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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

POPULATION DYNAMICS IN A SPATIALLY HOMOGENEOUS ENVIRONMENT

3. Continuous Models of Populations

4. Resource - Consumer Dynamics

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3. Continuous Models of Populations

3.0 Introduction to Exponential Growth

Let $x(t)$ denote the population size (or biomass) at time t; let b and d denote the birth rate and death rate respectively (that is, b is the number of births per individual per unit time interval and analogously for d) on the time interval $[t, t + \Delta t]$, $\Delta t > 0$

$$(3.1) \qquad x(t + \Delta x) - x(t) = b\, x(t)\, \Delta t + d\, x(t)\, \Delta t$$

Dividing by Δt in (3.1) and letting Δt approach zero, yields

$$(3.2) \qquad \frac{d\,x(t)}{dt} = r\, x(t)$$

where $r = b - d$ is the intrinsic growth rate of the population. The model (3.2) represents the traditional exponential growth $(r > 0)$ or decay $(r < 0)$ of a population. An important distinction between first order linear difference equations with constant coefficients and the analogous differential equation (3.2) is that (3.2) allows no oscillations. The deficiencies of (3.2) as a population model are delineated in Section 2.0.

3.1 A Density Dependent Growth Rate

In Section 2.1, for difference equations the assumption of density dependence was modelled by $r = r(x)$. The hypotheses that $r(x) \geq \delta > 0$ always leads to unbounded growth of the population while $r(x) < -\delta < 0$ always leads to extinction. As a canonical form for $r(x)$, the function represented by the graph in Figure 3.1 might serve as an initial approximation.

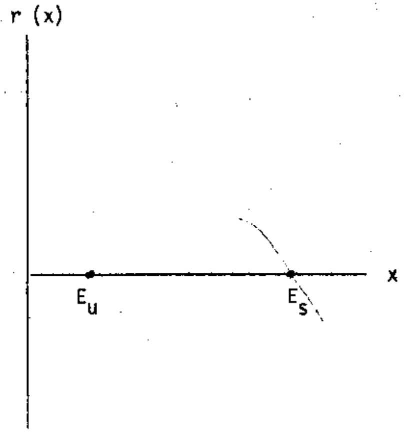

Fig. 3.1 The graph of a density dependent per capita growth rate.

It can be demonstrated by using linearization that the equilibrium E_u is unstable while the point E_s is locally asymptotically stable.

3.2 The Classical Logistic Equation

One of the first demographic studies that employed density dependent growth rates is that done by Pierre-Francois Verhulst (1838). In his book, G.E. Hutchinson (1978) eloquently presents the history of the logistic equation:

$$(3.3) \qquad \frac{dx}{dt} = r(x)x$$

where r is a linear function $r(x) = a - bx$. To try to improve any portion of that exposition is fruitless. We proceed directly to the theory of the equation (3.3). The traditional way of writing the logistic equation is with $r(x) = r_0 \, x \, (1 - \frac{x}{K})$ where r_0 (> 0) is the intrinsic growth rate and K (> 0) is called the carrying capacity of the population. When r_0 and K are constants, the equation may be solved by the variables separable method. This leads to

$$x(t) = \frac{K \, x_0}{x_0 - (x_0 - K) \, e^{-r_0 t}}$$

The geometrical structure of the positive quadrant of trajectories is given in Figure 3.1.

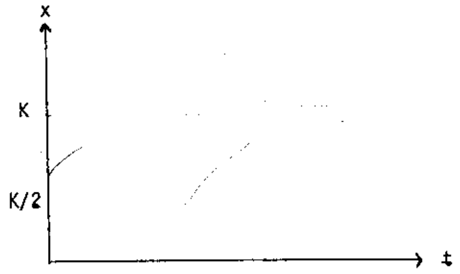

Fig. 3.1 Graphs of typical solutions of the logistic equation,
$\frac{dx}{dt} = x \, (r_0 - \frac{r_0 x}{K})$.

