



CHICAGO JOURNALS



The University of Chicago

Body Size and Consumer-Resource Dynamics

Author(s): P. Yodzis and S. Innes

Reviewed work(s):

Source: *The American Naturalist*, Vol. 139, No. 6 (Jun., 1992), pp. 1151-1175

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2462335>

Accessed: 08/11/2012 11:33

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

BODY SIZE AND CONSUMER-RESOURCE DYNAMICS

P. YODZIS* AND S. INNES†

*Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada;

†Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

Submitted September 5, 1990; Revised June 13, 1991; Accepted July 25, 1991

Abstract.—"Plausible" consumer-resource models, based on energetic reasoning and allometric empiricism, are formulated and their dynamics investigated. Most of the parameters in these models are determined by the body sizes and metabolic categories (endotherm, vertebrate ectotherm, invertebrate ectotherm, or plant) of the populations in question. The remaining parameters have clear biological meanings. The intent of these models is to provide maximum realism from minimum data when needed because of constraints of time or of resources for empirical research. The models also demonstrate the influence of physiological power and body size on consumer-resource dynamics. For a given metabolic type, we define *ecological scope* as the ratio of maximal ingestion rate to respiration rate. Invertebrate ectotherms have greater ecological scope than do vertebrate ectotherms, which have greater scope than do endotherms. Greater ecological scope implies ability to subsist on scarcer resources and a tendency to more stable dynamics. Changes in dynamics associated with increased resource carrying capacity K (the "paradox of enrichment") are investigated. Robust limit cycles (sustained oscillations) require a Type III functional response, but even in this case the cycles quickly "implode" (with respect to changes in K) to extremely small densities if the resource-consumer body mass ratio is too high. Estimates are given for resource-consumer body mass ratios that permit robust limit cycles, and some pertinent data are discussed. An analytic expression for the periods of limit cycles is derived. In terms of body mass, the periods scale as (consumer body mass)^{1/8} (resource body mass)^{1/8}.

Population modeling, if we are to apply it to the natural world, is beset with difficulties. There is the "curse of dimensionality" (if we may borrow a term from the theory of dynamic programming, which is similarly afflicted [Bellman 1957]): most populations in nature interact with many others, and the difficulty of working with models increases very rapidly as the number of interacting populations increases. Population models are also plagued with a surfeit of parameters. Even when we can for some purpose reasonably neglect all but a few interacting populations, even the simplest models contain so many parameters as to complicate the analysis and obscure application to nature. Moreover, the results of theoretical calculations can be alarmingly sensitive to parameter values (Yodzis 1988). This article is in part an attempt to address the "plague of parameters" in population modeling.

Two attitudes toward parameters are prevalent in the literature. One approach is to make detailed measurements on some particular population and to tailor a model for that population. The other is to leave the values of the parameters largely open, to create abstract models with very weak constraints, such as posi-

tivity, on the parameters. These represent extreme positions on a "tactical-strategic" spectrum of population modeling (Holling 1966). The one suffers from a lack of generality and a need for very extensive resources for research, the other from a remoteness from nature.

We develop here a treatment of parameters that is intermediate between these two extremes. We use energetic reasoning and allometric empiricism to construct models that might be termed *plausible*. Our approach makes it possible, given some guild of interacting populations with specified body sizes and metabolic categories (endotherm, vertebrate ectotherm, invertebrate ectotherm, or plant), to write down a simple, basic model embodying the trophic aspects of the interaction with a relatively small number of undetermined parameters.

Because we derive our parameters from empirical allometric scaling relationships of the form am^b , with a and b constants and m the body mass of an individual, these models can be used to explore the influence of body size and physiological power on population dynamics, a subject of much recent interest (Sheldon et al. 1973; Peters 1983; Schmitz and Lavigne 1983; Calder 1984; Ulanowicz and Platt 1985; Dickie et al. 1987).

If our models are intermediate in their approach to parameters, they are firmly strategic in form. Many details such as age structure and individual variation are neglected; the form of our basic equations (8) and (9) will be familiar to readers of strategically oriented texts (e.g., May 1981a; Yodzis 1989). But our approach moves these models somewhat away from the abstract, qualitative realm of conventional strategic modeling and toward a more concrete, quantitative realm. At the very least, we are able to exclude biologically impossible parameter combinations.

We illustrate our method here in the context of consumer-resource interactions. To be sure, in such a simple setting it is practicable to include a lot more detail (e.g., many of the articles cited at the end of the following section). But the strategic aspect of our approach makes it possible for us to gain some novel insights into the nature of large-scale comparisons among consumer-resource systems. Besides, our ultimate goal is to use these consumer-resource models as building blocks for the construction of plausible models for more complicated systems involving many interacting species. In that setting, one needs to be parsimonious with respect to detail, but we hope to do so without too great a sacrifice in realism.

AN ENERGETIC BASIS FOR POPULATION DYNAMICS

One way to think of an animal is as an energy processor: it acquires energy from its environment and allocates this energy among maintenance, growth, and reproduction, with the end result that a portion of the ingested energy is converted into (somatic or reproductive) biomass. Of course, individual nutrients may also be important resource factors (essential amino and fatty acids, vitamins, etc.), but one can argue (see, e.g., Calow and Townsend 1981) that energy is the most general measure of resources (e.g., all nitrogen compounds have potential energy, but not all resources contain nitrogen) and that organisms are often energy limited.

TABLE 1
EMPRICALLY DETERMINED MODEL PARAMETERS

Parameter	Carnivore	Herbivore	Endotherm	Vertebrate	Ectotherm	Invertebrate	Phytoplankton
δ	.15	.55
a_T	54.9	...	2.3	.5	...
a_J	89.2	...	8.9	9.7	...
a_r4

NOTE.—The quantity δ is the fraction of ingested energy that is lost to feces and urine; a_i (units $\text{kg}[\text{kg yr}]^{-1}\text{kg}^{0.25}$) are the coefficients in the allometric relationships (eqq. [5]–[7]).

There is a major empirical tradition that adopts this viewpoint by focusing on energy budgets for individual animals (Brody 1945; Kleiber 1975). If i is the energy ingested by an individual per unit time, then the energy metabolized per unit time is $(1 - \delta)i$, where δ is the fraction that is lost as feces and urine between ingestion and the metabolizable energy level (National Research Council 1981; Lavigne et al. 1982; Robbins 1983). This metabolizable energy is utilized either for respiration (q) or for production (p , which includes somatic growth, reproduction, and mortality): $(1 - \delta)i = q + p$. The energy fraction lost (δ) is influenced by diet type, but it does not depend on body size (Robbins 1983, p. 293; table 1). It is of course subject to nonsystematic individual variation, but this is not large and we will neglect it. Since diet is the major source of variation in δ and all members of our consumer population have identically the same diet, for our purposes δ can be treated as a constant whose value depends on whether the resource is animal or plant (table 1). If we then sum both sides of the previous equation over all members of the population, we obtain $(1 - \delta)I = Q + P$, where $I = \sum i$, $Q = \sum q$, and $P = \sum p$, the sums being over all members of the population.

Let B stand for the total biomass in the population. What is its time derivative? Biomass increases through production, and it decreases through starvation and death. So $dB/dt = P - L = -Q + (1 - \delta)I - L$, where L is the rate of loss of biomass due to causes other than starvation, which is already accounted for in the energy budget (see below). We can write this as

$$dB/dt = B[-T + (1 - \delta)J] - L, \quad (1)$$

where $T = Q/B$ is the mass-specific respiration rate of the population (respiration per unit biomass) and $J = I/B$ is the mass-specific ingestion rate of the population.

Population dynamics has been approached in something resembling this spirit by Sinko and Streifer (1969), Allan (1974), Lynch (1977), Silvert and Platt (1980), Paloheimo et al. (1982), Peters (1983), Kooijman (1986), Metz and Diekmann (1986), McCauley et al. (1989), and Maurer (1990), among others.

THE MODEL

Equation (1) looks simple, but it is not very useful as it stands. We need constitutive relations that express the quantities on the right-hand side in terms of B , and perhaps other dynamical variables, to convert equation (1) into a proper dynamical system.

We treat here a consumer-resource system: two species, one of which eats members of the other. The consumer species (with biomass density denoted henceforth by C rather than B) will have dynamics of the form (1). The resource species, with biomass density R , will be assumed to grow logistically $dR/dt = rR(1 - R/K)$ in the absence of the consumer. Here K is the resource carrying capacity, and r is the intrinsic production-biomass ratio of the resource. Our r differs from the intrinsic rate of increase, usually denoted r , of the conventional logistic model, because R is biomass density, not number density. For us, r expresses increases both in numbers and in individual body mass.

Losses of biomass from the consumer population might be caused by mortality from predation, accident, disease, as well as starvation. In this discussion, we are neglecting other populations that might account for predation or disease, and we assume accidental deaths to be negligible. Therefore, in equation (1) we will have $L = 0$.

The specific rates T and J are complicated functions of phylogeny, environmental parameters, activity, and age. In order to model these rates precisely, we would have to take all these factors into account. Quite a lot of work along these lines has been done for particular taxa, usually zooplankton (references at the end of the preceding section). The resulting models are complicated, and their application to nature, even for a single population, requires detailed information about the animals.

