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Processing the Images of a Typical Species of Bi-Dimensional Primary Producer

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Abstract

Experimental studies on bi-dimensional seaweeds revealed a scaling exponent of 0.472 for their length-biomass allometry. This was significantly higher than the value 0.25 which was proposed earlier as universal for all primary producers, based on the data for unicellular microalgae and vascular plants. Later, an exponent of 0.5 was theoretically derived, which agreed, to some extent, with experimental findings. Here, it is shown that there exists a power-law relation between two perpendicular length parameters along the directions of growth of a bi-dimensional organism. The length-biomass allometric parameters may be expressed in terms of this power index. A relation between the allometric scaling exponent and allometric constant, involving the mass per unit area, has been obtained. A method is proposed to determine the power index experimentally. Some mathematical expressions, relating mass, length and other parameters, have been formulated for a typical seaweed (namely Fucus vesiculosus) and these would be useful for experimental purposes in allometric studies. Analyzing images from an experimental study, a lot of parameters, regarding flat seaweeds, have been determined by analytical and numerical techniques. Assuming the seaweed species follows ontogenetic growth mechanism we solve such dynamical equation and express mass as a function of time. Numerical data on mass for that typical species has been fitted on the ontogenetic solution to make the time dependence of mass precise, the temporal behavior of sample area has also been proposed. Studying the images of three samples of Fucus vesiculosus we have predicted their ages from the model itself. Modifying some important earlier works on transport mechanism through linear networks for living organisms, those uses volume filling fractal (self-similar) like network the concept of surface filling fractals has been introduced. That the kind of sea-weeds under examination obeys Von Bertalanffy model which differs from the universal inter-specific trend defined by micro algae and vascular plants, has been clearly established.

Keywords: flat organism, power law dependence, ontogenetic growth model, allometric scaling, data analysis

1. INTRODUCTION:

In the biological world it is widely found that a variable (say length), often depends on the biomass (M) through a power law

$$L = \beta M^{\alpha} \qquad (1)$$

which is known to be length-biomass allometry (for an overview see [Ahluwalia A., 2017; Kwak H.S., Im H.G., Shim E.B., 2016; Germovsek E., Cheng M., Giragossian C., 2021]). According to Euclidean geometry, a D dimensional homogeneous object, having a linear size L possesses some mass M that scales as L^D. The surface area of such objects scales like $L^D/L = M^{(D-1)/D}$. Therefore, for three dimensional objects $L \propto M^{1/3}$. But it has been found that for systems having transportation networks, this simple $1/D$ scaling law is no longer valid [Banavar, J.R., Maritan, A., Rinaldo, A., 1999]. According to a scientific study [Niklas, K.J., Enquist, B.J., 2001], there is a universal scaling law $L \propto M^{0.25}$ for primary producers. But this law, declared as universal for primary producers, was proposed only on the basis of data for vascular plants and unicellular microalgae and a single macro algal species (Macrocystis, Laminariales). To test the applicability of this relation for macro algae, an experimental study [Scrosati, R., 2006] was conducted with four phylogenetically distinct seaweed species: Chondrus crispus Stackhouse, Pterocladiella capillacea (Gmelin) Santelices and Hommersand, Fucus vesiculosus Linnaeus and Laminaria saccharina (Linnaeus) J.V. Lamouroux. From the length-biomass data of these plants, a scaling relationship was proposed, namely

$$L = 7.811M^{0.472} \qquad (2)$$

The value of scaling exponent (1/4 or 0.25) proposed by Niklas and Enquist [Niklas, K.J., Enquist, B.J., 2001] was originally proposed for trees by West et. al.[West, G.B., Brown, J.H., Enquist, B.J., 1999], as a length-biomass relation between tree height and mass. The conceptual basis of this relation was another law, proposed for plants and animals in general, which claims that metabolic rate has an allometric dependence on organism's biomass, having a scaling exponent of 3/4 [West, G.B., Brown, J.H., Enquist, B.J., 1997]. Niklas and Spatz [Niklas, K.J., Spatz, H.C., 2004] later found that no single scaling rule applies to all species of vascular plants. An important assumption of the models developed by West [West, G.B., Brown, J.H., Enquist, B.J., 1999; West, G.B., Brown, J.H., Enquist, B.J., 1997] was that, biological organisms have fractal like distribution networks throughout the entire body for the internal transport of metabolites. Their models were based on studies of organisms where growth takes place along three dimensions. Their models were not meant to account for length-biomass allometry of bi-dimensional organisms.

