

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600



Order Number 9125455

A discrete size-structured competition model

Crowe, Kathleen Marie, Ph.D.

The University of Arizona, 1991

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106



A DISCRETE SIZE-STRUCTURED COMPETITION MODEL

by

Kathleen Marie Crowe

**A Dissertation Submitted to the Faculty of the
COMMITTEE ON APPLIED MATHEMATICS (GRADUATE)**

**In Partial Fulfillment of the Requirements
For the Degree of**

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 9 1

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Kathleen M. Crowe

entitled A Discrete Size-Structured Competition Model

and recommend that it be accepted as fulfilling the dissertation requirement
for the Degree of Doctor of Philosophy.

J M Cushing
J N Secomb

3-21-91
Date

Alwyn Scott

3-21-91
Date

3/20/91
Date

Date

Date

Final approval and acceptance of this dissertation is contingent upon the
candidate's submission of the final copy of the dissertation to the Graduate
College.

I hereby certify that I have read this dissertation prepared under my
direction and recommend that it be accepted as fulfilling the dissertation
requirement.

J M Cushing
Dissertation Director

3-21-91
Date

STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that accurate acknowledgement of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his or her judgement the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: _____

A handwritten signature in cursive script, written in black ink, is positioned over a horizontal line. The signature is somewhat stylized and difficult to read precisely, but appears to contain the name of the author.

ACKNOWLEDGMENTS

The list of people to whom I owe my thanks for helping me get through all of this schooling is virtually endless, but without a doubt it must begin with my family. Without the support (both moral and financial) of my parents, Rosalie and Tommy I might well have chosen to become a lifeguard instead. Thanks also to my brother David who put up with me during the worst of times, the years of my written and oral exams, and my sister Claudine, for keeping things lively.

Through the years I have been at this, it has been the day-to-day presence and encouragement of my fellow gauntlet runners (both past and present) that has kept reminding me why I was doing all this. Thanks to Lisa for convincing me that P.D.E.'s are not entirely black magic and putting up with me at school as well as at home, and John, Ted, and James for helpful hints about everything from jobs to the graduate degree check office. To all inhabitants of our corner of the "ghetto", particularly Janet and Mona, thanks for never making me clean my desk. Special thanks to ghetto-rat James for teaching me to juggle and Hannah for listening to all my grumbling. Finally, special thanks to John for all the encouragement and computer mail, the (often) silly, (occasionally) serious, and always helpful.

Several faculty members surely should be mentioned here for their help. Thanks to Professors Scott, Secomb, Young and Lomen for taking time to sit on committees, teach classes, assign classes, and all the other things that are so important to graduate students, and thanks to Professor Newell for all his help. Special thanks to Professor Flaschka for teaching me to learn, spending all sorts of time helping me, and continuing to believe in me even when I didn't.

The help from everyone on the staff, both in Mathematics and Applied Mathematics has been invaluable, but special mention must be made of Bob Condon, our local computer wizard. He has shown more patience with a variety of silly questions than anyone has a right to expect, and without his constant miracle-working this document would still be a stream of electrons running amok in the space-time continuum.

After all the hours spent at swimming pools with them, I cannot fail to mention my teammates who have always been there to provide support and encouragement for both my math and my swimming. Thanks to Alison and her family and Ryan and his family, who have virtually adopted me at times. Special thanks to Jeremy for everything, including a vast increase in my knowledge of basketball.

More gratitude than I can describe goes to my advisor, Jim Cushing, for teaching me to be (I hope) a mathematician, and putting up with my foolishness for the past few years. Without him none of this would have been possible.

TABLE OF CONTENTS

LIST OF FIGURES	7
LIST OF TABLES	8
ABSTRACT	9
1 Introduction	10
2 Model Derivation	17
2.1 General Discrete Model	17
2.2 Single Species Competition Model	24
2.3 Multispecies Competition Model	31
3 Equilibrium Dynamics	33
3.1 Single Species	33
3.2 Multispecies Dynamics	44
4 Nonequilibrium Dynamics	49
4.1 Single Species Equilibria	49
4.2 Multispecies Dynamics	58
5 Biological Considerations	63
5.1 Role of θ in the Dynamics	64
5.2 θ as a Function of β_i and γ_i	66
5.3 θ as a Function of Individual Physiological Parameters	70

	6
5.4 The Dependence of Body Size on Physiological Parameters	73
6 Concluding Remarks	79
A Appendix	84
REFERENCES	96

LIST OF FIGURES

3.1	Right- and left-hand sides of Equation (3.8) as functions of R^e	36
3.2	Equilibrium diagram for $c(P) \neq 1$	36
3.3	Equilibrium diagram for $c(P) \equiv 1$	37
3.4	Depleted Equilibrium Existence for $c(P) = e^{-dP}$	39
3.5	Depleted Equilibrium Existence for $c(P) = \frac{1}{1+dP}$	39
3.6	Depleted Equilibrium Existence for $c(P) = \frac{1}{1+dP^2}$	40
3.7	Bifurcation of Positive Equilibrium	43
3.8	Change to Depleted Equilibrium	43
3.9	Competitive Exclusion	48
4.1	Single species bifurcation to aperiodic dynamics	52
4.2	Two-cycle time series plots	53
4.3	Four-cycle time series plots	54
4.4	Aperiodic time series plots	55
4.5	Three-cycle time series plots	56
4.6	Bifurcation to two species coexistence	61
4.7	Two species coexistence in a two cycle	62
4.8	Two species coexistence with aperiodic dynamics	62

LIST OF TABLES

2.1	Size-specific Parameters	26
5.1	Size-Specific Parameter Dependence	72
5.2	Changes in θ and S with changes in κ_j	75
5.3	Changes in θ and S with changes in η_j	78

ABSTRACT

Matrix difference equations have been used to model the discrete time dynamics of a variety of populations whose individual members have been categorized into a finite number of classes based on, for example, age, size, or stage. Examples of such models include Leslie's age-structured model and the Usher model, a size-classified model which has been applied to trees, corals, sea turtles, copepods, and fish. These matrix difference equations can incorporate virtually any type of nonlinearity arising from the density dependence of fertility and survival rates and transition probabilities between classes. Under a fairly general set of assumptions, it can be shown that the normalized class distribution vector equilibrates, and thus an asymptotic or limiting equation for total population size can be derived.

In this research we assume the existence of a dynamically modeled resource in limited supply for which the members of the species compete, either exploitatively or through interference. The existence and stability of population size equilibria or cycles is then studied by means of bifurcation theory.

Several biological considerations are addressed, including the Size-Efficiency Hypothesis of Brooks and Dodson, the effects of changes in individual physiological parameters on the size and competitive success of a species, and the effects of delays on the viability of a species.

CHAPTER 1

Introduction

Since the development of the classical ordinary differential equation (O.D.E.) models of population dynamics by A. Lotka and V. Volterra in the early 1900's, systems of interacting populations have been modeled with varying assumptions and approaches. There have been O.D.E. models of, for example, competitive interactions, predator-prey interactions, cannibalism, and mutualism, as well as combinations of these in food web models. Delay-differential equations have been introduced to include phenomena such as maturation and gestation periods, while reaction diffusion models have been used to study populations under the assumption of spatial heterogeneity. Discrete models of populations have been studied as well and have focused interest on such topics as period-doubling bifurcations, symbolic dynamics, and chaos.

While much work has been done modeling systems of interacting populations, most of it has been carried out at the population level, using such aggregate measures as total population size and biomass as dynamic variables, and thus treating all individuals within a species as identical. These models, while exhibiting quite accurate qualitative behavior in many cases, unfortunately neglect the role that structure within a species plays on its dynamics. To some extent this has been a

necessary result of the trade-off between complexity of the model and tractability of the resulting equations; however, biologists have come to recognize that structure within a species can play a significant role in the dynamics of a species as a whole. This recognition can be seen in a wide variety of areas such as population dynamics, genetics, cell dynamics, and epidemiology. Indeed, a great deal of biological research involves measurements on individual organisms which can only be taken into account very qualitatively and phenomenologically in nonstructured models of the classical type. Thus there is currently a great deal of interest in models which bridge the gap between the physiological properties of the individual organisms and dynamics at the population level.

The earliest discrete population models which incorporated species structure were developed by Lewis [32] and Leslie [29]. These models divide the population into age classes; by following the dynamics of the vector of age-class densities, it is possible to discern the effects of individual age-specific physiological parameters on population level dynamics. These early matrix models were used primarily for human demography and were based on age-structure. In addition, these models were often linear. A fairly complete treatment of this subject is contained in the book by Impagliazzo [26].

In many cases, chronological age is not the most important structuring variable of a population. Many individual parameters depend heavily upon the size or life cycle stage of the individual. For example, metabolic rate usually scales as a power of weight (Calder [5]), home range has been shown to scale with body size (Linstedt, et al. [33]), and reproductive capability is often determined by body size or developmental stage. Since physical characteristics such as body size, weight, stage, and

reproductive capability may not correlate well with age, it is useful to consider parameters such as these as structuring variables. In addition, because linear models, while simple to analyze, yield exponential growth or decay, it is necessary for the consideration of long term dynamics to incorporate density (or nonlinear feedback) effects. Leslie [30] did study some nonlinear age-structured matrix models. More recently, a wide range of biological systems have been studied using nonlinear matrix models structured by age, size, and other variables. By means of such models, population-level behavior such as equilibration or oscillations, stability, and growth rates can be related to individual parameters such as rates of growth, resource uptake, birth, and death, conversion factors of resource, and metabolic rates, all of which can vary with the age, body size, weight, etc. of the individual.

One of the most fundamental interactions of interest in theoretical and field ecology is competition, both within a species and between different species, for a resource such as food, space, sunlight, etc. This competition can occur through exploitation, interference, or some combination of these, and is the focus of many of the classic principles and experiments in ecology. Experimental and field ecologists have provided us with many examples of complex competitive interactions in such species as the flour beetles *Tribolium castaneum* and *Tribolium confusum* (Park *et al.* [39]), the barnacles *Chthamalus stellatus* and *Balanus balanoides* (Connell [7]), the protozoans *P. aurelia*, *P. caudatum*, and *P. bursaria* (Gause [17],[18]), and the freshwater diatoms *Asterionella formosa* and *Synedra ulna* (Tilman *et al.* [43],[44]). The concepts of the ecological niche (Hutchinson [25]), niche differentiation and limiting similarity (MacArthur and Levins [35]), and the Principle of Competitive Exclusion are some examples of theories that have been developed in an attempt to

more fully understand the competitive interactions that are observed in nature.

It is important to the success of studies of such phenomena to acknowledge that competition takes place between *individuals* and to model the interactions accordingly. Most of the classical models, however, have treated species as completely homogeneous and thus have ignored the effects that differences between individuals can have on the dynamics of the population. It has been pointed out, most notably by Werner and Gilliam [51], that competition in the biological world at the level of the individual is exceedingly complex and heavily dependent on the physiological characteristics of the individuals involved in the competition. Discrete shifts in resource use based on size or life cycle stage changes have been shown to occur in amphibians and holometabolous insects (Wilbur [52]), fish such as the largemouth bass (Gilliam [19]) and the pinfish (Stoner *et al.* [41],[42]), and reptiles such as the watersnake *Nerodia* (Mushinsky, *et al.* [37]). The juvenile bottleneck phenomenon documented by Neill [38] is a mechanism by which the adults of a smaller species negatively affect the juveniles of a larger species by out-competing them, and among carnivorous species this bottleneck phenomenon may be further complicated by the adults of the larger species preying upon the smaller species. One example of a mixed competition/predation interaction is found between the rainbow trout *Salmo gairdneri* and the redbside shiner *Richardsonius balteatus* in Paul Lake, British Columbia [51]. Such complicated interactions at the level of the individual clearly affect the dynamics of the population as a whole, and it is important to consider population models that can study them.

In attempting to understand these complex interactions, many questions arise, including the following: What individual characteristics make a successful competi-

tor? Is body size correlated with competitive success? Can one predict the result of a competitive interaction from a knowledge of individual level characteristics? Few attempts have been made to develop models which address these questions.

The purpose of this research is to develop and study a general competition model for several structured species in order to promote some understanding of the questions listed above. Following Werner and Gilliam [51] we use size as the structuring variable. Many physiological parameters have been shown to scale to a power of body size τ (i.e. $\sim s^\tau$) with $\tau \in [2, 3]$ ([5],[51],[33]). For conciseness we will use specifically $\tau = 2$, although the methods could be used for other choices of τ with little or no mathematical change. The model to be studied here uses total body surface area as its structuring variable. It is similar to a model studied by Cushing [9], the primary difference being that the resource is no longer assumed to remain at a constant level, but is dynamically modelled.

The matrix difference equation for a single species is derived in Chapter 2, along with the difference equation governing the resource dynamics. Both of these equations are written in general terms, with the main assumption on the population that all newborns lie in the first size class. In addition, it is assumed that there is a constant input of resource at each time unit and that the unconsumed resource is subject to a degradation or washout process. This allows the system to be thought of as, for example, a model of an alpine lake which undergoes a seasonal snowcap runoff.

Also in Chapter 2 we state a Nonlinear Ergodic Theorem which states that, under some fairly general assumptions on the matrix equation governing a population, the normalized size-class distribution will equilibrate to a constant vector. Thus

for each species we are able effectively to reduce the matrix difference equation to a scalar equation for the dynamics of total population size, making analysis of the system much simpler. This theorem, a generalization of results obtained by Cushing [9] and Impagliazzo [26], is proved in the Appendix. By using the Nonlinear Ergodic Theorem we are able to discover the long-term behavior of the size-class distribution and the total population size separately, while still maintaining their interdependence. In addition, the resulting scalar equation for total population size involves a parameter (denoted by θ) which incorporates all the size structure of the species, enabling us to bridge the gap between individual and population level dynamics.

Making use of this reduction obtained from the Nonlinear Ergodic Theorem, we study in Chapter 3 the equilibrium dynamics of first the single species and then the multi-species systems by means of the resulting dynamical equations for total population size. In the single species case, the techniques of bifurcation theory are employed using the parameter θ to show the existence and stability of a nontrivial equilibrium. For more than one species the model suggests the usual result of competitive exclusion; only one species can exist under the assumption of all equilibrium dynamics.

We then turn to nonequilibrium dynamics and in Chapter 4 we study both single species and multi-species oscillatory and chaotic dynamics. It is shown that the nontrivial single species equilibrium can only lose stability via a flip bifurcation; i.e. a single eigenvalue leaving the unit circle through -1. Thus if a bifurcation occurs, it must be to a two-cycle, not an invariant circle, and we demonstrate such a bifurcation numerically. With this result we are able to study (using two bifurcation

theorems which are stated and proved in the Appendix) the existence of a “lift-off” of a stable k -cycle in n species to a stable k -cycle in $n+1$ species, thus demonstrating competitive coexistence in an oscillatory setting.

In Chapter 5 we make use of the dependence of the bifurcation parameter θ on all the individual physiological parameters to study the relationship between the population level dynamics of the species and the individual based, size-specific parameters upon which the model is based. In addition we examine how competitive success is related to the size of the species involved, using average adult size as a measure of species size; to life-cycle strategies involving growth and reproduction trade-offs; and to other size specific parameters such as resource-to-growth / reproduction conversion factors, size at birth, etc.

We conclude with a brief summary of results and a discussion of the relationship between these results and several important biological concepts such as the Size-Efficiency Hypothesis, Gause’s Principle, and the possibility of competitive coexistence of 2 or more species. In addition we include an Appendix that contains proofs of theorems stated in the chapters, as well as two additional theorems (along with proofs) for mathematical background.

CHAPTER 2

Model Derivation

2.1 General Discrete Model

We begin by describing a general discrete model for the dynamics of a single structured population with a finite number $m \neq 1$ of classes. Let $x_i(t)$ denote the number or density of individuals in class i , $1 \leq i \leq m$ at time t , for $t = 0, 1, 2, \dots$, and let $\vec{x}(t) = \text{col}(x_i(t))_{i=1}^m$ be the column vector of these densities. Then the dynamics of the population are described by the matrix difference equation

$$\vec{x}(t+1) = \mathcal{P} \vec{x}(t) \quad (2.1)$$

where the projection matrix \mathcal{P} can be decomposed into the sum of a class transition matrix \mathcal{T} and a fertility matrix \mathcal{B} ; i.e. $\mathcal{P} = \mathcal{T} + \mathcal{B}$.

A general form for the $m \times m$ transition \mathcal{T} is

$$\mathcal{T} = \begin{bmatrix} \pi_1(1-f_1) & \pi_2 f_{12} f_2 & \cdots & \pi_m f_{1m} f_m \\ \pi_1 f_{21} f_1 & \pi_2(1-f_2) & \cdots & \pi_m f_{2m} f_m \\ \vdots & \vdots & \ddots & \vdots \\ \pi_1 f_{m1} f_1 & \pi_2 f_{m2} f_2 & \cdots & \pi_m(1-f_m) \end{bmatrix} \quad (2.2)$$

representing the transitions among all classes that occur over one unit of time. Here π_j is the probability that an individual of class j survives one unit of time. We assume that after one unit of time a fraction f_j of the surviving individuals leave

class j , with a fraction f_{ij} of this group moving to class $i \neq j$. The fraction of j -class individuals who move into class $i \neq j$ is then $\pi_j f_{ij} f_j$, while the fraction that survives and remains in class j is $\pi_j(1 - f_j)$.

In addition to these transitions, classes may also obtain new members due to births. (We will ignore immigrations and emigrations.) Let b_{ij} be the number of births of i -class individuals per j -class individual in one unit of time. We assume that the census is taken immediately following reproduction by surviving individuals, so the class distribution vector of offspring at time $t + 1$ is given by $\mathcal{B} \bar{x}(t)$, where

$$\mathcal{B} = \begin{bmatrix} \pi_1 b_{11} & \pi_2 b_{12} & \cdots & \pi_m b_{1m} \\ \pi_1 b_{21} & \pi_2 b_{22} & \cdots & \pi_m b_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ \pi_1 b_{m1} & \pi_2 b_{m2} & \cdots & \pi_m b_{mm} \end{bmatrix} = [\pi_j b_{ij}]. \quad (2.3)$$

(If, on the other hand, the census were taken immediately before reproduction, then \mathcal{B} would be given by $[\pi_i b_{ij}]$.)

Several well-studied age- and size-structured models are included in this general model. One such model is the age-structured model of Leslie [29]. In this model the stages are age classes of one time unit in length so that $f_j = 0$ and $f_{ij} = 0$ if $i \neq j + 1$ in Equation (2.2); i.e. all surviving individuals must advance one age class in one unit of time. Since newborns have age 0 we have $b_{ij} = 0$ for all j and all $i \neq 1$ in Equation (2.3), and so \mathcal{P} becomes a Leslie matrix. Another example, a generalization of the Leslie model, is the Usher model, which occurs if individuals either remain in their class or move to the next class in one unit of time. This assumption yields a projection matrix called an ‘‘Usher’’, or ‘‘standard size-classified’’ matrix (Caswell [6]). Usher matrix models have been used in size-structured models of tree-forest dynamics (e.g. Usher [46], [47], [48], [49] and Ek *et al.* [13], [14]), and other studies of this general class of models include those by

Barclay [1], Buongiorno and Michie [3], Cushing [8]-[12], Levin and Goodyear [31], Liu and Cohen [34], Travis, *et al.* [45], and Hassell and Comins [21].

We now make several modeling assumptions. We are interested in the dynamics of structured populations of species competing for a common resource in limited supply when the species' ability to obtain this resource is class-dependent. In addition, we want to allow both fertility and transitions between classes to depend upon resource consumption and thus we assume that the birth rates b_{ij} and the fraction f_j of j -class individuals who leave class j in one unit of time are proportional to a "per unit resource uptake functional", $u = u(t)$. We write

$$\begin{aligned} b_{ij} &= \phi_{ij}u(t), & \phi_{ij} &\geq 0 \\ f_j &= \phi_j u(t), & \phi_j &\geq 0 \end{aligned} \quad (2.4)$$

where the time dependence of $u(t)$ can be explicit, or implicit, such as through a dependence on population density of the species or of a competing species. For example, consider a size-structured population for which resource consumption is dependent upon both body size and time dependent resource availability, such as the competing *ceriodaphnia* and *daphnia magna* populations discussed by Neill [38].

Here we will focus on differences in growth and fertility rates between individuals in different classes, as opposed to differences in survival rates. Thus we will also assume that the probability of surviving a unit of time is the same for all classes of a species and is constant (i.e. $\pi_j = \pi(t, \vec{x}(t)) \in (0, 1)$). While this assumption is simplistic and a bit unreasonable biologically, it will enable us to perform a good deal of analysis on a system that would otherwise be quite complicated. Although in many examples survivability is highly correlated with body size, in examples where this assumption is roughly accurate or where differences in survivability between classes are less significant than differences in fertility or growth rates this assumption

will yield a set of model equations which may be analyzed more completely. We hope that by focusing on class-dependent birth and transition rates alone we will gain some understanding of their impact on the dynamics of competing populations.

Now define the functions $a(t) = \pi(1 - \phi_q u(t))$ and $b(t) = \pi u(t)$ where ϕ_q is the largest ϕ_i (i.e. $\phi_q \geq \phi_i$ for all i). Under the modeling assumptions made above, Equation (2.1) can be written in the general form

$$\bar{x}(t+1) = \mathcal{P}(t) \bar{x}(t), \quad \mathcal{P}(t) = a(t)\mathcal{I} + b(t)\mathcal{L} \quad (2.5)$$

where \mathcal{L} is the matrix

$$\begin{bmatrix} \phi_q - \phi_1 + \phi_{11} & f_{12}\phi_2 + \phi_{12} & \cdots & f_{1q}\phi_q + \phi_{1q} & \cdots & f_{1m}\phi_m + \phi_{1m} \\ f_{21}\phi_1 + \phi_{21} & \phi_q - \phi_2 + \phi_{22} & \cdots & f_{2q}\phi_q + \phi_{2q} & \cdots & f_{2m}\phi_m + \phi_{2m} \\ \vdots & \vdots & & \vdots & & \vdots \\ -f_{q1}\phi_1 + \phi_{q1} & f_{q2}\phi_2 + \phi_{q2} & \cdots & \phi_{qq} & \cdots & f_{qm}\phi_m + \phi_{qm} \\ f_{m1}\phi_1 + \phi_{m1} & f_{m2}\phi_2 + \phi_{m2} & \cdots & f_{mq}\phi_q + \phi_{mq} & \cdots & \phi_q - \phi_m + \phi_{mm} \end{bmatrix}.$$

and \mathcal{I} is the $m \times m$ identity matrix. Note that \mathcal{L} is a constant nonnegative matrix.

Let \bar{w} be a given vector in \mathfrak{R}^n with $\bar{w} \geq \bar{0}$ and $\bar{w} \neq \bar{0}$. Then the inner product $\bar{w}^T \bar{x} = \sum_{j=1}^m w_j x_j(t)$ defines a “weighted population size”; call it $P(t)$. For example, if all the components of \bar{w} are 1, then $P(t) = \sum_{j=1}^m x_j(t)$ is the total population size at time t . Let $\bar{\eta}(t) = \frac{\bar{x}(t)}{P(t)}$ denote the “normalized class distribution”. We then have the following result, a proof of which appears in the Appendix.

Theorem 1 (Nonlinear Ergodic Theorem) *Assume that the following two hypotheses hold.*

H1 *There exist constants a_0 and b_0 such that $0 \leq a(t) \leq a_0$ and $0 < b_0 \leq b(t)$ for all $t = 0, 1, 2, \dots$.*

H2 *\mathcal{L} has a strictly dominant positive simple eigenvalue $\lambda^+ > 0$ with an associated positive eigenvector \bar{v}^+ , which is normalized so that $\bar{w}^T \bar{v}^+ = 1$.*

Also assume that $\bar{x}(t) \geq \bar{0}$ is a solution of Equation (2.5) such that $\bar{x}(0) \geq \bar{0}$, $\bar{x}(0) \neq \bar{0}$ and $P(t) > 0$ for $t \geq 0$. Then $\bar{\eta}(t) \rightarrow \bar{v}^+$ as $t \rightarrow +\infty$.

This is a generalization of a result of Cushing [9], who assumed the \mathcal{L} is diagonalizable, and in the special case of (age-structured) Leslie matrices this result is known as the *Fundamental Theorem of Demography*.

Before applying this theorem, a discussion of its second hypothesis is in order. It is well known from the theory of positive matrices that the dynamics of $\bar{x}(t)$ will be determined by the eigenvalue of largest magnitude of the transition matrix. If this eigenvalue has modulus greater than one then at least one solution of Equation (2.5) will tend to ∞ exponentially as $t \rightarrow +\infty$, while if this eigenvalue has modulus less than one then all solutions of Equation (2.5) will tend exponentially to zero as $t \rightarrow +\infty$. Since the transition matrix $\mathcal{P}(t)$ is just a shift of $b(t)\mathcal{L}$, we are concerned with the eigenvalues of \mathcal{L} .

Since \mathcal{L} is nonnegative, it must have a nonnegative real eigenvalue $\lambda_1 \geq 0$ with corresponding eigenvector \bar{v}_1 which is also nonnegative, and the moduli of all other eigenvalues cannot exceed λ_1 (cf. Gantmacher [16]). According to Perron's theorem, if \mathcal{L} strictly positive then so is λ_1 , and the moduli of all other eigenvalues are strictly less than λ_1 . However, in most applications to population dynamics \mathcal{L} will have some zero entries and so we must consider Frobenius' generalization to Perron's theorem in which the requirement of positivity of \mathcal{L} is replaced by the requirements of nonnegativity and irreducibility of \mathcal{L} .

