A COMPETITION MODEL FOR SIZE-STRUCTURED SPECIES*

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Abstract. The asymptotic dynamics of a system of ordinary differential equations describing the dynamics of n size-structured species competing for a single (unstructured) resource are studied. The system is based on a single species growth model for a size-structured species due to Diekmann, Metz, Kooijman, and Heijmans in which physiological parameters at the level of the individual are incorporated. It is shown that all trajectories asymptotically approach a lower-dimensional positive cone where the dynamics are governed by an easily determined lower-dimensional competition system of a type commonly studied in the literature for unstructured populations. It is also shown that, regardless of the asymptotic dynamics or the outcome of the competitive interaction, the average size of individuals for every species asymptotically equilibrates to a positive value. These results permit a study of competitive exclusion in terms of the physiological parameters and average size of individuals of the species. Illustrative applications are made to competing species in a chemostat and to species competing for a renewable resource. The relationship between competitive success and species size and other physiological parameters is discussed and related to the Size Efficiency Hypothesis (SEH) for zooplankton communities.

Key words. competition, size-structured population dynamics, ordinary differential equations, global asymptotic stability, average species size, competitive exclusion, Size Efficiency Hypothesis

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1. Introduction. Body size is one of the most important physical attributes of an organism. It is a significant factor in determining an organism's energetic requirements and ability to exploit resources. It has an important effect on the nature of an organism's interaction with the physical environment and with other biological species, including competitors and predators. Despite these obvious and recognized facts, relatively little mathematical theory of size-structured population interactions exists and virtually no dynamical models of competing size-structured species can be found in the literature. For a discussion of the importance of size-structure in population dynamics and multispecies interactions, particularly competitive interactions, see [20].

Zooplankton communities provide one example in which size structure has been of primary significance in the study of multispecies interactions. The observation that species of zooplankton tend to occur in associations characterized by body size and that large size species tend to predominate in zooplankton communities, at least in the absence of planktivorous fish, led Brooks and Dodson [1] to propose the *Size Efficiency Hypothesis* (SEH). The two basic tenets of this hypotheses are (1) that large size zooplankton species are more efficient at exploiting resources, which provides the potential for the competitive exclusion of smaller species, and (2) that size selective predation by large bodied (vertebrate) predators, which falls more heavily upon the larger zooplankton species, can allow for the survival of smaller species or even in some cases result in the elimination of larger species. This hypothesis has been the main theoretical framework of much zooplankton research since its formulation and many experimental studies have attempted to test its assumptions and verify its implications [9].

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While the second principle that (vertebrate or invertebrate) predator mediated competition plays an important role in shaping zooplankton community structure seems to be widely accepted, attempts to verify the first principle that larger species are more "efficient" competitors have been equivocal (e.g., see Dodson [7], Hall et al. [9], Neill [15], DeMott and Kerfoot [6] and the references cited therein). While some studies support this assumption, the ambiguities of other attempts at verification are usually attributed to any number of complications inevitably present in natural populations, such as habitat segregation, temporal environmental fluctuations, subtle specializations and life history adaptations, complex interspecies interactions, etc. It appears that available data is yet insufficient to determine the indisputable validity of this basic tenet of SEH [9], [8].

The purpose of this paper is to derive and analyze a general exploitative competition model for the dynamics of n size-structured species competing for a single (unstructured) resource and, by applying the results to specific models, hopefully shed some theoretical light on the first tenet of the SEH.

The model derived here is based on a model of Diekmann et al. [5] for the growth dynamics of simple (invertebrate) ectothermic animals whose resource uptake rate is proportional to body surface area (e.g., filter feeding species such as *Daphnia*), and is therefore particularly relevant to many competing zooplankton species. In the model of Diekmann et al. a system of partial integrodifferential equations describes the dynamics of the density of a size-structured (specifically length structured) population and its dynamical resource (also see Metz and Diekmann [14]). It is built from certain submodels at the level of the individual for birth, death, and growth processes. The exploitative competition model considered here is constructed by coupling n such systems together through their exploitation of the common resource.

In the derivation in § 2 two simplifying assumptions are made about the competing species: the energy utilized for metabolic maintenance is negligible relative to the energy used for growth and reproduction and there is no significant juvenile stage. From these assumptions a system of ordinary differential equations (2.9) for population level statistics (namely, total population numbers, length and area) is derived from the partial integrodifferential system.

In § 3 this ODE model is analyzed for general resource uptake rate functionals and fundamental properties of solutions are studied, including boundedness and positivity. The main result of § 3 (Theorem 2) is that all trajectories of the ODE model (3.3) asymptotically approach a lower-dimensional positive cone where dynamics are governed by a lower-order competitive system whose general structure is that of more familiar unstructured exploitative competition models. This lower-order system, however, governs the dynamics of certain weighted averages of the population level statistics, not simply total population numbers as is usually the case in ecological models. Known results about the asymptotic dynamics of such unstructured competition systems for various types of resource uptake functionals and inherent resource dynamics can be applied to this "reduced" system in order to obtain results concerning the asymptotic dynamics of the original size-structure competition model. This is done for the well-known chemostat model and for a two species model with a self-renewing resource in § 6.

One important feature of the competition model considered here is that important physiological parameters originating in the basic submodels for individual birth, growth, and death processes appear in the derived ODE model. As a result, we can relate these parameters at the individual level to the asymptotic dynamics at the population level and in particular to the outcome of the competitive interaction. These

parameters are encapsulated in the ODE model in what is termed below as the *efficiency coefficient* μ_i. Some necessary properties of this coefficient are given in § 4.

Another main result of the paper appears in § 5 (Theorem 4), where it is shown that regardless of the nature of the asymptotic dynamics the model implies that the average individual size (area or length) of each competing species equilibrates asymptotically. These equilibria depend only on the individual physiological reproductive and growth efficiencies and the size at birth and not on any other system parameters (death or resource uptake rates or the resource dynamics) nor on the presence or absence of competitors. An *average individual size* is thus defined for each species by the model and can be related to the competitive effectiveness of the species. This is done in § 6 for the chemostat model and for the self-renewing resource model.

The application made in § 6 to competition in a chemostat (which is often considered as a laboratory model of a simple natural lake) relies on and extends known model results for unstructured populations cultured in a chemostat to the case of size-structured species. As in the simpler case of unstructured populations, it is shown that only equilibrium asymptotic dynamics are possible. The results describe and fully account for the extinction or survival of all species on the basis of model parameters and they support the classical competitive exclusion principle in that at most one species can survive.

One point that clearly emerges from this application to the chemostat is the impossibility of relating average individual size in a simple, direct way to competitive success. It is not always true in the chemostat model below that the surviving competitor is the species with largest average individual size. In some extreme cases, such as when all other factors are identical for all species, it does in fact turn out that average individual size determines the competitive outcome (although the largest species is not always the winner). More generally, however, another criterion emerges as the determining factor of competitive success, namely that the surviving species is the one with the ability to exploit the resource to the lowest level while still being able to survive at that resource level. Thus the advantage of size afforded to largest individuals due to greater efficiency in total resource uptake can be mediated or even overcome by smaller individuals with physiological and per unit size resource uptake properties which allow it to survive at lower resource densities (a similar point is made by Wilson [21]). This simple (and rather intuitive) criterion for competitive effectiveness has been noted in the biological literature [15], [8] and, at least for the model considered here, is the real determining factor of the competitive outcome. Perhaps, then, the results obtained here provide some theoretical clue as to why species' size has been found to be an unreliable indicator of competitive success and suggest that this component of the SEH theory for zooplankton community structure is overly simplistic.

These conclusions are further strengthened by similar results obtained in § 6 for a competition model with a self-renewing resource, with the exception that there are ranges of parameter values for which competitors can coexist on a single resource, not in an equilibrium manner, but in an oscillatory limit cycle manner.

2. Model derivation. We begin with a capsule summary of the model of Diekmann et al. [5]. A full treatment can be found in Metz and Diekmann [14, Chap. I.3].

