

Received 1 September 1980; accepted 26 January 1981.

1. Hoering, T. C. in *Researches in Geochemistry* (ed. Abelson, P. H.) (Wiley, New York, 1967).
2. Rumble, D., Hoering, T. C. & Grew, E. S. *Yb. Carnegie Instn Wash.* 76, 623 (1977).
3. McKirdy, D. M. & Powell, T. G. *Geology* 2, 591 (1974).
4. Barghoorn, E. S., Knoll, A. H., Dembicki, H. & Meinschein, W. G. *Geochim. cosmochim. Acta* 41, 425 (1977).
5. Smith, J. W., Schopf, J. W. & Kaplan, I. R. *Geochim. cosmochim. Acta* 34, 659 (1970).
6. Degens, E. T. in *Organic Geochemistry* (eds Eglinton, G. & Murphy, M. T. J.) 304 (1969).
7. Galimov, E. in *Kerogen Insoluble Organic Matter from Sedimentary Rocks* (ed. Durand, B.) 271 (Edition Technique, Paris, 1980).
8. Goodwin, A. M., Monster, J. & Thode, H. G. *Econ. Geol.* 71, 870 (1976).
9. Krogh, T. E. & Davis, G. L. *Yb. Carnegie Instn Wash.* 70, 241 (1971).
10. Nunes, P. D. & Thurston, P. D. *Can. J. Earth Sci.* 17, 710 (1980).
11. Hoering, T. C. *Yb. Carnegie Instn Wash.* 61, 190 (1962).
12. Cloud, P. E. Jr, Gruner, J. W. & Hagen, H. *Science* 148, 1713 (1965).
13. Oehler, D. Z., Schopf, I. W. & Kvenvolden, K. A. *Science* 175, 1246 (1972).
14. Perry, E. C. Jr, Tan, F. C. & Morey, G. B. *Econ. Geol.* 68, 1110 (1973).
15. Schidlowski, M., Appel, P. W. U., Eichmann, R. & Junge, C. E. *Geochim. cosmochim. Acta* 43, 189 (1979).
16. Eichmann, R. & Schidlowski, M. *Geochim. cosmochim. Acta* 39, 585 (1975).
17. Schoell, M. & Hartmann, M. *Mar. Geol.* 14, 1 (1973).
18. Tietze, K., Geyh, M., Müller, H., Schröder, L. & Stahl, W. *Geol. Rdsch.* 69, 452-472 (1980).
19. Brooks, T. M., Bright, T. J., Bernard, B. B. & Schwab, C. R. *Limnol. Oceanogr.* 24, 735 (1979).
20. Sackett, W. M. *et al. Earth planet. Sci. Lett.* 44, 73 (1979).
21. Coleman, D. D., Risatti, J. & Schoell, M. (in preparation).
22. Barnes, R. O. & Goldberg, E. D. *Geology* 4, 297 (1976).
23. Martens, C. S. & Berner, R. A. *Limnol. Oceanogr.* 22, 10 (1977).
24. Fallon, R. D., Havrils, S., Hanson, R. S. & Brock, T. D. *Limnol. Oceanogr.* 25, 357 (1980).

Population density and body size in mammals

John Damuth

Committee on Evolutionary Biology, University of Chicago,
1103 E. 57 Street, Chicago, Illinois 60637, USA

There seems to be an inverse relationship between the size of an animal species and its local abundance. Here I describe the interspecific scaling of population density and body mass among mammalian primary consumers (herbivores, broadly defined). Density is related approximately reciprocally to individual metabolic requirements, indicating that the energy used by the local population of a species in the community is independent of its body size. I suggest that this is a more general rule of community structure.

Figure 1 shows the logarithm of mean population density plotted against the logarithm of mean adult body mass for 307 species of mammalian primary consumers. As far as possible, the density values represent 'ecological' densities, that is, those which apply to the habitat area actually used by the species. The

relationship is linear, with a slope of -0.75 , and species densities seem to be restricted to varying within about one order of magnitude from the value predicted by the regression line.