Recall that a matrix \mathcal{L} is *reducible* if the index set $I = \{0, \dots, m\}$ can be partitioned into two disjoint subsets $J = \{j_1, \dots, j_\alpha\}$ and $K = \{k_1, \dots, k_\beta\}$ such that the jk^{th} element of \mathcal{L} is zero for all $j \in J$, $k \in K$. In other words, a permutation of

\mathcal{L} (a permutation of rows together with the same permutation of columns) can be performed so that \mathcal{L} is placed in the block form

$$\mathcal{L} = \begin{bmatrix} \mathcal{A} & 0 \\ \mathcal{B} & \mathcal{C} \end{bmatrix}$$

where \mathcal{A} is $\alpha \times \alpha$, \mathcal{B} is $\beta \times \alpha$, and \mathcal{C} is $\beta \times \beta$. In terms of population models, this means that there exists a subset of classes which are unreachable from the remaining classes from transitions and births.

According to Frobenius' theorem, if \mathcal{L} is both nonnegative and irreducible then the (real) eigenvalue λ_1 is positive and algebraically simple, has a corresponding positive eigenvector, and is greater than or equal to the moduli of all other eigenvalues of \mathcal{L} . In addition, *all* eigenvectors of \mathcal{L} are nonnegative.

Another concept of importance is the *primitivity* of a matrix. The matrix \mathcal{L} is primitive if λ_1 is strictly larger than the moduli of all the other eigenvalues. There are several tests used to determine the primitivity (or imprimitivity) of matrices. According to Gantmacher, a matrix \mathcal{N} is primitive if and only if $\mathcal{N}^n > 0$ for some finite integer n . In addition, it is known that a Leslie matrix is primitive if it contains no two consecutive nonzero entries in its top row. The following result, applicable to the matrices considered here, is due to a comment by J. M. Cushing.

If \mathcal{N} is any nonnegative $m \times m$ matrix, it can be written as the sum of a nonnegative matrix \mathcal{Q} and a Leslie matrix \mathcal{L} . Then

$$\mathcal{N}^n = \mathcal{L}^n + \sum \text{nonnegative matrices.}$$

If \mathcal{N} has no two consecutive nonzero entries in its top row then neither does \mathcal{L} . Thus \mathcal{L} is primitive (i.e. there is some integer $n > 0$ such that $\mathcal{L}^n > 0$) and so $\mathcal{N}^n > 0$ and \mathcal{N} is primitive. Thus a sufficient condition for the primitivity of a nonnegative

matrix is that no two consecutive entries in its top row are zero.

The significance of the primitivity of \mathcal{L} is that it enables us to draw conclusions with regard to the ergodicity of the system. In fact, if \mathcal{L} is primitive then the dynamics of the total population size are governed by λ_1 and it is possible to completely describe the stable size distribution and the long-term behavior of the population using only λ_1 and its associated eigenvector \bar{v}_1 . We now apply this theory to our model.

Forming the inner product of the first equation of (2.5) with \bar{w}^T we obtain

$$P(t+1) = (a(t) \bar{w}^T \mathcal{I} + b(t) \bar{w}^T \mathcal{L}) \bar{x}(t)$$

and, noting that $\bar{w}^T \mathcal{L} \bar{x}(t) = \bar{w}^T \mathcal{L} \bar{\eta}(t) P(t)$, we have

$$P(t+1) = \left(a(t) + b(t) \bar{w}^T \mathcal{L} \bar{\eta}(t) \right) P(t). \quad (2.6)$$

By Theorem 1, we know that $\bar{w}^T \mathcal{L} \bar{\eta}(t) \rightarrow \bar{w}^T \mathcal{L} \bar{v}^+ = \lambda^+ \bar{w}^T \bar{v}^+ = \lambda^+$, and thus Equation (2.6) is asymptotic to the limit equation

$$P(t+1) = \left(a(t) + \lambda^+ b(t) \right) P(t), \quad (2.7)$$

and it is this equation that will be used to study the dynamics of the weighted population size $P(t)$ in our specific models. It should be noted that the question of the equivalence of solutions of Equations (2.6) and (2.7) is not a trivial one and, at least in the case of aperiodic trajectories of $P(t)$, has not been completely answered. For a treatment of this issue see LaSalle [28] or Cushing [10].

2.2 Single Species Competition Model

We now apply the results of the preceding section to a class of size-structured competition models in which the population is structured by size-classes according to body length s . Many species' resource uptake rates are proportional to s^τ with τ between 2 and 3 (Werner and Gilliam [51], Calder [5], Hall *et al.* [20]); i.e. an individual's ability to consume food scales with body surface area or volume. Here we assume that the resource uptake rate scales with body surface area, so $\tau = 2$ and

$$P(t) = \sum_{i=1}^m s_i^2 x_i(t)$$

is the total surface area at time t , although a similar analysis can be carried out for $\tau = 3$. (For $\tau = 3$ the structure of the model given below remains unchanged; only the expressions for the growth and reproductive coefficients β_i and γ_i are slightly different.) For conciseness we will give the details for only the case $\tau = 2$ in this dissertation. Examples of species for which resource uptake scales as body surface area are such filter feeders as zooplankton, mollusks, and anemones (Hall *et al.* [20]). We also assume that the resource in question, denoted by R , is in limiting supply, and that intraspecific competition, both exploitative and possibly interference, occurs. We first consider a model of the resource.

Model of Resource

We consider a resource in limited supply and denote the amount of resource available for consumption at time t by $R(t)$. We assume that there is a constant amount of resource I_0 input each unit of time and that the resource not consumed over the course of one unit of time is subject to a non-consumptive decrease or loss, for

example through degradation or through a washout process. Thus the amount of resource available at time $t + 1$ is given by

$$R(t + 1) = \xi \left[\begin{array}{c} \text{amount of resource} \\ \text{remaining after consumption} \end{array} \right] + I_0$$

where $\xi \in [0, 1)$ is the fraction of unconsumed resource remaining after one unit of time.

Let $r(R)$ be the inherent resource uptake rate per unit body surface area of consumer at resource level R and let $1 - c(P)$ be the fractional decrease in the uptake rate due to the presence of P competitors. We assume

$$\begin{array}{l} A1 \quad r(0) = 0, \quad r'(R) > 0, \quad \lim_{R \rightarrow +\infty} r(R) = r^0 < +\infty \\ A2 \quad c(0) = 1, \quad c'(P) \leq 0, \quad c(P) \leq 1 \text{ for } P > 0. \end{array}$$

An example of such an r is the Michaelis-Menten uptake function $r(R) = \frac{mR}{a+R}$ with $m, a > 0$. The density term $c(P)$ can also be modeled in various ways ranging from purely exploitative competition ($c(P) \equiv 1$) to strong nonlinear effects (e.g. $c(P) = e^{-dP}$, $d > 0$). In the models we consider, if $c(P) \neq 1$ we will assume that $c(P) < 1$ for $P > 0$ and that $c'(P) < 0$. As one example of such a function, let $1 - e^{-d}$ ($d > 0$) be the fractional decrease in resource uptake of an individual per unit body surface area of a competitor. Then at time t , a fraction $e^{-dP(t)}$ of the per unit inherent uptake $r(R(t))$ is actually consumed. Note that if $d = 0$ we have the purely exploitative case $c(P) \equiv 1$, and larger values of d result in stronger competitive or density effects.

Then the resource uptake rate per unit body surface area at time t becomes $u(R(t), P(t)) = r(R(t))c(P(t))$ as long as the total amount of resource consumed does not exceed $R(t)$; i.e. as long as $R(t) \geq r(R(t))c(P(t))P(t)$. Since the amount of resource available at time t is $R(t)$, the maximum resource consumption per unit

body surface area is $\frac{R(t)}{P(t)}$.

Thus we have the following model of the dynamics of the resource R :

$$R(t+1) = \xi[R(t) - u(R(t), P(t))P(t)] + I_0 \quad (2.8)$$

where

$$u(R, P) = \begin{cases} r(R)c(P) & \text{if } R \geq r(R)c(P)P \\ \frac{R}{P} & \text{if } R < r(R)c(P)P \end{cases} .$$

Models of Size-Structured Populations

Let $0 < \bar{s}_0 < \bar{s}_1 < \dots < \bar{s}_m$ define m size classes $[\bar{s}_{j-1}, \bar{s}_j)$, $j = 1, 2, \dots, m$. Let $x_j(t)$ denote the number or density of individuals in the j^{th} size class $[\bar{s}_{j-1}, \bar{s}_j)$, and let s_j be a representative length of an individual from size class j (e.g. $s_j = \bar{s}_j$ or $s_j = \frac{\bar{s}_{j-1} + \bar{s}_j}{2}$) and define the following size-specific parameters.

δ_j	length of the j^{th} size class ($\bar{s}_j - \bar{s}_{j-1}$)
μ_j	body density (assume uniform so that body weight is $\mu_j s_j^3$)
σ_j	constant of proportionality relating surface area to s_j^2
κ_j	fraction of consumed resource allocated to growth
η_j	conversion factor of resource units to body weight
ω_j	conversion factor of resource units to offspring body weight

Table 2.1: Individual size specific parameters for species j

We assume that all newborns lie in the smallest size class $[\bar{s}_0, \bar{s}_1)$, that no individual can shrink in size, and that the size class intervals have lengths δ_j such that an individual can grow in length no more than into the next size class in one unit of time. In addition, we assume that the resource uptake functional is dependent upon R and P explicitly, and thus is implicitly time-dependent; i.e. $u = u(R(t), P(t))$.

Then the transition matrix \mathcal{T} becomes

$$\mathcal{T} = \pi \begin{bmatrix} 1 - f_1 & 0 & 0 & 0 & \dots & 0 \\ f_1 & 1 - f_2 & 0 & 0 & \dots & 0 \\ 0 & f_2 & 1 - f_3 & 0 & \dots & 0 \\ 0 & 0 & \ddots & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \ddots & \ddots & \dots \\ 0 & 0 & \dots & 0 & f_{m-1} & 1 \end{bmatrix}$$

where the 1 in the lower right-hand corner signifies that no individual can grow larger than size \bar{s}_m and π represents the probability that an individual survives one unit of time.

Thus we need only model the fraction of survivors growing to the next size class. Since the body weight of a j -class individual is $W_j = \mu_j s_j^3$, the weight change of such an individual over one unit of time, ΔW_j , is approximately $3\mu_j s_j^2 \Delta s_j$, where Δs_j is the change in length of the individual over one unit of time. But the weight change can also be expressed in terms of resource consumption; i.e. $\Delta W_j = \kappa_j \sigma_j s_j^2 u(R, P) / \eta_j$. Solving for Δs_j we see that the growth rate per unit time of an individual of size s_j is $\Delta s_j = \frac{\kappa_j \sigma_j u(R, P)}{3\mu_j \eta_j} = \beta_j \delta_j u(R, P)$, where

$$\beta_j = \frac{\kappa_j \sigma_j}{3\mu_j \eta_j \delta_j}$$

is defined to be the "growth coefficient" of size class j . Thus the fraction f_j of individuals of size s_j growing to the next size class is

$$f_j = \frac{\beta_j \delta_j u(R, P)}{\delta_j} = \beta_j u(R, P),$$

and the transition matrix $\mathcal{T} \geq 0$ is the bidiagonal matrix given by

$$\pi \begin{bmatrix} 1 - \beta_1 u(R, P) & 0 & 0 & \cdots & 0 \\ \beta_1 u(R, P) & 1 - \beta_2 u(R, P) & 0 & \cdots & 0 \\ 0 & \beta_2 u(R, P) & 0 & \cdots & 0 \\ 0 & 0 & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & \beta_{m-1} u(R, P) & 1 \end{bmatrix}. \quad (2.9)$$

Now consider the fertility matrix \mathcal{B} . Under the assumptions above, \mathcal{B} will be given by

$$\mathcal{B} = \pi u(R, P) \begin{bmatrix} \gamma_1 & \gamma_2 & \cdots & \gamma_m \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix} \quad (2.10)$$

where

$$\gamma_j = \frac{(1 - \kappa_j) \sigma_j s_j^2}{\omega_j W_1}$$

is defined to be the "reproductive coefficient" for size class j . (Here $W_1 = \mu_1 s_1^3$ is the weight of an individual at birth.)

Thus the dynamics of the population surface area $P(t)$ and the population area vector $\vec{x}(t)$ are governed by Equation (2.5) with

$$a(t) = \pi(1 - \beta_q u(R(t), P(t))), \quad b(t) = \pi u(R(t), P(t))$$

where \mathcal{L} becomes the Usher matrix

$$\mathcal{L} = \begin{bmatrix} \beta_q - \beta_1 + \gamma_1 & \gamma_2 & \cdots & \gamma_q & \cdots & \gamma_{m-1} & \gamma_m \\ \beta_1 & \beta_q - \beta_2 & \cdots & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & \cdots & \beta_q - \beta_{m-1} & 0 \\ 0 & 0 & \cdots & 0 & \cdots & \beta_{m-1} & \beta_q \end{bmatrix}$$

with β_q defined to be the largest β_i .

Preliminary Results

Clearly $\mathcal{L} \geq 0$ and since the β_i are chosen so that $1 - \beta_i u(R, P) > 0$, we know that there exists an a_0 such that $0 \leq a(t) \leq a_0 = \pi$. Thus in order to apply Theorem 1 we need only show that $b(t)$ is bounded away from 0. To this end we consider the boundedness of $P(t)$ and $R(t)$.

Theorem 2 *If $\bar{x}(t)$ is a solution of Equation (2.1) with \mathcal{T} and \mathcal{B} given by Equations (2.9) and (2.10) where $c(P) \neq 1$ with $\bar{x}(0) \geq \bar{0}$ ($\neq \bar{0}$), then $\bar{x}(t) \geq \bar{0}$, $P(t) > 0$ and both sequences are bounded for all $t > 0$.*

Proof First, if $\bar{0} \leq \bar{x}(t) \neq \bar{0}$ then $P(t) \geq 0$ for all t , and Equation (2.1) gives $\bar{x}(t+1) \geq \bar{0}$. In addition, if $\bar{x}(t+1) = \bar{0}$ then $\bar{x}(t) = \bar{0}$, a contradiction of $\bar{x}(t) \neq \bar{0}$. Thus $\bar{x}(t+1) \neq \bar{0}$ and by induction $\bar{0} \leq \bar{x}(t) \neq \bar{0}$ for all t . Thus $P(t) > 0$ for all $t > 0$.

Now, to bound $\bar{x}(t)$ (and hence $P(t)$) above, consider $0 \leq s(t) \equiv \sum_{i=1}^m x_i(t)$. From Equations (2.1), (2.9), and (2.10) we see that

$$s(t+1) = \pi s(t) + \pi u(R(t), P(t)) \sum_{i=1}^m \gamma_i x_i(t)$$

and thus for $t \geq 0$ we obtain

$$0 \leq s(t+1) \leq F(s(t)) \tag{2.11}$$

with $s(0) = \sum x_i(0) > 0$ where $F(s) \equiv \pi(1 + \gamma^* r_0 c(s^* s))s$. Here we define $s^* \equiv \min \sigma_i s_i^2$ and $\gamma^* \equiv \max \gamma_i$. (Hence $u(R(t), P(t)) \sum \gamma_i x_i(t) \leq r_0 c(s^* s) \gamma^* \sum x_i(t) = r_0 c(s^* s) \gamma^* s$.) Clearly $F(s) \geq 0$ for all $s \geq 0$. In addition, there is an $s' \geq 0$ such that for $s > s'$ we have

- $F(s)$ is monotonically increasing
- $F(s) < s$
- $\max_{[0, s']} F(s) = F(s')$.

Now, if $s(t') \leq s'$ for some $t' \geq 0$ then by Equation (2.11) we have $s(t' + 1) \leq F(s(t')) \leq F(s') \leq s'$ and by induction $s(t) \leq s'$ for all $t \geq t'$. If, on the other hand, $s(t) > s'$ for all $t \geq 0$ then we see by Equation (2.11) that $s(1) \leq F(s(0)) \leq s(0)$ and by induction $s(t + 1) \leq F(s(t)) < s(t) < s(0)$. In either case, $s(t)$ is bounded and hence so are $\bar{x}(t)$ and $P(t)$. ♣

In the case where $c(P) \equiv 1$, boundedness depends upon the choice of parameters contributing to the γ_i . If we let $s(t)$ be defined as in the proof above, we arrive at the inequality

$$s(t + 1) < \pi\xi[1 + r_0\gamma^*]s(t) \quad (2.12)$$

where γ^* is again defined to be $\max \gamma_i$. Clearly for γ^* small enough, $\pi\xi[1 + r_0\gamma^*] < 1$, implying $s(t) \rightarrow 0$. While picking γ_i that small would be useless, this certainly shows that for γ_i small enough $s(t)$ (and hence $\bar{x}(t)$) is bounded above. In fact, there are ranges of parameters for which $\bar{x}(t)$ is bounded and $\bar{x}(t) \xrightarrow{t} \bar{0}$.

Now consider the boundedness of $R(t)$. While a lower bound on $R(t)$ is all that is needed to apply Theorem 1, for the sake of completeness we will include the upper boundedness proof here as well.

Theorem 3 *If $R(t)$ is a solution of Equation (2.8) with $u(R, P)$ as defined previously and with $r(R)$ and $c(P)$ satisfying assumptions A1 and A2 respectively, then for $R(0) \geq 0$ we have $R(t) \geq I_0$ for $t > 0$ and $R(t)$ bounded above.*

Proof Upon inspection of Equation (2.8) it is clear that $R(t) \geq I_0$ for all $t > 0$.

Now clearly $0 \leq R(t+1) \leq \xi R(t) + I_0$, so consider the difference equation $y(t+1) = \xi y(t) + I_0$ with $y(0) = R(0)$. This equation has the unique fixed point $\bar{y} = \frac{I_0}{1-\xi}$ and it is attracting since $\xi \in [0, 1)$. Then since $0 \leq R(t+1) \leq y(t+1)$, we have $\limsup R(t) \leq \frac{I_0}{1-\xi}$ and thus $R(t)$ is bounded above. ♣

If we let $b_0 = \pi r(I_0)c(P^\infty)$ where P^∞ is an upper bound for $P(t)$, we have $0 < b_0 \leq b(t)$ for all $t \geq 0$. Now as long as \mathcal{L} satisfies H2 of Theorem 1, the dynamics of $P(t)$ are determined by the scalar difference equation

$$P(t+1) = \pi(1 + \theta u(R(t), P(t)))P(t) \quad (2.13)$$

with $P(0) = \bar{w}^T \bar{x}(0) > 0$ where $\theta \equiv \lambda^+ - \beta_q$. Since $\lambda^+ > 0$ is the dominant eigenvalue of \mathcal{L} , θ is the eigenvalue of the matrix

$$\mathcal{M} \equiv \mathcal{L} - \beta_q \mathcal{I} = \begin{bmatrix} -\beta_1 + \gamma_1 & \gamma_2 & \cdots & \gamma_{m-1} & \gamma_m \\ \beta_1 & -\beta_2 & \cdots & 0 & 0 \\ 0 & \beta_2 & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & -\beta_{m-1} & 0 \\ 0 & 0 & \cdots & \beta_{m-1} & 0 \end{bmatrix}$$

with largest real part.

2.3 Multispecies Competition Model

We now consider a model of competition among n size-structured species for a common limiting resource. We describe the dynamics of each species by a model

of the type discussed above with species j represented by an m_j vector $\bar{x}_j(t) = \text{col}(x_{ij}(t))_{i=1}^{m_j}$ of size class densities. We use the same length scale for each species, but not necessarily the same size classes or number of size classes. We thus obtain a system of n coupled nonlinear matrix difference equations and one scalar difference equation (representing the resource). The ergodic theorem again applies to each matrix equation and we find that the normalized size distribution $\bar{\psi}_j(t)$ of each species asymptotically approaches the normalized positive eigenvector \bar{v}_j^+ of \mathcal{L}_j where

$$\mathcal{L}_j = \begin{bmatrix} \beta_{jq} - \beta_{j1} + \gamma_{j1} & \gamma_{j2} & \cdots & \gamma_{jq} & \cdots & \gamma_{jm-1} & \gamma_{jm} \\ \beta_{j1} & \beta_{jq} - \beta_{j2} & \cdots & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & \cdots & \beta_{jq} - \beta_{jm-1} & 0 \\ 0 & 0 & \cdots & 0 & \cdots & \beta_{jm-1} & \beta_{jq} \end{bmatrix}$$

and β_{jq} is the largest β for species j . Thus the dynamics of the population sizes $P_j(t)$ are governed by the system of equations

$$R(t+1) = \xi \left[R(t) - \sum_{j=1}^n u_j(R(t), \bar{P}(t)) P_j(t) \right] + I_0 \quad (2.14)$$

$$P_j(t+1) = \pi_j \left[1 + \theta_j u_j(R(t), \bar{P}(t)) \right] P_j(t) \quad (2.15)$$

with $u_j(R(t), \bar{P}(t))$ given by

$$u_j(R, \bar{P}) \equiv \begin{cases} r_j(R)c(\bar{P}) & \text{if } R \geq \sum_{i=1}^n r_i(R)c(\bar{P})P_i \\ \frac{R}{\sum P_i} & \text{if } R < \sum_{i=1}^n r_i(R)c(\bar{P})P_i \end{cases} \quad (2.16)$$

where $\bar{P}(t) = (P_1(t), \dots, P_n(t))$ is the vector of population sizes at time t .

CHAPTER 3

Equilibrium Dynamics

3.1 Single Species

First we consider the dynamics for one species. From Chapter 2 we have the limiting equations:

$$R(t+1) = \xi[R(t) - u(R(t), P(t))P(t)] + I_0 \quad (3.1)$$

$$P(t+1) = \pi[1 + \theta u(R(t), P(t))]P(t) \quad (3.2)$$

where $u(R(t), P(t))$, the resource uptake rate per unit area at time t , is given by:

$$u(R, P) = \begin{cases} r(R)c(P) & \text{if } R \geq r(R)c(P)P \\ \frac{R}{P} & \text{otherwise} \end{cases}$$

For all $\theta \geq 0$ Equations (3.1) and (3.2) have the trivial equilibrium $(R_0, 0)$, in which the population level is zero and R_0 is defined by $R_0 \equiv \frac{I_0}{1-\xi}$. To study the stability of this equilibrium, we first compute the Jacobian of Equations (3.1) and (3.2) for any equilibrium (R^e, P^e) satisfying $R^e \geq r(R^e)c(P^e)P^e$. At such an equilibrium we have

$$\mathcal{J}(R^e, P^e) = \begin{pmatrix} \xi[1 - P^e c(P^e) r'(R^e)] & -\xi r(R^e)[c(P^e) + c'(P^e)P^e] \\ \pi \theta r'(R^e) c(P^e) P^e & \pi[1 + \theta r(R^e)(c(P^e) + P^e c'(P^e))] \end{pmatrix} \quad (3.3)$$

At $(R_0, 0)$ we have

$$\mathcal{J}(R_0, 0) = \begin{pmatrix} \xi & -\xi r(R_0) \\ 0 & \pi(1 + \theta r(R_0)) \end{pmatrix}$$

which has eigenvalues ξ and $\pi(1 + \theta r(R_0))$. Since $\xi \in (0, 1)$, the stability of the trivial equilibrium is determined by $\pi(1 + \theta r(R_0))$, which is clearly positive. Thus the trivial equilibrium is asymptotically stable if $\pi(1 + \theta r(R_0)) < 1$; that is, if

$$\theta < \frac{1 - \pi}{\pi r(R_0)} \equiv \theta^{cr}.$$

Nondepleted Positive Equilibria

Next we look for a nontrivial equilibrium (R^e, P^e) , $P^e \neq 0$ such that $R^e > I_0$. Such equilibria will be called “nondepleted” since the equilibrium resource level is greater than the input amount; i.e. the resource is not being depleted at each time interval.

Interference Competition ($c(P) \neq 1$)

A nondepleted equilibrium (R^e, P^e) must satisfy $R^e > r(R^e)c(P^e)P^e$ as can be seen from Equations (3.1) and (3.2). Thus we obtain the equilibrium equations

$$R^e = \xi[R^e - r(R^e)c(P^e)P^e] + I_0 \quad (3.4)$$

$$\pi[1 + \theta r(R^e)c(P^e)] = 1 \quad (3.5)$$

Equation (3.5) can be rewritten as

$$r(R^e) = \frac{1 - \pi}{\pi\theta} \frac{1}{c(P^e)}. \quad (3.6)$$

Equation (3.4) can be rewritten as $R^e(1 - \xi) = I_0 - \xi r(R^e)c(P^e)P^e$, and upon substitution for $r(R^e)$ this becomes $R^e = R_0 - \frac{(1-\pi)\xi}{\pi\theta} P^e$, thus giving

$$P^e = \frac{\pi\theta}{(1 - \pi)\xi} (R_0 - R^e) \quad (3.7)$$

The equilibrium equations (3.4) and (3.5) are equivalent to Equations (3.6) and (3.7).

