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Mathematical Models of Predator/Prey/Plant Interactions in a Patch Environment

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ABSTRACT

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Several tritrophic systems are characterized by local over-exploitation of the food source. Interactions between predatory mites, spider mites and their host plants are an example of such systems: either the spider mites over-exploit local patches of host plants or the spider mites are exterminated by predatory mites. It is often stated that modelling the overall population dynamics of such systems in a realistic way would soon lead to an unmanageable edifice. We advocate, however, the use of physiologically structured population models as a both general and formal mathematical framework. The advantage is that analytically tractable models may be obtained from the complex 'master' model by time-scale arguments or special choices of model ingredients. In this way a network of models can be derived, each concentrating on a particular aspect, all inadequate to cover the entire spectrum, but together (we hope) providing a coherent set of insights the relative importance of which can be assessed by computer experiments on the 'master' model.

In this paper a rather realistic model of predator/prey interactions in an ensemble of host-plant patches is presented and, as an example of our approach, some special cases are derived from that model. Their analysis provided some first, useful insights. It is shown that prolonged duration of the prey-dispersal phase and prey dispersal from predator(-invaded prey) patches may result in a stable steady state, whereas a humped plant-production function may — under certain conditions — result in two stable steady states.

INTRODUCTION

To incorporate the inherent nonhomogeneous character of space and time in dynamic population models, one needs a mathematical language that is rich enough to allow for the translation of verbal descriptions of the relevant bio-

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logical processes into mathematical equations. In this paper we concentrate on a tritrophic system consisting of host plants, spider mites and predatory mites, and our aim is to exploit the framework of *physiologically structured population models* (Metz and Diekmann, 1986; the adverb 'physiologically' is used to indicate that we are dealing with structuring variables which are somehow 'internal' to the individuals making up a population, as opposed to 'external' variables characterizing, for example, the environment to which the individuals are exposed) to describe the interaction of phytophages and their natural enemies in an ensemble of local patches. Even though the patches reflect the *spatial* inhomogeneity of the lowest trophic level (i.e. the geographical distribution of plants) we shall not introduce spatial structure explicitly, but only deal with the subdivision of the population into local colonies. The key idea here is to consider the local colonies as 'individuals' characterized by such quantities as the available amount of food (or leaf area), the number of spider mites, and the number of predatory mites. Such 'individuals' will beget offspring since spider mites disperse and found new colonies in suitable patches whereas predatory mites disperse to invade spider-mite colonies (we shall introduce auxiliary variables to describe the aerial plankton consisting of searching spider and predatory mites). Such 'individuals' will grow (or shrink) since local densities change in the course of time according to food/prey/predator–interaction equations; thus one obtains a rather complicatedly structured population model.

Population models range from overly simplified, qualitative, ordinary differential equations to extremely complicated quantitative simulation models and, likewise, the group of population modellers is subdivided in categories. Communication between exponents of different categories usually is frustrated by the lack of a common language. The point of view advocated in this paper is that physiologically structured population models may serve as such a common language. On the one hand, one may implement the more comprehensive versions on a computer, choose parameter values and initial conditions, and simulate. In fact, many of the usual large simulation models are essentially crude implementations of structured population models. (Recently, De Roos (1988) has developed a numerically more sophisticated method for solving general structured population equations.) On the other hand, one may exploit special choices of model ingredients as well as time-scale arguments to derive stripped versions which one can analyse with pencil and paper or relatively simple computer programs. Thus one obtains networks of models, and qualitative insights derived from the simplest elements may be used to direct quantitative simulation studies and to guide the interpretation of the outcome of such studies.

This paper is a progress report on a joint research project which is far from finished. The paper of Sabelis and Laane (1986), presenting a simulation study of the regional dynamics of spider-mite populations that become extinct locally because of food source depletion and predation by phytoseiid mites, served as a starting point. An error in the implementation of the functions calculating the probability of predator invasion into a prey patch invalidates the simulation results reported in that paper.

In the following section we present a verbal description of the various processes that are to be considered, and in the next section we carry out the translation into mathematical equations (which automatically involves further specification and elaboration). Then we introduce, by means of some examples, the two main means of model simplification: (1) the choice of special submodels for which it just happens that the overall dynamics can be summarized by only a few variables; and (2) time-scale arguments. Subsequently, we reduce the full model to a system of three ordinary differential equations and show the stabilizing influence a prolonged prey-dispersal phase. We next demonstrate, in the context of another simplified model, the stabilizing influence of prey dispersal from predator-invaded patches. Finally, we use a third simplified model to call attention to the possibility that multiple stable steady-states may occur when regeneration of plant biomass becomes a limiting factor, a phenomenon which may have some relevance for biological control.

This paper does not survey existing knowledge derived from prey/predator/patch models (see Nachman, 1988, this volume). Neither does it claim to add substantially to such knowledge. Our chief aim is to introduce structured population equations as a modelling tool and to demonstrate the flexibility of this tool by means of some examples (see also Edelstein-Keshet (1986)).

INVENTORY OF RELEVANT PROCESSES

Consider a prey population consisting of many local colonies. The following processes are responsible for changes in the number of such colonies:

new colonies are founded by emigrants from existing colonies invading 'empty' patches;

colonies come to an end when the local food source is over-exploited; and

predator invasion will, after a while, lead to prey extermination.

The process of invasion by prey removes 'empty' patches available for colonization. We shall assume that these patches are replenished by some intrinsic dynamics. In the special cases discussed below, we shall also make specific assumptions about the replenishment process. Our terminology in describing the interpretation of empty patches is deliberately vague. Depending on the spatial scale under consideration, one may conceive of them as leaves, single plants or clusters of plants. Even though the numerical values of parameters may depend on the case at hand, the mathematical structure of the equations does not.

The invasion of a predator brings about an abrupt change in the 'state' of a local colony. When the local prey are extinct, all remaining predators disperse in search for other prey colonies.

So, apart from the usual processes in a system with three trophic levels: (1) food dynamics; (2) prey increase at the expense of food; and (3) predator increase at the expense of prey, we have to account for: changes in the number of uninhabited food patches (host plants); dispersal, i.e. the tendency to disperse, and survival of aerial plankton; foundation of prey colonies; and predator invasion in prey colonies. We illustrate these processes in Fig. 1.

Our ideal is to answer the following general question: how do all these factors contribute to the dynamics of the global populations, conceived as an ensemble of local subpopulations? Our motivation partly derives from biological pest control where, in particular, one wants to know whether the system: (a) will have a stable steady state (with, preferably, the prey at a very low level); or (b) will exhibit wild oscillations leading to global extinction either of the predator or of both the prey and the predator; and (c) how the answer to this question depends on the various factors involved.