The seaweeds studied by Scrosati [Scrosati, R., 2006] are essentially flat and grow mostly across two dimensions. Therefore, it may be inferred that due to the bi-dimensional nature of growth of these seaweeds, there is very little effect of internal architecture on inter-specific allometric exponent for length-biomass relationship, leading to the validity of Euclidean geometry. Thus, for bi-dimensional growth ($D = 2$), one may expect a relation like $L \propto M^{1/2}$ as an average behavior all samples of such species.

2. MODELING AND COMPUTATION REGARDING BI-DIMENSIONAL GROWTH MECHANISM:

A bi-dimensional organism (like seaweed) has two different length parameters (length and breadth) which are not generally found to have the same allometric dependence on mass. In most cases, it is a common observation that growth does not take place at the same rate along two perpendicular directions for organisms having two dimensional growths. Hence, the lengths along two perpendicular directions cannot generally be proportional to each other. In the present study we have attempted to explain the theoretical basis of the allometric expression obtained from Scrosati's experimental observations. We have found it reasonable to consider a power-law relation namely [Majumdar P., Roy S., 2010]

$$L_2 = kL_1^{\lambda} \qquad (3)$$

(in our earlier work) with two growth dimensions (maximum value), having different power indices for different species. The surface area (A) of the organism having the above dimensions is simply a fraction of the area of the rectangle, having sides L_1 and L_2, and it is of the following form [Majumdar P., Roy S., 2010]

$$A = fL_1L_2 = kfL_1^{\lambda+1} \qquad (4)$$

Introducing the new parameter mass per unit area m and keeping in mind the fact that the species have constant thickness one obtains [Majumdar P., Roy S., 2010]

$$L_1 = (1/mfk)^{1/1+\lambda}M^{1/1+\lambda} \qquad (5)$$

Comparison of (5) and (1) may easily yield both α and β. Also we may obtain the mass as a function of the other parameters as [Majumdar P., Roy S., 2010]

$$M = A/\left(\beta^{1/\alpha}fk\right) \qquad (6)$$

If we use the average estimate of Scrosati [6] over four samples (names were mentioned earlier) namely $\alpha = 0.472$ (see (2)) it yields $\lambda = 1.119$. According to Euclidian geometry, for a bi-dimensional ($D = 2$) compact organism with uniform density $\alpha = 1/D = 0.5$, implying $\lambda = 1$. Here, for flat seaweeds clearly λ deviates slightly from this mean value.

In our present work we have made a partial analysis of some data and images provided by Scrosati's study [Scrosati, R., 2006]. Table 1 of [Scrosati, R., 2006] presents the actual values of different parameters corresponding to different samples. Figure3 of the same paper has images of three samples of Fucus vesiculosus. Using the mean values of α and β from Table1 of [Scrosati, R., 2006] the length-biomass allometry for Fucus vesiculosus may be expressed as [Majumdar P., Roy S., 2010]

$$L = 2.41M^{0.376} \qquad (7)$$

yielding $\lambda = 1.6596$ which may be treated as an average estimate of the parameter. As a consequence we may obtain $A/L_1^{\alpha} = 0.0964/\mathrm{m}$. The images of the samples in figure 3 of [Scrosati, R., 2006] have been traced on a mm graph with natural scaling. Counting the smallest squares, we have found different dimensions (with the help of the scale shown in the same figure of the samples). Hence one obtains the following numerical equation for three different samples of the species Fucus vesiculosus with obviously three different exponents [Majumdar P., Roy S., 2010]

$$0.010377/0.21852^{1/\alpha} = 0.002737/0.09630^{1/\alpha'} = 0.001454/0.08148^{1/\alpha''} = 0.0964/\mathrm{m}. \quad (8)$$

