

SOME COMPETITION MODELS FOR SIZE-STRUCTURED POPULATIONS

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1. Introduction. Ordinary differential equations (ODE's) have long played a central role in the history of theoretical ecology. Nonlinear systems of ordinary differential equations, as exemplified by either the famous classical models of A. Lotka and V. Volterra or any of the vast number of other models that can be found in the literature, have been used to provide theoretical support for many of the well established principles in both theoretical and field ecology, principles such as competitive exclusion, ecological niche, predator-prey oscillations, etc. Such models continue today to serve, and will no doubt continue to serve for some time to come, as valuable tools for investigating the qualitative implications of various ecological assumptions and situations.

ODE models for the dynamics of multispecies interactions are, of course, based upon a great many simplifying assumptions. It was, in fact, an explicit goal of the early investigators to attempt to provide some measure of understanding of the extraordinarily complex biological world by focusing on simple, but key, principles. As a part of the natural development of the subject researchers extended and continue to extend the models in such a way as to incorporate more realistic features, while always being confronted by the brutal trade-off between complexity and analytical tractability.

Most of the sophistications of the classical ODE models (and their innumerable offspring) address the assumed homogeneities in these models. ODE models are almost exclusively based upon a description of the rates of change of some population level statistic such as number of individuals, total biomass or dry weight, etc. They generally assume a homogeneous environment, in space and time, and homogeneous populations made up of identical individuals. Spatial inhomogeneities have been widely investigated in recent years by means of partial differential ("reaction-diffusion") equations (and by compartmental

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ODE models as well). To a lesser degree the effects of environmental fluctuations, both stochastic and regularly periodic, have also been studied using nonautonomous versions of established model equations.

Almost totally unexplored, however, are the effects of inhomogeneities within species on multispecies interactions due to important physiological differences between individual members of both the same and different species making up the community. Such physiological differences can be due to any number of factors: chronological age, body size or weight, life-cycle stages, morphological differences, genetical variants, etc. A fundamental question in so-called “structured” population dynamics is how such physiological differences at the level of the individual relate to the dynamics of population level statistics.

Although models of structured populations have only relatively recently attracted a great deal of attention and interest, there is a long research tradition dealing with one type of structured population, namely age-structured populations. Developed mainly by demographers interested in human populations, age-structured population dynamics was, until recently, primarily a linear theory for the growth of a single isolated population. Within the last few years the fundamental theory of nonlinear age-structured populations and even interacting age-structured populations has reached a high level of sophistication and completeness (Webb [7]). Nonetheless, with the exception of some age-structured predator-prey models, the detailed investigation of specific age-structured ecological models is still in its infancy. For example, there is very little in the literature dealing with models of competition between age-structured species.

It is frequently pointed out by biologists that age, however, often is not (some would say rarely is) the important determining factor in a population’s dynamics, but that body “size” is the relevant physiological factor. Clearly size is one of the most important attributes of an individual organism. It is significant in determining an organism’s energetic requirements and ability to exploit resources for growth and reproduction and its interaction with its physical and biological environment, including predators, prey, and competitors (Werner and Gilliam [8]).

Zooplankton communities provide one example in which size structure has been of primary significance in the study of multispecies in-

teractions. The importance of individual body size in determining the structure of zooplankton communities can be found in the overwhelming attention paid to it in zooplankton research literature and in the formulation of the so-called “size efficiency hypothesis” (SEH) (Brooks and Dodson [1]). The basic tenets of this hypothesis are that large size zooplankton species are more efficient resource exploiters, providing the means for competitively excluding smaller species, and that size specific predation by large bodied predators, which falls more heavily on the large bodied zooplankton, can mediate this exclusion of small 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 (Hall et al. [4]). Although the SEH has fallen somewhat into disuse in recent years, it is not due to the lack of importance of size structure in zooplankton communities, but, on the contrary, to the realization that the dynamics is even more complicated than had been originally thought.

The importance of body size in competition interactions in a broad range of taxa is stressed in the survey article by Werner and Gilliam [8]. They also discuss the importance of body size in other types of interactions as well and, even more interestingly, how size- and stage-structured populations can have such complicated interactions as to defy the usual classifications of competition, predator-prey, mutualism, etc. Werner and Gilliam point out the almost total lack of mathematical modeling of size-structured ecological interactions.

The purpose of this paper is to derive and study a competition model for m size-structured species attempting to exploit a single (unstructured) resource. Under certain explicitly stated simplifying assumptions, including a key assumption that resource uptake rates are proportional to a power of body length, it is shown how the dynamics of certain population level statistics are governed by a system of ODE's. The assumptions of the model, while retaining a certain degree of generality, are particularly relevant to small organisms such as zooplankton.

