological laws. In *Macroecology: Concepts and Consequences* (ed. T. M. Blackburn and K. J. Gaston), pp. 64-84. Cambridge: Cambridge University Press.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.

Burness, G. P., Diamond, J. and Flannery, T. (2001). Dinosaurs, dragons and dwarfs: the evolution of maximal body size. *Proc. Nat. Acad. Sci. USA* **98**, 14518-14523.

Canning, D., Amaral, L. A. N., Lee, Y., Meyer, M. and Stanley, H. E. (1998). A power law for scaling the volatility of GDP growth rates with country size. *Economics Lett.* **60**, 335-341.

Calder, W. A., III (1983). Ecological scaling: mammlas and birds. *Annu. Rev. Ecol. Syst.* **14**, 213-230.

Calder, W. A., III (1984). *Size, Function and Life History*. Harvard University Press.

Calder, W. A. III (2000). Diversity and convergence: scaling for conservation. In *Scaling in Biology* (ed. J. H. Brown and G. B. West), pp. 297-323. New York: Oxford University Press.

Carbone, C. and Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science* **295**, 2273-2276.

Cardillo, M. and Bromham, L. (2001). Body size and risk of extinction in Australian mammals. *Conserv. Biol.* **15**, 1435-1440.

Carpenter, S. R. and Kitchell, J. F. (1984). Plankton community structure and limnetic primary production. *Am. Nat.* **124**, 159-172.

Cassey, P. (2001). Are there body size implications for the success of globally introduced land birds? *Ecography* **24**, 413-420.

Charnov, E. L. (1993). *Life History Invariants*. Oxford, UK: Oxford University Press.

Charnov, E. L., Haskell, J. and Ernest, S. K. M. (2001). Density-dependent invariance, dimensionless life histories and the energy-equivalence rule. *Evol. Ecol. Res.* **3**, 117-127.

Chave, J. and Levin, S. (2003). Scale and scaling in ecological and economic systems. *Environ. Resource Econ.* **26**, 527-557.

Cofré, H. and Marquet, P. A. (1999). Conservation status, rarity and geographic priorities for conservation of Chilean Mammals: an assessment. *Biol. Cons.* **88**, 1-16.

Cohen, J. E., Jonsson, T. and Carpenter, S. R. (2003). Ecological community description using the food web, species abundance and body size. *Proc. Natl. Acad. Sci. USA* **100**, 1781-1786.

Cohen, J. E., Jonsson, T., Muller, C. B., Godfray, H. C. J. and Savage, V. M. (2005). Body size of hosts and parasitoids in individual feeding relationships. *Proc. Natl. Acad. Sci. USA* **18**, 684-689.

Cotgreave, P. (1993). The relationship between body size and population density. *Trends Ecol. Evol.* **8**, 244-248.

Cousins, S. H. (1980). A trophic continuum derived from plant structure, animal size and a detritus cascade. *J. Theor. Biol.* **82**, 607-618.

Cousins, S. H. (1985). Ecologists build pyramids again. *New Sci.* **1463**, 50-54.

Cushing, D. H. (1975). *Marine Ecology and Fisheries*. Cambridge, UK: Cambridge University Press.

Cyr, H. (2000). Individual energy use and the allometry of population density. In *Scaling in Biology* (ed. J. H. Brown and G. B. West), pp. 267-295. New York: Oxford University Press.

Cyr, H. and Pace, M. L. (1993). Allometric theory: extrapolations from individuals to communities. *Ecology* **74**, 1234-1245.

Cyr, H., Downing, J. A. and Peters, R. H. (1997). Density-body size relationships in local aquatic communities. *Oikos* **79**, 333-346.

Damuth, J. (1981). Population density and body size in mammals. *Nature* **290**, 699-700.

Damuth, J. (1987). Interspecific allometry of population density in mammals and others animals: the independence of body mass and population energy use. *Biol. J. Linn. Soc.* **31**, 193-246.

Damuth, J. (1991). Of size and abundance. *Nature* **351**, 268-269.

Damuth, J. (1998). Common rules for animals and plants. *Nature* **395**, 115-116.

Damuth, J. (2003). Cope's rule, the island rule and the scaling of mammalian population density. *Nature* **365**, 748-750.

de Boer, W. F. and Prins, H. H. T. (2002). The community structure of a tropical intertidal mudflat under human exploitation. *ICES J. M. Sci.* **59**, 1237-1247.

Diamond, J. M. (1984a). 'Normal' extinctions of isolated populations. In *Extinctions* (ed. M. H. Nitecki), pp. 191-246. Chicago: The University of Chicago Press.

Diamond, J. M. (1984b). Historic extinctions: a Rosetta stone for understanding prehistoric extinctions. In *Quaternary Extinctions: A Prehistoric Revolution* (ed. P. S. Martin and R. G. Klein), pp. 824-862. Tucson: The University of Arizona Press.

Diamond, J. M. and Case, T. (eds) (1986). *Community Ecology*. New York: Harper and Row.

Dickie, L. M., Kerr, S. R. and Boudreau, P. R. (1987). Size-dependent processes underlying regularities in ecosystem structure. *Ecol. Monog.* **57**, 233-250.