A fundamental dilemma presents itself: in how much detail do we have to model the various processes mentioned above? Our strategy will be to neglect this dilemma to some extent: we build a relatively detailed and complicated master model and then discuss various simplified versions obtained by i.a. timescale arguments. However, both for the sake of simplicity and for the sake of exposition, we shall from the very beginning model rather superficially both the food biomass growth within a host-plant patch as well as the creation of new uninhabited patches of host plant; the same holds for the survival of the aerial plankton.

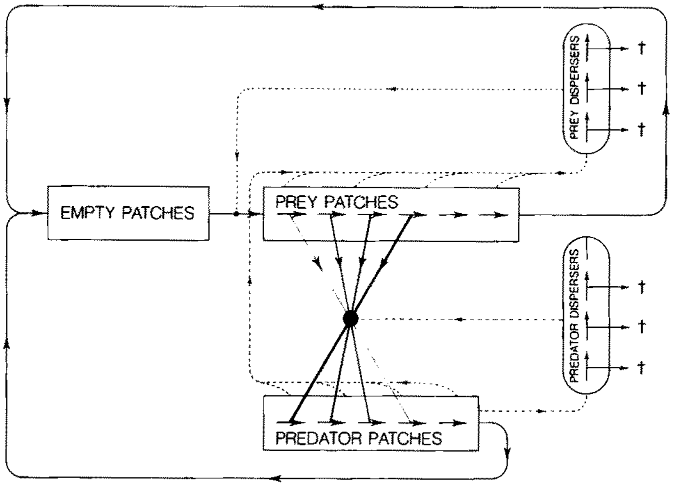

Fig. 1.Flow diagram of relevant processes.

TRANSLATION INTO MATHEMATICAL LANGUAGE

We first concentrate on patches in which only prey are present. Let x denote the number of prey in such a patch. We introduce a density function $n(t,x)$ such that the number of prey patches at time t with prey population level between x_1 and x_2 is given by

$$\int_{x_1}^{x_2} n(t,\xi)\mathrm{d}\xi$$

For instance, $\int_0^\infty n(t,\xi)\mathrm{d}\xi$ is the total number of prey patches at time t.

As an idealization, assume that the local food availability is either a fixed constant (in space and time) or zero (so we imagine over-exploitation as an instantaneous and complete 'crash' of the host plant; before the crash the rate at which individual prey consume food is constant; after the crash this rate is zero). Let $v(x)$ denote the rate at which a local prey population of size x increases in the presence of food and the absence of predators. If we follow any particular prey patch, its x-variable changes according to the ordinary differential equation $\mathrm{d}x/\mathrm{d}t=v(x)$. Bookkeeping arguments (see Metz and Diekmann (1986) p.15 and pp. 92–96) then show that the process of growth of local prey colonies contributes a term $-\frac{\mathrm{d}}{\mathrm{d}x}(v(x)n(t,x))$ to the rate of change of $n(t,x)$; that is

$$\frac{\mathrm{d}n}{\mathrm{d}t}(t,x)=-\frac{\mathrm{d}}{\mathrm{d}x}(v(x)n(t,x))+...$$

At $x=1$ we have an influx of newly founded colonies. Let $n_0(t)$ denote the number of suitable empty patches at time t and let $P(t)$ denote the number of potential prey colonists around at time t; then, assuming mass action kinetics, the rate at which new prey colonies are founded is given by

$$\zeta n_0(t)P(t)$$

where ζ denotes a 'reaction' constant. The flux away from $x=1$ is given by $v(x)n(t,x)$, the product of the 'velocity' v and the density n. Consequently, the founding of new prey colonies is described by the boundary condition

$$v(1)n(t,1)=\zeta n_0(t)P(t) \tag{1}$$

Let us, for the time being, leave the possibility of over-exploitation of the host plant out of consideration, and concentrate on predator invasion only. Let $Q(t)$ denote the number of potentially invading predators around, then the rate at which prey colonies of size x are invaded is, again assuming mass action kinetics, given by $\eta(x)Q(t)n(t,x)$, where the 'vulnerability' η is an x-dependent reaction coefficient describing how attractive (or, conspicuous) a prey patch of size x, is; hence

$$\frac{\mathrm{d}n}{\mathrm{d}t}(t,x)=-\frac{\mathrm{d}}{\mathrm{d}x}(v(x)n(t,x))-\eta(x)Q(t)n(t,x) \tag{2}$$

Any invaded prey patch becomes a (prey/)predator patch. To describe such patches we introduce y, the number of predators, as another state variable and we define the density function $m(t,x,y)$ such that

$$\int_{x_1}^{x_2}\int_{y_1}^{y_2} m(t,x,y)\mathrm{d}y\mathrm{d}x$$

equals the number of predator patches with predator level between y_1 and y_2 and prey level between x_1 and x_2. Let $g(x,y)$ and $h(x,y)$ be such that for any particular predator patch

$$\frac{\mathrm{d}x}{\mathrm{d}t}=g(x,y),\quad \frac{\mathrm{d}y}{\mathrm{d}t}=h(x,y) \tag{3}$$

In other words, g and h describe the local prey–predator interaction. (Note that by definition $v(x)=g(x,0)$.) The (assumed) fact that the number of predator patches changes only due to influx at the 'invasion' boundary $y=1$ (and outflux at the 'extermination' boundary $x=0$) is expressed by the conservation law

$$\frac{\mathrm{d}}{\mathrm{d}t}m(t,x,y)+\frac{\mathrm{d}}{\mathrm{d}x}(g(x,y)m(t,x,y))+\frac{\mathrm{d}}{\mathrm{d}y}(h(x,y)m(t,x,y))=0 \tag{4}$$

and the boundary condition

$$h(x,1)m(t,x,1)=\eta(x)Q(t)n(t,x) \tag{5}$$

The system (3) defines curves in the (x,y)-plane and individual predator patches follow such curves (Fig. 2). The observation that the predators drive their prey locally to extinction translates into the assumption that these curves connect the invasion boundary $y=1$ with the extermination boundary $x=0$.

This completes our description of the dynamics of prey- and predator patches, but we have yet to specify the dynamics of the free patches n_0 and the aerial plankton variables P and Q.