The positivity and boundedness of solutions are proved (Theorems 1 and 3), and it is shown that the asymptotic dynamics are governed by a reduced, transformed competition ODE system of a general type appearing in the literature for unstructured populations (Theorem 3). However, the models considered here, unlike the usual ODE

competition models, include parameters related to basic physiological properties of individual members of the species.

Regardless of the asymptotic dynamics of these models, it is proved that the average size of individuals in each species (i.e., average individual body length, surface area or volume) asymptotically equilibrates to a positive value. This result provides a way by which the “size” of a species can be compared to its competitive effectiveness or vulnerability. These results are illustrated by an application to competition in a chemostat, to which results of Butler and Wolkowicz [2] can be applied.

2. Models of size-structured population growth. In order to build a dynamical model for the growth of a population it is necessary to specify submodels for the rate of additions to and removals from the population, i.e., to describe how these vital rates depend on physical environmental parameters, on interactions with other biological species, on physiological properties of individuals, etc. For “structured” populations in which individuals have been categorized within the population, it is also necessary to describe rates at which individuals transfer between the specified categories. In particular, for populations in which an individual’s size is an important factor affecting vital birth and survival rates (or is otherwise of interest), it is necessary to build a submodel for the growth rate of individuals.

When these submodels are given, the dynamics of a population density $\rho = \rho(t, s)$ can be described by means of balance equations involving the hyperbolic first order partial differential equations below. Here, t is time and s is a measure of size, such as body length, surface area, or volume. If b and d denote per unit density birth and removal rates and if $g = ds/dt$ denotes the growth rate, then

$$(2.1) \quad \partial_t \rho + \partial_s (g\rho) = -d\rho, \quad t > 0, s > s_B,$$

$$(2.2) \quad g\rho|_{s=s_B} = \int_{S_J}^{\infty} b\rho ds, \quad t > 0,$$

describe the rate of change of density (due to removals) and the rate of additions (due to births), respectively, under the assumption that

all newborns have the same length s_B and only individuals of length greater than a juvenile length $s_J \geq s_B$ reproduce. In general, the submodels must specify g , b , and d as functions of t , s , and ρ , as well as possibly other important parameters such as food resource densities, densities of other interacting populations, physiological parameters of individuals such as metabolic rates, resource uptake rates, reproductive efficiencies, etc. Thus, these equations are, in general, nonlinear. Coupled with an initial condition $\rho(0, s) = \rho_0(s)$, they presumably determine the future density as a function of time. See Metz and Diekmann [5] for an in-depth treatment of this modeling procedure.

The growth rate g depends on the ability of an individual to obtain and assimilate food resources. This ability may depend significantly on the size of the individual as well as on the density of the resource, which we denote by R . The assimilated resource is then allocated between growth, reproductive, and metabolic (respiration) processes (assimilated food can also be stored, but this is ignored here). There is considerable biological evidence that growth, reproductive, and metabolic rates scale exponentially to body length l (Werner and Gilliam [8], Hall et al. [4]).

Suppose that the resource uptake rate is given by ul^γ i.e., is proportional to l^γ for some $\gamma > 0$. If some portion of consumed resource is utilized for metabolism, then there is a net amount of resource available for growth and reproduction. Hall et al. conclude (for microorganisms such as appear in zooplankton communities at least) that "it is generally safe to express the difference between assimilation rate . . . and respiration rate as an increasing exponential function of body length." In accordance with this law suppose that the resource utilized for growth and reproduction is assimilated at a net rate nl^γ so that weight change is given by $dw/dt = \kappa nl^\gamma/\eta$, where κ is the fraction of this available resource allocated to growth and η is a conversion factor relating weight to resource units. Then

$$g = \frac{\kappa nl^\gamma}{\eta} \frac{ds}{dw}.$$

The remaining fraction of available resource is assumed allocated to reproduction so that

$$b = \frac{1 - \kappa}{\omega w_B} nl^\gamma.$$

Here ω is a resource to offspring conversion factor and w_B is the weight of newborns. If volume (via an appropriate choice of units) is interpreted as weight, then $w = l^3$ and $w_B = l_B^3$, where l_B is the length at birth.

The dependence of resource uptake on resource density R is expressed by $u = u(R)$, $n = n(R)$.

