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Cross-scale ecological dynamics and microbial size spectra in marine ecosystems

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Evaluating the component features of 'scaling' planktonic size spectra, commonly observed in marine ecosystems, is crucial for understanding the ecological and evolutionary processes from which they emerge. Here, we develop a theoretical framework that describes such spectra in terms of the size distributions of individual species, and test it against actual datasets of microbial size spectra from the Atlantic Ocean. We describe characteristics of size probability distributions of component species that are sufficient to support the observational evidence and infer that, when a power law describes the community size spectrum (thus suggesting critical self-organization of microbial ecosystem structure and function), a related power law links the total number of individuals of a given species to its mean size.

Keywords: marine microbial ecosystems; scaling size spectra; species size distribution; finite-size scaling

1. INTRODUCTION

Ecological processes shape the size distributions of organisms that comprise natural communities. The lack of preferential sizes and a continuous spectrum without gaps therein, implies scaling size distributions, i.e. those that can be described by a power law in a finite range of sizes. Such distributions emerge as ubiquitous properties of complex marine food webs (e.g. Sheldon *et al.* 1972; Platt 1985; Prothero 1986; Rodriguez & Mullin 1986; Chisholm 1992; Blanco *et al.* 1994; Rodriguez 1994; Vidondo *et al.* 1997; Cavender-Bares *et al.* 2001; Rodriguez *et al.* 2001).

Why should a continuous spectrum of organism size emerge from the ecological and evolutionary processes that have shaped ecosystems over evolutionary time? One wonders about the origins and implications of the absence of preferential sizes (e.g. Levin *et al.* 1997; Banavar *et al.* 1999; Solé *et al.* 1999; Marquet 2000; Norberg *et al.* 2001), which is routinely observed in marine ecosystems regardless of a wide range of forcing environmental conditions (e.g. Cavender-Bares *et al.* 2001). This feature, the signature of scale invariance, is detected by the regularity of the community size spectrum, i.e. the probability distribution of sizes regardless of species, lacking troughs and peaks that signal rare or frequent occurrences—and hence absence, or excess, of certain ranges of size. Such features may have their dynamic origin in the self-organization of complex adaptive systems, possibly to self-organized critical phenomena, because they are robust in the face of environmental fluctuations (see Bak 1997; Rodriguez-Iturbe & Rinaldo 1997; Levin 1999; Solé *et al.* 1999). In this context, size distributions may provide a powerful synthesis of structure and function of an ecosystem, because size matters for rates of metabolic activity and predator–prey dynamics (e.g. McMahon & Bonner 1983; Levin 1999) and because diversity and abundance control individual species' and community size spectra (e.g. Holling 1992).

In this study, we propose sufficient conditions for the establishment of scaling community-size spectra for ecosystems composed of an arbitrary number of species, possibly overlapping in size, in terms of size distributions of individual species (i.e. species' size distributions, SSDs). We address theoretical consistency and finite-size scaling analyses based on the study of measured microbial-size spectra comprised organisms ranging in size from bacteria to nano-phytoplankton in marine ecosystems.

2. THEORETICAL FRAMEWORK

It is commonly assumed in the literature on planktonic size distributions, that body density ρ is constant and species independent. Quasi-spherical particles are measured and counted, increasingly through flow cytometry. This means that the volume and the characteristic linear size are equivalent, size being proportional to the cubic root of volume for Eulerian geometries. In this paper, all measured properties are related to cell volume, and the term 'size distributions' is used freely in this context.

We assume that organisms (individuals) of arbitrary size, described for convenience by their volume v, can be attributed to different 'species' k. Although we refer to 'species' throughout our discussion, we intend this to include functional groups, i.e. groups that have a collec-

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tive, macroscopic behaviour coherent with that of a single species. In our actual experimental analysis, we can, at best, resolve functional groups and, at worst, resolve ensembles of similar species (see § 3). We note that for prokaryotic microbes, in general, species distinctions are imprecise and, in any event, a species-based approach necessarily ignores intraspecific variations (e.g. Norberg *et al.* 2001). By contrast, a continuum approach that accounts for features within a functional group has been speculated to allow for better understanding of group behaviour (Fisher 1958; Levin 1999), and the same assumption has recently been used to derive equations that describe the aggregate properties of a group of species in changing environments (Norberg *et al.* 2001). Therefore, in what follows, we will term SSD as the size distribution of a functional group.

We thus define the kth SSD as $p_k(v)$, i.e. $p_k(v)\mathrm{d}v$ is the fraction of individuals of the kth species with volumes in $(v,v + \mathrm{d}v)$. Let N_k be the total number of individuals of species k within a sample, which we term the population abundance of k. This abundance is determined by the balance between growth and mortality in the species, and as such is an emergent property of the dynamics of the food web. The community-size spectrum of all organisms describes the relative proportion of sizes regardless of species. It is defined as the probability density $f(v)$ of volume, v, of all the organisms, i.e. $f(v)\mathrm{d}v$ is the number of organisms of any species with size in the range $(v,v + \mathrm{d}v)$. SSDs may overlap in size, and thus different species contribute to each size class v. The definition of community-size spectrum thus follows as

$$f(v) = \frac{\Sigma_k N_k p_k(v)}{\Sigma_k N_k}, \tag{2.1}$$

where the index k spans the species defining the arbitrary community of the ecosystem sampled. Notice that the denominator is the total number of individuals of all 'species' (or functional groups). In practice, to avoid problems due to binning and to the number of individuals in each sample, one samples the probability of exceedence of a given size, i.e. $P[V \geqslant v]$ or the proportion of the total number of organisms whose size exceeds v within a large sample. One thus has $f(v) = -\mathrm{d}P[V \geqslant v]/\mathrm{d}v$.

