EXTINCTION IN A STRUCTURED PREDATOR-PREY MODEL

WITH SIZE-DEPENDENT PREDATION

THOMAS G. HALLAM

Department of Mathematics and Graduate Program in Ecology, University of Tennessee
Knoxville, Tennessee 37996-1300, U.S.A.

and

SHANDELLE M. HENSON

Department of Mathematics, University of Tennessee
Knoxville, Tennessee 37996-1300, U.S.A.

DEDICATION
In memory of the friendship and science of
Stavros Busenberg

ABSTRACT

Two age-size structured, individual-based, partial differential equation population models are coupled to form a predator-prey model, which is parametrized for a *Daphnia*-trout (*Daphnia magna-Oncorhynchus mykiss*) community. Lethal effects chemical uptake models for fish and *Daphnia* are coupled to the community, and *Daphnia* population extinction thresholds due to predation are computed as a function of chemical concentration in the water. Predation of fish on *Daphnia* is size dependent, and *Daphnia* population extinction thresholds are also computed as a function of size-dependent predation.

1. Introduction

1.1. The Problem

Interactions between species are mechanistically complex because they depend upon numerous environmental, physiological, behavioral, and trophic factors. This article focuses on two possible controlling agents in the predation process, physiological processes and exogenous chemical stressors. Predation, a fundamental structuring process in ecological systems, is often influenced by size of both the predator and its prey. This attribute, along with the ecotoxicological aspects of our study, require an individual-based perspective.

Dynamics of structured population models are difficult to ascertain because of the spectrum of possible behaviors. Our efforts focus on persistence and extinction phenomena obtained from consideration of size-governed feeding and chemical toxicity in an age-size structured predator-prey model. The results are obtained via

simulations of the community model.

1.2 The Model

The predator-prey model is composed of two age-size structured population models, one for each of the predator and prey populations, and the trophic interactions between them. The population models are partial differential equation models of McKendrick-von Foerster type and are individual-based in that the growth rate of an individual organism appears in the population equation.

The individual growth rate models are mechanistic representations of individual energy budgets, and rely on parameters estimated from empirical data collected at the individual level. Individual biology is important for risk assessment because environmental influences such as toxic stress affect populations by affecting the population's individual members. Lipophilic chemicals, for example, affect individual organisms according to their fat content[1].

The predator model is constructed and parametrized for the rainbow trout, *Oncorhynchus mykiss*[2], and the prey model is constructed and parametrized for *Daphnia magna*[3]. The two population models are coupled through the feeding of the fish on the *Daphnia* and the consequent mortality imposed on the prey population. Predator resource density is computed from prey density, and one component of prey mortality is due to predation. Once the predation interaction has been specified, a given predator feeds according to the uptake term(s) in its individual growth model, and the resulting mortality on the prey population is computed[4].

Assume (ρ, q) is the unique solution of the age-size structured model

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \sum_{i=1}^{j} \frac{\partial}{\partial m_i}(g_i \rho) = -\mu \rho$$

$$\rho(0, a, \vec{m}) = \hat{\rho}(a, \vec{m})$$

$$\rho(t, 0, \vec{m}_0) = \int_{\Omega} \int_{0}^{\infty} \beta(a, \vec{m}, \vec{m}_0) \rho(t, a, \vec{m}) da d\vec{m}$$

$$\quad (1)$$

$$\frac{\partial q}{\partial t} + \frac{\partial q}{\partial a} + \sum_{i=1}^{k} \frac{\partial}{\partial n_i}(h_i q) = -v q$$

$$q(0, a, \vec{n}) = \hat{q}(a, \vec{n})$$

$$q(t, 0, \vec{n}_0) = \int_{\Gamma} \int_{0}^{\infty} B(a, \vec{n}, \vec{n}_0) q(t, a, \vec{n}) da d\vec{n} \quad ,$$

where $\vec{m} = (m_1, m_2, \cdots, m_j)$ and $\vec{n} = (n_1, n_2, \cdots, n_k)$ are vectors of j physiological variables for the prey and k physiological variables for the predator. $\rho(t, a, \vec{m})$ is the age-mass (but not volumetric) density at time t, age a, and mass vector $\vec{m}$ of