Dobson, F. S., Zinner, B. and Silva, M. (2003). Testing models of biological scaling with mammalian population densities. *Can. J. Zool.* **81**, 844-851.

Dodds, P. S., Rothman, D. H. and Weitz, J. S. (2001). Re-examination of the '3/4-law' of metabolism. *J. Theor. Biol.* **209**, 9-27.

Drgas, A., Radziejewska, T. and Warzocha, J. (1998). Biomass size spectra of near-shore shallow-water benthic communities in the Gulf of Gdansk (Southern Baltic Sea). *Mar. Ecol.* **19**, 209-228.

Dugan, J. E., Hubbard, D. M. and Page, H. M. (1995) Scaling population density to body size: tests in 2 soft sediment intertidal communities. *J. Coastal Res.* **11**, 849-857.

Dulvy, N. K. and Reynolds, J. D. (2002). Predicting extinction vulnerability in Skates. *Conserv. Biol.* **16**, 440-450.

Duncan, R. P., Blackburn, T. M. and Veltman, C. J. (1999). Determinants of geographical range sizes: a test using introduced New Zealand birds. *J. Anim. Ecol.* **68**, 963-975.

Duncan, R. P., Bomford, M., Forsyth, D. M. and Conibear, L. (2001). High predictability in introduction outcomes and the geographical range size of introduced Australian birds: A role for climate. *J. Anim. Ecol.* **70**, 621-632.

Duncan, R. P., Blackburn, T. M. and Sol, D. (2003). The ecology of bird introductions. *Annu. Rev. Ecol. Evol. S.* **34**, 71-98.

Duplisea, D. (2000). Benthic organism biomass size-spectra in the Baltic Sea in relation to the sediment environment. *Limnol. Oceanogr.* **45**, 558-568.

Duplisea, D. E. and Kerr, S. R. (1995). Application of a biomass size spectrum model to demersal fish data from the Scotian Shelf. *J. Theor. Biol.* **177**, 263-269.

Duplisea, D. and Kerr, S. (2000). Application of a biomass size spectrum model to demersal fish data from the scotian shelf. *J. Theor. Biol.* **177**, 263-269.

Durán, L. R. and Castilla, J. C. (1989). Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Biol.* **103**, 555-562.

Echevarría, F., Carrillo, P., Jimenez, F., Sanchez-Castillo, P., Cruz-Pizarro, L. and Rodriguez, J. (1990). The size-abundance distribution and taxonomic composition of plankton in an oligotrophic, high mountain lake (La Caldera, Sierra Nevada, Spain). *J. Plankton Res.* **12**, 415-422.

Elton, C. (1927). *Animal Ecology*. Macmillan, New York.

Enquist, B. J. and Niklas, K. J. (2001). Invariant scaling relations across tree-dominated communities. *Nature* **410**, 655-660.

Enquist, B. J., Brown, J. H. and West, G. B. (1998). Allometric scaling of plant energetics and population density. *Nature* **395**, 163-165.

Enquist, B. J., Haskell, J. P. and Tiffney, B. H. (2002). General patterns of taxonomic diversity and biomass partitioning across tree dominated communities. *Nature* **219**, 610-613.

Enquist, B. J., Economo, E. P., Huxman, T. E., Allen, A. P., Ignace, D. D. and Gillooly, J. F. (2003). Scaling metabolism from organisms to ecosystems. *Nature* **423**, 639-642.

Ernest, S. K., Enquist, B. J., Brown, J. H., Charnov, E. L., Gillooly, J. F., Savage, V. M., White, E. P., Smith, F. A., Hadly, E. A., Haskell, J. P. et al. (2003). Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecol. Lett.* **6**, 990-995.

Ferrier, R. and Cazelles, B. (1999). Universal power laws govern intermittent rarity in communities of interacting species. *Ecology* **80**, 1505-1521.

Fisher, D. O., Blomberg, S. P. and Owens, I. P. F. (2003). Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. Roy. Soc. Lond. B.* **270**, 1801-1808.

Forsyth, D. M., Duncan, R. P., Bomford, M. and Moore, G. (2004). Climatic suitability, life-history traits, introduction effort and the establishment and spread of introduced mammals in Australia. *Conserv. Biol.* **18**, 557-569.

France, R., Chandler, M. and Peters, R. (1998). Mapping trophic continua of benthic food webs: body size d15N relationships. *Mar. Ecol. Prog. Ser.* **174**, 301-306.

Frontier, S. (1985). Diversity and structure in aquatic ecosystems. *Oceanog. Mar. Biol. Annu. Rev.* **23**, 253-312.

Fry, B. and Quiñones, R. A. (1994). Biomass spectra and stable-isotope indicators of trophic level in zooplankton of the northwest Atlantic. *Mar. Ecol. Prog. Ser.* **112**, 201-204.

Gaedke, U. (1993). Ecosystem analysis based on biomass size distributions: a case study of a plankton community in a large lake. *Limnol. Oceanogr.* **38**, 112-127.

