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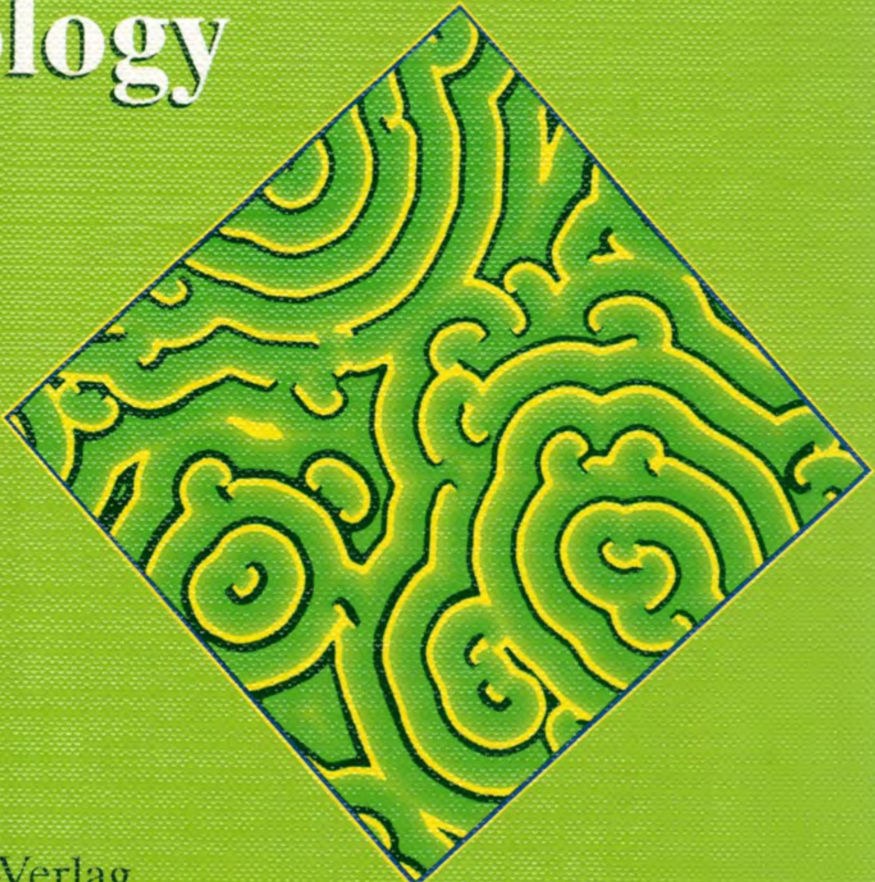

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STRUCTURED POPULATION DYNAMICS

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INTRODUCTION

Population dynamics attempts to account for changes in the sizes of biological populations. This is a fundamental problem in biology that has occupied scientists' attention since at least Aristotle. It is a problem of not only intrinsic interest, but of fundamental importance in other biological investigations as well. Models of population dynamics form the bases of models in ecology, genetics, theories of evolution, cell dynamics, epidemiology, resource management, bioeconomics, ecotoxicology, sociobiology and many other disciplines of the biological, medical, and environmental sciences. Given a biological population's natural propensity for exponential growth and the finiteness of our natural world, at the heart of this problem is the fundamental problem of how population numbers are "regulated", i.e. how they are kept from growing without bound.

Although a few well-known mathematicians formulated simple models for some specific problems earlier (e.g. Fibonacci and Euler), the use of mathematical models to study population growth flourished only after the "Golden Age" that occurred during the decades of 1920-1940 (Scudo & Ziegler (1978)). This period is associated with the names Volterra, Lotka, Kostitzin, and Kolmogorov. The resulting explosion in theoretical models for the dynamics of single populations and multi-species interactions, while undoubtedly excessive, nonetheless resulted in theoretical support (and in some cases the original impetus) for many basic tenets of population dynamics and theoretical ecology that are still central to much of the thinking in these subjects today. Examples include "logistic" growth and the accompanying notions of carrying capacity and **r** and **K** selectors; competitive exclusion, ecological niche, and limiting similarity; and the oscillatory nature of predator-prey interactions.

