

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

Regularidad del escalamiento metabólico en ecosistemas acuáticos

RESUMEN. Se contrastó la hipótesis de que el metabolismo de un ecosistema sigue una relación de escalamiento análoga a la existente en los organismos. La relación entre el logaritmo de la razón Producción/Biomasa (B/P) y el nivel trófico (TL) se estimó para 98 modelos tróficos de los ecosistemas acuáticos. Una distribución normal de las pendientes de esta relación produjo un valor modal de 0.64 que es significativamente diferente del valor teórico de 0.75 ($p < 0.05$). Después de realizar una corrección considerando la eficiencia de transferencia entre niveles tróficos, se obtuvo un valor modal de 0.726, el cual fue obtenido a través de un algoritmo de mínimos cuadrados, que generó un valor significativamente ($p > 0.05$) similar al teórico esperado. También se contrastó la hipótesis de existencia de error en ambas variables, logaritmo (B/P) y TL, a través de la técnica de regresión denominada "Reduced Major Axis", con resultados similares según el valor modal de 0.756, sin diferencia estadísticamente significativa ($p > 0.05$) del valor teórico. Se exploró la existencia de algún patrón en la distribución geográfica, sin obtenerse relación significativa ($p > 0.05$) con la latitud, o con diferentes regiones del mundo. Las conclusiones son: a) el metabolismo del ecosistema sigue la regla de escalamiento metabólico de 3/4; b) la eficiencia de la transferencia entre TL desempeña un papel relevante, representando los atributos locales del metabolismo del ecosistema; c) no hay una diferencia latitudinal o geográfica. Estos resultados confirman la existencia de una regularidad en el escalamiento metabólico en ecosistemas acuáticos.

Palabras clave: Ecosistema, metabolismo, factor de escalamiento, eficiencia de transferencia.

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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 indi-

vidual 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:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} + EX_i + E_i + BA_i$$

where B_i is biomass of group i ; $\left(\frac{P}{B}\right)_i$ 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_i 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 ; $\left(\frac{Q}{B}\right)_j$ is the consumption/biomass ratio of predator j ; DC_{ji} is the proportion of prey i in the diet of predator j ; EX_i 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 $\log\left(\frac{B}{P}\right)_i$, 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 respi-

ration 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:

$$TL_j = 1 + \sum_{i=1}^n DC_{ji} \cdot TL_i$$

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:

$$TE_i = \frac{Y_i + \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} + E_i + BA_i}{\left(\frac{Q}{B}\right)_i}$$

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

Correction of the exponent

We used the slope (β_{TE}) of the relationship $\log TE_i$ vs. TL_i to correct the slope (β_0) of the relationship $\log\left(\frac{B}{P}\right)_i$ vs. TL_i as

$$\log\left(\frac{B}{P}\right)_i = \alpha_0 + \beta_0 TL_i, \text{ where } \beta_0 = \beta_{BP} (1 + \beta_{TE}),$$

where β_{BP} and β_{TE} are the slopes in figure 2 of $\log\left(\frac{B}{P}\right)_i$ and $\log TE_i$ changes with TL_i , and α_0 , is a normalization constant independent of TL_i .

RESULTS AND DISCUSSION

$\log\left(\frac{B}{P}\right)_i$ vs. TL_i expresses a linear equation (Figure 2A), where the slope represents the exponential rate of change of $\left(\frac{B}{P}\right)_i$ 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.*, 1997; 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.