For the dynamics of the number of suitable empty patches n_0 we can make various assumptions. We shall simply take n_0 to be constant, so here we ignore the possible lack of patches at which new colonies can be formed. This is justified whenever the predators keep the number of prey colonies at such a low

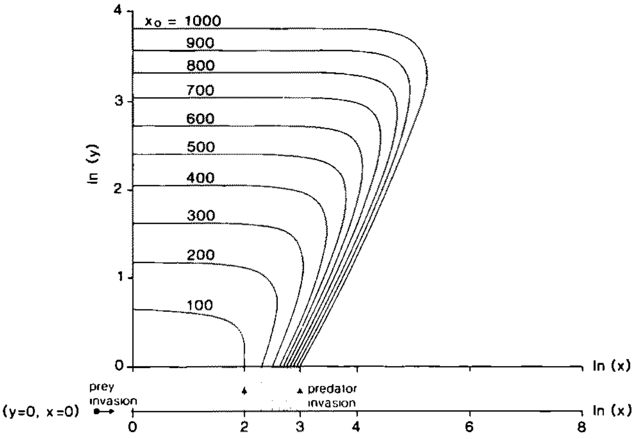

Fig. 2. The lower x-axis corresponds to prey population size on a logarithmic scale in the absence of predators. Note the jump from $x=0$ to $x=1$ representing prey invasion in an empty patch. The upper x-axis and the y-axis correspond to, respectively, prey and predator population size after predator invasion (both on a logarithmic scale). Note the jump from $y=0$ to $y=1$ representing predator invasion in a prey colony.
The curves in the $\ln x - \ln y$ plane are obtained by solving (3) for the special choice $g(x,y)=\alpha x-\beta y$, $h(x,y)=\gamma y$ with the (for spider and predatory mites) more or less realistic parameter values $\alpha=0.28$ day^{-1}, $\beta=20$ day^{-1} (prey/predator) and $\gamma=0.32$ day^{-1}.

level that the number n_0 of uninhabited host-plant patches remains effectively at the carrying capacity; in the next section (third limiting case) we use

$$\frac{dn_0}{dt}=f(n_0)-\zeta n_0 P \tag{6}$$

where f is , for example, the familiar logistic function: $f(n_0)=rn_0(1-\frac{n_0}{K})$.

It is perfectly possible to take the 'age' structure of the aerial plankton into account, where 'age' refers to the time elapsed since dispersal (see Metz and Diekmann (1986) p.122). But in this paper we just assume that all members of the aerial plankton are equivalent.

Let $\pi(x,y)$ denote the overall rate at which prey disperse from a given patch of prey size x and predator size y then we will take either

$$\frac{dP}{dt}(t)=\int_1^\infty \pi(x,0)n(t,x)dx+\int_0^\infty\int_1^\infty \pi(x,y)m(t,x,y)dydx-\mu P(t) \tag{7a}$$

where μ denotes a death rate or

$$P(t)=\frac{1}{\mu}\left(\int_1^\infty \pi(x,0)n(t,x)\mathrm{d}x+\int_0^\infty\int_1^\infty \pi(x,y)m(t,x,y)\mathrm{d}y\mathrm{d}x\right) \tag{7b}$$

which is the quasi-steady-state approximation to (7a) for both very large π and μ.

We assume (for simplicity) that predators remain in the patch until the very last prey individual is found, and then leave collectively. So the rate of production of predator aerial plankton equals the weighted (with weight y) outflux at the boundary $x=0$. Thus we obtain (note that $g(0,y)<0$!)

$$\frac{\mathrm{d}Q}{\mathrm{d}t}(t)=-\int_1^\infty yg(0,y)m(t,0,y)\mathrm{d}y-\nu Q(t) \tag{8a}$$

or

$$Q(t)=-\frac{1}{\nu}\int_1^\infty yg(0,y)m(t,0,y)\mathrm{d}y \tag{8b}$$

if we make a quasi-steady-state approximation.

In (7) and (8) we incorporate changes in P and Q due to 'landing' in suitable patches in the terms μP and νQ, respectively. So, in a sense, we assume random landing. Alternatively one may add terms like $-\zeta n_0(t)P(t)$ and

$-\int_1^\infty \eta(x)n(t,x)\mathrm{d}xQ(t)$ to, respectively, (7) and (8).

Along the same lines as followed above one may introduce the food (leaf area $\simeq$ host-plant biomass) in a given patch as another state variable z and work with densities $n_0(t,z)$, $n(t,x,z)$ and $m(t,x,y,z)$. In doing so one increases not only the generality but also the complexity of the model considerably. For the time being we have, therefore, abstained from describing local food dynamics. In particular we assume that all empty patches offer an identical prospect for the prey.

Strictly speaking, the aerial plankton Equations (7) and (8) should contain additional source terms corresponding to, respectively, prey and predators leaving crashing patches. As a consequence of our assumption that empty patches are identical, a prey patch will crash exactly when x reaches a certain level $x_{\max}$. This observation will be the basis for the alternative version of (7) which we shall use in Appendix II (but below we shall take $x_{\max}=\infty$ or, in other words, no crash at all). Of course there has to be a 'crash' boundary in the (x,y)-plane as well, corresponding to prey patches being invaded by a predator so late in their development that over-exploitation of the host plant cannot be prevented. To compute this resource-exhaustion boundary from a mechanistic submodel for food/prey/predator interaction may be rather difficult (see Metz and Diekmann (1986) p.82 for the simplest example). Here we do not go into such exercises but confine ourselves to remarking that the presence of a resource-exhaustion boundary yields a considerable complication.

Our modelling exhibits a strange but deliberate inconsistency. Whereas prey colony growth is described by a differential equation for a *continuous* variable x, the founding of the colony is described by a *discrete* change $x=0 \rightarrow x=1$. So we are not very precise about the short phase of colony up-building in which a more detailed demographic description involving age structure (and possibly stochastic effects) seems more appropriate. Yet such a more detailed description can in principle be incorporated in the present approach, by adopting the alternative parametrization of patches by the age of the colony and the age at the moment of predator invasion (see Metz and Diekmann (1986) pp. 110,111,136,137 and 345–375). We do not feel motivated to actually carry this out. A related point is that we have systematically neglected the effects of prey aerial plankton landing in prey or predator patches and of predator aerial plankton landing in predator patches The argument here is that, after a very short initial phase, population growth by reproduction is far larger than population growth by immigration.

The ideal is to understand the global dynamical behaviour of the presented model and, in particular, how this behaviour is affected by the various ingredients and submodels. In reality this is an impossible task since we are dealing with a nonlinear infinite dimensional dynamical system with many parameters; so we shall look for simplifications.

In three different limiting cases we shall investigate how the qualitative behaviour depends on the model parameters which are treated as constants. These constants may be considered as set by the species under consideration, the particular experimental arena, temperature, relative humidity etc.

SOME LIMITING CASES

The processes of dispersal, prey colony growth and local prey/predator interaction all have their characteristic time-scales, and these need not be the same. If some of these scales are widely different, we may use either quasi-steady-state approximations or neglect some of the delays between cause and effect to obtain less-complicated models. Moreover, even if these time scales are actually *not* very different one may still adopt the sound mathematical strategy of studying limiting special cases first before tackling the full problem. Most of the time, insight obtained from special simplified cases is of much help in the analysis of the general case. Last but not least, any qualitative understanding of close relatives of complicated models can be a key factor in the design and sensitivity analysis of computer experiments.