We find this work fascinating and important, but we think it is also worthwhile to investigate less exact but simpler models within this general framework. Therefore, we are going to make the following approximation: as an estimate of the rates T and J per unit biomass in the population, we will use the corresponding rates per unit biomass of a typical adult individual.

The accuracy of such a procedure is difficult to assess with a high degree of confidence, but we would point out the following. If all individuals in the population had the same mass-specific rate for some quantity (say metabolism), then the mass-specific rate of the population for that quantity would be the same as the individual-specific rate. In actual fact, apart from random variation among individuals of comparable body sizes, which we can reasonably neglect, there tends to be systematic variation in the specific rates as an individual animal grows (Brody 1945; Wieser 1984; Innes et al. 1987). As a first approximation, the specific rates tend to vary as an animal grows as the -0.25 power of body mass, though the slope of the curve tends to be shallower at earlier ages. Because -0.25 is a small power, the specific rates should not vary a great deal from one individual to another, even among individuals of quite different body sizes. Therefore, the mass-specific rates for the population as a whole should not differ greatly from the specific rates for a typical individual.

One needs to bear in mind as well an important question of scale, not only for our models but for allometric reasoning generally. If we compare two populations whose mean adult body masses are very close together, the (relatively small) interpopulational variation in body mass and in contributions to the model parameters might be swamped by intrapopulational variation. This would not be a sensible use of our models. On the other hand, for relatively large interpopula-

tional differences in body mass, the intrapopulation variation in body mass will matter far less. This is the context for which our models are intended.

Henceforth, then, T will denote the mass-specific respiration rate and J the mass-specific ingestion rate of a typical adult individual.

A different conceptualization that yields the same models would be to think of a population of fully grown adult individuals only. Then with number density $N = C/m_C$, where m_C is the adult body mass, our models would be equivalent to conventional ones.

Specific respiration T varies with the activity level of the animal. Also, T can vary significantly with environmental parameters such as ambient temperature (Robinson et al. 1983). But it is not an outrageous approximation to take T constant for a given body size, and we will do so.

The specific ingestion rate J depends strongly on the resource density R and possibly on the consumer density C as well. We will assume that consumers do not interfere with one another's consumption, which implies that J does not depend on C . Ingestion must be zero when $R = 0$, ought to increase monotonically with R , and will not increase beyond some maximum value. We express these properties with functions of the form

$$J(R) = J_{\max} R^n / (R^n + R_0^n). \quad (2)$$

For $n = 1$, this has the form of a Holling Type II functional response; for $n = 2$, it has the form of a Holling Type III functional response (Real 1977, 1978; May 1981a). The constant J_{\max} is the asymptotic (saturation) rate of ingestion, and R_0 is the half-saturation density—the resource density at which half the saturation ingestion rate is attained.

The resulting dynamical system is

$$dC/dt = C[-T + (1 - \delta)J(R)] \quad (3)$$

and

$$dR/dt = rR(1 - R/K) - CJ(R)/f_e, \quad (4)$$

where $J(R)$ is given by equation (2) and f_e is the fraction of biomass removed from the resource population that is actually eaten. This fraction would be close to one for a grazer but might be significantly less than one for a predator that kills its prey but does not consume the entire carcass.

Physiological rates such as respiration tend to scale like m^b , where m is body mass and b is generally in the range 0.6–0.8 (Lavigne 1982; Peters 1983; Calder 1984). Some authors have suggested that behind these data lurks a general law, with the “true” exponent b either 0.67 (Heusner 1982a, 1982b) or 0.75 (Feldman and McMahon 1983). For our purposes, it will not make a great deal of difference exactly what the exponent is, so long as it does not vary overmuch in nature, and we have chosen to analyze the data using a fixed exponent of 0.75 (see Peters 1983). Of course, this means that the *mass-specific* rates in our model scale as $m^{-0.25}$.

This is our second major simplification. If we wanted to investigate some particular group of animals and the best allometric relationships we could find for

that group deviated slightly from the -0.25 power, this would introduce small mass-dependent corrections to our model. We have neglected these small corrections in favor of the simplicity and economy of a uniform exponent. If one did want to focus on some particular group of animals with greater accuracy, one could incorporate the particular allometric relationships into our formalism.

Thus, we assume

$$T = a_T m_C^{-0.25}, \quad (5)$$

$$(1 - \delta)J_{\max} = f_J a_J m_C^{-0.25}, \quad (6)$$

and

$$r = f_r a_r m_R^{-0.25}, \quad (7)$$

where m_C and m_R are adult body masses for the consumer and resource populations, a_i are empirically determined "universal" constants for each metabolic type of organism (next section), and f_i represent certain fractional properties of specific populations.

The maximum *feasible* metabolizable energy obeys an allometric law of the form $a_J m^{-0.25}$ (next section). This relationship represents the maximum (specific) rate at which the animal could possibly metabolize food. It is an upper bound, a constraint on what is biologically possible within a given metabolic group. But of course not every population is limited by its physiological capacity to metabolize food. In nature, animals require time to capture and otherwise handle prey, or they are subject to other ecological limitations on food intake. For these animals, the saturation level $(1 - \delta)J_{\max}$ will be some fraction of the physiological capacity, and f_J in equation (6) is that fraction. Similarly, a_r in equation (7) is derived from the physiological capacity for production, and f_r is a fraction that depends on each particular population's ecology (see the next section). Both fractions f_i lie in the interval $(0, 1]$.

With the relations (5)–(7), our model becomes

$$dC/dt = F_C = Cx[-1 + yR^n/(R^n + R_0^n)] \quad (8)$$

and

$$dR/dt = F_R = R(1 - R/K) - (xy/(1 - \delta)f_e)CR^n/(R^n + R_0^n), \quad (9)$$

where we have chosen units of time such that $r = 1$ and

$$x = (a_T/f_r a_r)(m_R/m_C)^{0.25} \quad (10)$$

and

$$y = f_J a_J / a_T. \quad (11)$$

The parameter x is a *relative* specific rate of respiration, normalized to the production-biomass ratio of the consumer population; y is dimensionless.

Equations (8) and (9) are invariant under the transformation $C \rightarrow C/K$, $R \rightarrow R/K$, $R_0 \rightarrow R_0/K$. (This is equivalent to choosing units of area in which $K = 1$.) This implies that the solutions can always be rescaled so that they do not depend on

R_0 and K separately but only on the combination R_0/K . Therefore, given the metabolic types and adult body masses of the consumer and resource individuals, the shape parameter n , and the fraction eaten f_e (all of which are relatively straightforward to obtain), equations (8)–(11) define a three-parameter family of models for the consumer-resource interaction. The three parameters are x , y , and R_0/K ; or f_r , f_j , and R_0/K .

ESTIMATION OF THE ALLOMETRIC COEFFICIENTS

We have divided the variety of organisms into four groupings of “metabolically similar” animals based on the division by Robinson et al. (1983). Specifically, these are endothermic vertebrates (homeotherms), ectothermic vertebrates (active fish and reptiles), ectothermic invertebrates (poikilotherms), and phytoplankton (unicells). Although these groupings are more general than those proposed by Humphreys (1979), they represent a minimum representation of the general metabolic groupings of heterotrophic organisms and an autotrophic base to the food web. May (1981*b*), reexamining Humphreys’ results, arrived at a similar categorization to ours.

The model’s parameters of mass-specific field metabolic rate T , maximum rate of energy metabolism $(1 - \delta)J_{\max}$, and maximum production-biomass ratio r can be expressed by equations of the form $E = am^{-0.25}$, where E is the rate of energy exchange expressed in the units $\text{kg}(\text{kg yr})^{-1}$, a is a coefficient with the units of $\text{kg}(\text{kg yr})^{-1} \text{kg}^{0.25}$, and m is body mass (kg).

We estimated the allometric coefficients (a in the preceding equation) from data by fixing the mass exponent at -0.25 and determining the mean of the transformed rates as the rate coefficient. Alternately, when only the allometric equation was given (i.e., ectothermic invertebrates), the equation was evaluated at the logarithmic midrange of the body sizes used, and this value was used to determine the appropriate coefficient. This does not mean that our model requires a rigorous “ $-1/4$ law” to be sensible. As we explained earlier, it is in the nature of an approximation: slight deviations in the mass exponents would result in slight corrections to the population dynamics. Figure 1 shows the data points used in our analyses of maximum rate of ingestion at the metabolizable energy level, $(1 - \delta)J_{\max}$, along with our $m^{-0.25}$ summaries, from which the reader can judge for him- or herself the adequacy of our approximation. The greatest deviation is present in the feeding rates of the invertebrates. However, these observations are for a limited range of body size.

All coefficients are expressed in the units of $\text{kg}(\text{kg yr})^{-1} \text{kg}^{0.25}$ and represent data collected when the representative animals were active. The variety of energy units used in the various literature studies required conversion to $\text{kg}(\text{kg yr})^{-1}$ ($1 \text{ kcal} = 4,186 \text{ J}$ [Yarwood and Castle 1972], $1 \text{ kg wet mass} = 7 \times 10^6 \text{ J}$, $1 \text{ mol O}_2 = 450.2 \text{ kJ}$ [Peters 1983, his App. Ia]).