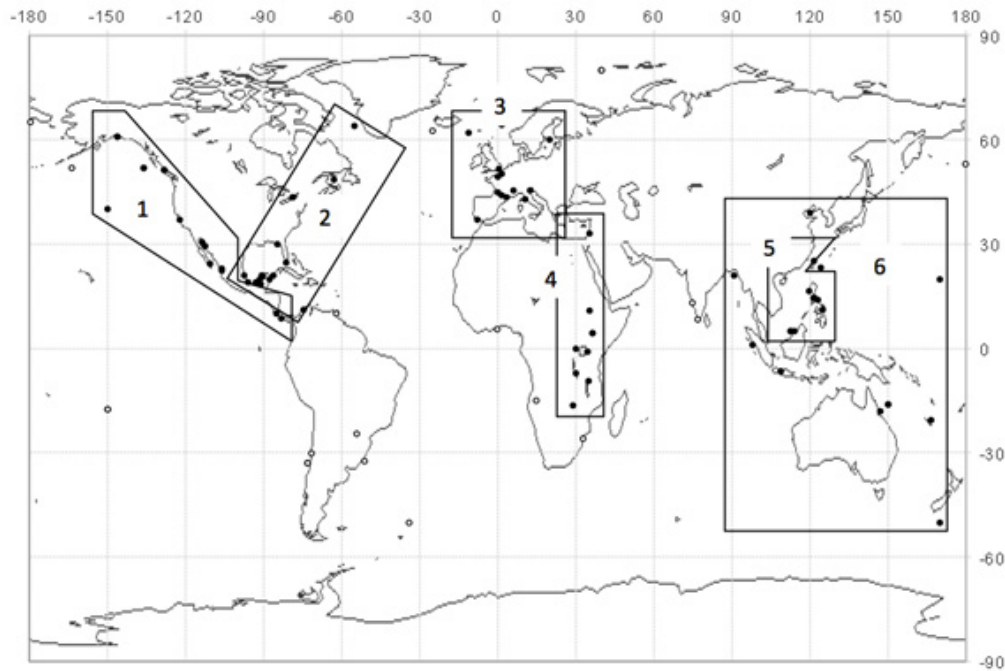


Figure 1 Ecosystem distribution of 98 models used in this paper (see annex for details). Numbered areas indicate regions used to look for geographic patterns. Black dots indicates models used for computations, white dots not used models.

Distribution of β values for the 98 ecosystems (see Annex) is shown in figure 3A, with a mean of $\beta=0.64$ (standard deviation of $\delta=0.19$) significantly different to the expected 0.75 value ($p<0.05$). $\beta<2/3$ 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 $\text{Log}(\frac{B}{P})_i$, increases for higher TL_i 's or diminishes for lower TL_i 's. In theory this could happen with biomass changes accumulated within respective TL_i 's, process,

which is inherent to Transfer Efficiencies (TE_i) between TL_i 's. It has been demonstrated that changes in TE_i would alter scaling exponent of abundance (*i.e.* as biomass) with mass (Jennings *et al.*, 2002; Jennings & Mackinson, 2003), and particularly that changes in TE_i from 0.05 to 0.30 would alter scaling exponent by ± 0.2 (25% of the exponent theoretical value of 0.75).

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

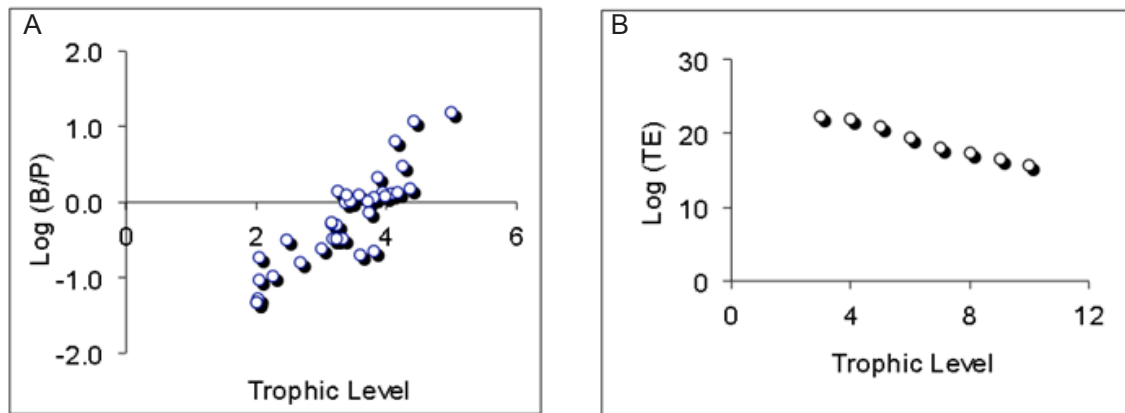


Figure 2. A) Trend of Biomass / Production ratio over trophic level, and B) Trend of transfer efficiency with trophic level for the Central Pacific ecosystem (Kitchell *et al.*, 2002).