Mathematical models necessarily entail simplifying assumptions. This is particularly true for "analytically tractable" models, i.e. for models involving mathematical equations from which one is analytically able to derive some useful information about their solutions. Modelers are continually struggling between model tractability and "accuracy" or "realism". Models of population growth that assume some kind of regulation of the unbounded exponential growth to which biological populations have a natural propensity are generally nonlinear and therefore can easily lead to difficult and intractable equations. This is true for models of even the "simplest" controlled laboratory populations from which have been eliminated any further complexities found in natural populations. It comes, then, as no surprise that models in population dynamics usually entail very restrictive assumptions (often very severe ones from a biologist's point of view).

For example, "classical" type of models, such as the famous Lotka-Volterra equations (or, more generally, "Kolmogorov type equations") utilize systems of autonomous nonlinear ordinary differential equations to describe the rates of changes of total population size (May (1974), Freedman (1980)). No matter how large or complicated these systems of equations are, they still make very restrictive assumptions (whether explicitly stated or not) about the homogeneity of both the environment and the individuals of the populations involved. Assumed environmental homogeneities in these models include, for example, spatial and temporal uniformity. The effect of habitat heterogeneities has been and continues to be addressed by a large literature by means of a variety of types of modeling equations, including partial differential equations, integro-differential equations, and compartmental type ordinary differential equations. Temporal variations in environmental parameters has also been investigated, although to a lesser extent, usually by modifying classical models to include time dependent model parameters, either in a stochastic manner or in a deterministic manner such as periodic oscillations (e.g. see P.L. Chesson (1986), Cushing (1982)).

Another restrictive simplification made in classical type population models, and with which we are concerned in this article, is that populations are assumed to be homogeneous collections of entirely identical individuals. Physiological and behavioral characteristics of individuals, whether due to significant life cycle changes during development or simply to natural variations between individuals, are ignored. In reality, however, an individual's interactions with its environment and with members of its own and other species is likely to depend critically on its physiological condition or behavioral attributes. Vital birth, death, and growth rates of individuals in most plants and animals usually depend, for example, on age and/or on body size.

Classical demography (which deals primarily with human populations), the one sub-discipline in population dynamics that has focused on differences between individuals, uses chronological age as an internal structuring parameter. Throughout the biological world, however, individual body size is usually the more significant factor affecting an individual's vital rates than is age (Ebenman & Lennart (1988c), Bonner (1988), Caswell (1989)). Body size can determine an individual's competition effectiveness for resources, its probability of survival or escape from predation (including cannibalistic) attacks and other hazards, its metabolic demands and efficiency, etc. Since body size can vary as much as four orders of magnitude within some species, a greater variation than is in fact often found between species (Werner & Gilliam (1984)), it is clear that body size (and consequently individual growth rates) can be the single most important physiological characteristic during the life cycle of individuals and hence in ultimately determining the dynamics of the entire population.

Of course, in some cases, body size can closely correlate with age. In other cases, it has been found that both age and size are needed to account adequately for the dynamics (Schoen (1988)). Furthermore, while size and age are often the single most significant variables affecting an individual's vital rates, other variables or categorizations can also be as or more important in other cases or under different circumstances. Life cycles stages or the amount of certain chemicals present in the body are examples of additional variables that can and have been used to internally "structure" the population in order to understand its dynamics.