Now we study the conditions under which a solution (R^e, P^e) of Equations (3.7) and (3.6) will exist. A substitution of (3.7) into (3.6) yields the equation

$$r(R^e) = \frac{1 - \pi}{\pi\theta} \frac{1}{c\left(\frac{\pi\theta}{(1-\pi)\xi}(R_0 - R^e)\right)}, \quad (3.8)$$

a solution R^e on the interval $I_0 < R^e < R_0$ of which yields a positive nondepleted equilibrium. By the assumptions on $r(R)$, the left-hand side of (3.8) is increasing with R^e . Also, as R^e increases, $R_0 - R^e$ must decrease, so $c\left(\frac{\pi\theta}{(1-\pi)\xi}(R_0 - R^e)\right)$ increases. This in turn implies that the right-hand side of (3.8), $RHS(R^e)$, is a decreasing function of R^e .

Upon inspection of Figure (3.1) it is clear that an equilibrium (R^e, P^e) (determined by an intersection of the curves) will exist if and only if $r(I_0) < RHS(I_0)$ and $RHS(R_0) < r(R_0)$. The first of these conditions can be expressed as

$$\frac{\pi\theta I_0}{1 - \pi} c\left(\frac{\pi I_0\theta}{(1 - \pi)(1 - \xi)}\right) < \frac{I_0}{r(I_0)} \quad (3.9)$$

while the second condition simplifies to give

$$\theta > \frac{1 - \pi}{\pi r(R_0)} (\equiv \theta^{cr}). \quad (3.10)$$

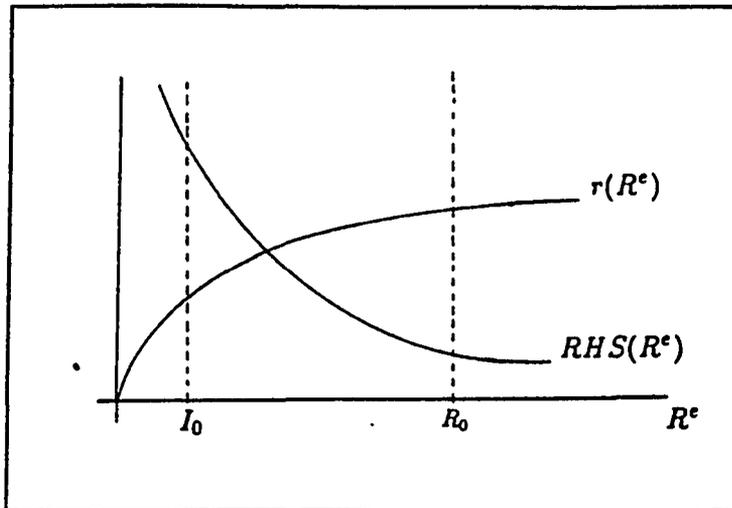


Figure 3.1: Right- and left-hand sides of Equation (3.8) as functions of R^e .

By the monotonicity of $r(R)$ and $c(P)$ it is clear that such an intersection must be unique; hence a positive nondepleted equilibrium exists and is unique for each $\theta > \theta^{cr}$ such that Equation (3.9) holds, which is true at least for $\theta \approx \theta^{cr}$. We thus have the following equilibrium diagram:

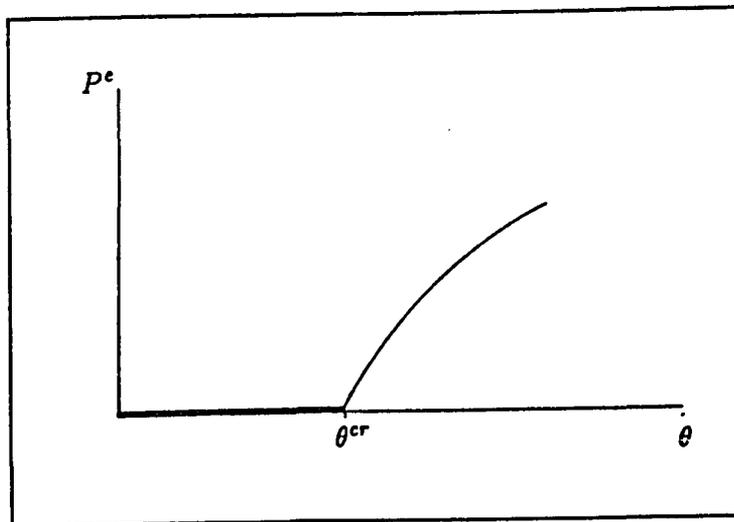


Figure 3.2: Equilibrium diagram for $c(P) \neq 1$.

Exploitative Competition ($c(P) \equiv 1$)

In this case the nondepleted equilibrium equations become

$$R^e = \xi[R^e - r(R^e)P^e] + I_0 \quad (3.11)$$

$$\pi[1 + \theta r(R^e)] = 1 \quad (3.12)$$

From Equation (3.12) we see that $r(R^e) = \frac{1-\pi}{\pi\theta}$ and since $r(R)$ is one-to-one this gives a unique R^e with $R^e < R_0$ for $\theta \leq \theta^b$, where $\theta^b \equiv \frac{1-\pi}{\pi r(I_0)}$. (Note that $\theta > \theta^b$ implies that $r(R^e) < r(I_0)$, which in turn gives $R^e < I_0$, a contradiction to Equation (3.11).) Then since $r(R^e) = r(R_0)$ at $\theta = \theta^{cr}$, we have $(R^e, P^e) = (R_0, 0)$, while for $\theta \in (\theta^{cr}, \theta^b]$ we have $R^e < R_0$ and thus $P^e > 0$. Also, from the equations for $r(R^e)$ and P^e it is clear that R^e decreases monotonically and P^e increases monotonically with increasing θ .

We thus have the following equilibrium diagram for exploitative competition:

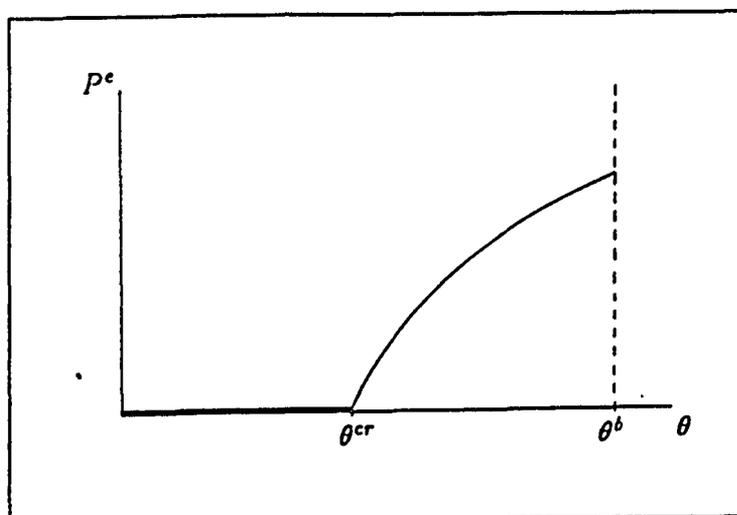


Figure 3.3: Equilibrium diagram for $c(P) \equiv 1$.

Depleted Equilibria

Now we consider an equilibrium (R^e, P^e) with $P^e \neq 0$, such that $r(R^e)c(P^e)P^e \geq R^e$ and $u(R^e, P^e) = \frac{R^e}{P^e}$. Call such an equilibrium "depleted". The depleted equilibrium equations are

$$R^e = I_0 \quad (3.13)$$

$$\pi \left[1 + \theta \frac{I_0}{P^e} \right] = 1 \quad (3.14)$$

and Equation (3.14) then yields

$$P^e = \frac{\pi \theta I_0}{1 - \pi}.$$

The inequality $r(R^e)c(P^e)P^e \geq R^e$ becomes

$$\gamma \theta c(\gamma \theta) \geq \frac{I_0}{r(I_0)} \quad (3.15)$$

where $\gamma \equiv \frac{\pi I_0}{1 - \pi}$ is a constant. Upon comparison of Equations (3.9) and (3.15) we see that when a depleted equilibrium exists, it arises from an equilibrium for which the resource remains undepleted, and this switch occurs at a value of θ such that $\gamma \theta c(\gamma \theta) = \frac{I_0}{r(I_0)}$. We examine several examples of competition functions $c(P)$ to show the possible changes of equilibrium type which might occur.

Example 1 For $c(P) = e^{-dP}$, Equation (3.15) becomes $\gamma \theta e^{-d\gamma \theta} = \frac{I_0}{r(I_0)}$. In this case, a depleted equilibrium will occur if and only if $\frac{1}{de} \geq \frac{I_0}{r(I_0)}$, and then only for a finite range of θ values, $\theta \in [\underline{\theta}, \bar{\theta}]$, as shown below.

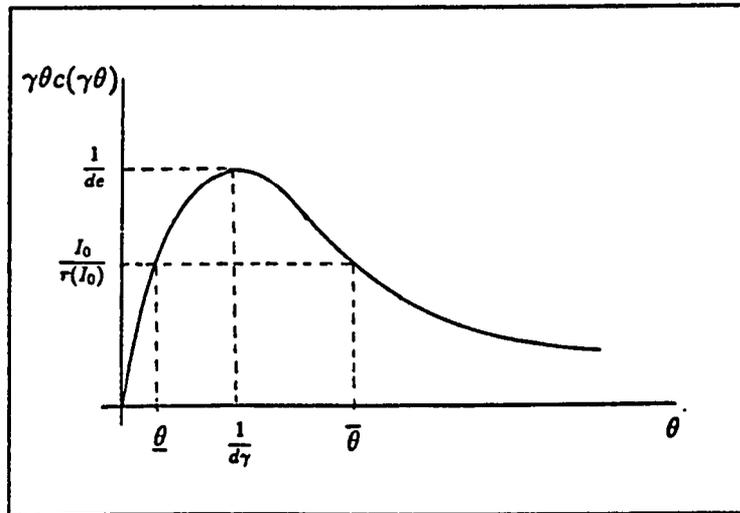


Figure 3.4: Range of θ for which a depleted equilibrium will exist for $c(P) = e^{-dP}$.

Example 2 For $c(P) = \frac{1}{1+dP}$, Equation (3.15) becomes $\frac{\gamma\theta}{1+d\gamma\theta} \geq \frac{I_0}{r(I_0)}$. In this case, a depleted equilibrium will occur if and only if $\frac{1}{d} \geq \frac{I_0}{r(I_0)}$. If this condition is met, then there will exist a depleted equilibrium for all $\theta \geq \underline{\theta}$, as shown below.

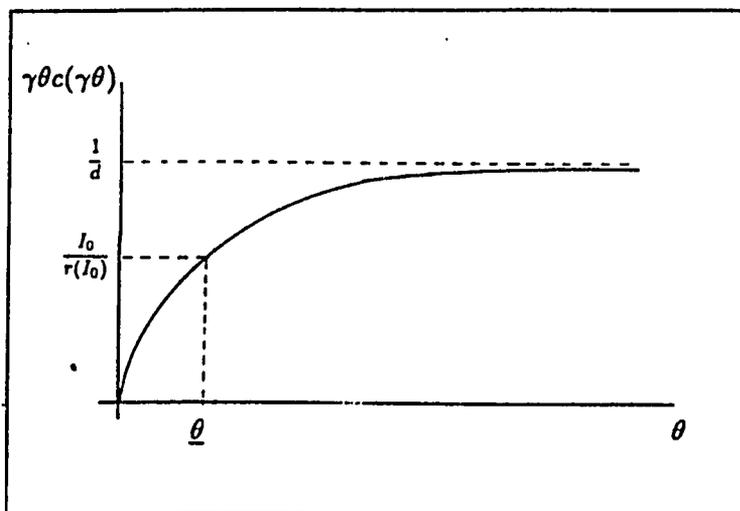


Figure 3.5: Range of θ for which a depleted equilibrium will exist for $c(P) = \frac{1}{1+dP}$.

Example 3 For $c(P) = \frac{1}{1+dP^2}$, Equation (3.15) becomes $\frac{\gamma\theta}{1+d(\gamma\theta)^2} \geq \frac{I_0}{r(I_0)}$, and a depleted equilibrium will always occur for θ large enough.

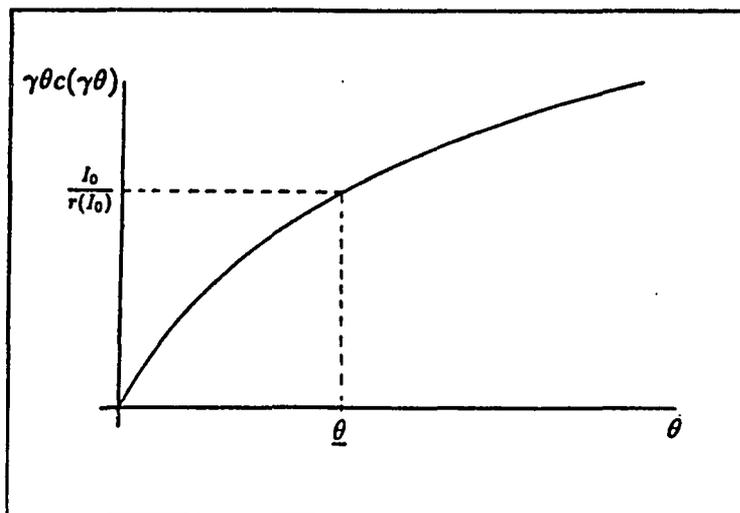


Figure 3.6: Range of θ for which a depleted equilibrium will exist for $c(P) = \frac{1}{1+dP^2}$.

Example 4 For $c(P) \equiv 1$, we see from Equation (3.15) that a necessary and sufficient condition for a depleted equilibrium to exist is $\gamma\theta \geq \frac{I_0}{r(I_0)}$, but this can be rewritten as $\theta \geq \frac{1-\pi}{\pi r(I_0)} = \theta^b$, and solutions of the limiting equations are unbounded there. Thus under the restriction to purely exploitative competition where $c(P) \equiv 1$, the only type of equilibrium which may occur is nondepleted.

Stability Results

We now state the following existence and stability results for trivial, nondepleted, and depleted equilibria. Parts (i) - (iii) of Theorem 4 have already been shown, while the proof of part (iv) is contained in the Appendix. We begin with the results for the trivial and nondepleted equilibria.

Theorem 4 *For the system given by Equations (3.1) and (3.2), there exists a value $\theta = \theta^{cr}$ such that the following statements hold.*

- i. There exists a unique equilibrium $(R_0, 0)$ for all $\theta \geq 0$.*
- ii. The trivial equilibrium $(R_0, 0)$ is locally asymptotically stable if $\theta < \theta^{cr}$.*
- iii. A positive nontrivial equilibrium (R^e, P^e) exists if and only if $\theta > \theta^{cr}$.*
- iv. This equilibrium is locally asymptotically stable for $\theta \gtrsim \theta^{cr}$.*

The next theorem deals with the stability of depleted equilibria.

Theorem 5 *A depleted equilibrium (R^e, P^e) of Equations (3.1) and (3.2) is asymptotically stable whenever it exists.*

Proof The Jacobian of Equations (3.1) and (3.2) at a depleted equilibrium (R^e, P^e) is given by

$$\mathcal{J}(R^e, P^e) = \begin{bmatrix} 0 & 0 \\ \pi\theta I_0 & \pi \end{bmatrix},$$

which has eigenvalues 0 and π . Since both of these eigenvalues are between -1 and 1 and independent of θ , the depleted equilibrium (R^e, P^e) is asymptotically stable.

♣

While the stability results given above for the nontrivial equilibria are local, a global result may be obtained for the trivial equilibrium.

Theorem 6 For $\theta < \theta^{cr}$, $(R_0, 0)$ is globally attracting.

Proof Let $(R(t), P(t))$ be any solution of Equations (3.1) and (3.2), and let $\theta < \theta^{cr}$. Then for any $\varepsilon > 0$ there exists a $T(\varepsilon) > 0$ such that for $t \geq T(\varepsilon)$

$$\begin{aligned} 0 \leq P(t+1) &= \pi [1 + \theta u(R(t), P(t))] P(t) \\ &\leq \pi [1 + \theta r(R(t))] P(t) \\ &< \pi [1 + \theta r(R_0 + \varepsilon)] P(t) \end{aligned}$$

since by Theorem 3 in the previous chapter $\limsup R(t) \leq R_0$. If ε is chosen small enough that $\pi [1 + \theta r(R_0 + \varepsilon)] < 1$ (which is possible since $\theta < \theta^{cr}$), we then have $0 < P(t+1) < \pi [1 + \theta r(R_0 + \varepsilon)] P(t)$ and thus $P(t) \rightarrow 0$ and $R(t) \rightarrow R_0$ as $t \rightarrow +\infty$. ♣

We now have the following bifurcation diagrams. Figure (3.7) shows the equilibrium dynamics for a nondepleted equilibrium, while Figure (3.8) shows the dynamics for a depleted equilibrium.

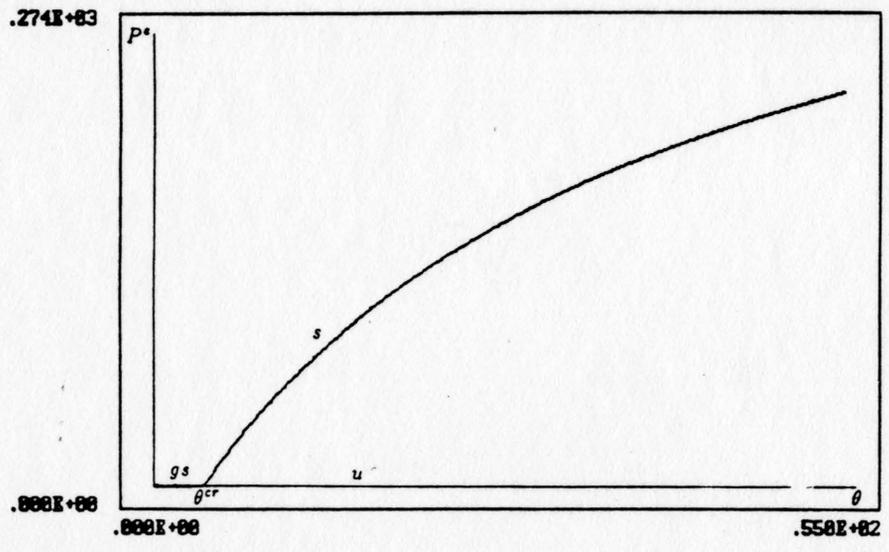


Figure 3.7: Bifurcation diagram showing the exchange of stability from the trivial equilibrium $(R_0, 0)$ to the positive (nondepleted) equilibrium (R^e, P^e)

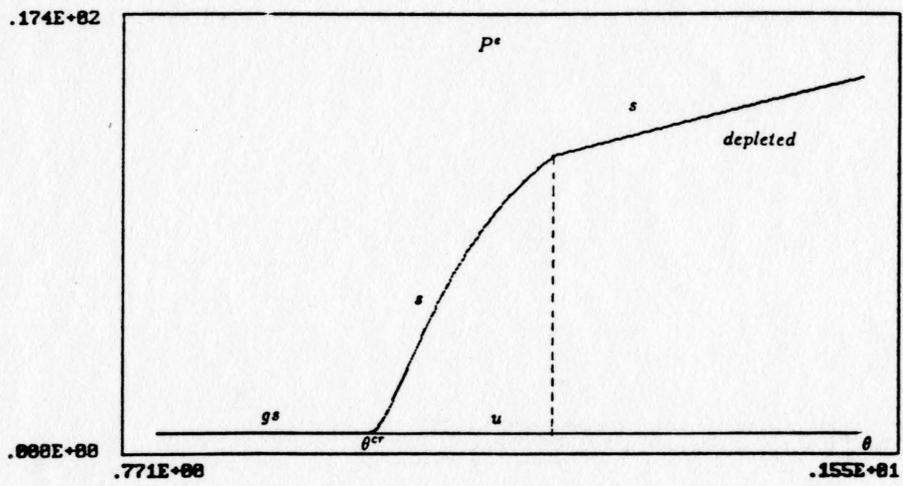


Figure 3.8: Diagram showing the change of equilibrium type from nondepleted to depleted

3.2 Multispecies Dynamics

We now study the equilibrium dynamics for the multispecies case. For n species we have the system:

$$R(t+1) = \xi \left[R(t) - \sum_{j=1}^n u_j(R(t), \bar{P}(t)) P_j(t) \right] + I_0 \quad (3.16)$$

$$P_j(t+1) = \pi_j \left[1 + \theta_j u_j(R(t), \bar{P}(t)) \right] P_j(t) \quad j = 1, \dots, n \quad (3.17)$$

where $\bar{P}(t) \equiv (P_1(t), \dots, P_n(t))$ and $c(\bar{P}(t))$ is such that $c(\bar{0}) = 1$ and $\frac{\partial c}{\partial P_j} < 0$ for $j = 1, \dots, n$. The per unit body surface area uptake rate for species j , denoted by $u_j(R(t), \bar{P}(t))$, is given by

$$u_j(R, \bar{P}) \equiv \begin{cases} r_j(R) c(\bar{P}) & \text{if } R \geq \sum_{j=1}^n r_j(R) c(\bar{P}) P_j \\ \frac{R}{\sum_{j=1}^n P_j} & \text{otherwise} \end{cases}$$

For $j = 1, \dots, n$, let θ_j^{cr} be given by

$$\theta_j^{cr} \equiv \frac{1 - \pi_j}{\pi_j r_j(R_0)}$$

Lemma 1 *If $P_j(0) > 0$ and $\theta_j < \theta_j^{cr}$ then $P_j(t) \rightarrow 0$ as $t \rightarrow +\infty$.*

Proof Let $(R(t), \bar{P}(t))$ be any solution of the system (3.16), (3.17). Then for any $\varepsilon > 0$ there exists a $T(\varepsilon) > 0$ such that for $t \geq T(\varepsilon)$

$$\begin{aligned} 0 \leq P_j(t+1) &= \pi_j \left[1 + \theta_j u_j(R(t), \bar{P}(t)) \right] P_j(t) \\ &\leq \pi_j [1 + \theta_j r_j(R(t))] P_j(t) \\ &< \pi_j [1 + \theta_j r_j(R_0 + \varepsilon)] P_j(t) \end{aligned}$$

since $\limsup R(t) \leq R_0$. If we choose ε such that $\pi_j [1 + \theta_j r_j(R_0 + \varepsilon)] < 1$ (possible since $\theta_j < \theta_j^{cr}$), we then have $0 < P_j(t+1) < \pi_j [1 + \theta_j r_j(R_0 + \varepsilon)] P_j(t)$. Thus $x(t) \rightarrow 0$ as $t \rightarrow +\infty$, and so $P_j(t) \rightarrow 0$ as $t \rightarrow +\infty$ as well. ♣

The preceding lemma shows that if $\theta_j < \theta_j^{cr}$ then species j will go extinct, so we assume without loss of generality that

$$\theta_j > \theta_j^{cr} \quad \text{for } j = 1, \dots, n.$$

The next lemma shows that the only possible equilibria are the trivial equilibrium and the n one-species equilibria.

Lemma 2 *Let $(R^e, P_1^e, \dots, P_n^e)$ be an equilibrium of the system given by Equations (3.16) and (3.17). For a generic choice of parameters ξ, π_j, θ_j , $P_j^e \neq 0$ for at most one j .*

Proof Without loss of generality, we consider an equilibrium $(R^e, P_1^e, \dots, P_k^e, 0, \dots, 0)$ with $P_j^e \neq 0$ for $j = 1, \dots, k$ $k \geq 2$. Then

$$\pi_j \left[1 + \theta_j r_j (R^e) c(\bar{P}^e) \right] = 1$$

for the nondepleted case and

$$\pi_j \left[1 + \theta_j \frac{R^e}{\sum_{j=1}^k P_j^e} \right] = 1$$

for a depleted equilibrium. In either case, we have $k \geq 2$ equations in one unknown, namely $c(\bar{P}^e)$ in the undepleted case, and $\sum_{j=1}^k P_j^e$ in the depleted case, and thus the system of equations is not solvable for a generic choice of parameters. ♣

In light of the preceding lemma, we need only consider the trivial equilibrium $(R_0, 0, \dots, 0)$ and the n axis equilibria given by

$$(R_j^e, P_j^e \vec{e}_j) \equiv (R_j^e, 0, \dots, 0, P_j^e, 0, \dots, 0)$$

where the pair (R_j^e, P_j^e) is an equilibrium of the single species system for species j . We say that $(R_j^e, P_j^e, \bar{e}_j)$ is *inherently asymptotically stable* if (R_j^e, P_j^e) is asymptotically stable in the single species system.

We begin to study the stability of these equilibria by first noting that due to the assumption $\theta_j > \theta_j^{cr}$ for $j = 1, \dots, n$, the trivial equilibrium $(R_0, \bar{0})$ is unstable since the Jacobian at that equilibrium has eigenvalues ξ and $\pi_j(1 + \theta_j r_j(R_0))$, $j = 1, \dots, n$, the last n of which have magnitude greater than one. We now state a stability result for $(R_j^e, P_j^e, \bar{e}_j)$.