the prey in numbers per unit age per unit mass, and $q(t, a, \vec{n})$ is the density at time t, age a, and mass vector n of the predators. $g_i(a, \vec{m})$ and $h_i(a, \vec{n})$ are the growth rates of the ith mass variables m_i and n_i, respectively, in an individual prey and predator. $\beta(a, \vec{m}, \vec{m}_0)$ and $B(a, \vec{n}, \vec{n}_0)$ are the birth rates of the prey and predators, respectively; $\mu(t, a, \vec{m}, \rho(t, \cdot, \cdot), q(t, \cdot, \cdot))$ and $v(t, a, \vec{n}, q(t, \cdot, \cdot))$ are the mortality rates for the prey and predators, respectively; and $\hat{\rho}$ and $\hat{q}$ are the initial distributions of prey and predators.

Variation among individuals can be introduced by modelling an arbitrary number of ecotypes in the populations. Each ecotype is modelled with a partial differential equation and is distinguished by its distinct individual growth rate.

1.3 Relative Foraging Volumes

Because the predator-prey model is solved numerically, it is difficult to simulate the large number of *Daphnia* required to provide resources for a reasonable number of fish; therefore, only a fraction of the *Daphnia* are simulated and the model is appropriately scaled. The fish population is associated with a volume parameter V_F representing predator foraging range. The simulated representative daphnids are associated with another (possibly the same, but probably smaller) volume parameter V_D. The *Daphnia* population is assumed to be distributed uniformly over volume V_F, but the simulation only tracks a representative fraction of the whole *Daphnia* population. If $V_D = V_F$, then the simulation follows the entire *Daphnia* population. If not, interactions between the predator and prey communities must be modified by the scaling factor V_D / V_F.

1.4 Predator Feeding

An individual fish is assumed to only eat daphnids whose length L_D falls within a certain prey size window that depends linearly on the length of the fish[5]. In particular, the fish can consume daphnids whose length satisfies the inequality

$$10 \cdot k_{min} \cdot L_F \leq L_D \leq 10 \cdot k_{max} \cdot L_F, \tag{2}$$

where k_{min} and k_{max} are parameters. Smaller and larger daphnids either are not pursued by the fish or are transported through the gills. A daphnid of length L_D therefore can (only) be consumed by a fish whose length satisfies the inequality

$$0.1 \cdot k_{max}^{-1} \cdot L_D \leq L_F \leq 0.1 \cdot k_{min}^{-1} \cdot L_D. \tag{3}$$

For both species, length is computed allometrically from structural mass, one of the mass variables computed in both the fish and *Daphnia* models. Let $\Omega(\vec{n})$ denote the range of masses of *Daphnia* which a fish of mass $\vec{n}$ can consume, and let $\Gamma(\vec{m})$ denote the range of masses of fish which can consume a daphnid of mass $\vec{m}$.

The fish respond to the volumetric density of the prey, and are assumed to divide the resource among themselves by an intraspecific competitive mechanism, with larger fish receiving larger shares. A fish of mass $\vec{n}_F$ responds to the following resource density of *Daphnia* of mass $\vec{m}$:

$$x_{\vec{n}_F, \vec{m}} = \frac{\int_0^\infty \left(\sum \vec{m}\right) \rho(t, a, \vec{m}) da}{V_D} \cdot \frac{\sum \vec{n}_F}{\int_{\Gamma(\vec{m})} \int_0^\infty \left(\sum \vec{n}\right) q(t, a, \vec{n}) \, d\vec{n} \, da} \tag{4}$$

grams per unit volume per unit mass, where $\sum \vec{m}$ is the total mass of the organism having mass vector $\vec{m}$. A fish of mass $\vec{n}_F$ thus responds to a total resource density of

$$x_{\vec{n}_F} = \frac{\sum \vec{n}_F}{V_D} \int_{\Omega(\vec{n}_F)} \frac{\int_0^\infty \left(\sum \vec{m}\right) \rho(t, a, \vec{m}) \, da}{\int_{\Gamma(\vec{m})} \int_0^\infty \left(\sum \vec{n}\right) q(t, a, \vec{n}) \, d\vec{n} \, da} \, d\vec{m} \tag{5}$$

grams per unit volume.