At one opposite extreme from the classical models that treat individuals as identical are models that distinguish and account for the dynamics of each and every individual. Thus, if a population consisting of 10,000 individuals were of interest then a model with 10,000 state variables, one for each individual, could be conceived together with rules governing how these variables move or change in time. With the computing power now available such "individual based" models are easy to construct and use for simulations. Many models of this or similar type have been built for the dynamics of specific populations and for large scale communities of populations, which, after "calibration" by the adjustment of model parameters until known data sets are acceptably fit, are then used to make predictions. One of the shortcomings that critics often find with these kinds of computer models is that it is difficult to gain real understanding and insight from them, primarily because they are so large and complex (and partly because of the way the models are used and analyzed, or are not analyzed). It is as if a complicated biological system that one does not understand is replaced by a "black box" computer program that one equally does not understand. Of course, the computer program is available for simulations, which the real world biological entity probably is not, but beyond using it as an elaborate curve fitting device it can be difficult to use such models to identify and understand the significant features and crucial model parameters and components that are most important in determining the behavior of the model.

Intermediate between these two extremes are models that are based upon sub-groupings or categories determined by specified physiological traits of individuals. Such models permit the gap betweem the level of individual organisms and the level of the total population to be spanned while at the same time allowing for a reasonable amount of analytical tractability. In so doing they introduce the possibility of incorporating the vast amount of biological data that exists at the level of the individual organism into models for population level dynamics, something that the classical models do not do well, if at all.

Modeling methodologies are now well developed for the derivation of both "continuous" and "discrete" models for structured populations. Models for the continuous time dynamics of populations structured by continuous structuring variables can be described by means of mass balance equations (Metz & Diekmann (1986)) which, in simpler cases, take the form of the so-called "McKendrick/von Foerster" equation (McKendrick (1926), von Foerster (1959), Hoppensteadt (1975), Sinko & Streifer (1967))

$$\frac{\partial}{\partial t}\rho+\frac{\partial}{\partial s}(g\rho)=-d\rho \qquad \textbf{(MvF)}$$

In these models the population is described by means of a density distribution $\rho(t,s)$ (per unit of s) which, as a function of time t and the structuring variable s satisfies this first order hyperbolic partial differential equation. This equation accounts for "transitions" out of and between structuring classes measured by the single real variable s under the assumption that the population is closed to immigration and emigration and suffers losses only through death, modeled by the per unit death rate d. Transitions between classes are modeled by the rate $g = ds/dt$ (e.g. in a size-structured population in which s is some measure of body size, g is the individual's growth rate). In the McKendrick/von Foerster model, births are modeled by the boundary condition

$$(g\rho)_{s=s_b}=\int_{s_b}^{\infty} b\rho ds \qquad \textbf{(B)}$$

where b is the per unit birth rate. Here it is assumed that all newborns belong to the same class s_b.

Because birth, death, and transition rates are in general affected by population density the equation (**MvF**) will in general be a nonlinear equation as will the boundary condition (**B**). Moreover, because an individual's vital rates b, d and g are likely to be affected by individuals of classes other than its own, density dependence is most often expressed in the model by weighted integrals of the density distributions taken over an appropriate interval of s. Thus, the equation (**MvF**) is in general a complicated nonlinear, integro-partial differential equation which is accompanied by the nonlinear, integral boundary condition (**B**).

Such complicated nonlinear equations can pose difficult (but not insurmountable) mathematical problems concerning even the fundamental questions of existence and uniqueness of solutions, to say nothing of questions about the properties of solutions, such as, for example, their asymptotic long time behavior (equilibria, stability, oscillations, persistence, etc.). The fundamental mathematical theory for some classes of models has been rather thoroughly developed (see Gurtin & MacCamy (1974), Webb (1985) for the case of age-structured models and Tucker & Zimmerman (1988) for certain kinds of age- and size-structured models). With regard to biological applications one can attempt to analyze models based on these kinds of equations directly or one can, by making suitable simplifying assumptions, use these equations as the basis for deriving simpler model equations, such as autonomous ordinary differential equations, delay differential equations, integral equations, etc., for which analytical tools are more readily available and the analysis is more tractable. For example, certain classes of models, based upon specialized assumptions about the nonlinear density terms and/or the age/size dependence of the vital rates, have been analyzed in this way (e.g. "separable" death rates (Simmes (1978), Busenberg & Iannelli (1985); the "linear chain trick" (Gurtin & MacCamy (1979), Metz & Diekmann (1986)); hierarchical age and size classes (Cushing (19983)).