The solution approaches the carrying capacity, K, as t approaches infinity, independent of initial population size, x_0. The sigmoid behavior represented by the bottom trajectory in Fig. 3.1 occurs for those solutions with x_0 satisfying $0 < x_0 < K/2$ (K/2 is the ordinate at which any inflection point of a solution occurs). When x is small, the solutions exhibit exponential growth for a period of time, then density dependent effects take over and the population saturates at carrying capacity. This saturation effect occurs monotonically for all trajectories.

Many of the populations whose graphs are shown in Section 2 exhibit the sigmoid characteristics of the logistic trajectories (e.g. Figures 1.4-1.12). There are many hypotheses that a population must satisfy for the logistic model to serve as a valid model. Most of these are not valid for any population; nevertheless, the logistic remains the most widely used population model. Some hypotheses that are employed in formulating the logistic equation are given below.

1. Biotic and abiotic parameters are constant for all time. Birth and death rates are affected by many exogenous factors and will tend to vary with these effects so a constant intrinsic growth rate and carrying capacity will not reflect this time variation.

2. Stochastic events are not considered in the model (of course not - it is a deterministic model).

3. All individuals of the population are treated equivalently. They are not differentiated by sex, age, social role, or physical location. This ecological homogenity is probably not valid for any population.

4. The per capita growth rate responds instantaneously to changes in density. The assumption that no time delays occur in any process is probably invalid as well.

5. Resources are nonexpendable or are continuously renewed.

Each of these general objections to the logistic can be overcome through modification of the model. There are other changes that also need to be implemented. For example, if r is not restricted to be positive, weird things can happen; when r is negative, any solution with $x_0 > K$ is unbounded. How can a population, which cannot survive under ideal conditions of no intraspecific competition, $(r_0 < 0)$ thrive and explode when the density dependence is strong? The logistic equation presents one way but, from a modelling perspective, it is not a feasible one.

The logistic equation has provided motivation for some of the early theoretical developments in evolutionary ecology. The idea of r- and K-selection are in direct reference to the parameters of the logistic equation (Roughgarden, 1979). Theoretical developments direct from this classical form of the logistic equation are frought with difficulties. These difficulties are explored in Section 3.4 on the non-autonomous logistic equation.

3.3 The Logistic Equation with Harvesting

Suppose there is an exogeneous force which removes members of a population at a constant rate h. This physical process is called harvesting and can, for example, be effected by hunters or fisherperchildren. If the population is governed by the logistic equation the model is (3.3) with harvesting included:

$$(3.4) \qquad \frac{dx}{dt} = x\,(a - bx) - h$$

Harvesting models have played an important role in the management of renewable resources (C. Clark, 1976) and are developed later by Dr. J. Conrad in these notes.

Equation (3.4) can be analyzed by employing a stability analysis. The equilibria are given as roots of $b\,x^2 - a\,x + h = 0$. The roots of this equation, x_*, x^* are real if and only if h satisfies the inequality $0 \leq h \leq a^2/4b$. The smaller root $x_* = [\,a - (a^2 - 4bh)\,]^{\frac{1}{2}}/\,2b$ is unstable and the root $x^* = [\,a + (a^2 - 4bh)^{\frac{1}{2}}] / 2b$ is asymptotically stable. The solution space of (3.4) has a configuration given in Figure 3.2.

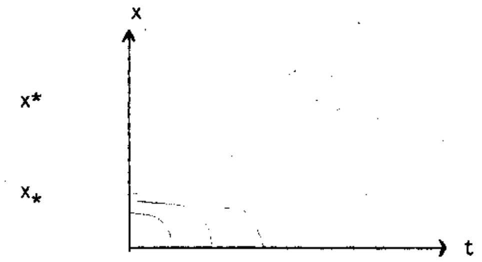

Fig. 3.2 The solution space of the logistic equation with harvesting.

The model has a threshold of extinction (x_*) below which extinction occurs in a finite time. If the initial population exceeds this threshold, the solution, $x(t)$, approaches the equilibrium population, x^*, as t tends to infinity.

Much will be said later about this situation but one concluding remark is given here. When the harvesting rate exceeds the critical value $h = a^2 / 4b$, extinction results independent of the initial population; hence, if (3.4) is biologically meaningful there is a critical harvesting rate. Certainly, for values of the harvest rate parameter near critical value, the model is interesting both from a mathematical and a bioeconomic viewpoint.