This analysis combines data from a wide variety of habitats throughout the world, and it is important that we know whether this overall pattern accurately reflects that found within individual communities; few, if any, mammal communities have been completely studied. To obtain a representative sample, I extracted from my data those sets yielding densities of three or more species within the same habitat type; these 'constructed' communities are shown in Table 1, with regression statistics. They include representatives of almost the whole range of habitat structures and primary productivity levels encountered by terrestrial mammals. None of the individual slopes, which vary from -0.56 to -0.95 , differ significantly from -0.75 , and Levene's test¹ and an analysis of covariance² reveal no significant differences in variance about the regression, in slope, or in intercept. Pooling the data from the communities gives an estimated slope of -0.70 , which is not significantly different from the value obtained for the overall regression (*t*-test). Thus, the overall trend gives a reasonable representation of that which we are likely to find within individual communities.

Knowledge of population density scaling in communities allows us to consider the relative energy use of species among primary consumers of different sizes. Individual basal metabolic requirements are related to body mass by the power of 0.75 (refs 3, 4). Estimates of the metabolic requirements of free-living mammals in natural habitats roughly parallel basal requirements, but at a higher level, varying between ~ 1.5 and 3.0 times basal values⁵⁻¹³. Thus they will also be related to body mass by the power of ~ 0.75 . The energy used by the local population of a species equals the population density (*D*) multiplied by individual metabolic requirements (*R*), which yields the following relationship to body mass (*W*): $DR \propto W^{-0.75}W^{0.75}$. The exponents of *W* cancel each other, which gives the important result that the amount of energy that a species population uses in the community is independent of its body size. No mammal herbivore species, on an ecological time scale, has an energetic advantage over any other solely as a result of size differences.

There are two important corollaries of this relationship. First, because secondary productivity for a given amount of assimilated energy is independent of body size in mammals (Kleiber's Law)³, it follows from the above that the secondary productivity of a herbivore species' local population, and hence the energy that it yields to the next higher trophic level, is also independent of body size. Second, the standing-crop biomass of a species (population density multiplied by body mass) is positively related to body mass by the ~ 0.25 power; this is a

Table 1 Habitat types and constructed communities

Community/habitat type	a	s.e.	r	b	n
Sonoran desert, USA	-0.63	0.16	-0.76	3.37	14
Mesquite grassland, USA and Mexico	-0.56	0.086	-0.95	3.73	7
Boreal and subalpine forest, N. America	-0.79	0.080	-0.95	4.43	12
Lowland tropical rainforest, Malaysia	-0.60	0.089	-0.90	2.61	13
Transvaal lowveld (woodland-savanna), S. Africa	-0.61	0.089	-0.93	3.78	10
Mixed temperate forest, Poland	-0.79	0.080	-0.97	4.33	8
Temperate grassland, USA	-0.67	0.13	-0.92	3.28	7
Tropical grassland, Rwenzori N.P., Uganda	-0.79	0.17	-0.81	3.59	13
Tropical grassland, Sri Lanka*	-0.79	0.19	-0.92	4.59	5
Ichu grassland, Altiplano, Peru*	-0.82	0.34	-0.99	3.93	4
High arctic tundra, Canada*	-0.95	0.21	-0.96	4.71	4
Sub-arctic birch forest and meadows, Norway*	-0.83	0.72	-0.99	4.41	3
Southern pine-hardwood forest, USA*	-0.91	0.46	-0.89	4.23	3
Northern hardwoods, USA*	-0.57	0.11	-0.98	3.11	3
Oaks and chapparal, USA*	-0.72	0.021	-0.99	4.83	3
Means of statistics	-0.74	0.20	-0.93	3.93	—
Pooled data from above regressions	-0.70	0.040	-0.86	3.71	109

Statistics are for standard least-squares regression equations: $\log D = a(\log W) + b$; s.e., standard error of the slope (a); r, correlation coefficient; n, number of species. Note that in the pooled regression, as some species are found in more than one habitat type, $n = 109$ includes only 92 separate species.