Typical values for γ for many species of zooplankton lie between 2 and 3 (Hall et al. [4]). The two cases $\gamma = 2$ and 3 will be considered here, i.e., resource uptake and net resource availability for growth and reproduction scale to body surface area and body volume or weight, respectively.

MODEL I. For $\gamma = 3$, it is convenient to use volume $s = w = l^3$ as the structuring variable in the model above. Thus

$$(2.3a) \quad g = \beta n(R)s$$

$$(2.3b) \quad b = \alpha s_B^{-1} n(R)s,$$

where

$$\alpha = (1 - \kappa)/\omega, \quad \beta = \kappa/\eta.$$

MODEL II. For $\gamma = 2$, simpler equations result if we use length $s = l$, so that

$$(2.4a) \quad g = \frac{\beta}{3} n(R)$$

$$(2.4b) \quad b = \alpha s_B^{-3} n(R)s^2.$$

Finally, in this paper the simple assumption that deaths or removals occur independently of size or time is made so that

$$(2.5) \quad 0 < d = \text{constant}.$$

Equations (2.1)–(2.2), together with (2.5) and (2.3) or (2.4), constitute the basic size-structured growth model to be considered here.

They will be coupled with a dynamical equation for the growth of the resource species $R = R(t)$ of the form

$$\frac{dR}{dt} = k(R) - u(R)S,$$

where $k(R)$ describes the resource dynamics in the absence of the predator species and where

$$S(t) = \begin{cases} \int_{s_B}^{\infty} w\rho(t, w) dw = \text{total population volume for } \gamma = 3 \\ \int_{s_B}^{\infty} l^2\rho(t, l) dl = \text{total population surface area for } \gamma = 2. \end{cases}$$

More generally, we will be interested in the case when $m \geq 1$ species utilize and compete for the resource R , in which case m systems of these equations are coupled:

$$(2.6) \quad \partial_t \rho_i + \partial_s (g_i \rho_i) = -d_i \rho_i, \quad t > 0, s > s_{B_i}$$

$$(2.7) \quad g_i \rho_i|_{s=s_{B_i}} = \int_{s_{J_i}}^{\infty} b_i \rho_i ds, \quad t > 0$$

$$(2.8) \quad \frac{dR}{dt} = k(R) - \sum_{i=1}^m u_i(R)S_i,$$

where

$$(2.9) \quad g_i = \begin{cases} \beta_i n_i(R) s & \text{for Model I when } s = w \\ \beta_i n_i(R) / 3 & \text{for Model II when } s = l \end{cases}$$

$$(2.10) \quad b_i = \begin{cases} \alpha_i s_{B_i}^{-1} n_i(R) s & \text{for Model I when } s = w \\ \alpha_i s_{B_i}^{-3} n_i(R) s^2 & \text{for Model II when } s = l. \end{cases}$$

Let $\mathbf{R}_+ = [0, +\infty)$. It will be assumed throughout that

$$(H1) \quad u_i, n_i : \mathbf{R}_+ \rightarrow \mathbf{R}_+ \text{ and } k : \mathbf{R}_+ \rightarrow \mathbf{R} \text{ are once continuously differentiable with } u_i(0) = 0, n_i(0) = 0, k(0) \geq 0.$$

3. Two specific models. The treatment of the model equations (2.6)–(2.10) will be carried out by reducing them to an equivalent and more tractable system of ordinary differential equations for appropriate population level statistics for each species. This will be done under the simplifying assumption that the juvenile period is insignificant, i.e., that

$$s_{J_i} = s_{B_i}.$$

Define $s_i = s_{B_i}$, $w_i = w_{B_i}$, and $l_i = l_{B_i}$.

(a) *Model I.* Equations for the rates of change of the moments

$$S_i = W_i = \int_{w_i}^{\infty} \rho_i(t, w) w \, dw, \quad P_i = \int_{w_i}^{\infty} \rho_i(t, w) \, dw,$$

can be derived by integrating equation (2.6), multiplied by w^ν for $\nu = 0$ and 1, with respect to w from $w = w_i$ to ∞ and using (2.7). This results in

$$(3.1) \quad R' = k(R) - \sum_{i=1}^m u_i(R) W_i$$

$$(3.2) \quad W_i' = (-d_i + (\alpha_i + \beta_i) n_i(R)) W_i$$

$$(3.3) \quad P_i' = -d_i p_i + \alpha_i w_i^{-1} n_i(R) W_i$$

$$(3.4) \quad R(0) > 0, \quad W_i(0) > 0, \quad P_i(0) > 0.$$

The parameters

$$\alpha_i = (1 - \kappa_i)/\omega_i, \quad \beta_i = \kappa_i/\eta_i$$

will be referred to as *reproductive and growth efficiency coefficients*, respectively.