Instantaneous prey extermination after predator invasion

By way of example, assume that the time between predator invasion and prey extermination is negligible compared to the average time of dispersal and prey colony growth. Then we may forget about (4) and (5), drop the term involving m in (7), and describe the dynamics of Q by

$$\frac{\mathrm{d}Q}{\mathrm{d}t}(t) = \delta Q(t) \int_1^\infty x\eta(x) n(t,x)\,\mathrm{d}x - \nu Q \tag{8c}$$

where δ is the prey-to-predator conversion factor.

As a further simplification, we may consider the special case where both $\nu(x)$ and $\pi(x,0)$ are proportional to x and η is constant. More precisely, let us take

$$\nu(x) = \alpha x, \quad \pi(x,0) = \epsilon x \quad \text{and} \quad \eta(x) = \theta \tag{9}$$

If we now introduce

$$O(t) := \int_1^\infty x n(t,x)\,\mathrm{d}x \tag{10}$$

we can derive a *closed* system of ordinary differential equations for O,P,Q and n_0 (this is called linear chain trickery; see e.g. Metz and Diekmann (1986) IV.5). Indeed, if we multiply Equation (2) by x and integrate over x from 1 to ∞ we obtain, using integration by parts and the boundary condition (1),

$$\frac{\mathrm{d}O}{\mathrm{d}t} = \zeta n_0 P + \alpha O - \theta Q O \tag{11a}$$

while (7a) and 8c) can be rewritten as

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \epsilon O - \mu P \tag{11b}$$

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = \delta\theta Q O - \nu Q \tag{11c}$$

If we take n_0 to be constant the system (11a–c) has a unique nontrivial steady state given by

$$\bar{O} = \frac{\nu}{\delta\theta}, \quad \bar{P} = \frac{\epsilon\nu}{\delta\theta\mu}, \quad \bar{Q} = \frac{1}{\theta}\left(\alpha + \frac{\zeta n_0 \epsilon}{\mu}\right) \tag{12}$$

The stability of this steady state is determined by the position of the roots of the *characteristic equation*

$$\lambda^3+\lambda^2(\mu+\frac{\zeta n_0\epsilon}{\mu})+\lambda\nu(\frac{\zeta n_0\epsilon}{\mu}+\alpha)+\mu\nu(\frac{\zeta n_0\epsilon}{\mu}+\alpha)=0 \tag{13}$$

in the complex λ-plane. According to the Routh-Hurwitz criteria (see, for instance, May (1973) and Appendix II) all roots lie in the left half-plane and consequently the steady state (12) is *asymptotically stable.*

If both ϵ and μ are very large we may replace (11b) by the quasi-steady-state approximation $P=\frac{\epsilon}{\mu}O$. Effectively this amounts to the assumption that prey dispersal is instantaneous. As a result, (11) reduces to the two-dimensional system

$$\frac{\mathrm{d}O}{\mathrm{d}t}=O\{\frac{\zeta n_0\epsilon}{\mu}+\alpha-\theta Q\} \tag{14a}$$

$$\frac{\mathrm{d}Q}{\mathrm{d}t}=Q\{\delta\theta O-\nu\} \tag{14b}$$

which is precisely the familiar Volterra-Lotka system. The steady state of (14) is still given by (12) but the corresponding characteristic equation

$$\lambda^2+\nu(\frac{\zeta n_0\epsilon}{\mu}+\alpha)=0 \tag{15}$$

has two roots precisely on the imaginary axis implying that the system (14) is on the borderline of stability. Comparing (14) and (11) we therefore conclude that *a prey dispersal phase of non-negligible duration has a stabilizing effect on the global prey–predator interaction.* We can easily understand this result intuitively. Indeed, the prey dispersal phase acts as a temporary *refuge* since, during this phase the prey are, notwithstanding all kinds of other dangers (death of starvation, drowning etc.), safe as far as predation is concerned. We note that, in contrast, the predator dispersal phase acts as a destabilizing delay (compare the following subsection).

Constant interaction time, predator yield, vulnerability and prey dispersal rate

The prey/predator interaction time (i.e. the time between predator invasion and prey extermination), as well as the predator yield at the end of the interaction, depend on the prey colony size at the time of predator invasion. The precise form of this dependence is determined by the solutions of the ordinary differential system (3). The partial differential equation (4) adds to this no more and no less than the bookkeeping of the number of patches.

The interaction time and the predator yield are the relevant quantities and, if we make alternative assumptions for these, we may forget about (3) and (4). In this subsection we shall assume that both are constant, i.e. independent of the prey colony size at the time of predator invasion.

Under the above assumption, prey colony size is still relevant since it determines the vulnerability η, the prey dispersal rate π and, finally, whether or not the patch will crash. But if we assume that η is a constant, π is a constant π_1 for prey patches and a constant π_2 for predator patches, and that host plants are never over-exploited, the size of the prey colonies becomes totally irrelevant. We may then dispose of n and work with the total number of prey patches

$$N(t)=\int_0^\infty n(t,x)\mathrm{d}x \tag{16}$$

instead. Adopting, moreover, the quasi-steady-state approximations for P and Q we arrive at the system of differential delay equations

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t}&=\zeta n_0 P-\eta QN \\ P(t)&=\frac{1}{\mu}(\pi_1 N(t)+\pi_2 M(t)) \\ Q(t)&=\frac{\epsilon\eta}{\nu}Q(t-\tau)N(t-\tau) \\ M(t)&=\eta\int_{t-\tau}^{t} Q(\sigma)N(\sigma)\mathrm{d}\sigma \end{aligned} \tag{17}$$

where τ denotes the interaction time, ϵ the yield coefficient (the number of predators dispersing after prey extermination) and M the total number of predator patches. This system has a nontrivial steady state

$$\bar{N}=\frac{\nu}{\epsilon\eta},\ \bar{Q}=\frac{\zeta n_0\pi_1}{\eta(\mu-\zeta n_0\pi_2\tau)},\ \bar{M}=\frac{\tau\zeta n_0\pi_1\nu}{\epsilon\eta(\mu-\zeta n_0\pi_2\tau)},\ \bar{P}=\frac{\pi_1\nu}{\epsilon\eta(\mu-\zeta n_0\pi_2\tau)} \tag{18}$$

provided $\zeta n_0\pi_2\tau/\mu<1$ (if this inequality is not satisfied the number of prey patches will grow exponentially). The stability of this steady state is governed by the compound parameter $\zeta n_0\pi_2\tau/\mu$. More precisely, $\zeta n_0\pi_2\tau/\mu>\frac{1}{2}$ guarantees stability (see Appendix I). The compound parameter is the product of $\zeta n_0/\mu$, which is the probability that a dispersing prey individual will found a new colony, and $\pi_2\tau$ which is the number of prey dispersing from a predator patch during the entire interaction period. So the parameter $\zeta n_0\pi_2\tau/\mu$ itself can be interpreted as the number of prey patches found by one predator patch. We conclude that *the founding of new prey colonies by prey dispersing from predator patches is a stabilizing mechanism.*

