METABOLIC SCALING REGULARITY IN AQUATIC ECOSYSTEMS

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ABSTRACT. We tested the hypothesis that ecosystem metabolism follows a quarter power scaling relation, analogous to organisms. Logarithm of Biomass/Production (B/P) to Trophic Level (TL) relationship was estimated to 98 trophic models of aquatic ecosystems. A normal distribution of the slopes gives a modal value of 0.64, which was significantly different of the theoretical value of 0.75 (p<0.05). After correction for transfer efficiency among trophic levels a modal value of 0.726 was obtained through a least squares algorithm which was not significantly different from the theoretical one (p>0.05). We also tested for error in both variables, Log (B/P) and TL through a Reduced Major Axis regression with similar results, with a modal value of 0.756 (p>0.05). We also explored a geographic distribution showing no significant relation (p>0.05) to latitude and between different regions of the world. We conclude that: a) ecosystem metabolism follows the quarter-power scaling rule; b) transfer efficiency between TL plays a relevant role characterizing local attributes to ecosystem metabolism; and c) there is neither latitudinal nor geographic differences. These findings confirm the existence of a metabolic scaling regularity in aquatic ecosystems.

Keywords: Ecosystem, metabolism, scaling factor, transfer efficiency

INTRODUCTION

Mass and size of organisms are key attributes associated to metabolism and consequently of great interest for managing natural resources. A number of contributions discuss metabolic regularities in a wide range of living organisms, from unicellular to higher complex living systems, including plants and animals, individuals and populations (West et al., 2001; Savage et al., 2004; Brown et al., 2004). The concept has also been extended to ecosystems accounting for the metabolism of individual organisms with different life histories (Ernest et al., 2003; West & Brown, 2004; Brown et al., 2002). Such metabolic regularities are represented by the allometric relation \( Y \propto M^b \), where \( Y \) = metabolic rate, \( M \) = body mass and \( b = 0.75 \). The concept behind the slope value is referred as “quarter-power” scaling or “3/4-power law” (Savage et al., 2004) and represents the scaling factor between metabolic rate and individual mass, where the quarter scaling, instead of 2/3 derived from size dimensions, is associated to network constrains for energy transport and their assimilation within the living systems which are characterized by having a hierarchical branching structure through which energy flows (West & Brown, 2004; West et al., 1997; Banavar et al., 2002).

A similar process has been suggested at ecosystem level where trophic relationships are arranged like a branching structure with a source of energy represented by primary producers on the base of the trophic pyramid, and the prey-predator relations as the branches or pathways through which energy flows; such structures representing the food web. In an ecosystem context the 3/4-power law is also expected to represent metabolism as a process analogous to that of individual organisms (West & Brown, 2005).
Some authors (West & Brown, 2004; 2005) present an allometric relation representing several species for different levels of complexity suggesting metabolic regularity at ecosystem level such as that observed for individuals and populations.

**MATERIALS AND METHODS**

The information used comes from 98 trophic models for aquatic ecosystems worldwide (see list of models in Annex) comprising lakes, oceanic waters, continental shelf, coral reefs, coastal lagoons, rivers, bays, reservoirs and insular systems (Figure 1), most of them exploited and few unexploited. It is not possible to know the quality of the data in most models, because it does not have an estimate of the pedigree index. However, only eight models have an average pedigree index of 0.53, which indicates that they possess an acceptable quality. Trophic models were constructed using Ecopath with Ecosim suite of programs (Christensen & Pauly, 1992), which is based in one master equation that represents the balance between production and losses for each functional groups and the whole ecosystem:

\[
B_i \cdot \left( \frac{P}{B_i} \right) \cdot EE = \sum B_j \cdot \left( \frac{Q}{B_j} \right) \cdot DC_{ji} + EX_{ji} + E_i + BA_i
\]

where \( B_i \) is biomass of group \( i \), \( P/B_i \) is production/biomass ratio of \( i \), which is equal to the total mortality coefficient (\( Z \)) under steady-state conditions (Allen, 1971; Merz & Myers, 1998); \( EE \) is ecotrophic efficiency which is the part of the total production that is consumed by predators or exported out of the system; \( B_j \) is the biomass of predator \( j \); \( DC_{ji} \) is the consumption/biomass ratio of predator \( j \); \( DC_{ji} \) is the proportion of prey \( i \) in the diet of predator \( j \); \( EX_{ji} \) is the export of group \( i \), which in this study consists of fisheries catch when a group is exploited; \( E_i \) is net migration and \( BA_i \) is biomass accumulation.

To test for metabolic regularity at ecosystem level, we used the relationship between metabolic rate, expressed by \( \log_{10}(B/P) \), in respect to size, represented by trophic level of group \( i \) (\( TL_i \)). This assumes that a trophic level has a direct and negative relationship with the biomass of the compartment according to the pyramid of biomass (Lindeman, 1942).