2. Results: Extinction Thresholds

2.1. Definition

In order to analyze some of the effects of size-dependent predation, we now assume 1) the *Daphnia* population has a constantly abundant resource density, and 2) all mortality is due to predation, starvation, or old age.
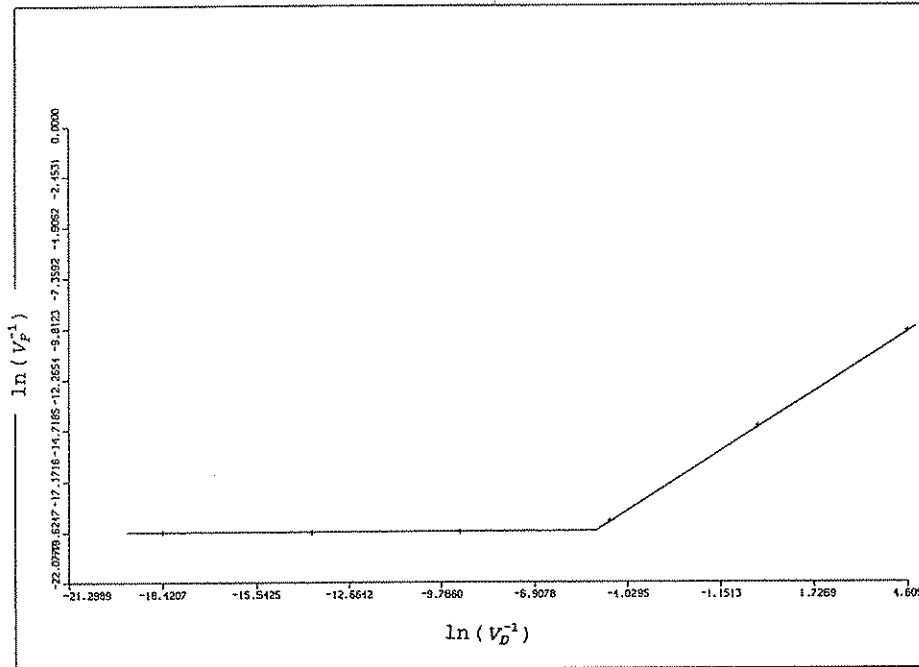

Fig. 1.   Extinction threshold $\ln V_F^{-1}$ as a function of $\ln V_D^{-1}$ for 100-day runs.

Because of these hypotheses, extinction can occur in only two ways. The first extinction scenario is also found in aggregated models: the fish eat all the available daphnids, the *Daphnia* population goes to extinction, and then the fish starve. The second extinction scenario is completely due to size structure in the model, specifically size-dependent predation: the fish do not find sufficient *Daphnia* of the appropriate size to eat, and thus starve while the *Daphnia* population survives[4]. This paper concerns the first extinction scenario, which corresponds to the extinction of the *Daphnia* and necessarily leads to the extinction of the fish.

Let $\hat{\rho}$ and $\hat{q}$ be nominal initial population distributions of prey and predator, respectively, in units of numbers per unit age per unit mass. While keeping these distributions the same, we vary the initial population densities by varying the volumes V_D and V_F, and calculate the extinction threshold. Given an initial *Daphnia* population density distribution $\hat{\rho}/V_D$, the extinction threshold is the infimum of the V_F^{-1} such that an initial fish density distribution of $\hat{q}/V_F$ drives the *Daphnia* population to extinction within a prescribed number of days.
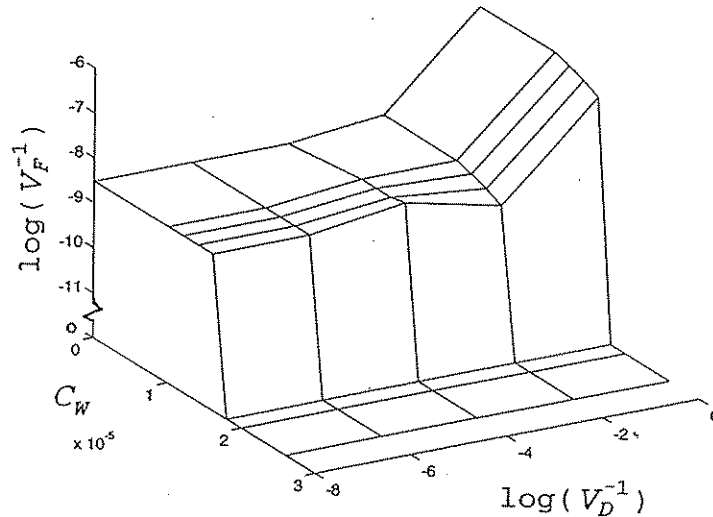