García, C. M., Jiménez-Gomez, F., Rodríguez, J., Bautista, B., Estrada, M., García-Braun, J., Gasol, J. M., Gómez-Figueiras, F., Guerrero, F., Jiménez-Montes, F. et al. (1994). The size structure and functional composition of ultraplankton and nanoplankton at a frontal station in the Alborán Sea. Working Group 2 and 3 Report. *Sci. Mar.* **58**, 43-52.

Garlaschelli, D., Caldarelli, G. and Pietronero, L. (2003). Universal scaling relations in food webs. *Nature* **423**, 165-168.

Gasol, J. M., Guerrero, R. and Pedrós-Alió, C. (1991). Seasonal variations in size structure and procaryotic dominance in sulfurous Lake Ciso. *Limnol. Oceanogr.* **36**, 860-872.

Gaston, K. J. and Blackburn, T. M. (1995). Birds, body-size and the threat of extinction. *Phil. Trans. Roy. Soc. B.* **347**, 205-212.

Gaston, K. J. and Blackburn, T. M. (1996). Conservation implications of geographic range size body size relationships. *Conserv. Biol.* **10**, 638-646.

Gaston, K. J. and Blackburn, T. M. (2000). *Patterns and Processes in Macroecology*. Blackwell Science Limited, Oxford.

George-Nascimento, M., Muñoz, G., Marquet, P. A. and Poulin, R. (2004). Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecol. Lett.* **7**, 527-531.

Ghilarov, M. S. (1944). Correlation between size and number of soil animals. *Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS XLIII* **6**, 267-269.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. and Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science* **293**, 2248-2251.

Gisiger, T. (2001). Scale invariance in biology: coincidence or footprint of an universal mechanism? *Biol. Rev.* **76**, 161-209.

Goodman, D. (1987). The demography of chance extinction. In *Viable Populations for Conservation* (ed. M. E. Soulé), pp. 11-34. Cambridge, UK: Cambridge University Press.

Griesbach, S., Peters, R. H. and Youakim, S. (1982). An allometric model for pesticide bioaccumulation. *Can. J. Fish. Aquat. Sci.* **39**, 727-735.

Hajagos, J. and Ferson, S. (2001). *RAMAS® Ecorisk: Software for Rapid Ecological Risk Analysis*. Setauket, New York: Applied Biomathematics.

Hall, D. J., Threlkeld, S. T., Burns, C. W. and Crowley, P. H. (1976). The size-efficiency hypothesis and the size structure of zooplankton communities. *Annu. Rev. Ecol. Syst.* **7**, 177-208.

Halley, J. (1996). Ecology, evolution and 1/f noise. *Trends Ecol. Evol.* **11**, 33-37.

Halley, J. and Inchausti, P. (2002). Lognormality in ecological time series. *Oikos* **99**, 518-530.

Halley, J. and Inchausti, P. (2004). The increasing importance of 1/f noises as models of ecological variability. *Fluct. Noise Lett.* **4**, R1-R26.

Han, B. P. and Straskraba, M. (2001). Size dependence of biomass spectra and abundance spectra: the optimal distributions. *Ecol. Model.* **145**, 175-187.

Hanski, I. and Tiainen, J. (1989). Bird ecology and Taylor variance-mean regression. *Ann. Zool. Fennici* **26**, 213-217.

Harte, J., Kinzig, A. and Green, J. (1999). Self-similarity in the distribution and abundance of species. *Science* **157**, 374-386.

Harte, J., Blackburn, T. and Ostling, A. (2001). Self-similarity and the relationship between abundance and range size. *Am. Nat.* **157**, 374-386.

Haskell, J. P., Ritchie, M. E. and Olff, H. (2002). Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* **418**, 527-530.

Havens, K. E. (1992). Acidification effects on the plankton size spectrum: an *in situ* mesocosm experiment. *J. Plankton Res.* **14**, 1687-1696.

Havlicek, T. and Carpenter, S. R. (2001). Pelagic species size distributions in lakes: are they discontinuous? *Limnol. Oceanogr.* **46**, 1021-1033.

Hubbell, S. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forest and coral reefs. *Coral Reefs* **16**, 9-21.

Hubbell, S. P. (2001). *A Unified Theory of Biodiversity and Biogeography.* Princeton, NJ: Princeton University Press.

Inchausti, P. and Halley, J. (2001). Investigating long-term ecological variability using the global population dynamics database. *Science* **293**, 655-657.

Isaacs, J. D. (1972). Unstructured marine food webs and 'pollutant analogues'. *Fish. Bull.* **70**, 1053-1059.

Isaacs, J. D. (1973). Potential trophic biomasses and trace-substance concentrations in unstructured marine food webs. *Mar. Biol.* **22**, 97-104.

Jennings, S. and Mackinson, S. (2003). Abundance–body mass relationships in size-structured food webs. *Ecol. Lett.* **6**, 971-974.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. and Boon, T. (2001). Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J. Anim. Ecol.* **70**, 934-944.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. and Warr, K. J. (2002). Linking size-based and trophic analyses of benthic community structure. *Mar. Ecol. Prog. Ser.* **226**, 77-85.

Jetz, W., Carbone, C., Fulford, J. and Brown, J. H. (2004). The scaling of animal space use. *Science* **306**, 266-268.