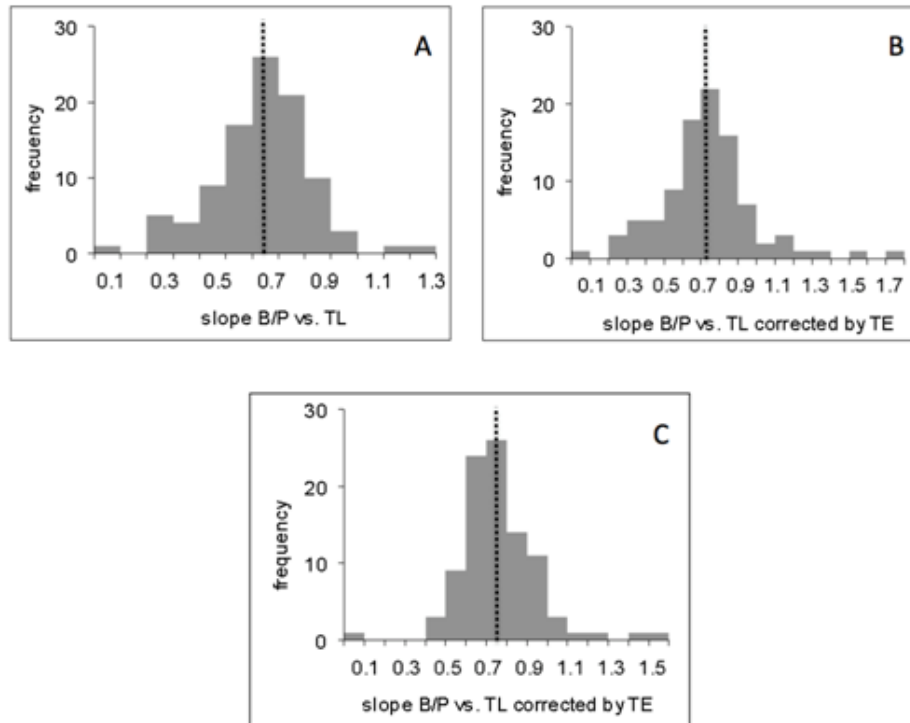


Figure 3. Slope distribution of $\log(B/P)$ versus TL for ecosystem models showing a normal-type distribution with (A) a modal value $\beta_0 = 0.64$ and $\delta = 0.19$, (B) modal value $\beta_0 = 0.726$ and $\delta = 0.25$ after TE correction, both solved by a least squares algorithm, (C) a modal value 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 ($p > 0.05$).

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 TE_i tends to decrease with TL_i (Figure 2B). For this reason the slopes (β_0) were corrected obtaining a new set of $\log(\frac{B}{P})_i$ vs. 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 β_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 β_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 TL_i 's were estimated through diet composition data. Slopes of $\log(\frac{B}{P})_i$ and $\log TE_i$, with 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

Table 1. Results for the relationships between β_0 (slope of the relationship $\log(B/P)$ vs. TL corrected by β_{TE}) vs. Latitude for selected regions of the world shown in figure 1. No one slope was significantly different of $b=0$ ($p > 0.05$) around $\beta_0 = 0.75$. C.I. is the confidence interval of the β_0 and the coefficient of correlation.