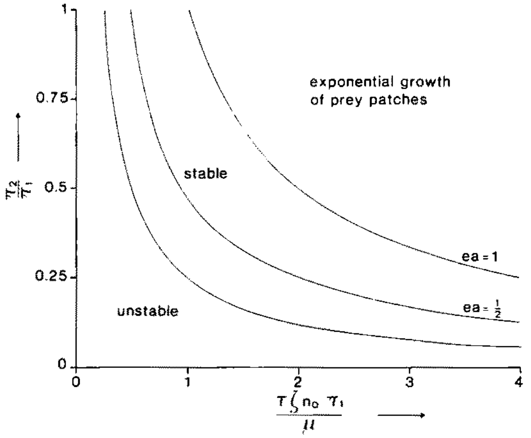

Fig. 3. Stability boundaries for two models: (1) upper and lower hyperbolic curves apply to the case of uniform predator dispersal during the interaction period; (2) upper and intermediate hyperbolic curves apply to the case of predator dispersal at the end of the interaction period. The symbols a and e are shorthand for, respectively, the horizontal and vertical variable (see Appendix I).

If we put $\pi_2 = 0$, the steady state is unstable due to the delay between predator invasion and the yield of new dispersing predators. So we may also say that this destabilizing effect of the interaction period can be overcome if prey disperse from predator patches. However, if too many prey disperse the predator is no longer able to keep the prey in check.

In Sabelis and Diekmann (1987) essentially the same conclusions were obtained in the context of a slightly different model. There we assumed that the predator aerial plankton Q is proportional to the total number of predator patches M or, in other words, that predators disperse from predator patches uniformly during the interaction period (and not, as in the model of this paper, all together at the end of the interaction period). The stability boundaries of both models are drawn in Fig. 3. It appears that the stability region is larger in the case of uniform predator dispersal. We conclude that *postponement of predator dispersion to the end of the interaction period is a destabilizing mechanism.*

Instantaneous host plant destruction, possibly defeated by predator invasion

Whenever the prey exhaust their host plant very quickly, we may employ a somewhat more sophisticated time-scale argument. In the absence of predators, the founding of a prey colony now leads instantaneously to the production of new searching prey. When predators are around they may invade, and then the instantaneous yield consists of predators rather than prey. In Appendix II we derive the following simplified system, starting from the assumption that $g(x,y)=\alpha x-\beta y$ and $h(x,y)=\gamma y$:

$$\begin{aligned}\frac{\mathrm{d}P}{\mathrm{d}t}&=x_{\max}\zeta n_0 P e^{-\omega Q}-\mu P\\ \frac{\mathrm{d}Q}{\mathrm{d}t}&=\zeta n_0 P h(Q)-\nu Q\end{aligned}\tag{19}$$

where by definition

$$\omega=\int_1^{x_{\max}}\frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma\tag{20}$$

and

$$h(Q)=\frac{\beta}{\gamma}\int_{1+(\gamma/\beta)}^{1+(\gamma/\beta)x_{\max}} y\mathrm{d}\left[1-\exp\left(-Q\int_1^{\beta/\gamma(y-1)}\frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma\right)\right]\tag{21}$$

Note in particular that ω and h depend on the function η so that the simplified system inherits certain characteristics from its structured mother.

If we now supplement (19) with

$$\frac{\mathrm{d}n_0}{\mathrm{d}t}=\mathrm{f}(n_0)-\zeta n_0 P\tag{22}$$

we are describing the system by following the number of empty patches as well as the prey and predator aerial plankton as a function of time, while the rise and annihilation of a local colony reduces to a point event.

The equilibria of (19)–(22) fall into three categories:

(1) When $\mathrm{f}(\bar{n}_0)=0$, $\bar{P}=\bar{Q}=0$ the empty patches are in a steady state, and there are neither prey nor predators. If $\bar{n}_0$ is stable with respect to the equation $\frac{\mathrm{d}n_0}{\mathrm{d}t}=\mathrm{f}(n_0)$ it is stable with respect to prey invasion if and only if $\bar{n}_0<\frac{\mu}{x_{\max}\zeta}$.

(2) The steady state $\bar{n}_0=\frac{\mu}{x_{\max}\zeta}$, $\bar{P}=\frac{\mathrm{f}(\bar{n}_0)}{\zeta\bar{n}_0}$, $\bar{Q}=0$ corresponds to the situation in which the density of empty patches is completely determined by the 'predation pressure' of the spider mites, while there are no predatory mites. With respect to the system

$$\begin{aligned}\frac{\mathrm{d}n_0}{\mathrm{d}t}&=\mathrm{f}(n_0)-\zeta n_0 P\\ \frac{\mathrm{d}P}{\mathrm{d}t}&=x_{\max}\zeta n_0 P-\mu P\end{aligned}\tag{23}$$

this steady state is stable if and only if $\bar{n}_0 f(\bar{n}_0) < f'(\bar{n}_0)$. For the usual density-dependent growth rates f, like the logistic $f(n_0) = rn_0(1 - \frac{n_0}{K})$, this condition holds for any $\bar{n}_0$. The steady state is stable with respect to predator invasion if and only if $f(\frac{\mu}{x_{\max}\zeta})h'(0) - \nu < 0$.

(3) Any solution $\bar{n}_0 > \frac{\mu}{x_{\max}\zeta}$ of the scalar equation

$$F(n_0) := f(n_0) g(\frac{1}{\omega} \ln \frac{x_{\max}\zeta}{\mu} n_0) - \nu = 0 \tag{24}$$

where by definition

$$g(Q) = \begin{cases} \frac{h(Q)}{Q} & \text{for } Q > 0 \\ h'(0) & \text{for } Q = 0 \end{cases} \tag{25}$$

yields a steady state with

$$\bar{P} := \frac{f(\bar{n}_0)}{\zeta \bar{n}_0} \quad \text{and} \quad \bar{Q} := \frac{1}{\omega} \ln \frac{x_{\max}\zeta}{\mu} \bar{n}_0$$

or, in other words, a steady state with all three trophic levels present. Note that

$$F(\mu/x_{\max}\zeta) = f(\mu/x_{\max}\zeta)h'(0) - \nu$$

and that, consequently, predators are able to establish themselves when confronted with a steady state of empty and prey patches if and only if $F(\mu/x_{\max}\zeta) > 0$. Note, furthermore, that if f has a zero greater than $\mu/x_{\max}\zeta$ and $F(\mu/x_{\max}\zeta) > 0$ then necessarily at least one solution of (24) exists.