Assimilation Efficiency

The model required information on the conversion of food energy (ingested energy, IE; National Research Council 1981) into metabolic energy used for respi-

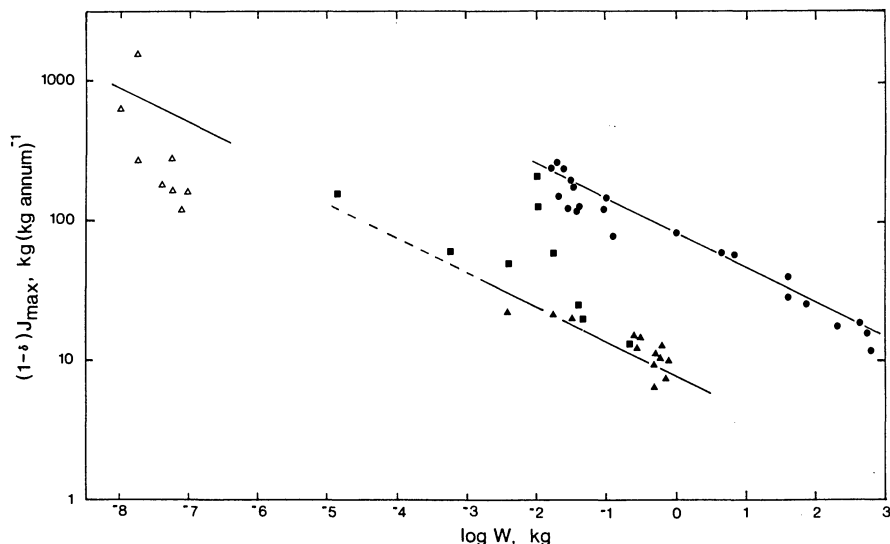


FIG. 1.—Allometric scaling of the maximum rate of metabolizable energy $(1 - \delta)J_{\max}$ for invertebrates (open triangles; Ikeda 1977), reptiles, and fishes, based on maximum oxygen consumption rate (solid triangles; Bennett and Dawson 1976; Brett and Groves 1979; Gerking and Lee 1983), feeding rate for fish (squares; Brett 1971), and maximum feeding rates for mammals and birds (circles; Kirkwood 1983).

ration and production. Energy (or biomass) lost between the ingested level and the metabolizable level (our parameter δ ; National Research Council 1981) was taken to be 55% for herbivores and 15% for carnivores (table 1). These two values summarize the digestibilities of plant and animal food sources (Calow 1977, table 4; Bjørndal 1979, 1987; Greenwald and Kanter 1979; Harwood 1979; Ruppert 1980; Schroeder 1981; Lavigne et al. 1982; Robbins 1983; Waldschmidt et al. 1986), which are independent of the consumer's taxon and body size. The differential in the heat increment of feeding between carnivores and herbivores is listed as part of the field metabolic rate (respiration) and was not factored into δ .

Maximal Ingestion

There is a limit to the amount of energy that can be consumed, processed, and converted into either production or respiration. The maximal rate of energy ingestion was defined after Kirkwood (1983) as the greatest sustained rate of ingestion, usually associated with maximal production of the individual, often over a limited time frame. This maximum rate of energy ingestion was expressed at the metabolizable level, that is, $(1 - \delta)J_{\max}$, to account for the significant difference between carnivores and herbivores in assimilation efficiency (Kirkwood 1983; see above).

Kirkwood (1983) reviewed the magnitude of metabolizable energy consumed by homeothermic animals (mammals and birds) during maximal production. The maximal rate of metabolism for this group is equivalent to approximately six

times the basal metabolic rate of $3.39 \text{ W kg}(\text{kg yr})^{-1} \text{ kg}^{-0.75}$ (Kleiber 1975). This is "metabolic scope" in the sense of McNab (1980). The coefficient a_j computed for the observations published in Kirkwood (1983) setting the mass-specific relationship's exponent to -0.25 was $89.2 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$.

The maximal ingestion rate for the ectothermic vertebrates has not been summarized as it has been for birds and mammals. This may be partially due to the preoccupation of investigators with the significant effects of environmental temperature and species' adaptation to temperature on the rates of energy transformation. The coefficient a_j for the ectothermic vertebrates was set at $8.9 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$, which represents the average of the maximal rate of oxygen consumption for lizards (Bennett and Dawson 1976) and salmon (Brett 1971). This coefficient, although somewhat arbitrary, is similar to coefficients for the maximum ingestion rates for fishes of $10.37 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ at the metabolizable level (Brett 1971; Brett and Groves 1979; Gerking and Lee 1983; fig. 1) and the predicted $10 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$, based on the anatomical differences between mammals and reptiles (Karasov and Diamond 1985). However, this a_j coefficient is well above that for mean maximal ingestion rate of $2.4 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ observed in lizards (Harwood 1979; Waldschmidt et al. 1986). This difference may be due to the timing of the observations relative to the circannual pulse of production in lizards (i.e., not measured during maximal growth); these lower ingestion rates of the lizards were associated with very low rates of somatic production, which were close to maintenance levels.

The average maximal rates of energy ingestion for eight ectothermic invertebrates, corrected to the metabolizable level, yielded $a_j = 9.7 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ (Ikeda 1977). Implicit in this analysis was the assumption of a 10% dry weight (fig. 1).

Respiration

The baseline for respiration (energy expenditure during free existence) was either the observed field metabolic rates (Nagy 1982, 1987) or the rates of respiration under conditions similar to free existence, again at the metabolizable energy level. These rates of energy expenditure pool basal metabolism, energy expended in activity, thermoregulation, and the heat increments of production and feeding.

The field metabolic rate for mammals and birds is approximately 2.5–3.5 times the basal metabolic rate (Nagy 1987). The mean coefficient a_T computed from observations in Nagy (1987) was $54.9 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$.

Field metabolic rates were established by the doubly labeled water technique for a wide range of lizards (Nagy 1982) and oxygen consumption for salmon (Brett and Glass 1973). The average coefficient a_T was $2.30 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$. This represented an increase of 2–2.5 times the respiration measured in the laboratory and 2.5–3.1 times the resting metabolic rates of these lizards at 35°C (Bennett and Nagy 1977).

The field metabolic rate for the ectothermic invertebrates was determined for the midpoint of the regression between body size and respiration rate for crustaceans at 20°C (Ikeda 1971, as cited in Parsons et al. 1979). This coefficient $a_T = 0.51 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ was considerably greater than the similar estimate by

TABLE 2
DERIVED MODEL PARAMETERS

Parameter	Endotherm	Vertebrate Ectotherm	Invertebrate	Phytoplankton
a_r	34.3	6.6	9.2	...
f_m	1.0	.2	.3	.01
y_{\max}	1.6	3.9	19.4	...

NOTE.—The allometric coefficient for maximal production-biomass ratio is $a_r = a_J - a_T$. This is expressed as a fraction of the coefficient for endotherms by f_m . The ecological scope $y_{\max} = a_J/a_T$.

Robinson et al. (1983) of $0.1 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$. Such variation is common among allometric studies of ectothermic animals because of the conditions of measurements.

Maximal Production-Biomass Ratio

The role of body size on the rate of biomass production for autotrophic unicellular organisms and plants is insufficiently documented. Most studies of phytoplankton deal with the effects of incident light, temperature, salinity, and nutrients for particular species and do not consider body size important. The coefficient for rate of increase, a_r , was $0.386 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ for diatoms ranging in cell size from 10^{-11} to 10^{-14} kg (Williams 1964).

For heterotrophs, the maximal production-biomass ratio r is the difference between maximal metabolizable energy and respiration. Thus, $f_r a_r$ in equation (7) can be expressed as $f_J a_J - a_T$, with a_J and a_T taken for the metabolic type of the resource population. Since the fraction $f_r = 1$ results if the fraction $f_J = 1$, we have then $a_r = a_J - a_T$. These coefficients are summarized in table 2. Of course, a_r , which corresponds to the maximum possible production-biomass ratio for each metabolic type, is much larger than coefficients obtained from typical field data (Banse and Mosher 1980; Peters 1983). This circumstance is expressed in the fraction f_r in equation (7), which would typically be on the order of 0.1 for a field population.

DYNAMICS OF THE MODEL

Phase space analysis of the model (eqq. [8] and [9]) is a standard part of basic theoretical ecology (see, e.g., Yodzis 1989). There is at most one equilibrium point with both species present. When that point is stable, it is a global attractor; when it is unstable, it is surrounded by a stable limit cycle that is a global attractor.