Fig. 2. Extinction threshold $\log V_F^{-1}$ as a function of chemical concentration C_W in the water and $\log V_D^{-1}$ for 100-day runs. The planes $C_W = 1.62 \times 10^{-5}$ and $C_W = 1.78 \times 10^{-5}$ form vertical asymptotes for the surface; and for $C_W ¿ 1.78 \times 10^{-5}$, $V_F^{-1} = 0$ (see Figure 3 for a cross section).

Figure 1 shows the extinction threshold as a function of V_D^{-1} for 100-day runs with nominal initial population distributions. The initial *Daphnia* distribution con-

tains 26 ecotypes of relatively fast growers and reproducers, and 1 ecotype of slow growers which reproduce only once before dying of old age at 50 days. The lower part of the curve, which has small slope, corresponds to the extinction of the slow-growing ecotype, and the upper part, which has a larger slope, corresponds to extinction of the faster-growing ecotypes.

V_D and V_F must be interpreted as volumes, and not just scaling factors on the initial distributions, because they appear as parameters in their own right in the resource partitioning for fish, where fish numbers respond to *Daphnia* density.

2.2 Extinction threshold as a function of toxicant

We now allow toxicant-induced mortality in both the predator and prey populations by engaging the lethal effects models for fish and *Daphnia*[1,2].

Figure 2 shows the 100-day extinction threshold for the predator-prey model (with the nominal initial population distributions) as a function of C_W (concentration of chemical in the water) and V_D^{-1}. At 2600 days, both populations were given a 3 day exposure to a chemical with octanol-water coefficient 10^4. k_{max} and k_{min} had values of 0.2 and 0.007, respectively.
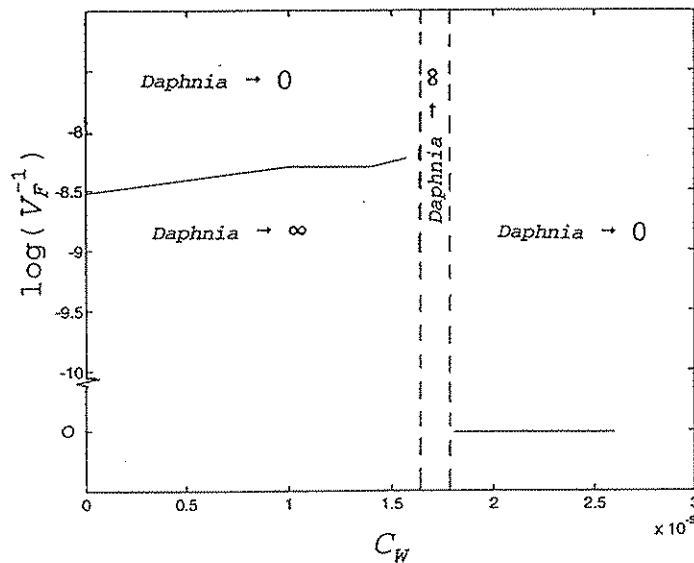

Fig. 3. Cross section of Figure 2 with initial *Daphnia* density held constant at $V_D^{-1} = 10^{-4}$.