Biomass/Production ratio (B/P) reflects the proportion of production (P) sustaining a given biomass (B), related to organisms size and longevity (Pauly & Christensen, 1993) reflecting attributes related to metabolism. For a given population, energy is gained through assimilation stored as biomass and removed by respiration and biomass mortality (Allen, 1971). In a stable population mortality equals production, meaning sustained biomass through metabolism. Evidently, for consumers, energy gained comes from preys and in an ecosystem this is represented by trophic relationships between individuals and the food web as a structural attribute.

In our case, the trophic level is estimated as:

\[
TL_j = 1 + \sum_i DC_{ji} \cdot TL_i
\]

where \( TL_j \) is the trophic level of predator \( j \), \( DC_{ji} \) represents the proportion of preys \( i \) in the diet of predator \( j \), \( TL_i \) is the trophic level of prey \( i \); and the sum represents diet composition of predator.

In addition, transfer efficiency (\( TE_i \)), between TL’s was also considered since this process can be different for similar groups between ecosystems depending of the topological and functional configuration of each system. \( TE_i \) is computed as follows:

\[
TE_i = \frac{Y_i + \sum_{j=1}^{n} DC_{ji} \cdot EX_{ji} + E_i + BA_i}{Q/E_i}
\]

\( TE_i \) being the proportion of energy transferred by predation and export.

**Correction of the exponent**

We used the slope (\( \beta_{BP} \)) of the relationship \( \log B/P \) vs. \( TL_i \) to correct the slope (\( \beta_0 \)) of the relationship \( \log B/P \) vs. \( TL_i \) as:

\[
\log B/P = \alpha_0 + \beta_0 TL_i
\]

where \( \beta_0 = \beta_{BP} (1+\beta_{TE}) \),

where \( \beta_{BP} \) and \( \beta_{TE} \) are the slopes in figure 2 of \( \log B/P \), and \( \log TE_i \) changes with \( TL_i \), and \( c_0 \) is a normalization constant independent of \( TL_i \).

**RESULTS AND DISCUSSION**

\( \log B/P \) vs. \( TL_i \) expresses a linear equation (Figure 2A), where the slope represents the exponential rate of change of \( B/P \) with \( TL_i \), meaning how production is used to sustain biomass when flowing through the food web in a process that reflects ecosystem metabolism; and \( TL_i \) linearly relates to logarithm of biomass (Jennings et al., 2001). Based on literature (West et al., 1999; West & Brown, 2005; Banavar et al., 1999), it is expected as null hypothesis (metabolic regularity) a slope value of \( \beta=0.75 \), while the ordinate is assumed normalization constant.
Distribution of β values for the 98 ecosystems (see Annex) is shown in figure 3A, with a mean of β = 0.64 (standard deviation of 0.19) significantly different to the expected 0.75 value (p < 0.05). β < 2/3 has been interpreted as that the network is not fully representing a real ecosystem (Bendoricchio & Palmeri, 2005); or that differences from 0.75 are stemming from network inefficiencies (Banavar et al., 2002). Taking into account the process shown in figure 2A, the slope may approach 0.75 if log($\beta / p$) increases for higher TLi's or diminishes for lower TLi's. In theory this could happen with biomass changes accumulated within respective TLi's, process, which is inherent to Transfer Efficiencies (TEi) between TLi's. It has been demonstrated that changes in TEi would alter scaling exponent of abundance (i.e. as biomass) with mass (Jennings et al., 2002; Jennings & Mackinson, 2003), and particularly that changes in TEi from 0.05 to 0.30 would alter scaling exponent by ±0.2 (25% of the exponent theoretical value of 0.75).

TEi's in ecosystem models, as estimated by Ecopath, vary between TLi's, despite of the 10% reported as average value, and between ecosystems (Pauly & Christensen, 1995). The 3/4-power law assumes distribution of energy

Figure 1 Ecosystem distribution of 98 models used in this paper (see annex for details). Numbered areas indicate regions used to look for geographic patterns. Black dots indicates models used for computations, white dots not used models.

Figure 2. A) Trend of Biomass / Production ratio over trophic level, and B) Trend of transfer efficiency with trophic level for the Central Pacific ecosystem (Kitchell et al., 2002).
along living systems having the same efficiency (in circulatory system it is expressed as maintenance of a constant nutrient deliverable rate per unit volume of body; Banavar et al., 2002). This assumption is not fulfilled in many trophic webs represented by biomass flows, where $\text{TE}_i$ tends to decrease with $\text{TL}_i$ (Figure 2B). For this reason the slopes ($\beta_0$) were corrected obtaining a new set of $\log(\beta_0)$ vs. $\text{TL}_i$ for 95 ecosystems (Figure 3B) with a mean value of $\beta_0=0.726 (\delta=0.25)$, showing a non-significant difference from the 0.75 value ($p>0.05$).

Since ecosystem models used here come from different parts of the world, we searched for geographic patterns of $\beta_0$ values; specifically for latitudinal changes. Figure 1 shows ecosystems locations, and areas drawn indicate latitudinal groups for selected regions to explore for patterns. Values for $\beta_0$ (Table 1) did not show statistical differences between them ($p>0.05$) nor with zero, which means there is not latitudinal gradient and confirm existence of a global pattern.