The equilibrium biomasses are

$$R_e = R_0/(y - 1)^{1/n} \quad (12)$$

and

$$C_e = (f_e(1 - \delta)/x)R_e(1 - R_e/K). \quad (13)$$

In order to have a feasible two-species equilibrium (both R_e and C_e positive),

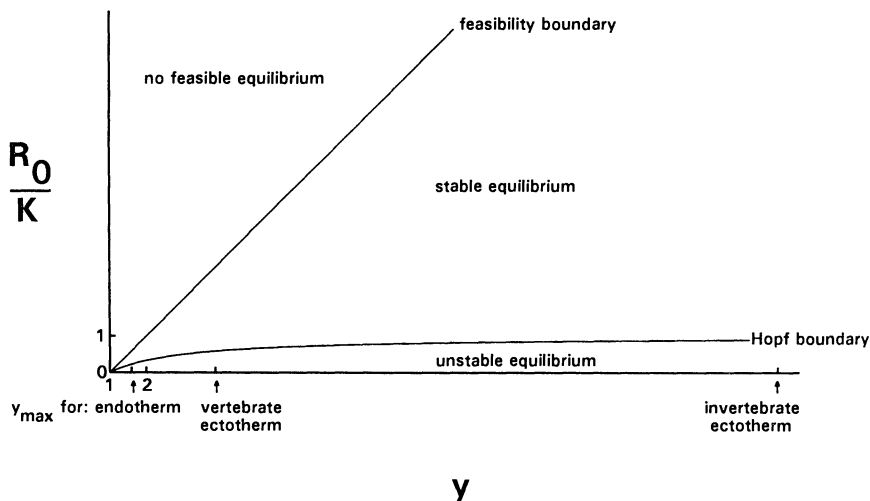


FIG. 2.—Equilibrium feasibility and stability for a Holling Type II functional response ($n = 1$ in eq. [2]). Half the saturation level of ingestion is attained when the resource density is R_0 . The quantity y is defined by eq. (18); the smaller it is, relative to its maximum value for a given metabolic type, the more strongly the consumer is limited by ecological rather than physiological factors in its resource acquisition.

we need $R_0 < R_{0F}$, where

$$R_{0F} = (y - 1)^{1/n} K. \quad (14)$$

We will call the boundary defined by $R_0/K = R_{0F}/K$ in $y - R_0/K$ parameter space the *feasibility boundary*.

The equilibrium is locally stable if and only if $R_0 > R_{0H}$, where

$$R_{0H} = \begin{cases} (y - 1)/(y + 1)K, & n = 1 \text{ (Holling Type II)} \\ (y - 1)^{1/2}(1 - y/2)K, & n = 2 \text{ (Holling Type III)} \end{cases} \quad (15)$$

Across the boundary in $y - R_0/K$ parameter space defined by $R_0/K = R_{0H}/K$, which we will call the *Hopf boundary*, there is a Hopf bifurcation between a stable focus and an unstable focus surrounded by a stable limit cycle (Freedman 1980). The feasibility and Hopf boundaries and the resultant stability domains in $y - R_0/K$ parameter space are depicted in figures 2 and 3. Since the two parameters y and R_0/K do not depend on body size, feasibility and local stability depend only on metabolism and functional response.

The two dimensions of the parameter space shown in figures 2 and 3 have clear biological interpretations. We may think of R_0/K as an inverse measure of *resource abundance* (as perceived by the consumer population). As for y , recall that, for a given metabolic category, a_j and a_T are fixed. Variation along the Y -axis is then due to variations in f_j (eq. [11]), which measures the consumer's saturation level of consumption as a fraction of its physiological maximum. Thus, position on the Y -axis is a measure of ecological limitation of resource acquisition. If y takes on its maximum possible value for a given metabolic type (correspond-

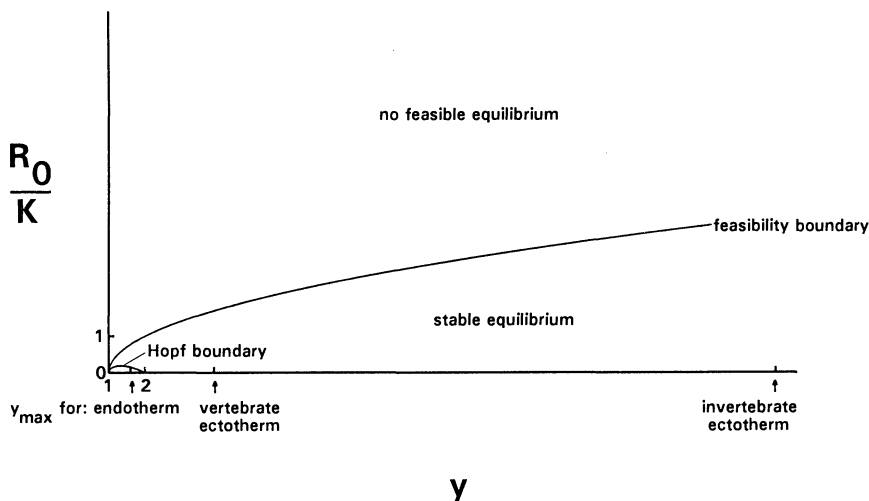


FIG. 3.—Same as fig. 2, but for a Holling Type III functional response ($n = 2$ in eq. [2])

ing to $f_j = 1$), the rate at which the consumer takes in resources is limited only by its physiological capacity to assimilate those resources; the smaller y is, relative to its maximum possible value, the more the consumer's resource intake is limited by ecological factors to rates that are smaller than those that the animals are capable of assimilating. The maximal values y_{\max} for y (corresponding to $f_j = 1$) for our three metabolic types are indicated in figures 2 and 3 and tabulated in table 2. We call y_{\max} the *ecological scope* of a metabolic type.

The equilibrium point with both species present, when it is feasible, can be either a focus or a node with two tangents. In the case of a focus, the trajectories spiral into a stable equilibrium or out from an unstable equilibrium; if the equilibrium is a node, it is approached (or departed from) more or less "radially" (see, e.g., Yodzis 1989).

For a system with a stable equilibrium, the difference is this: when the equilibrium is a focus, the biomass densities approach equilibrium as damped oscillations; when it is a node, the densities approach equilibrium monotonically, without oscillating. Strictly speaking, these statements apply only when the densities are sufficiently close to equilibrium, but numerical integrations suggest that they characterize the global behavior of the approach to equilibrium in these systems.

Denote the community matrix at the two-species equilibrium by \mathbf{A} : $\mathbf{A}_{ij} = [\partial F_i / \partial N_j]_e$, where i, j are either C or R , F_i is given by equations (8) and (9), and $N_C = C$, $N_R = R$. Then the local behavior of the equilibrium is determined by the two eigenvalues of \mathbf{A} . These are

$$\lambda = [\mathbf{A}_{RR} \pm (\mathbf{A}_{RR}^2 + 4\mathbf{A}_{CR}\mathbf{A}_{RC})^{1/2}]/2. \quad (16)$$

If the quantity in the square root is negative, we have a focus; if it is positive, we have a node. The boundary between node and focus is then

$$\mathbf{A}_{RR}^2 + 4\mathbf{A}_{CR}\mathbf{A}_{RC} = 0,$$

which is

$$\begin{aligned} & [1 - 2n(1 + 2x)(y - 1)/y + n^2(y - 1)^2/y^2] \\ & + [-4 + 2n(3 + 2x)(y - 1)/y - 2n^2(y - 1)^2/y^2]R_e/K \\ & + [4 - 4n(y - 1)/y + n^2(y - 1)^2/y^2](R_e/K)^2 = 0, \end{aligned} \quad (17)$$

with R_e given by equation (12). This expression depends not just on R_0 and y but also on x , which in turn depends both on metabolic parameters and the ratio of resource and consumer body sizes (eq. [10]).

The parameter x is a measure of the rate of consumer metabolism relative to the rate of resource dynamics. Another way of viewing it, through equation (10), is as an expression of the ratio of resource and consumer body sizes (given their metabolic categories). For numerical analyses such as we will describe later in this section, it is convenient to express resource body mass, hence the ratio of resource to consumer body mass, for all metabolic types in terms of the mass of an equivalent endotherm operating at its physiological limit ($f_J = 1$). First, we can express $a_r = f_m a_{r(\text{endotherm})}$, where the fractions f_m are as given in table 2. Then

$$\begin{aligned} r &= f_r f_m a_{r(\text{endotherm})} m_R^{-0.25} \\ &= a_r m_{ER}^{-0.25}, \end{aligned}$$

where

$$m_{ER} = f_r^{-4} f_m^{-4} m_R \quad (18)$$

is the equivalent physiologically limited endotherm body mass. For multicellular plants where the very meaning of "body size" is obscure, one can similarly think in terms of a physiologically limited endotherm with the same production-biomass ratio as the plants in question.

In our numerical work, we used $f_r = 1$ and the endothermic value for a_r , expressing all variation in relative rates of consumer and resource populations in terms of an equivalent body mass ratio m_{ER}/m_C . Because the negative fourth powers of the fractions f_r and f_m appear in the equivalent physiologically limited body mass m_{ER} , this mass can be very large relative to the actual body mass m_R , particularly for resource species whose own foraging activities are severely limited by ecological factors (small f_r) or for very "slow" organisms such as vertebrate ectotherms or phytoplankton (both of which have small f_m).

Figures 4 and 5 show the boundaries (eq. [17]) for a vertebrate ectotherm feeding on a physiologically limited endotherm. The qualitative behavior is similar for the other metabolic categories. There are always two boundaries: one, which we will call the *stable focus-node boundary*, above the Hopf bifurcation boundary but below the feasibility boundary; the other (the *unstable focus-node boundary*) below the Hopf bifurcation boundary. The boundaries are depicted for the equivalent body mass ratios (eq. [18]) $m_{ER}/m_C = 10^{-9}, 10^{-3}, 10^3, 10^9$. When this ratio is 10^9 , the unstable focus-node boundary is a little peak near the origin of our graph, too small to be seen at the depicted degree of resolution.