Jimenez, F., Rodriguez, J., Bautista, B. and Rodriguez, V. (1987). Relations between chlorophyll, phytoplankton cell abundance and biovolume during a winter bloom in Mediterranean coastal waters. *J. Exp. Mar. Biol. Ecol.* **105**, 161-173.

Jimenez, F., Rodriguez, J., Jimenez-Gomez, F. and Bautista, B. (1989). Bottlenecks in the propagation of a fluctuation up the planktonic size-spectrum in Mediterranean Coastal waters. *Scient. Mar.* **53**, 269-275.

Johst, K. and Brandl, R. (1997). Body size and extinction in a stochastic environment. *Oikos* **78**, 612-617.

Keeling, M. J. (2000). Simple stochastic models and their power-law type behaviour. *Theor. Pop. Biol.* **58**, 21-31.

Keitt, T. H. and Marquet, P. A. (1996). Extinction cascades in introduced Hawaiian birds suggest self-organized criticality. *J. Theor. Biol.* **182**, 161-167.

Keitt, T. H. and Stanley, H. E. (1998). Dynamics of North American breeding bird populations. *Nature* **393**, 257-260.

Keitt, T. H., Amaral, L. A. N., Buldyrev, S. V. and Stanley, H. E. (2002). Scaling in the growth of geographically subdivided populations: invariant patterns from a continent-wide biological survey. *Phil. Trans. R. Soc. Lond. B.* **357**, 627-633.

Kelt, D. A. and Van Vuren, D. H. (1999). Energetic constraints and the relationship between body size and home range area in mammals. *Ecology* **80**, 337-340.

Kelt, D. A. and Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *Am. Nat.* **157**, 637-645.

Kerr, S. R. (1974). Theory of size distribution in ecological communities. *J. Fish. Res. Bd. Can.* **31**, 1859-1862.

Kerr, S. R. and Dickie, L. M. (2001). *The Biomass Spectrum: A Predator–Prey Theory of Aquatic Production.* NewYork, NY: Columbia University Press.

King, A. W., Johnson, A. R. and O'Neill, R. V. (1991). Transmutation and functional representation of heterogeneous landscapes. *Land. Ecol.* **5**, 239-253.

Lawton, J. H. (1989). What is the relationship between population density and animal abundance? *Oikos* **55**, 429-434.

Lawton, J. H. (1990). Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. *Philos. Trans. R. Soc. London Ser. B* **330**, 283-291.

Lawton, J. H. (1995). Population dynamic principles. In *Extinction rates* (ed. J. H. Lawton and R. M. May), pp. 147-163. Oxford: Oxford University Press.

Lawton, J. H. (1999). Are there general laws in ecology? *Oikos* **84**, 177-192.

Lawton, J. H. and Brown, K. C. (1986). The population and community ecology of invading insects. *Philos. Trans. R. Soc. London Ser. B* **314**, 607-617.

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

Levin, S. A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* **1**, 431-436.

Levin, S. A. (1999). *Fragile Dominion: Complexity and the Commons.* Reading, MA: Perseus Books.

Levin, S. A. (2002). Complex adaptive systems: exploring the known, the unknown and the unknowable. *Bull. Am. Math. Soc.* **40**, 3-19.

Li, W. K. W. (2002). Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* **419**, 154-157.

Lindeman, R. L. (1942). The trophic dynamic aspect of ecology. *Ecology* **23**, 399-417.

Longhurst, A. R. (1989). Pelagic ecology: definition of pathways for material and energy flux. In *Oceanologie: Actualit, et prospective* (ed. M. M. Denis), pp. 263-288. Marseille: Centre d'Oceanologie de Marseille.

Longhurst, A. R. (1991). Role of marine biosphere in the global carbon cycle. *Limnol. Oceanog.* **36**, 1507-1526.

Maris, H. J. and Kadanoff, L. P. (1978). Teaching the renormalization group. *Am. J. Phys.* **46**, 652-657.

Marquet, P. A. (2000). Invariants, scaling laws and ecological complexity. *Science* **289**, 1487-1488.

Marquet, P. A. (2002a). The search for general principles in ecology. *Nature* **418**, 723.

Marquet, P. A. (2002b). Of predators, prey and power laws. *Science* **295**, 2229-2230.

Marquet, P. A. and Cofre, H. (1999). Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos* **85**, 299-309.

Marquet, P. A. and Taper, M. L. (1998). On size and area: patterns of mammalian body size extremes across landmasses. *Evol. Ecol.* **12**, 127-139.

Marquet, P. A., Navarrete, S. A. and Castillla, J. C. (1990). Scaling population density to body size in rocky intertidal communities. *Science* **250**, 1125-1127.

Marquet, P. A., Navarrete, S. A. and Castilla, J. C. (1995). Body size, population density and the energetic equivalence rule. *J. Anim. Ecol.* **64**, 325-332.

Marquet, P. A., Keymer, J. E. and Cofre, H. (2003). Breaking the stick in space: of niche models, metacommunities and patterns in the relative abundance of species. In *Macroecology: Concepts and Consequences* (ed. T. M. Blackburn and K. J. Gaston), pp. 64-84. Cambridge: Cambridge University Press.