Theorem 7 *The axis equilibrium $(R_j^e, P_j^e, \bar{e}_j)$ is asymptotically stable if and only if it is inherently asymptotically stable and $\frac{r_k(R_j^e)}{r_k(R_0)} \frac{\theta_k}{\theta_k^{cr}} < \frac{r_j(R_j^e)}{r_j(R_0)} \frac{\theta_j}{\theta_j^{cr}}$ for $k \neq j$.*

Proof Without loss of generality we consider the case $j = 1$. The proof is given for the nondepleted case, but the extension to the depleted case can be made by considering $r(R) \equiv R$ and $c(\bar{P}) \equiv \sum_j P_j$. The $(n+1) \times (n+1)$ Jacobian is upper block triangular

$$\mathcal{J} = \begin{bmatrix} \mathcal{A} & \mathcal{B} \\ 0 & \mathcal{C} \end{bmatrix}$$

where \mathcal{C} is the $(n-1) \times (n-1)$ diagonal matrix

$$\mathcal{C} = \text{Diag} \left[\pi_i \left(1 + \theta_i r_i(R_1^e) c(P_1^e, \bar{e}_1) \right) \right], \quad i = 2, \dots, n$$

and \mathcal{A} is the 2×2 matrix

$$\mathcal{A} = \begin{bmatrix} \xi [1 - r'_1(R_1^e) P_1^e c(P_1^e, \bar{e}_1)] & -\xi r_1(R_1^e) \left[c(P_1^e, \bar{e}_1) + \frac{\partial c}{\partial P_1} P_1^e \right] \\ \pi_1 P_1^e \theta_1 r'_1(R_1^e) c(P_1^e, \bar{e}_1) & \pi_1 \left[1 + \theta_1 r_1(R_1^e) \left(c(P_1^e, \bar{e}_1) + \frac{\partial c}{\partial P_1} P_1^e \right) \right] \end{bmatrix}.$$

The submatrix \mathcal{A} is simply the Jacobian of the single species equilibrium (R^e, P^e) .

Thus for an equilibrium $(R_1^e, P_1^e, \bar{e}_1)$, stability occurs if and only if

1. The single species equilibrium (R_1^e, P_1^e) is asymptotically stable in the absence of competition, and
2. $\pi_k [1 + \theta_k r_k(R_1^e) c(P_1^e \bar{e}_1)] < 1$ for all $k \neq 1$.

Condition 2 occurs if and only if

$$\theta_k < \frac{1 - \pi_k}{\pi_k r_k(R_1^e) c(P_1^e \bar{e}_1)} \quad \text{for } k \neq 1,$$

and since from the equilibrium equations $\theta_1 = \frac{1 - \pi_1}{\pi_1 r_1(R_1^e) c(P_1^e \bar{e}_1)}$, Condition 2 occurs if and only if

$$\frac{\pi_k r_k(R_1^e)}{1 - \pi_k} \theta_k < \frac{\pi_1 r_1(R_1^e)}{1 - \pi_1} \theta_1$$

or

$$\frac{r_k(R_1^e) \theta_k}{r_k(R_0) \theta_k^{cr}} < \frac{r_1(R_1^e) \theta_1}{r_1(R_0) \theta_1^{cr}} \quad (3.18)$$

for $k \neq 1$. ♣

Note that if the inherent dynamics of all the species are equilibria then Condition (3.18) can be rewritten as $\frac{r_k(R_1^e)}{r_k(R_k^e)} \theta_k < 1$ or $R_1^e < R_k^e$ for $k \neq 1$. Thus the winning species is that species which can deplete the resource to the lowest level. In addition, since at equilibrium we have $\theta_k = \frac{1 - \pi_k}{\pi_k r_k(R_k^e) c(P_k^e \bar{e}_k)}$, in the depleted equilibrium case Condition (3.18) becomes $P_1^e > P_k^e$ for $k \neq 1$; that is, the species that wins is the one that can maintain the highest equilibrium level on the resource amount I_0 .

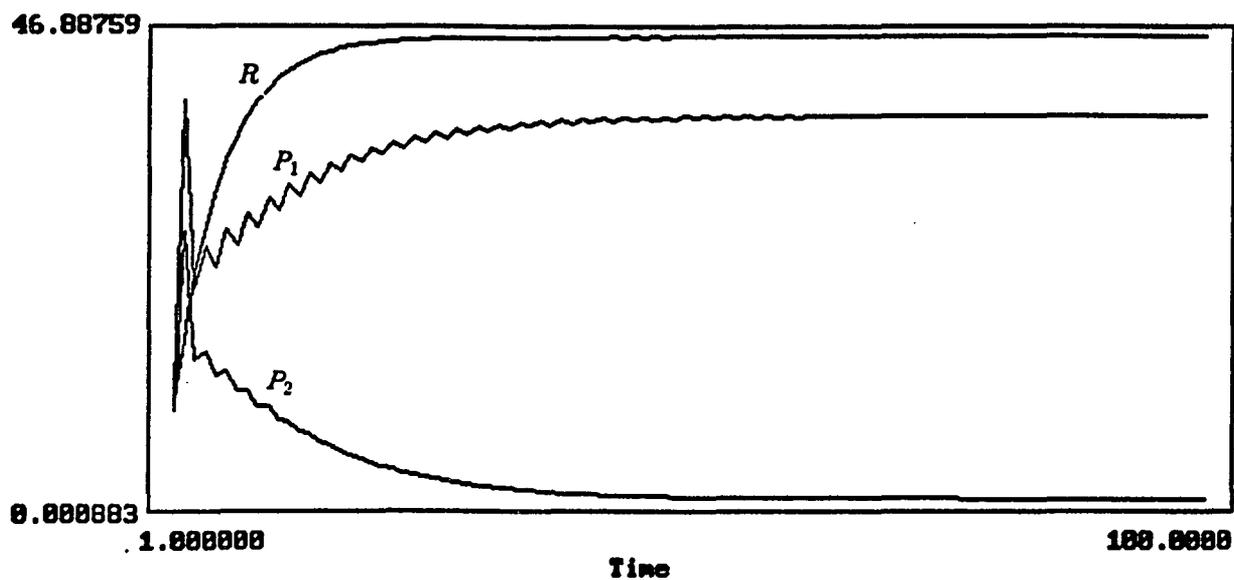


Figure 3.9: Two species competition with species 1 winning and species 2 going extinct. In this example $r_1(R) = r_2(R) = \frac{R}{1+R}$, $c(P) = e^{-0.1(P_1+P_2)}$, $\pi_1 = \pi_2 = 0.5$, and $\xi = 0.8$. $\theta_1 = 50$, corresponding to the eventual winner, and $\theta_2 = 40$.

CHAPTER 4

Nonequilibrium Dynamics

In this chapter we investigate, both analytically and numerically, the existence and stability of nonequilibrium solutions of both the single species and the multispecies models. We begin by studying the loss of stability of the single species equilibrium, recalling that only nondepleted equilibria can lose stability.

4.1 Single Species Equilibria

Theorem 8 *Let λ and μ be the eigenvalues of the linearization of the system given by Equations (3.1) and (3.2) at a nondepleted equilibrium (R^e, P^e) . Suppose that both λ and μ lie inside the unit circle for $\theta < \theta^h$ and $|\lambda| > 1$ for $\theta > \theta^h$. Then at $\theta = \theta^h$, $\lambda = -1$ and $|\mu| < 1$.*

Proof Let \mathcal{J} be the Jacobian of Equations (3.1) and (3.2) at (R^e, P^e) . Then by assumption, at $\theta = \theta^h$ we have $|\lambda| = 1$. We now state the following lemma concerning the determinant of \mathcal{J} .

Lemma 3 At $\theta = \theta^h$, $Det \mathcal{J} \neq 1$.

Proof

$$Det \mathcal{J} = \left[\xi - (R_0 - R^e) \frac{r'(R^e)}{r(R^e)} \right] \left[1 + \frac{\pi \theta}{\xi} (R_0 - R^e) \frac{c'(P^e)}{c(P^e)} \right] + \frac{r'(R^e)}{r(R^e)} (R_0 - R^e) \left[1 - \pi + \frac{\pi \theta}{\xi} (R_0 - R^e) \frac{c'(P^e)}{c(P^e)} \right]$$

After some simplification this yields

$$Det \mathcal{J} = \xi + \pi (R_0 - R^e) \left[\theta \frac{c'(P^e)}{c(P^e)} - \frac{r'(R^e)}{r(R^e)} \right] < \xi < 1$$

since $\left(\theta \frac{c'(P^e)}{c(P^e)} - \frac{r'(R^e)}{r(R^e)} \right) < 0$. Thus $Det \mathcal{J} \neq 1$. ♣

Returning to the proof of the theorem, we see that since $Det \mathcal{J} \neq 1$, we cannot have a complex conjugate pair of eigenvalues on the unit circle, so any eigenvalues of unit modulus must be real, hence equal to 1 or -1. We now state a lemma concerning the possible eigenvalues of \mathcal{J} .

Lemma 4 At $\theta = \theta^h$, 1 is not an eigenvalue of \mathcal{J} .

Proof Suppose $\lambda = 1$ is an eigenvalue of \mathcal{J} at $\theta = \theta^h$. By the characteristic equation $\lambda^2 - (Tr \mathcal{J})\lambda + Det \mathcal{J} = 0$, we have $Tr \mathcal{J} = 1 + Det \mathcal{J}$. This gives

$$1 + \xi - (R_0 - R^e) \frac{r'(R^e)}{r(R^e)} + \frac{\pi \theta}{\xi} (R_0 - R^e) \frac{c'(P^e)}{c(P^e)} = 1 + \xi - \pi (R_0 - R^e) \frac{r'(R^e)}{r(R^e)} + \theta \pi (R_0 - R^e) \frac{c'(P^e)}{c(P^e)}$$

which reduces to

$$(1 - \pi) \frac{r'(R^e)}{r(R^e)} = \pi \theta \frac{c'(P^e)}{c(P^e)},$$

which is clearly impossible since $r'(R^c) > 0$ and $c'(P^c) < 0$. ♣

Returning to the proof of Theorem 8, we see by Lemma 4 that $\lambda \neq 1$, and $|\mu| = \frac{|Det\mathcal{J}|}{|\lambda|}$. Since both λ and μ are inside the unit disk for $\theta < \theta^h$, we know that $|Det\mathcal{J}| = |\lambda\mu| < 1$ for $\theta < \theta^h$. By continuity $|Det\mathcal{J}| \leq 1$ at $\theta = \theta^h$ and hence $|\mu| = \frac{|Det\mathcal{J}|}{|\lambda|} = |Det\mathcal{J}| \leq 1$. Suppose $|\mu| = 1$. By Lemma 4, $\mu = -1$ and hence -1 is a double root. This implies $Det\mathcal{J} = \mu\lambda = 1$, in contradiction to Lemma 3. Thus $|\mu| < 1$. ♣

Since the loss of stability occurs through an eigenvalue crossing at -1 , we are led to suspect that the equilibrium bifurcates to a two-cycle. Unfortunately, a formal proof of this conjecture does not seem to be mathematically tractable; however, numerical studies, some examples of which follow, bear out this hypothesis for the model with interference competition (i.e. $c(P) \neq 1$).

Interference Competition ($c(P) \neq 1$)

Here we show a typical bifurcation diagram (Figure 4.1) illustrating the loss of stability of a nondepleted equilibrium and the resulting periodic and aperiodic behavior of the system.

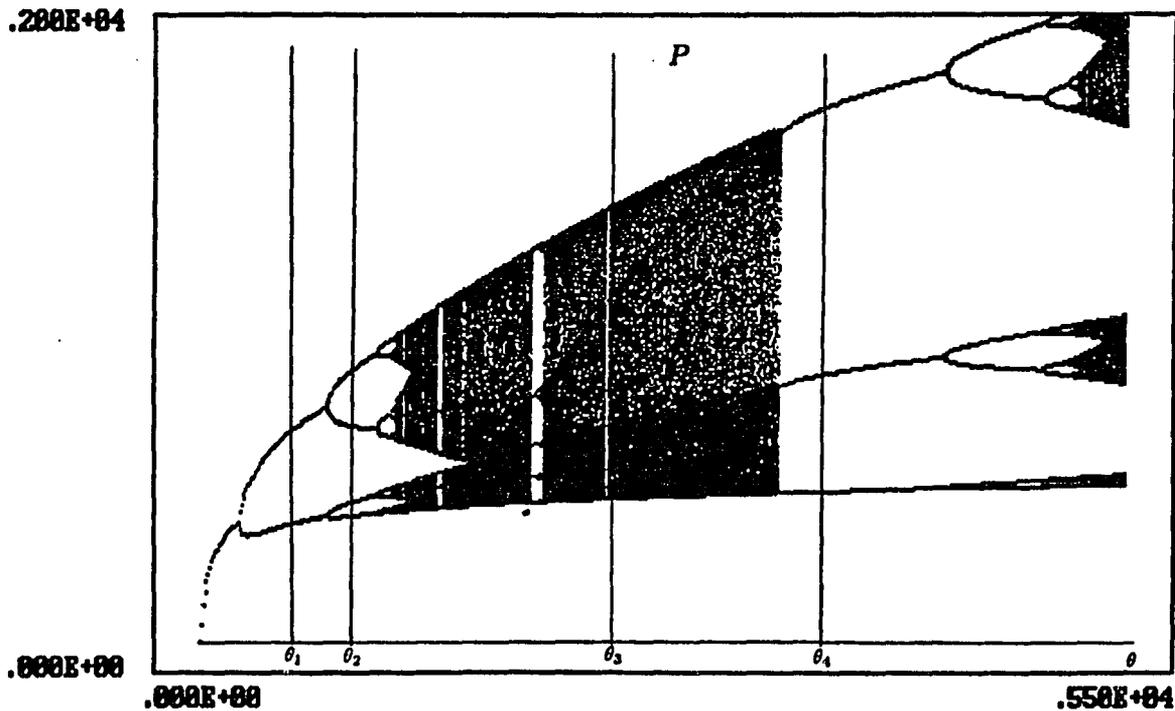


Figure 4.1: Bifurcation diagram for a single species with $\xi = .8$, $\pi = .5$, $r(R) = \frac{R}{1+R}$, $c(P) = e^{-dP}$. Time series for the indicated values of θ are shown on the following pages.

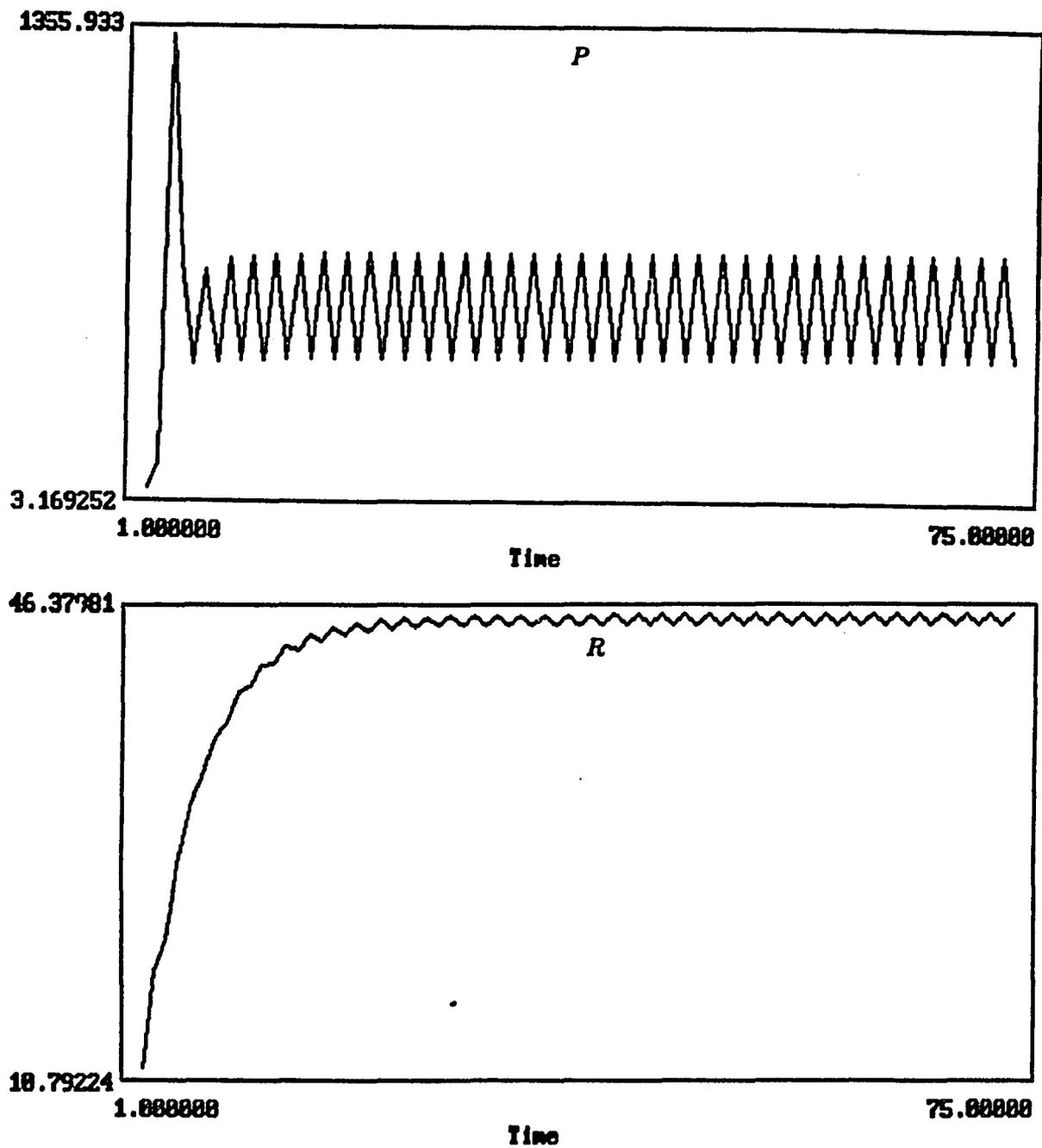


Figure 4.2: Time series of $P(t)$ and $R(t)$ under two-cycle dynamics. $\theta_1 = 550$

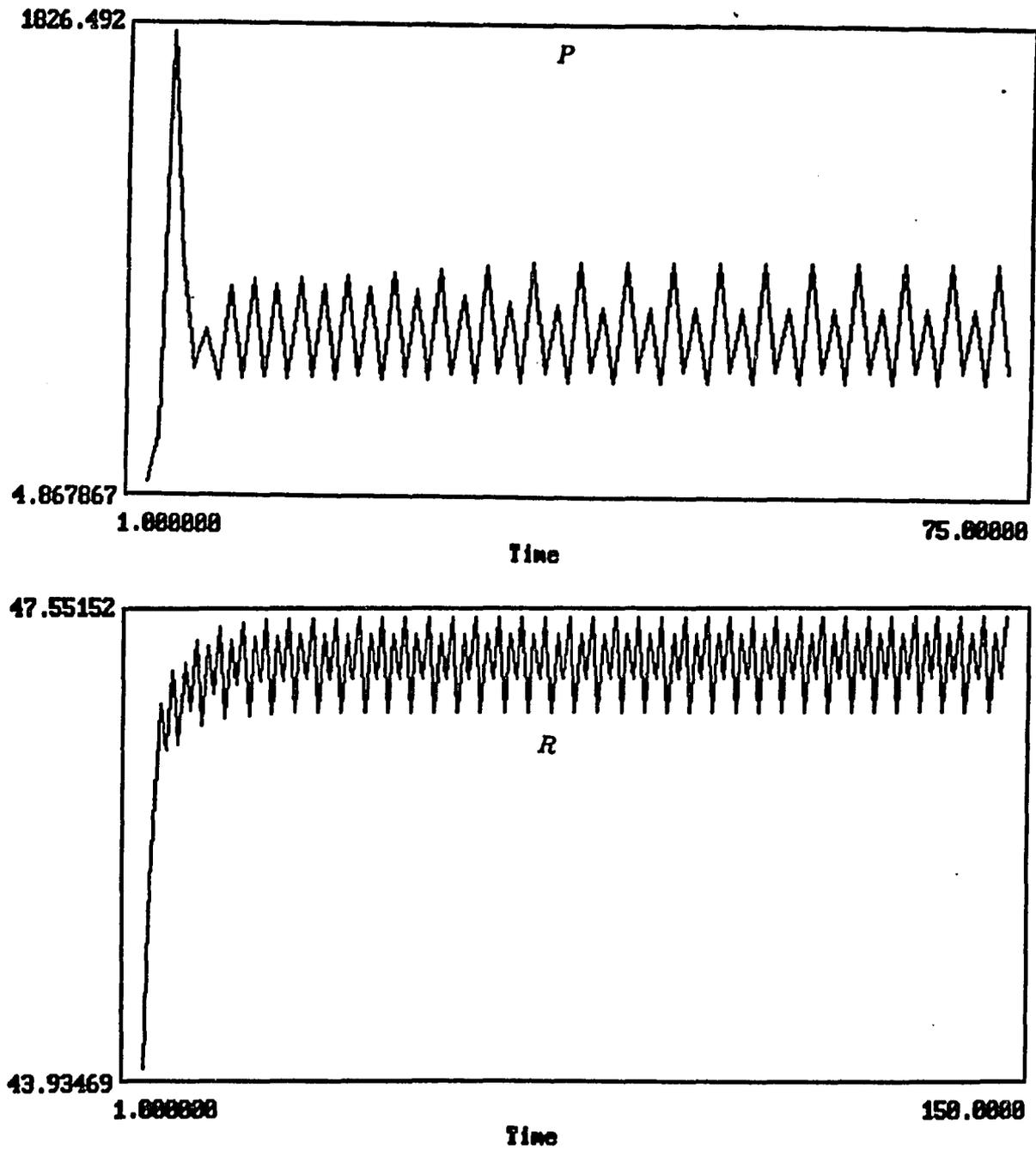


Figure 4.3: Time series of $P(t)$ and $R(t)$ under four-cycle dynamics. $\theta_2 = 900$

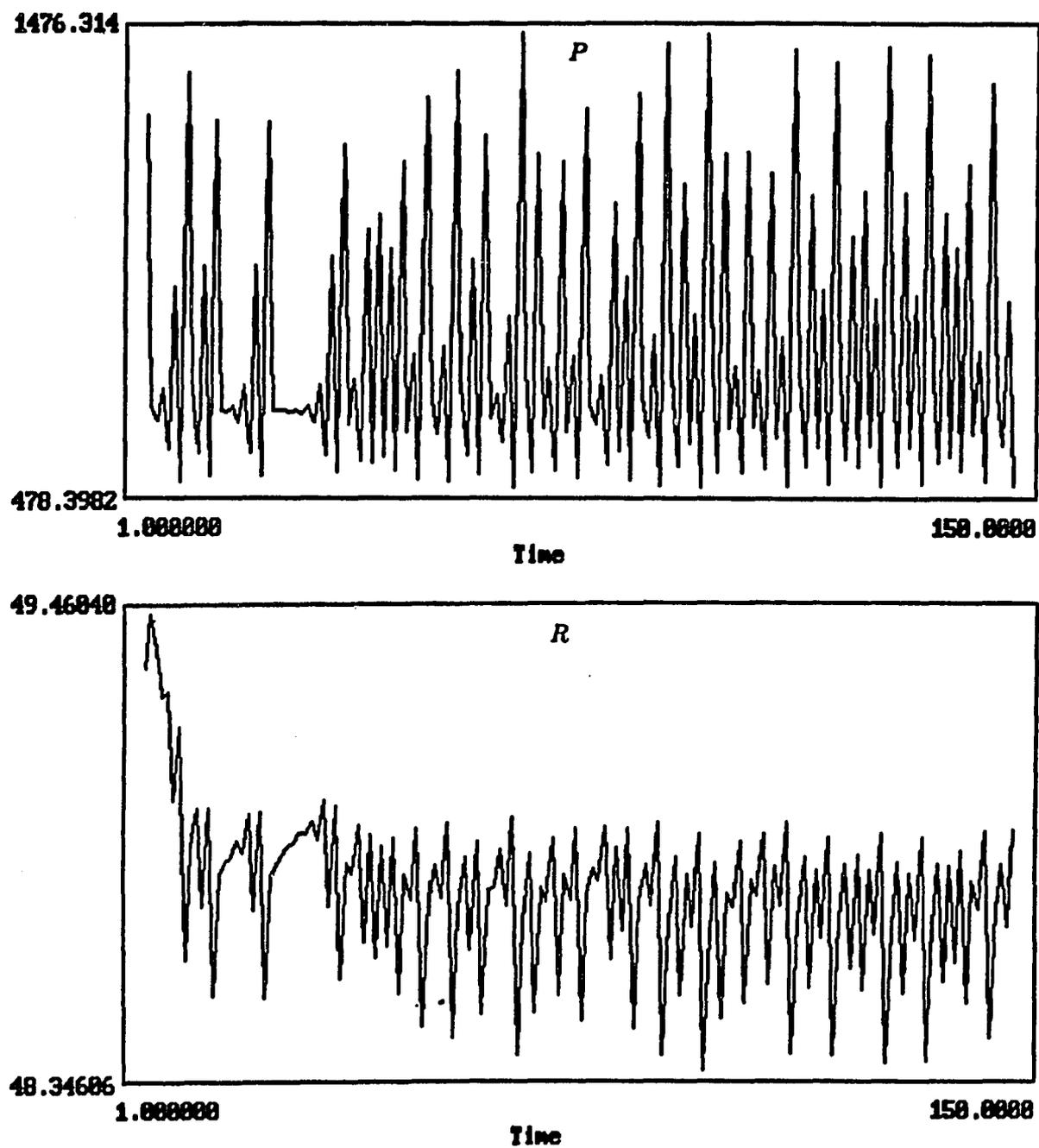


Figure 4.4: Time series of $P(t)$ and $R(t)$ under aperiodic dynamics. $\theta_3 = 2500$