Region	β_0	β_{TE}	+/-95% C.I.	r
1	0.6786	-0.0016	0.0052	0.15
2	0.7763	-0.0043	0.0072	0.27
3	1.2897	-0.0083	0.0253	0.21
4	0.9550	-0.0083	0.0154	0.36
5	0.8250	-0.0082	0.0243	0.18
6	0.6495	-0.0031	0.0038	0.35

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 β_0 , we alternatively applied the Reduced Major Axis (RMA) analysis (Sokal & Rohlf, 1981; Bohonak & van der Linde, 2004) on both, $\text{Log}\left(\frac{B}{P}\right)_i$ and $\text{Log } TE_i$, with TL_i relationships. RMA assumes both variables are measured with error. Results indicate an estimation of $\beta_0=0.756$ ($\delta=0.193$) 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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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; β_{PP} = slope relationship Log(B/P) vs. TL; β_{TE} = slope relationship Log(TE) vs. TL; β_0 = slope of the relationship Log(B/P) vs. TL corrected by β_{TE} . (least squares regression); $\beta_{0,RMA}$ = slope of the relationship Log(B/P) vs. TL corrected by β_{TE} (Reduced Major Axis regression).

Ecosystem name	Longitude	Latitude	Type of ecosystem	Number of functional groups	Number of PP (including detritus)	β_{PP}	β_{TE}	β_0	$\beta_{0,RMA}$	Reference
Region I										
Prince William Sound Ecosystem, Alaska	-146	61	Continental shelf	48	4 (2)	0.6517	-0.0662	0.6949	0.727	(1)
Prince William Sound old model, Alaska	-146	61	Continental shelf	19	2 (1)	0.7354	-0.0637	0.7823	0.809	(2)
North British Columbia 1750, Canada	-136	52	Continental shelf	53	2 (1)	0.2598	-0.1032	0.2866	0.642	(3)
North British Columbia 1900, Canada	-136	52	Continental shelf	53	2 (1)	0.2583	-0.1091	0.2865	0.648	(3)
Alto Golfo de California, Mexico	-113.5	30.5	Continental shelf	29	2 (1)	0.7674	0.0322	0.7921	0.748	(4)
Central Gulf of California, Mexico	-112.5	29.5	Continental shelf	27	1 (1)	0.578	-0.0044	0.5805	0.79	(5)
Southern of Gulf California, Mexico	-105.8333	22.3667	Continental shelf	37	2 (1)	0.3416	0.0172	0.3475	0.548	(6)
Gulf of Nicoya, Costa Rica	-85	10.0167	Continental shelf	21	3 (1)	0.5492	0.0615	0.583	0.905	(7)
Golfo Dulce, Costa Rica	-83.2667	8.5	Continental shelf	21	2 (1)	0.7867	0.1285	0.8878	0.932	(8)
Monterey Bay, United States	-122	37	Bay	16	3 (1)	0.7021	-0.071	0.752	0.725	(9)
La Paz Bay, Mexico	-110.5	24.5	Bay	22	2 (1)	0.5318	-0.0263	0.5458	0.612	(10)
Rivers Inlet 1950, Canada	-128	51.3333	River	32	2 (1)	0.5662	-0.174	0.653	0.597	(11)
Rivers Inlet 1990, Canada	-128	51.3333	River	32	2 (1)	0.5626	-0.1461	0.6448	0.602	(11)
Huizache-Caimanero, Mexico	-106.05	23	Coastal lagoon	26	2 (1)	0.6528	-0.0754	0.702	0.686	(12)
Sharks in Central Pacific	-150	40	Oceanic	22	1 (1)	0.6132	-0.2244	0.7508	0.484	(13)
Region II										
Campeche Sound, Mexico	-93	19	Continental shelf	25	2 (1)	0.5152	-0.0876	0.5603	0.657	(14)
Northern Gulf of St. Lawrence, Canada	-63	48.5	Continental shelf	32	1 (1)	0.5911	-0.0183	0.6019	0.575	(15)
Seagrass in St. Marks, United States	-84.5	30	Bay	49	5 (1)	0.2889	-0.2218	0.353	0.686	(16)
Bahia Ascension, Mexico	-87.5	19.75	Bay	19	2 (1)	0.763	-0.0879	0.83	0.853	(17)
Celestun Mangrove, Mexico	-90.25	20.75	Coastal lagoon	19	2 (1)	0.4079	-0.1576	0.4722	0.663	(18)
Terminos Lagoon, Mexico	-91.1667	18.3333	Coastal lagoon	16	2 (1)	0.7912	0.0949	0.8663	1.047	(19)
Loos Key National Marine Sanctuary, United States	-81.4	24.5333	Coral reef	20	2 (1)	0.4467	-0.1969	0.5347	0.721	(20)
Coral Reef Mexican Caribbean	-86	21	Coral reef	18	2 (1)	0.4518	-0.2789	0.5778	0.562	(21)
Lake Ontario, Canada	-78.5	43.5	Lake	14	1 (1)	0.6086	-0.0626	0.6467	0.752	(22)
Upwelling Gulf of Salamanca, Colombia	-74.5	11.0833	Continental shelf	18	2 (1)	0.6006	0.0441	0.6271	0.637	(23)
Weat Greenland	-55	64	Continental shelf	12	1 (1)	0.5034	0.0797	0.5435	0.657	(24)
Campeche Sound, Mexico	-91.5	20	Continental shelf	19	1 (1)	0.6469	-0.0796	0.6984	0.736	(25)
Terminos Lagoon, Mexico	-91.5	18.5	Continental shelf	20	2 (1)	0.8613	0.0245	0.8824	1.047	(26)
Mandinga Lagoon, Mexico	-96	19	Coastal lagoon	20	1 (1)	0.8523	-0.5165	1.2925	0.481	(27)
Tampamachoco Lagoon, Mexico	-97.5	21	Coastal lagoon	23	2 (1)	0.4242	-0.1662	0.4947	0.484	(28)
Celestun Lagoon, Mexico	-90.5	21	Coastal lagoon	16	2 (1)	0.6187	0.0195	0.6307	0.808	(29)