A basic assumption is that individual food ingestion is proportional to its size or, more specifically, to its surface area. If s denotes length and R denotes resource or food density then resource uptake rate is $f(R)s^2$ where the resource uptake rate (per unit area) $f(R)$ is dependent on resource density R. It is assumed that this rate is

positive whenever the resource density is nonzero:

$$f(0) = 0, \quad f(R) > 0 \quad \text{for } R > 0.$$

A typical such relationship is the Michaelis–Menten or Holling type II expression:

$$(2.1) \qquad\qquad f(R) = c \frac{R}{a + R}, \quad c > 0, \quad a > 0.$$

It is further assumed that ingested food is allocated between metabolic maintenance, individual growth, and reproduction. Energy reserves are ignored. If metabolic maintenance needs are assumed proportional to weight (or, up to a scaling factor, to volume), if a fraction κ of ingested food is utilized for individual growth and if η is a conversion factor relating weight to food units then we arrive at a von Bertalanffy type growth equation:

$$\frac{ds}{dt} = g(R, s) \quad \text{where } g(R, s) = \frac{1}{3\eta} [\kappa f(R) - \zeta s]_{+},$$

$$\eta > 0, \quad \zeta > 0, \quad 0 < \kappa < 1$$

where $[x]_{+} = x$ for $x > 0$ and 0 otherwise. Here ζ is the metabolism rate, i.e., the rate (per unit volume) of food units needed for metabolic maintenance.

With regard to reproduction it is assumed that the remaining fraction $(1 - \kappa)f(R)$ of ingested food is channeled to reproduction. If s_b and s_j denote the length at birth of all individuals and the length at which reproduction starts, respectively, and if reproduction ceases when the grow rate drops to zero (i.e., growth and maintenance take precedence over reproduction), then the individual birth rate is given by

$$m(R, s) = \begin{cases} 0, & s_b \leqq s < s_j, \\ (\omega s_b^3)^{-1}(1 - \kappa)f(R)s^2, & s_j \leqq s \leqq \underline{s}(R), \\ (\omega s_b^3)^{-1}(f(R)s^2 - \zeta s^3), & \max\{s_j, \underline{s}(R)\} \leqq s \leqq \bar{s}(R). \end{cases}$$

Here ω is a conversion factor relating food units to weight for reproduction, i.e., ωs_b^3 is the amount of food needed to produce one offspring, $\underline{s}(R)$ is the size at which growth stops at food density R and $\bar{s}(R)$ is the size at which all food is needed just for maintenance, i.e.,

$$\underline{s}(R) = \zeta^{-1} \kappa f(R) \leqq \zeta^{-1} f(R) = \bar{s}(R).$$

Finally it is assumed that the individual death rate $d > 0$ is a constant independent of size, time, and resource density R.

The above submodels for the growth, birth, and death rates can be incorporated into dynamical equations for population level growth dynamical equations by using the modeling principles and techniques of Metz and Diekmann [14] (also see Sinko and Streifer [16]). If $\rho(t, s)$ denotes population density as a function of time t and length s, so that $\int_{s_2}^{s_1} \rho(t, s)\, ds$ denotes the number of individuals with lengths between s_1 and s_2, then

$$\frac{\partial}{\partial t} \rho(t, s) + \frac{\partial}{\partial s}(g(R, s)\rho(t, s)) = -d\rho(t, s), \qquad s_b < s < \bar{s}(R), \quad t > 0,$$

$$(2.2) \qquad \rho(t, s) = 0, \quad s > \bar{s}(R), \quad t > 0,$$

$$g(R, s_b)\rho(t, s_b) = \int_{s_j}^{\bar{s}} m(R, s)\rho(t, s)\, ds, \qquad t > 0.$$

To complete the formulation of the model the dynamics of the resource must be specified. The simplest assumption is that the food resource density R is somehow held constant over time. This case is investigated in some detail by Metz and Diekmann [14]. The more realistic case when resource density can change due to the feeding activity of the population and to other external causes will be considered here. If $k(R)$ denotes the inherent density dependent growth rate of the resource $R = R(t)$ in the absence of feeding by the population ρ, then

$$(2.3) \qquad \frac{dR}{dt} = k(R) - f(R) \int_{s_b}^{\bar{s}} \rho(t, s) s^2 \, ds.$$

A typical resource growth law is

$$(2.4) \qquad k(R) = (R_0 - R)d, \qquad R_0 > 0, \quad d > 0,$$

which corresponds to a constant replenishing of (nonreproducing) food particles and a constant food loss (by, for example, dilution in a continuous flow culture such as in a chemostat). Another is the classical logistic law

$$(2.5) \qquad k(R) = r\left(1 - \frac{R}{K}\right)R, \qquad r > 0, \quad K > 0$$

for a self-renewing resource. These will be utilized in § 6.

Equations (2.2)–(2.3) constitute the starting point for the competition model to be considered in this paper. We are interested in the dynamics of several competing species of the type meeting the assumptions described above all of which attempt to utilize the same limiting resource R. It will be assumed that the n interacting species, whose densities will be denoted by ρ_i, $1 \leq i \leq n$, interact with each other by means of this common limited food resource and in no other way so that the interaction is of the type usually referred to as "exploitative." Thus, it is assumed that there is no significant interference between individuals of opposing species that affect growth dynamics (such as aggressive behavior, the production of toxic wastes, etc.). In this way we can model the multispecies interaction by means of uncoupled equations (2.2) for each individual species together with a modified resource equation (2.3) that affects the coupling and the competition. Thus, for $i = 1, \cdots, n$ we have the following equations:

$$(2.6) \quad \begin{aligned} &\frac{\partial}{\partial t} \rho_i(t, s) + \frac{\partial}{\partial s} (g_i(R, s)\rho_i(t, s)) = -d_i \rho_i(t, s), \qquad s_{b_i} < s < \bar{s}_i(R), \quad t > 0, \\ &\rho_i(t, s) = 0, \quad s > \bar{s}_i(R), \quad t > 0, \\ &g_i(R, s_{b_i})\rho_i(t, s_{b_i}) = \int_{s_{l_i}}^{\bar{s}_i} m_i(R, s)\rho_i(t, s) \, ds, \qquad t > 0, \\ &\frac{dR}{dt} = k(R) - \sum_{i=1}^{n} f_i(R) \int_{s_{b_i}}^{\bar{s}_i} \rho_i(t, s) s^2 \, ds, \qquad t > 0. \end{aligned}$$

Here the subscripted quantities represent the corresponding species specific quantity from the single species model.

Partial integrodifferential equations of the type (2.2)–(2.3) or (2.6) and the study of the implied asymptotic dynamics, even for specialized functional responses f and resource dynamics k such as (2.1) and (2.4) or (2.5), present significant mathematical difficulties and offer a stimulating challenge to applied mathematicians. Even the basic

theory of these equations needs further development, although headway has been made on similar equations (cf. Metz and Diekmann [14]).

The purpose of this paper is to give a complete global analysis of the asymptotic dynamics of a simplified version of the competition equations (2.6). This will be done under two simplifying assumptions. First, it will be assumed that the amount of ingested food needed for metabolic maintenance is negligible compared to that utilized for growth and reproduction. Thus, mathematically $\zeta = 0$ and accordingly $s(R) = \bar{s}(R) = +\infty$. Second, it will be assumed that individuals need not grow significantly before being capable of reproduction so that $s_{b_i} = s_{j_i} = s_i$. Then so long as R remains positive the model equations become for $i = 1, \cdots, n$ the following:

(2.7) (a) $\dfrac{\partial}{\partial t} \rho_i(t, s) + \dfrac{\kappa_i}{3\eta_i} f_i(R) \dfrac{\partial}{\partial s} \rho_i(t, s) = -d_i \rho_i(t, s), \quad s_i < s, \quad t > 0,$

(b) $\rho_i(t, s_i) = \dfrac{3\eta_i(1 - \kappa_i)}{\kappa_i \omega_i s_i^3} \displaystyle\int_{s_i}^{\infty} \rho_i(t, s) s^2 \, ds, \qquad t > 0,$

(c) $\dfrac{dR}{dt} = k(R) - \displaystyle\sum_{i=1}^{n} f_i(R) \int_{s_i}^{\infty} \rho_i(t, s) s^2 \, ds, \qquad t > 0.$

In lieu of the compact support implied in (2.6) it is assumed that $\rho_i(t, s)$ vanishes at $s = +\infty$ and has finite moments

$$A_i(t) = \int_{s_i}^{\infty} \rho_i(t, s) s^2 \, ds, \quad L_i(t) = \int_{s_i}^{\infty} \rho_i(t, s) s \, ds, \quad P_i(t) = \int_{s_i}^{\infty} \rho_i(t, s) \, ds$$

that represent the total area of all individuals, the total length of all individuals, and the total number of individuals in the population, respectively. Rather than treat equations (2.7)(a)–(2.7)(c) directly, an equivalent system of ordinary differential equations for the quantities A_i, L_i, and P_i will be derived.