Another modeling approach is based upon the description of a discrete, vector distribution of classes that is followed dynamically through discrete time steps. This matrix methodology was originated by Lewis (1942) and Leslie (1945, 1948) for age-structured populations and is developed for arbitrarily structured populations in the recent book by Caswell (1989) (also see Lefkowitz (1965), Cushing (1988)). Matrix or difference equations models have some nice advantages; they present no annoying technical problems concerning existence and uniqueness of solutions, they are extremely easy to program for use on computers, and they are easily understood and used by those with no training or familiarity with differential equations. As pointed out by Caswell (1989), however, because the models do not continuously account for the dynamics between discrete time steps, one must be careful in their formulation and in the interpretation of model parameters.

Occasionally mixed discrete and continuous models are found to be useful, i.e. models that are continuous in some variables and discrete in others (e.g. see Impagliazzo (1980)).

Since the McKendrick/von Foerster equation is simply a balancing law it can be viewed as a unifying model in population dynamics. All the classical, unstructured models can be derived from the equation by simply postulating that all vital rates and parameters are structure variable independent and by integrating over the structure variable domain, thereby obtaining a dynamical equation for total population size. Discrete matrix models can be derived by making suitable discretation approximations to the derivatives and integrals in the McKendrick/von Foerster equation. This is easy to do formally; but in order to obtain a matrix model which is a rigorous (consistent, stable, and convergent) discretation of the McKendrick/von Foerster equation, care has to be taken. For example, some discretizations mentioned in the literature for the age-structured equation (**MvF**) which result in the classical Leslie matrix model are not convergent. The connection between matrix models and continuous models has not been thoroughly studied; (see Saints (1987) for the linear age-structured case and Leslie models and Uribe (1993) for the non-linear size-structured case and Usher models).

The most commonly used model of single species, density regulated growth is the "logistic" or Pearl/Verhulst equation. The inadequacies of this famous equation in accounting for population self-regulation through individual interactions is discussed by Lomnicki (1988). Since interactions take place between individual organisms, what is needed are models based upon differences between individuals, as is the case, for example, in Lomnicki's simple models which are based upon an ranking hierarchy within the population that determines an individual's access to and consumption of food resources. Such a ranking might be age, or perhaps more importantly throughout the biological world, body size. Model equations that attempt to take into account effects of internal population structure should not be too casually constructed, however, and careful modeling methodologies (e.g. based upon equations (**MvF**) and (**B**)) should be followed.

For example, in studying the effects of time delays that might be caused by age or size determined factors (such as gestation or maturation delays), modelers and mathematicians must do more than stick a time lag in their favorite classical type differential equation. S uch models more often than not give no new insights that are not by now well known about the effects of time delays in dynamical models. The famous delay logistic equation is a prime example. This equation has served an important purpose in the history of population dynamics in that it illustrates, in a relatively simple way, the general qualitative effects of time delays in basic differential equation models, namely that they can destabilize equilibrium states and lead to sustained oscillations. It has provided the impetus for many sophisticated mathematical analyses and generalizations and has served as an obligatory "application" in mathematical papers on delay equations (usually for the wrong biological reasons, however). But attempts to use it to explain oscillatory phenomena in biological data of specific species (May (1974)) have been unconvincing, because lacking the necessary biological underpinnings with regard to the causes of the delay these applications are really nothing more than elaborate curve fitting exercises. The delay logistic equation is a special case of a distributed delay equation introduced by Volterra for the study of a specific biological problem, namely the failure of certain cultured bacterial populations to follow a standard logistic saturation curve because, it was hypothesized, of the toxic effects of the accumulated remains of dead individuals, effects which made the current growth rate of the population depend upon past populations (see Scudo & Ziegler 1978)). This problem has nothing to do with gestation or maturation delays (to the contrary, it had to do with accumulated effects of past populations on the death rate), the most often stated apology for the casual placing of a time delay in the logistic and similar differential equations. Such delays require a structured model, which in fact show that the delay logistic is inappropriate for delays due to these causes (Cushing (1979)).