Our aim is to fix the value of m, as it must not vary among the members of a species and also to keep the allometric parameters within the specific ranges ($0.349 < \alpha < 0.404$ with 95 percent confidence level as prescribed by Scrosati [Scrosati, R., 2006]) as mentioned in Table1 of [Scrosati, R., 2006]. Numerical solution to (8) using MATLAB yields $= 0.1134\ \mathrm{kg}\cdot\mathrm{mt}^{-2}$ [Majumdar P., Roy S., 2010]. Considering the growth process of the seaweed to be ontogenetic [Moses M.E. et. al., 2008; West G.B., Brown J.H., Enquist B.J., 2001], one may expresses the differential equation obeyed by the time dependent mass as

$$dM(t)/dt = qM(t)^{\sigma_1} - rM(t)^{\sigma_2}. \qquad (9)$$

Although most of the studies [van der Meer J., 2006; Sebens K.P., 2002] including the early studies of Bertalanffy [von Bertalanffy L., 1938; von Bertalanffy L., 1960] agreed that $\sigma_2 = 1$ but there were lot of debates about the exact value of σ_1. Introducing two limiting masses namely, initial mass M_0 and the maximum attainable mass (obtained when dM/dt becomes zero) M_a, one obtains the solution to the above equation

$$M(t) = \left[M_a^{1-\sigma_1}\left(1 - e^{-r(1-\sigma_1)t}\right) + M_0^{1-\sigma_1}e^{-r(1-\sigma_1)t}\right]^{1/1-\sigma_1}, \qquad (10)$$

clearly the maximum attainable mass namely, $M_a = (q/r)^{1/1-\sigma_1}$ is obtainable at $t \to \infty$.

3. DETERMINATION OF METABOLIC EXPONENT:

To determine σ_1 we now follow the idea proposed by Brown et. al. [West, G.B., Brown, J.H., Enquist, B.J., 1999; West, G.B., Brown, J.H., Enquist, B.J., 1997] on transport mechanism through linear networks for all living organisms where the basic assumptions made by them were related to some volume filling fractal (self-similar) like network; the size invariance of the final branches of the network (capillaries) and minimization of energy while transporting the resources throughout the network, like all other minimization principles in nature. But because of the typical bi-dimensional nature (with constant thickness h) of the seaweeds we have to introduce the width parameter w_k instead of the branch radius r_k [West, G.B., Brown, J.H., Enquist, B.J., 1997] (which should in general be applicable for branches of circular cross-section $(D = 3)$) in order to determine the cross-section hw_k for the k th level branching [West, G.B., Brown, J.H., Enquist, B.J., 1997]. Consequently the volume rate of flow will become

$$Q_k = hw_k\bar{u}_k \qquad (11)$$

In the above equation $\bar{u}_k$ is the mean flow speed through the k th level branch. According to Brown [West, G.B., Brown, J.H., Enquist, B.J., 1997] the network has N levels of branching starting from the trunk (level $= 0$) to capillary (level $k = N$). Also each branch at k th level splits into n_k sub-branch, in other words

$$N_k = n_0 n_1 \dots n_k \qquad (12)$$

Following [West, G.B., Brown, J.H., Enquist, B.J., 1997], equation of continuity yields

$$\dot{Q}_0 = N_k\dot{Q}_k = N_k hw_k\bar{u}_k = N_c hw_c\bar{u}_c \qquad (13)$$

where the last part of (13) are the quantities corresponding to the extreme branch (capillary) and is invariant (except N_c) according to Brown [West, G.B., Brown, J.H., Enquist, B.J., 1997]. The initial rate of fluid transport $\dot{Q}_0$ is directly scalable to B.M.R., which in turn scales as M^a, where M and a are the mass of the organism and its metabolic exponent respectively, implying $N_c \propto M^a$. Also the self similar fractal-like Fucus Vesiculosus (ref. to the image in fig.3 of [Scrosati, R., 2006]) shows $n_k = n = 2$, implying $N_k = n^k$. Hence $N_c = n^N$ and we may have [West, G.B., Brown, J.H., Enquist, B.J., 1997]