Marquet, P. A., Labra, F. and Maurer, B. A. (2004). Metabolic ecology: linking individuals and ecosystems. *Ecology* **85**, 1794-1796.

May, R. M. (1986). The search for patterns in the balance of nature: advances and retreats. *Ecology* **67**, 1115-1126.

McArdle, B. H., Gaston, K. J. and Lawton, J. H. (1990). Variation in the size of animal populations: patterns, problems and artefacts. *J. Anim. Ecol.* **59**, 439-454.

McClain, C. R. (2004). Connecting species richness, abundance and body size in deep-sea gastropods. *Global Ecol. Biogeogr.* **13**, 327-334.

McKinney, M. L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Evol. S.* **28**, 495-516.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**, 133-140.

McNab, B. K. (1994). Resource use and the survival of land and freshwater vertebrates on oceanic islands. *Am. Nat.* **144**, 643-660.

Medel, R. G., Bozinovic, F. and Novoa, F. F. (1995). The mass exponent in

population energy use: the fallacy of averages reconsidered. *Am. Nat.* **145**, 155-162.

Milne, B. T. (1998). Motivation and beliefs of complex systems approaches in ecology. *Ecosystems* **1**, 449-456.

Milne, B. T., Turner, M. G., Wiens, J. A. and Johnson, A. R. (1992). Interactions between the fractal geometry of landscapes and allometric herbivory. *Theor. Pop. Biol.* **41**, 337-353.

Miramontes, O. (1995). Order-disorder transitions in the behavior of ant societies. *Complexity* **1**, 56-60.

Miramontes, O. and Rohani, P. (1998). Intrinsically generated coloured noise in laboratory insect populations. *Proc. Roy. Soc. Lond. B* **265**, 785-792.

Mitzenmacher, M. (2001). A brief history of generative models for power law and log normal distributions. In *Proceedings of the 39th Annual Allerton Conference on Communication, Control and Computing*, pp. 182-191. Urbana-Champagne: University of Illinois.

Mohr, C. O. (1940). Comparative populations of game, fur and other mammals. *Am. Midl. Nat.* **24**, 581-584.

Moloney, C. L. and Field, J. G. (1985). Use of particle-size data to predict potential pelagic-fish yields of some Southern African areas. *S. Afr. J. Mar. Sci.* **3**, 119-128.

Mulder, C., Cohen, J. E., Setälä, H., Bloem, J. and Breure, M. (2005). Bacterial traits, organism mass and numerical abundance in the detrital soild food web of Dutch agricultural grasslands. *Ecol. Lett.* **8**, 80-90.

Murawski, S. A. and Idoine, J. S. (1989). Multispecies size composition: a conservative property of exploited fishery systems? NAFO SCR Doc. 89/76.

Navarrete, S. A. and Menge, B. A. (1997). The body size population density relationship in tropical rocky intertidal communities. *J. Anim. Ecol.* **66**, 557-566.

Nee, S., Read, A. F. Greenwood, J. J. D. and Harvey, P. H. (1991). The relationship between abundance and body size in British birds. *Nature* **351**, 312-313.

Niklas, K. J. (1994). *Plant Allometry*. Chicago, IL: University of Chicago.

Niklas, K. J. and Enquist, B. J. (2001). Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Nat. Acad. Sci. USA* **98**, 2922-2927.

O'Neill, R. V. (1979). Transmutations across hierarchical levels. In *Systems Analysis of Ecosystems* (ed. G. S. Innis and R. V. O'Neill), pp. 58-78. Fairland, Maryland: International Cooperative Publishing House.

Pahl-Wostl, C. (1995). *The Dynamic Nature of Ecosystems: Chaos and Order Entwined.* Chichester, UK: Wiley.

Pascual, M. and Guichard, F. (2005). Criticality and disturbance in spatial ecological systems. *Trends Ecol. Evol.* **20**, 88-95.

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge, UK: Cambridge University Press.

Peters, R. H. and Raelson, J. V. (1984). Relations between individual size and mammalian population density. *Am. Nat.* **124**, 498-517.

Peterson, I. and Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* **41**, 1117-1120.

Pimm, S. L. (1992). *The Balance of Nature*. Chicago, IL: The University of Chicago Press.

Pimm, S. L., Jones, H. L. and Diamond, J. (1988). On the Risk of Extinction. *Am. Nat.* **132**, 757-785.

Platt, T. and Denman, K. (1977). Organization in the pelagic ecosystem. *Helgol. Wiss. Meeresunters.* **30**, 575-581.

Platt, T. and Denman, K. (1978). The structure of pelagic ecosystems. *Rapp. P-V. Reun. Cons. Int. Explor. Mer.* **173**, 60-65.

Platt, T., Lewis, M. and Geider, R. (1984). Thermodynamics of the pelagic ecosystem: elementary closure for biological production in the open ocean. In *Flows of Energy and Materials in Marine Ecosystems* (ed. M. J. R. Fasham), pp. 49-84. New York: Plenum Publishing Corporation.

Platt, T. (1985). Structure of the marine ecosystem: its allometric basis. *Can. Bull. Fish. Aquat. Sci.* **213**, 55-64.