(b) *Model II.* Equations for the rates of change of the moments

$$S_i = A_i = \int_{l_i}^{\infty} \rho_i(t, l) l^2 \, dl,$$

$$L_i = \int_{l_i}^{\infty} \rho_i(t, l) l \, dl, \quad P_i = \int_{l_i}^{\infty} \rho_i(t, l) \, dl,$$

which are the total area, total length and total number of all individuals, respectively, can be derived from (2.6) by integrating equation

(2.6), multiplied by $l^\nu, \nu = 0, 1,$ and $2,$ with respect to l from $l = l_i$ to ∞ and using (2.7). The resulting equations can be written in matrix form:

$$(3.5) \quad \frac{dR}{dt} = k(R) - \sum_{i=1}^m u_i(R)A_i$$

$$(3.6) \quad P_i' = -d_i p_i + n_i(R)M_i^t p_i$$

$$(3.7) \quad R(0) > 0, \quad p_i(0) > 0$$

where $p_i = \text{col}(A_i, L_i, P_i)$ and

$$(3.8) \quad M_i = \begin{pmatrix} \alpha_i/l_i & \alpha_i/l_i^2 & \alpha_i/l_i^3 \\ 2\beta_i/3 & 0 & 0 \\ 0 & \beta_i/3 & 0 \end{pmatrix}.$$

For each i the matrix M_i has the form of a Leslie matrix. Some facts about this matrix will be needed below. The Perron-Frobenius theory tells us that M_i possesses a positive, strictly dominant eigenvalue, which we will denote by $\mu_i > 0,$ and that this eigenvalue is associated with strictly positive right and left eigenvectors $v_i > 0, w_i > 0.$ An investigation of the cubic characteristic polynomial of M_i shows that the remaining two eigenvalues are complex conjugates with negative real part $\gamma_i < 0$ and imaginary part $\nu_i \neq 0.$

The eigenvalue μ_i will play an important role below. It is important to notice that it depends on (and only on) the physiological parameters $l_i, \alpha_i,$ and β_i of the i -th species. In particular, it does not depend upon the resource uptake rates u_i and n_i or the resource dynamics $k.$ Thus μ_i encapsulates the physiological properties of individuals in the model for the population level dynamics.

The nature of the dependence of μ_i on the length at birth $l_i,$ the reproductive efficiency coefficient α_i and the growth rate efficiency coefficient β_i was studied by Cushing [3]. It turns out that it can be written in the form

$$(3.9) \quad \mu_i = \alpha_i z_i(r_i)/l_i, \quad r_i = \beta_i/\alpha_i,$$

where z_i is a strictly increasing function of its argument with $z_i(0) = 1.$ Thus μ_i is an increasing function of β_i and a decreasing function of $l_i.$ It can also be shown that μ_i is an increasing function of $\alpha_i.$

4. Positivity. First we show that the positive cone is positively invariant under the dynamics of Models I and II.

THEOREM 1. *The solutions of Models I and II, respectively, remain positive for all time $t > 0$.*

PROOF. (a). From equations (3.1)–(3.3) it is easy to see that $W_i(t)$ and $P_i(t)$ are positive. If $R(t)$ vanishes at a first point $t_0 > 0$, then $0 \geq R'(t_0) = k(0)$, which is an immediate contradiction if $k(0) > 0$. If $k(0) = 0$, then, by uniqueness, $R(t) \equiv 0$, another contradiction.

(b). A similar argument shows $R(t) > 0$ for equations (3.5)–(3.7) as well. Let i be arbitrary but fixed. Suppose now that $t_i > 0$ is the first point at which at least one component of p_i vanishes. Say $A_i(t_i) = 0$, the following argument being similar if it should be that either L_i or P_i vanishes first. Then $A_i(t) > 0$, $L_i(t) > 0$, and $P_i(t) > 0$ for $0 \leq t < t_i$. From the first component of the system (3.6), follows

$$A_i(t) = A_i(0)e^{-d_i t} + \int_0^t e^{-d_i(t-s)} \psi(s) ds$$

$$\psi(t) = n_i(R) \left(\frac{\alpha_i}{s_i} A_i + \frac{2}{3} \beta_i L_i \right).$$

Since $\psi(t) \geq 0$ on $[0, t_i]$ it follows that $A_i(t_i) > 0$. This contradiction shows that no such t_i exists. \square

5. Asymptotic average size. It is proved in this section that, regardless of the asymptotic dynamics implied by either Model I or II, the average “size” of individuals in each species asymptotically equilibrates. This result permits a comparison between competitive success and the “size” of a species, where, by “size,” is meant the asymptotic average volume, surface area or length of an individual.