$$N = a\ln(pM)/\ln(n) \qquad (14)$$

where p is the scaling constant. Analyzing the images of Fucus vesiculosus as provided in figure3 of [Scrosati, R., 2006] we have determined the mean branch lengths l_k and mean branch width w_k for all possible k values (using the scale fitted in the said figure). We now introduce the scale factors $A_k = w_{k+1}/w_k$ and $B_k = l_{k+1}/l_k$ similar to [West, G.B., Brown, J.H., Enquist, B.J., 1997] and compute their respective values for all such k. The majority of the data suggests that both these scale factors are actually invariant with k. The entire fluid volume passing through the network (with a total of N level branching) is

$$V = \sum_{k=0}^{N} V_k N_k = h\sum_{k=0}^{N} w_k l_k n_k^k = \frac{(nAB)^{-(N+1)}-1}{(nAB)^{-1}-1} n^N V_c. \qquad (15)$$

where V_k and V_c are the volume passing through the k th level and capillary in respective order. For a fully grown organism $N >> 1$ (however for the largest of the samples of the seaweed species Fucus Vesiculosus provided by Scrosati we observe from figure 3 of [6] that $N = 6$, which may not be fully grown yet). Application of this inference and also the fact that $nAB < 1$ (which may be obtained by computing the mean values of the parameters A and B from out data set), (15) leads to $V \propto (AB)^{-N} \propto M$. The last relation is obtained using the energy minimization principle [West, G.B., Brown, J.H., Enquist, B.J., 1997]. Applying this result to (14) one obtains (for some new scaling constant p' which may be set to unity)

$a = -\ln n / \ln (p' AB)$. (16)

Brown [West, G.B., Brown, J.H., Enquist, B.J., 1997] introduced the concept of space-filling fractal for the branched organism so that all the groups of cells (service volume) are transported by the capillaries. In his interpretation since the radii of each branch is sufficiently smaller than its length hence for large N the volume serviced by the entire network may be approximated by the sum of the spheres whose diameters are equal to the length of the k th-level branch. For large N, this estimate is independent of k. The fractal is volume-preserving from one generation to the next. For bi-dimensional seaweeds however, the phenomenon of space filling are performed by flat fractals hence instead of the service volume, now we have to think about service area which must be circular in nature of radius $l_k/2$, for the k th level, consequently

$\pi (l_k/2)^2 N_k \approx \pi (l_{k+1}/2)^2 N_{k+1}$, (17)

which yields $B_k \approx (N_k/N_{k+1})^{-1/2} = n^{-1/2} = B$. The area-preserving branching from parent to daughter branch obtains

$hw_k = nhw_{k+1}$, (18)

implying $A_k = n^{-1} = A$. Both the values of A and B match with our measured mean values obtained from the data set ($A = 0.5$ and $B = 0.7$). Hence following (16) $a = 2/3$, implying that the B.M.R. for these typical bi-dimensional seaweed species varies as the two-third power of the mass, following Bertallanfy model [14, 15]. Also the width and length parameters yield (from trunk to capillary) $w_0 = A^{-N} w_c = N_c w_c$ and $l_0 = B^{-N} l_c = N_c^{1/2} l_c$ (since $N_c = n^N$), yielding finally $w_0 \propto M^{2/3}$ and $l_0 \propto M^{1/3}$ (as $N_c \propto M^a$). Hence the length-mass allometric exponent predicted by this theory is likely to be 0.33, which is in well agreement with the experimental finding of Scrosati [Scrosati, R., 2006] (0.37 for Fucus Vesiculosus [Scrosati, R., 2006]). Also the metabolic theory of ecology confirms that $\sigma_1 = a = 2/3$.