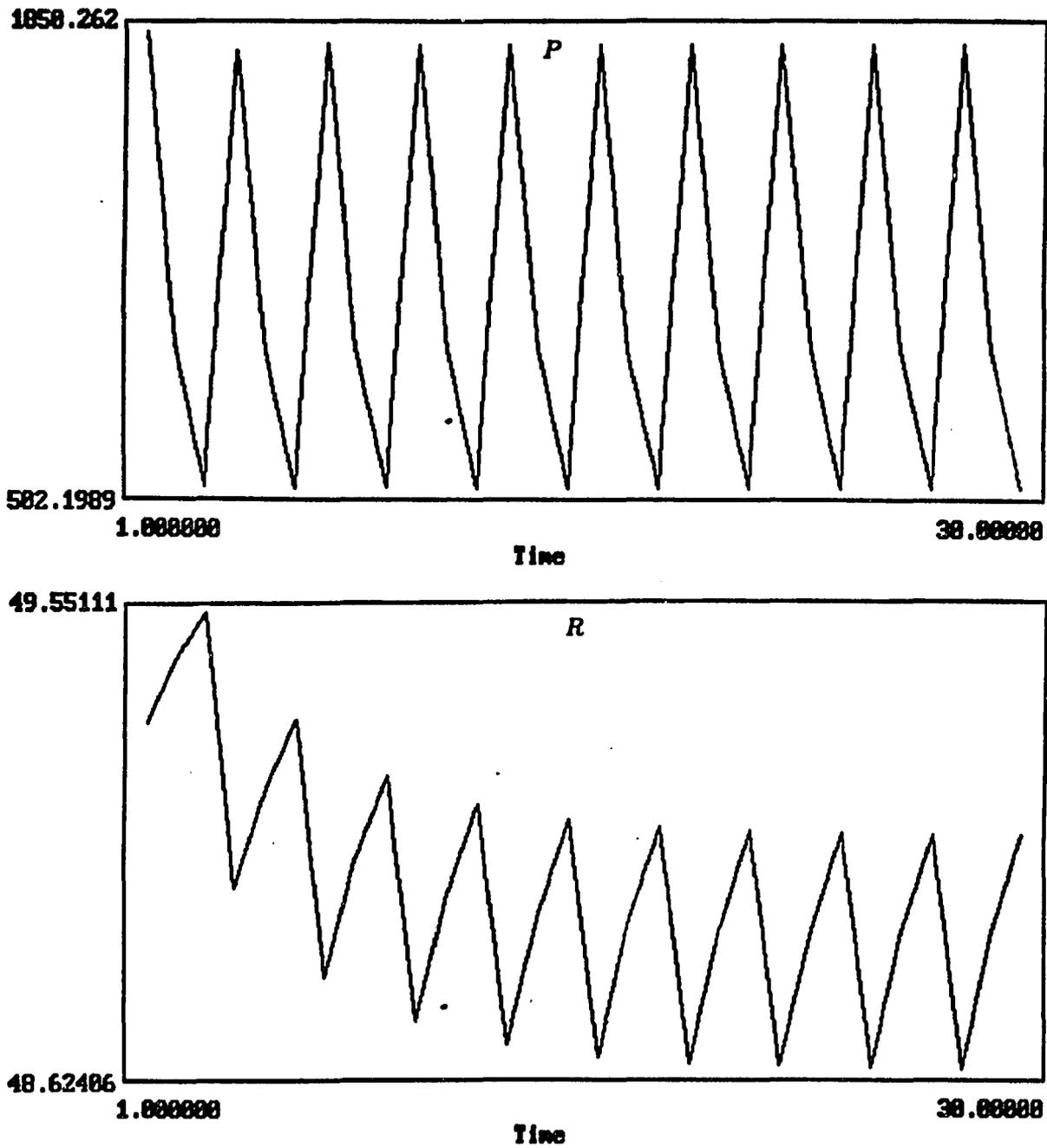


Figure 4.5: Time series of $P(t)$ and $R(t)$ under three-cycle dynamics. $\theta_4 = 3800$

Exploitative Competition ($c(P) \equiv 1$)

For the case $c(P) \equiv 1$ we know that the only equilibria must be nondepleted, hence we can easily explore the existence of the bifurcation point. In this case, we have

$$r(R^e) = \frac{1 - \pi}{\pi\theta} \quad (4.1)$$

$$P^e = \frac{\pi\theta}{(1 - \pi)\xi}(R_0 - R^e) \quad (4.2)$$

For purposes of contradiction, suppose that the equilibrium (R^e, P^e) loses stability at $\theta = \theta^h$. Referring to Theorem 8, we let μ be the eigenvalue of the Jacobian lying inside the unit circle. Then at $\theta = \theta^h$ we obtain

$$\text{Det } \mathcal{J} = \xi [1 - \pi r'(R^e)P^e] = -\mu$$

$$\text{Tr } \mathcal{J} = 1 + \xi - \xi r'(R^e)P^e = \mu - 1.$$

These equations imply

$$r'(R^e)P^e = \frac{2(1 + \xi)}{(1 + \pi)\xi}. \quad (4.3)$$

Equations (4.1), (4.2), and (4.3) yield, at $\theta = \theta^h$, the Jacobian

$$\mathcal{J} = \begin{bmatrix} \frac{\xi^2(1+\pi) - 2(1+\xi)}{\xi(1+\pi)} & -\frac{(1-\pi)\xi}{\pi\theta} \\ \frac{2\pi\theta(1+\xi)}{\xi(1+\pi)} & 1 \end{bmatrix}$$

which, since -1 is an eigenvalue, satisfies $\text{Det}(\mathcal{J} + \mathcal{I}) = 0$. But

$$\text{Det}(\mathcal{J} + \mathcal{I}) = \frac{4(\xi^2 - 1)}{\xi(1 + \pi)}$$

and $\xi \in (0, 1)$, so that $\text{Det}(\mathcal{J} + \mathcal{I}) \neq 0$, a contradiction. Thus there is no θ^h at which a bifurcation through -1 occurs, and thus we have the following corollary to Theorem 8.

Corollary 9 *For $c(P) \equiv 1$, the (nondepleted) equilibrium (R^e, P^e) does not lose stability.*

4.2 Multispecies Dynamics

We now turn to the case of several species exhibiting oscillatory dynamics. We will again use bifurcation theory techniques to arrive at some general analytical results, and then show some numerical results. We begin by stating the main result of this section.

Theorem 10 *Let $k \in N, k > 1$, and assume there is a stable k -cycle of Equations (3.16) and (3.17) in \mathfrak{R}^{n+1} with $P_n \equiv 0$. Then there exists a critical value θ_n^{bif} at which there bifurcates from this k -cycle a locally asymptotically stable k -cycle in $int(\mathfrak{R}^{n+1})^+$.*

Proof Let $\vec{q} = (R^*, P_1^*, \dots, P_{n-1}^*, 0)$ be an element of a stable k -cycle of Equations (3.16) and (3.17). Then it is also a stable fixed point of the k -composed system, so we have a system of equilibrium equations

$$\begin{aligned} R &= F_0(R, P_1, \dots, P_n) \\ P_1 &= F_1(R, P_1, \dots, P_n) \\ &\vdots \\ P_n &= F_n(R, P_1, \dots, P_n) \end{aligned} \tag{4.4}$$

where the F_i are the functions giving the equilibrium equations of the k -composed system derived from Equations (3.16) and (3.17). We can expand about the equilibrium $(R^*, P_1^*, \dots, P_{n-1}^*, 0)$ as follows:

Let $x_0 = R - R^*$, $x_i = P_i - P_i^*$ for $i = 1, \dots, n$, where $P_n^* = 0$ by definition.

Then we have

$$\vec{x} = \vec{F}_{\vec{x}}(0) \vec{x} + \mathcal{O}(\|\vec{x}\|^2) \tag{4.5}$$

where

$$\begin{bmatrix} \mathcal{A} & \mathcal{B} \\ 0 & \mathcal{C} \end{bmatrix}$$

with \mathcal{A} is an $n \times n$ matrix and \mathcal{C} is a scalar. The submatrix \mathcal{A} of $\bar{F}_{\bar{x}}(\bar{0})$ arises from the linearization of Equations (4.4) restricted to \mathfrak{R}^n about $(R^*, P_1^*, \dots, P_{n-1}^*)$ and by assumption all eigenvalues of this matrix lie within the unit circle. Thus we turn our attention to \mathcal{C} , the $n + 1^{\text{st}}$ eigenvalue, which arises from the linearization of $P_n = F_n(R, P_1, \dots, P_n)$.

The k -cycle is completely given by

$$\text{Orb}(\bar{q}) = \{\bar{q}, \bar{F}(\bar{q}), \bar{F}^{(2)}(\bar{q}), \dots, \bar{F}^{(k-1)}(\bar{q})\}.$$

Now the last equation of System (4.4) can be expressed as

$$\begin{aligned} P_n &= \pi_n^k \left[1 + \theta_n r_n (R(t+k-1)) c(\bar{P}(t+k-1)) \right] \\ &\quad \dots \left[1 + \theta_n r_n (R(t)) c(\bar{P}(t)) \right] P_n \end{aligned} \quad (4.6)$$

and upon expansion about \bar{q} , this becomes

$$\begin{aligned} z &= \pi_n^k \left[1 + \theta_n r_n \left(\bar{F}^{(k-1)}(\bar{q}) \right) c \left(\bar{F}^{(k-1)}(\bar{q}) \right) \right] \\ &\quad \dots \left[1 + \theta_n r_n(\bar{q}) c(\bar{q}) \right] z + \mathcal{O}(\|\bar{x}\|^2) \\ &\equiv \mathcal{C}z + \mathcal{O}(\|\bar{x}\|^2). \end{aligned}$$

Upon inspection of this expression for \mathcal{C} , it is clear that at $\theta_n = 0$, we have $\mathcal{C} = \pi_n^k \in (0, 1)$. As θ_n increases, so does \mathcal{C} , until at some $\theta_n = \theta_n^{bif}$ we have $\mathcal{C} = 1$. We can now turn to Theorems 14 and 15 in the Appendix.

Let \bar{v} and \bar{w} be the (respectively) right and left eigenvectors of $\bar{F}_{\bar{x}}(\bar{0}, \theta_n^{bif})$, and consider the derivative of $\bar{F}_{\bar{x}}$ with respect to θ_n . Since the only

equation in the k -composed system (4.4) that depends on θ_n is the last one, the derivative of $\bar{F}_{\bar{x}}$ will appear as

$$\bar{F}_{\bar{x}, \theta_n}(\bar{0}, \theta_n^{bif}) = \begin{bmatrix} 0 & 0 \\ 0 & \frac{\partial C}{\partial \theta_n} \end{bmatrix}.$$

According to Theorems 14 and 15, we need to study the quantity $-\bar{w} \cdot \bar{F}_{\bar{x}, \theta_n}(\bar{0}, \theta_n^{bif}) \bar{v}$, which is equal to

$$\mu = -w_{n+1} \left(\frac{\partial C}{\partial \theta_n} \Big|_{\theta_n^{bif}} \right) v_{n+1}.$$

The left eigenvector, \bar{w} , of $\bar{F}_{\bar{x}}(\bar{0})$ has the form $(0, \dots, 0, w_{n+1})$, while the right eigenvector, \bar{v} , must be a solution of the n equations in $n+1$ unknowns given by $(\bar{F}_{\bar{x}}(\bar{0}) - \mathcal{I}) \bar{v} = \bar{0}$, so we can assume that $v_{n+1} = 1$. Then to make $\bar{w} \cdot \bar{v} = 1$, we need only let $w_{n+1} = 1$ as well.

By Theorems 14 and 15 the existence and direction of bifurcation are determined by the sign of μ . Here we have

$$\begin{aligned} \mu &= - \frac{\partial C}{\partial \theta_n} \Big|_{\theta_n = \theta_n^{bif}} \\ &= -\pi_n^k \sum_{j=1}^{k-1} \theta_n^{bif} r_n \left(\bar{F}^{(j)}(\bar{q}) \right) c \left(\bar{F}^{(j)}(\bar{q}) \right) \\ &\quad \prod_{i \neq j} \left[1 + \theta_n^{bif} r_n \left(\bar{F}^{(i)}(\bar{q}) \right) c \left(\bar{F}^{(i)}(\bar{q}) \right) \right] \\ &< 0 \end{aligned}$$

So by Theorem 14, the bifurcation of a k -cycle occurs, and by Theorem 15, the resulting k -cycle in the positive cone of \mathfrak{R}^{n+1} is locally asymptotically stable. ♣

The preceding theorem shows that it is possible to “lift off” a k -cycle ($k \geq 2$) from \mathfrak{R}^n to \mathfrak{R}^{n+1} dimensions (for $n \geq 2$). Thus we can see oscillatory coexistence

of any number of species in certain parameter ranges. While this theorem does not include the lifting off of a chaotic orbit, it is possible to demonstrate such a lifting-off (and hence chaotic coexistence) numerically. In Figure 4.6 below we see a typical example of a bifurcation diagram illustrating the “lift-off” of a stable two-cycle from one to two species. Figures 4.7 and 4.8 show time series of two species coexisting with oscillations.

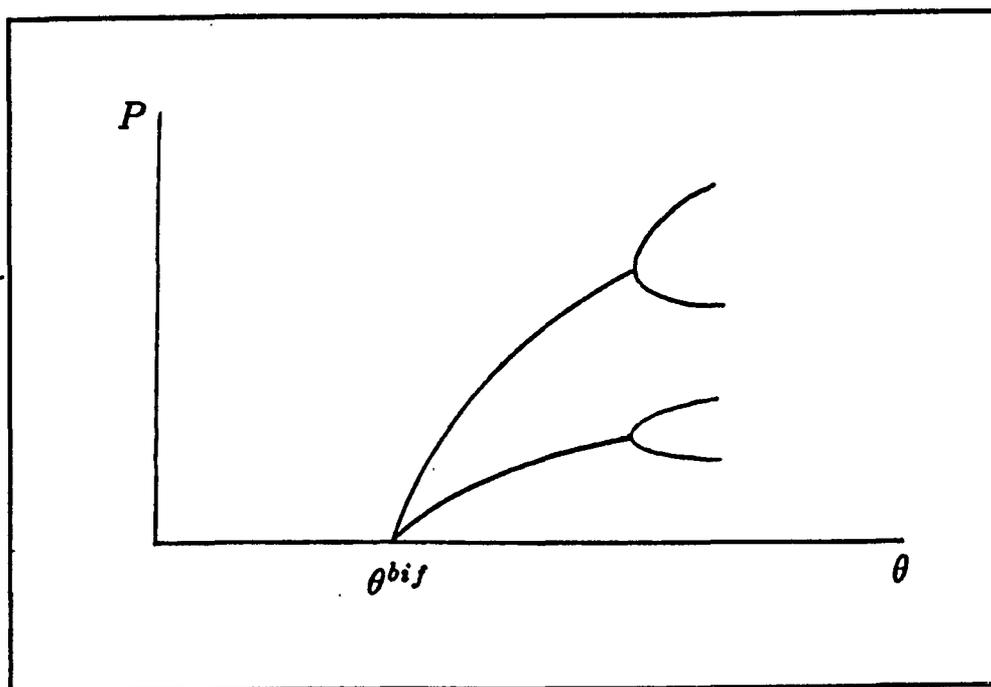


Figure 4.6: Bifurcation diagram illustrating the “lift-off” of a stable 2-cycle from one species to two species

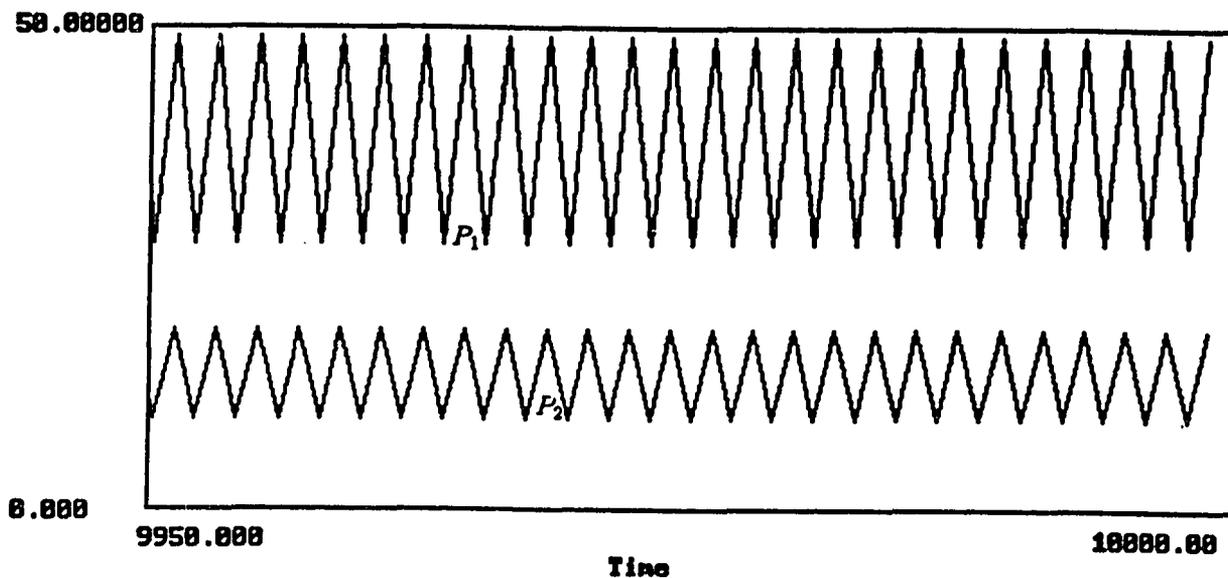


Figure 4.7: Time series showing two species coexisting with two-cycle dynamics. Here $\xi = .8$, $\pi_1 = .5$, $\pi_2 = .4$, $r_1(R) = \frac{R}{1+R}$, $r_2(R) = \frac{5R}{1+R}$, and $c(P_1, P_2) = e^{-.1P_1 - .1P_2}$. Also $\theta_1 = 100$ and $\theta_2 = 33$.

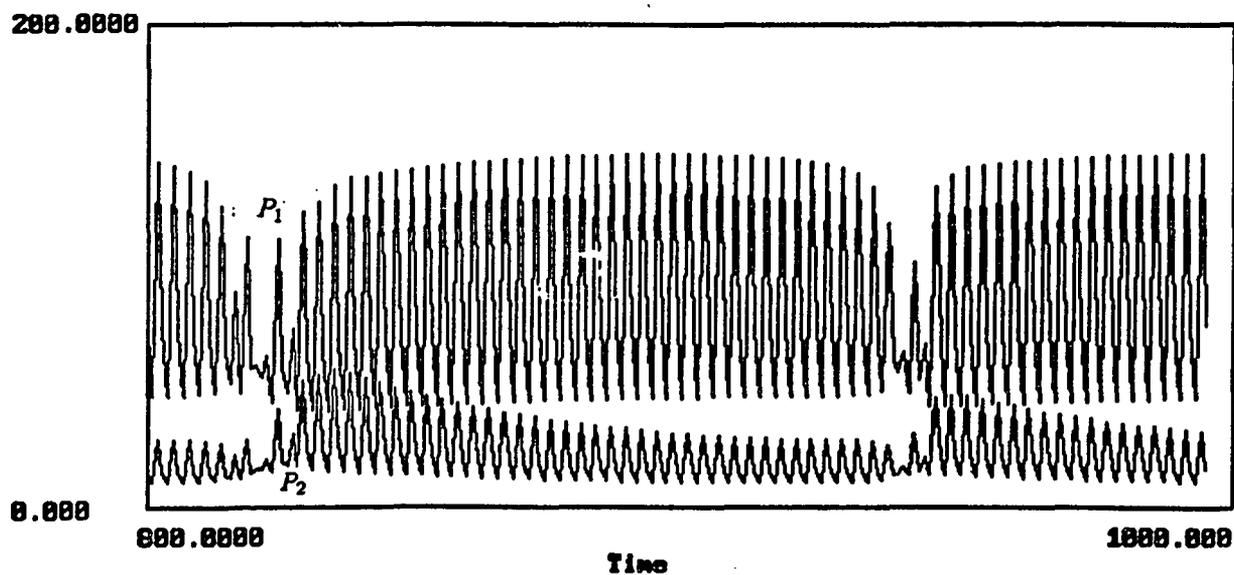


Figure 4.8: Time series showing two species coexisting with aperiodic dynamics. All parameters are as in Figure 4.7, with $\theta_1 = 200$ and $\theta_2 = 55$.

CHAPTER 5

Biological Considerations

While models for competing species have been studied in a variety of forms and under a multitude of assumptions, most of these studies have been modeled at the population level only, without consideration of the structure within the species. On the other hand, nonlinear models of structured populations tend to become unwieldy, and rigorous analytical results are hard to come by. By reducing the matrix difference equations of Chapter 2 to a scalar equation via a nonlinear ergodic theorem, we have derived a model of the dynamics of the population for which considerable analysis can be accomplished, yet which still incorporates the crucial size-specific physiological parameters through the quantity θ . Thus by relating the dynamics of the system to the value of θ (in our case by using θ as a bifurcation parameter for the system) and then examining the dependence of θ on individual physiological parameters, we can address some of the biological considerations associated with these models.

5.1 Role of θ in the Dynamics

We begin the study of the relationship between θ and the dynamics of the model by first considering the single species model with θ small; i.e. $\theta \approx \theta^{cr}$. It was shown in Section 3.1 that regardless of the strength of the competition, a positive equilibrium (R^e, P^e) will bifurcate from the trivial equilibrium $(R_0, 0)$ at $\theta = \theta^{cr}$. Thus for small values of θ , an increase in θ is clearly to the benefit of the species, allowing it to survive on the amount of resource available to it. In addition, for $\theta \gtrsim \theta^{cr}$, an increase in θ results in an increase in P^e , making the species more likely to survive fluctuations in the environment and hence contributing to its viability. Also, since the bifurcation to a positive equilibrium occurs transversely, the stability of the equilibrium increases with increases in θ for $\theta \gtrsim \theta^{cr}$.

As θ is increased beyond θ^{cr} , its effect on the equilibrium (R^e, P^e) depends upon the type and strength of competition present. In the case of purely exploitative competition ($c(P) \equiv 1$), an increase in θ causes an increase in P^e for all $\theta \in (\theta^{cr}, \theta^b)$. As was shown previously, the equilibrium exists for all θ in this range without losing stability, so an increase in θ can only help the species to survive.

When interference competition also occurs ($c(P) \neq 1$), the effect of increases in θ on species survivability is slightly ambiguous. At first, increases in θ produce the previously noted increases in equilibrium level. Further along, these increases may even be strengthened if the species equilibrium becomes depleted, since P^e grows linearly with θ in a depleted regime. Thus if interference competition occurs only weakly (e.g. $c(P) = \frac{1}{1+d\sqrt{P}}$), then increases in θ will certainly produce a more viable equilibrium since the eigenvalues of the linearized system remain fixed and within the unit circle while the population size increases. On the other hand, in

the presence of strong interference competition (e.g. $c(P) = e^{-dP}$), (R^e, P^e) will be depleted for only a finite range of θ values, if at all. Eventually the equilibrium will revert to a nondepleted type (with a correspondingly lesser increase with increase in θ) and from there will bifurcate to a 2-cycle, 4-cycle, and on to chaotic dynamics with increases in θ (See Figure (4.1)). While the range of values of such a cycle is still quite high, and such cycles appear to be strongly stable, a change from equilibrium to nonequilibrium dynamics may nevertheless be considered destabilizing.

We now consider the role of the θ values in the multispecies model. In general, the j^{th} species will equilibrate and win the competition, thus driving the other species extinct, (i.e. the axis equilibrium $(R_j^e, P_j^e, \bar{e}_j)$ is asymptotically stable) only if its equilibrium is inherently asymptotically stable and θ_k is small enough (less than some multiple of θ_k^{cr}) for $k \neq j$. Hence an increase in θ_k for some other species k will enhance its competitive efficiency and promote its chances of being the winner and hence not being driven extinct. In the case of nonequilibrium dynamics, it was proven in Chapter 4 that any number of species can coexist in an oscillatory fashion; again the techniques of bifurcation theory were employed. It was shown there that the species k is able to "invade" and exist in a $k - 1$ species oscillating system if θ_k is larger than θ_k^{bif} . Clearly, then, it is to the advantage of species k for θ_k to increase. In addition, if θ_k is increased enough, species k will out-compete the other $k - 1$ species and become the only species to survive, while experiencing an increase in the level of its population.

Thus in almost every instance, an increase in the θ value of a species is to its benefit, either allowing it to survive on a low resource level, increasing its equilibrium level, or enabling it to better compete with other species. Recalling that θ is

the largest eigenvalue of the matrix \mathcal{M} , which is comprised of the growth and reproductive efficiency parameters, β_i and γ_i , we turn our attention to the dependence of θ on these parameters.

5.2 θ as a Function of β_i and γ_i

We begin this section by recalling that θ is the (real) eigenvalue with largest real part of the $m \times m$ matrix

$$\mathcal{M} = \begin{bmatrix} -\beta_1 + \gamma_1 & \gamma_2 & \cdots & \gamma_{m-1} & \gamma_m \\ \beta_1 & -\beta_2 & \cdots & 0 & 0 \\ 0 & \beta_2 & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & -\beta_{m-1} & 0 \\ 0 & 0 & \cdots & \beta_{m-1} & 0 \end{bmatrix} = [\mathcal{M}_{ij}].$$

According to Caswell [6],

$$\frac{\partial \theta}{\partial \mathcal{M}_{ij}} = \frac{w_i^+ v_j^+}{\langle \bar{w}^+, \bar{v}^+ \rangle} \quad (5.1)$$

where \bar{w}^+ and \bar{v}^+ are the (respectively) left and right eigenvectors of \mathcal{M} corresponding to θ . Thus we next find general forms for the eigenvectors of \mathcal{M} .