Define the averages

$$[W_i](t) = W_i(t)/P_i(t), \quad [A_i](t) = A_i(t)/P_i(t), \quad \text{etc.}$$

For Model I an easy calculation using equations (3.2)–(3.3) shows that $[W_i]$ solves the equation

$$[W_i]' = n_i(R) \left(\alpha_i + \beta_i - \frac{\alpha_i}{w_i} [W_i] \right) [W_i].$$

A change of variables $\tau_i = \int_0^t d\sigma/n_i(R(\sigma))$ yields the logistic equation

$$\frac{d}{d\tau_i}[W_i] = \left(\alpha_i + \beta_i - \frac{\alpha_i}{w_i}[W_i] \right) [W_i].$$

Consider Model II. From the component equations of (3.6) one can straightforwardly calculate

$$\begin{aligned} [A_i]' &= n_i(R) \left(l_i^{-1} \alpha_i [A_i] + \frac{2}{3} \beta_i [L_i] - l_i^{-3} \alpha_i [A_i]^2 \right) \\ [L_i]' &= n_i(R) \left(\frac{1}{3} \beta_i + l_i^{-2} \alpha_i [A_i] - l_i^{-3} \alpha_i [A_i] [L_i] \right). \end{aligned}$$

Using the same change variable $t \rightarrow \tau_i$, we can transform this system to the plane autonomous system

$$(5.1) \quad \begin{aligned} \frac{d}{d\tau_i}[A_i] &= l_i^{-1} \alpha_i [A_i] + \frac{2}{3} \beta_i [L_i] - l_i^{-3} \alpha_i [A_i]^2 \\ \frac{d}{d\tau_i}[L_i] &= \frac{1}{3} \beta_i + l_i^{-2} \alpha_i [A_i] - l_i^{-3} \alpha_i [A_i] [L_i]. \end{aligned}$$

It is easy to verify from the direction field associated with (5.1) that the positive quadrant $[A_i], [L_i] \geq 0$ is positively invariant and all trajectories in the positive quadrant are bounded. It is also easy to show that there exists a unique equilibrium in this quadrant (which is given by the limits in the statement of Theorem 2 below) and that this equilibrium is locally asymptotically stable. If the divergence of the vector field defined by the right-hand sides of (5.1) multiplied by $[A_i]^{-1}[L_i]^{-1}$ is taken, then it will be found that the result is negative in the positive quadrant. Consequently, by Dulac's principle, there are no limit cycles in this quadrant.

These facts, together with an application of the Poincaré-Bendixson theorem, imply that all positive trajectories approach the unique positive equilibrium.

We summarize these facts in the following Theorem.

THEOREM 2. *For all solutions of Model I,*

$$[W_i](t) \rightarrow (1 + \beta_i/\alpha_i)w_i$$

and, for all solutions of Model II,

$$[A_i](t) \rightarrow \mu_i l_i^3 / \alpha_i > 0, \quad [L_i](t) \rightarrow l_i + \beta_i / 3\mu_i > 0$$

as $t \rightarrow +\infty$.

6. Asymptotic dynamics. We've already seen that all solutions of Models I and II remain positive for $t > 0$. Under the hypothesis

(H2) Every solution of $R' = k(R)$ with $R(0) > 0$
is bounded for $t > 0$,

we can show that these solutions also remain bounded for $t > 0$. Consider first Model I.

LEMMA 1. *Under hypotheses (H1)–(H2), every solution of Model I is bounded for all $t > 0$.*

PROOF. Since $R' \leq k(R)$ for any solution of (3.1)–(3.4), it follows from familiar comparison theorems that $R > 0$ is bounded for $t > 0$. Set $U = R + \sum_{i=1}^m W_i / (\alpha_i + \beta_i) \geq 0$. From (3.1)–(3.2),

$$U' = - \sum_{i=1}^m d_i \frac{1}{\alpha_i + \beta_i} W_i + k(R) - \sum_{i=1}^m (u_i(R) - n_i(R)) W_i.$$