Because it provides the means to model population self regulation on the basis of individual differences, the McKendrick/von Foerster equation should probably be viewed as the fundamental equation of population growth instead of the simplistic logistic equation. By specifying submodels for birth, death, and growth rates, as not only density dependent rates but structure variable dependent rates, a modeler can explore the implications of various types of intraspecific interactions on the dynamics and regulation of the population. This remains true for discrete matrix models and other types of models derivable from the McKendrick/von Forester equation as well. Models so derived have their biological underpinnings at the level of the individual organism. Namely, they contain model parameters related to individual physiological and behavioral characteristics, even if they should by simplification ultimately take the form of classical kinds of models. See Cushing (1989) for an example.

One of the legacies of the classical, non-structured models for single species density regulated growth dynamics, and in particular of the logistic equation, is that until recently little attention has been paid to the complexities of intraspecific interactions. Intraspecific competition has been little studied in comparison to interspecific competition, which has received a tremendous amount of attention. Nor has much attention been paid to intraspecific predation. The type and nature of intraspecific interactions can be diverse, both in different species and within the same species (particularly those whose life cycles involve significant morphological and hence niche changes) and can even change during an individual's life cycle. I nteractions between individuals of the same species can be and often are more complex than those between individuals of different species. Furthermore, the effects of environment can vary greatly among individuals within a single species.

Thus, the nonlinear mathematical equations that arise from density regulated, structured single species population models can be quite complicated and can allow for a broad range of dynamical possibilities, ranging from equilibration to oscillations to aperiodic "chaotic" dynamics (unlike the mathematically trivial monotonic equilibrium dynamics of the classical logistic). Their analysis can be mathematically very challenging.

One problem that has recently been studied is that of competition between juvenile and adult members of a population for a limited resource and of the effects that this competition has on the population's dynamics. One broad question that has been addressed is whether such juvenile vs. adult competition is a "stabilizing" or "destabilizing" influence on the population dynamics. This problem has been investigated by several authors using nonlinear model equations of many different sorts, including difference equations, ordinary and delay differential equation, and the McKendrick/von Foerster equations directly. Age-structured models were studied by May et al. (1974), Tschumy (1982), Ebenman (1987,1988a), Cushing & Li (1989), and Cushing (1992) and size-structured models by Ebenman (1988b), Cushing (1991a), Cushing & Li (1992). These studies have shown that usually juvenile vs. adult intraspecific competition is destabilizing (with respect to several different meanings of this word), although in some cases and parameter ranges it can be viewed as stabilizing. The full range of the dynamics of most of these models has not been investigated, however. And the question of how such destabilizing interactions could have evolved has received little attention (Ebenman (1988a, 1988c)).

Another problem that has recently been investigated is that of interspecific predation or cannibalism. The survey articles of Fox (1974) and Polis (1981) discuss cannibalism in depth and argue that it is should not be dismissed are rare). Many dynamical consequences have been attributed to cannibalism, including: stabilization (i.e. cannibalism is a means of self regulation); destabilization (causing oscillations in population numbers); multiple stable equilibrium states and hence hysteresis effects; "life boat" effects (i.e. cannibalism can help a population survive in circumstances when it would otherwise be in danger of extinction); and dominance of single age or size classes over long periods of time. It is an interesting challenge to try to understand the effects of cannibalism and to explain these (and other) dynamical consequences on the bases of mathematical models (see Gurtin & Levine (1982), Levine (1983), Diekmann et al. (1986), Hastings (1987), Costantino & Hastings (1987), Costantino & Desharnais (1991), van den Bosch et al. (1988), Cushing (1991b, 1993)).