Annex. Continued.

Ecosystem name	Longitude	Latitude	Type of ecosystem	Number of functional groups	Number of PP (including detritus)	β_{PB}	β_{TE}	β_0	$\beta_{0,RMA}$	Reference
Region III										
Iceland 1950	-11	62	Continental shelf	24	2 (1)	0.808	-0.0876	0.8788	0.777	(30)
Seine Estuary, France	0.1667	49.4417	Coastal lagoon	15	2 (1)	0.5473	-0.2172	0.6662	0.829	(31)
Lagoon of Venice, Italy	12.5	45.5	Coastal lagoon	16	2 (1)	0.5443	-0.1148	0.6068	0.836	(32)
Gironde Estuary, France	0	45	Coastal lagoon	18	2 (1)	0.9351	0.0223	0.956	1.502	(33)
Etang de Thau, France	3.5	43.5	Coastal lagoon	11	2 (1)	0.4755	0.1567	0.55	0.777	(34)
Orbetello Lagoon, Italy	10.5	43	Coastal lagoon	12	2 (1)	0.6486	-0.1473	0.7442	0.693	(35)
Garonne River, France	1.5	44	River	10	2 (1)	0.8197	-0.8516	1.5178	0.093	(36)
Lake Aysdat, France	6	45.5	Lake	11	2 (1)	0.787	0.0473	0.8242	0.669	(37)
Ria Formosa lagoonal system, Portugal	-7.8	37.0333	Reservoir	14	1 (1)	1.2186	-0.0686	1.3022	0.894	(38)
Region IV										
Baltic Sea	20	60	Oceanic	16	2 (1)	0.782	-0.1419	0.893	0.816	(39)
Region V										
Lake Kinneret, Israel	35.5	33	Lake	14	2 (1)	0.585	-0.2667	0.741	1.008	(40)
Lake Turkana 1973, Kenya	36.5	4.5	Lake	8	1 (1)	0.7669	-0.2898	0.9892	0.643	(41)
Lake Turkana 1987, Kenya	36.5	4.5	Lake	8	1 (1)	0.7675	-0.3224	1.015	0.604	(41)
Lake George, Uganda	30.2	0	Lake	14	2 (1)	0.6739	0.0406	0.7012	0.958	(42)
Lake Victoria, Kenya	34.5	-1	Lake	16	2 (1)	0.6889	-0.166	0.8033	0.782	(43)
Lake Tanganyica, Africa	30	-7	Lake	7	1 (1)	0.8654	-0.028	0.8896	0.846	(44)
Lake Kariba, Zimbabwe	29	-16.5	Lake	10	3 (1)	0.6669	-0.2188	0.8128	0.917	(45)
Lake Malawi	35	-9.5	Lake	9	1 (1)	1.1651	-0.5119	1.7615	0.658	(46)
Sri Lankan Reservoir, Sri Lanka	35.3333	10.75	Reservoir	17	4 (1)	0.6517	0.1129	0.7253	1.267	(47)
Region VI										
Brunei Darussalam, Philippines	114	5	Continental shelf	13	1 (1)	0.6865	-0.1483	0.7883	0.732	(48)