* Due to small sample size and/or a single point at one end of the size range, the individual values for these regressions are not very reliable.

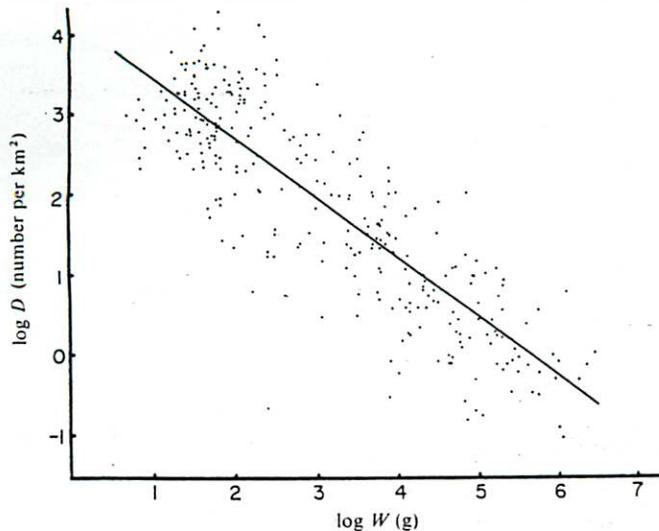


Fig. 1 Population density (D) compared with the mean adult body mass (W) for 307 mammal primary consumers; each point represents one species. Density values for each species are the mean of the means from each locality from which data were reported for the particular species. (Data are from the literature for the years 1950–79, derived from 115 journals and numerous books, ~650 references in all.) The line represents the least-squares regression line, $\log D = -0.75 (\log W) + 4.23$; $r = -0.86$, standard error of the slope = 0.026.

quantitative measure of a qualitative relationship that has been known for some time but only sporadically appreciated¹⁴. Species of small mammals are able to produce, on average, the same amount of biomass over time as do species of large mammals, whereas at a given moment their standing-crop biomass is considerably less, because the population turnover rates and individual growth rates per unit weight of small species are much greater^{15–17}.

The widespread occurrence of an approximately reciprocal relationship between population density and individual metabolic requirements among mammalian herbivores suggests that a general principle is involved. The independence of species energy control and body size revealed by this reciprocal relationship implies that random environmental fluctuations and interspecific competition act over evolutionary time to keep energy control of all species within similar bounds. It is unlikely that the occurrence of competition among species of different body sizes is restricted to herbivorous mammals. Along with the ubiquity of allometric scaling of metabolic rate with body size⁴, this suggests that a reciprocal relationship, and particularly a value of ~ -0.75 , characterizes a broader range of taxa and trophic levels. These points will be discussed more fully elsewhere.

I thank I. L. Heisler, V. C. Maiorana, D. M. Raup, V. L. Roth and L. Van Valen for comments, and acknowledge support from the University of Chicago and Field Museum of Natural History.

Received 6 October 1980; accepted 27 January 1981.

1. Van Valen, L. *Evol. Theory* **4**, 33–44 (1978).
2. Brownlee, K. A. *Statistical Theory and Methodology in Science and Engineering* 2nd edn (Wiley, New York, 1965).
3. Kleiber, M. *The Fire of Life* 2nd edn (Krieger, New York, 1975).
4. Hemmingen, A. M. *Rep. Steno meml Hosp.* **4**, 7–58 (1950).
5. Brody, S. *Bioenergetics and Growth* (Reinhold, New York, 1945).
6. Chew, R. M. & Chew, A. E. *Ecol. Monogr.* **40**, 1–21 (1970).
7. Gessaman, J. A. in *Ecological Energetics of Homeotherms* (ed. Gessaman, J. A.) (Utah University Press, 1973).
8. King, J. R. in *Avian Energetics* (ed. Paynter, R. A. Jr) (Nuttall Ornithological Club, Massachusetts, 1974).
9. McKay, G. M. *Smithson. Contr. Zool.* **125**, 1–113 (1973).
10. Moen, A. N. *Wildlife Ecology: an Analytical Approach* (Freeman, San Francisco, 1973).
11. Mullen, R. K. *Comp. Biochem. Physiol.* **39**, 379–390 (1971).
12. Mullen, R. K. & Chew, R. M. *Ecology* **54**, 633–637 (1973).
13. Nagy, K. A. & Milton, K. *Ecology* **60**, 475–480 (1979).
14. Odum, E. P. *Fundamentals of Ecology* 3rd edn (Saunders, Philadelphia, 1971).
15. Fenichel, T. *Oecologia* **14**, 317–326 (1974).
16. Western, D. *Afr. J. Ecol.* **17**, 185–204 (1978).
17. Case, T. J. *Q. Rev. Biol.* **53**, 243–282 (1978).