Cannibalism and juvenile vs. adult competition afford only two examples of the challenging and interesting problems that can arise concerning the dynamics of single species structured populations. Questions involving different modes of competition (interference, exploitative, contest, scramble), conflict (territoriality, aggression, predation), mutualism (herding, nurturing), and, even more intriguing, interactions which change during the life cycle of an individual (Werner & Gilliam (1984)) also raise challenging problems that have been little investigated by means of structured models, if at all. Competition and conflict take place at the individual level. It has been argued that body size is one of the most significant factors in determining an individual's success or failure in dealing with its physical and biological environment (Ebenman & Lennart

(1988c)). Generally, smaller (or, if size correlates closely with age, younger) individuals are less efficient metabolizers of food resources, but are larger in total numbers and therefore can assert significant competitive pressure on larger (older) individuals for food resources (Polis (1988)). What are possible responses of larger (older) individuals to the competitive pressure of smaller (younger) individuals? Delayed or earlier reproduction? Slower or faster growth? Interference or contest competition (Lomnicki (1988))? Aggressive behavior or even cannibalism (Fox (1974), Polis (1981, 1988))? What are the effects of different strategies on the dynamics of the population? Beyond understanding the dynamical implications of various kinds of intraspecific interactions, one would like to know how these strategies arose evolutionarily (Ebenman & Lennart (1988c)). The concept of "evolutionarily stable strategy" has not been extensively applied to structured populations and could perhaps help explain the evolution of the often complex life cycles that individuals undergo (see chapter 11 of the book by Maynard Smith (1982), Bonner (1988), Caswell (1989)).

Very few dynamical models have been formulated, let alone thoroughly analyzed, with regard to these questions.

If individual differences among conspecifics can result in complicated intraspecific interactions and have profound consequences on the dynamics at the population level, then it is no surprise that the same is true for interactions between members of different species. Werner & Gilliam (1984) and the many authors in the book by Ebenman & Lennart (1988c) forcibly argue for the necessity of taking individual differences and life cycles into account in order to fully understanding the dynamics of many, if not most, biological populations and their interactions with their physical and biological environments.

Consider the problem of competition between species for limited resources. Despite the huge literature dealing with interspecific competition models, competition between structured populations has been virtually unexplored by means of mathematical models (some exceptions are Cushing (1989, 1991a), Crowe (1992), and selected papers in DeAngelis & Gross (1992)). This is a shortcoming in the attempt to understand interactions between species since, as is pointed out by Bonner (1988, p. 20), competition takes place between individuals and only indirectly do species compete as separate entities. Physiological characteristics such as age or body size can directly affect an individual's success in winning vital resources in competitive confrontations with other individuals and can also indirectly determine its competitive effectiveness by correlating with parameters such as resource uptake rates, resource allocation to growth vs. reproduction, onset of reproduction, offspring size and viability, etc.

The derivation and analysis of structured models could help identify those parameters crucial for competitive success under different circumstances and lead to the understanding of how and why various life cycle strategies have evolved.

As an example, the studies of Cushing (1989, 1991a) and Crowe (1992) consider the problem of species size and competitive effectiveness. There is some evidence that, at least under some circumstances, larger species will have a competitive advantage over smaller species (Dodson (1965), Werner & Gilliam (1984), Bonner (1988)). The size-structured competition models of Cushing & Crowe show when this is and is not the case by illuminating how various size dependent physiological parameters determine species size (average adult size, in this case) and competitive superiority and under what conditions these two occur or do not occur together. However, the models considered by Cushing and Crowe require some restrictive assumptions (e.g. size independent mortality) and many questions and problems remain. For example, one strategy that smaller species have been observed to adopt in order to out compete a larger species is for the adults of the smaller species to exert sufficient competitive pressure on the similar sized juveniles of the larger species, thereby decreasing the reproductive output of the larger species (Werner & Gilliam (1984), Neill (1988), Persson (1988)). This "juvenile bottleneck" phenomenon has not been investigated by dynamical models.