Coast of Sarawak, Malaysia	112.5	4.8333	Continental shelf	29	2 (1)	0.6245	-0.0914	0.6816	0.741	(49)
Coast of Sabah, Malaysia	112.5	4.8333	Continental shelf	29	2 (1)	0.5432	-0.0659	0.579	0.658	(49)
Kuosheng Bay, Taiwan	121.6667	25.2167	Bay	17	2 (1)	0.2796	-0.1168	0.3123	1.138	(50)
San Miguel Bay, Philippines	123	14	Bay	16	1 (1)	0.6384	0.0361	0.6615	0.755	(51)
San Pedro Bay, Philippines	125	11.0917	Bay	16	2 (1)	0.3798	0.1122	0.4224	0.546	(52)
Bolinao Coral Reef, Philippines	119.9167	16.4167	Coral reef	26	3 (1)	0.2825	0.0242	0.2893	0.614	(53)
Laguna de Bay 1820, Philippines	121.5	14.5	Lake	30	2 (1)	0.8666	-0.1297	0.979	0.652	(54)
Laguna de Bay 1920, Philippines	121.5	14.5	Lake	26	2 (1)	0.8694	0.1759	1.0223	0.874	(54)
Laguna de Bay 1950, Philippines	121.5	14.5	Lake	21	2 (1)	0.8308	0.0136	0.8421	0.719	(54)
Laguna de Bay 1968, Philippines	121.5	14.5	Lake	16	2 (1)	0.6789	0.1975	0.813	0.548	(54)
Laguna de Bay 1980, Philippines	121.5	14.5	Lake	17	2 (1)	0.8196	0.2024	0.9855	0.763	(54)
Laguna de Bay 1990, Philippines	121.5	14.5	Lake	20	2 (1)	0.7523	0.2787	0.962	0.801	(54)
Region VII										
Brunei Darussalam, Philippines	114	5	Continental shelf	13	1 (1)	0.6865	-0.1483	0.7883	0.732	(48)
Coast of Sarawak, Malaysia	112.5	4.8333	Continental shelf	29	2 (1)	0.6245	-0.0914	0.6816	0.741	(49)
Coast of Sabah, Malaysia	112.5	4.8333	Continental shelf	29	2 (1)	0.5432	-0.0659	0.579	0.658	(49)
Peninsula Malaysia, Malaysia	98	1	Continental shelf	15	1 (1)	0.4885	0.0257	0.5011	0.62	(55)
North Coast of Central Java, Indonesia	109	-6.5	Continental shelf	27	2 (1)	0.4502	0.0663	0.4801	0.961	(56)
Kuosheng Bay, Taiwan	121.6667	25.2167	Bay	17	2 (1)	0.2796	-0.1168	0.3123	1.138	(50)
San Miguel Bay, Philippines	123	14	Bay	16	1 (1)	0.6384	0.0361	0.6615	0.755	(51)
San Pedro Bay, Philippines	125	11.0917	Bay	16	2 (1)	0.3798	0.1122	0.4224	0.546	(52)
Bohai Sea, China	120	39	Bay	13	1 (1)	0.5968	-0.0097	0.6026	0.626	(57)

Annex. Continued.