Theorem 11 *Let λ be any eigenvalue of the $m \times m$ matrix \mathcal{M} . Then the corresponding right eigenvector \bar{v} is given (up to scalar multiplication) by $\bar{v} = (v_1, v_2, \dots, v_m)^T$ where*

$$v_m = \beta_1 \cdots \beta_{m-1}$$

$$v_{m-j} = \lambda \prod_{i=m-j+1}^{m-1} (\lambda + \beta_i) \prod_{i=0}^{m-j-1} \beta_i \text{ for } j = 2, \dots, m-1$$

$$v_{m-1} = \lambda \beta_1 \cdots \beta_{m-2}.$$

(Here β_0 is defined to be 1).

Proof Since \bar{v} is the right eigenvector of \mathcal{M} corresponding to λ we have $\mathcal{M} \bar{v} = \lambda \bar{v}$ and writing this equation out, we obtain

$$\begin{bmatrix} -\beta_1 v_1 + \gamma_2 v_2 + \cdots + \gamma_m v_m \\ \beta_1 v_1 - \beta_2 v_2 \\ \beta_2 v_2 - \beta_3 v_3 \\ \vdots \\ \beta_{m-2} v_{m-2} - \beta_{m-1} v_{m-1} \\ \beta_{m-1} v_{m-1} \end{bmatrix} = \lambda \begin{bmatrix} v_1 \\ v_2 \\ v_3 \\ \vdots \\ v_{m-1} \\ v_m \end{bmatrix}. \quad (5.2)$$

If we let $v_m = \beta_1 \cdots \beta_{m-1}$ then the last line of Equation (5.2) gives

$$v_{m-1} = \frac{\lambda}{\beta_{m-1}} v_m = \lambda \beta_1 \cdots \beta_{m-2}$$

while the next to last line gives

$$v_{m-2} = \frac{\beta_{m-1} + \lambda}{\beta_{m-2}} v_{m-1} = \lambda(\lambda + \beta_{m-1}) \beta_1 \cdots \beta_{m-3},$$

so the general form in Theorem 11 of the eigenvector entry is true for $j = 2$. For purposes of induction we assume the form is true for $j = k - 1$. At $j = k$ the characteristic equation gives

$$\beta_{m-k} v_{m-k} - \beta_{m-k+1} v_{m-k+1} = \lambda v_{m-k+1}$$

and hence

$$\begin{aligned} v_{m-k} &= \frac{(\lambda + \beta_{m-k+1}) v_{m-k+1}}{\beta_{m-k}} \\ &= \lambda \frac{\lambda + \beta_{m-k+1}}{\beta_{m-k}} \prod_{i=m-k+2}^{m-1} (\lambda + \beta_i) \prod_{i=0}^{m-k} \beta_i \\ &= \lambda \prod_{i=m-k+1}^{m-1} (\lambda + \beta_i) \prod_{i=0}^{m-k-1} \beta_i \quad \clubsuit \end{aligned}$$

Theorem 12 Let λ be any eigenvalue of the $m \times m$ matrix \mathcal{M} . Then the corresponding left eigenvector \bar{w} is given (up to scalar multiplication) by $\bar{w} = (w_1, \dots, w_m)$ where

$$w_1 = \frac{\lambda}{\gamma_j} w_m$$

$$w_2 = \frac{\lambda(\lambda + \beta_1)}{\beta_1 \gamma_m} w_m$$

$$w_3 = \left(\frac{\lambda(\lambda + \beta_2)(\lambda + \beta_1)}{\beta_1 \beta_2 \gamma_m} - \frac{\lambda \gamma_2}{\beta_2 \gamma_m} \right) w_m$$

$$w_j = \left(\frac{\lambda(\lambda + \beta_{j-1}) \dots (\lambda + \beta_1)}{\beta_1 \dots \beta_{j-1} \gamma_m} - \frac{\lambda \gamma_{j-1}}{\beta_{j-1} \gamma_m} - \sum_{i=2}^{j-2} \frac{\lambda \gamma_i}{\gamma_m \beta_i} \prod_{l=i+1}^{j-1} \frac{\lambda + \beta_l}{\beta_l} \right) w_m$$

for $j = 4, \dots, m - 1$.

Proof The characteristic equation $\bar{w} \mathcal{M} = \lambda \bar{w}$ gives the system

$$\begin{bmatrix} -\beta_1 w_1 + \beta_1 w_2 \\ \gamma_2 w_1 - \beta_2 w_2 + \beta_2 w_3 \\ \gamma_3 w_1 - \beta_3 w_3 - \beta_3 w_4 \\ \vdots \\ \gamma_{m-1} w_1 - \beta_{m-1} w_{m-1} + \beta_{m-1} w_m \\ \gamma_m w_1 \end{bmatrix}^T = \lambda \begin{bmatrix} w_1 \\ w_2 \\ w_3 \\ \vdots \\ w_{m-1} \\ w_m \end{bmatrix}^T, \quad (5.3)$$

the last line of which gives

$$w_1 = \frac{\lambda}{\gamma_m} w_m.$$

Then the first line of Equation (5.3) can be solved to give

$$w_2 = \frac{\lambda + \beta_1}{\beta_1} w_1 = \frac{\lambda(\lambda + \beta_1)}{\beta_1 \gamma_m} w_m,$$

and substituting these two equations into the second equality of Equation (5.3) we obtain

$$w_3 = \frac{\lambda + \beta_2}{\beta_2} w_2 - \frac{\gamma_2}{\beta_2} w_1 = \left(\frac{\lambda(\lambda + \beta_2)(\lambda + \beta_1)}{\beta_1 \beta_2 \gamma_m} - \frac{\lambda \gamma_2}{\beta_2 \gamma_m} \right) w_m.$$

For $k = 3, \dots, m-1$ we see that

$$w_k = \frac{\lambda + \beta_{k-1}}{\beta_{k-1}} w_{k-1} - \frac{\gamma_{k-1}}{\beta_{k-1}} w_1$$

and for $j = 4$ this becomes

$$\begin{aligned} w_j &= \frac{\lambda + \beta_3}{\beta_3} w_3 - \frac{\gamma_3}{\beta_3} w_1 \\ &= \left(\frac{\lambda(\lambda + \beta_1)(\lambda + \beta_2)(\lambda + \beta_3)}{\beta_1 \beta_2 \gamma_m} - \frac{\lambda(\lambda + \beta_3)\gamma_2}{\beta_2 \beta_3 \gamma_4} - \frac{\lambda \gamma_3}{\beta_3 \gamma_m} \right) w_m \end{aligned}$$

so the closed form solution is true for $j = 4$. Now assume that this solution is true for $j = k-1$. Then for $j = k$ we have

$$\begin{aligned} w_k & \tag{5.4} \\ &= \frac{\lambda + \beta_{k-1}}{\beta_{k-1}} \left(\frac{\lambda(\lambda + \beta_{k-2}) \cdots (\lambda + \beta_1)}{\beta_1 \cdots \beta_{k-2} \gamma_m} - \frac{\lambda \gamma_{k-2}}{\beta_{k-2} \gamma_m} - \sum_{i=2}^{k-3} \frac{\lambda \gamma_i}{\beta_i \gamma_m} \prod_{l=i+1}^{k-2} \frac{\lambda + \beta_l}{\beta_l} \right) \\ & \quad w_m - \frac{\lambda \gamma_{k-2}}{\beta_{k-2} \gamma_m} w_m \\ &= \left(\frac{\lambda(\lambda + \beta_{k-1}) \cdots (\lambda + \beta_1)}{\beta_1 \cdots \beta_{k-1} \gamma_m} - \frac{\lambda \gamma_{k-2}(\lambda + \beta_{k-1})}{\gamma_m \beta_{k-2} \beta_{k-1}} - \sum_{i=2}^{k-3} \frac{\lambda \gamma_i}{\beta_i \gamma_m} \left(\prod_{l=i+1}^{k-2} \frac{\lambda + \beta_l}{\beta_l} \right) \right. \\ & \quad \left. \frac{\lambda + \beta_{k-1}}{\beta_{k-1}} - \frac{\lambda \gamma_{k-2}}{\beta_{k-2} \gamma_m} \right) w_m \\ &= \left(\frac{\lambda(\lambda + \beta_{k-1}) \cdots (\lambda + \beta_1)}{\beta_1 \cdots \beta_{k-1} \gamma_m} - \sum_{i=2}^{k-2} \frac{\lambda \gamma_i}{\gamma_m \beta_i} \left(\prod_{l=i+1}^{k-1} \frac{\lambda + \beta_l}{\beta_l} \right) - \frac{\lambda \gamma_{k-2}}{\beta_{k-2} \gamma_m} \right) w_m. \clubsuit \end{aligned}$$

Note that all entries of \bar{w}^+ and \bar{v}^+ are nonnegative and the vectors are both nonzero; hence $\langle \bar{w}^+, \bar{v}^+ \rangle > 0$. Following Caswell [6] we calculate $\frac{\partial \theta}{\partial \beta_j}$ and $\frac{\partial \theta}{\partial \gamma_j}$.

For $j = 1, \dots, m - 1$,

$$\frac{\partial \theta}{\partial \beta_j} = \frac{1}{\langle \bar{w}^+, \bar{v}^+ \rangle} (-w_j v_j + w_{j+1} v_j) = \frac{v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} (w_{j+1} - w_j) \quad (5.5)$$

and since $\frac{v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} > 0$, the sign of $\frac{\partial \theta}{\partial \beta_j}$ is determined by the difference $w_{j+1} - w_j$. This says that θ will increase with an increase in β_j if and only if the reproductive value of an individual in size class $j + 1$ is greater than the reproductive value of an individual in size class j .

Similarly, for $j = 2, \dots, m$,

$$\frac{\partial \theta}{\partial \gamma_j} = \frac{1}{\langle \bar{w}^+, \bar{v}^+ \rangle} w_1 v_j > 0 \quad (5.6)$$

In other words, an increase in γ_j (reproductive efficiency of an individual in size class j) increases θ . However, it must be remembered that γ_j is composed of several physiological parameters, some of which also appear in β_j . Thus we must consider the effects of physiological parameters such as κ_j (fraction of consumed resource allocated to growth), ω_j (conversion factor of resource units to offspring body weight), and η_j (conversion factor of resource units to body weight) on θ in order to obtain an accurate picture of how a species can become more (or less) able to survive.

5.3 θ as a Function of Individual Physiological Parameters

We now study the dependence of θ on the individual physiological parameters κ_j , ω_j , and η_j , beginning with the growth allocation fraction κ_j . Recall first that the definitions of β_j and γ_j are

$$\beta_j = \frac{\kappa_j \sigma_j r_j}{3 \mu_j \eta_j \delta_j} \quad \text{and} \quad \gamma_j = \frac{(1 - \kappa_j) r_j \sigma_j s_j^2}{\omega_j W_1}.$$

Note that both β_j and γ_j depend upon κ_j and that

$$\frac{\partial \beta_j}{\partial \kappa_j} = \frac{\sigma_j r_j}{3\mu_j \eta_j \delta_j} = \frac{\beta_j}{\kappa_j}$$

and

$$\frac{\partial \gamma_j}{\partial \kappa_j} = -\frac{r_j \sigma_j s_j^2}{\omega_j W_1} = -\frac{\gamma_j}{1 - \kappa_j}.$$

We then have the following theorem relating changes in κ_j to changes in θ .

Theorem 13 For $j = 2, \dots, m - 1$, $\frac{\partial \theta}{\partial \kappa_j} > 0$ (< 0) if and only if

$$w_{j+1} - w_j - \frac{3\mu_j \delta_j \eta_j}{\omega_j W_1} w_1 > 0 \quad (< 0).$$

Proof Following Caswell,

$$\begin{aligned} \frac{\partial \theta}{\partial \kappa_j} &= \frac{\partial \theta}{\partial \beta_j} \frac{\partial \beta_j}{\partial \kappa_j} + \frac{\partial \theta}{\partial \gamma_j} \frac{\partial \gamma_j}{\partial \kappa_j} \\ &= \frac{v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[\frac{\beta_j}{\kappa_j} (w_{j+1} - w_j) - \frac{\gamma_j}{1 - \kappa_j} w_1 \right] \end{aligned}$$

and thus the sign of $\frac{\partial \theta}{\partial \kappa_j}$ will be determined by the sign of the bracketed term; i.e.

$\frac{\partial \theta}{\partial \kappa_j} > 0$ if and only if $\frac{\beta_j}{\kappa_j} (w_{j+1} - w_j) - \frac{\gamma_j}{1 - \kappa_j} w_1 > 0$, which occurs if and only if

$$w_{j+1} > w_j + \frac{\kappa_j \gamma_j}{\beta_j (1 - \kappa_j)} w_1 = w_j + \frac{3\mu_j \delta_j \eta_j}{\omega_j W_1} w_1. \quad \clubsuit$$

Thus an increase in κ_j will increase θ if and only if the reproductive value of an individual in size class $j + 1$ exceeds the reproductive value of an individual in size class j by a sufficient amount.

As another example, consider the effect on θ of a change in the conversion factor ω_j . Since ω_j occurs only in γ_j , we have

$$\frac{\partial \theta}{\partial \omega_j} = \frac{\partial \theta}{\partial \gamma_j} \frac{\partial \gamma_j}{\partial \omega_j} = -\frac{w_1 v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left(\frac{(1 - \kappa_j) r_j \sigma_j s_j^2}{\omega_j^2 W_1} \right) = -\frac{w_1 v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} \frac{\gamma_j}{\omega_j}$$

and hence $\frac{\partial \theta}{\partial \omega_j} < 0$ and an increase in ω_j must always decrease θ .

As a final example, consider the result of a change in the η_j . Since η_j occurs only in β_j , we have

$$\begin{aligned} \frac{\partial \theta}{\partial \eta_j} &= \frac{\partial \theta}{\partial \beta_j} \frac{\partial \beta_j}{\partial \eta_j} = -\frac{v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} (w_{j+1} - w_j) \frac{\kappa_j \sigma_j r_j}{3\mu_j \delta_j \eta_j^2} \\ &= \frac{v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} \frac{\beta_j}{\eta_j} (w_j - w_{j+1}) \end{aligned}$$

and so θ will increase with an increase in η_j if and only if $w_j > w_{j+1}$; i.e. the reproductive value of an individual in size class $j + 1$ is less than the reproductive value of an individual in size class j .

In summary we present the results obtained thus far:

parameter φ_j	$\frac{\partial \beta_j}{\partial \varphi_j}$	$\frac{\partial \gamma_j}{\partial \varphi_j}$	$\frac{\partial \theta}{\partial \varphi_j}$
κ_j	$\frac{\beta_j}{\kappa_j} > 0$	$-\frac{\gamma_j}{1-\kappa_j} < 0$	$\frac{\beta_j}{\kappa_j} (w_{j+1} - w_j) - \frac{\gamma_j}{1-\kappa_j} w_1$
ω_j	0	$-\frac{\gamma_j}{\omega_j} < 0$	$-\frac{\gamma_j}{\omega_j} < 0$
η_j	$-\frac{\beta_j}{\eta_j} < 0$	0	$w_j - w_{j+1}$

Table 5.1: In this table we summarize the dependence of the parameters β_j , γ_j , and θ on the individual parameters κ_j , ω_j , and η_j . The entries in the table are the quantities upon which the sign of the partial derivatives depend. If the partial derivative is always of one sign, it is noted.

5.4 The Dependence of Body Size on Physiological Parameters

Having obtained results describing the effects of changes in size-specific parameters on θ (and hence species survivability), we now explore the effects that those same changes have on species size. In doing so we hope to draw some conclusions concerning the relationship between a species size and its competitive success. We begin by defining what we mean by species size.

Several different notions of species size have been used in biological studies. These include maximal adult size, maturation size, average individual size, and average adult size. Here we will use the last of these, average adult size. We know that as $t \rightarrow +\infty$, the normalized size distribution will approach \bar{v}^+ , the right eigenvector of \mathcal{M} corresponding to θ , where $\|\bar{x}(t)\| = \sum_{i=1}^m s_i^2 x_i(t)$ is the total surface area of the population at time t and $\|\bar{v}^+\| = \sum_{i=1}^m s_i^2 v_i = 1$. Then the average adult size of the species is

$$\mathcal{S} = \sum_{i=j}^m s_i^2 v_i \quad (5.7)$$

where j is the number of the first reproducing size class; i.e. γ_j is the first nonzero γ .

We now want to consider the effects of the changes in κ_j , ω_j , and η_j on \mathcal{S} . For the sake of simplicity we will look at the case when $m = 4$ (i.e. there are four size classes) with $\kappa_1 = 1$ so that individuals in the first size class do not reproduce. Thus the matrix \mathcal{M} is given by

$$\mathcal{M} = \begin{bmatrix} -\beta_1 & \gamma_2 & \gamma_3 & \gamma_4 \\ \beta_1 & -\beta_2 & 0 & 0 \\ 0 & \beta_2 & -\beta_3 & 0 \\ 0 & 0 & \beta_3 & 0 \end{bmatrix}$$

and the right and left eigenvectors of \mathcal{M} corresponding to θ are

$$\bar{v}^+ = \begin{bmatrix} \theta(\theta + \beta_2)(\theta + \beta_3) \\ \theta\beta_1(\theta + \beta_3) \\ \theta\beta_1\beta_2 \\ \beta_1\beta_2\beta_3 \end{bmatrix} \quad \text{and} \quad \bar{w}^+ = \begin{bmatrix} \theta\beta_1\beta_2 \\ \theta\beta_2(\theta + \beta_2) \\ \theta(\theta + \beta_2)(\theta + \beta_1) - \theta\beta_1\gamma_2 \\ \beta_1\beta_2\gamma_4 \end{bmatrix}^T.$$

Then in this case, $\mathcal{S} = s_2^2\theta\beta_1(\theta + \beta_3) + s_3^2\theta\beta_1\beta_2 + s_4^2\beta_1\beta_2\beta_3$.

First we consider the results of changes in κ_j . For $j = 2$ we obtain

$$\begin{aligned} \frac{\partial \mathcal{S}}{\partial \kappa_2} &= s_2^2\beta_1 \left[\theta \frac{\partial \theta}{\partial \kappa_2} + (\theta + \beta_3) \frac{\partial \theta}{\partial \kappa_2} \right] + s_3^2\beta_1 \left[\theta \frac{\partial \beta_2}{\partial \kappa_2} + \beta_2 \frac{\partial \theta}{\partial \kappa_2} \right] + s_4^2\beta_1\beta_3 \frac{\partial \beta_2}{\partial \kappa_2} \\ &= \left[s_2^2\beta_1(2\theta + \beta_3) + s_3^2\beta_1\beta_2 \right] \frac{\partial \theta}{\partial \kappa_2} + \left[s_3^2\beta_1\theta + s_4^2\beta_1\beta_3 \right] \frac{\partial \beta_2}{\partial \kappa_2}. \end{aligned}$$

Since from the preceding section we know that

$$\frac{\partial \theta}{\partial \kappa_2} = \frac{v_2}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[\frac{\beta_2}{\kappa_2}(w_3 - w_2) - \frac{\gamma_2}{1 - \kappa_2}w_1 \right] \quad \text{and} \quad \frac{\partial \beta_2}{\partial \kappa_2} = \frac{\beta_2}{\kappa_2},$$

we obtain

$$\begin{aligned} \frac{\partial \mathcal{S}}{\partial \kappa_2} &= \frac{v_2}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[s_2^2\beta_1(2\theta + \beta_3) + s_3^2\beta_1\beta_2 \right] \left[\frac{\beta_2}{\kappa_2}(w_3 - w_2) - \frac{\gamma_2}{1 - \kappa_2}w_1 \right] \\ &\quad + \frac{\beta_2}{\kappa_2} \left[s_3^2\beta_1\theta + s_4^2\beta_1\beta_3 \right] \end{aligned}$$

and thus $\frac{\partial \mathcal{S}}{\partial \kappa_2} > 0$ if and only if

$$w_3 > w_2 + \frac{\gamma_2\kappa_2}{\beta_2(1 - \kappa_2)}w_1 - C_2$$

where

$$C_2 = \frac{s_3^2\beta_1\theta + s_4^2\beta_1\beta_3}{\frac{v_2}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[s_2^2\beta_1(2\theta + \beta_3) + s_3^2\beta_1\beta_2 \right]} > 0.$$

Similarly for κ_3 we have that $\frac{\partial \mathcal{S}}{\partial \kappa_3} > 0$ if and only if

$$w_4 > w_3 + \frac{\gamma_3\kappa_3}{\beta_3(1 - \kappa_3)} - C_3$$

where

$$C_3 = \frac{s_2^2 \beta_1 \theta + s_4^2 \beta_1 \beta_2}{\frac{v_3}{\langle w^+, v^+ \rangle} [s_2^2 \beta_1 (2\theta + \beta_3) + s_3^2 \beta_1 \beta_2]} > 0.$$

Recalling from the previous section that $\frac{\partial \theta}{\partial \kappa_j} > 0$ if and only if $w_{j+1} > w_j + \frac{\gamma_j \kappa_j}{\beta_j (1 - \kappa_j)} w_1$, we see that for an intermediate range of w_{j+1} , $\frac{\partial \theta}{\partial \kappa_j} < 0$ while $\frac{\partial S}{\partial \kappa_j} > 0$. See Table 5.2 below.

	$w_j + \frac{\kappa_j \gamma_j}{\beta_j (1 - \kappa_j)} w_1 - C_j$	$w_j + \frac{\kappa_j \gamma_j}{\beta_j (1 - \kappa_j)} w_1$
0		w_{j+1}
$\frac{\partial \theta}{\partial \kappa_j} < 0$	$\frac{\partial \theta}{\partial \kappa_j} < 0$	$\frac{\partial \theta}{\partial \kappa_j} > 0$
$\frac{\partial S}{\partial \kappa_j} < 0$	$\frac{\partial S}{\partial \kappa_j} > 0$	$\frac{\partial S}{\partial \kappa_j} > 0$

Table 5.2: Changes in θ and S with changes in κ_j over varying ranges of w_{j+1} (reproductive value of class $j + 1$)

Thus for w_{j+1} in the region $(w_j + \frac{\gamma_j \kappa_j}{\beta_j (1 - \kappa_j)} - C_j, w_j + \frac{\gamma_j \kappa_j}{\beta_j (1 - \kappa_j)})$ an increase in species size via an increase in κ_j , the proportion of consumed resource allocated to growth in the j^{th} size class, results in a decrease in that species θ -value.

Next consider the effects of changes in w_j on S . Since β_j is independent of w_j ,

we have

$$\begin{aligned}\frac{\partial \mathcal{S}}{\partial \omega_j} &= s_2^2 \beta_1 \left[\theta \frac{\partial \theta}{\partial \omega_j} + (\theta + \beta_j) \frac{\partial \theta}{\partial \omega_j} \right] + s_3^2 \beta_1 \beta_2 \frac{\partial \theta}{\partial \omega_j} \\ &= -\frac{w_1 v_j}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[s_2^2 \beta_1 (2\theta + \beta_3) + s_3^2 \beta_1 \beta_2 \right] \frac{\gamma_j}{\omega_j} \\ &< 0\end{aligned}$$

Thus a decrease in θ caused by an increase in ω_j is always accompanied by a corresponding decrease in body size.