The SSDs of individual species need no specific restriction, in particular concerning the mean, spread and range of sizes allowed to any given species, apart from proper normalization (i.e. $\int_0^\infty p_k(v)\mathrm{d}v = 1$). In fact, different species may indeed have overlapping ranges of size. We do not constrain the bulk and the tails of the distributions of individual species, and their relative position and spread across scales. We also assume that $p_k(v)$ depends strictly on volume and, say, not on time. This implies that the relative proportion of cells of a given size within a species does not change substantially from sample to sample, and from place to place. As we shall see in § 3, this assumption, although never entirely true, is a reasonable working assumption, often supported by data for true species. Notice that the mean size $\langle v\rangle_k$ is directly computed from the SSD via $\langle v\rangle_k = \int_0^\infty \mathrm{d}v \times v p_k(v)$. The population abundance of species k is defined by the number of organisms, N_k. The number of individuals of species k and of size v is $N_k p_k(v)$ and the total biomass in species k is $M_k = \rho N_k \langle v\rangle_k$, with the usual symbol notation. Finally, the total biomass is $M = \Sigma_k M_k$, where the summation spans all species. Notice that one may interpret our results regardless of whether or not the ecosystem is in a steady state where the observed species abundance (and their relative proportions) remains stable in time, implying that regulatory environmental conditions (e.g. nutrient availability, light and temperature) are maintained long enough relative to the generation times of the organisms.

Scaling-size spectra, i.e. distributions showing an algebraic decay $f(v) \propto v^{-\alpha} (\alpha > 0)$ for large values of v, lack a preferential size and size gaps, and are a requisite for self-organized dynamic origins (Bak 1997; Levin 1999; see Vidondo *et al.* (1997) in the context of microbial size spectra). In general, a homogeneous power function such as $f(x) = Cx^\alpha$ (with C and α constant) is intrinsically self-similar: if x is rescaled (multiplied by a constant), then $f(x)$ is still proportional to x^α albeit with a different constant of proportionality. Such functions reproduce themselves upon rescaling, and therefore lack natural scales, do not harbour a characteristic unit and are said to be scale free, or 'true on all scales'. In this sense, power laws are sources of scale invariance or self-similarity. Power-law probability distributions of size may imply an infinite mean unless a finite range of sizes is assumed. In such a case (depending on the value of the scaling exponent), the mean, the variance and progressive moments of the distributions diverge in the infinite range—in order to be finite they must depend on a finite interval of sizes sampled, and thus the mean makes no sense as a property of a population. This 'syndrome of infinite variance' (i.e. the progressive divergence of the variance of a self-similar signal as the sample size is enlarged) is widely held as the typical signature of scale invariance. Similarly, it has been observed that the operational computation of mean phytoplankton size may depend on the sample size (Chisholm 1992).

It is widely debated whether scaling-size spectra represent some central tendency of natural ecosystems (e.g. Holling 1992; Rodriguez 1994; Marquet 2000; Niklas & Enquist 2001). It is generally assumed that this is not the case for terrestrial ecosystems, where gaps in size spectra are ubiquitous and uneven relative abundances of organisms result in bumpy distributions which clearly depart from a power-law type and its implications, such as the lack of characteristic sizes (Holling 1992). Invariant scaling relationships for interspecific plant biomass (an analogue to community-size spectra) have instead been documented (Niklas & Enquist 2001). For marine ecosystems, however, a continuous, power-law type spectrum is commonly observed in samples of plankton collected from seawater (e.g. Sheldon *et al.* 1972; Platt 1985; Rodriguez & Mullin 1986; Cavender-Bares *et al.* 2001). This important difference between terrestrial and marine ecosystems is not conclusively explained (e.g. Holling 1992), although it is of central importance to the understanding of the ecological processes that shape the respective communities.

3. DATA

We examined microbial-size spectra, including bacteria through nano-phytoplankton (Cavender-Bares *et al.* 2001), in samples from the western North Atlantic Ocean. Microbial size and abundance were measured using flow