Plerou, V., Amaral, L. A. N., Gopikrishnan, P., Meyer, M. and Stanley, H. E. (1999). Similarities between the growth dynamics of university research and of competitive economic activities. *Nature* **400**, 433-437.

Pope, J. G., Stokes, T. K., Murawski, S. A. and Iodine, S. I. (1988). A comparison of fish size-composition in the North Sea and on Georges Bank. In *Ecodynamics: Contributions to Theoretical Ecology* (ed. W. Wolff, C. J. Soeder and F. R. Drepper), pp 146-152. Berlin: Springer Verlag.

Quiñones, R. A. (1992). Size-distribution of planktonic biomass and metabolic activity in the pelagic system. PhD Thesis, Dalhousie University, Halifax, Canada.

Quiñones, R. A. (1994). A comment on the use of allometry in the study of

pelagic ecosystem processes. *Sci. Mar.* **58**, 11-16.

Quiñones, R. A., Platt, T., Ruiz, J. and Echevarría, F. (1991). Biomass size-spectra and metabolism in the pelagic zone. *Can. Tech. Rep. Fish. Aquat. Sci.* **1844**, 16-17.

Quiñones, R. A., Blanco, J. M., Echevarría, F., Fernandez-Puelles, M. L., Gilabert, J., Rodriguez, V. and Valdés, L. (1994). Metabolic size-spectra at a frontal station in the Alboran Sea. *Sci. Mar.* **58**, 53-58.

Quiñones, R. A., Platt, T. and Rodríguez, J. (2003). Patterns of biomass-size spectra from oligotrophic waters of the Northwest Atlantic. *Progr. Oceanog.* **57**, 405-427

Quintana, X. D., Comín, F. A. and Moreno-Amich, R. (2002). Biomass-size spectra in aquatic communities in shallow fluctuating Mediterranean salt marshes (Emporda wetlands, NE Spain). *J. Plankton Res.* **24**, 1149-1161.

Quiroga, E., Quiñones, R. A., Palma, M., Sellanes, J., Gallardo, V. A., Gerdes, D. and Rowe, G. (2005). Biomass size-spectra of macrobenthic communities in the oxygen minimum zone off Chile. *Est. Coast. Shelf. Sci.* **62**, 217-231.

Raffaelli, D., Hall, S., Emes, C. and Manly, B. (2000). Constraints on body size distributions: an experimental approach using a small-scale system. *Oecologia* **122**, 389-398.

Rassouldagan, F. and Sheldon, R. W. (1986). Predator–prey interactions of nanozooplankton and bacteria in an oligotrophic marine environment. *Limnol. Oceanogr.* **31**, 1010-1021.

Rhodes, C. J. and Anderson, R. M. (1996). Power laws governing epidemics in isolated populations. *Nature* **381**, 600-602.

Rhodes, C. J., Jensen, H. J. and Anderson, R. M. (1997). On the critical behavior of simple epidemics. *Proc. Roy. Soc. Lond. B* **264**, 1639-1646.

Rice, J. C. (2000). Evaluating fishery impacts using metrics of community structure. *ICES J. Mar. Sci.* **57**, 682-688.

Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science* **235**, 167-171.

Rinaldo, A., Maritan, A., Cavender-Bares, K. K. and Chisholm, S. W. (2002). Cross-scale ecological dynamics and microbial size spectra in marine ecosystems. *Proc. Roy. Soc. Lond. B.* **269**, 2051-2059.

Ritchie, M. E. and Olff, H. (1999). Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* **400**, 557-560.

Rodriguez, J. (1994). Some comments on the size-based structural analysis of the pelagic ecosystem. *Sci. Mar.* **58**, 1-10.

Rodriguez, J. and Mullin, M. (1986a). Diel and interannual variation of size-distribution of oceanic zooplanktonic biomass. *Ecology* **67**, 215-222.

Rodriguez, J. and Mullin, M. (1986b). Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol. Oceanog.* **31**, 361-370.

Rodriguez, J., Jimenez, F., Bautista, B. and Rodriguez, V. (1987). Planktonic biomass spectra dynamics during a winter production pulse in Mediterranean coastal waters. *J. Plankton Res.* **9**, 1183-1194.

Rodriguez, J., Echevarría, F. and Jiménez-Gómez, F. (1990). Physiological and ecological scalings of body size in an oligotrophic, high mountain lake (La Caldera. Sierra Nevada, Spain. *J. Plankton Res.* **12**, 593-599.

Rosenzweig, M. L. (1995). *Species Diversity in Time and Space*. Cambridge, UK: Cambridge University Press.

Roy, K., Jablonski, D. and Valentine, J. W. (2002). Body size and invasion success in marine bivalves. *Ecol. Lett.* **5**, 163-167.

Roy, M., Pascual, M. and Franc, A. (2003). Broad scaling region in a spatial ecological system. *Complexity* **8**, 19-27.

Saiz-Salinas, J. I. and Ramos, A. (1999). Biomass size-spectra of macrobenthic assemblages along water depth in Antarctica. *Mar. Ecol. Prog. Ser.* **178**, 221-227.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C. et al. (2001). The population biology of invasive species. *Annu. Rev. Ecol. Evol. S.* **32**, 305-332.

