Scaling and Zipf's Law in ecological size spectra

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Size distributions in some ecosystems follow a power (Zipf-)law behavior spanning up two ten decades. A model for the origins of this scaling behavior is presented. The model shows that the intrinsic dynamics of the system leads to a power law distribution, $N(m) \sim m^{-\alpha}$, with $\alpha \approx 2$, in agreement with field data. We assume that each individual is eventually the predator of any smaller individual, thereby connecting all elements in the food web among themselves. We consider reproduction and death coming from predation and natural death. It is shown that the most important mechanism generating the exponent $\alpha \approx 2$ is predation.

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Scaling phenomena are widespread in nature. From the spatial distribution of cities [1] [2] to the patterns of evolution in the biosphere [3] [4] power laws have been shown to be a common feature of many complex systems. The most famous of all these distributions is the so called Zipf's law [1]. Over the last decades several mechanisms leading to power law behavior have been reported, such as intermittency [5] , coherent noise [4], coagulation-fragmentation dynamics [6], self-organized criticality [7] or multiplicative processes arising from systems with interacting units with complex internal structure [8].

Understanding the origins of scaling can provide valuable information about the origins of complexity and its implications. Power laws are well known in physics but their statistical quality in biology [9] is often less satisfactory. A remarkable exception is provided by the size spectra of ecosystems. Field data from aquatic environments show a power law in size-abundance spectrum $N(m)$ of organisms (mostly plankton) of size m: $N(m) \sim m^{-\alpha}$, with $\alpha \approx 2$ [10]. In other words, size spectra in ecology also display the Zipf's law. This value has been shown to have some range of variation: In inland lakes, $\alpha \in (1.90, 2.16)$ [11] [12]; in the north Pacific Central Gyre, $\alpha \in (2.13, 2.32)$ [13]. An example [14] is shown in figure 1.

Some previous studies have introduced different types of specific assumptions to derive the size-abundance spectrum [15] [16] [17]. There is a range of values for α in these studies [18] but no general, simple mechanism has been provided. Here a simple model is presented and it is shown to be able to explain both the origins of the scaling and the range of observed values for α.

An ecological community is a complex food web where an individual can be a prey or a predator of the same species at different stages of its life [19]. From the trophic point of view, the food web contains basically three type of organisms: (1) phytoplankton, organisms growing from inorganic matter; (2) zooplankton, which feed on themselves and on phytoplankton; and (3) at the bottom, detritivorous bacteria, that eat some organic matter generated at other levels. Thus, biomass is created in the phytoplankton, flows up to the zooplankton through predation, and is recycled by detritivorous bacteria. We simplify the food web complexity by assuming that a zooplankton organism is the predator of any smaller organism.

If we neglect migration, we may write a steady balance equation for the abundance distribution:

$$\frac{\partial \left(N \dot{m} \right)}{\partial m} = -N p_m + R(m) \tag{1}$$

where R indicate reproduction terms, $\dot{m}$ denotes the growth rate of an organism of mass m, and p_m its death rate (the sum of the predation and natural death rates). The term in the left-hand-side accounts for the variation in N due to the growth of organisms, while the right side contains the source terms: the substraction of individuals by death, and reproduction. Strictly speaking, the quantities $\dot{m}$ and p_m depend not only on the mass but also on the species; however, experimental measurements put in evidence that their averages follow simple power laws, $\dot{m} \sim m^{\delta}$ and $p_m \sim m^{-\gamma}$, with $\delta \in (0.7, 1.0)$ and $\gamma \in (-0.3, 0)$ [20], [21].

Let us start ignoring reproduction and natural death (i. e. organisms die only due to predation). If individuals from zooplankton eat any organism smaller than them, one may write:

$$p_m = \int_m^{\infty} N_z(m_1) b(m, m_1) dm_1 \tag{2}$$

where $N_z(m)$ is the zooplankton abundance density. Here $b(m, m_1)$ is the probability per unit time for a predator of mass m_1 to eat a prey of mass m. One can express p_m in terms of N by taking adavantage of the fact that, under the conditions of our study, zooplankton biomass is roughly the same as phytoplankton's (Sprules et al measurements provide a value a bit smaller than 60% for the zooplankton biomass in summer [22]). This approximation yields:

$$p_m \simeq a_1 \int_m^\infty N(m_1) b(m, m_1) dm_1, \text{with } a_1 \approx 1/2 \qquad (3)$$