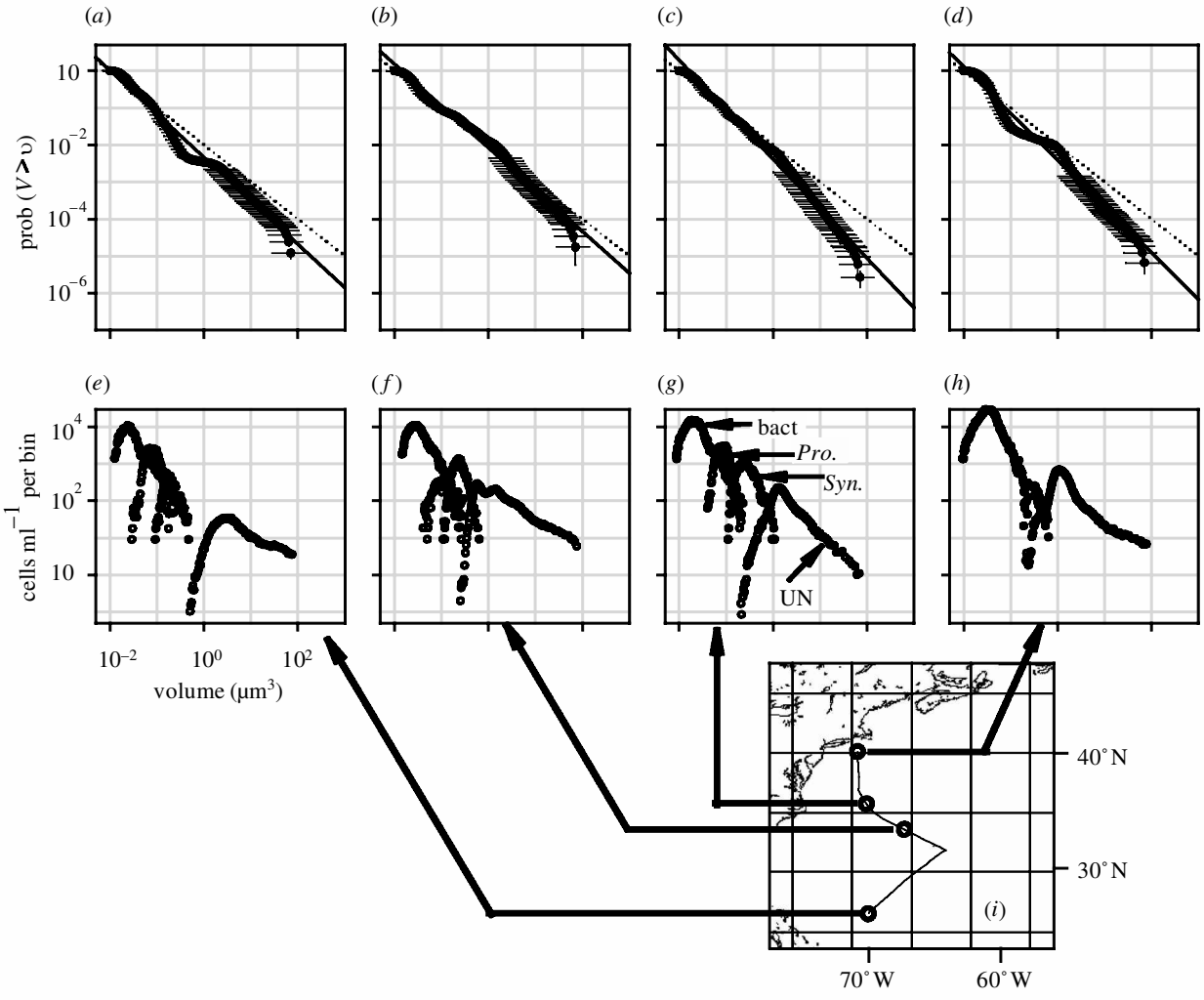

Figure 1. A sample of the experimental database. (*a–d*) Ensemble averages of the probability of exceedence spectra, $P[V \geqslant v]$ based on several ($\geqslant 10$) realizations based on the number of samples taken in the various locations in the Atlantic Ocean: (*a*) the Southern Sargasso Sea; (*b*) the Northern Sargasso Sea; (*c*) the Gulf Stream; (*d*) coastal waters. We choose to represent the spectra via axes, for $P[V \geqslant v]$ and volume, equally scaled for all panels. Confidence intervals on the estimation of cell sizes are shown by horizontal lines for each point via the experimental techniques described in Appendix A; variations among individual spectra are shown by vertical error bars (1 s.d.). In all cases, a 1 : 1 dotted line is included beginning at the smallest cell measured. We note that the relative conformity of the spectra to a power law—a straight line in the plot—varies depending on sites. (*e–h*) Individual realizations of plots of cell concentration against volume for the regions in (*a–d*). Four groups are shown here, respectively from small to large: (i) heterotrophic bacteria (bact); (ii) *Prochlorococcus* (*Pro.*); (iii) *Synechococcus* (*Syn.*); and (iv) ultra- and nano-plankton (UN). Details on the tools to extract such information are in the literature (Cavender-Bares *et al.* 2001). Note the absence of cells of certain size classes, for example the size gap in panel (*e*) for spectrum (*a*) and in panel (*h*) for spectrum (*d*), and how the gap is filled by a sub-population of ultra- and nano-plankton appearing in spring bloom waters for (*g*). (*i*) A map of the sampling stations in the western Atlantic Ocean during March 1998.

cytometry (see Appendix A), and the spectra were represented as probability of exceedence of cell volume (see Appendix A). A sample of the results is shown in figure 1 where we distinguish the community size spectrum ($P[V \geqslant v]$ versus v: figure 1*a–d*) and the observed (ensemble mean) SSD $p_k(v)$ (figure 2*a*) computed from measured cell concentration plots (figure 1*e–h*).

We can distinguish four distinct types of microbes using our methodology: bacteria, *Prochlorococcus* (*Pro.*), *Synechococcus* (*Syn.*) and ultra- and nano-phytoplankton (UN). The bacteria (more properly, bacteria and archaea) represent an ensemble of many different species—unresolved by our methods—which have a diversity of functional roles in the ecosystem. *Pro.* and *Syn.*, on the other hand, can be properly referred to as functional groups. UN represents an unknown number of eukaryotic species, which we can only partially resolve into subgroups based on their size and pigment content. For the purpose at hand, we refer to these four groups as 'species' ($k = 1,4$: bacteria, *Pro.*, *Syn.*, UN), but as is revealed later, only *Pro.* and *Syn.* behave as such in our analysis, as would be expected (see Appendix A). The volume range resolved in our analysis is four orders of magnitude, not as large as one might prefer, but still meaningful for scaling analyses because it is significantly large relative to the range of individual species (figure 1).

We observe (Cavender-Bares *et al.* 2001) that spectral shapes often conform closely to a power law, for example during the bloom in the Sargasso Sea and in the waters of the Gulf Stream (figure 1*b*,*c*). In coastal waters, and in the permanently stratified waters of the Sargasso Sea, this is not observed as we see peaks and troughs in the spectra

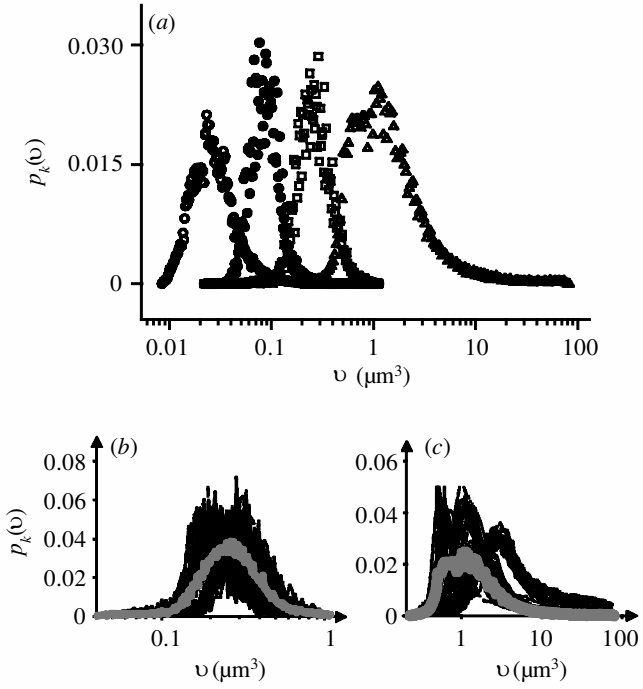

Figure 2. (*a*) Ensemble mean size probability distributions $p_k(v)$ for the four species investigated. Forty-five different realizations have been sampled from the transects shown in figure 1; (*b*) and (*c*) show individual realizations departing from the ensemble mean, allowing a control of the ergodic conditions (i.e. where no single realization differs substantially from the ensemble mean). Note that suitable binning is required to produce the ensemble averages. Also, note that bacteria and especially ultra- and nano-plankton show irregular features, probably because these populations contain multiple species that could not be resolved using flow cytometry. (*b*) The plot shows 45 individual realizations of the SSD $p_3(v)$ where $k = 3$ indicates *Synechococcus* (thin lines). A thick solid grey line shows the ensemble average $\langle p_3(v)\rangle$. Deviations from any sample to the ensemble mean are minor, and thus we substantiate the basic assumption $p_k(v) \sim \langle p_k(v)\rangle$ as we have done in this paper. (*c*) The plot shows 45 individual realizations of the size spectrum of ultra- and nano-plankton, together with their ensemble mean (solid grey line). Three broad classes of spectral features emerge, suggesting either the instability of the size spectrum over time, or the relative presence of at least three different species. We favour the latter, and we conclude that the group ultra- and nano-plankton does not characterize a single species. Triangles, ultra- and nano-plankton; filled circles, *Prochlorococcus*; squares, *Synechococcus*; open circles, bacteria.