4. DETERMINATION OF LENGTH, AGE AND AREA:

Following the idea of Brown [West, G.B., Brown, J.H., Enquist, B.J., 1997] we may say that the length Le of the organism is equivalent to the length of a tube running from the base to the capillary and is given by

$Le = \sum_{k=0}^{N} l_k = \frac{l_0}{1-B} \propto M^{1/3}$. (19)

In order to compute the length of the plant we may note that using the available data we may have only four complete paths which connect the trunk to the capillary. Computation for the largest sample shows (all the lengths are measured in m) $Le_1 = 0.2290, Le_2 = 0.2290, Le_3 = 0.1984, Le_4 = 0.1984$. Computation of lengths for the medium of the three samples of Fucus Vesiculosus can not be performed because of the unclearness of the trunk size. However those for the smallest is $Le = 0.1032$. One may verify (19) from [Majumdar P., Roy S., 2010] and find that the masses of the largest and the smallest samples are $M^L = 0.0012$ kg and $M^S = 0.00016$ kg implying $Le^L/Le^S \sim (Me^L/Me^S)^{1/3}$.

In figure3 of [Scrosati, R., 2006] three images of Fucus vesiculosus were provided with different sizes. We may safely assume that the possible differences in sizes are occurring only due to the differences in their ages and obviously the sample with the largest size must be the oldest one. From the logarithmic plot of length against bio-mass of Fucus vesiculosus in figure5 of [Scrosati, R., 2006] we observe the maximum and minimum values of the data points corresponding to bio-masses are respectively $M_{\max} = 1.5 \times 10^{-3}$ kg and $M_{\min} = 1.0 \times 10^{-6}$ kg. Considering the largeness of the sample size examined by

Scrosati we may safely assume that $M_a = M_{\max}$ and $M_0 = M_{\min}$. Hence using the relation (obtained from (10))

$$rt = 3\ln\left[\frac{M_a^{1/3} - M_0^{1/3}}{M_a^{1/3} - M^{1/3}}\right]. \tag{20}$$

We may obtain the corresponding ages as $7.6323, 2.4096$ and 1.6546 (the data corresponding to the individual masses are brought from [Scrosati, R., 2006; Majumdar P., Roy S., 2010] and here the age of the sample is considered as dimensionless and having a scale factor). Again following (9) and the linear relation between M and A the growth equations with scaled time rt for mass and surface area are