Finally we consider the effects of changes in η_j . For $j = 1$ we have

$$\begin{aligned}\frac{\partial \mathcal{S}}{\partial \eta_1} &= s_2^2 \left[\theta \beta_1 \frac{\partial \theta}{\partial \eta_1} + (\theta + \beta_3) \left(\theta \frac{\partial \beta_1}{\partial \eta_1} + \beta_1 \frac{\partial \theta}{\partial \eta_1} \right) \right] \\ &\quad + s_3^2 \beta_2 \left[\theta \frac{\partial \beta_1}{\partial \eta_1} + \beta_1 \frac{\partial \theta}{\partial \eta_1} \right] + s_4^2 \beta_2 \beta_3 \frac{\partial \beta_1}{\partial \eta_1} \\ &= \left[s_2^2 \theta \beta_1 + s_2^2 \beta_1 (\theta + \beta_3) + s_3^2 \beta_1 \beta_2 \right] \frac{\partial \theta}{\partial \eta_1} + \left[s_2^2 \theta (\theta + \beta_3) s_3^2 \theta \beta_2 + s_4^2 \beta_2 \beta_3 \right] \frac{\partial \beta_1}{\partial \eta_1}\end{aligned}$$

We know from the previous section that

$$\frac{\partial \theta}{\partial \eta_1} = \frac{v_1}{\langle \bar{w}^+, \bar{v}^+ \rangle} \frac{\beta_1}{\eta_1} (w_1 - w_2) \quad \text{and} \quad \frac{\partial \beta_1}{\partial \eta_1} = -\frac{\beta_1}{\eta_1}$$

and so

$$\begin{aligned}\frac{\partial \mathcal{S}}{\partial \eta_1} &= \frac{v_1}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[s_2^2 \theta \beta_1 + s_2^2 \beta_1 (\theta + \beta_3) + s_3^2 \beta_1 \beta_2 \right] \frac{\beta_1}{\eta_1} (w_1 - w_2) \\ &\quad - \left[s_2^2 \theta (\theta + \beta_3) + s_3^2 \theta \beta_2 + s_4^2 \beta_2 \beta_3 \right] \frac{\beta_1}{\eta_1},\end{aligned}$$

so $\frac{\partial \mathcal{S}}{\partial \eta_1} > 0$ if and only if

$$w_1 > w_2 + \mathcal{D}_1$$

where

$$\mathcal{D}_1 = \frac{s_2^2 \theta (\theta + \beta_3) + s_3^2 \theta \beta_2 + s_4^2 \beta_2 \beta_3}{\frac{v_1}{\langle \bar{w}^+, \bar{v}^+ \rangle} \left[s_2^2 \theta \beta_1 + s_2^2 \beta_1 (\theta + \beta_3) + s_3^2 \beta_1 \beta_2 \right]} > 0.$$

Similarly we have $\frac{\partial S}{\partial \eta_2} > 0$ if and only if

$$w_2 > w_3 + \mathcal{D}_2$$

where

$$\mathcal{D}_2 = \frac{s_3^2 \theta \beta_1 + s_4^2 \beta_1 \beta_3}{\frac{v_2}{\langle \bar{w}^+, \bar{v}^+ \rangle} [s_2^2 \beta_1 (2\theta + \beta_3) + s_3^2 \beta_1 \beta_2]} > 0$$

and also $\frac{\partial S}{\partial \eta_3} > 0$ if and only if

$$w_3 > w_4 + \mathcal{D}_3$$

where:

$$\mathcal{D}_3 = \frac{s_3^2 \theta \beta_1 + s_4^2 \beta_1 \beta_2}{\frac{v_3}{\langle \bar{w}^+, \bar{v}^+ \rangle} [s_2^2 \beta_1 (2\theta + \beta_3) + s_3^2 \beta_1 \beta_2]} > 0.$$

Recalling from the previous section that $\frac{\partial \theta}{\partial \eta_j} > 0$ if and only if $w_j > w_{j+1}$, we see that for an intermediate range of w_{j+1} , $\frac{\partial \theta}{\partial \eta_j} > 0$ while $\frac{\partial S}{\partial \eta_j} < 0$ as in Table 5.3 below. Thus for w_j in the region $(w_{j+1}, w_{j+1} + \mathcal{D}_j)$ an increase in θ caused by an increase in η_j is accompanied by a decrease in the size of the species.

Here we have seen three different types of relationships between a species size and its ability to survive. In the first case, in which the growth allocation fraction κ_j was changed, there exist regions where size and survivability increase and decrease together, along with an intermediate parameter range in which an increase in size corresponds to a decrease in survivability. The second case, involving changes in the conversion factor of resource units to offspring body weight ω_j , shows a monotonic relationship between species size and survivability. Finally, in the case involving changes in the conversion factor of resource units to body weight η_j , there are again parameter ranges where θ and S increase and decrease together, along with an intermediate parameter range in which a decrease in size corresponds to an increase in survivability.

	w_{j+1}	$w_{j+1} + D_j$	w_j
0	$\frac{\partial \theta}{\partial \eta_j} < 0$	$\frac{\partial \theta}{\partial \eta_j} > 0$	$\frac{\partial \theta}{\partial \eta_j} > 0$
	$\frac{\partial S}{\partial \eta_j} < 0$	$\frac{\partial S}{\partial \eta_j} < 0$	$\frac{\partial S}{\partial \eta_j} > 0$

Table 5.3: Changes in θ and S with changes in η_j over varying ranges of w_{j+1} (reproductive value of class $j + 1$)

Thus there is no consistent relationship between increases (or decreases) in species size and corresponding increases (or decreases) in the species' ability to survive. In fact, it is the means by which a species changes these quantities (i.e. what individual physiological parameter is changed) that determines how its size and survivability are related.

CHAPTER 6

Concluding Remarks

As more interest has been focused on modeling the structure within a species, whether age-, size-, or stage-classified, the use of discrete models such as those introduced by Leslie and Lewis has increased. These models lend themselves more easily to analysis than do even the most simple of continuous models incorporating species structure. Several mathematical tools play key roles in this analysis, including the theory of positive matrices, Perron-Frobenius theory, and the ergodic theorems developed by Cushing and Impagliazzo and generalized here.

Here we have been concerned with a model of size structured competition among n species for a limited resource which has been dynamically modeled. Using the aforementioned techniques, specifically the Nonlinear Ergodic Theorem, for each population the matrix difference equation for the size distribution vector is reduced to a (limiting) scalar difference equation for the total population size. This scalar equation contains a crucial parameter θ which is related to the eigenvalue of the transition matrix with maximal real part and hence encapsulates all of the size specific demographic parameters of the model. The parameter θ is used as a bifurcation parameter in our study of the population level dynamics.

In the single species case, a supercritical (and hence stable) bifurcation from the

trivial equilibrium to a positive equilibrium occurs at a unique critical value of θ . Depending upon the strength of the competition present, this equilibrium will either persist or lose stability via a bifurcation to a 2-cycle as θ increases. If this secondary bifurcation occurs, we then see the usual period doubling cascade.

By analyzing the dependence of both the bifurcation parameter θ and average adult size \mathcal{S} on the individual physiological parameters κ_i (the fraction of consumed resource allocated to growth by the i^{th} size class), ω_i (the conversion factor of resource units consumed by the i^{th} size class to offspring body weight), and η_i (the conversion factor of resource units consumed by the i^{th} size class to body weight), we are able to comment on some biological issues related to structured population models, the Size-Efficiency Hypothesis, and the effects of delays on the species dynamics.

The Size-Efficiency Hypothesis was proposed by Brooks and Dodson [2] in an attempt to explain the differences between lakes in the average individual sizes of their zooplankton populations. It suggested that, at least under low predation, the relatively greater foraging efficiency of the larger zooplanktors, combined with their ability to ingest a greater range of particle sizes, would cause them to be the eventual winner of the competition for resource. Since in the model we consider, an increase in θ virtually always increases a species' chances of surviving, we compare the changes in θ and body size \mathcal{S} resulting from changes in various of the individual physiological parameters. The results are mixed, with ranges of parameters existing where an increase in species size \mathcal{S} is actually detrimental to the species.

When there are two or more species present in the system, the number of species that can survive depends upon the inherent dynamics of the species. If in the

absence of interspecific competition the species would exhibit equilibrium dynamics, then our model corroborates one facet of the “Competitive Exclusion Principle”, or “Gause’s Principle”; i.e. there is no differentiation of the species’ niches and a single species survives. On the other hand, if the species are allowed to exhibit oscillatory dynamics, then competitive coexistence becomes possible. This was shown via the bifurcation theorems which allowed a stable k -cycle in n species to be “lifted off” into the positive cone, thus forming a stable k -cycle in $n + 1$ species.

The concept of oscillatory coexistence among competing species is not new. A partial reference list for this subject includes studies by McGehee and Armstrong [36], Cushing [11], [8], Hsu, Hubbell, and Waltman [22],[24],[23], Keener [27], Smith [40], Waltman [50], Freedman, So, and Waltman [15], and Tilman [44]. One of the main conclusions to be drawn from these references is that the type of resource dynamics present in the system plays an important role in determining the possible coexistence of the species. It was shown by Butler and Wolkowicz [4] that competitive coexistence can not occur in the chemostat (having a nonself-renewing resource). On the other hand, if the resource in the chemostat is allowed to be self-renewing (through, for example, a logistic growth term) it has been shown that 2 or more species can coexist in an oscillatory fashion ([27],[50],[40]). One interesting exception to this result is given by Freedman, So, and Waltman [15], who show numerically that under nonself-renewing resource dynamics species can coexist in the chemostat through the introduction of a delay term.

With the exception of the results due to Cushing, all of the aforementioned studies deal with continuous nonstructured models. Here we consider a discrete structured population model with “chemostat-like” dynamics. It is characteristic

of structured models that delay mechanisms can be more explicitly modeled and accounted for, and included in this model are time delays, both a delay in the maturation of the individuals and a built-in delay of one time unit in the conversion of resource to body mass (a characteristic of all discrete models). It was found to be possible for two or more species to coexist under oscillatory dynamics but, unlike the delay model proposed by Freedman *et al.* [15] (in which a vague "conversion" delay is the source of oscillations in the system), increasing the maturation delay time is not necessarily responsible for the ability of the species to coexist. In fact, as was discussed in Chapter 5, the effects of changes in such parameters as reproductive efficiency are highly dependent upon the individual parameters which were altered and it is in fact possible that a lengthening of the maturation delay could result in a decrease in θ , making oscillations less likely to occur.

Finally in conclusion, we mention the two main assumptions upon which this model and the analysis are based, and give some indication as to how the model could be generalized. One of the assumptions concerns the dynamics of the resource. We have considered only a nonself-renewing resource which is only replenished through a constant input each time unit, and it would be fairly straightforward to modify the model for the case of a self-renewing resource. Since even simple logistic renewal of the resource in the chemostat can result in oscillations in the system, it is anticipated that a similar change in the discrete model would cause the appearance of nonequilibrium dynamics for the weak competition cases which presently exhibit purely equilibrium behavior.

The other main assumption concerns the appearance of the nonlinearities in the matrix difference equations. It was required that the nonlinearity be the same for all

size classes; in effect that the survival rate and the density effects were independent of the size of the individual. While this can of course be justified if the differences between survival rates and between density effects are relatively small, it is a restrictive assumption that inhibits our ability to study some biological phenomena. For example, another tenet of the Size-Efficiency Hypothesis is that the competitive advantages of being a larger species can be outweighed by the disadvantages when faced with size-specific predation. As another example we have the juvenile bottleneck phenomenon described by Werner and Gilliam [51] in which the adults of the smaller species are able to out-compete the juveniles of the larger species and actually drive the larger species to extinction. Unfortunately, neither of these phenomena can be modeled without allowing the survival rates and competitive effects to be size-class dependent, and in doing so the matrix difference equation ceases to meet the requirements of the nonlinear ergodic theorem and we are forced to deal with the full matrix difference equations rather than their limiting equations.

APPENDIX A

Proof of Theorem 1 Recall that Equations (2.5) were given by

$$\bar{x}(t+1) = \mathcal{P}(t) \bar{x}(t),$$

$$\mathcal{P}(t) = a(t)\mathcal{I} + b(t)\mathcal{L}.$$

Together these give

$$\bar{x}(t+1) = (a(t)\mathcal{I} + b(t)\mathcal{L}) \bar{x}(t). \quad (A.1)$$

Now assume that \mathcal{L} has eigenvalues $\lambda_1 = \lambda^+, \lambda_2, \dots, \lambda_q$, each with multiplicity $m(i)$ so that $m(1) = 1$ and $\sum_{i=1}^q m(i) = m$. Then λ_1 has corresponding eigenvector \bar{v}^+ , and λ_i has eigenvectors (and/or generalized eigenvectors) $\bar{v}_{i,1}, \bar{v}_{i,2}, \dots, \bar{v}_{i,m(i)}$ such that

$$Q \equiv \left\{ \bar{v}^+, \bar{v}_{2,1}, \dots, \bar{v}_{2,m(2)}, \bar{v}_{3,1}, \dots, \bar{v}_{3,m(3)}, \dots, \bar{v}_{q,1}, \bar{v}_{q,m(q)} \right\}$$

is linearly independent and thus spans \mathfrak{R}^m . The coefficient matrix $a(t)\mathcal{I} + b(t)\mathcal{L}$ has eigenvalues $a(t) + b(t)\lambda_i$ with the same set, Q , of eigenvectors as given above. Then for each $k \geq 0$ there is a Jordan matrix $\mathcal{J}(k)$ similar to $a(k)\mathcal{I} + b(k)\mathcal{L}$ (i.e. $a(k)\mathcal{I} + b(k)\mathcal{L} = T\mathcal{J}(k)T^{-1}$ for some nonsingular matrix T) of the form

$$\mathcal{J}(k) = \text{diag} [\mathcal{J}_1(k), \mathcal{J}_2(k), \dots, \mathcal{J}_q(k)]$$

where $\mathcal{J}_1(k) = [a(k) + b(k)\lambda^+]$ and for $i = 2, \dots, q$, $\mathcal{J}_i(k)$ is given by

$$\mathcal{J}_i(k) = \text{diag} [\mathcal{J}_{i1}(k), \dots, \mathcal{J}_{id(i)}(k)].$$

Here \mathcal{J}_{ij} is a square matrix of order k_{ij} given by

$$\mathcal{J}_{ij}(k) = \begin{bmatrix} a(k) + b(k)\lambda_i & & & & \\ & 1 & \cdots & & \mathcal{O} \\ & \mathcal{O} & \ddots & \ddots & \\ & & & 1 & a(k) + b(k)\lambda_i \end{bmatrix}$$

where $k_{i1} \geq k_{i2} \geq \dots \geq k_{id(i)}$ and $\sum_{j=1}^{d(i)} k_{ij} = m(i)$.

Now Equation A.1 has solution

$$\begin{aligned} \bar{x}(t) &= \prod_{k=0}^{t-1} (a(k)\mathcal{I} + b(k)\mathcal{L}) \bar{x}(0) \\ &= \mathcal{T} \left(\prod_{k=0}^{t-1} \mathcal{J}(k) \right) \mathcal{T}^{-1} \bar{x}(0) \end{aligned}$$

where

$$\prod_{k=0}^t \mathcal{J}(k) = \text{diag} \left[\prod_{k=0}^t \mathcal{J}_1(k), \prod_{k=0}^t \mathcal{J}_{21}(k), \dots, \prod_{k=0}^t \mathcal{J}_{2d(2)}(k), \dots, \prod_{k=0}^t \mathcal{J}_{qd(q)}(k) \right].$$

Let $\mathcal{J}'_{ij}(k) \equiv \frac{\mathcal{J}_{ij}(k)}{a(k) + b(k)\lambda^+}$. Then

$$\prod_{k=0}^t \mathcal{J}'_{ij}(k) = \left(\prod_{k=0}^t \frac{1}{a(k) + b(k)\lambda^+} \right) \prod_{k=0}^t \mathcal{J}_{ij}(k)$$

and

$$\prod_{k=0}^t \mathcal{J}'(k) = \left(\prod_{k=0}^t \frac{1}{a(k) + b(k)\lambda^+} \right) \prod_{k=0}^t \mathcal{J}(k).$$

Note that since the first column of \mathcal{T} is \bar{v}^+ , we have

$$\mathcal{T} \begin{bmatrix} 1 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix} \mathcal{T}^{-1} \bar{x}(0) = a_1 \bar{v}^+$$

where $\bar{a} = (a_1, a_2, \dots, a_m) = \mathcal{T}^{-1} \bar{x}(0)$, and hence

$$\begin{aligned} \bar{x}(t) = & a_1 \left(\prod_{k=0}^{t-1} (a(k) + b(k)\lambda^+) \right) \bar{v}^+ \\ & + \sum_{i=2}^q \sum_{j=1}^{d(i)} \mathcal{T} \begin{bmatrix} 0 & \mathcal{O} & \dots & \mathcal{O} & \dots & \mathcal{O} \\ \vdots & \vdots & & \vdots & & \vdots \\ \mathcal{O} & \mathcal{O} & \dots & \prod_{k=0}^{t-1} \mathcal{J}_{ij}(k) & \dots & \mathcal{O} \\ \vdots & \vdots & & \vdots & & \vdots \\ \mathcal{O} & \mathcal{O} & \dots & \mathcal{O} & \dots & \mathcal{O} \end{bmatrix} \mathcal{T}^{-1} \bar{x}(0). \end{aligned} \quad (\text{A.2})$$

If we define Π_t as

$$\Pi_t \equiv \prod_{k=0}^{t-1} \frac{1}{a(k) + b(k)\lambda^+}$$

then multiplying Equation A.2 by Π_t , we obtain

$$\Pi_t \bar{x}(t) = a_1 \bar{v}^+ + \sum_{i=2}^q \sum_{j=1}^{d(i)} \mathcal{T} \begin{bmatrix} 0 & \mathcal{O} & \mathcal{O} \\ \mathcal{O} & \prod_{k=0}^{t-1} \mathcal{J}'_{ij}(k) & \mathcal{O} \\ \mathcal{O} & \mathcal{O} & \mathcal{O} \end{bmatrix} \begin{bmatrix} a_1 \\ \vdots \\ a_n \end{bmatrix}.$$

Lemma 5 For $i = 2, \dots, q$ and $j = 1, \dots, d(i)$, each element of $\prod_{k=0}^{t-1} \mathcal{J}'_{ij}(k)$ goes to 0 as $t \rightarrow +\infty$.

Proof First note that $\prod_{k=0}^{t-1} \mathcal{J}'_{ij}(k)$ is a lower triangular matrix for all i and j , so the rc^{th} element of each will be 0 for $r < c$. For $r \geq c$ we have

$$\begin{aligned} & \left| rc^{\text{th}} \text{ element of } \prod_{k=0}^{t-1} \mathcal{J}'_{ij}(k) \right| \\ &= \left| \binom{t}{r-c} \text{products of } \frac{a(k) + b(k)\lambda_i}{a(k) + b(k)\lambda^+} \text{ of degree } t - r + c \text{ in} \right. \\ & \quad \left. \text{numerator and denominator} \right| \\ &\leq \frac{t^{r-c}}{(r-c)!} \left| \text{products of } \frac{\lambda_i + \rho(k)}{\lambda^+ + \rho(k)} \dots \right| \end{aligned}$$

where $\rho(k) \equiv \frac{a(k)}{b(k)}$.

It can be seen in the complex plane that $\lambda^+ > |\lambda_1|$ implies that $\frac{|\lambda_i + x|}{\lambda^+ + x} < 1$ for all $x > 0$. Since this ratio is continuous in x , we can choose some $m_i < 1$ such that for

all $x \in [0, \rho_0]$, $0 < \frac{\lambda_1 + x}{\lambda_1 + x} < m_i$. Here ρ_0 is the upper bound of ρ ; i.e. $\rho_0 = \frac{a_0}{b_0}$, which exists and is finite due to the assumptions on $a(k)$ and $b(k)$. Thus we obtain

$$\left| r c^{th} \text{ element of } \prod_{k=0}^{t-1} \mathcal{J}'_{ij}(k) \right| \leq \frac{t^{r-c}}{(r-c)!} m_i^t$$

which approaches 0 as $t \rightarrow +\infty$. ♣

Thus as $t \rightarrow +\infty$, $\bar{x}(t) \rightarrow a_1 \Pi_t^{-1} \bar{v}^+$, and the normalized size distribution $\eta(t) = \frac{\bar{x}(t)}{\|\bar{x}(t)\|}$ approaches $\frac{a_1 \Pi_t \bar{v}^+}{a_1 \Pi_t} = \bar{v}^+$ as $t \rightarrow +\infty$. Note that $a_1 > 0$ since $a_1 = \bar{w}_1^T \bar{x}(0)$ where \bar{w}_1 is the left eigenvector of \mathcal{L} corresponding to $\lambda_1 = \lambda^+$, a positive vector.

♣

Proof of Theorem 4, part iv Since at $\theta = \theta^{cr}$ the trivial equilibrium has eigenvalue 1, by considering θ as a bifurcation parameter we have a bifurcation point $(R_0, 0)$ with bifurcation value θ . We use the expansions

$$\begin{aligned} r(R^e) &= r(R_0) + r'(R_0)(R^e - R_0) + \frac{1}{2} r''(R_0)(R^e - R_0)^2 + \dots \\ c(P^e) &= 1 + c'(0)P^e + \frac{1}{2} c''(0)P^{e2} + \dots \end{aligned}$$

to rewrite the Jacobian as

$$\mathcal{J} = \begin{bmatrix} \xi + \xi^2(1 - \xi)(R^e - R_0) \frac{r'(R^e)}{r(R^e)} & -\frac{1 - \pi\xi}{\pi\theta} + (1 - \xi)(R^e - R_0) \frac{c'(P^e)}{c(P^e)} \\ -\pi\xi^2\theta(1 - \xi)(R^e - R_0) \frac{r'(R^e)}{r(R^e)} & 1 - \pi\theta(1 - \xi)(R^e - R_0) \frac{c'(P^e)}{c(P^e)} \end{bmatrix} + \dots$$

Plugging in the expansions for $r(R^e)$ and $c(P^e)$, we get a 2×2 matrix $\mathcal{J} = (\mathcal{J}_{i,j})$ with entries as follows:

$$\mathcal{J}_{1,1} = \xi - \xi^2 \frac{1 - \pi\xi}{\pi\theta} P^e \left(\frac{r'(R_0) - \frac{1 - \pi\xi}{\pi(1 - \xi)\theta} P^e r''(R_0) + \dots}{r(R_0) - \frac{1 - \pi\xi}{\pi(1 - \xi)\theta} P^e r'(R_0) + \dots} \right)$$

$$\begin{aligned}
\mathcal{J}_{1,2} &= -\frac{1-\pi\xi}{\pi\theta} \left(1 + P^e \frac{c'(0) + c''(0)P^e + \dots}{1 + c'(0)P^e + \dots} \right) \\
\mathcal{J}_{2,1} &= \xi^2(1-\pi\xi)P^e \left(\frac{r'(R_0) - \frac{1-\pi\xi}{\pi(1-\xi)\theta} P^e r''(R_0) + \dots}{r(R_0) - \frac{1-\pi\xi}{\pi(1-\xi)\theta} P^e r'(R_0) + \dots} \right) \\
\mathcal{J}_{2,2} &= 1 + (1-\pi\xi)P^e \left(\frac{c'(0) + c''(0)P^e + \dots}{1 + c'(0)P^e + \dots} \right)
\end{aligned}$$

If we then expand $P^e = \varepsilon + \varepsilon^2 p_1 + \dots$ and $\theta = \theta^{\text{cr}} + \varepsilon \theta_1 + \dots$ with $\varepsilon > 0$, we have an epsilon expansion for the Jacobian:

$$\begin{aligned}
\mathcal{J} = \mathcal{J}(\varepsilon) &= \\
&\begin{bmatrix} \xi & -\xi r(R_0) \\ 0 & 1 \end{bmatrix} + \varepsilon \begin{bmatrix} \xi^3 r'(R_0) & r(R_0) \frac{\theta}{\xi} \left(c'(0) - \frac{\pi \xi r(R_0)}{1-\pi\xi} \right) \\ \xi^2(1-\pi\xi) \frac{r'(R_0)}{r(R_0)} & (1-\pi\xi) c'(0) \end{bmatrix} + \dots
\end{aligned}$$

Now let $\mu(\varepsilon) = 1 + \varepsilon \mu_1 + \dots$ be the eigenvalue of $\mathcal{J}(\varepsilon)$ with $\mu(0) = 1$ and let $\bar{w}(\varepsilon) = \bar{w}_0 + \varepsilon \bar{w}_1 + \dots$ and $\bar{v}(\varepsilon) = \bar{v}_0 + \varepsilon \bar{v}_1 + \dots$ be the right and left (resp.) eigenvectors of $\mathcal{J}(\varepsilon)$ corresponding to $\mu(\varepsilon)$, so that

$$\mathcal{J}(\varepsilon) \bar{w}(\varepsilon) = \mu(\varepsilon) \bar{w}(\varepsilon) \quad (\text{A.3})$$

and

$$\bar{v}(\varepsilon) \mathcal{J}(\varepsilon) = \mu(\varepsilon) \bar{v}(\varepsilon). \quad (\text{A.4})$$

Letting $\varepsilon = 0$ in Equation A.3 we get

$$\bar{w}_0 = \begin{bmatrix} -\frac{1-\xi}{\xi} \frac{1}{r(R_0)} \\ 1 \end{bmatrix}$$

while letting $\varepsilon = 0$ in Equation A.4 and requiring that $\bar{v}_0 \cdot \bar{w}_0 = 1$ we get

$$\bar{v}_0 = \begin{bmatrix} 0 & 1 \end{bmatrix}.$$

Dividing Equation A.3 by ε and letting $\varepsilon \rightarrow 0$ we obtain

$$(\mathcal{J}_0 - \mathcal{I}) \bar{w}_1 = (-\mathcal{J}_1 + \mu_1) \bar{w}_0.$$

By the Fredholm alternative, this equation is solvable if $(-\mathcal{J}_1 + \mu_1) \bar{w}_0$ is orthogonal to the null space of $(\mathcal{J}_0 - \mathcal{I})^T$; that is, if $(-\mathcal{J}_1 + \mu_1) \bar{w}_0 \perp \bar{v}_0$. This in turn is equivalent to $\bar{v}_0 \cdot (\mathcal{J}_1 + \mu_1) \bar{w}_0 = 0$, or

$$\begin{aligned} \mu_1 &= \bar{v}_0 \cdot \mathcal{J}_1 \bar{w}_0 \\ &= \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} -\xi^3 r'(R_0) & r(R_0) \frac{\theta}{\xi} \left(c'(0) - \frac{\pi \xi r(R_0)}{1 - \pi \xi} \right) \\ \xi^2 (1 - \pi \xi) \frac{r'(R_0)}{r(R_0)} & (1 - \pi \xi) c'(0) \end{bmatrix} \begin{bmatrix} -\frac{1 - \xi}{\xi} \frac{1}{r(R_0)} \\ 1 \end{bmatrix} \\ &= -\xi(1 - \pi \xi)(1 - \xi) \frac{r'(R_0)}{r(R_0)} + (1 - \pi \xi) c'(0) \\ &< 0. \end{aligned}$$

Thus the branch of equilibria bifurcating from $(R_0, 0)$ at $\theta = \theta^{cr}$ is locally asymptotically stable for $\theta \gtrsim \theta^{cr}$. ♣

Theorem 14 Let $\bar{F}: \mathbb{R}^n \times \mathbb{R}^+ \rightarrow \mathbb{R}^n$ be given by $\bar{F} = \bar{F}(\bar{x}, \theta)$. Assume the following are true.