implying preferential sizes in the distribution (figure 1*a*,*d*). Overall, the individual spectra within large regions characterized by similar ecological conditions show remarkable consistency, and suggest a picture in substantial agreement with the observed tendency towards a uniform distribution of biomass among size classes (Platt 1985; Prothero 1986; Blanco *et al.* 1994; Rodriguez 1994; Vidondo *et al.* 1997; Rodriguez *et al.* 2001). In such cases a size spectrum inclusive of all relevant organisms has been suggested (Rodriguez 1994) to approach the algebraic form $f(v) \propto v^{-2}$.

The ensemble averages of the SSD $p_k(v)$ from 45 samples ($k = 1$ bacteria; $k = 2$ *Pro.*; $k = 3$ *Syn.*; $k = 4$ UN) are shown in figure 2*a*. A comparison of ensemble averages with the individual realizations from the batch of measurements in the above samples is shown in figure 2*b* for *Syn.* and figure 2*c* for UN. The data suggest that for *Syn.* (and indeed for *Pro.*, data not shown)—the two groups that correspond to 'species' by our definition—there exists a stable species' size distribution $p_k(v)$ that does not change substantially from sample to sample, and departures from the ensemble average are not major. This does not apply to bacteria (data not shown) and UN (figure 2*c*) that are characterized by a heterogeneous mix of cell types. The cluster of cells measured as bacteria, and as UN, identified by the flow cytometer, undoubtedly comprise numerous species, and there are probably more in the bacteria than in the UN. We note that the particular structure of the individual realizations of the SSDs of UN (figure 2*c*) indicates the probable inclusion of at least three different species that cannot be distinguished from each other on their flow cytometric signatures.

4. THE MODEL

There exist many alternative mathematical ways in which individual spectra can produce composite community-size spectra of the power-law type. One, for instance, could be that the number of species increases with decreasing (log-) size while population abundance in each species remains constant. This is clearly not supported by ecological data (e.g. Damuth 1981). Other mathematical assumptions could constrain the spacing of the bulk of the SSDs, provided their tails decay sufficiently fast, i.e. implying self-similarity of individual spectra and an unlikely regular spacing of the body of the SSDs. This also seems unrealistic (e.g. May & Stumpf 2000). It has also been observed (Solé *et al.* 1999) that mixing of distributions may account for most empirical power laws reported in the ecological literature. For instance, mixing lognormal distributions (a particular case of equation (4.1)) may produce a power law if the means are identical but the variances vary among distributions contributing to the mixture (Allen *et al.* 2001). This requirement would hardly be met in the case at hand, for different functional groups generally have different mean size.

We propose the following assumptions: the SSD $p_k(v)$ has a finite-size scaling form, obtained by the product of two terms, an algebraic power of size multiplied by a suitable scaling function, i.e.

$$p_k(v) = \frac{1}{v}\mathscr{F}\left(\frac{v}{v_k}\right), \tag{4.1}$$

where $\mathscr{F}$ is the scaling function and v_k is a typical size acting as a scaling factor (not the maximum size of the kth species), which we show to be proportional to the mean size, i.e. $v_k \propto \langle v\rangle_k$ (see Appendix A). It is important to note that $\mathscr{F}$ is a scaling function whose detailed specification is not needed (Fisher 1972). Specific and popular choices of distributions, like the lognormal or the generalized gamma, belong in the class of distributions defined by equation (4.1). Standard finite-size scaling arguments imply that in equation (4.1) the exponent of the prefactor at the right-hand side must be 1 ($f(v) \propto v^{-1}$) to ensure that $p_k(v) \to 0$ for $v \to 0$. If the exponent were greater than 1, this would imply, unsuitably, that $p_k(v) \to$ constant for for $v \to 0$. Notice that the

domain of $\mathscr{F}$ in equation (4.1) is not necessarily a bounded interval, hence what follows is not relevant only to groups of species for which the ratio of the maximum to the minimum volume for each species is the same; population abundance in the kth species' scales as

$$N_k \propto \langle v \rangle_k^{-1/\phi}, \tag{4.2}$$

where $\phi > 0$ formalizes the obvious observation that the total number of individuals decreases with increasing typical size. Equation (4.2) relates to allometric scaling of biological quantities (McMahon & Bonner 1983; Peters 1983; Damuth 1981, 1987, 1998; Brown *et al.* 1993; Ritchie & Olff 1999; Brown & West 2000; Schmid *et al.* 2000; May & Stumpf 2000; Burness *et al.* 2001; Maurer 2002), i.e. simple and systematic empirical scaling laws that dictate how biological features change with an organism's size.

The finite-size scaling form of equation (4.1) is a sufficient condition for a power-law size spectrum $f(v)$ to emerge. In fact, straightforward manipulations (see Appendix A) yield

$$f(v) \propto v^{-(1+1/\phi)}, \tag{4.3}$$

valid from a lower to an upper cut-off size. Note that, from equations (4.2) and (4.3), the biomass of the kth species is $M_k \simeq \langle v \rangle_k N_k \propto \langle v \rangle_k^{1-1/\phi}$ and that the value $\phi = 1$ would agree with the assumption (e.g. Chisholm 1992; Blanco *et al.* 1994; Rodriguez 1994) of biomass being independent of the size class, i.e. $M_k \simeq$ constant, and $f(v) \propto v^{-2}$ (see Appendix A). Notice also that the specific value of the scaling exponent (i.e. $\phi = 1$ and hence, from equation (4.3), $\alpha = 2$ for $f(v) \propto v^{-\alpha}$) is immaterial to the validity of our analysis.