$$dM(rt)/d(rt) \quad = 0.1147M(rt)^{\frac{2}{3}} - M(rt), \tag{21}$$

$$dA(rt)/d(rt) \quad = 0.2370A(rt)^{\frac{2}{3}} - A(rt). \tag{22}$$

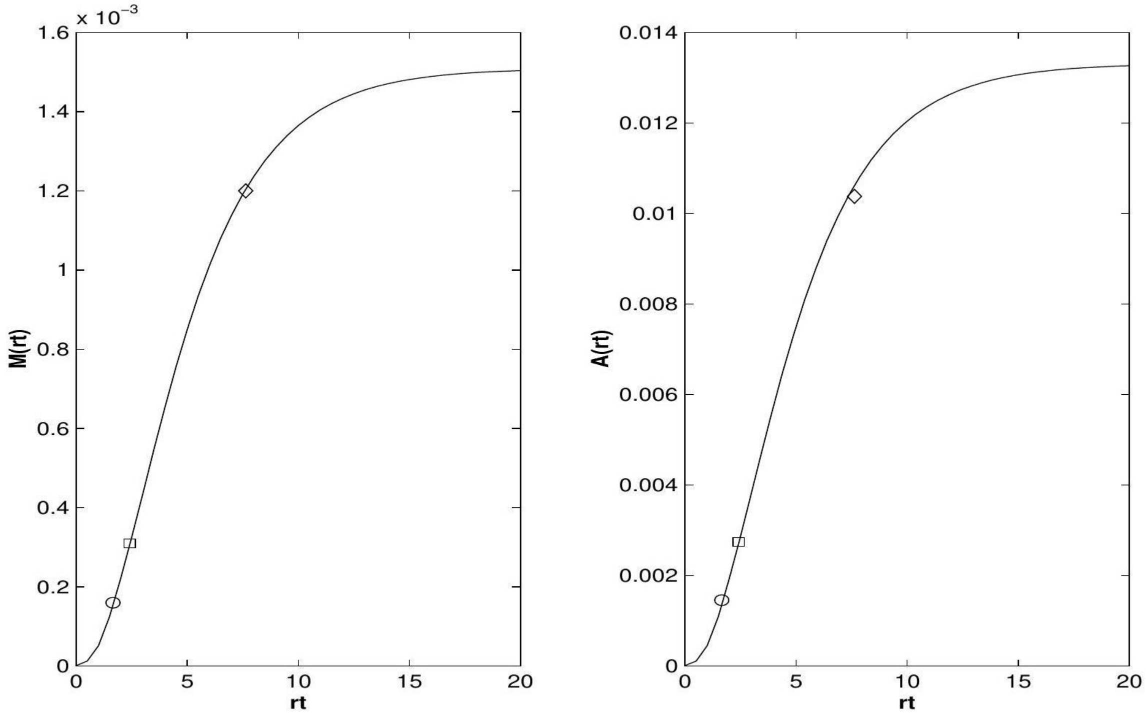

FIG. 1: Figue shows the growth dynamics of Fucus vesiculosus both in terms of mass (left) as well as area (right). The diamond, square and the circle shapes are the data points corresponding to the largest, medium and the smallest of the samples respectively.

After simulating (21) and (22) in MATLAB we obtain the simulation outputs as shown in fig.1 where the discrete data points are the positions corresponding to the samples of Fucus Vesiculosus which justifies the fact that although the shape of the flat organism may vary irregularly, its area may show a smooth variation over time because it is directly scalable to the mass within the same species.

5. OUTLOOK AND CONCLUDING REMARKS:

We have proposed a way for the computation of the scaling exponent of length-biomass allometry of a bi-dimensional organism following some ontogenetic growth mechanism. Scrosati in his article [Scrosati, R., 2006] pointed out the length-biomass allometric exceptionality of the typical species of plants, namely seaweeds, from other plants. We have explained that exceptionality for a particular member of such species, namely Fucus vesiculosus, using some necessary modifications of metabolic theory predicted by Brown et. al. [West, G.B., Brown, J.H., Enquist, B.J., 1997]. Based on common observations, we have adopted a new approach where the basic assumption is that, different length parameters of an organism have different allometric dependences on mass. Hence two length parameters of a bi-dimensional organism may have a power-law relation between them. The power index (λ) plays an important role in the determination of length-biomass scaling exponent. One may determine λ and k experimentally for a certain species using the technique that we have discussed. Using this value of λ, one can compute the scaling exponents for the two length parameters. We have also derived expressions relating M with L_1 and L_2, which would be useful for studying the properties of these parameters experimentally. Another major finding of this study is that the allometric scaling exponent α and constant β depend upon each other. We have developed a theoretical way of measuring m (the mass per unit area), which may become useful for other studies of the same kind.

There are limitations of this study caused by inadequacy of experimental data. We have made a thorough analysis of a secondary set of data obtained from the article of Scrosati [Scrosati, R., 2006]. It is hard to make definite conclusions from such a small set of data that we have dealt with. The important parameters namely the width, area, mass per unit area of the samples of different species could not be obtained from Scrosati's study. We have estimated them mathematically from the figures given in Scrosati's article. Hence, there was no scope for their direct verification, although they have been verified by indirect methods. We have estimated values of those variables (L_2, A, m) for the samples analyzed by Scrosati on the basis of the supplied variables (M, L_1) for those species and the mean values of the allometric parameters (α, β). However, the consistency of results, determined by indirect methods, shows clearly the validity and usefulness of our theoretical model. More such experiments need to be performed and their data should be made widely available for an improvement of the theoretical model presented in this article. We may merely guess the time dependence of some parameters of our model (in fact we have discussed the topic for two parameters, namely mass and area) for the samples analyzed by Scrosati.

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