Let $d = \min d_i > 0$. Then

$$U' \leq -dU + \phi(R) - \sum_{i=1}^m \phi_i(R) W_i,$$

where $\phi(R) = dR + k(R)$ and $\phi_i(R) = u_i(R) - n_i(R)$. Inasmuch as $\phi_i(R) \geq 0$ and R (and hence $\phi(R)$) is bounded for $t \geq 0$, we have from $U' \leq -dU + \phi(R)$ that $U \geq 0$ is bounded above for $t \geq 0$. Since R and W_i are positive it follows that W_i is bounded for $t \geq 0$. \square

Since equation (3.3) decouples from the system (3.1)–(3.4), the asymptotic dynamics of this model can be determined by the equations (3.1)–(3.2) and (3.4) which have the form

$$(6.1) \quad R' = k(R) - \sum_{i=1}^m c_i u_i(R) x_i$$

$$(6.2) \quad x'_i = (-d_i + \mu_i n_i(R)) x_i$$

$$(6.3) \quad R(0) > 0, \quad x_i(0) > 0,$$

where $c_i = 1, \mu_i = \alpha_i + \beta_i$ and $x_i = W_i$.

Next we show that the asymptotic dynamics of Model II are also governed by a system of this same form (6.1)–(6.3). Let T_i be a matrix for which

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

The first column in T_i is the right eigenvector $v_i > 0$ and the first row in T_i^{-1} is the left eigenvector $w_i > 0$. Let $\xi_i = \text{col}(c_{1i}, c_{2i}, c_{3i})$ denote the first column of T_i^{-1} . Note that c_{1i} is the first component of w_i and therefore, $c_{1i} > 0$. If the change of variables $q_i = T_i^t p_i = \text{col}(x_i, y_i, z_i)$ is made in equation (3.2), then Model I equations (3.1)–(3.3) become

$$(6.4) \quad \frac{dR}{dt} = k(R) - \sum_{i=1}^m u_i(R) \xi_i \circ q_i$$

$$(6.5) \quad x'_i = -d_i x_i + \mu_i n_i(R) x_i$$

$$(6.6) \quad y'_i = -d_i y_i + n_i(R) (\gamma_i y_i - \nu_i z_i)$$

$$(6.7) \quad z'_i = -d_i z_i + n_i(R) (\nu_i y_i + \gamma_i z_i)$$

$$(6.8) \quad R(0) > 0, \quad x_i(0) = v_i \circ p_i(0) > 0.$$

If we define $\tilde{y}_i = y_i/\Gamma_i, \tilde{z}_i = z_i/\Gamma_i$, where

$$\Gamma_i(t) = \exp \left(-d_i t + \gamma_i \int_0^t n_i(R) ds \right),$$

then it follows from (6.6)–(6.7) that

$$\frac{d}{dt} (\tilde{y}_i^2 + \tilde{z}_i^2) = 0,$$

and, hence, $y_i^2(t) + z_i^2(t) = (y_i^2(0) + z_i^2(0)) \Gamma_i(t)$. Since $\gamma_i < 0$ we have proved the following lemma.

LEMMA 2. *For any solution of (6.4)–(6.7), it is true for all i that*

$$y_i(t) \rightarrow 0, z_i(t) \rightarrow 0 \quad \text{as } t \rightarrow +\infty.$$

The next lemma can be proved using only slight modifications of the proof of Lemma 1.

LEMMA 3. *Under hypotheses (H1)–(H2), every solution of (6.4)–(6.8) is bounded for all $t > 0$.*

COROLLARY. *Under hypotheses (H1)–(H2), every solution of Model II is bounded for all $t > 0$.*

By Lemmas 2–3, the omega limit set of every solution of (6.4)–(6.8) lies in the face $y_i = z_i = 0$, which is easily seen to be an invariant set of (6.4)–(6.8) on which the dynamics are given by the reduced system obtained by setting $y_i = z_i = 0$ in (6.4)–(6.8). The resulting equations have the form (6.1)–(6.2) with μ_i equal to the dominant positive eigenvalue of M_i and $c_i = c_{1i}$, $x_i = v_i \circ p_i$.

The results of this section are summarized in the following theorem.

THEOREM 3. *Under hypotheses (H1) and (H2), all solutions of Models I and II are positive and bounded for $t > 0$. Moreover, the asymptotic dynamics of these two systems are determined by (6.1)–(6.3) with*

$$(6.9) \quad \begin{aligned} \mu_i &= \begin{cases} \alpha_i + \beta_i & \text{for Model I} \\ \text{the dominant positive eigenvalue of } M_i & \text{for Model II} \end{cases} \\ c_i &= \begin{cases} c_{1i} > 0 & \text{for Model I} \\ 1 & \text{for Model II} \end{cases} \end{aligned}$$

where $x_i = W_i =$ total population volume or weight for Model I and $x_i = v_i \circ p_i =$ a weighted average of A_i, L_i, P_i for Model II.