A discussion of this situation and an interesting application may be found in Brauer 1976.

3.4 The Nonautonomous Logistic Equation

Nearly Constant Coefficients

An hypothesis of the classical logistic model is that the ecology of the population is constant. The time-varying version of the logistic equation is

$$(3.5) \qquad \frac{dx(t)}{dt} = r(t)\, x(t) \left[1 - \frac{x(t)}{K(t)} \right]$$

This equation is of Bernoulli-type and is solvable in closed form if r and K are piecewise continuous on $\mathbb{R}_+ = [o, \infty)$. The solution of (3.5) which passes through (t_o, x_o) is

$$(3.6) \qquad x(t, t_o, x_o) = \frac{x_o \exp\left[\int_{to}^{t} r(s)\, ds \right]}{1 + x_o \int_{to}^{t} \exp\left[\int_{to}^{s} r(s_1) ds_1 \right] \frac{r(s)}{K(s)}\, ds}$$

When r and K satisfy the inequalities

$$(3.7a) \qquad 0 \le r_* \equiv \inf_{t_1 \in \mathbb{R}_+} K(t) \le K(t) \le K^* \equiv \sup_{t_1 \in \mathbb{R}_+} K(t) < \infty$$

$$(3.7b) \qquad 0 \le K_* \equiv \inf_{t_1 \in \mathbb{R}_+} K(t) \le K(t) \le K^* \equiv \sup_{t_1 \in \mathbb{R}_+} K(t) < \infty$$

then the asymptotic behavior of (3.5) is much like the logistic with constant ecology (Coleman, 1979). There exists a solution of (3.5)

$$\tilde{x}(t) = \left[\int_0^{\infty} \exp\left[- \int_0^{s} r(t - \gamma) d\gamma \right] \frac{r(t - s)}{K(t - s)}\, ds \right]^{-1}$$

that is globally asymptotically stable. The solution $\tilde{x}$ depends upon the complete past history of r and K. If r and K are periodic then so is $\tilde{x}$.

A Deteriorating Environment

The behavior of the nonautonomous logistic equation is not always similar to the classical logistic model. This can be demonstrated by considering the deteriorating environment situation.

A deteriorating environment is modelled here by functions K with the properties that $K > 0$ on $\mathbb{R}_+$ and $\lim_{t \to \infty} K(t) = 0$. For convenience of illustration, assume for the present that $r > 0$ on $\mathbb{R}_+$.

Remark 1. If $\int^{\infty} r(s)ds = \infty$ then each solution of (3.5) satisfies $\lim_{t \to \infty} x(t,t_0,x_0) = 0$. Hence, a relatively large growth rate coupled with a deteriorating environment causes a population to track its environment to extinction. This plausible and expected result can be demonstrated directly from (3.6) by using L'Hospitals Rule.

Remark 2. If $\int_0^{\infty} r(t)dt < \infty$ then each solution of (3.5) converges; that is, $\lim_{t \to \infty} x(t, t_0, x_0) = x_\infty$. This result is valid even without the deteriorating environment hypothesis. In the case that K is constant, it can be shown that given any terminal value x_∞, with $x_\infty < K \{ 1 - \exp [-\int_{t_0}^{\infty} r(s)\, ds] \}^{-1} \equiv M$. Hence, if $\int_{t_0}^{\infty} r(s)ds$ is sufficiently small, M can be arbitrarily large and K is exceeded by the limit of any solution that is initially above K. For a deteriorating environment, there exist cases where the terminal value of every solution of (3.5) exceeds the terminal density of the carrying capacity.

If one attempts to interpret the above comments biologically, the following puzzle arises. A growth rate that is large can lead to extinction while a small growth rate can result in persistence independent of initial population (and can lead to large terminal densities which exceed the terminal values of the carrying capacity). By interpreting r as the growth rate of the population in the absense of environmental stress, a situation arises where a population, because of a small intrinsic growth rate, is barely able to persist under the best of conditions. However, it is able to survive and even flourish in an intolerable environment. These conclusions again vividly indicate the inadequacy of (3.2) as a model of logistic growth. The difficulties here are easy to bypass in that a proper parameterization of the logistic equation does not lead to these dilemmas.