Finally, we have studied the periods and magnitudes of the sustained oscillations corresponding to limit cycles in those systems where the two-species equi-

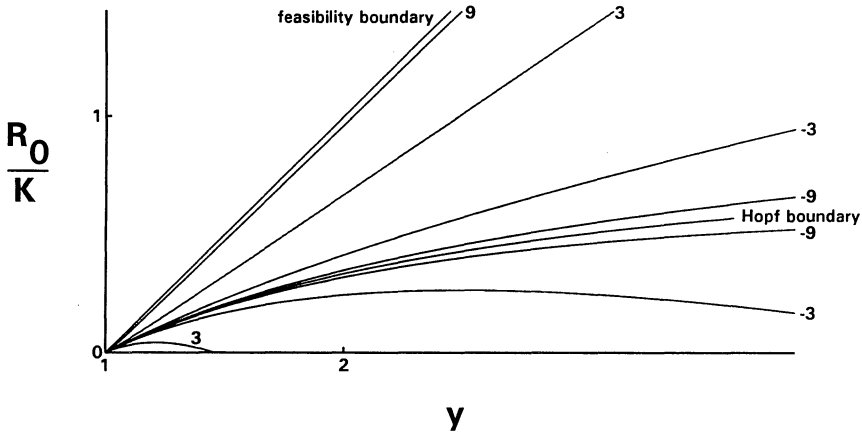


FIG. 4.—The stable (above the Hopf boundary) and unstable (below the Hopf boundary) focus-node boundaries, superimposed onto fig. 2 (Holling Type II), for several values of the equivalent body mass ratio m_{ER}/m_C (eq. [13]). The curves are labeled with $\log_{10}(m_{ER}/m_C)$.

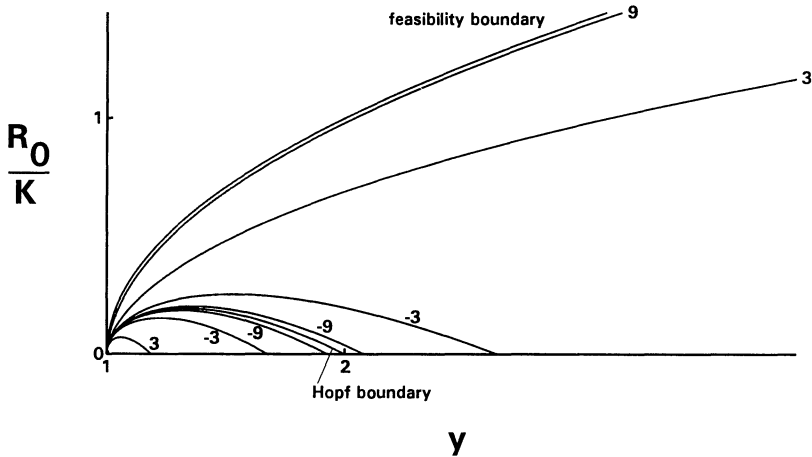


FIG. 5.—The stable (above the Hopf boundary) and unstable (below the Hopf boundary) focus-node boundaries, superimposed onto fig. 3 (Holling Type III), for several values of the equivalent body mass ratio m_{ER}/m_C (eq. [13]). The curves are labeled with $\log_{10}(m_{ER}/m_C)$.

librium is unstable. For this purpose, it is convenient to ask how the magnitude and period of the limit cycle vary as we let R_0/K decrease from the Hopf bifurcation value R_{0H}/K (eq. [15]), all other parameters being held fixed.

Near the bifurcation, the oscillations are small, and the period T is close to $T_0 = 2\pi/\omega_0$, where $\omega_0 = |\text{Im}(\lambda)|$, the magnitude of the imaginary parts of the eigenvalues (eq. [19]) (Iooss and Joseph 1980). We find

$$T_0 = 2\pi m_C^{1/8} m_R^{1/8} / G(f, a, a_T)^{1/2}, \quad (19)$$

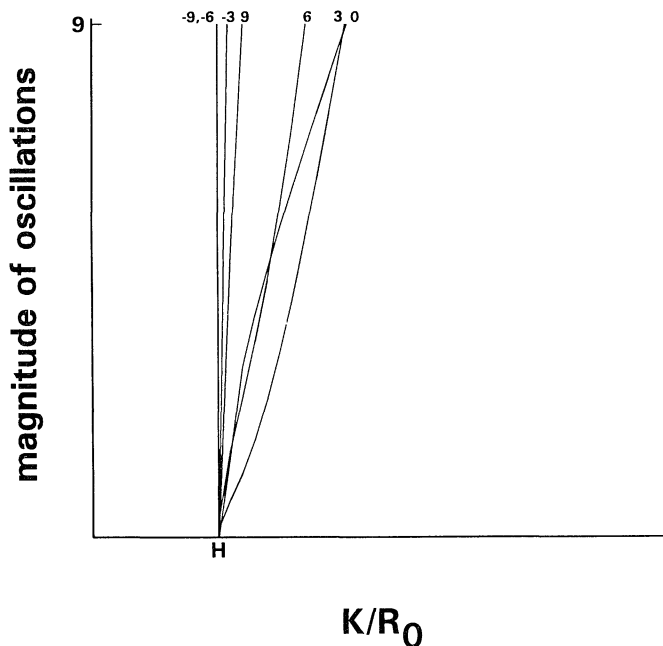


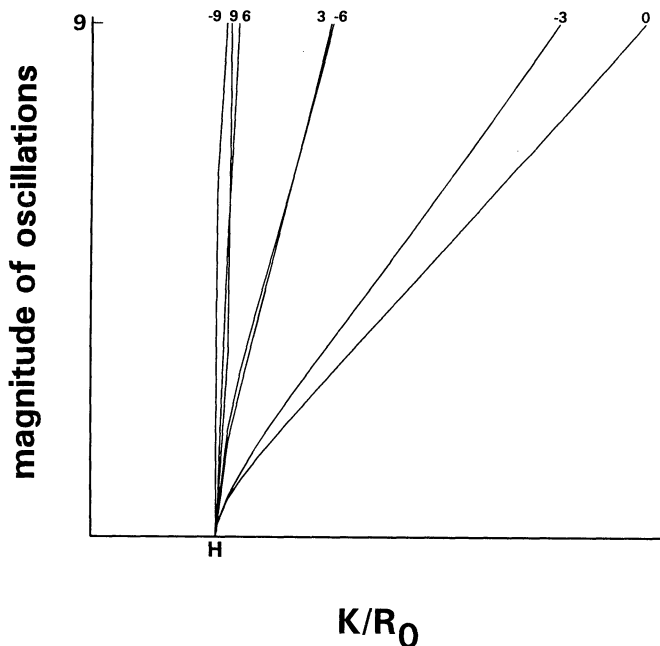
FIG. 6.—Dependence of magnitude of oscillations on K/R_0 for an endothermic consumer ($y = 1.06$) and a Holling Type II functional response ($n = 1$). The magnitude of oscillations in population density is plotted vs. the resource carrying capacity K (measured in units of the half-saturation density R_0 of the consumer's functional response) for a selection of equivalent body mass ratios m_{ER}/m_C . The curves are labeled with $\log_{10}(m_{ER}/m_C)$. The magnitude of oscillations is measured as the \log_{10} of the ratio of maximum to minimum density for the population density that varies more strongly (the resource when $\log_{10}[m_{ER}/m_C] < 0$, otherwise the consumer). The Hopf bifurcation occurs at the point labeled H (at which $K/R_0 = K/R_{0H}$); for $K/R_0 < H$ the magnitude of oscillations is zero because the system has a stable equilibrium rather than a limit cycle.

where

$$G = \begin{cases} [(y - 1)/(y + 1)]^{1/2}, & n = 1 \text{ (Holling Type II)} \\ (y - 1)^{1/2}, & n = 2 \text{ (Holling Type III)}. \end{cases} \quad (20)$$

We have studied, by means of an extensive set of computer integrations of the system (eqq. [8]–[11]), the behavior of the cycles as R_0/K moves farther away from the bifurcation. In all of the following results, there is no significant difference between carnivores ($\delta = 0.15$) and herbivores ($\delta = 0.55$). Nor is there any significant dependence on the fraction eaten, f_e , for values ranging from 0.1 to 1. Where quantitative results are given, they are for an herbivore with $f_e = 1$.

The half-saturation density R_0 is an intrinsic property of the biology of the consumer species, whereas the resource carrying capacity K depends on both intrinsic and extrinsic environmental factors. Because the value of K may be relatively fluid in a field situation, we will emphasize the dependence on K in what follows by expressing results in terms of K/R_0 rather than the inverse.

FIG. 7.—Same as fig. 6, but with $y = 1.6$

Recall that when K/R_0 is above the Hopf bifurcation value K/R_{0H} (which corresponds, of course, to R_0/K below the Hopf boundary R_{0H}/K in figs. 2–5), the system has a stable limit cycle: asymptotically the population densities experience sustained oscillations. The higher the value of K/R_0 , the larger those oscillations are in both period and magnitude. One can think of the period and magnitude of sustained oscillations corresponding to each value of K/R_0 as functions of K/R_0 . In terms of such functions, we find that the magnitude increases much more rapidly than the period: at K/R_0 values where a density varies by a factor of 10^9 , the period will typically be a factor somewhere between 2 and 10 times the Hopf period (eq. [19]).