Ecosystem name	Longitude	Latitude	Type of ecosystem	Number of functional groups	Number of PP (including detritus)	β_{PB}	β_{TE}	β_0	$\beta_{0,RMA}$	Reference
Bay of Bengal, Bangladesh	91	21	Bay	15	1 (1)	0.6806	0.1966	0.8144	0.533	(58)
Bolinao Coral Reef, Philippines	119.9167	16.4167	Coral reef	26	3 (1)	0.2825	0.0242	0.2893	0.614	(53)
Northern Great Barrier Reef, Australia	150	-16	Coral reef	25	2 (1)	0.6528	-0.133	0.7397	0.913	(59)
Central Great Barrier Reef, Australia	147	-18	Coral reef	25	2 (1)	0.6869	-0.131	0.7771	0.899	(60)
Uvea Atoll Loyalty Islands, New Caledonia	166.5	-20.5	Coral reef	25	3 (2)	0.7128	-0.102	0.7853	0.743	(61)
Central Pacific Ocean	170	20	Oceanic	26	1 (1)	0.6399	-0.0207	0.6532	0.7	(62)
Subantarctic water Plateau, New Zealand	170	-50	Oceanic	19	1 (2)	0.7164	-0.103	0.7902	0.705	(63)
Laguna de Bay 1990, Philippines	121.5	14.5	Lake	20	2 (1)	0.7523	0.2787	0.962	0.801	(54)
Models used for BP vs TL but not for latitudinal analysis										
Central Chile 1992, Chile	-73	-33	Continental shelf	21	1 (1)	0.6288	-0.165	0.7326	0.607	(64)
Central Chile 1998, Chile	-73	-33	Continental shelf	21	1 (1)	0.5728	-0.183	0.6778	0.701	(64)
Iceland's fisheries, Iceland	-25	62.5	Continental shelf	21	1 (1)	0.9818	-0.147	1.126	1.009	(65)
South Orkneys/Georgia, Antarctic Territory	-34	-50	Continental shelf	30	1 (1)	0.7456	-0.131	0.8436	0.682	(66)
Northern Benguela, Namibia	12	-22	Continental shelf	24	1 (2)	0.0269	-0.05	0.0282	0.705	(67)
Eastern Bering Sea, United States	-163.5	52	Continental shelf	38	1 (3)	0.7134	-0.194	0.852	0.707	(68)
Western Bering Sea, United States	-179.5	65	Continental shelf	36	1 (3)	0.7002	-0.147	0.8031	0.812	(68)
Venezuela shelf, Venezuela	-62	10	Continental shelf	16	2 (1)	0.7141	-0.108	0.7909	0.732	(69)
Southern Brazil, Brazil	-51	-32.5	Continental shelf	13	1 (1)	0.7557	0.1855	0.8959	0.989	(70)
Barents Sea 1990	40	80	Continental shelf	41	2 (3)	0.669	-0.138	0.7613	0.813	(71)
Barents Sea 1995	40	80	Continental shelf	41	2 (3)	0.672	-0.119	0.752	0.788	(71)
Southwest coast of India, India	75	13	Continental shelf	11	1 (1)	0.6101	0.2447	0.7594	0.815	(72)
Tongo Bay, Chile	-71.5	-30.2417	Bay	17	2 (1)	0.606	0.0074	0.6105	0.9	(73)
Bay of Somme, France	1.55	50.2333	Bay	9	2 (1)	0.7796	-	-	-	(74)
Maputo bay, Mozambique	33	-26	Bay	10	2 (1)	0.7397	-0.275	0.9431	0.719	(75)
Sandy Barrier Lagoon Chiku, Taiwan	124.0667	23.1333	Coastal lagoon	13	2 (1)	0.9072	0.1296	1.0247	1.491	(78)
Sakumo Lagoon, Ghana	0.0333	5.6167	Coastal lagoon	13	1 (1)	0.8797	-	-	-	(76)
Mangrove in Celestun Lagoon, Mexico	-90.25	20.75	Coastal lagoon	19	2 (1)	0.4059	-0.079	0.438	0.545	(77)

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