A1 $\bar{F} \in C^2(\bar{x}, \theta)$, $\bar{F}(\bar{0}, \theta) = \bar{0}$ for all θ .

A2 $\bar{F}_{\bar{x}\theta}(\bar{0}, \theta^{cr})$ (the Jacobian of \bar{F} with respect to \bar{x} at $\theta = \theta^{cr}$ and $\bar{x} = \bar{0}$) has a simple eigenvalue of 1.

Then there exists a solution of $\bar{F}(\bar{x}, \theta) = \bar{x} = \bar{0}$ with $\bar{x} \neq \bar{0}$ locally about $(\bar{x}, \theta) = (\bar{0}, \theta^{cr})$.

Proof First note that $\bar{F}(\bar{x}, \theta)$ can be written as

$$\bar{F}(\bar{x}, \theta) = \mathcal{L}(\theta) \bar{x} + \bar{H}(\bar{x}, \theta)$$

where $\bar{H}(\bar{x}, \theta) = \mathcal{O}(\|\bar{x}\|^2)$. Then by assumption **A2**, there exist $\bar{v} \neq \bar{0}, \bar{w} \neq \bar{0}$ such that $\mathcal{L}(\theta^{cr}) \bar{v} = \bar{v}$ and $\bar{w} \mathcal{L}(\theta^{cr}) = \bar{w}$.

Now look for a solution of $\bar{F}(\bar{x}, \theta) - \bar{x} = \bar{0}$ of the form

$$\begin{aligned}\bar{x} &= \bar{x}(\varepsilon) = \varepsilon \bar{v} + \varepsilon \bar{z}(\varepsilon); & \bar{z}(\varepsilon) &= \mathcal{O}(\varepsilon), \quad \bar{z} \perp \bar{v} \\ \theta &= \theta(\varepsilon) = \theta^{cr} + \eta(\varepsilon).\end{aligned}$$

This must solve the equation

$$\mathcal{L}(\theta(\varepsilon)) \bar{x}(\varepsilon) + \bar{H}(\bar{x}(\varepsilon), \theta(\varepsilon)) - \bar{x}(\varepsilon) = \bar{0} \quad (\text{A.5})$$

where $\mathcal{L}(\theta) = \mathcal{L}(\theta^{cr}) + \mathcal{L}'(\theta^{cr})\eta(\varepsilon) + \kappa(\varepsilon)$ with $\kappa(\varepsilon) = \mathcal{O}(\varepsilon^2)$. Collecting terms in Equation A.5 we obtain

$$\varepsilon^1 \quad \mathcal{L}(\theta^{cr}) \bar{v} - \bar{v} = \bar{0},$$

which is true by assumption **A2**, and

$$\begin{aligned}\mathcal{O}(\varepsilon^2) \quad & \mathcal{L}(\theta^{cr})\varepsilon \bar{z}(\varepsilon) + \mathcal{L}'\eta(\varepsilon) (\varepsilon \bar{v} + \varepsilon \bar{z}(\varepsilon)) \\ & + \kappa(\eta) (\varepsilon \bar{v} + \varepsilon \bar{z}(\varepsilon)) + \bar{H}(\bar{x}(\varepsilon), \theta(\varepsilon)) - \varepsilon \bar{z}(\varepsilon) = \bar{0} \quad (\text{A.6})\end{aligned}$$

Canceling an ε in the last equation, we obtain

$$\begin{aligned}(\mathcal{L}(\theta^{cr}) - \mathcal{I}) \bar{z}(\varepsilon) &= -\mathcal{L}'(\theta^{cr})\eta(\varepsilon) \bar{v} - \mathcal{L}'(\theta^{cr})\eta(\varepsilon) \bar{z}(\varepsilon) \\ &\quad - \kappa(\eta) (\bar{v} + \bar{z}(\varepsilon)) - \frac{1}{\varepsilon} \bar{H}.\end{aligned} \quad (\text{A.7})$$

Then Equation A.7 is solvable if and only if $RHS(\text{A.7})$ is orthogonal to the null space of $(\mathcal{L}(\theta^{cr}) - \mathcal{I})^T$; that is, if and only if

$$\begin{aligned}\bar{w} \cdot (\mathcal{L}'(\theta^{cr})\eta(\varepsilon)) \bar{v} + \bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{z}(\varepsilon) \\ + \bar{w} \cdot \kappa'(\eta) (\bar{v} + \bar{z}(\varepsilon)) + \bar{w} \cdot \frac{1}{\varepsilon} \bar{H} = 0.\end{aligned} \quad (\text{A.8})$$

According to the Implicit Function Theorem, Equation (A.8) can be solved for $\eta = \eta(\varepsilon, \bar{z})$ where $\eta(0, \bar{0}) = 0$ if $\frac{\partial}{\partial \eta} LHS(A.8) \neq 0$ at $(0, \bar{0})$.

$$\begin{aligned} \frac{\partial}{\partial \eta} LHS(A.8) = \\ \bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{v} + \bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{z}(\varepsilon) + \bar{w} \cdot \kappa'(\eta) (\bar{v} + \bar{z}(\varepsilon)) + \bar{w} \cdot \frac{1}{\varepsilon} \bar{H} \end{aligned}$$

and at $\varepsilon = 0, \bar{z} = \bar{0}$ we have $\frac{\partial}{\partial \eta} LHS(A.8) = \bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{v}$.

Thus Equation (A.8) can be solved for $\eta = \eta(\varepsilon, \bar{z})$ if

$$\bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{v} \neq 0. \quad (A.9)$$

If we assume that Equation (A.9) holds, we then have $\eta = \eta(\varepsilon, \bar{z}(\varepsilon))$, and Equation (A.7) must now be solved for $\bar{z} = \bar{z}(\varepsilon)$. Let \mathcal{S} denote the solution operator of Equation (A.7); that is,

$$\bar{z}(\varepsilon) = -\mathcal{S} \left(\mathcal{L}'(\theta^{cr}) \eta(\varepsilon) \bar{v} + \mathcal{L}'(\theta^{cr}) \eta(\varepsilon) \bar{z}(\varepsilon) + \kappa(\eta) (\bar{v} + \bar{z}(\varepsilon)) + \frac{1}{\varepsilon} \bar{H} \right)$$

or

$$\begin{aligned} \mathcal{S}(\mathcal{L}'(\theta^{cr}) \eta(\varepsilon)) \bar{v} + \mathcal{S}(\mathcal{L}'(\theta^{cr}) \eta(\varepsilon)) \bar{z}(\varepsilon) \\ + \mathcal{S}(\kappa(\eta)) (\bar{v} + \bar{z}(\varepsilon)) + \mathcal{S} \left(\frac{1}{\varepsilon} \bar{H} \right) + \bar{z}(\varepsilon) = 0 \end{aligned} \quad (A.10)$$

Equation (A.10) can then be solved for $\bar{z} = \bar{z}(\varepsilon)$ if it is solved by $\varepsilon = 0$ and $\frac{\partial}{\partial \bar{z}} LHS(A.10)$ is nonsingular at $\varepsilon = 0$. At $\varepsilon = 0$, we have that $\eta = 0, \bar{z} = \bar{0}, \kappa(\eta) = 0$, and $\bar{H}(\bar{x}(\varepsilon), \theta(\varepsilon)) = \bar{0}$ since all of these terms are at least order ε , and thus at $\varepsilon = 0, RHS(A.10) = 0$, so $\varepsilon = 0$ solves Equation (A.10).

Now consider $\frac{\partial}{\partial \bar{z}} LHS(A.10)$.

$$\begin{aligned} \frac{\partial}{\partial \bar{z}} LHS(A.10) = & \\ & \mathcal{S}(\mathcal{L}'(\theta^{cr})\eta(\varepsilon)) + \left(\frac{\partial}{\partial \bar{z}} \mathcal{S}(\mathcal{L}'(\theta^{cr})\eta(\varepsilon)) \right) \bar{z}(\varepsilon) + \mathcal{S}(\kappa(\eta)) \\ & + \left(\frac{\partial}{\partial \bar{z}} \kappa(\eta) \right) (\bar{v} + \bar{z}(\varepsilon)) + \frac{\partial}{\partial \bar{z}} \mathcal{S}\left(\frac{1}{\varepsilon} \bar{H}\right) + \mathcal{I}, \end{aligned}$$

and at $\varepsilon = 0$ this becomes

$$\frac{\partial}{\partial \bar{z}} LHS(A.10) = \mathcal{S}(\kappa(\eta(0))) + \left(\frac{\partial}{\partial \bar{z}} \kappa(\eta) \right) \bar{v} \Big|_{\varepsilon=0} + \frac{\partial}{\partial \bar{z}} \mathcal{S}\left(\frac{1}{\varepsilon}\right) \Big|_{\varepsilon=0} + \mathcal{I}.$$

Now $\kappa(0) = 0$ implies that $\mathcal{S}(0) = 0$, and $\bar{H} = \mathcal{O}(\|\bar{z}\|^2)$ implies that $\frac{\partial}{\partial \bar{z}} \mathcal{S}\left(\frac{1}{\varepsilon}\right) \Big|_{\varepsilon=0} = 0$. In addition, since $\kappa(\eta) = \mathcal{O}(\varepsilon^2)$ and $\bar{z} = \mathcal{O}(\varepsilon)$, we have that $\frac{\partial}{\partial \bar{z}} \kappa(\eta) = 0$ at $\varepsilon = 0$. Thus $\frac{\partial}{\partial \bar{z}} LHS(A.10) = \mathcal{I}$ at $\varepsilon = 0$ and so by the Implicit Function Theorem, $\bar{z} = \bar{z}(\varepsilon)$ (and hence $\eta = \eta(\varepsilon)$).

So we have shown that there is a solution

$$\begin{cases} \bar{x} = \bar{x}(\varepsilon) = \varepsilon \bar{v} + \varepsilon \bar{z}(\varepsilon) \\ \theta = \theta(\varepsilon) = \theta^{cr} + \eta(\varepsilon) \end{cases}, \quad (\bar{x}, \theta) \in C^2(\mathfrak{R}^n \times \mathfrak{R})$$

of $\bar{F}(\bar{x}, \theta) - \bar{x} = \bar{0}$ with $\bar{x} \neq \bar{0}$ locally about $(\bar{0}, \theta^{cr})$ if $\bar{w} \cdot \mathcal{L}'(\theta^{cr}) \bar{v} \neq 0$. ♣

Theorem 15 *Let $\bar{F}: \mathfrak{R}^n \times \mathfrak{R}^+ \rightarrow \mathfrak{R}^n$. Assume that **A1** and **A2** from the previous theorem hold. In addition, assume that $\bar{w}\bar{F}_{\bar{x},\theta}(\bar{0},\theta^{cr})\bar{v} > 0$ (resp. < 0). Then the eigenvalue $\mu(\theta)$ of the Jacobian $\bar{F}_{\bar{x}}(\bar{x},\theta)$ evaluated at the solution (\bar{x},θ) of $\bar{F}(\bar{x},\theta) - \bar{x} = \bar{0}$ guaranteed by Theorem 14 satisfies*

- $\mu(\theta^{cr}) = +1$
- $\mu(\theta) < 1$ (resp. > 0) for $\theta \gtrsim \theta^{cr}$
- $\mu(\theta) > 1$ (resp. < 0) for $\theta \lesssim \theta^{cr}$.

Proof By the preceding theorem, we can parametrise the branch of nontrivial solutions of $\bar{F}(\bar{x},\theta) = \bar{x}$:

$$\begin{aligned}\bar{x} &= \varepsilon \bar{v} + \varepsilon^2 \bar{x}_2 + \dots \\ \theta &= \theta^{cr} + \varepsilon \theta_1 + \dots\end{aligned}$$

Equating powers of ε in $\bar{F}(\bar{x},\theta) = \bar{x}$ we get

$$\varepsilon^0: \quad \bar{F}(\bar{0},\theta^{cr}) = \bar{0}$$

which is true by assumption **A3**, and

$$\varepsilon^1: \quad \bar{F}_{\bar{x}}(\bar{x}(0),\theta(0))\bar{x}_\varepsilon(0) + \bar{F}_\theta(\bar{x}(0),\theta(0))\theta_\varepsilon(0) = \bar{v}$$

which implies that

$$\bar{F}_{\bar{x}}(\bar{0},\theta^{cr})\bar{v} + \bar{F}_\theta(\bar{x}(0),\theta^{cr})\theta_1 = \bar{v}$$

or $\bar{v} = \bar{v}$, which is clearly true.

$$\varepsilon^2: \quad \bar{F}_{\bar{x}}(\bar{x}(0),\theta(0))\bar{x}_{\varepsilon\varepsilon}(0)$$

$$\begin{aligned}
& + \left[\bar{F}_{\bar{x}\bar{x}} (\bar{x}(0), \theta(0)) \bar{x}_\varepsilon(0) + \bar{F}_{\bar{x}\theta} (\bar{x}(0), \theta(0)) \theta_\varepsilon(0) \right] \bar{x}_\varepsilon(0) \\
& + \bar{F}_\theta (\bar{x}(0), \theta(0)) \theta_{\varepsilon\varepsilon}(0) \\
& + \left[\bar{F}_{\theta\bar{x}} (\bar{x}(0), \theta(0)) \bar{x}_\varepsilon(0) + \bar{F}_{\theta\theta} (\bar{x}(0), \theta(0)) \theta_\varepsilon(0) \right] \theta_\varepsilon(0) = \bar{x}_{\varepsilon\varepsilon}(0)
\end{aligned}$$

implies

$$\begin{aligned}
& \bar{F}_{\bar{x}} (\bar{0}, \theta^{cr}) 2 \bar{x}_2 + \left[\bar{F}_{\bar{x}\bar{x}} (\bar{0}, \theta^{cr}) \bar{v} + \bar{F}_{\bar{x}\theta} (\bar{0}, \theta^{cr}) \theta_1 \right] \bar{v} \\
& + \bar{F}_\theta (\bar{0}, \theta^{cr}) 2\theta_2 + \left[\bar{F}_{\theta\bar{x}} (\bar{0}, \theta^{cr}) \bar{v} + \bar{F}_{\theta\theta} (\bar{0}, \theta^{cr}) \theta_1 \right] \theta_1 = 2 \bar{x}_2
\end{aligned}$$

and hence

$$\begin{aligned}
& \left[\bar{F}_{\bar{x}} (\bar{0}, \theta^{cr}) - \mathcal{I} \right] \bar{x}_2 = \\
& -\frac{1}{2} \left[\bar{F}_{\bar{x}\bar{x}} (\bar{0}, \theta^{cr}) \bar{v} + \bar{F}_{\bar{x}\theta} (\bar{0}, \theta^{cr}) \theta_1 + \bar{F}_{\theta\bar{x}} (\bar{0}, \theta^{cr}) \theta_1 \right] \bar{v}. \quad (A.11)
\end{aligned}$$

By the Fredholm alternative, for Equation A.11 to be solvable it is required that

$$-\frac{1}{2} \left[\bar{F}_{\bar{x}\bar{x}} \bar{v} + \bar{F}_{\bar{x}\theta} \theta_1 + \bar{F}_{\theta\bar{x}} \theta_1 \right] \bar{v}$$

be orthogonal to the null space of

$$\left[\bar{F}_{\bar{x}} (\bar{0}, \theta^{cr}) - \mathcal{I} \right]^T,$$

that is,

$$\bar{w} \cdot \left[\bar{F}_{\bar{x}\bar{x}} \bar{v} + \bar{F}_{\bar{x}\theta} \theta_1 + \bar{F}_{\theta\bar{x}} \theta_1 \right] \bar{v} = 0. \quad (A.12)$$

Then since μ, \bar{w} , and \bar{v} must be continuous functions of $\bar{F}_{\bar{x}}$, write

$$\mu(\varepsilon) = 1 + \varepsilon\mu_1 + \dots, \quad \bar{v}(\varepsilon) = \bar{v} + \varepsilon\bar{v}_1 + \dots, \quad \bar{w}(\varepsilon) = \bar{w} + \varepsilon\bar{w}_1 + \dots$$

We want $\bar{v}(\varepsilon)$ to solve $\bar{F}(\bar{x}(\varepsilon), \theta(\varepsilon)) \bar{v}(\varepsilon) = \mu(\varepsilon) \bar{v}(\varepsilon)$, so equating powers of ε again we obtain:

$$\varepsilon = 0: \quad \bar{F}_{\bar{x}} \bar{v} = \bar{v}$$

which is true by assumption **A3**, and

$$\varepsilon^1 : \quad \bar{F}_{\bar{x}} \bar{v}_1 + \left[\bar{F}_{\bar{x}\bar{x}} \bar{v} + \bar{F}_{\bar{x}\theta} \theta_1 \right] \bar{v} = \bar{v}_1 + \mu \bar{v}$$

which implies

$$\left[\bar{F}_{\bar{x}} - \mathcal{I} \right] \bar{v}_1 = - \left[\bar{F}_{\bar{x}\bar{x}} \bar{v} + \bar{F}_{\bar{x}\theta} \theta_1 \right] \bar{v} + \mu_1 \bar{v} .$$

So by the Fredholm alternative we must have

$$\bar{w} \cdot \left[\bar{F}_{\bar{x}\bar{x}} \bar{v} + \bar{F}_{\bar{x}\theta} \theta_1 \right] = \bar{w} \mu_1 \bar{v} .$$

This equation, substituted into Equation A.12, gives $\bar{w} \mu_1 \bar{v} + \bar{w} \bar{F}_{\theta\bar{x}} \theta_1 \bar{v} = 0$, which upon simplification gives $\bar{w} \mu_1 \bar{v} = -(\bar{w} \bar{F}_{\theta\bar{x}} \bar{v}) \theta_1$, or

$$\mu_1 = -(\bar{w} \bar{F}_{\theta\bar{x}} \bar{v}) \theta_1. \quad \clubsuit$$

REFERENCES

- [1] H. Barclay. Models of host-parasitoid interactions to determine the optimal instar for pest control. *Natural Resource Modeling*, 1(1):81–104, 1986.
- [2] J. L. Brooks and S. I. Dodson. Predation, body size, and composition of plankton. *Science*, 150:28–35, 1965.
- [3] J. Buongiorno and B. R. Michie. A matrix model of uneven-aged forest management. *Forest. Sci.*, 26(4):609–625, 1980.
- [4] G. J. Butler and G. S. K. Wolkowicz. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM J. Appl. Math.*, 45(1):138–151, 1985.
- [5] William A. Calder III. *Size, Function and Life History*. Harvard University Press, Cambridge, Massachusetts, USA, 1984.
- [6] H. Caswell. *Matrix Population Models*. Sinauer Associates Inc., Sunderland, MA, 1989.
- [7] J. H. Connell. The influence of interspecific competition and other factors on the distribution of the barnacle *chthamalus stellatus*. *Ecology*, 42:710–723, 1961.

- [8] J. M. Cushing. A competition model for size-structured species. *SIAM J. Appl. Math.*, 49(3):838–858, 1983.
- [9] J. M. Cushing. Nonlinear matrix models and population dynamics. *Natural Resource Modeling*, 2(4), 1988.
- [10] J. M. Cushing. A Strong Ergodic Theorem for some nonlinear matrix models for structured population growth. *Natural Resource Modeling*, 3(3):331–357, 1989.
- [11] J. M. Cushing. Some competition models for size-structured populations. *Rocky Mountain Journal of Mathematics*, 20(4), 1990.
- [12] J. M. Cushing. A discrete model of competing size-structured species (invited paper). *Theo. Pop. Biol.*, (to appear), 1991.
- [13] A. Ek. Nonlinear models for stand table projection in northern hardwood stands. *Can. J. For. Res.*, 4:23–27, 1974.
- [14] A. Ek and R. A. Monserud. Performance and comparison of stand growth models based on individual tree and diameter class growth. *Ca. J. For. Res.*, 9:231–244, 1979.
- [15] H. Freedman, J. So, and P. Waltman. Coexistence in a model of competition in the chemostat incorporating discrete delays. *SIAM J. A. M.*, 49(3):859–870, June 1989.
- [16] F. R. Gantmacher. *Applications of the Theory of Matrices*. Interscience Publishers, New York, 1959.

- [17] G. F. Gause. *The Struggle for Existence*. Williams and Wilkins, Baltimore, 1934. Reprinted 1964 by Hafner, New York.
- [18] G. F. Gause. Experimental demonstration of Volterra's periodic oscillation in the number of animals. *J. Exp. Biol.*, 12:44-48, 1935.
- [19] J. F. Gilliam. *Habitat Use and Competitive Bottlenecks in Size-structured Fish Populations*. PhD thesis, Michigan State University, East Lansing, Michigan, 1982.
- [20] Donald J. Hall, Stephen T. Threlkeld, Carolyn W. Burns, and Philip H. Crowley. The Size-Efficiency Hypothesis and the structure of zooplankton communities. *Ann. Rev. Ecol. Syst.*, 7:177-208, 1976.
- [21] M. P. Hassell and H. N. Comins. Discrete time models for two competing species. *Theoret. Pop. Biol.*, 9:202-221, 1976.
- [22] S. B. Hsu, S. Hubbell, and P. Waltman. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. Appl. Math.*, 32:366-383, 1977.
- [23] S. B. Hsu, S. Hubbell, and P. Waltman. Competing predators. *SIAM J, Appl. Math.*, 35:617-625, 1978.
- [24] S. B. Hsu, S. Hubbell, and P. Waltman. A contribution to the theory of competing predators. *Ecol. Monogr.*, 48:337-349, 1978.
- [25] G. E. Hutchinson. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, 22:415-427, 1957.

- [26] J. Impagliazzo. *Deterministic Aspects of Mathematical Demography*, volume 13 of *Biomathematics*. Springer, Berlin, 1980.
- [27] J. P. Keener. Oscillatory coexistence in the chemostat: a codimension-two unfolding. *SIAM J. Appl. Math.*, 43:1005–1019, 1983.
- [28] J. P. LaSalle. *The Stability of Dynamical Systems*. Reg. Conf. Series in Appl. Math. SIAM, Philadelphia, 1976.
- [29] P. H. Leslie. On the use of matrices in certain population mathematics. *Biometrika*, 33:183–212, 1945.
- [30] P. H. Leslie. Some further notes on the use of matrices in population mathematics. *Biometrika*, 35:213–245, 1948.
- [31] S. A. Levin and C. P. Goodyear. Analysis of an age-structured fishery model. *J. Math. Biol.*, 9:245–274, 1980.
- [32] E. G. Lewis. On the generation and growth of a population. *Sankhya*, 6:93–96, 1942.
- [33] S. L. Linstedt, B. J. Miller, and S. W. Buskirk. Home range, time, and body size in mammals. *Ecology*, 67(2):413–418, 1986.
- [34] L. Liu and J. E. Cohen. Equilibrium and local stability in a logistic matrix model for age-structured populations. *J. Math. Biol.*, 25:73–88, 1987.
- [35] R. H. MacArthur and R. Levins. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101:377–385, 1967.

- [36] R. McGehee and R. A. Armstrong. Some mathematical problems concerning the ecological principle of competitive exclusion. *J. Differential Equations*, 23:30–52, 1977.
- [37] H. R. Mushinsky, J. J. Hebrard, and D. S. Vodopich. Ontogeny of water snake foraging ecology. *Ecology*, 63:1624–1629, 1982.
- [38] W. E. Neill. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology*, 56:809–826, 1975.
- [39] T. Park, D. B. Mertz, W. Grodzinski, and T. Prus. Cannibalistic predation in populations of flour beetles. *Physiological Zoology*, 38:289–321, 1965.
- [40] H. L. Smith. Competitive coexistence in an oscillating chemostat. *SIAM J. Appl. Math.*, 40:498–522, 1981.
- [41] A. W. Stoner. Feeding ecology of *lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. *Fish. Bull.*, 78:337–352, 1980.
- [42] A. W. Stoner and R. J. Livingston. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*, pages 174–187, 1984.
- [43] D. Tilman. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*, 58:338–348, 1977.
- [44] D. Tilman. *Resource Competition and Community Structure*. Princeton University Press, Princeton, N. J., 1982.

- [45] C. C. Travis, W. M. Post, D. L. DeAngelis, and J. Perkowski. Analysis of compensatory Leslie matrix models for competing species. *Theoret. Pop. Biol.*, 18:16–30, 1980.
- [46] M. B. Usher. A matrix model for forest management. *Biometrics*, 25:309–315, 1969a.
- [47] M. B. Usher. A matrix approach to the management of renewable resources, with special reference to selection forests. *J. Appl. Ecol.*, 3:355–367, 1969b.
- [48] M. B. Usher. A matrix approach to the management of renewable resources, with special references to selection forests - two extensions. *J. Appl. Ecol.*, 6:247–248, 1969c.
- [49] M. B. Usher. *Developments in the Leslie matrix model*. Mathematical Models in Ecology. Blackwell Scientific Publishers, London, 1972.
- [50] P. Waltman. *Competition Models in Population Biology*, volume 45 of *Regional Conference Series in Applied Mathematics*. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania 19103, 1983.
- [51] E. Werner and J.F. Gilliam. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.*, 15:393–425, 1984.
- [52] H. M. Wilbur. Complex life cycles. *Ann. Rev. Ecol. Syst.*, 11:67–93, 1980.