3.5 A Modified Logistic Equation

Modelling deficiencies of the classical logistic equation [(3.5), with constant coefficients], are promulgated by the role of both model parameters r and K. The model defects in the previous section are consequences of the domination of the intrinsic growth rate r in the equation. An equation, of modified logistic type, which does not allow solution behavior to be subjugated by r is

$$(3.8) \qquad \frac{dx(t)}{dt} = x(t)\left(r - \frac{c}{K}x(t)\right).$$

In equation (3.8), the intrinsic growth rate, r, is expressed in units $(\text{time})^{-1}$ as is the positive parameter c. This new independent parameter c is a measure of the population response to environmental stress as represented by the ratio x/K.

A problem with the parameter K in the classical logistic equation is that it can be ambiguously interpreted as either a population carrying capacity or a steady state of the population. Since these interpretations need not be equivalent, it is convenient to reformulate the model as

$$(3.9) \qquad \frac{dx(t)}{dt} = x(t)\left[r(t) - c\frac{x(t)}{B(t)}\right]$$

where B denotes the maximum population which the environment can support; that is, the environment can provide all necessary requirements for the maintenance of B individuals but it will not support $B + 1$ individuals. When r and B are constants, equation (3.9) has a stable equilibrium at $x = rB/c$. This motivates the definition of the (ultimate) population level parameter K as

$$(3.10) \qquad K = \begin{cases} rB/c & \text{if } r > 0 \\ 0 & \text{if } r \leq 0. \end{cases}$$

It must be the case that $r \leq c$ in equation (3.9). For species that have evolved in a manner which allows the population to exploit the full potential of the environment, one would expect to have $K = B$ and $r = c$; that is, the traditional logistic equation is applicable.

Equation (3.9) can be shown to palliate some of the modelling difficulties associated with the classical logistic equation as it yields plausible results in many instances where the traditional logistic does not. For example, when $r < 0$, all solutions of the autonomous equation (3.9) approach zero as t approaches infinity while for the logistic some solutions blow up in a finite time.

In the nonautonomous case, it can be shown that the undesirable attributes exhibited in the deteriorating environment setting no longer hold (Hallam and Clark, 1982). For example, either a deteriorating growth rate or a deteriorating environment assures extinction of the population.

There have been many who criticize the logistic equation for its deficiencies (e.g. Gray, 1929; Kavanagh and Richards, 1934; Andrewartha and Birth, 1945; Pielou, 1977; Murray, 1979). However, despite the criticisms and obvious deficiencies, the equation continues to be the most frequently used continuous deterministic model of single species population growth in a limited environment. Its advantages are its analytical simplicity, the elementary interpretation of its biological parameters, and the fact that it often can be fit to data.

The reparameterization suggested in (3.9) might prove beneficial for modelling populations with small growth rates or where the environment is changing in an unfavorable manner.

3.6 What Should a "Discrete" Logistic Model Look Like?

A comparison between the discrete logistic equation and the classical logistic equation indicates that the behaviors are considerably different. To find a difference equation that has the same behavior as the logistic, E.C. Pielou (1979) starts with the solution

$$x(t) = \frac{Kx_0}{x_0 - (x_0 - K)e^{-r_0 t}}$$

and considers this as the solution to the desired difference equation:

$$y_n = \frac{K}{1 + c\lambda^{-n}} \qquad (\lambda = e^{-r_0})$$

It can be shown that

$$y_{n+1} = \frac{\lambda y_n}{1 + \frac{\lambda - 1}{K} y_n}$$

This equation has a behavior that is similar to the traditional logistic equation.

3.7 Density Dependent Representations

Smith's Modification of the Logistic Model.

The per capita growth rate of the logistic equation is a linear function of the population density. F. E. Smith (1963), studying a population of Daphnia magna by an elegant set of experiments found that his data did not support the linearity hypothesis (Figure 3.3).