Differences among individuals can also play an important role in predator-prey interactions. Smaller (younger) individuals are generally more vulnerable to predation, as are older weaker individuals; predators are usually larger than prey (except in the case of cooperative hunting); larger (older) predators are likely to be more successful, etc. There have been some studies of age-structured predator-prey interactions (Gurtin & Levine (1979), Levine (1983), van den Bosch & Diekmann (1986), Cushing & Saleem (1982), Hastings (1983), Hastings & Wollkind (1982)), but as with the case of competitive interactions, predator-prey interactions between structured populations remains largely unexplored. There have been, for example, virtually no model studies of size-structured predator-prey interactions.

When individual differences and developmental changes during life cycles are taken into account, the familiar ecological classifications of competition, predator-prey, etc. can break down. It is not uncommon for the nature of intra- and interspecific interactions to change, even reverse, over the course of an individual's life history. Werner & Gilliam (1984) document many examples of such "mixed" interactions (also see Werner (1988)). Individuals of different species may compete as juveniles, but interact as predator and prey as adults; juveniles of one species may be prey to the adults of another, who are in turn prey for the adults of their prey; competing adults can be predators on each others juveniles; etc. No model studies seem to have been made of such mixed interactions.

The attempt to connect the individual level to the population and community levels, i.e. to span the distance between the physiological and behavior characteristics of individual organisms and the dynamics of total populations, pose important and significant challenges to theoretical population dynamics and ecology. Some basic modeling methodologies have already been set forth in recent years. These methods provide mathematical descriptions of populations through dynamical equations based upon more fundamental submodels for vital individual level attributes such as birth (additions), death (removals), and growth rates (transition rates along structuring variables). What will be needed in future modeling investigations is careful attention to the derivation of these submodels with respect to the biological particulars of the species and circumstances of interest.

Mathematically, the challenge will be to analyze the complicated equations that arise from these models. This challenge can be met either by using familiar methods on these equations (linearized stability techniques, Liapunov functions, Hopf bifurcation theory, persistence theory, etc.); by developing analytic "tricks" to manipulate the equations into equations of more tractable form (ordinary or functional differential equations, integral equations, etc.); or by discovering altogether new analytical techniques. Numerical simulations are, of course, a powerful tool in indicating what possible dynamical properties solutions of equations have and will undoubtedly play an increasingly important role.

Models inevitably require simplifying assumptions. Successful modeling applications will involve a careful balance between biological detail and analytical tractability. Such successes, while of course not yielding an ultimate description of any biological problem, will provide insights into the implications of the particular modeling assumptions made and therefore further understanding of more extensive problems. Classical type models formulated at the population level probably have taken us about as far as they can, with their phenomenological character and many homogeneity assumptions. Further significant advances will come from allowing more heterogeneity in models, such as internal population structure due to differences in individual organisms.

Several advances will accrue from these efforts. Not only will more theoretical insights into the older accepted tenets of population biology will be gained (e.g. competitive exclusion, limiting similarity, etc.), but so will further corroboration and or even contradictions and modifications of these tenets. They will also permit the investigation of new phenomena that were not amenable to unstructured models (e.g. juvenile bottlenecks and other life history strategies, body size relationships to competitive and predation efficiencies, mixed species interactions, etc.). Structured models will better allow modelers and analysts to utilize the masses of biological data available on physiological properties of organisms in their models, something that has long been recognized as a shortcoming of the vast majority of models in population dynamics and ecology. This will in turn make the models less qualitative and more quantitative in their predictions. This increased predictive capability of structured models will make them considerably more useful than classical models in their use in today's critical environmental and medical problems.

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