The asymptotic dynamics of (6.1)–(6.3) are not obvious and, in fact, can be quite complicated. There are some special cases, however, that have been thoroughly studied in the literature. One such case is treated in the next section.

7. An application: size-structured competition in a chemostat. Models for competing species of microorganisms being continuously cultured in a chemostat have been studied by many authors (e.g., see Butler and Wolkowicz [2], Paul Waltman [6] and the cited references). However, none of the literature deals with models which attempt to account for size dependent physiological properties of individual members of the species, many of which are widely recognized as important determining factors of the dynamics of, for example, zooplankton communities. (The chemostat, incidentally, can be thought of as a simple experimental model of a zooplankton community in a natural lake.)

Models for the chemostat will be considered here which, by means of the results above, reduce asymptotically to a type of chemostat model for unstructured species extensively studied in the literature. The variables and parameters in our model, however, will have different interpretations. This will allow the outcome of the competition to be related to physiological properties of individuals, including average size.

For simplicity, only the case when the resource uptake rates $u_i(R)$ are monotonically increasing in R will be considered (although the more complicated case of non-monotonic rates could be studied in a similar way using the results of Butler and Wolkowicz [2]). The class of monotonic resource uptake rates include the frequently utilized Holling II or Michaelis-Menten case $u_i = c_i R / (a_i + R)$.

In the chemostat model the resource (or substrate) dynamics are given by $k(R) = (R_0 - R)d$, where $R_0 > 0$ is the input concentration and d is the washout (and input) rate. It is also assumed that the inherent death rate of all species is small compared to this washout rate, so that $d_i = d$ for all i .

One last assumption will be made, namely that the metabolic demands of individuals of all species are small compared to the resource demands of growth and reproduction. We will, in fact, assume that metabolic demands are negligible and set $n_i(R) = u_i(R)$.

According to the results in §6, the asymptotic dynamics of the resulting Models I and II are determined by the reduced equations

$$(7.1) \quad \begin{aligned} \frac{dR}{dt} &= (R_0 - R)d - \sum_{i=1}^m c_i u_i(R) x_i, & R(0) > 0, \\ x_i' &= -dx_i + \mu_i u_i(R) x_i, & x_i(0) > 0. \end{aligned}$$

As can be seen from Theorem 3, the coefficients c_i and μ_i depend only upon the reproductive and growth efficiency coefficients α_i and β_i and, in the case of Model II, the size at birth l_i .

The results of Butler and Wolkowicz [2] imply that the asymptotic dynamics of (7.1) are determined by the break even values λ_i of the species' growth rate as defined by the equation

$$(7.2) \quad \mu_i u_i(\lambda_i) = d.$$

These results, together with the results of §6, imply that all species densities will equilibrate and all species will asymptotically die out with the possible exception of one. Thus this size-structured competition model is commensurate with the ecological principle of competitive exclusion which asserts that at most one species can survive on one resource.

More specifically, if there is a smallest λ_i , say, without loss in generality $\lambda_1 < \lambda_i$ for $i \neq 1$, then $(A_i(t), L_i(t), P_i(t)) \rightarrow 0$ as $t \rightarrow +\infty$ for $i \neq 1$. Species $i = 1$ will also equilibrate, but whether it survives or not depends on whether λ_1 is less than or greater than the input concentration R_0 as follows:

Model I. $(R, W_1, P_1) \rightarrow (R_\infty, W_\infty, P_\infty)$ as $t \rightarrow +\infty$, where

$$\begin{aligned} \lambda_1 > R_0 &\implies R_\infty = R_0, & W_\infty = P_\infty = 0 \\ \lambda_1 < R_0 &\implies R_\infty = \lambda_1, \\ W_\infty &= (R_0 - \lambda_1)(\alpha_1 + \beta_1), & P_\infty = (R_0 - \lambda_1)\alpha_1/w_1. \end{aligned}$$

Model II. $(R, A_1, L_1, P_1) \rightarrow (R_\infty, A_\infty, L_\infty, P_\infty)$ as $t \rightarrow +\infty$, where

$$\begin{aligned} \lambda_1 > R_0 &\implies R_\infty = R_0, \quad A_\infty = L_\infty = P_\infty = 0 \\ \lambda_1 < R_0 &\implies R_\infty = \lambda_1, \quad A_\infty = (R_0 - \lambda_1)\mu_1, \\ &L_\infty = (R_0 - \lambda_1)(1 + \beta_1/3\mu_1 l_1)\alpha_1/l_1^2, \\ &P_\infty = (R_0 - \lambda_1)\alpha_1/l_1^3. \end{aligned}$$