Previous references to scaling regularity for ecosystem metabolism have used information of specific species (West & Brown, 2004; 2005) and their masses not belonging to the same food web. Here we used information of 95 aquatic ecosystems of different regions of the world where their $\text{TL}_i$'s were estimated through diet composition data. Slopes of $\log(\beta_0)$ and Log $\text{TE}_i$, with $\text{TL}_i$, represent ecosystem attributes related to ecosystem structure and function. In contrast with some previous analysis (Garlaschelli et al., 2003) our results confirm the hypothesis that ecosystems metabolism follows the $3/4$-power law, transfer efficiency being a key process.

Considering the quantitative analysis, ordinary least squares regression assumes that the values $\beta_0$ and $\text{TE}_i$ are independent and normally distributed. Table 1 shows results for the relationship $\log(\beta_0)$ vs. $\text{TL}_i$ after TE correction, both solved by a least squares algorithm. First modal value was significantly different from the theoretical value of 0.75 ($p<0.05$), other were not significantly different ($p>0.05$).

![Figure 3: Slope distribution of log (B/P) versus TL for ecosystem models showing a normal-type distribution with (A) a modal value $|\beta|=0.64$ and $\delta=0.19$, (B) modal value $|\beta|=0.726$ and $\delta=0.25$ after TE correction, both solved by a least squares algorithm, (C) a modal value of $\beta_0=0.756$ and $\delta=0.193$, solved by Reduced Major Axis regression. First modal value was significantly different of the theoretical value of 0.75 ($p<0.05$), other were not significantly different ($p>0.05$).](image-url)

### Table 1: Results for the relationships between $\beta_0$ and $\text{TL}_i$ after TE correction

<table>
<thead>
<tr>
<th>Region</th>
<th>$\beta_0$</th>
<th>$\beta_{\text{TE}}$</th>
<th>+/-95% C.I.</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.6786</td>
<td>-0.0016</td>
<td>0.0052</td>
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</tr>
<tr>
<td>2</td>
<td>0.7763</td>
<td>-0.0043</td>
<td>0.0072</td>
<td>0.27</td>
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<tr>
<td>3</td>
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<td>-0.0063</td>
<td>0.0253</td>
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</tr>
<tr>
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<td>-0.0083</td>
<td>0.0154</td>
<td>0.36</td>
</tr>
<tr>
<td>5</td>
<td>0.8250</td>
<td>-0.0082</td>
<td>0.0243</td>
<td>0.18</td>
</tr>
<tr>
<td>6</td>
<td>0.6495</td>
<td>-0.0031</td>
<td>0.0038</td>
<td>0.35</td>
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</tbody>
</table>
error exists only in the dependent variable, resulting potentially in biased results when the assumption is not met. In our data trophic level was probably also measured with error. To test for this effect in our estimates of β₀, we alternatively applied the Reduced Major Axis (RMA) analysis (Sokal & Rohlf, 1981; Bohonak & van der Linde, 2004) on both, log(T_i) and log(TE_i), with T_i relationships. RMA assumes both variables are measured with error. Results indicate an estimation of β₀ = 0.756 (σ = 0.193) and, after the same consideration with respect to TE_i, results shows a non-significant difference from the 0.75 value (p > 0.05), which confirm the 3/4-power law (Figure 3C).

Results provide evidence of regularity of aquatic ecosystems metabolism. Such regularity is maintained independently of the type of ecosystem or the region of the world. Despite of their emergent metabolism regularity, there are particularities for individual ecosystems given by specific transfer efficiencies, attribute that could be of relevance for local considerations. As conclusion, our findings confirm the concept that complex living systems also follow the 3/4-metabolism scaling rule as a global regularity (West & Brown, 2005; Brown et al., 2007; Banavar et al., 2010).

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REFERENCES


Pauly, D. & V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255-257. DOI: 10.1038/374255a0


Annex. Names and some attributes for the ecosystems used in this contribution. For more details about models and documentation related please visit www.ecopath.org. PP = primary producers; $\beta_{BP}$ = slope relationship Log(B/P) vs. TL; $\beta_{TE}$ = slope relationship Log(TE) vs. TL; $\beta_0$ = slope of the relationship Log(B/P) vs. TL corrected by $\beta_{TE}$. (least squares regression); $\beta_{0,RMA}$ = slope of the relationship Log(B/P) vs. TL corrected by $\beta_{TE}$ (Reduced Major Axis regression).

<table>
<thead>
<tr>
<th>Ecosystem name</th>
<th>Longitude</th>
<th>Latitude</th>
<th>Type of ecosystem</th>
<th>Number of functional groups</th>
<th>Number of PP (including detritus)</th>
<th>$\beta_{BP}$</th>
<th>$\beta_{TE}$</th>
<th>$\beta_0$</th>
<th>$\beta_{0,RMA}$</th>
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<td>61</td>
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<td>48</td>
<td>4 (2)</td>
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<td>0.642</td>
<td>(3)</td>
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<td>Coral reef</td>
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<td>0.6778</td>
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<td>2 (1)</td>
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<td>Campeche Sound, Mexico</td>
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