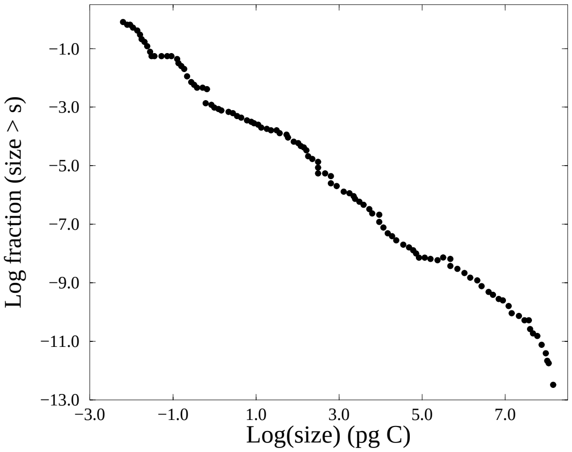

FIG. 1. Fraction of organisms with mass greater than m(in our model, slope $-\alpha + 1$) versus the mass m (measured in dry Carbon weight). One observes a power law dependence over 10 decades.

On the other hand, the growth rate for zooplankton can be expressed as

$$\frac{dm}{dt} = a_2 \int_{m_0}^{m} N(m_1) m_1 b(m, m_1) dm_1 \qquad (4)$$

m_0 being the mass of the smallest organisms, and a_2 the fraction of ingested food which is actually transformed into biomass by the predator (a_2 is roughly 20% for zooplankton, maybe less [18] [23] [24]).

Let us now consider the interaction rate $b(m, m_1)$. It must be an increasing function of the predator mass, m_1, since the larger the organism, the larger its energy requirements. Besides, larger preys are likely to be more attractive to predators than small ones. In what follows, we consider a function of the type:

$$b(m, m_1) \propto m^\beta m_1^\beta \qquad (5)$$

with β some positive exponent, but the results that one obtains are quite the same if one uses functions $b_{m,m_1}$of the type $m^\rho m_1^\beta$, or $m^{2\beta} + m_1^{2\beta}$, for instance.

By proposing a solution $N(m) \sim m^{-\alpha}$ and introducing expression (5) in (3), one finds:

$$p_m = C a_1 \Big(\frac{m^{1+2\beta-\alpha}}{\alpha - 1 - \beta} \Big) \qquad (6)$$

C being the product of the prefactors in $N(m)$ and $b(m, m_1)$. In order p_m to decrease with m, as it must due to the predation process, one has $\alpha > 1 + 2\beta$. Similarly, (4) yields:

$$\frac{dm}{dt} = C a_2 \frac{m^{2+2\beta-\alpha}}{2 + \beta - \alpha}, \text{ for } m \gg m_0 \qquad (7)$$

Since $\dot{m}$ is an increasing funtion of m, it is necessary that $\alpha < 2 + \beta$. Then, $1 + 2\beta < \alpha < 2 + \beta$. Let us also notice that, expressions (6) and (7) lead to $\delta + \gamma = 1$, in agreement with experimental observations [20] [23].

The introduction of (6) and (7) into (1) supplies:

$$\frac{a_2}{a_1} \frac{2 + 2\beta - 2\alpha}{2 + \beta - \alpha} = \frac{1}{1 + \beta - \alpha}$$

Its solution, under constraints $1 + 2\beta < \alpha < 2 + \beta$,is:

$$\alpha = \beta + 1 + \frac{-1 + \sqrt{1 + 8x}}{4x} \qquad (8)$$

that allows to find α if one knows $x \equiv a_2/a_1$, and β. For $a_2 = 0.2$ and $a_1 = 0.5$ as good estimates, and $\beta = 0.4$, (8) provides $\alpha = 2.06$. With this value of the β parameter, the growth exponent δ is, from (7), $\delta = 2 + 2\beta - \alpha = 0.74$, in the range of observations. Fig.2 displays α obtained through (8) and δ versus the parameter x for $\beta = 0.4$. One observes that exponents α and δ fall well into the observational ranges for all reasonable values of x, with $\alpha \simeq 2$.