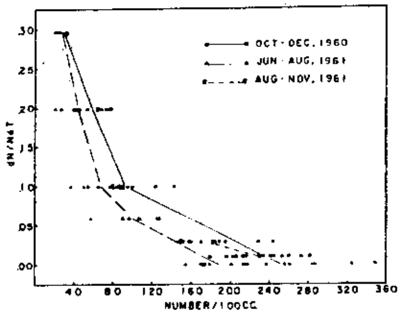

Fig. 3.3 Observed densities of D. magna at various specific rates of growth, using number of individuals as the measure of density. Data are combined from three sets of experiments.

To find an adequate model, Smith argues as follows. The classical logistic equation contains the assumption that the growth rate is proportional to $(K - x)/K$, the proportion of maximal attainable population size still unrealized. This seems somewhat unrealistic and it might be more appropriate to have a growth rate that depends on the proportion of some limiting factor not yet consumed. A natural candidate for a limiting factor is the food supply not yet utilized. The hypothesis employed by Smith is that the per capita growth rate of a population is proportional to the rate of food supply not momentarily being used. This results in the model:

$$\frac{1}{x}\frac{dx}{dt} = r\left(1 - \frac{F}{T}\right),$$

where F is the rate at which a population of biomass x consumes resources, and T is the rate at which the population uses food when it is at the equilibrium K.

At this point, it is prudent to observe that this model shares some modelling difficulties whth the logistic equation. The proportionality constant factor r can result in false feedback when r is negative or in suspecious behavior if r is close to zero. Hence we assume that the per capita growth rate is a linear function of the ratio of the rates F/T; consequently,

$$(3.11) \qquad \frac{1}{x}\frac{dx}{dt} = a - b\,\frac{F}{T}\,.$$

The rates of comsumption, F and T, depend, at least, upon the population biomass and upon the rate at which the population is growing. As a first approximation, let $F = c_1 x + c_2 \frac{dx}{dt}$. Since T is the rate of consumption at equilibrium K, $T = c_1 K$. Substitution of these values into (3.11) gives

$$\frac{1}{x}\frac{dx}{dt} = a - b\,\frac{\left(c_1 x + c_2 \frac{dx}{dt}\right)}{c_1 K}$$

Simplifying the equation results in

$$\frac{dx}{dt} = x\left[\frac{a - \frac{b}{B}\,x}{1 + \frac{bc_2}{c_1 B}\,x}\right]$$

This formulation, in an analoguous manner to the logistic, yields a population carrying capacity K defined by

$$K = \begin{cases} \frac{aB}{b} & \text{if } a > 0 \\ 0 & \text{if } a \leq 0 \end{cases}.$$

It can be readily demonstrated that each solution of this model approaches K as t tends to infinity.

This model emphasizes a new saturation aspect to the role of density dependence in the theory of populations. There are in the literature many other representations of the per capita growth rate that reflect effects of density dependence. These include:

1. B. Gompertz (1825) used

$$r(x) = cx(\ln \frac{B}{x}).$$

2. M. Rosenzweig (1971) used

$$r(x) = cx((\frac{B}{x})^{-g} - 1), \quad 0 < g \leq 1.$$

3. Goel, Maitra, and Montroll (1971) use the negative of Rosenzweig's model:

$$r(x) = 1 - (\frac{N}{B})^{g}, \quad 0 < g \leq 1.$$

4. T. Schoener (1973) takes $g = -1$ in the above formulation of Rosenzweig.

Resource - Consumer Dynamics

4.0 Introduction

The quantity and quality of a population's resources determine many aspects of the growth of the population. Of the population models described previously, only the Smith model makes any pretence to explicitly consider the food supply as an important parameter. In this section, we will explore the dynamics of resource - consumer interactions from a modelling perspective.

First, some general principles that govern most resource - consumer relationships are indicated.

1. When a resource is rare relative to the magnitude of the consumer population, the rate of consumption should be determined solely by the amount of available resources.

2. When the resource is abundant, the rate of consumption is determined solely by the density of the consumer population.

3. When the resource is neither rare nor abundant, the rate of consumption is a function of both the amount of available resources and the density of the consumers.

4.1 A Model of a Resource - Consumer Interaction

Gallopin (1971) developed a rudimentary model that utilizes some of these principles to describe a single dynamic resource and a consumer population.

The Resource, A.

