

Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants

Andrea Belgrano,^{1*} Andrew P. Allen,¹ Brian J. Enquist,^{2,3} and James F. Gillooly¹

¹Department of Biology, University of New Mexico, 167 Castetter Hall, Albuquerque, NM 87131-1091 USA.

²Department of Ecology and Evolutionary Biology, University of Arizona, BioSciences West, Tucson, AZ 85721 USA.

³Center for Applied Biodiversity Science, 1919 M. St. NW, Suite 600, Washington, DC 20036 USA.

*Correspondence:

E-mail: belgrano@unm.edu

Abstract

A primary goal of macroecology is to identify principles that apply across varied ecosystems and taxonomic groups. Here we show that the allometric relationship observed between maximum abundance and body size for terrestrial plants can be extended to predict maximum population densities of marine phytoplankton. These results imply that the abundance of primary producers is similarly constrained in terrestrial and marine systems by rates of energy supply as dictated by a common allometric scaling law. They also highlight the existence of general mechanisms linking rates of individual metabolism to emergent properties of ecosystems.

Keywords

Allometry, energetic equivalence, marine phytoplankton, metabolic scaling theory, population abundance, terrestrial plants.

Ecology Letters (2002) 5: 611–613

The scaling of organismal form and function is a central feature of biological diversity (Brown & West 2000). Empirical data indicate that the rate of resource use by an individual plant, Q , is proportional to its metabolic rate, B , and increases with its body size, M , as $Q \propto B \propto M^{3/4}$ (Enquist *et al.* 1998). This observation has been attributed to the fractal-like geometry of biological distribution networks (West *et al.* 1997), although alternative views have also been expressed (Whitfield 2001). Empirical data also indicate that for terrestrial plants, total abundance per unit area, N , declines with increasing body size as $N \propto M^{-3/4}$ (Enquist *et al.* 1998). This implies that N is regulated such that the total energy flux of the population, Q_{Tot} , is invariant with respect to body size and equal to the rate of limiting resource supply, R , from the environment ($R = Q_{Tot} = N \times Q \propto M^{-3/4} \times M^{3/4} = M^0$) (Enquist *et al.* 1998). Species of vastly different size are thus 'energetically equivalent' in terms of population energy flux (Damuth 1981).

Recent work demonstrates that unicellular algae and vascular plants adhere to the same allometric relationship for rates of individual biomass production, G , where $G \propto M^{3/4}$ (Niklas & Enquist 2001). This relationship is predicted by allometric theory under the assumption that $G \propto Q \propto B \propto M^{3/4}$. The equations above therefore predict that the two groups should also share a common power function relating abundance to body size.

We test this prediction by combining a global compendium of terrestrial plant size and abundance (Enquist *et al.* 1998; Enquist & Niklas 2002) with an 11-year survey (1986–95) of marine phytoplankton in Sweden (Belgrano *et al.* 1999). The maximum abundance of marine phytoplankton (black points, Fig. 1) is well predicted by the power function describing the maximum abundance–body size relationship for terrestrial plants ($N = 948 \times M^{-0.757}$, $n = 365$, 95% confidence interval (CI) for the normalization constant: 796 to 1130, 95% CI for the exponent: -0.773 to -0.741). Indeed, if we fit the same model using maximum abundance data for the terrestrial plants and phytoplankton combined, the updated parameter estimates are well within the 95% confidence limits of those calculated for the terrestrial plant model ($N = 1020 \times M^{-0.765}$, $n = 376$). The implication is that maximum plant abundance is similarly constrained in terrestrial and marine systems by energy supply.

The $-3/4$ -power scaling relationship observed here between maximum abundance and body size contrasts with previous work conducted in aquatic systems (Duarte *et al.* 1987; Cyr 2000). These other studies showed a steeper slope (i.e. $N \propto M^{-\alpha}$, $\alpha > 3/4$), but are not comparable to the present study because they aggregated data across trophic groups. Steeper abundance–body size relationships may exist for heterotrophic consumers than for autotrophs because of allometric relationships between predator size,