Samuelsson, K., Berglund, J., Haecky, P. and Andersson, A. (2002). Structural changes in an aquatic microbial food web caused by inorganic nutrient addition. *Aquat. Microb. Ecol.* **29**, 29-38.

Savage, V. M. (2004c). Improved approximations to scaling relationships for species, populations and ecosystems across latitudinal and altitudinal gradients. *J. Theor. Biol.* **227**, 525-534.

Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist, B. J. and Brown, J. H. (2004a). The predominance of quarter-power scaling in ecology. *Funct. Ecol.* **18**, 257-282.

Savage, V. M., Gillooly, J. F., Charnov, E. L., Brown, J. H. and West, G.

B. (2004b). Effects of body size and temperature on population growth. *Am. Nat.* **163**, 429-441.

Schmid, P. E. (2000). Fractal properties of habitat and patch structure in benthic ecosystems. *Adv. Ecol. Res.* **30**, 339-401.

Schmid, P. E., Tokeshi, M. and Schmid-Araya, J. M. (2000). Relation between population density and body size in stream communities. *Science* **289**, 1557-1560.

Schmidt, N. M. and Jensen, P. M. (2003). Changes in mammalian body length over 175 years – adaptations to a fragmented landscape? *Conserv. Ecol.* **7**, 6. [online] URL: http://www.consecol.org/vol7/iss2/art6.

Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size so Important*? Cambridge University Press.

Schwinghamer, P. (1981). Characteristic size distributions of integral benthic communities. *Can. J. Fish. Aquat. Sci.* **38**, 1255-1263.

Schwinghamer, P. (1985). Observations on size structure and pelagic coupling of some shelf and abyssal benthic communities. In *Proceedings 19th European Marine Biology Symposium* (ed. P. E. Gibbs), pp. 347-359. Cambridge, UK: Cambridge University Press.

Sheldon, R. W., Prakash, A. and Sutcliffe, W. H. Jr (1972). The size distribution of particles in the ocean. *Limnol. Oceanogr.* **17**, 327-340.

Sheldon, R. W., Sutcliffe, W. H., Jr and Prakash, A. (1973). The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. *Limnol. Oceanogr.* **18**, 719-733.

Sheldon, R. W., Sutcliffe, W. H., Jr and Paranajape, M. A. (1977). Structures of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Board Can.* **34**, 2344-2355.

Sheldon, R. W., Nival, P. and Rassoulzadegan, F. (1986). An experimental investigation of a flagellate-ciliate-copepod food chain with some observations relevant to the linear biomass hypothesis. *Limnol. Oceanogr.* **31**, 184-188.

Siemann, E., Tilman, D. and Haarstad, J. (1996). Insect species diversity, abundance and body size relationships. *Nature* **380**, 704-706.

Silva, M. and Downing, J. A. (1994). Allometric scaling of minimal mammal densities. *Conserv. Biol.* **8**, 732-743.

Silva, M. and Downing, J. A. (1995). The allometric scaling of density and body-mass – a nonlinear relationship for terrestrial mammals. *Am. Nat.* **145**, 704-727.

Silva, M., Brimacombe, M. and Downing, J. A. (2001). Effects of body mass, climate, geography and census are on population density of terrestrial mammals. *Global Ecol. Biogeogr.* **10**, 469-485.

Silvert, W. and Platt, T. (1978). Energy flux in the pelagic ecosystem: a time dependent equation. *Limnol. Oceanogr.* **18**, 813-816.

Silvert, W. and Platt, T. (1980). Dynamic energy-flow model of the particle size-distribution in pelagic ecosystems. In *Evolution and Ecology of Zooplankton Communities* (ed. W. C. Kerfoot), pp. 754-763. Hanover, NH: The University Press of New England.

Simberloff, D. (2004). Community ecology. Is it time to move on? *Am. Nat.* **163**, 787-799.

Solé, R. V., Manrubia, S. C., Luque, B., Delgado, J. and Bascompte, J. (1996). Phase transitions and complex systems. *Complexity* **1**, 13-26.

Solé, R. V., Manrubia, S. C., Kauffman, S., Benton, M. and Bak, P. (1999). Criticality and scaling in evolutionary ecology. *Trends Ecol. Evol.* **14**, 156-160.

Solé, R. V., Alonso, D. and McKane, A. (2002). Self-organized instability in complex ecosystems. *Phil. Trans. Roy. Soc. Lond. B* **357**, 667-681.

Sornette, D. (2000). *Critical Phenomena in Natural Sciences. Chaos Fractals, Selforganization and Disorder: Concepts and Tools*. Heidelberg, Germany: Spring-Verlag.

Sprules, W. G. and Knoechel, R. (1984). Lake ecosystem dynamics based on functional representations of trophic components. In *Trophic Interactions within Aquatic Ecosystems* (ed. D. G. Meyers and J. R. Strickler), pp. 383-403. Boulder, CO: Westview Press.

Sprules, W. G. and Munawar, M. (1986). Plankton size spectra in relation to ecosystem productivity, size and perturbation. *Can. J. Fish. Aquat. Sci.* **43**, 1789-1794.