The exogeneous rate of input of resource into the system is assumed to be $f(t)$; actually, in the analysis, f is taken to be constant. The amount of available resource A is, by a conservation of mass, the difference between the resource that has entered the system and the resource that has been ingested by consumers. It is assumed that the excreted resource is not available for consumption.

The ingestion rate, c, should be a function of the amount of available food A; some measure of the population, either density or biomass, M; the rate of change of the population (growing organisms consume more resources per unit mass than nongrowing ones); and, perhaps, other factors. Thus,

$$c = c(A, M, \frac{dM}{dt}, \ldots)$$

In order to further specify c, it is convenient to introduce the parameter a, the ingestion rate per unit mass which corresponds to maintenance at complete satiation. If a population is satiated, an increase in food supply will not increase the ingestion rate. However, if the population is hungry, an increase in food will produce a significant increase in the ingestion rate. It is assumed that the change in the ingestion rate per unit change in available food is proportional to the hunger of the population:

$$\frac{\partial c}{\partial A} = h(M,A)\ (aM - c). \tag{4.1}$$

The proportionality parameter h depends only upon biomass M and available resources A. Note aM is the total ingestion rate at satiation. A choice of h that results in many desirable properties of resource - consumer systems is that made by Gallopin $h = \alpha/M$. For example, an increase in A has a greater effect on consumption when M is small than when M is large. Equation (4.1) with $h(A,M) = \alpha/M$ (in fact, for arbitrary h) is solvable as a first order differential equation in c; for $M > 0$, this yields

$$c(A,M) = aM + K(M)\exp(-\alpha A/M)$$

where $K(M)$ is a constant of integration that may depend upon M (because the integration is with respect to A). Since $c(0,M) = 0$ for all $M > 0$, $K(M) = -aM$; hence

$$C(A,M) = aM(1 - \exp(-\alpha A/M)) \tag{4.2}$$

This formulation for rate of consumption has the following properties:

1. When food is abundant (A large) the ingestion rate is a function of M only: $\lim_{A\to\infty} C(A,M) = aM$.

2. When resources are scarce (A small) the ingestion rate is small: $\lim_{A\to\infty} C(A,M) = 0$.

3. When population biomass is small, the consumption rate is also: $\lim_{\substack{M\to 0\\ A\neq 0}} C(A,M) = 0$.

4. When the biomass is very large, consumption rate will be proportional to available food: $\lim_{M\to\infty} C(A,M) = a\,\alpha\,A$.

Population Dynamics:

Conservation of mass implies that

$$(4.3) \qquad \frac{dM}{dt} = c(A,M) - \lambda(A,M)$$

where λ represents the losses of resource from the population. The losses include egestion, respiration, excretion, and mortality.

The following hypotheses are imposed. Egestion rate is proportional to consumption rate. The totality of the remaining losses are required to be proportional to the population biomass. The equation (4.3) with these hypotheses imposed becomes

$$(4.4) \qquad \frac{dM}{dt} = (1 - u)c + kM = Bc + kM$$

The conservation of mass law can be used to find a dynamic equation for A:

$$\frac{dA}{dt} = f - c$$

When (4.2) is substituted in (4.4) the differential equations become a coupled system for A and M:

$$(4.5) \qquad \frac{dM}{dt} = BaM(1 - \frac{k}{Ba} - \exp(-\alpha A/M))$$

$$\frac{dA}{dt} = f - aM(1 - \exp(-\alpha A/M))$$

The system (4.5) can be analyzed by analytical methods if $f(t) \equiv f_o$ is a positive constant. There exists an equilibrium

$$(4.6) \qquad M_o = \frac{\beta f_o}{k}$$

$$A_o = \frac{-\beta f_o}{k\alpha} \ln(1 - \frac{k}{a\beta})$$

provided $k < a\beta$. If $k > a\beta$ then no (positive) equilibrium exists and extinction may be demonstrated by use of the comparison principle for differential inequalities (Lakshmikantham and Leela, 1969) applied to the M-equation in (4.5). The parameter k is a maintenance cost per unit mass of the population; extinction results if the maintenance cost exceeds the assimilation rate per unit mass ($a\beta$). [Most ecologists could have told us this before the mathematics started].