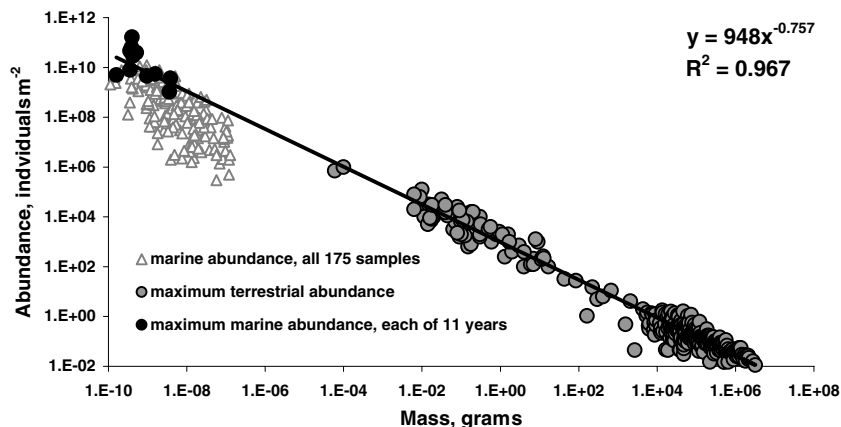


Figure 1 Relationship between maximum plant abundance and average body size for terrestrial plants (grey circles) and marine phytoplankton (black circles and grey triangles). The terrestrial plant data included estimates of maximum abundance (individuals m^{-2}) and body size (g) for diverse plants including woody gymnosperms and angiosperms (Enquist & Niklas 2002) and non-woody plants (Enquist *et al.* 1998). The maximum of total phytoplankton abundance was calculated for each of 11 years (black circles) based on a total of 175 samples (grey circles) taken approximately once each month. Total phytoplankton abundance per unit area was calculated based on average phytoplankton abundance per unit volume over depths of 0–20 m. For each sample, the average body mass across all individuals was calculated based on estimates of phytoplankton size (Edler 1977) for the 40 species sampled during the survey. The model in the figure was fitted to the terrestrial plant data using reduced major-axis regression (Isobe *et al.* 1990) after applying a logarithmic transformation to both variables.

prey size, and productivity of the prey base (Carbone & Gittleman 2002).

We note that phytoplankton abundance varies by more than 2 orders of magnitude among samples even after controlling for body size (grey triangles, Fig. 1). This is consistent with other studies showing that phytoplankton abundance and body size exhibit pronounced intra-annual variation in response to changes in nutrient supply (Lindahl *et al.* 1998) and vertical mixing of the water column (Rodríguez *et al.* 2001). Nevertheless, our results clearly show that marine phytoplankton and terrestrial plants adhere to the same power function relating maximum abundance to body size. This result, combined with previous work on rates of individual biomass production (Niklas & Enquist 2001), suggests that maximum rates of productivity are identical for terrestrial and marine ecosystems.

ACKNOWLEDGEMENTS

AB, APA and JFG acknowledge the support of an NSF Biocomplexity grant (DEB-0083422). BJE was supported by an NSF Career award (DEB-133974) and a Fellowship from the Center for Applied Biodiversity Science, Conservation International. We thank James H. Brown, Nils Chr. Stenseth, and Paul Falkowski for commenting on earlier versions of the manuscript, and Odd Lindahl for providing the phytoplankton data. We are also grateful for the constructive comments of two anonymous referees and Pablo Marquet.

REFERENCES

- Belgrano, A., Lindahl, O. & Hernroth, B. (1999). North Atlantic Oscillation (NAO) primary productivity and toxic phytoplankton in the Gullmar Fjord, Sweden (1985–96). *Proc. Roy. Soc. Lond. B*, 266, 425–430.
- Brown, J.H. & West, G.B. (2000). *Scaling in Biology*. Oxford University Press, New York.
- Carbone, C. & Gittleman, J.L. (2002). A common rule for the scaling of carnivore density. *Science*, 295, 2273–2276.
- Cyr, H. (2000). Individual energy use and the allometry of population density. In: *Scaling in Biology* (eds Brown, J.H. & West, G.B.). Oxford University Press, New York, pp. 267–295.
- Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.
- Duarte, C.M., Agusti, S. & Peters, R.H. (1987). An upper limit to the abundance of aquatic organisms. *Oecologia*, 74, 272–276.
- Edler, L. (1977). Phytoplankton and primary production in the sound. In: *Department of Marine Botany*. University of Gothenburg, Gothenburg, p. 82.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998). Allometric scaling of plant energetics and population density. *Nature*, 395, 163–165.
- Enquist, B.J. & Niklas, K.J. (2002). Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, 295, 1517–1520.
- Isobe, T., Feigelson, E.D., Akritas, M.G. & Babu, G.J. (1990). Linear regression in astronomy I. *Astrophys. J.*, 364, 104–113.
- Lindahl, O., Belgrano, A., Davidsson, L. & Hernroth, B. (1998). Primary production, climatic oscillations and physico-chemical processes: the Gullmar Fjord data-set (1985–96). *ICES J. Mar. Sci.*, 55, 723–729.

- Niklas, K.J. & Enquist, B.J. (2001). Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Nat. Acad. Sci. USA*, 98, 2922–2927.
- Rodriguez, J., Tintore, J., Allen, J.T., Blanco, J.M., Gomis, D., Reul, A. *et al.* (2001). Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature*, 410, 360–363.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126.
- Whitfield, J. (2001). All creatures great and small. *Nature*, 413, 342–344.
- Editor, P. A. Marquet
Manuscript received 3 May 2002
First decision made 15 May 2002
Manuscript accepted 30 May 2002