The function g defined by (25) and (21) is monotone-decreasing, no matter the precise form of η. However, when f is a humped function the function F may be humped as well and multiple (stable) steady states are possible.

We intend to report in another paper on a detailed investigation of Equation (24) as well as the characteristic equation determining the stability for the special case where $f(n_0) = rn_0(1 - (n_0/K))$ and η is proportional to x. Here we shall only summarize the main results obtained so far: it turns out that indeed the system admits two stable steady states (as well as one unstable steady coexistence state) in a large domain of parameter space. In one of the stable steady states the predators are absent and the prey keep the plants (i.e. the empty patches n_0) far below the carrying capacity K. If one tries to achieve biological control by introducing a small number of predators, the stability of this steady state prevents success. However, the introduction of a large number of predators may bring the system into the other stable steady state in which the plants are almost at carrying capacity while the prey are kept at a low level by the predators. There also exist regions in parameter space in which the latter steady state is unstable and, presumably, stable oscillations around this steady state exist.

DISCUSSION

Structured population theory provides a framework for the formulation of complex realistic models in terms of mathematical equations. Given a 'master' model one can try to use experimental and field observations to obtain quantitative specification of the ingredients (submodels) or one can perform a multitude of thought experiments which produce more tractable caricatures. In this paper we illustrated the second approach because we feel it is somewhat neglected. By using time-scale arguments and special choices of model ingredients, analytically tractable models were obtained. An important advantage of this indirect approach to simple models is illustrated by the system of Equations (19) derived in the last section and Appendix II. Had we started by constructing simplified models directly, this system would have escaped our attention. So this is one good reason to formulate a 'master' model which incorporates many aspects of the 'real' system and then to proceed by deriving various caricatures which concentrate on some particular aspect while neglecting many others. Another good reason is that the 'master' model brings about coherence in the network of models and that it bridges the gap with simulation models.

In this paper we investigated a few elements and links of the network and some first insights were obtained. We found that, whereas the predator-dispersal phase acts as a destabilizing delay, the prey dispersal phase acts as a stabilizing refuge. The destabilizing effect of the predator-dispersal phase is reinforced by postponement of predator dispersion to the end of the interaction period. On the other hand, the founding of new prey patches by prey escaping from predator-invaded patches during the interaction period constitutes a stabilizing mechanism. Finally, we observed that a humped plant-production curve at the large spatial scale may lead to a bistable situation in which predators may or may not be successful in controlling the prey, depending on the initial conditions.

Among the more specific problems to be studied in the near future are the following:

(1) The role of an aggregative response of predators to local prey density

One can incorporate a temporary refuge by taking the vulnerability index η to be zero for $x \leqslant x_{\mathrm{crit}}$, where x_{crit} is the critical prey colony size below which, by assumption, predators are unable to detect and invade the colony. More generally, one can include an *aggregative response* by allowing η to increase with x. We plan to investigate the effect of the shape of η on the stability of the steady state. Note that the present model does not fix the prey colony size distribution n a priori (compare Hassell and May, (1974); May, (1978); Hassell, (1984); and Chesson and Murdoch, (1986)), but that n is dynamically influenced by the predation process.

(2) The role of interception of dispersers in already colonized patches

So far we have neglected the interception of prey in prey or predator patches and of predators in predator patches. What influence does this interception have?

(3) Evolutionary questions

Such as: "Why do predatory mites drive local prey-mite populations to extinction?" and "Under what conditions does selection favour predators with properties causing a delay of local prey extermination?"

In working together on this paper we directly experienced how mathematics and biology act as symbionts. We hope that the paper itself radiates that feeling.

APPENDIX I. STABILITY ANALYSIS OF SYSTEM 17

In order to simplify the notation we first perform a scaling of variables. Define

$$X(t)=\frac{\delta\eta}{\nu}N(\tau t),\quad Y(t)=\tau\eta Q(\tau t),\quad Z(t)=\frac{\delta\eta}{\nu}M(\tau t),$$

$$a=\frac{\zeta n_0 \pi_1 \tau}{\mu},\quad e=\frac{\pi_2}{\pi_1}$$

then (17) can be rewritten as

$$\frac{\mathrm{d}X}{\mathrm{d}t}(t)=a(X(t)+eZ(t))-X(t)Y(t)$$

$$Y(t)=Y(t-1)X(t-1)$$

$$Z(t)=\int_{t-1}^{t} X(\sigma)Y(\sigma)\mathrm{d}\sigma$$

The linearization about the steady state $\bar{X}=1$, $\bar{Y}=\frac{a}{1-ea}$, $\bar{Z}=\frac{a}{1-ea}$ (which is positive provided $ea=\frac{\zeta n_0 \pi_2 \tau}{\mu}<1$) is given by

$$\frac{\mathrm{d}\Xi}{\mathrm{d}t}(t)=a(\Xi(t)+Z(t))-H(t)-\bar{Y}\Xi(t)$$

$$H(t)=H(t-1)+\bar{Y}\Xi(t-1)$$

$$Z(t)=\int_{t-1}^{t} H(\sigma)\mathrm{d}\sigma+\bar{Y}\int_{t-1}^{t}\Xi(\sigma)\mathrm{d}\sigma$$

The characteristic equation is obtained by looking for a solution of the linearized system of the special form

$$\begin{bmatrix}\Xi(t)\\ H(t)\\ Z(t)\end{bmatrix}=e^{\lambda t}\begin{bmatrix}\Xi_0\\ H_0\\ Z_0\end{bmatrix}$$

By substitution and straightforward manipulation it follows that such a solution exists if and only if λ satisfies

$$\lambda(1-e^{-\lambda})+ae^{-\lambda}+d\frac{e^{-\lambda}-1+\lambda}{\lambda}=0$$

where

$$d=\frac{a^2 e}{1-ea}$$

Our first objective is to divide the positive (a,d)-parameter plane into the stable region where all roots of the above characteristic equation lie in the left half-plane and the unstable region in which at least one root lies in the right half-plane. The boundary of these two regions necessarily consists of curves which are characterized by the fact that a root lies precisely on the imaginary axis. Therefore we study such curves first.