Competitive ability influences habitat choice in marine invertebrates

Richard K. Grosberg

Department of Biology, Yale University, 260 Whitney Avenue, PO Box 6666, New Haven, Connecticut 06511, USA

Patterns of distribution and abundance of sessile marine epibenthic invertebrates are controlled by three factors: (1) the presence and abundance of larvae which are competent to settle, (2) the choice of settling sites by recruiting larvae, and (3) the biotic and physical events occurring during and after settlement. Although there is much information on the distribution of larvae and seasons of recruitment^{1–3}, substratum selection^{4–6} and post-settlement events^{7–15}, very little is known of the ecological and evolutionary relationships between these factors^{5,16–18}. Natural selection acts on entire life cycles, thus information about these relationships is essential for understanding patterns of recruitment and survival. For example, sessile organisms can modify the course of post-recruitment events by selective settlement and directional growth¹⁹. Here, I present evidence that the larvae of several taxa of marine invertebrates avoid substrata where there is a high probability of death caused by a superior spatial competitor.

I found, as did Grave²⁰, that in the Eel Pond at Woods Hole, Massachusetts (USA), the two compound ascidians *Botryllus schlosseri* (Pallas) Savigny and *Botrylloides leachii* (Savigny) cover, by area, over 50%, and sometimes 100%, of hard substrata during the spring and summer. This period includes the season of recruitment for most other colonizers. Thus, settling larvae are likely to contact a botryllid ascidian at some time during their lives. A common result of contacts between colonists is overgrowth of one organism by another^{21–29}. In this way, overgrowth is a consequence of competition for space (and perhaps other resources³⁰), and therefore can be an important factor in the distribution and abundance of encrusting species.

B. schlosseri is the most successful overgrower (along with *B. leachii*) in the Eel Pond (Table 1) and is rarely overgrown by other species. As it is such an important member of the Eel Pond epibenthic assemblage (considering the post-settlement events of overgrowth and coverage), I investigated the effects of its density on the recruitment of other taxa.

B. schlosseri collected from the Eel Pond were placed in finger-bowls where they released larvae which were then transferred to 10-ml polycarbonate dishes. Two hours after settlement on the sides of the dishes, the juveniles were teased off and re-attached to 5 × 5 cm glass plates. I set up three densities of juvenile *Botryllus* with three replicates of each: (1) 15 regularly spaced *Botryllus* juveniles, with all subsequent botryllid settlement removed daily; (2) 5 regularly spaced *Botryllus* juveniles with all subsequent botryllid recruits removed daily; and (3) no *Botryllus* juveniles with daily removal of all botryllid recruits. Three additional glass plates which initially carried no juveniles, but on which all recruits were allowed to remain, served as controls.

Experimental and control plates were positioned horizontally in a Latin square arrangement³¹ below a floating dock at 1 m depth. The experiment was started on 20 July, 24 h after the larvae had been transplanted. The lower side of each plate (which carried the juvenile *Botryllus*) was censused non-destructively until 28 July on a daily basis—this allowed me to distinguish between failure to settle and all but the earliest post-settlement mortality.

Figure 1 shows the numbers of each species that settled on the glass plates. To determine if there were any differences between each of the three density treatments and the controls, the data for each species were analysed using the null hypothesis that