Figures 6–9 show typical dependences of the magnitude of oscillations on K/R_0 . The quantity that is plotted is the common logarithm of the ratio of maximum to minimum biomass density over a cycle for the population for which this quantity is the larger. There are several curves in each figure that correspond to differing values of the equivalent body mass ratio m_{ER}/m_C , with each curve labeled by the common logarithm of this quantity. Figures 6 and 8 are for $y = 1.06$, which might represent a typical field endotherm. Figures 7 and 9 are for $y = 1.6$, which would represent an ideal endotherm operating at its maximum physiological capacity or a typical field invertebrate.

All four of these figures are for an endotherm consumer. There is no need to redo the computations for other consumer metabolic types: for a given y , each of these plots would be identical for any other of the metabolic types, except that the equivalent body mass ratio associated with each curve would need to be

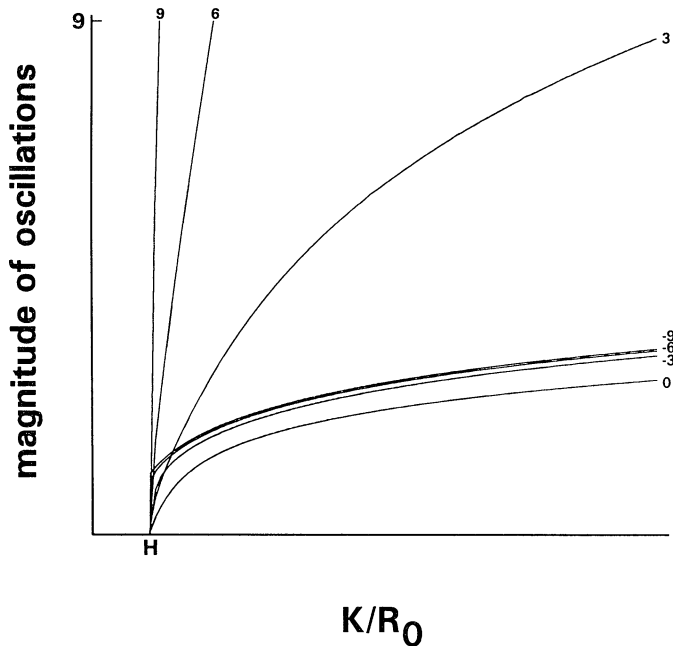


FIG. 8.—Dependence of magnitude of oscillations on K/R_0 for an endothermic consumer ($y = 1.06$) and a Holling Type III functional response ($n = 2$). The magnitude of oscillations in population density is plotted vs. the resource carrying capacity K (measured in units of the half-saturation density R_0 of the consumer's functional response) for a selection of equivalent body mass ratios m_{ER}/m_C . The curves are labeled with $\log_{10}(m_{ER}/m_C)$. The magnitude of oscillations is measured as the \log_{10} of the ratio of maximum to minimum density for the population density that varies more strongly (the resource when $\log_{10}[m_{ER}/m_C] < 3$, otherwise the consumer). The Hopf bifurcation occurs at the point labeled H (at which $K/R_0 = K/R_{0H}$); for $K/R_0 < H$ the magnitude of oscillations is zero because the system has a stable equilibrium rather than a limit cycle.

changed. A change in metabolic type with y fixed amounts to a change in the value of x . From equations (10) and (18),

$$x = a_T/a_{r(\text{endotherm})}(m_{ER}/m_C)^{0.25}, \quad (21)$$

where m_{ER} is the equivalent resource body mass (eq. [18]). Therefore, for any change in x due to a change in metabolic type, the same change in x could have been generated by a change in m_{ER}/m_C . To obtain the corresponding equivalent body mass ratio for some metabolic type 2, with $a_T = a_{T2}$, from the ratio for some metabolic type 1, with $a_T = a_{T1}$, multiply the body mass ratio by the factor $(a_{T1}/a_{T2})^4$.

Using this procedure together with the conversion in equation (18), one can, for each pair of metabolic types, work out an approximate (to within an order of magnitude) conversion factor to take an actual body mass ratio m_R/m_C into our endothermic consumer's equivalent body mass ratio m_{ER}/m_C . The results, assuming "typical field" resources ($f_r = 0.1$), are summarized in table 3. These esti-

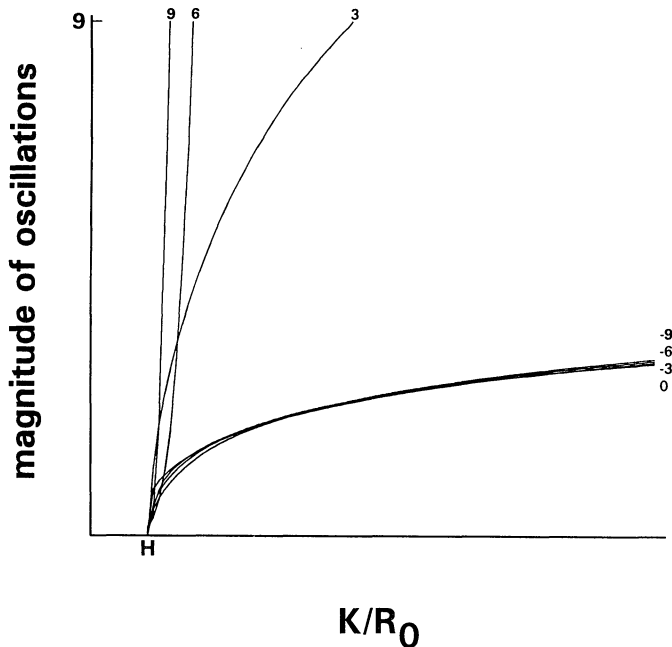
FIG. 9.—Same as fig. 8, but with $y = 1.6$

TABLE 3

CONVERSION FACTORS THAT TAKE ACTUAL BODY MASS RATIOS m_R/m_C INTO EQUIVALENT BODY MASS RATIOS m_{ER}/m_C FOR ENDOTHERMIC CONSUMERS

CONSUMER	RESOURCE			
	Endotherm	Vertebrate Ectotherm	Invertebrate	Phytoplankton
Endotherm	10^4	10^7	10^6	10^{12}
Vertebrate ectotherm	10^9	10^{12}	10^{11}	10^{17}
Invertebrate ectotherm	10^{12}	10^{15}	10^{14}	10^{20}

NOTE.—Data are estimated for “typical field” populations ($f_r = 0.1$).

mates are quite robust, except for the very sensitive dependence on the ecological limitation factor f_r for the resource population in equation (18). Variation in this factor could plausibly change the conversion factors by two or perhaps even three orders of magnitude.

The following trends can be seen in figures 6–9 (and further computations not depicted):

1. The most striking trend is a contrast between the behavior with a Type II functional response (figs. 6, 7) and a Type III functional response (figs. 8, 9). With a Type II functional response, the magnitude of oscillations increases steadily and rather rapidly; at best (fig. 7) the magnitude reaches nine (max/min = 10^9) by the time K/R_0 is four times its value at the Hopf bifurcation. With a Type III func-

tional response, if $m_{ER}/m_C \leq 1$, the magnitude of oscillations remains relatively steady over at least an order of magnitude of variation in K/R_0 .

2. When m_{ER}/m_C is very small, the magnitude of oscillations in the resource population is larger than the magnitude of oscillations in the consumer population; this trend is reversed when m_{ER}/m_C is very large.

3. The rapidity with which the magnitude of oscillations increases as K/R_0 increases is greater for smaller values of y .

4. The rapidity with which the magnitude of oscillations increases as K/R_0 increases has a dependence on the equivalent body mass ratio m_{ER}/m_C . With a Type II functional response, the magnitude has its slowest increase with respect to K/R_0 when m_{ER}/m_C is around 10^0 . With a Type III functional response, sufficiently small values of m_{ER}/m_C result in very robust oscillations whose magnitude increases quite rapidly to about three orders of magnitude, then grows only very slowly with further increases in K/R_0 , whereas larger values of m_{ER}/m_C are associated with oscillations that grow rapidly with respect to K/R_0 .

Of course, to apply these results to real populations, one needs to convert the actual mass ratio m_R/m_C to the endothermic values m_{ER}/m_C used to label figures 6–9, using equations (18) and (21) or, approximately, table 3.

DISCUSSION

The nature of consumer-resource dynamics as we have modeled it depends on five biological factors: the metabolic types—endotherm, vertebrate ectotherm, or invertebrate ectotherm—of the populations, the type (in the sense of Holling) of consumer functional response, resource abundance, ecological limitation on resource acquisition, and the relative rates of consumer and resource dynamics.

In our model, resource abundance, as perceived by the consumer, is expressed through R_0/K , the ratio of half-saturation density of the consumer functional response to resource carrying capacity. Ecological limitation on resource acquisition is expressed through the parameter y (eq. [11]), whose upper limit y_{\max} , which corresponds to physiologically limited resource intake, depends on the metabolic type as indicated in table 2 and figures 2 and 3. The smaller y is relative to y_{\max} , the more strongly the consumer's saturation level of intake is limited by ecological factors. The relative rates of consumer and resource dynamics are summarized in the relative mass-specific metabolic rate x (eq. [10]) of the consumer.