5. RESULTS AND DISCUSSION

We have tested the validity of the basic rescaling condition implied by equation (4.1) on the data shown in figures 1 and 2. In particular, the theoretical results derived from the guide of the data imply that the ensemble mean SSDs shown in figure 2 should collapse onto a single curve when plotted in the scaling form $v \times p_k(v)$ versus $v/\langle v \rangle_k$. The result of the rescaled collapse of the SSDs is shown in figure 3. As expected, such collapse is remarkable only for *Pro.* and *Syn.* (see, in particular, the logarithmic enlargement in figure 3*b*). These are the only true 'species' (i.e. functional groups) that our experimental procedure can resolve (Cavender-Bares *et al.* 2001). Somewhat surprising to us was the fact that bacterial spectra are close to collapse onto the predicted curve although they are known to blend numerous species together, thus yielding an unclear attribution to the same functional group. The heterogeneous mix of cell types labelled as UN is far from collapsing owing, in particular, to a much larger range of sizes covered. Given the departure of the ensemble average of UN from single realizations (figure 2*c*) clearly representative of a collection of species, it is not surprising that the ensemble mean SSDs do not align with those for *Pro.* and *Syn.* However, an overall consistent picture of observational and theoretical results emerges.

Our theoretical results suggest that when a power law $f(v) \propto v^{-\alpha}$ describes the community-size spectrum, the relationship between the total number of individuals of the

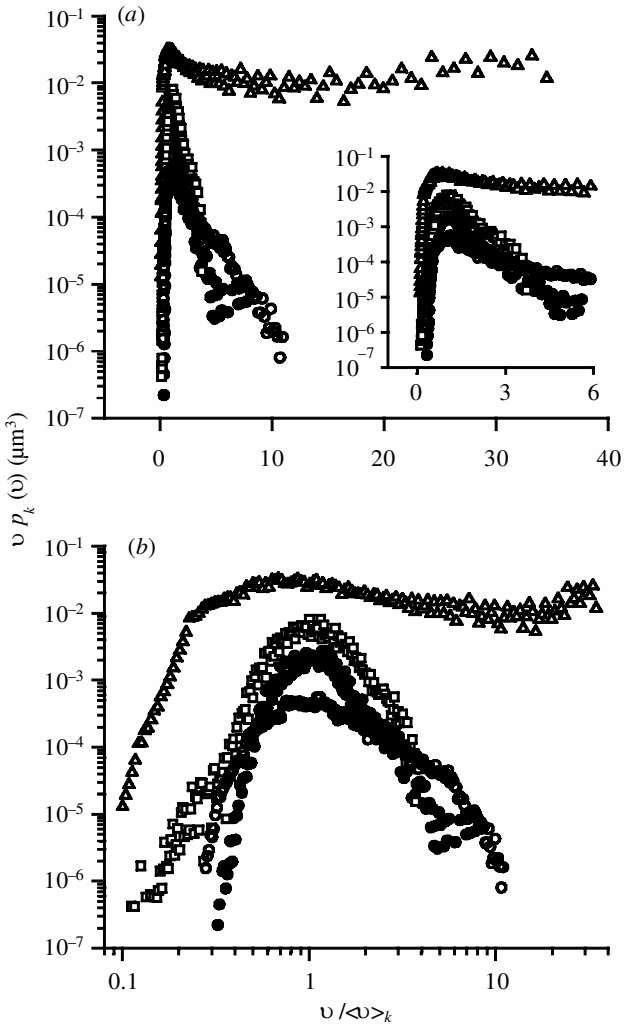

Figure 3. Collapse of rescaled SSD. (*a*) A suitable collapse of the ensemble mean size distributions of the four species measured tests the validity of equation (4.3). Here, we plot $v \times p_k(v)$ versus $v/\langle v \rangle_k$ for the four ensemble mean distributions which, according to equation (4.3), should collapse onto the same curve $\mathscr{F}$ even though the mean sizes differ by orders of magnitude. The inset enlarges the section of the plot around the maximum value of the scaling function. (*b*) A logarithmic expansion of the x-axis allows an enlargement of the key region from $0.1 \leqslant v/\langle v \rangle_k \leqslant 10$. It is seen that the collapse is remarkable only for *Prochlorococcus* and *Synechococcus*, which are the only true species that our experimental techniques can distinguish. Symbols as in figure 2.

kth species, N_k, versus its mean size $\langle v \rangle_k$ should also be described by a power law with exactly the scaling exponent $1/\phi = \alpha - 1$. The related observational relationships, which relate to cross-scale ecosystem dynamics controlling the population abundance N_k, can be seen in figure 4 for the spectra shown in figure 1. We observe that when the size spectrum closely conforms to a power law (e.g. figure 1*c*,*g*), the relationship between the number of cells (N_k) and mean size ($\langle v \rangle_k$) becomes linear after logarithmic transformation (figure 4*g*) and the predicted relationship between the scaling exponents holds, i.e. $\phi \simeq 1$ yielding, $N_k \propto \langle v \rangle_k^{-1}$, $f(v) \propto v^{-2}$ and $P[V \geqslant v] \propto v^{-1}$. This case, known to imply roughly equal biomass per bin of size (see Appendix A), shows that the total biomass of