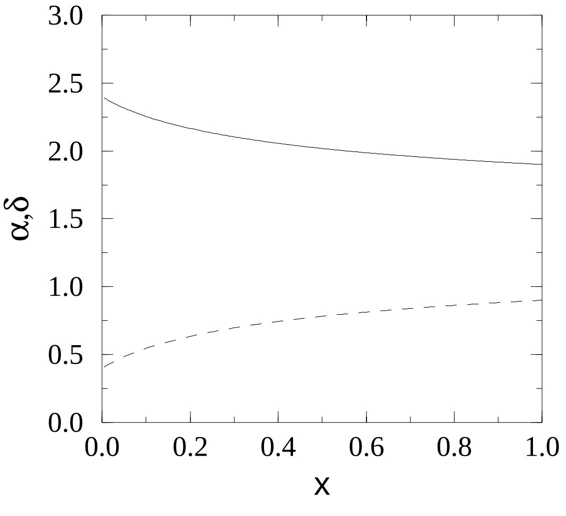

FIG. 2. Exponents α (—) and δ (– –), corresponding to the abundance and growth rate spectra, respectively, versus $x \equiv a_2/a_1$, by solving eq. 8. For reasonable values of x around our estimate $x = 0.4$, α and δ fall well into observational ranges, with $\alpha \simeq 2$.

One can also analyze the sensitivity of the results to the chosen value of β. Starting from our best estimate for x, $x = 0.4$, some direct manipulations supply: $\delta = 0.34 + \beta$, $\alpha = 1.65 + \beta$, so that $\alpha = 1.31 + \delta$. Then, for values of δ between 0.7 and 1.0, α ranges from 2.0 to 2.3, perfectly in the observational range. For $\delta = 0.75$, maybe the more accepted value for its relation with Kleiber's law, $\alpha \cong 2.0$, as corresponds to data for lakes.

An additional ingredient, natural death, can be easily added to the model. It seems reasonable to think that natural death rates may be some fraction of predation death rates; since very few individuals may survive more than, let us say, $5(p_m^{pred})^{-1}$, it is not likely that evolution have supplied natural lifetimes longer than a few $(p_m^{pred})^{-1}$. Then, if one takes $p_m^{nat} = 1/4 p_m^{pred}$, for instance, coefficient a_1 in (6) should increase in a factor 5/4, and x decreases in a factor 4/5. This change affects very little the results, as discussed above, since α is weakly sensitive to small changes in x (see also fig. 3). For instance, for the values of the parameters used above, α changes from 2.06 to 2.09.

The model assumptions can be completed by considering reproduction. The introduction of reproduction adds new contributions to the right-hand-side of the balance equation (1).

By one hand, the individuals that reproduce have a final mass which is a fraction, say b_1^{-1}, of the initial mass; this introduces two terms, namely, $-N(m)p_m^r + b_1 N(b_1 m) p_{b_1 m}^r$, with p_m^r the average reproduction rate of an organism of mass m. On the other hand, there is an increase in the mass class corresponding to egg masses; if we denote with b_2^{-1} the fraction of parent mass corresponding to an egg, and with $b_3 \equiv (1 - 1/b_1) b_2$ the number of offspring in a single reproduction event, one must add a term $b_3 b_2 N(b_2 m) p_{b_2 m}^r$.

Therefore equation (1) including reproduction reads:

$$\begin{aligned} \frac{\partial (N\dot{m})}{\partial m} &= -N(m)p_m - N(m)p_m^r \\ &+ b_1 N(b_1 m) p_{b_1 m}^r + b_3 b_2 N(b_2 m) p_{b_2 m}^r \end{aligned} \tag{9}$$

Now, it is biologically sensible to assume that death rates, p_m, and reproduction rates, p_m^r are related: the longer a species lives, the longer its generation time. The simplest hypothesis is to assume that both rates are simply proportional: $p_m^r = d p_m$, d being a constant. Observational data may support this hypothesis. Fenchel [20] provides $p_m^r \sim m^{-0.28}$, i.e an exponent for reproduction rates similar to the ones observed for death rates (let us recall that the later ranges from -0.3 to 0). In particular, it is quite close to the 1/4 exponent, maybe the more accepted exponent for p_m [23], [25]. With this assumption, by using (6) and $N(m) \sim m^{-\alpha}$, it is direct to rewrite right-hand side of (9) as:

$$-N(m)p_m \left[1 + d\left(1 - b_1^{2+2\beta-2\alpha} - b_3 b_2^{2+2\beta-2\alpha}\right)\right] \tag{10}$$