As we see in figures 2 and 3, if resources are very scarce (R_0/K above the feasibility boundary), the consumer and resource cannot coexist; if resources are moderately abundant (R_0/K below the feasibility boundary but above the Hopf boundary), there will be a stable equilibrium; and if resources are sufficiently abundant (R_0/K below the Hopf boundary), there will be an unstable equilibrium and sustained oscillations, which might, however, be so strong as to drive the resource or the consumer to local extinction (see below).

The set of all plausible consumer-resource models (in the sense that we are using the term, including the simplifying assumptions discussed in the introductory sections of this article) is parameterized by the three parameters x , y , R_0/K , which we may think of as defining a three-dimensional Euclidian space. The

region of this space corresponding to $y < y_{\max}$, $R_0 < R_{0F}$ delimits the set of biologically possible systems of the form we are discussing. But, for other biological reasons, not all points in this region are equally probable in nature. Unfortunately, these other reasons are complex, and one has little notion what the probability distribution of actual consumer-resource systems looks like. But for the sake of discussion, one may draw conclusions that are valid, all other things being equal, if this probability distribution is uniform.

For instance, if R_0/K lies above the stable focus-node boundary in figure 4 or 5 but below the feasibility boundary, the system will tend to approach equilibrium monotonically; otherwise, there will be some sort of oscillatory behavior. As we see from these figures, all other things being equal, the smaller the ratio m_{ER}/m_C , the more likely monotonic dynamics, because the smaller this ratio, the larger the area in figures 4 and 5 that corresponds to monotonic dynamics, relative to the area that corresponds to oscillatory dynamics.

Ecological Scope

Because the physiologically constrained maximal value y_{\max} is larger for invertebrate ectotherms than for vertebrate ectotherms than for endotherms (table 2), the invertebrate ectotherms as a group have more of what we might call ecological scope than do the vertebrate ectotherms than do the endotherms, and we will apply this term to the quantity y_{\max} .

This term is an attempt to express the following circumstances. The maximum value of R_0/K that permits any sort of coexistence is the value R_{0F}/K , which corresponds through equation (14) to $y = y_{\max}$ for a given metabolic type. Since R_{0F}/K is an increasing function of y , this means that the larger the ecological scope of a metabolic type, the larger the value of R_0/K (hence, the scarcer the resource levels) that members of that metabolic type can tolerate.

There is another sense in which what we are calling ecological scope is favorable. The sustained oscillations associated with the region of "unstable equilibrium" in figures 2 and 3 can easily become so large as to lead to local extinction. The larger the ecological scope is, the greater the area is in parameter space that corresponds to stable equilibrium relative to the area that corresponds to unstable equilibrium; hence, all other things being equal, the more likely such a metabolic type is to persist.

This line of thinking suggests that we ought to see more invertebrate populations than vertebrate ectotherm populations than endotherm populations in nature. This happens to be the case, but there are many factors involved, and we do not mean to suggest that ecological scope is necessarily the most important of them.

The Paradox of Enrichment

Rosenzweig (1972) noticed that (in our terminology), if we increase the K of a consumer-resource system that initially is in the region of parameter space corresponding to existence of a stable equilibrium, we can push it over the Hopf boundary into the region of sustained oscillations. For large enough K , the oscillations may be so big that one population or the other will die out due to demo-

graphic stochasticity. Rosenzweig called this the paradox of enrichment. As we have seen in the discussion surrounding figures 6–9, this kind of destabilization depends on several factors: metabolic type, the ecological limitation of ingestion as expressed through the value of y , relative body size, and especially the form of functional response.

The character of sustained oscillations and of the paradox of enrichment for consumer-resource systems is very different with a Type II or a Type III functional response. In either case, for certain ratios of resource to consumer body mass the oscillations “blow up” essentially at the Hopf boundary (figs. 6–9). Consumer-resource systems with these body mass ratios will never be observed to cycle. With a Type II functional response, even at favorable body mass ratios the magnitude of oscillations is quite sensitive to the value of K/R_0 (figs. 6, 7). Because of this sensitivity, we expect that with a Type II functional response, sustained oscillations will be quite rare, will be observed only for limited ranges of body mass ratios (which can be read off from figs. 6 and 7 and table 3), and will be “noisy” when they do occur.

With a Type III functional response, below a certain body mass ratio any destabilization due to enrichment will occur far beyond the Hopf boundary (figs. 8, 9). These cycles are moderate in magnitude and quite robust. We expect that most observed consumer-resource cycles, especially those that are not very “noisy,” will be associated with Type III functional responses and with equivalent body mass ratios $m_{ER}/m_C < 3$.

This upper limit, together with table 3, gives some notion of where Type III paradox of enrichment behavior—or simply robust limit cycles—might be observed. Although there are certainly exceptions, Peters (1983) suggests that predators tend to fall into two groups: large prey eaters (mammals and birds of prey), with $m_R/m_C \approx 10^{-1}$, and small prey eaters (lizards, amphibians, piscivorous and insectivorous birds), with $m_R/m_C \approx 10^{-3}$. On this basis, table 3 would suggest that robust consumer-resource limit cycles should be rather widespread taxonomically. However, for wolves preying on moose, $m_{ER}/m_C \approx 10^5$, which renders wolf-moose predator-prey cycles (Peterson and Page 1983) highly implausible and lends credence to the notion that the observed fluctuations might be driven instead by the extrinsic influence of winter snowfall (Mech et al. 1987).

There have been surprisingly few empirical studies of the paradox of enrichment. McAllister et al. (1972) added 5 tons of fertilizer per week, over a 20-wk period, to a 4,850-ha oligotrophic lake, mean depth 200 m. They observed no change in stability (consistent with the simple hypothesis that they did not enrich enough to cross the Hopf boundary), but, very interestingly, they did find that, although phytoplankton standing crop did not change, zooplankton standing crop increased by a factor of eight, consistent with equations (12) and (13) and with standard predator-prey theory (Rosenzweig 1972). McCauley and Murdoch (1990) unsuccessfully sought paradox of enrichment style behavior in the *Daphnia*-algae interaction. It is not clear whether this was because they did not use a large enough range of algal biomasses or because of other, confounding effects that they discuss. However, Luckinbill's (1974) experiments with *Didinium nasutum* preying on *Paramecium aurelia* in large-volume laboratory enclosures seem to

demonstrate paradox of enrichment behavior, with oscillations that progressively increase in amplitude as the carrying capacity increases and extinction when K is too large.

The Allometry of Population Cycles

Our numerical explorations have shown that the Hopf period T_0 , equation (19), will generally be a reasonable approximation to the period of any consumer-resource cycles whose magnitude is small enough to be safe. This enables us to predict how the period of such cycles ought to scale with body size.

For many predators, there is a close relationship between predator body size and prey body size (Peters 1983; Vézina 1985). In this context, $m_R \approx \alpha m_C$ for some constant α , so T_0 is proportional to $m_C^{1/4}$. For grazers, on the other hand, very little has been documented about this relationship. An extreme possibility would be for m_C and m_R in equation (19) to be completely decoupled. In such a group, periods would scale like $m_C^{1/8}$, with a lot of scatter, if only m_C is observed.

Calder (1984) suggested that cycle periods should scale like $m_C^{1/4}$ and found this relationship in a rather small data set. Peterson et al. (1984) found a similar relationship in a much larger set of data. Calder's data are restricted to grazers. Peterson et al. do not indicate what their mix of predators and grazers is, but it seems likely that grazers are well represented. These data suggest, then, the existence of a large-scale relationship between grazer body mass and plant "body mass" (in the sense of an equivalent body mass derived from population production/biomass with, say, the allometric relationship for endotherms, as we did in the discussion just after eq. [18]).

Of course, not all population cycles are consumer-resource cycles. It should be borne in mind that our comments both in this and in the preceding subsection apply to consumer-resource cycles only.

CONCLUSION

For practitioners seeking maximum potential understanding of a system of interacting populations from a relatively modest field program, we would emphasize the importance of consumer functional responses that have been measured in the field situation (so that one is working with the appropriate ecologically determined f_j). The other parameters required for our model are relatively easy to estimate.

Even with the simple point of view we have adopted here, the possibilities are rather numerous and complex in that several different factors interact in producing a given behavior. With more than two interacting populations, the complication will be far greater. Models that incorporate more detail than ours quickly require so much information about any given real population that very substantial empirical programs are needed to provide it. That is not to say that such models or such programs are to be avoided; quite to the contrary, often they are necessary. However, when constraints of time or research resources call for maximum realism from minimum data, plausible models such as we have discussed here may be a valid recourse.

ACKNOWLEDGMENTS

We thank D. M. Lavigne for numerous discussions of these matters and for his comments on our manuscript. The comments of anonymous referees on an earlier manuscript are greatly appreciated.

