Testing Size-Abundance Rules in a Human Exclusion Experiment

RICHARD R. STRATHMANN

THE SIZE OF ORGANISMS IS A GOOD PREDICTOR OF THE rates at which they produce and consume materials. Size, as weight or length, is easily measured, and biologists who deal with diverse and poorly known species have therefore seized on scaling relationships of organisms for general quantitative predictions. Their size can also be related to their abundance (*1, 2*), and this relation is especially interesting to ecologists because it extends predictions from individual organisms to natural populations and communities (*3*). Dependence of a property on size is usually expressed by the allometric equation, in which (variable of interest) = a (measure of size)^b. The allometric exponent (b) is usually estimated as the slope of a log-log plot. For size abundance relationships, b has been reported in the neighborhood of -0.75 to -1.0 (*1*), although in some cases no relationship has been found (*4*). The elevation of the line, as measured by a, can also be of interest, for size-abundance relationships, poikilotherms are reported to have higher population densities than homeotherms of the same size (*1*).

A deficiency of this approach is that the underlying causes of these scaling relations are seldom well understood. For size-abundance relationships, this is particularly true for the allometric exponent, b. Confidence in the generality of such relationships depends largely on the extent to which the biological world has been sampled, not on a knowledge of underlying processes. Speculative explanations of the underlying processes are prompted by the value of b, but these hypotheses are seldom adequately tested, and the generality of the measured relations is therefore often in doubt. For size-abundance relationships, explanations have involved limited resources (*2, 4*), predation (*3*), the minimum size for viable populations (*4*), or merely sampling biases (*4*). The arguments linking these phenomena to a particular exponent are not strong. Comparisons of different types of organisms or organisms in different environments have not resolved questions about underlying processes (*3, 4*). Experiments would seem in order, but allometric relations have rarely been tested experimentally. Experiments seem particularly applicable to size-abundance relationships because sizes of populations and the ways in which they interact with one another can be easily manipulated. As a start, one can ask whether size-abundance relationships are changed for an assemblage of organisms when predation or competition are changed (*6*).

An experiment of this sort has changed size and abundance in an intertidal community of organisms by exclusion of people. The impact of human foraging on communities of marine organisms is insufficiently appreciated because controlled experiments are rare. In a series of studies in Chile (*6–8*), people have been excluded from some stretches of coastline while adjacent shores have been left open to foraging. Rocky intertidal shores have been ideal testing grounds for ecological principles because the organisms are sedentary, of small size, and easily removed, added, enclosed, or excluded. Direct and indirect effects of predation and competition have been well demonstrated in numerous field experiments. At the site in Chile, people eat a large predatory snail, which in turn controls the abundance of a mussel which dominates in competition for space on the shore. In the absence of people, the snails increased in density and the percentage of shore occupied by the mussel decreased (*7*). People also harvest a large kelp, and in the absence of people, the kelp are larger (*8*). The changes in populations of harvested organisms produced a cascade of indirect effects that changed the size or abundance of numerous species in this community through changes in the intensity of predation and competition for different populations. Nevertheless, the size-abundance relationships remained the same inside and outside the exclusion sites. The lack of any change in size-abundance relationships during pronounced changes in predation and competition within the community casts doubt on hypotheses that depend solely on one or the other of these processes. The test would be stronger if the hypotheses were more explicit about mechanisms; there is no clear prediction on how far these processes must be shifted before the size-abundance relationship is changed.

There are several pitfalls in testing hypotheses about size-abundance relationships from estimates of allometric coefficients (*4, 5*). One difficulty is that variation about size-abundance regression lines is so great that quite different estimated slopes are not significantly different (*6*). Size is a very rough predictor of abundance in this intertidal community (*6*) and in other assemblages that have been sampled (*1*); many hypotheses on underlying processes could be consistent with the data.

Another difficulty is that estimates of b from ordinary least squares regression models can be inappropriate for describing relationships between two variables. Reduced major axis regression has been recommended for many cases (*5, 9*), with the choice depending partly on the nature of variation in the data and partly on the relation that one is trying to describe or predict. With reduced major axis regression, the slopes of reported size-abundance relationships are steeper (*5*), closer to -1 than -0.75. This is true also for the intertidal organisms of the human exclusion experiment (*10*), for which the slopes steepen to -1.08 to -1.22. They are still in agreement with the revised estimates of previous studies, but those who look to the allometric exponent for inspiration about processes underlying the allometric relations must carefully examine their choice of regression models (*5*).

There are formidable methodological difficulties in obtaining comparable samples from very different environments and in interpreting allometric exponents for size-abundance relationships. Experiments on selected natural communities can circumvent these difficulties and should provide greater insight into the processes that produce such relationships.

Department of Zoology and Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250.

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10. Exponents from ordinary least squares regression in (*6*) were converted to exponents from reduced major axis by dividing b by r.