The introduction of (10) in the balance equation supply a power law dependence for $N(m)$ with exponent α satisfying:

$$\frac{a_2}{a_1}\frac{2+2\beta-2\alpha}{2+\beta-\alpha} = \frac{\left[1 + d\left(1 - b_1^{2+2\beta-2\alpha} - b_3 b_2^{2+2\beta-2\alpha}\right)\right]}{1+\beta-\alpha} \tag{11}$$

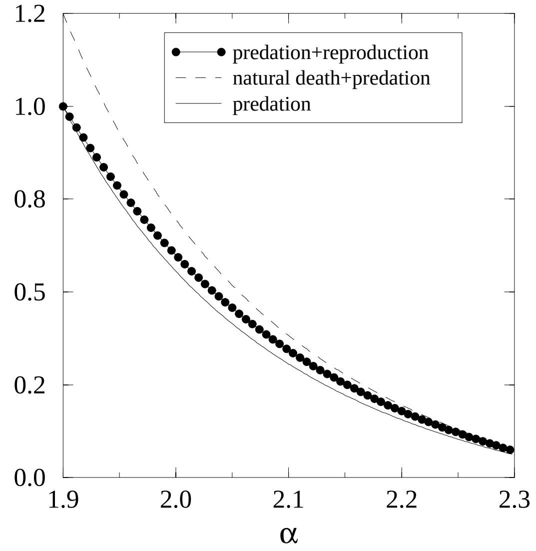

FIG. 3. Exponent α versus x ($\beta = 0.4$): only predation (solid line), predation and natural death (broken line, $p_m^{nat} = 1/4 p_m^{pred}$), and predation plus reproduction (dotted line; $d = 1, b_1 = 10/9, b_2 = 100$). Natural death and reproduction modify very little the exponent α obtained through predation only.

In order to analyze the effects of reproduction in exponent α, we must solve (11) by using realistic values for parameters d and $b's$. Huntley and Lopez [26] provide for copepods: $\dot{m}/m \simeq 4p_m^r$, since $\dot{m}/m \simeq p_m$ (with a factor of order unity [23] [17]), one has $d \lesssim 1$. The quotient parent mass/egg mass is roughly of order 100 [26]. If we also consider that each time new offspring are born, the parent looses about 10% of its weight(11), only negligible variations in the parameter α (see fig.3) are observed. Even considering fission, that is to say, that individuals break into two equal parts, α hardly changes in a few hundreths. Therefore, the inclusion of reproduction does not modify significantly the exponent α obtained by only taking into account growth and death rates.

In summary, we have shown a simple model describing the size abundance spectrum of plankton which is in agreement with observational data. The model is based in very simple assumptions about the trophic relationship among species. We have assumed that each individual is eventually the predator of any other smaller, thereby connecting all elements in the food web among themselves.

We have considered death coming from predation, natural death and reproduction, and we may conclude that the most important mechanism generating the exponent $\alpha \approx 2$ is predation.

This paper generalizes previous studies in several ways. First, we have introduced reproduction and natural death. Second, we have allowed that any smaller organism may be a prey of a larger individual. As previously mentioned, the specific form of the interaction matrix b_{m,m_1} only introduces slight changes in the final results. The robustness of our results strongly suggests that a rather generic mechanism is at work.

Finally, let us have a mention of the role of the smallest organisms, such as detritivorous bacteria and picophytoplankton. Since they are at the bottom of the food web, they do not appear explicitly in our equations. However, their role is essential since they are the basic source of individuals. Eventually, the big ones eat the small ones, so that there must be a continuous source at the small-size level in order for the system to maintain a stationary situation. Since the percentage of organic matter recycled by detritivorous bacteria affects the rate at which these small organisms enter the system, one would expect that this should modify the value of the slope α. Indeed, the rate at which the smallest organisms enter the system only modifies the prefactor in the size-abundance spectrum (i.e. the total biomass of the ecosystem), but not the slope. This is similar to what happens in aggregation problems, where this is proved theoretically and through numerical simulations [6].

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