$\lambda=0$ is a root if and only if $a=0$. If $\lambda=\mathrm{i}\omega,\omega\neq 0$ is a root then

$$-\omega^2(1-\cos\omega+\mathrm{i}\sin\omega)+a\mathrm{i}\omega(\cos\omega-\mathrm{i}\sin\omega)$$
$$+\mathrm{d}(\cos\omega-\mathrm{i}\sin\omega-1+\mathrm{i}\omega)=0$$

Splitting this equation into its real and its imaginary part yields the system of equations

$$-\omega^2(1-\cos\omega)+a\omega\sin\omega+d(\cos\omega-1)=0$$
$$-\omega^2\sin\omega+a\omega\cos\omega-d\sin\omega+d\omega=0$$

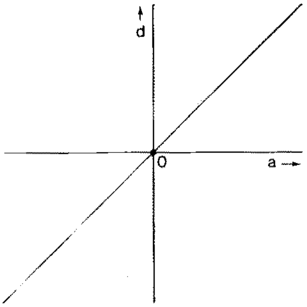

Fig. 4. The stability region is shaded.

which is linear in a and d. Solving for a and d we find

$$a=d=\omega^2\frac{1-\cos\omega}{\omega\sin\omega+\cos\omega-1}$$

provided $\omega\sin\omega+\cos\omega-1\neq 0$. If $\sin\omega=0$ and $\cos\omega=1$ we find $a=-d$. If $\omega\sin\omega+\cos\omega-1=0$ and $\sin\omega\neq 0$ there are no solutions. So the stability boundary is composed of pieces of the lines $a=0$, $a=d$ and possibly $a=-d$. As we shall show in the next proposition, the stability region is as depicted in Fig. 4.

Proposition

All roots of the characteristic equation lie in the left half-plane if and only if $d>a>0$ or $d<a<0$.

Proof

We first compute which way the root $\lambda=0$ goes if we perturb away from the line $a=0$. So for fixed d we look for a root $\lambda=\theta a+$ HOT, where HOT indicates higher order terms in a. A straightforward computation shows that necessarily $\theta=-2/d$. Hence a necessary and sufficient condition for $\operatorname{Re}\lambda<0$ is $d>0$ for a small but positive and $d<0$ for a small but negative.

If $a=d=0$ all roots lie on the imaginary axis. Indeed, they are given by $2k\pi i, k\in\mathrm{Z}$. We now compute where these roots go if we perturb along a line $d=\alpha a$. In order to do so we put $\lambda=2k\pi i+\theta_1 a+\theta_2 a^2+$ HOT, substitute and make Taylor expansions. We find

$$\theta_1=\frac{1+\alpha}{2k\pi}i;\quad \theta_2=\frac{1+\alpha}{4k^2\pi^2}\left(\frac{1-\alpha}{2}-\frac{1+2\alpha}{2k\pi}i\right)$$

Consequently $\operatorname{Re}\lambda<0$ if and only if either $\alpha>1$ or $\alpha<-1$.

So in a neighbourhood of $(a,d)=(0,0)$ we have stability precisely when $d>a>0$ or $d<a<0$. Since stability can change only at the lines $a=0$, $a=d$, $a=-d$ this local characterization remains globally valid.

Remarks

(i) $d > a > 0$ if and only if $\frac{1}{2} < ea = \frac{\zeta n_0 \pi_2 \tau}{\mu} < 1$. Note that the right inequality corresponds to the condition for the existence of an equilibrium. The case $d < a < 0$ has no biological meaning.

(ii) At the line $a = d$ stability is lost by complex conjugated pairs of roots crossing the imaginary axis. An unusual aspect of the present system is that passage of the line $a = d$ in parameter space is accompanied with a simultaneous passing of the imaginary axis in the complex plane by a multitude (in fact infinitely many) of pairs of roots. This is due to the fact that one of the equations is a pure difference equation. As a consequence one cannot apply standard Hopf bifurcation theorems about the existence of periodic solutions.

APPENDIX II. DERIVATION OF THE LIMITING EQUATIONS DESCRIBING INSTANTANEOUS INTERACTION

When $\nu(x) = \alpha x$ the solution of

$$\begin{cases} \frac{\mathrm{d}}{\mathrm{d}t}(t,x) = -\frac{\mathrm{d}}{\mathrm{d}x}(\nu(x)n(t,x)) - \eta(x)Q(t)n(t,x) \\ \nu(1)n(t,1) = \zeta n_0(t)Q(t) \end{cases}$$

is given explicitly by

$$n(t,x) = \frac{\zeta n_0(t - \frac{1}{\alpha}\ln x)P(t - \frac{1}{\alpha}\ln x)}{\alpha x} \exp\left(-\int_0^{\frac{1}{\alpha}\ln x} \eta(\mathrm{e}^{\alpha\sigma})Q(t - \frac{1}{\alpha}\ln x + \sigma)d\sigma\right)$$

(The basic technique to obtain such explicit expressions is integration along characteristics; see Metz and Diekmann (1986, Ch. III, section 4.1).

When $g(x,y) = \alpha x - \beta y$ and $h(x,y) = \gamma y$ the solution of

$$\begin{cases} \frac{\mathrm{d}}{\mathrm{d}t}m(t,x,y) + \frac{\mathrm{d}}{\mathrm{d}x}(g(x,y)m(t,x,y)) + \frac{\mathrm{d}}{\mathrm{d}y}(h(x,y)m(t,x,y)) = 0 \\ h(x,1)m(t,x,1) = \eta(x)Q(t)n(t,x) \end{cases}$$

is given explicitly by

$$m(t,x,y) = \frac{1}{\gamma}y^{-(1+\frac{\alpha}{\gamma})}\eta(x_0(x,y))Q(t - \frac{1}{\gamma}\ln y)n(t - \frac{1}{\gamma}\ln y, x_0(x,y))$$

where, by definition

$$x_0(x,y) = xy^{-\frac{\alpha}{\gamma}} + \frac{\beta}{\alpha - \gamma}(1 - y^{1-\frac{\alpha}{\gamma}})$$

We assume that a prey patch which is not invaded by predators will nevertheless crash after a fixed period due to local food over-exploitation, and that all prey will disperse at that very instant (whereas earlier no prey emigrate from the colony). Let $x_{\max}$ denote the number of prey in a crashing colony. (So $x_{\max}$ is the maximal realisable colony size and, as such, it is an indirect measure of the value of an empty patch with regard to exploitable energy.) Then the rate R at which new prey aerial plankton is produced is given by the product of $x_{\max}$ and the 'flux' $\nu(x_{\max})n(t,x_{\max})$ which is the rate at which prey patches reach $x_{\max}$:

$$R(t)=x_{\max}\nu(x_{\max})n(t,x_{\max})=\alpha x_{\max}^2 n(t,x_{\max})$$

Similarly, the rate at which new predator aerial plankton is produced is given by

$$S(t)=-\int_{y_{\min}}^{y_{\max}} yg(0,y)m(t,0,y)\mathrm{d}y$$

where $y_{\min}$ and $y_{\max}$ are the minimal and maximal possible local predator population sizes.

We ignore the possibility of host plant exhaustion for a predator-invaded patch (which would result in the simultaneous production of prey and predator aerial plankton) because this possibility becomes negligible in the limiting case that we will consider here.