If (2.7a) is multiplied by s^2 and the result integrated with respect to s from s_i to $+\infty$, the equation

$$A_i' = -d_i A_i + \dfrac{(1 - \kappa_i)}{\omega_i s_i} f_i(R) A_i + \dfrac{2\kappa_i}{3\eta_i} f_i(R) L_i \quad \text{where } ' = \dfrac{d}{dt}$$

is obtained after an integration by parts and a utilization of (2.7)(b) in the boundary term. If similar manipulations are carried out, but with multiples of s and one instead, and if the notation

(2.8) $$\alpha_i = \dfrac{(1 - \kappa_i)}{\omega_i}, \qquad \beta_i = \dfrac{\kappa_i}{\eta_i}$$

is introduced, then we arrive at the following system of ordinary differential equations:

(2.9) (a) $R' = k(R) - \displaystyle\sum_{i=1}^{n} f_i(R) A_i, \qquad R(0) > 0,$

(b) $A_i' = -d_i A_i + s_i^{-1} \alpha_i f_i(R) A_i + \tfrac{2}{3}\beta_i f_i(R) L_i, \qquad A_i(0) > 0,$

(c) $L_i' = -d_i L_i + s_i^{-2} \alpha_i f_i(R) A_i + \tfrac{1}{3}\beta_i f_i(R) P_i, \qquad L_i(0) > 0,$

(d) $P_i' = -d_i P_i + s_i^{-3} \alpha_i f_i(R) A_i, \qquad P_i(0) > 0.$

To summarize, in the model system (2.9)(a)-(2.9)(d) for n size-structured species competing for a single resource we have the following:

$R(t)$ = the resource density at time t;

$A_i(t)$ = the total area of all individuals of the ith species at time t;

$L_i(t)$ = the total length of all individuals of the ith species at time t;

$P_i(t)$ = the total number of individuals of the ith species at time t;

$k(R)$ = resource growth rate in the absence of predation by all n competing species;

$f_i(R)$ = resource uptake rate of the ith species;

d_i = death or removal rate of the ith species;

and the coefficients α_i and β_i are defined by (2.8) with the following:

κ_i = fraction of ingested resource utilized for individual growth by individuals of the ith species;

η_i = conversion factor relating weight to food units for individual growth by individuals of the ith species;

ω_i = conversion factor relating weight to food units for reproduction by individuals of the ith species.

The quantities α_i and β_i are *reproductive and growth efficiency coefficients* that measure the efficiency of an individual's utilization of food resources for reproduction and growth respectively. Greater values of these parameters correspond to greater efficiency.

3. The competition equations (2.9). Assume that the resource uptake functional $f(R)$ and the inherent resource growth rate $k(R)$ are continuously differentiable functions of $R \geq 0$ and that

$$k(0) \geq 0 \text{ and } f(0) = 0, f(R) > 0 \text{ for } R > 0.$$

Under these conditions it will be shown in this section that the long-time asymptotic dynamics of the system (2.9) are governed and completely determined by the asymptotic dynamics of a certain lower-dimensional (viz., $n+1$) system. This lower-dimensional or "reduced" system (3.3) is of a type that is amenable to considerable global analysis and in fact has been thoroughly studied in the literature for selected $f(R)$ and $k(R)$. By this result we have a means for studying the global dynamics of size-structured competition models of the form (2.7). This approach is illustrated by the applications in §§ 4 and 5.

The quantities A_i, L_i, P_i are only biologically meaningful when nonnegative. The proof of the following theorem appears in the Appendix.

THEOREM 1. *The solution of the initial value problem* (2.9) *is positive for all time, i.e.,* $R(t) > 0, A_i(t) > 0, L_i(t) > 0, P_i(t) > 0$ *for all* $t > 0$.

To study equations (2.9)(a) and (2.9)(d) further a linear transformation will be performed. Let $p_i = \text{col}(A_i, L_i, P_i)$ denote the column vector of the population variables for the ith species and write the last three equations (2.9)(b)-(2.9)(d) in the matrix form

$$(3.1) \qquad\qquad p_i' = -d_i p_i + f_i(R) M_i^t p_i$$

where M_i^t denotes the transpose of the Leslie matrix

$$(3.2) \qquad\qquad M_i = \begin{pmatrix} s_i^{-1}\alpha_i & s_i^{-2}\alpha_i & s_i^{-3}\alpha_i \\ \frac{2}{3}\beta_i & 0 & 0 \\ 0 & \frac{1}{3}\beta_i & 0 \end{pmatrix}.$$

Note that this matrix depends only on the individual physiological properties s_i, α_i, and β_i. If T_i is a nonsingular matrix and new dependent variables $q_i = \mathrm{col}\,(x_i, y_i, z_i)$ are defined by $q_i = T_i' p_i$, then equation (3.1) becomes

$$q_i' = -d_i q_i + f_i(R) T_i' M_i' (T_i')^{-1} q_i = -d_i q_i + f_i(R)(T_i^{-1} M_i T_i)' q_i.$$

Thus the linear change of variables $q_i = T_i' p_i$ results in a similarity transformation of the coefficient matrix M_i in (3.1) and consequently introduces a means of simplifying the system. The real form of the Jordan canonical form will be utilized and for this purpose the following lemma concerning the eigenvalues and eigenvectors of M_i (whose proof appears in the Appendix) is of use.

LEMMA 1. *The Leslie matrix M_i has a strictly dominant positive eigenvalue $\mu_i > 0$ that possesses associated strictly positive right and left unit eigenvectors $v_i > 0$, $w_i > 0$. The remaining two eigenvalues $\gamma_i \pm \nu_i \sqrt{-1}$ are complex with negative real parts: $\gamma_i < 0$, $\nu_i \neq 0$.*

As a result of this lemma it follows that there exists a nonsingular matrix T_i such that $T_i^{-1} M_i T_i$ has the form

$$T_i^{-1} M_i T_i = \begin{pmatrix} \mu_i & 0 & 0 \\ 0 & \gamma_i & \nu_i \\ 0 & -\nu_i & \gamma_i \end{pmatrix}, \qquad \gamma_i < 0.$$

The first column of T_i is the positive right eigenvector $v_i > 0$ and the first row of T_i^{-1} is the positive left eigenvector $w_i > 0$. If c_{1i}, c_{2i}, c_{3i} denote the entries in the first column of T_i^{-1} then the transformed system becomes the following:

(3.3) (a) $R' = k(R) - \sum_{i=1}^{n} f_i(R)(c_{i1} x_i + c_{i2} y_i + c_{i3} z_i),$ $R(0) > 0,$

  (b) $x_i' = -d_i x_i + \mu_i f_i(R) x_i,$ $x_i(0) > 0,$

  (c) $y_i' = -d_i y_i + f_i(R)(\gamma_i y_i - \nu_i z_i),$

  (d) $z_i' = -d_i z_i + f_i(R)(\nu_i y_i + \gamma_i z_i).$

Note that $x_i(0) > 0$ follows from $x_i(0) = v_i' p_i(0)$. Also note that c_{i1} is the first component of w_i, and hence is positive.

THEOREM 2. *For any solution of (3.3)(a)-(3.3)(d), $y_i \to 0$ and $z_i \to 0$ exponentially as $t \to +\infty$.*

The proof of this theorem, as well as that of the following theorem, appear in the Appendix.

THEOREM 3. *Assume the following:*

(H)   *all solutions of $R' = k(R)$, $R(0) > 0$, are bounded for $t \geq 0$.*

Then all solutions of (3.3)(a)-(3.3)(d) are bounded for $t \geq 0$.