Thus for both Models I and II the outcome of the competitive interaction is determined by the resource equilibrium level λ_i defined by (7.2). The winning species is the one that can exploit the resource to the lowest positive level λ_i and still survive at that resource level. For a given washout rate d and given uptake rates u_i , the crucial parameter λ_i depends upon the physiological parameters α_i, β_i and, in the case of Model II, on the length at birth l_i through the dependence of μ_i on these parameters. Any change in a species' model parameters which decreases λ_i will enhance that species' chances for surviving.

Given the assumption that u_i is monotonically increasing in its argument, it follows from (7.2) that λ_i is inversely related to μ_i . A species' survival chances are thus improved by an increase in its parameter value μ_i as defined by (6.9), i.e., by an increase in either its reproductive or growth efficiency coefficients α_i, β_i .

Comparing this result with the results about the asymptotic size of each species in §5 we find that, for these models at least, there is no general correlation between competitive success and species size.

To illustrate this point consider the case when all species have identical resource uptake rates $u_i(R) = u(R)$. By (7.2), the smallest λ_i corresponds to the largest μ_i , and, hence, the surviving species is determined solely by the physiological parameters α_i, β_i and size at birth w_i or l_i .

For Model I it is clear that the largest $\mu_i = \alpha_i + \beta_i$ does not necessarily correspond to the largest asymptotic weight $[W_i] = (1 + \beta_i/\alpha_i)w_i$.

Under some further restrictions it can happen that the largest species will always be the competitive survivor. For example, if the species are made even more similar by assuming that they all have the same weight at birth, $w_i = w$, and the same reproductive efficiencies, $\alpha_i = \alpha$, then $\mu_i = \alpha + \beta_i$ and $[W_i] = (1 + \beta_i/\alpha)/w$ are simultaneously maximal as a function of the growth efficiency coefficient β_i .

However, under other restrictions, the complete opposite can hold. For example, if all species have the same weight at birth, $w_i = w$, and identical growth efficiencies, $\beta_i = \beta$, then $\mu_i = \alpha_i + \beta$ is maximized when $[W_i] = (1 + \beta/\alpha_i)w$ is minimized, namely for the largest reproductive efficiency coefficient α_i . In this case the smallest species is the winning competitor.

Identical conclusions can be shown to hold for Model II by using formula (3.9) for μ_i and using, as a measure of species size, any weighted average of the asymptotic area and length as given in Theorem 2. For more details see Cushing [1988], where the case of a logistically growing resource $k(R) = r(1 - R/K)R$ is also considered.

8. Concluding remarks. We have seen how an ODE competition model for m size-structured species exploiting a single resource can be derived under certain simplifying assumptions from integro-partial differential equations for size specific densities that describe size specific birth and death processes. Mathematically, it was shown that solutions of the model are positive and bounded and that the asymptotic dynamics are governed by a more tractable reduced system of ODE's. Moreover, it was found that the model implied that the average size of individuals in all species asymptotically equilibrates to a positive value, regardless of the asymptotic dynamics and the outcome of the competition. This average size was compared to competitive effectiveness in the application to competition in a chemostat, and it was found that species "size" was a poor indicator of competitive success under general circumstances. This result can perhaps be interpreted as providing some theoretical evidence as to why attempts at experimental verification of the SEH have been equivocal.

The key assumptions in the model studied here are that the consumed resource is allocated (after metabolic demands are met) between growth and reproduction, that resource uptake scales to an integer power of body length (viz. to power 2 or 3), and that there is no appreciable juvenile, nonreproductive stage. That resource scales to a power of body length seems well established (Werner and Gilliam [8]), particularly for small organisms like zooplankton (Hall et al. [4]). The latter assumption of no juvenile stage is a serious restriction in the model, but seems a necessary one for the mathematical analysis carried

out above. Juvenile stages, being a source of time delay, can significantly affect the resulting dynamics, and models which include them would be of interest. It would be of interest to incorporate many other important features into size structured models as well, including a finite adult size (which is usually the measure of species size referred to in the biological literature), resource storage capability (Metz and Diekmann [5]), starvation and growth cessation (dormancy), size-structured resources, and size-specific predation, to name just a few.

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