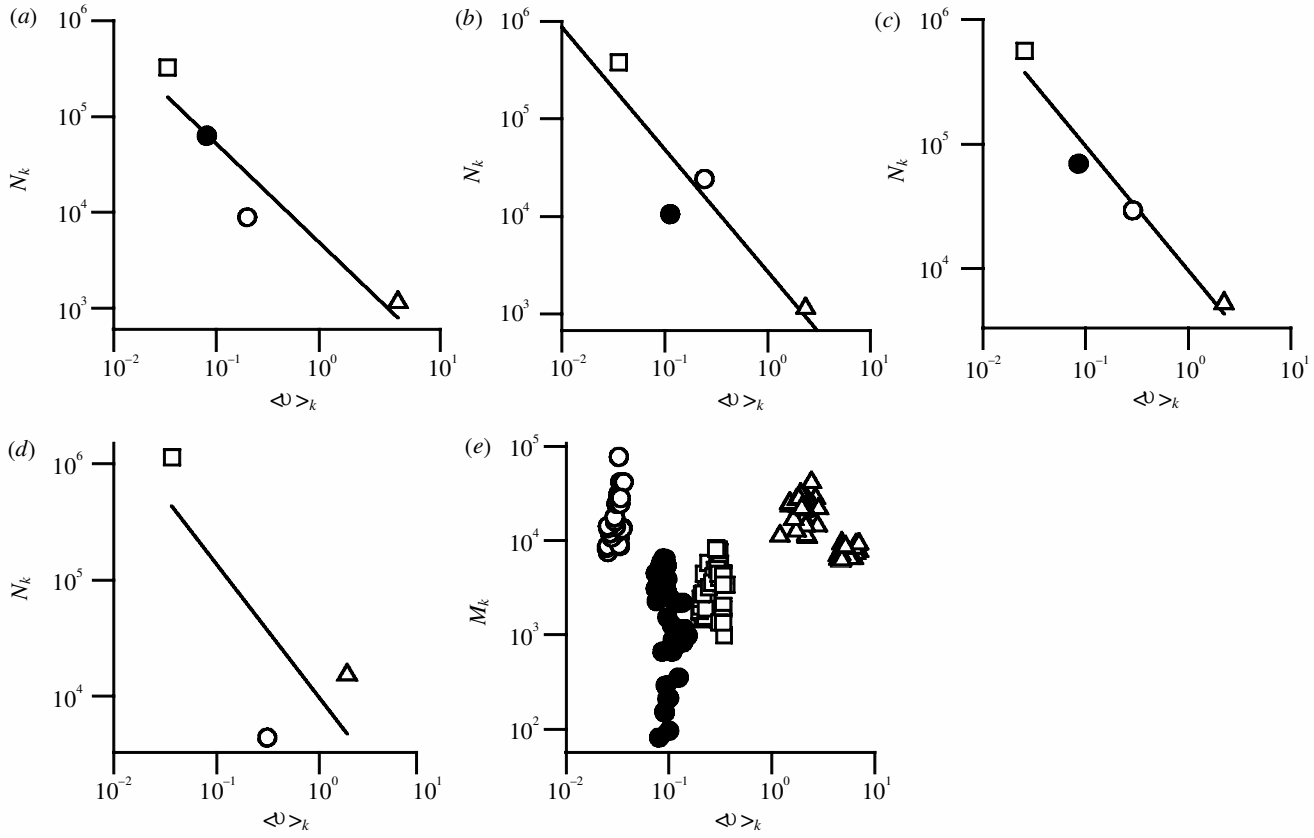

Figure 4. Allometric relationships in marine microbial communities. (*a–d*) Total number of cells for each of the four 'species' measured ((i) heterotrophic bacteria; (ii) *Prochlorococcus*; (iii) *Synechococcus*; and (iv) ultra- and nano-plankton) within different samples (figure 1*e–h*) as a function of the mean species' size, computed via the ensemble averages shown in figure 2. (*a*) Number of cells in the cell concentration plot in figure 1*e*; (*b*) relative to figure 1*f*; (*c*) relative to figure 1*g*; (*d*) relative to figure 1*h*. We note that as the relationship tends to a power law (*a–d*), $N_k \propto \langle v \rangle_k^{-1/\phi}$, the global size distribution (figure 1*a–d*) tends to $P[V \geqslant v] \propto v^{-1/\phi}$, as predicted by equations (2.1) and (4.1)–(4.3). Where a clear scaling relationship is found (e.g. case C, figure 1*c*,*g*), the scaling exponent approximates to $\phi = 1$ and therefore $N_k \propto \langle v \rangle_k^{-1}$. (*e*) The relationship between the total biomass $M_k \propto N_k \langle v \rangle_k$ in the *k*-species and its mean volume $\langle v \rangle_k$. It is interesting to notice the wide fluctuations in total biomass in the different samples. Depending on the blooming conditions, *Prochlorococcus* biomass may in fact change by almost two orders of magnitude. One also notices that the observed tendency towards a value of $\phi \sim 1$ implies $M_k \propto \langle v \rangle_k^0 \sim$ constant, or roughly equal biomass versus mean size, which is a corollary of the known observation of roughly equal biomass per bin of size classes of all organisms. The lack of manifest trends in (*e*) supports the above argument, and the mean of the observational points shown does not scale with size. Symbols as in figure 2.

every species is roughly independent of its mean size (figure 4*i*). Finally, it should be noted that the above linear relationship holds, surprisingly, even for bacteria and UN. This probably stems from a correct identification of the mean size of the cluster of species clumped together under the same label—and from the fact that the related species' abundances are measured correctly.

The finite-size scaling framework in ecology is stimulating and leads to possibly important insights in ecology. If, for instance, the total number of species within A is $N(A) \propto A^z$, a different, and related, finite-size scaling argument has been proposed (Banavar *et al.* 1999). In fact, the number of individuals of all species within an area A_i, N_i, must be finite and is described by a species-abundance distribution $P_i(n)$ (the probability that any given species on a biome A_i has n individuals). It has been suggested that P_i is well described by a relationship of the type $P_i(n) = n^{-1}\mathscr{G}(n/N_i^{\Phi})$ where Φ is another scaling exponent. Significantly, the size distribution cannot extend to infinity, thus possibly yielding diverging moments of the distribution. Ecosystem size must determine an upper cut-off to the sustainable maximum size and to the food-chain length. This would postulate that no preferential sizes would exist in the ecosystem apart from those dictated by the upper and lower cut-off. In turn, the dependence of the mean size on the range of sizes allowed would sustain the so-called 'syndrome of infinite variance'. The relationship between ecosystem size and the food-chain length has been documented in lakes (Post *et al.* 2000), and that the largest organism within an ecosystem depends on the ecosystem's size is a commonly accepted tenet (Burness *et al.* 2001; Maurer 2002). Thus, one would have a size distribution of the type

$$f(v) \propto v^{-\alpha} F(v/V^{\beta}), \tag{5.1}$$

where F is an appropriate finite-size scaling function, V is the characteristic size of the ecosystem and α,β are suitable finite-size scaling exponents. It has recently been suggested (Burness *et al.* 2001) that $\beta = 1/2$ and V is simply the size of the landmass supporting the maximal body size. This ansatz, once demonstrated conclusively, would bear fundamental consequences on cross-scale dynamics of

ecosystems including mass extinctions due to biome alteration (e.g. by glaciations).