Sprules, W. G., Casselman, J. M. and Shuter, B. J. (1983). Size distribution of pelagic particles in lakes. *Can. J. Fish. Aquat. Sci.* **40**, 1761-1769.

Sprules, W. G., Munawar, M. and Jin, E. H. (1988). Plankton community structure and size spectra in the Georgian Bay and North Channel ecosystems. *Hydrobiologia* **163**, 135-140.

Sprules, W. G., Brandt, S. B., Stewart, D. J., Munawar, M., Jin, E. H. and Love, J. (1991). Biomass size-spectrum of the Lake Michigan pelagic food web. *Can. J. Fish. Aquat. Sci.* **48**, 105-115.

Stanley, H. E., Amaral, L. A. N., Gopikrishnan, P., Ivanov, P. Ch., Keitt, T. H. and Plerou, V. (2000). Scale invariance and universality: organizing principles in complex systems. *Physica A* **281**, 60-68.

Stanley, M. H. R., Amaral, L. A. N., Buldyrev, S. V., Havlin, S., Leschhorn, H., Maass, P., Salinger, M. A. and Stanley, H. E. (1996). Scaling behavior in the growth of companies. *Nature* **379**, 804-806.

Stenseth, N. C. (1979). Where have all the species gone? On the nature of extinction and the Red Queen hypothesis. *Oikos* **33**, 196-227.

Storch, D. and Gaston, K. J. (2004). Untangling ecological complexity on different scales of space and time. *Basic Appl. Ecol.* **5**, 389-400.

Storch, D., Gaston, K. J. and Cepak, J. (2002). Pink landscapes: 1/f spectra of spatial environmental variability and bird community composition. *Proc. Roy. Soc. Lond. B* **269**, 1791-1796.

Strogatz, S. H. (2001). Exploring complex networks. *Nature* **410**, 268-276.

Taper, M. L. and Marquet, P. A. (1996). How do species really divide resources? *Am. Nat.* **147**, 1072-1086.

Taylor, L. R. (1961). Aggregation, variance and the mean. *Nature* **189**, 732-735.

Taylor, L. R. and Woiwod, I. P. (1980). Temporal stability as a density-dependent species characteristic, *J. Anim. Ecol.* **49**, 209-224.

Torres, J.-L., Sosa, V. J., Equihua, M. and Torres, L. (2001). On the conceptual basis of the self-thinning rule. *Oikos* **95**, 544-548.

Thiebaux, M. L. and Dickie, L. M. (1993). Structure of the body-size spectrum of the biomass in aquatic ecosystems: a consequence of allometry in predatory-prey interactions. *Can. J. Fish. Aquat. Sci.* **50**, 1308-1317.

Thomann, R. V. (1979). An analysis of PCB in Lake Ontario using a size-dependent food chain model. In *Perspectives on Lake Ecosystem Modelling* (ed. D. Scavia and A. Robertson), pp. 293-320. Ann Arbor, MI: Ann Arbor Science.

Thomann, R. V. (1981). Equilibrium model of fate of microcontaminants in diverse aquatc food chains. *Can. J. Fish. Aquat. Sci.* **38**, 280-296.

Ulanowicz, R. E. (1986). *Growth and Development: Ecosystems Phenomenology*. San Jose, CA: Excel Press.

Van Valen, L. (1976). Energy and evolution. *Evol. Theor.* **1**, 179-229.

Van Valen, L. (1977). The Red Queen. *Am. Nat.* **111**, 809-810.

Van Valen, L. (1980). Evolution as a zero-sum game for energy. *Evol. Theor.* **4**, 289-300.

Vanni, M. J. (1986). Fish predation and zooplankton demography: indirect effects. *Ecology* **67**, 337-354.

Vezina, A. F. (1986). Body size and mass flow in freshwater plankton: models and tests. *J. Plankton Res.* **8**, 939-956.

Vidondo, B., Prairie, Y. T., Blanco, J. M. and Duarte, C. M. (1997). Some aspects of the analysis of size spectra in aquatic ecology. *Limnol. Oceanogr.* **42**, 184-192.

Warwick, R. M. (1984). Species-size distributions in marine benthic communities. *Oecologia* **61**, 32-41.

Welsh, A. H., Peterson, A. T. and Altmann, S. A. (1988) The fallacy of averages. *Am. Nat.* **132**, 277-288.

Weng, G., Bhalla, U. S. and Iyenagr, R. (1999). Complexity in biological signaling systems. *Science* **284**, 92-96.

West, G. B. (1999). The origin of universal scaling laws in biology. *Physica A* **263**, 104-113.

West, G. B., Brown, J. H. and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122-126.

West, G. B., Brown, J. H. and Enquist, B. J. (1999). The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* **284**, 1677-1679.

Wiesenfeld, K. (2001). Scaling laws. *Am. J. Phys.* **69**, 938-942.

Witek, Z. and Krajewska-Soltys, A. (1989). Some examples of epipelagic plankton size structure in high latitude oceans. *J. Plankton Res.* **11**, 1143-1155.

Zwanenburg, K. C. T. (2000). The effects of fishing on demersal fish communities of the Scotian Shelf. *ICES J. Mar. Sci.* **57**, 503-509.