LITERATURE CITED

- Allan, J. D. 1974. Balancing predation and competition in cladocerans. *Ecology* 55:622–629.
- Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs* 50:355–379.
- Bellman, R. 1957. *Dynamic programming*. Princeton University Press, Princeton, N.J.
- Bennett, A. F., and W. R. Dawson. 1976. Metabolism. Pages 127–224 in C. Gans and W. R. Dawson, eds. *Biology of the Reptilia*. Vol. 5. Academic Press, London.
- Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697–700.
- Bjorndal, K. A. 1979. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. *Comparative Biochemistry and Physiology A, Comparative Physiology* 63:127–133.
- . 1987. Digestive efficiency in a temperate herbivorous reptile, *Gopherus polyphemus*. *Copeia* 1987:714–720.
- Brett, J. R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* 28:409–415.
- Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *Journal of the Fisheries Research Board of Canada* 30:379–387.
- Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pages 279–352 in W. S. Hoar, D. J. Randall, and J. R. Brett, eds. *Fish physiology*. Vol. 8. Bioenergetics and growth. Academic Press, New York.
- Brody, S. 1945. *Bioenergetics and growth*. Hafner, London.
- Calder, W. A., III. 1984. *Size, function, and life history*. Harvard University Press, Cambridge, Mass.
- Calow, P. 1977. Conversion efficiencies in heterotrophic organisms. *Biological Reviews of the Cambridge Philosophical Society* 52:385–409.
- Calow, P., and C. R. Townsend. 1981. Energetics, ecology and evolution. Pages 3–19 in C. R. Townsend and P. Calow, eds. *Physiological ecology*. Sinauer, Sunderland, Mass.
- Dickie, L. M., S. R. Kerr, and P. R. Boudreau. 1987. Size-dependent processes underlying regularities in ecosystem structure. *Ecological Monographs* 57:233–250.
- Feldman, H. A., and T. A. McMahon. 1983. The 3/4 mass exponent for energy metabolism is not a statistical artifact. *Respiration Physiology* 52:149–163.
- Freedman, H. I. 1980. *Deterministic mathematical models in population ecology*. Dekker, New York.
- Gerking, S. D., and R. M. Lee. 1983. Thermal limits for growth and reproduction in the desert pupfish *Cyprinodon n. nevadensis*. *Physiological Zoology* 56:1–9.
- Greenwald, O. E., and M. E. Kanter. 1979. The effects of temperature and behavioral thermoregulation on digestive efficiency and rate in corn snakes (*Elaphe guttata guttata*). *Physiological Zoology* 52:398–408.
- Harwood, R. H. 1979. The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. *Comparative Biochemistry and Physiology A, Comparative Physiology* 63:417–433.
- Heusner, A. A. 1982a. Energy metabolism and body size. I. Is the 0.75 exponent of Kleiber's equation a statistical artifact? *Respiration Physiology* 48:1–12.
- . 1982b. Energy metabolism and body size. II. Dimensional analysis and energetic non-similarity. *Respiration Physiology* 48:13–25.
- Holling, C. S. 1966. The strategy of building models of complex ecological systems. Pages 195–214 in K. E. F. Watt, ed. *Systems analysis in ecology*. Academic Press, New York.

- Humphreys, W. F. 1979. Production and respiration in animal populations. *Journal of Animal Ecology* 48:427–453.
- Ikeda, T. 1971. Relationship between respiration rate and body size in marine plankton animals as a function of temperature of the habitat. *Bulletin of the Faculty of Fisheries, Hokkaido University* 21:91–112.
- . 1977. Feeding rates of planktonic copepods from a tropical sea. *Journal of Experimental Marine Biology and Ecology* 29:263–277.
- Innes, S., D. M. Lavigne, W. M. Earle, and K. M. Kovacs. 1987. Feeding rates of seals and whales. *Journal of Animal Ecology* 56:115–130.
- Iooss, G., and D. D. Joseph. 1980. *Elementary stability and bifurcation theory*. Springer, New York.
- Karasov, W. H., and J. M. Diamond. 1985. Digestive adaptations for fueling the cost of endothermy. *Science* (Washington, D.C.) 228:202–204.
- Kirkwood, J. K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comparative Biochemistry and Physiology A, Comparative Physiology* 75:1–3.
- Kleiber, M. 1975. *The fire of life: an introduction to animal energetics*. Krieger, Huntington, N.Y.
- Kooijman, S. A. L. M. 1986. Energy budgets can explain body size relations. *Journal of Theoretical Biology* 121:269–282.
- Lavigne, D. M. 1982. Similarity in energy budgets of animal populations. *Journal of Animal Ecology* 51:195–206.
- Lavigne, D. M., W. Barchard, S. Innes, and N. A. Øritsland. 1982. Pinniped bioenergetics. FAO (Food and Agriculture Organization of the United Nations) Fisheries Series 5. *Mammals in the Seas* 4:191–235.
- Lavigne, D. M., S. Innes, G. A. J. Worthy, K. M. Kovacs, O. J. Schmitz, and J. P. Hickie. 1986. Metabolic rates of seals and whales. *Canadian Journal of Zoology* 64:279–284.
- Luckinbill, L. S. 1974. The effects of space and enrichment on a predator-prey system. *Ecology* 55:1142–1147.
- Lynch, M. 1977. Fitness and optimal body size in zooplankton population. *Ecology* 58:763–774.
- Maurer, B. A. 1990. *Dipodomys* populations as energy processing systems: regulation, competition, and hierarchical organization. *Ecological Modelling* 50:157–176.
- May, R. M. 1981*a*. Models for two interacting populations. Pages 78–104 in R. M. May, ed. *Theoretical ecology*. 2d ed. Sinauer, Sunderland, Mass.
- . 1981*b*. Patterns in multi-species communities. Pages 78–104 in R. M. May, ed. *Theoretical ecology*. 2d ed. Sinauer, Sunderland, Mass.
- McAllister, C. D., R. J. LeBrasseur, and T. R. Parsons. 1972. Stability of enriched aquatic ecosystems. *Science* (Washington, D.C.) 175:562–564.
- McCauley, E., and W. W. Murdoch. 1990. Predator-prey dynamics in environments rich and poor in nutrients. *Nature* (London) 343:455–457.
- McCauley, E., W. W. Murdoch, R. M. Nisbet, and W. S. C. Gurney. 1989. The physiological ecology of *Daphnia*: development of a model of growth and reproduction. *Ecology* 71:703–715.
- McNab, B. K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist* 116:106–124.
- Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. *Journal of Animal Ecology* 56:615–627.
- Metz, J. A. J., and O. Diekmann, eds. 1986. *The dynamics of physiologically structured populations*. Springer, New York.
- Nagy, K. A. 1982. Energy requirements of free-living iguanid lizards. Pages 49–59 in G. M. Gurchardt and A. S. Rand, eds. *Iguanas of the world: their behavior, ecology, and conservation*. Noyes, Park Ridge, N.J.
- . 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111–128.
- National Research Council. 1981. *Nutritional energetics of domestic animals and a glossary of terms*. National Academy, Washington, D.C.
- Paloheimo, J. E., S. J. Crabtree, and W. D. Taylor. 1982. Growth model of *Daphnia*. *Canadian Journal of Fisheries and Aquatic Sciences* 39:598–606.

- Parsons, T. R., M. Takahashi, and B. Hargrave. 1979. Biological oceanographic processes. 3d ed. Pergamon, Oxford.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.
- Peterson, R. O., and R. E. Page. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, U.S.A. *Acta Zoologica Fennica* 174:251–253.
- Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. *Science* (Washington, D.C.) 224:1350–1352.
- Real, L. A. 1977. The kinetics of functional response. *American Naturalist* 111:289–300.
- . 1978. Ecological determinants of functional response. *Ecology* 60:481–485.
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York.
- Robinson, W. R., R. H. Peters, and J. Zimmermann. 1983. The effects of body size and temperature on metabolic rate of organisms. *Canadian Journal of Zoology* 61:281–288.
- Rosenzweig, M. L. 1972. Stability of enriched aquatic ecosystems. *Science* (Washington, D.C.) 175:564–565.
- Ruppert, R. M. 1980. Comparative assimilation efficiencies of two lizards. *Comparative Biochemistry and Physiology A, Comparative Physiology* 67:491–496.
- Schmitz, O. J., and D. M. Lavigne. 1984. Intrinsic rate of increase, body size, and specific metabolic rate in marine mammals. *Oecologia* (Berlin) 62:305–309.
- Schroeder, L. A. 1981. Consumer growth efficiencies: their limits and relationships to ecological energetics. *Journal of Theoretical Biology* 93:805–828.
- Sheldon, R. W., W. H. Sutcliffe, Jr., and A. Prakash. 1973. The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. *Limnology and Oceanography* 18:719–733.
- Silvert, W., and T. Platt. 1980. Dynamic energy-flow model of the particle size distribution in pelagic ecosystems. Pages 754–763 in W. C. Kerfoot, ed. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, N.H.
- Sinko, J. W., and W. Streifer. 1969. Applying models incorporating age-size structure of a population to *Daphnia*. *Ecology* 50:608–615.
- Ulanowicz, R. E., and T. Platt, eds. 1985. Ecosystem theory for biological oceanography. *Canadian Bulletin of Fisheries and Aquatic Sciences* 213.
- Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* (Berlin) 67:555–565.
- Waldschmidt, S. R., S. M. Jones, and W. P. Porter. 1986. The effects of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. *Physiological Zoology* 59:376–383.
- Wieser, W. 1984. A distinction must be made between the ontogeny and the phylogeny of metabolism in order to understand the mass exponent of energy metabolism. *Respiration Physiology* 55:1–19.
- Williams, R. B. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. *Ecology* 45:877–880.
- Yarwood, T. M., and F. Castle. 1972. Physical and mathematical tables. 3d ed. G. R. Noakes, ed. Macmillan, Basingstoke.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508–515.
- . 1989. *Introduction to theoretical ecology*. Harper & Row, New York.

Associate Editor: Stephen W. Pacala