COROLLARY. *Under hypothesis (H) all solutions of (2.9) are positive and bounded for $t \geq 0$.*

Theorems 1-3 and $x_i(t) = v_i' p_i(t)$ imply that the ω-limit sets of all solutions of (3.3) lie in the set $R \geq 0$, $x_i \geq 0$, $y_i = 0$, $z_i = 0$ for all i. Moreover, this set is easily seen to be a positively invariant set on which the dynamics of (3.3) are governed by the following "reduced" system.

(3.4) (a) $R' = k(R) - \sum_{i=1}^{n} c_{i1} f_i(R) X_i,$ $R(0) > 0,$

  (b) $X_i' = -d_i X_i + \mu_i f_i(R) X_i,$ $X_i(0) > 0.$

Consequently, the asymptotic dynamics of the competition equations (2.9) can be studied by means of this associated lower-dimensional system.

The transformed variable $x_i(t) = v_i^t p_i(t)$ is a weighted average of the population parameters A_i, L_i, P_i. From (3.4) it is seen that the contribution of the physiological parameters s_i, α_i, β_i to the dynamics of the competitive interaction is through the coefficients μ_i, c_{i1} that are determined by the matrix M_i. The eigenvalue μ_i will be referred to as the *physiological efficiency coefficient* of the ith species.

Note that by Theorem 2 an equilibrium of (3.3) must have $y_i = z_i = 0$ for all i, and hence must be an equilibrium of (3.4). There is, of course, a one-to-one correspondence between the equilibria of (2.9) and those of (3.3).

4. The efficiency coefficient. In what follows it will be important to understand how the physiological efficiency coefficient μ_i depends on model parameters. Since the matrix M_i depends only on the physiological parameters s_i, α_i, β_i, the same is true of its eigenvalue μ_i. In this section some simple facts concerning the relationship between these parameters and μ_i will be derived.

The characteristic polynomial of M_i is

$$(4.1) \qquad h_i(\mu) = \mu^3 - s_i^{-1}\alpha_i\mu^2 - \frac{2}{3}s_i^{-2}\alpha_i\beta_i\mu - \frac{2}{9}s_i^{-3}\alpha_i\beta_i^2$$

and μ_i is the unique positive root of this polynomial. If the characteristic equation $h(\mu) = 0$ is multiplied by $(s_i/\alpha_i)^3$ and if $z = \mu s_i/\alpha_i$, then this equation is equivalent to

$$(4.2) \qquad z^3 - z^2 - \frac{2}{3}r_i z - \frac{2}{9}r_i^2 = 0, \; r_i = \frac{\beta_i}{\alpha_i}.$$

The unique positive root of this equation $z = z_i(r_i)$ is analytic in r_i with $z_i(0) = 1$ and is strictly increasing. This latter fact can be seen from an implicit differentiation of (4.2) and

$$z_i'(r_i) = \frac{2}{9}(3z_i + 2r_i) \bigg/ \left(3z_i^2 - 2z_i - \frac{2}{3}r_i\right) = \frac{2}{9}(3z_i + 2r_i) \bigg/ \left(\frac{3}{z_i}\left(z_i^3 - \frac{2}{3}z_i^2 - \frac{2}{9}r_i z_i\right)\right)$$

$$= \frac{2z_i}{27}(3z_i + 2r_i) \bigg/ \left(\frac{1}{3}z_i^2 + \frac{4}{9}r_i z_i + \frac{2}{9}r_i^2\right) > 0.$$

From this and from $\mu_i = z_i(r_i)\alpha_i/s_i$ it follows that

$$\frac{\partial \mu_i}{\partial \alpha_i} = \frac{z_i}{3s_i}\frac{9z_i^2 + 6r_i z_i + 2r_i^2}{3z_i^2 + 4r_i z_i + 2r_i^2} > 0.$$

LEMMA 2. *The physiological efficiency coefficient μ_i can be written in the following form*:

$$\mu_i = \alpha_i z_i(r_i)/s_i, \qquad r_i = \beta_i/\alpha_i$$

where z_i is a strictly increasing function of its argument and $z_i(0) = 1$. The efficiency coefficient μ_i is an increasing function of both the reproductive efficiency α_i and the growth efficiency β_i and is a decreasing function of the size at birth s_i.

5. Average individual size. Let

$$[A_i](t) = A_i(t)/P_i(t), \qquad [L_i](t) = L_i(t)/P_i(t)$$

denote the average area and length of an individual in the ith species at time t. A simple differentiation shows that these averages satisfy the following differential

equations:

(5.1)
$$[A_i]' = f_i(R(t))(s_i^{-1}\alpha_i[A_i] + \tfrac{2}{3}\beta_i[L_i] - s_i^{-3}\alpha_i[A_i]^2),$$
$$[L_i]' = f_i(R(t))(s_i^{-2}\alpha_i[A_i] + \tfrac{1}{3}\beta_i - s_i^{-3}\alpha_i[A_i][L_i]).$$

Fix i. Using the fact that R is bounded by Theorem 3, we find that under the change of independent variable from t to τ defined by

$$\tau = \int_0^t \frac{ds}{f_i(R(s))}$$

the nonautonomous system (5.1) is transformed to the plane autonomous system

(5.2)
$$[A_i]' = s_i^{-1}\alpha_i[A_i] + \tfrac{2}{3}\beta_i[L_i] - s_i^{-3}\alpha_i[A_i]^2,$$
$$[L_i]' = s_i^{-2}\alpha_i[A_i] + \tfrac{1}{3}\beta_i - s_i^{-3}\alpha_i[A_i][L_i]$$

where "′" now denotes differentiation with respect to τ.

This planar system can be completely analyzed with regard to its global asymptotic dynamics in the positive first quadrant. It is an undergraduate exercise to deduce from the direction field for this system that the closure of the positive quadrant is positively invariant and that there exists a unique nonnegative equilibrium, which is in fact strictly positive. This equilibrium is given analytically in Theorem 4 below.

The 2×2 coefficient matrix of the linearization of (5.2) at the positive equilibrium is straightforwardly shown to have a negative trace and positive determinant, which implies that this equilibrium is locally asymptotically stable. Furthermore, if $V([A_i], [L_i])$ denotes the vector field determined by the right-hand sides of (5.2), then it is easily calculated that the divergence of $[A_i]^{-1}[L_i]^{-1} V([A_i], [L_i])$ is strictly negative in the positive quadrant. Thus the Dulac principle rules out the existence of cyclic trajectories in the positive quadrant. The Poincaré–Bendixson Theorem now implies that all positive solutions of (5.2) approach the unique positive equilibrium.

These facts, together with Lemma 2, yield the following result.

THEOREM 4. *Suppose* (H) *holds. Then for any solution of* (2.9) *we have*

$$\lim_{t \to +\infty} [A_i](t) = \frac{\mu_i s_i^3}{\alpha_i} = z_i(r_i)s_i^2,$$

$$\lim_{t \to +\infty} [L_i](t) = s_i + \frac{\beta_i}{3\mu_i} = \left(1 + \frac{1}{3} \frac{r_i}{z_i(r_i)}\right) s_i.$$

This theorem implies that regardless of the nature of the asymptotic dynamics and of the outcome of the competition governed by the model equations (2.9) the average areas and lengths of the individuals of each species asymptotically approach positive limits. This is true even if an individual species tends to extinction.

Using this result, we can introduce in a meaningful way a measure of the "size" of a species with the idea of studying how this size is related to a species' competitive advantage or disadvantage. For example, we could use the asymptotic average area of an individual as given by Theorem 4 for this purpose; or we could as well use the asymptotic average length of an individual given by the same theorem. For our purposes either of these choices is suitable and leads us to the same qualitative results as does, in fact, any weighted average of these two measures. Consequently, we define the *average individual size* σ_i *of the ith species* to be a weighted average of asymptotic average area and length of individuals as given by Theorem 4.

Note that σ_i depends only on the individual physiological parameters α_i, β_i, and s_i (actually the ratio $r_i = \beta_i / \alpha_i$ and s_i). It does not depend on the resource uptake f_i or the death rate d_i (although the time scale in (5.2), and hence the rate of asymptotic approach to σ_i, does). It has been shown in § 4 that z_i is a strictly increasing function of r_i. It is not difficult to show that the same is true of $r_i / z_i(r_i)$.