The formulas above allow us to express R and S in past values of n_0, P and Q and consequently we can derive a closed system of delay-differential equations for these three variables. In order to simplify these expressions and to obtain ordinary differential equations we are going to take the limit $\alpha,\beta,\gamma,\eta\to\infty$ with $\alpha/y\to 0$ but β and γ of the same order, and α and η of the same order.

In this limit we have

$$R(t)=x_{\max}\zeta n_0(t)P(t)\exp(-Q(t)\int_1^{x_{\max}}\frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma)$$

and

$$S(t)=\frac{\beta}{\gamma}\zeta n_0(t)P(t)\int_{y_{\min}}^{y_{\max}} yQ(t)\frac{\eta(x_0(0,y))}{\alpha x_0(0,y)}\exp(-Q(t)\int_1^{x_0(0,y)}\frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma)\,\mathrm{d}y$$

$$=\frac{\beta}{\gamma}\zeta n_0(t)P(t)\int_{y_{\min}}^{y_{\max}} y\mathrm{d}[1-\exp(-Q(t)\int_1^{x_0(0,y)}\frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma)]$$

The biological interpretation is as follows. We assume that both prey and predators reproduce infinitely fast, but predators still an order faster than prey. The rate of production of prey aerial plankton R equals the product of the yield factor $x_{\max}$, the rate of founding of new prey colonies $\zeta n_0(t)P(t)$ and a reduction factor $\exp(-Q(t)\int_1^{x_{\max}} \frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma)$ due to predator invasion. Similarly, the rate of production of predator aerial plankton S is proportional to the rate of founding of new colonies with a proportionality constant which is the mean yield

$$h(Q(t)) := \frac{\beta}{\gamma}\int_{y_{\min}}^{y_{\max}} y\mathrm{d}[1-\exp(-Q(t)\int_1^{x_0(0,y)} \frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma)]$$

Note that the mean yield depends on Q and the vulnerability index η. The point is that the yield in predators depends on the size of the prey colony at the moment of invasion, while the probability for invasion at some particular size depends on both η, a descriptive model ingredient, and the dynamical variable Q.

We now specialize, by way of example, η to be $\eta(x)=\alpha\theta x$ or, in other words, we take the probability of predator invasion to be proportional with prey colony size. Then

$$\int_1^x \frac{\eta(\sigma)}{\alpha\sigma}\mathrm{d}\sigma = \theta(x-1) \quad \text{and} \quad R(t) = x_{\max}\zeta n_0(t)P(t)\exp(-\theta(x_{\max}-1)Q(t))$$

Since in the limit $x_0(0,y) = \frac{\beta}{\gamma}(y-1)$

(and therefore $y_{\min} = 1+\frac{\gamma}{\beta}$, $y_{\max} = 1+\frac{\gamma}{\beta}x_{\max}$) we obtain

$$\frac{S(t)}{\zeta n_0(t)P(t)} = (\frac{\beta}{\gamma}+x_{\max})(1-\mathrm{e}^{-\omega Q(t)}) + \frac{1-\mathrm{e}^{-\omega Q(t)}}{\theta Q(t)} + 1 - x_{\max}$$

where, by definition, $\omega = \theta(x_{\max}-1)$.

Taking $\delta = \frac{\beta}{\gamma}+x_{\max}$ and $\rho = \frac{\omega}{\delta\theta} = \frac{x_{\max}-1}{x_{\max}+\beta/\lambda} < 1$ we obtain

$$\delta^{-1}h(Q) = 1-\mathrm{e}^{-\omega Q} + \rho(\frac{1-\mathrm{e}^{-\omega Q}}{\omega Q}-1),\ Q>0$$

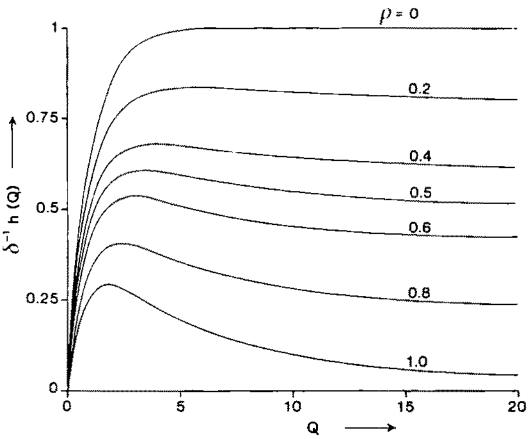

Fig. 5. The relation between h and Q for $\omega = 1$, $\delta = 1$ and various values of ρ.

and $h(0) = \lim_{Q \downarrow 0} h(Q) = 0$. The graph of h is sketched in Fig. 5.

Note that an increase in the number of searching predators may actually lead to a decrease of the production of new predator aerial plankton, since prey colonies may be invaded so early in their development that they produce, at the end of the interaction period, few predators.

Similarly, the assumption that η is constant, say $\eta(x) = \alpha\theta$, leads to

$$h(Q) = \frac{\beta}{\gamma}\left(1 + \frac{\gamma}{\beta}x_{\max}\right)\left(1 - x_{\max}^{-\theta Q}\right) + 1 - x_{\max} + \frac{x_{\max}^{1-\theta Q} - 1}{1 - \theta Q}$$

REFERENCES

Chesson, P. and Murdoch, W.W., 1986. Aggregation of risk: relationships among host-parasitoid models. Am. Nat., 127: 696–715.

De Roos, A.M., 1988. Numerical methods for structured population models: the escalator box-car train. Numer. Methods Part. Differ. Equations, 4: 173–195.

Edelstein-Keshet, L., 1986. Mathematical theory for plant-herbivore systems. J. Math. Biol., 24: 25–58.

Hassell, M.P., 1984. Parasitism in patchy environments: inverse density-dependence can be stabilizing. IMA J. Math. Appl. Med. Biol., 1: 123–133.

May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton Univ. Press, Princeton, NJ.

May, R.M., 1978. Host-parasitoid systems in patchy environments: a phenomenological model. J. Anim. Ecol., 47: 833–843.

Metz, J.A.J. and Diekmann, O. (Editors), 1986. The Dynamics of Physiologically Structured Populations. Lecture Notes in Biomathematics, 68; Springer, Berlin, 511 pp.

Nachman, G., 1988. Regional persistence of locally unstable predator/prey populations. Exp. Appl. Acarol., 5: 293–318.

Sabelis, M.W. and Diekmann, O., 1987. Overall population stability despite local extinction: the stabilizing influence of prey dispersal from predator-invaded patches.

Sabelis, M.W. and Laane, W.E.M., 1986. Regional dynamics of spider-mite populations that become extinct locally because of food-source depletion and predation by phytoseiid mites. In: J.A.J. Metz and O. Diekmann (Editors), The Dynamics of Physiologically Structure Populations. Lecture Notes in Biomathematics, 68; Springer, Berlin, pp. 345–375.