Persistence can occur for the population whose dynamics are modelled by (4.5). A linearization shows that the equilibrium (4.6) is locally asymptotically stable if and only if $k < a\beta$.

The Dulac-Bendixson Nonexistence Criteria (with auxiliary function M^{-1}) can be used to demonstrate that no limit cycles exist for (4.5). Consequently, by the Poincaré-Bendixson Theorem, (A_0,M_0) is globally asymptotically stable.

There is a relationship between the hypotheses of the model of Smith (Section 3.7) and this one in that both formulations are concerned with consumption rates at a variable density and at equilibrium or satiation.

4.2 Other Model Mechanisms for Feeding Relationships

Representations without Consumer Interference Mass Action.

Among the earliest modelling efforts devoted to feeding mechanisms were important contributions of A. Lotka, an American biologist, and V. Volterra, an Italian mathematician. They assumed that the ingestion rate, F, is proportional to the product of the magnitudes of consumer density, x_c, and resource density, x_r:

$$F = f\, x_c\, x_r.$$

One criticism of this feeding representation is that when the resource is abundant, the rate of consumption does not depend solely upon the consumer population. Holling (1959) overcomes this objection by maintaining the linear response for low density resource but imposes at saturation effect for large densities (Figure 4.1).

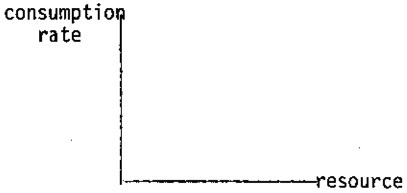

Fig. 4.1 A linear functional response (Holling).

Hyperbolic Responses

In a model of a fishery V. S. Ivlev (1961) used a formulation that allowed consumers to feed at a mass rate when food is abundant:

$$F = f x_c (1 - e^{-\gamma x_r})$$

The models of Monod (1949), Watt (1959), and Holling (1959) all relate to the formulation

$$F = f \frac{x_c x_r}{c + x_r}$$

This representation is referred to as a Michaelis-Menten-Monod formulation (M^3 for short; M^2 got into the act from enzyme kinetics).

Sigmoid Responses

Holling (1959), Murdoch and Oaten (1975) describe a sigmoid type functional response.

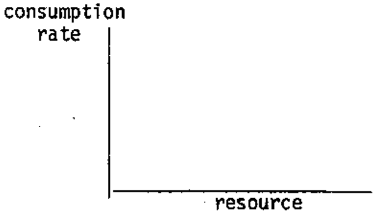

Fig. 4.2 A sigmoid response for resource-consumer interactions

The hyperbolic response seems to be most prevalent and occurs in some insects, some invertebrates (snails on mussels, starfish on snails) and some vertebrates (carp on bream roe); see Murdoch and Oaten (1975). Some phytoplankton respond in this way to various nutrients (Frost, 1974).

The sigmoid response has been observed in some parasitic insects and some vertebrates (deermouse on sawfly pupae). Hassell (1977) argues that this type of response is more common than originally believed.

The linear response type is claimed to occur for some invertebrates (crustacea on algae or yeast) although it is difficult to differentiate data fits to the linear response and the hyperbolic response.

4.3 Representations with Consumer Interference

Situations can occur in which consumer density increases but the feeding rate does not increase proportionately because of mutual interference between consumers. Consumption efficiency must decrease in these settings. Salt (1967, 1974), in studies of the effects of the ciliate Woodruffia metabolica, on the species Paramecium and Didinium nasutum on Paramecium aurelia, found that feeding rates per unit consumer F/x_c react strongly to changes in density of consumers. Hassell (1971) has demonstrated that the searching effeciency of the insect parasite Nemeritis canescens decreases at high parasite densities.

With these examples in mind, DeAngelis, Goldstein, and O'Neill (1975) suggest that F/x_c should depend upon x_c and propose a consumption formulation of

$$F = \frac{fx_rx_c}{b + x_c + dx_r}$$

It should be recalled that Gallopin's formulation also has this consumer-interference feature with his formulation

$$F = ax_c(1 - e^{-\alpha\frac{x_r}{x_e}}).$$