LEMMA 3. *The asymptotic size σ_i is a decreasing function of reproductive efficiency α_i and an increasing function of both growth efficiency β_i and the size at birth s_i.*

6. Some applications. In this section two cases are considered for which the reduced system has been well studied in the literature. An application of the results above allow conclusions about these cases in which the competing species are size-structured.

6.1. Size-structured species competing in a chemostat. A chemostat is a laboratory device used for culturing micro-organisms into which a resource (nutrient or substrate) is pumped at a constant rate while a constant volume is maintained by pumping the (assumed well mixed) contents out at the same rate. The rate of change of the resource concentration in the absence of any consumption by micro-organisms in the chemostat is determined by the simple law (2.4) where R_0 is the input concentration of resource rate and d is the washout or dilution rate. It is assumed that the death rate of the competing species is negligible compared to the washout rate so that $d_i = d$ for all i. The chemostat model is also considered to be a reasonable laboratory simulation of a simple naturally occurring lake.

Although a more general case could be analyzed by utilizing the results of Butler and Wolkowicz [3], for simplicity only the case of monotonic resource uptake rates will be considered here, i.e., it is assumed that

$$(6.1) \qquad\qquad f_i(0) = 0, \quad f_i'(R) > 0 \quad \text{for } R > 0.$$

These conditions are certainly satisfied by the frequently used Michaelis–Menten (or Holling type II) uptake rate (2.1). A more detailed discussion of this chemostat model as well as the usefulness of the Michaelis–Menten uptake law can be found in Hsu, Hubbell, and Waltman [10], Waltman [19], Metz and Diekmann [14] and the references cited therein.

The resulting size-structured competition system

$$R' = (R_0 - R)d - \sum_{i=1}^{n} f_i(R)A_i, \qquad\qquad R(0) > 0,$$

$$A_i' = -dA_i + f_i(R)\left(s_i^{-1}\alpha_i A_i + \frac{2}{3}\beta_i L_i \right), \quad A_i(0) > 0,$$

$$(6.2)$$

$$L_i' = -dL_i + f_i(R)\left(s_i^{-2}\alpha_i A_i + \frac{1}{3}\beta_i P_i \right), \quad L_i(0) > 0,$$

$$P_i' = -dP_i + f_i(R)s_i^{-3}\alpha_i A_i, \qquad\qquad P_i(0) > 0$$

can be linearly transformed to the system

$$R' = (R_0 - R)d - \sum_{i=1}^{n} f_i(R)(c_{i1}x_i + c_{i2}y_i + c_{i3}z_i), \qquad R(0) > 0,$$

$$x_i' = -dx_i + \mu_i f_i(R)x_i, \qquad x_i(0) > 0,$$

$$(6.3)$$

$$y_i' = -dy_i + f_i(R)(\gamma_i y_i - \nu_i z_i),$$

$$z_i' = -dz_i + f_i(R)(\nu_i y_i + \gamma_i z_i),$$

which is associated with the reduced system

(6.4)
$$R' = (R_0 - R)d - \sum_{i=1}^{n} c_{i1}f_i(R)X_i, \qquad R(0) > 0,$$

$$X_i' = -dX_i + \mu_i f_i(R)X_i, \qquad X_i(0) > 0.$$

This system has the form of that studied by Butler and Wolkowicz [3] and their results can be used to describe the global asymptotic dynamics of all its solutions. These results can in turn be used to obtain the global asymptotic dynamics of (6.3), and hence (6.2).

For each i define the positive numbers λ_i by the equation

(6.5)
$$d = \mu_i f_i(\lambda_i), \qquad \lambda_i > 0.$$

By the assumed monotonicity of f_i the number λ_i is unique, if it exists. If λ_i does not exist for some i, then $-d + \mu_i f_i(R) < 0$ for all $R > 0$ and it is easy to see from (6.3) that $x_i(t) \to 0$, as $t \to +\infty$. By Theorem 2 this implies that $(A_i(t), L_i(t), P_i(t)) \to 0$, i.e., species i suffers extinction. Thus if λ_i fails to exist for all i then all species suffer extinction. The constant λ_i is the "break even" resource density for species i at which the growth rate of its weighted average x_i is zero; for resource densities below (above) the level λ_i, x_i decreases (increases).

Assume that at least one λ_i exists. Furthermore, assume that these λ_i are distinct. Without loss in generality, the species can be ordered so that

(6.6)
$$\lambda_1 < \lambda_2 < \lambda_3 < \cdots < \lambda_m, \qquad 1 \leqq m \leqq n.$$

Corollary 3.5 of Butler and Wolkowicz [3] implies that $X_i(t) \to 0$ for all $i \geqq 2$ and that

$$R(t) \to \begin{cases} R_0 & \text{if } \lambda_1 > R_0, \\ \lambda_1 & \text{if } \lambda_1 < R_0, \end{cases} \quad \text{and} \quad X_1(t) \to \begin{cases} 0 & \text{if } \lambda_1 > R_0, \\ X_1^* > 0 & \text{if } \lambda_1 < R_0, \end{cases}$$

where $X_i^* = \mu_i(R_0 - \lambda_i)/c_{i1}$. This result for the reduced system (6.4) together with Theorem 2 are used in the Appendix to prove the following result for the competitive system (6.2).

THEOREM 5. *Assume that the uptake rates $f_i(R)$ satisfy (6.1). Let $\mu_i > 0$ be the physiological efficiency coefficient of the ith species, i.e., the dominant eigenvalue of the Leslie matrix M_i given by (3.2). Let I be the set of indices for which equation (6.5) has a positive solution $\lambda_i > 0$ and assume that the λ_i and R_0 are all distinct. Then for every solution of (6.2) the following alternatives hold:*

(a) *If $I = \varnothing$ then $R(t) \to R_0$ and $(A_i(t), L_i(t), P_i(t)) \to 0$ for all i as $t \to +\infty$.*

(b) *Suppose $I \neq \varnothing$ and the species are ordered so that (6.6) holds. Then*

$$(A_i(t), P_i(t), L_i(t)) \to 0 \quad \text{for all } i \geqq 2 \quad \text{as } t \to +\infty$$

and

$$\lambda_1 > R_0 \Rightarrow R(t) \to R_0 \quad \text{and} \quad (A_1(t), L_1(t), P_1(t)) \to 0,$$

$$\lambda_1 < R_0 \Rightarrow R(t) \to \lambda_1 \quad \text{and} \quad (A_1(t), L_1(t), P_1(t)) \to (A_1, L_1, P_1) > 0$$

where

$$A_1 = \mu_1(R_0 - \lambda_1), \qquad L_1 = s_1^{-2}\alpha_1(R_0 - \lambda_1)(3\mu_1 + s_1^{-1}\beta_1)/3\mu_1,$$

$$P_1 = s_1^{-3}\alpha_1(R_0 - \lambda_1).$$

This theorem is consistent with the fundamental competitive exclusion principle in that it implies that at most one species can survive on a single limiting resource. The surviving species is the one with the smallest λ_i value provided this value is less than the input concentration R_0. That is, the winning species is the one that can exploit resource R to the lowest level and survive at that resource level, provided it is below the input concentration R_0.

From the defining equation (6.5) and the assumed monotonicity of the uptake rate f_i it follows that λ_i is inversely related to the efficiency coefficient μ_i. Thus it is to a species' advantage to increase μ_i. By Lemma 2 this can be accomplished by an increase in either the reproductive or the growth efficiency α_i, β_i or by a decrease in the length at birth s_i.

An increase in the efficiency coefficient μ_i does not necessarily correspond to a larger average individual size σ_i, however. By Lemma 3 this would occur if the growth efficiency β_i is increased, but a decrease in average individual size occurs if μ_i is increased by means of either an increase in reproductive efficiency α_i or a decrease in the length at birth s_i.

Thus it is seen that, at least for this competition model, there is no clear cut relationship between competitive success and a species' average individual size σ_i. Competitive success is determined by the parameter λ_i, which is determined through (6.5) not only by the physiological parameters encapsulated in the efficiency coefficient μ_i, but by the resource uptake rate f_i.

At one extreme all species could have identical efficiency coefficients (although quite different physiological parameters α_i, β_i, s_i, and hence different average individual sizes σ_i) in which case the surviving species would be determined solely by the per unit area uptake rate f_i. In this case average individual size is clearly not relevant to competitive exclusion.