The universality and consistency of scaling microbial community-size spectra observed in marine ecosystems is very surprising given the variability in the physical and chemical processes that dictate their structure. The features of these size spectra are determined by—indeed emerge from—the dynamics of the food web, which is in turn forced by the abiotic environment. That such a complex web of interacting factors, acting locally and over evolutionary time, should result in such universal patterns begs explanation, and suggests a tendency of ecosystems to self-organize into states that lack a characteristic size—regardless of initial conditions and of transient disturbances. This ecological process is driven by cross-scale population dynamics, which shape natural selection and species' abundance, which in turn regulate the mean, spread and range of organism sizes covered, whose connected features we have proposed.

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6. APPENDIX A

(a) *Material and methods*

The details of the experimental methodology can be found in Cavender-Bares *et al.* (2001). Briefly, a modified Epics V flow cytometer (Beckman–Coulter) was used both at sea and in the laboratory for all plankton analyses (Cavender-Bares *et al.* 1998). Four groups of plankton were distinguished by these analyses. Bacteria (including Archaea) were enumerated by staining samples with a nucleic-acid-specific stain (SYBR-Green I, Molecular Probes) following the protocol of Marie *et al.* (1997). These samples were preserved using 0.1% glutaraldehyde and were frozen in liquid nitrogen. *Prochlorococcus* and *Synechococcus* were analysed either at sea or on similarly preserved, but unstained samples. The ultra- and nanoplankton, which are not well preserved, were analysed in fresh samples at sea. We applied a calibration curve (Cavender-Bares *et al.* 2001) to the raw flow cytometry data in order to convert from forward angle light scattering (FALS) to cell volume.

Each data point resulted from sorting (via flow cytometry) a subset of cells in a preserved field sample away from the other cells and then sizing those cells using a Coulter Counter (Model ZM, Beckman–Coulter). A fit to the data based on the equations of Bohren and Huffman for Mie theory, has been produced along with our estimate of 95% confidence intervals on predicting volume from FALS. The points at low FALS correspond to populations of *Prochlorococcus*. Instrument limitations did not permit the sorting and sizing of bacteria, however, the slope of the Mie fit to the data extrapolated in this region agrees with previous work relating FALS to the volume of marine bacteria (Cavender-Bares *et al.* 2001).

Although flow cytometry is a useful tool for generating highly resolved and statistically significant abundance versus size data, as configured for this study it is limited to analyses of the lower end of the plankton size spectrum. Although most of the oceanographic provinces we examined are indeed dominated by very small cells, our study would have benefited from the inclusion of the larger-size end of the microbial spectrum, and we will work towards this in the future.

(b) *Mathematical details*

We regard as interesting the investigation of the properties required of individual species for the whole ecosystem to lack a preferential size because of a scaling community-size spectrum. Here, we show sufficient and plausible, data-supported conditions for the individual SSDs, $p_k(v)$, to yield a power-law-distributed size spectrum $f(v)$.

The scaling form of equation (4.1) implies that the only species dependence of $p_k(v)$ occurs through the quantity $\langle v\rangle_k$. In fact, equation (4.1) implies, by direct integration, that the nth moment of the distribution scales as v_k^n as $\langle v^n\rangle_k \sim v_k^n$ (or $\langle v^n\rangle_k = C_n v_k^n$, where the constant $C_n = \int x^{n-1}\mathscr{T}(x)\mathrm{d}x$ is finite and independent of the species considered).

The above equation implies that the larger the mean size of the species, the larger its size spread around the mean. In such cases, one notes that the increasing variance of sizes would be overlooked by allometric relationships (or macroecological datasets) addressing mean values only (e.g. McMahon & Bonner 1983; Peters 1983; Burness *et al.* 2001). In fact the standard deviation of sizes in the kth species is

$$(\sigma_v)_k = \sqrt{\langle v^2\rangle_k - \langle v\rangle_k^2} \propto v_k.$$

Thus, the scaling factor v_k is proportional to the range of sizes covered, which in turn is solely proportional to the mean value $\langle v\rangle_k$.

Notice, with reference to a general ecosystem, that the use of SSDs precisely relates the mean (e.g. adult) mass of each species with the mass of the largest known individual in probabilistic terms, and may compare with studies providing only a range of masses (Burness *et al.* 2001). Equation (4.1) is equivalent to the assumption that for two arbitrary species k,j the relationship $p_k(v) = \Lambda_{kj} p_j(\Lambda_{kj} v)$ holds, where Λ_{kj} depends solely on the ratio v_j/v_k. Given two different species j and k characterized by different mean and range, defined by their scaling factors v_j, v_k, the following basic condition must relate the behaviour of the SSDs under changes of scale (where, owing to normalization, Λ_{kj} must be a constant dependent only on the ratio v_k/v_j, i.e. $\Lambda_{kj} = \Lambda(v_k/v_j)$; notice that $\Lambda(1) = 1$). Let us consider three distinct species i,j,k. It thus follows that $p_j(v) = \Lambda_{ij}\Lambda_{ki} p_k(\Lambda_{ij}\Lambda_{ki} v)$, which yields $\Lambda(v_k/v_j) = \Lambda(v_i/v_j)\Lambda(v_k/v_i)$, suggesting that the term v_i at the right-hand side can be chosen arbitrarily because the left-hand side does not depend on it. One can further show that the above equations imply $\Lambda_{kj} = (v_k/v_j)^{-\phi}$, where ϕ is the exponent appearing in equation (4.1). Assuming a reference species, say denoted by 0, characterized by unit population, one thus has $\mathscr{T}(x) = xN_0^{-\phi} p_0(xN_0^{-\phi})$, and $\langle v\rangle_k \propto N_k^{-\phi}$. By differentiating the previous relationship with respect to v_k and then setting $v_i = v_k$ we obtain

$$\frac{1}{v_j}\Lambda'(v_k/v_j) = \frac{1}{v_k}\Lambda'(1)\Lambda(v_k/v_j),$$

which is equivalent to

$$\frac{\mathrm{d}}{\mathrm{d}x}\log\Lambda(x) = \frac{\Lambda'(1)}{x}.$$

The unique solution of the above equation with $\Lambda(1) = 1$ is $\Lambda(x) = x^{-\phi}$, with $\phi = -\Lambda'(1)$. This demonstrates that $\Lambda_{kj} = (v_k/v_j)^{-\phi}$.