Another case is when the species are identical in their per unit area resource uptake rates $f_i = f$ and differ only in their physiological parameters. In this case the ordering (6.6) is equivalent to

$$\mu_1 > \mu_2 > \cdots > \mu_m$$

and the winning species is the one with the largest efficiency coefficient (provided it exceeds a critical value)

$$\mu_1 > \mu_{cr} = d/f(R_0).$$

As can be seen by means of Lemmas 2 and 3, however, the species possessing the largest efficiency coefficient may or may not be the species with the largest average individual size.

For example, consider the case when all species are the same length at birth $s_i = s$ and have the same reproductive efficiency coefficients $\alpha_i = \alpha$. By Lemma 2, μ_i is an increasing function of the growth efficiency coefficient β_i. In this case the surviving species is the one with the largest growth efficiency coefficient (provided it exceeds a critical value) which is in turn, by Lemma 3, the species with the largest average individual size at equilibrium. This conclusion, for this special case, is in agreement with the SEH in that the larger species eliminates the smaller species.

On the other hand, if instead the species differ in this case only in their reproductive efficiency coefficients α_i, then the winning species has the largest α_i, but by Lemma 3 the *smallest* average individual size. In a similar fashion we can see that if the species differ only in their lengths at birth, then the surviving species has the smallest length at birth s_i and again the smallest species average individual size. These cases are not

commensurate with the SEH in that they imply that the smallest competitor eliminates the larger competitors.

Although the model studied in this paper explicitly ignores juvenile states, the results for this latter case could perhaps be interpreted in a very crude way as lending some support for the so-called "juvenile bottleneck" phenomenon [20]. The reasoning is that, all other things being equal, the species with the greatest reproductive efficiency or the smallest length at birth survives by producing a population with a large proportion of young individuals who, by the weight of numbers, exert insurmountable competitive pressure on the other species and prevent them from producing population levels large enough for their larger average individual sizes to become significant.

6.2. Competition for a self-renewable resource. As a second application consider the case when the resource R is a self-renewing population whose inherent dynamics are governed by the logistic equation (2.5). If Michaelis–Menten uptake rates are used, the model equations are as follows:

$$R' = r\left(1 - \frac{R}{K}\right)R - \sum_{i=1}^{n} c_i \frac{R}{a_i + R} A_i, \qquad R(0) > 0,$$

$$A_i' = -d_i A_i + c_i \frac{R}{a_i + R}\left(s_i^{-1}\alpha_i A_i + \frac{2}{3}\beta_i L_i\right), \qquad A_i(0) > 0,$$

(6.7)

$$L_i' = -d_i L_i + c_i \frac{R}{a_i + R}\left(s_i^{-2}\alpha_i A_i + \frac{1}{3}\beta_i P_i\right), \qquad L_i(0) > 0,$$

$$P_i' = -d_i P_i + c_i \frac{R}{a_i + R} s_i^{-3}\alpha_i A_i, \qquad P_i(0) > 0.$$

For the case $n = 2$ of just two competing predator species the reduced transformed system (3.4) becomes

$$R' = r\left(1 - \frac{R}{K}\right)R - \sum_{i=1}^{2} c_{i1} c_i \frac{R}{a_i + R_i} X_i, \qquad R(0) > 0,$$

(6.8) $$X_1' = -d_1 X_1 + \mu_1 c_1 \frac{R}{a_1 + R} X_1, \qquad X_1(0) > 0,$$

$$X_2' = -d_2 X_2 + \mu_2 c_2 \frac{R}{a_2 + R} X_2, \qquad X_2(0) > 0,$$

a system extensively studied by many authors, including Hsu, Hubbell, and Waltman [19], Butler [2], Smith [17], Keener [12], and Waltman [19]. As for the case of the chemostat model, in § 6.1 the results of these authors concerning this reduced system (6.8) can be used to derive corresponding results concerning the asymptotic behavior of solutions of the original size-structure model (6.7). The details for this case will be omitted.

Unlike for the chemostat model in § 6.1, however, the case of a self-renewable resource does not necessarily possess only equilibrium dynamics. The dynamics in this case can be more complicated and do not seem to be completely known for all parameter ranges, although many results have been obtained. Depending on parameter values, cases that can arise are the following: both species go extinct; only one species survives, either in an equilibrium state or in a nonconstant periodic oscillatory state with the resource; or *both* species survive in a nonconstant periodic oscillatory state with the resource. The last case is interesting because it is in opposition to the familiar tenet that only one species can survive on a single resource.

These various cases are determined primarily by the break even concentrations:

$$\lambda_i = a_i d_i / (\mu_i c_i - d_i), \qquad i = 1, 2.$$

In terms of the parameters of (6.8) known results yield the following (see, e.g., Smith [18]). Assume, without loss of generality, that the first species has the smaller λ_i value: $0 < \lambda_1 < \lambda_2$.

If $\mu_i < d_i / c_i$ then $X_i(t) \to 0$, so that the only case of interest is $\mu_i > d_i / c_i$.

If

$$\mu_1 < \mu_1^{cr} = \frac{d_1}{c_1}\left(1 + \frac{a_1}{K}\right),$$

then both species go extinct, i.e., $(X_1, X_2, R) \to (0, 0, K)$. If however $\mu_1 > \mu_1^{cr}$ then the nature of the asymptotic dynamics and the outcome of the competition depends on μ_2 as follows.

If

$$\mu_2 < \mu_2^{cr} = \frac{d_2}{c_2}\left(1 + \frac{a_2}{K}\right),$$

then species X_1 wins, i.e., $X_2(t) \to 0$. In this case there are two possibilities: either X_1 equilibrates or (X_1, X_2, R) approaches (except for a one-dimensional manifold of initial conditions) a nonconstant limit cycle in the face $X_2 = 0$. The former occurs if $K < a_1$ or if $K > a_1$ and $\mu_1 < d_1 c_1^{-1}(K + a_1)(K - a_1)^{-1}$, in which case

$$(X_1, X_2, R) \to (X_1^*, 0, \lambda_1) \quad \text{where } X_1^* = \frac{\lambda_1}{d_1}\left(1 - \frac{\lambda_1}{K}\right) > 0$$

while the latter occurs if $K > a_1$ and $\mu_1 > d_1 c_1^{-1}(K + a_1)(K - a_1)^{-1}$.

If, on the other hand, $\mu_2 > \mu_2^{cr}$ then again X_1 wins with exactly the same possibilities as above if in addition

$$(6.9) \qquad\qquad\qquad \mu_2 < \frac{c_1 d_2}{c_2 d_1} \mu_1.$$

However if the opposite of this inequality holds, then it is possible that both species survive in the sense that there exists a stable nonconstant limit cycle in the positive (X_1, X_2, R) cone. This is analytically known to occur only under certain further parameter constraints, namely for $\lambda_1 \approx \lambda_2$ and for small $a_2 - a_1 > 0$ [18], [12].

If we view these various cases as constraints on the physiological efficiency coefficients μ_i then, as with the chemostat model in § 6.1, we again find that to survive, a species must possess an efficiency coefficient greater than a critical value. If two such species compete then the species with the smaller λ_i value wins (unless the other species has a sufficiently large efficiency coefficient and, in addition, if other system parameter values are appropriately related, in which case the two species might coexist in limit cycle sense).

By Theorem 4 the average individual size of each species is

$$\sigma_i = \frac{d_i s_i^3}{c_i \alpha_i}\left(1 + \frac{a_i}{\lambda_i}\right).$$

Just as in § 6.1 we see that there is in general no definite relationship between the species' average individual sizes and the outcome of the competition.

In passing it is interesting to note that the limit cycle coexistence case can occur only if the species are sufficiently different in the sense that if $s_1 = s_2$, $c_1 = c_2$, $a_1 = a_2$, and $d_1 = d_2$, then $\lambda_1 < \lambda_2$ is equivalent to $\mu_1 > \mu_2$ which implies that (6.9) holds.

7. Concluding remarks. It has been shown above that under certain simplifying assumptions the asymptotic dynamics' of a complicated model for the interaction of an arbitrary number of size-structured species competing for a single resource, can be studied by means of a system of ordinary differential equations for the population level statistics of total number of individuals, total population length, and total population area. Trajectories of the ODE system have been shown to approach an invariant, lower-dimensional positive cone on which the dynamics are governed by a lower-dimensional (transformed) system more amenable to analysis and, in many cases, subject to known global results. This approach is used in § 6 to study two specific size-structured competition systems that are appropriate for zooplankton communities.

Two simplifying assumptions have been made in the derivation of the ODE system (2.9)(a)-(2.9)(d). It has been assumed that for the individuals of each species the energy utilized for metabolic maintenance is negligible relative to the energy used for growth and reproduction. Second, juvenile stages have been ignored.

With a slight modification in the model a similar methodology can be carried out, to a certain point at least, on a model that includes metabolic maintenance costs. In the model (2.6) of Diekmann et al. the growth of individuals is never permitted to be negative, i.e., while growth may cease, individuals do not shrink in size. This is a reasonable assumption for organisms of the type that Diekmann et al. had in mind (*Daphnia* have a hard external shell that does not appreciably shrink even during periods of starvation). If, on the other hand, the growth rate is allowed to assume negative values and we replace $g(R, s)$ in § 2 by

$$g(R, s) = \frac{1}{3\eta} \left(\kappa f(R) - \zeta s \right)$$

then the same manipulations that lead to the system (2.9) for A_i, L_i, and P_i, now lead to the same system again but with modified death rates d_i. Specifically, the d_i in equations (2.9)(b) and (2.9)(c) are replaced by $d_i + 2\zeta_i/3\nu_i\eta_i$, $d_i + \zeta_i/3\nu_i\eta_i$. Unfortunately a linear change of variables no longer uncouples the system as it did in § 2. Nonetheless we still have a more tractable size-structured competition model of ordinary differential equations and one that may be useful in analyzing this case.

The inclusion of a juvenile period in size-structured competition models would be of interest since the presence of juveniles is known to be important for many species interactions [20]. The juvenile bottleneck phenomenon mentioned in § 6 is one case in point. The key points of the approach taken above can be derived heuristically in another manner that in fact does allow for the inclusion of a juvenile period. Write the PDE in (2.6) as follows:

$$\frac{d}{dt} \rho_i = -d_i \rho_i + f_i(R) B_i \rho_i$$

where B_i is the appropriate differential operator. If the "ansatz"

$$\rho_i(t, \cdot) = a_i(t) n_i \left(\int_0^t f_i(R) \, d\tau, \cdot \right)$$

is plugged into this equation, the result can be decoupled into the following pair of equations:

$$\frac{d}{dt} n_i = B_i n_i - \mu_i n_i, \qquad \frac{d}{dt} a_i = (-d_i + \mu_i f_i(R)) a_i.$$

Here μ_i is an arbitrary constant, but under suitable hypotheses on B_i, if μ_i is taken as the dominant eigenvalue, then we can show that n_i converges as $t \to +\infty$ to the dominant eigenvector of B_i and consequently that the asymptotic behavior of ρ_i is determined by the scalar equation for a_i. Presumably, with enough work, this heuristic approach can be made mathematically rigorous and in this way we can arrive at the asymptotic equations (3.4) and the "ergodic" results of § 5 even with a juvenile stage, although information about the important dominant eigenvalue μ_i may be more difficult to obtain in this case.

In this paper we have considered only one of the basic tenets of the Size Efficiency Hypothesis (SEH), namely that larger species have a competitive edge over smaller species. The other primary assumption of the SEH, that size specific predation can determine the structure of a competitive community of size-structured species, is not addressed. By the addition of a predator species to the model system, the approach taken here should be fruitful for this problem as well, especially in light of recent results on predator mediated competition for unstructured populations [4] which could be used to study the asymptotic limiting equations.

Another interesting modification of the model would be the incorporation of size-structure in the resource population R, as there is a great deal of biological literature on the importance of food particle size in the population dynamics of micro-organisms [9].

Appendix.

Proof of Theorem 1. Suppose R is not positive for all time and let $T > 0$ be the first time at which R vanishes. Then $R'(T) \leqq 0$ and $R'(T) = k(0)$ by (2.9)(a). If $k(0) > 0$, this is a contradiction. If $k(0) = 0$, then by uniqueness $R \equiv 0$, which contradicts $R(0) > 0$. Thus R must be positive for all time.

Next, suppose that A_i is not positive for all time and let $T_A > 0$ be the first time at which A_i vanishes. Then $A_i'(T_A) \leqq 0$ and (2.9)(b) imply $L_i(T_A) \leqq 0$. If $T_L > 0$ is the first time at which L_i vanishes, then it follows that $T_L \leqq T_A$. A similar argument using equation (2.9)(c) shows that P_i must have a first time $T_P \leqq T_L$ at which it vanishes and $P'(T_P) \leqq 0$. Finally the last equation (2.9)(d) with $t = T_P$ shows that $A(T_P) \leqq 0$, and hence $T_A \leqq T_P$, which in turn implies $T_A = T_L = T_P = T$. Thus A_i, L_i, and P_i simultaneously vanish at this time $T > 0$. It follows from equations (2.9)(b)–(2.9)(d) and uniqueness that A_i, L_i, and P_i are all identically zero for all time, in contradiction to the positivity of their initial conditions. Thus A_i is positive for all time.

Suppose that L_i is not positive for all time and has a first zero $T_L > 0$ where $L_i'(T_L) \leqq 0$. Equation (2.9)(c) implies that $P_i(T_L) \leqq 0$ and consequently that P_i has a first zero at a time $T_P \leqq T_L$ at which $P_i'(T_P) \leqq 0$. Equation (2.9)(d) now implies the contradiction that $A(T_P) \leqq 0$. Thus L_i is positive for all time.

Finally suppose that P_i is not positive for all time and has a first zero $T_P > 0$ where $P_i'(T_P) \leqq 0$. Equation (2.9)(d) implies the contradiction that $A(T_P) \leqq 0$. $\square$

Proof of Lemma 1. Since both α_i and β_i are nonzero, the Leslie matrix M_i is irreducible and primitive and as a result the well-known Perron–Frobenius theory implies the first sentence in Lemma 1.

With regard to the other two eigenvalues of M_i consider the characteristic polynomial (4.1). Since

$$h'(\mu) = 3\mu^2 - 2s_i^{-1}\alpha_i\mu - \tfrac{2}{3}s_i^{-2}\alpha_i\beta_i,$$

the following facts are easily seen: $h(0) < 0$, $h'(0) < 0$, and h has two critical points $\mu_- < 0$, $\mu_+ > 0$ at which h has a relative maximum and minimum, respectively. Clearly,

if $h(\mu_-) < 0$, then h has only one real root, namely the positive root μ_i. But from $h'(\mu_-) = 0$ follows

$$\frac{2}{3} s_i^{-2} \alpha_i \beta_i \mu_- + \frac{2}{9} s_i^{-3} \alpha_i \beta_i^2 = \frac{\beta_i}{s_i} \mu_-^2,$$

which when substituted into $h(\mu_-)$ yields

$$h(\mu_-) = \mu_-^2 (\mu_- - s_i^{-1}(\alpha_i + \beta_i)) < 0.$$

Finally from the first-order coefficient in $h(\mu)$ it is seen that

$$0 > -\tfrac{2}{3} s_i^{-2} \alpha_i \beta_i = 2\mu_i \gamma_i + \gamma_i^2 + \nu_i^2,$$

which implies $\gamma_i < 0$.   □

Proof of Theorem 2. If equations (3.3)(c)–(3.3)(d) are multiplied by

$$\Gamma_i(t) = \exp\left(d_i t - \gamma_i \int_0^t f_i(R(u))\, du \right)$$

and if

$$\bar{y}_i(t) = y_i(t)\Gamma_i(t), \quad \bar{z}_i(t) = z_i(t)\Gamma_i(t),$$

then equations (3.3)(c)–(3.3)(d) can be rewritten as

$$\bar{y}_i' = -\nu_i f_i(R)\bar{z}_i, \quad \bar{z}_i' = \nu_i f_i(R)\bar{y}_i$$

from which it follows that $\bar{y}_i^2 + \bar{z}_i^2$ is constant, i.e., $\bar{y}_i^2(t) + \bar{z}_i^2(t) = \bar{y}_i^2(0) + \bar{z}_i^2(0)$ or $y_i^2(t) + z_i^2(t) = (y_i^2(0) + z_i^2(0))/\Gamma_i^2(t)$. Since $f_i(R)$ is positive and γ_i is negative this implies

$$y_i^2(t) + z_i^2(t) \leq (y_i^2(0) + z_i^2(0)) \exp(-2d_i t).   □$$

Proof of Theorem 3. It has already been shown that $y_i(t)$ and $z_i(t)$ are bounded and that $R(t)$ is positive for $t \geq 0$. Since the eigenvector v_i is positive and since $p_i(t)$ is positive by Theorem 1, $x_i(t) = v_i^t p_i(t)$ is positive for all $t \geq 0$ and all i. From Theorem 1 and (2.9)(a) it follows that $R' \leq k(R)$ and hence by (H) and standard comparison theorems that $R(t)$ is bounded for $t \geq 0$.