(c) *Allometry*

From the definitions, we can write

$$f(v) \propto \sum_k N_k p_k(v) \propto \sum_k \langle v\rangle_k^{-1/\phi}(1/v)\mathscr{F}(v/\langle v\rangle_k),$$

which can be rewritten as

$$f(v) \sim \frac{1}{v}\int \mathrm{d}\hat{v}\hat{v}^{-1/\phi}\mathscr{F}(v/\hat{v})g(\hat{v}),$$

where $g(\hat{v})$ is the probability density of species with typical size $\hat{v}$. The fact that no gaps in size occur and that the size variance of every species is proportional to its typical size leads us to propose that g behaves like

$$g(\hat{v}) \sim \frac{1}{\sigma_{\hat{v}}} \sim \frac{1}{\hat{v}}$$

(valid between an upper and lower cut-off in order to allow normalization) because one observes that equal biomass per size bin and larger variances calls for a decreasing density of mean and typical sizes. From the above one obtains

$$f(v) = v^{-1/\phi}\int \mathrm{d}x x^{-1/\phi}\mathscr{F}(1/x)g(xv) \sim \frac{1}{v^{1+1/\phi}},$$

because the resulting size spectrum $f(v)$ in the scaling regime obeys the relationship $f(v)\mathrm{d}v \sim v^{-1/\phi}g(v)\mathrm{d}v$ since the population with mean v is proportional $v^{-1/\phi}$. Indeed, the left-hand side above is the percentage of individuals with size comprised in the interval $(v, v + \mathrm{d}v)$. The number of individuals per species with mean v is $v^{-1/\phi}$ and the number of species with size about v is $g(v)\mathrm{d}v$, hence the above equation. Thus, combining the above two equations one obtains equation (4.3).

(d) *On equal biomass in each size class*

If $\phi = 1$ one obtains a slope -1 of a log–log plot of the probability of exceedence $P[V \geqslant v]$ versus v, which is the slope of the normalized size spectrum. This describes a system in which there is roughly equal biomass in each size class, a remarkable emergent property of the system that is a well-known observational feature in many marine ecosystems (e.g. Rodriguez 1994). In fact the total mass in a range $(v, v + \Delta v)$ with $\Delta v/v \sim 1$ is

$$\int_v^{v+\Delta v} \mathrm{d}v' f(v')v' \sim \log\left(1 + \frac{\Delta v}{v}\right) \sim 1,$$

i.e. the total biological mass in a range between v and $v + \Delta v$, Δv being the typical variance at scale v, is independent of v.

REFERENCES

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

Bak, P. 1997 *How nature works. The science of self-organized criticality*. Berlin: Copernicus–Springer.

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

Blanco, J. M., Echevarría, F. & Garcia, C. M. 1994 Dealing with size spectra: some conceptual and mathematical problems. *Sci. Mar.* **58**, 17–24.

Brown, J. H. & West, G. B. 2000 *Scaling in biology*. Oxford University Press.

Brown, J. H., Marquet, P. & Taper, M. 1993 Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584.

Burness, G. P., Diamond, J. & Flannery, T. 2001 Dinosaurs, dragons and dwarfs: the evolution of maximal body size. *Proc. Natl Acad. Sci. USA* **98**, 14 518–14 523.

Cavender-Bares, K., Frankel, S. L. & Chisholm, S. W. 1998 A dual sheath flow cytometer for shipboard analyses of phytoplankton communities from the oligotrophic oceans. *Limnol. Oceanogr.* **43**, 1383–1391.

Cavender-Bares, K., Rinaldo, A. & Chisholm, S. W. 2001 Microbial size spectra from natural and enriched ecosystems. *Limnol. Oceanogr.* **46**, 778–789.

Chisholm, S. W. 1992 Phytoplankton size. In *Primary productivity and biogeochemical cycles in the sea* (ed. G. Falkowski & A. D. Woodhead), pp. 213–237. New York: Plenum.

Damuth, J. 1981 Population density and body size in mammals. *Nature* **290**, 699–703.

Damuth, J. 1987 Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* **31**, 193–201.

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

Fisher, M. E. 1972 Finite-size scaling. In *Critical phenomena* (ed. M. S. Green), pp. 271–295. New York: Academic.

Fisher, R. A. 1958 *The genetical theory of natural selection*. New York: Dover.

Holling, C. S. 1992 Cross-scale morphology, geometry and dynamics of ecosystems. *Ecol. Monogr.* **62**, 447–465.

Levin, S. A. 1999 *Fragile dominion: complexity and the commons*. Reading, MA: Perseus Books.

Levin, S. A., Grenfell, B., Hastings, A. & Perelson, A. S. 1997 Mathematical and computational challenges in population biology and ecosystem science. *Science* **275**, 334–343.

McMahon, T. A. & Bonner, J. T. 1983 *On size and life*. New York: Scientific American Library.

Marie, D., Partenski, F., Jacquet, S. & Vaulot, D. 1997 Enumeration and cell cycle analysis of natural populations of marine picoplankton by flow cytometry using the nucleic acid stain SYBR Green I. *Appl. Environ. Microbiol.* **63**, 186–198.

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

Maurer, B. 2002 Big thinking. *Nature* **415**, 489–491.

May, R. M. & Stumpf, M. P. H. 2000 Species–area relations in tropical forests. *Science* **290**, 2084–2088.

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

Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R. & Levin, S. A. 2001 Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl Acad. Sci. USA* **98**, 11 376–11 381.

Peters, R. H. 1983 *The ecological implications of body size*. Cambridge University Press.

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

Post, D. M., Pace, M. L. & Hairston, N. G. 2000 Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1051.

Prothero, J. 1986 Morphological aspects of scaling in biology. *J. Theor. Biol.* **118**, 259–262.

Ritchie, M. E. & 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. & Mullin, M. M. 1986 Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol. Oceanogr.* **31**, 361–370.

Rodriguez, J., Tintoré, J., Allen, J. T., Blanco, J. M., Gomis, D., Reul, A., Ruiz, J., Rodriguez, V., Echevarría, F. & Jimenez-Gomez, F. 2001 Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature* **410**, 360–364.

Rodriguez-Iturbe, I. & Rinaldo, A. 1997 *Fractal river basins: chance and self-organization*. New York: Cambridge University Press.

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

Sheldon, R. W., Prakash, A. & Sutcliff, W. H. 1972 The size distribution of particles in the ocean. *Limnol. Oceanogr.* **17**, 327–340.

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

Vidondo, B., Prairie, Y. T., Blanco, J. M. & Duarte, C. M. 1997 Some aspects of the analysis of size spectra in aquatic ecology. *Limnol. Oceanogr.* **2**, 184–192.

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