Add together equations (3.3)(b) multiplied by c_{i1}/μ_i and add the result to equation (3.3)(a) to obtain

$$R' + \sum_{i=1}^n \frac{c_{i1}}{\mu_i} x_i' = k(R) - \sum_{i=1}^n d_i \frac{c_{i1}}{\mu_i} x_i - \phi(t)$$

where

$$\phi = -\sum_{i=1}^n f_i(R)(c_{i2} y_i + c_{i3} z_i) \to 0 \quad \text{as } t \to +\infty.$$

Let $d = \min\{d_i\} > 0$ and

$$w(t) = R(t) + \sum_{i=1}^n c_{i1} x_i(t)/\mu_i.$$

Then $w(t) \geq 0$ and $w' \leq k(R) - d \sum_{i=1}^n c_{i1} x_i/\mu_i - \phi$ or

$$w'(t) + dw(t) \leq \psi(t), \qquad \psi = k(R) + dR - \phi.$$

Since $\psi = \psi(t)$ is bounded and $d > 0$ it follows that $w(t)$ is bounded for $t \geq 0$. From this and the positivity of R and x_i follows the boundedness of x_i. □

Proof of Theorem 5. (a) If $I = \varnothing$ then, as was shown just preceding Theorem 5, $(A_i(t), L_i(t), P_i(t)) \to 0$ for all i as $t \to +\infty$. It follows easily from (6.2)(a) that $R(t) \to R_0$.

(b) If $I \neq \varnothing$, then the remarks preceding Theorem 5 show that $(A_j(t), L_j(t), P_j(t)) \to 0$ for all $j > m$. Let Γ be the trajectory associated with a solution $(R, x_1, y_1, z_1, \cdots, x_n, y_n, z_n)$ of the transformed system (6.3) and let Ω be its ω-limit set. Theorems 1–3 imply that Ω lies in the invariant face $R \geq 0$, $x_i \geq 0$, $y_i = z_i = 0$ for all i. Let e_0 denote the equilibrium $(R_0, 0, 0, \cdots, 0)$ of (6.3) and let e_j, for $j \in I$, denote the equilibrium of (6.3) for which $R = \lambda_j$, $y_i = z_i = 0$ for all i, $x_i = 0$ for all $i \neq j$ and $x_j = X_j^* > 0$. Finally let

$$E_j = \begin{cases} e_0 & \text{if } j \notin I \quad \text{or} \quad j \in I \quad \text{and } \lambda_j > R_0, \\ e_j & \text{if } j \in I \quad \text{and} \quad \lambda_j < R_0. \end{cases}$$

(i) First suppose that Ω contains a point P whose x_1 component is positive. The trajectory Γ_P associated with the solution of (6.3) through P is also a trajectory of the reduced system (6.4) through P because $P \in \Omega$ lies in the invariant face $y_i = z_i = 0$ for all i. The invariance of the w-limit set Ω implies $\Gamma_P \subseteq \Omega$. Corollary 3.5 of Butler and Wolkowicz [3] implies, since the x_1 component of P is positive, that the ω-limit set of Γ_P is the equilibrium E_1. Thus $E_1 \in \Omega$. A straightforward linearization of (6.3) at E_1 shows that E_1 is asymptotically stable. Thus $\Omega = \{E_1\}$ and $\Gamma \to E_1$.

In summary, in this case, $1 \in I$ and $\lambda_1 < R_0$ implies $\Gamma \to e_1$, while either $1 \notin I$ or $1 \in I$ and $\lambda_1 > R_0$ leads to a contradiction since $E_1 = e_0$ has a zero x_1 component. We conclude that in the latter event Ω must lie in the face $x_1 = 0$, $y_i = z_i = 0$ for all i, a case that is considered next.

(ii) Suppose that Ω lies in the face $x_1 = 0$, $y_i = z_i = 0$ for all i. Suppose, however, that there exists a point $P \in \Omega$ with a positive x_2 component. The trajectory Γ_P of (6.3) through $P \in \Omega$ lies in this face and is also a trajectory of the reduced system (6.4) reduced further by elimination of x_1 (i.e., (6.4) with $x_1 = 0$) for which Corollary 3.5 of Butler and Wolkowicz [3] implies that the ω-limit set of Γ_P is the equilibrium E_2.

Next it will be shown that Γ approaches E_2, i.e., $\Omega = \{E_2\}$. Since Γ approaches its ω-limit set, it follows by Theorem 2 that $x_1(t) \to 0$ and $y_i(t) \to 0$, $z_i(t) \to 0$. Consequently, the system

$$R' = (R_0 - R)d - \sum_{i=2}^{n} c_{i1} f_i(R) x_i$$
$$+ \left(-c_{11} f_1(R) x_1 + \sum_{i=1}^{n} f_i(R)(c_{i2} y_i + c_{i3} z_i) \right),$$
$$x_i' = -dx_i + \mu_i f_i(R) x_i, \qquad i = 2, \cdots, n$$

obtained from (6.3) by ignoring the equation for x_1, which the solution $(R, x_1, y_1, z_1, \cdots, x_n, y_n, z_n)$ automatically solves, is asymptotic to the system

$$R' = (R_0 - R)d - \sum_{i=2}^{n} c_{i1} f_i(R) X_i,$$
$$X_i' = -dX_i + \mu_i f_i(R) X_i, \qquad i = 2, \cdots, n.$$

A straightforward linearization of this system shows that E_2 is asymptotically stable in the face $x_1 = 0$ as an equilibrium of this system. Since $P \in \Omega$, the invariance and compactness of the limit set Ω implies $\Gamma_P \subset \Omega$ and $E_2 \in \Omega$. A theorem of Markus [13]

(see also Hsu et al. [11]) applied to these two systems yields the desired result that $\Omega = \{E_2\}$.

If $2 \notin I$ or $2 \in I$ and $\lambda_2 > R_0$, then $\Omega = \{e_0\}$, which is a contradiction since e_0 does not have a positive x_2 component.

If $2 \in I$ and $\lambda_2 < R_0$, then $\Omega = \{e_2\}$. However, a linearization of (6.3) at e_2 shows that the stable manifold of e_2 lies in the invariant face $x_1 = y_i = z_i = 0$. This is also a contradiction since Γ does not lie in this face.

Consequently, in this case there exists no point P in Ω which has a positive x_2 component, i.e., Ω must lie in the invariant face $x_1 = x_2 = 0$, $y_i = z_i = 0$.

The above argument can be repeated, with obvious modifications and with E_2 replaced by E_3, if Ω contains a point P with a positive x_3 component, and so on until the conclusion that $\Omega = \{e_0\}$ is reached.

(iii) Suppose $1 \in I$ and $\lambda_1 < R_0$. By (i) and (ii) either $\Omega = \{e_1\}$ or $\{e_0\}$. But a linearization of (6.3) shows that in this case e_0 is unstable with its stable manifold contained in the invariant face with $x_1 = 0$. Since Γ is not in this face Ω cannot be $\{e_0\}$ and hence $\Omega = \{e_1\}$.

(iv) The following conclusions result from (i)-(iii): If either $1 \notin I$ or $1 \in I$ and $\lambda_1 > R_0$ then $\Omega = \{e_0\}$, while if $1 \in I$ and $\lambda_1 < R_0$ then $\Omega = \{e_1\}$. This is equivalent to Theorem 5(b).

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