Figure 3 shows a typical cross section of Figure 2 with initial *Daphnia* density held constant at $V_D^{-1} = 10^{-4}$. When $1.62 \times 10^{-5} \leq C_W \leq 1.78 \times 10^{-5}$, all the

young fish die from the toxicant and the remaining fish are too large to eat any of the juvenile daphnids. Thus, each daphnid is able to reproduce at least once, and hence the *Daphnia* population grows no matter how high the fish density. When $C_W > 1.78 \times 10^{-5}$, the toxicant kills all the *Daphnia*.

2.3 Extinction threshold as a function of size-dependent predation

Figure 4 shows the extinction threshold for constant V_D^{-1} as a function of k_{max} when k_{min} is set at 0. At low values of k_{max}, none of the daphnids are small enough to fall in the prey windows of any of the fish, and so no density of fish is large enough to control the *Daphnia* population. At intermediate values of k_{max}, all juvenile daphnids and some adult daphnids are consumed by the fish, and so the extinction threshold is finite. At large values of k_{max}, all sizes of *Daphnia* are consumed by all fish, and so the extinction threshold becomes constant with increasing k_{max}.
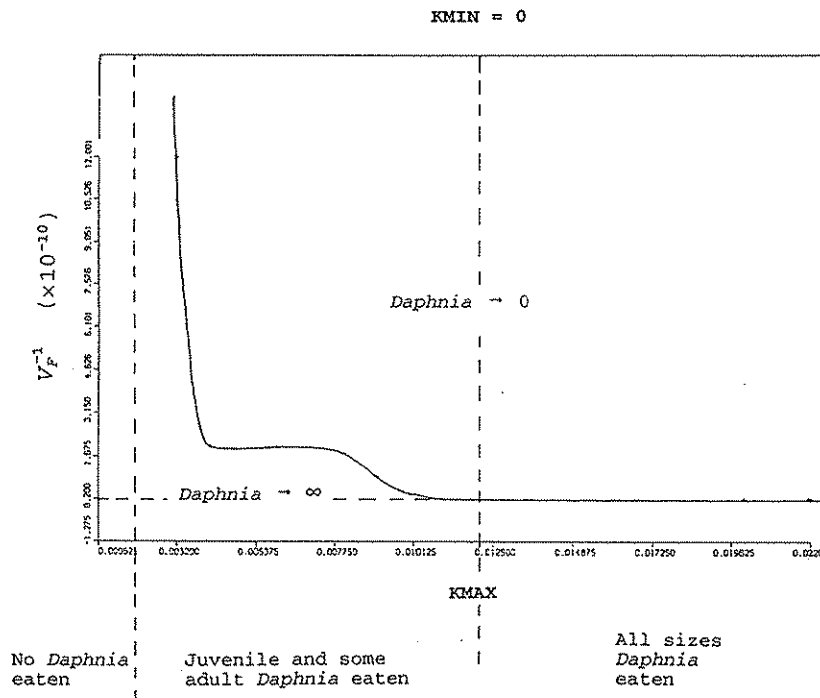

Fig. 4.   Extinction threshold as a function of k_{max} when $k_{min} = 0$.

Figure 5 shows the extinction threshold for constant V_D^{-1} as a function of k_{min} when k_{max} is set at ∞. At low values of k_{min}, all sizes of *Daphnia* are consumed by all fish, so the threshold corresponds to the threshold at high k_{max} in Figure 4. At intermediate values of k_{min}, adult and some juvenile daphnids are consumed. When k_{min} is sufficiently high, no juvenile daphnids are consumed. At this point, no finite fish density can control the *Daphnia* population since each daphnid is allowed to

reproduce at least once.

3. Summary

When mortality is restricted to predation, starvation, and old age, causes of extinction in the structured community model are restricted to over-exploitation of prey and starvation. When the prey are assumed to have a constantly abundant resource, extinctions can only result from extinction of prey due to predation, or extinction of predators due to lack of sufficient prey of appropriate consumption size. The extinction thresholds obtained are of the former type, and are functions of the size-dependent predation mechanism.

If lethal effects of chemicals are introduced, the densities and size distributions of the populations are perturbed, causing changes in the extinction thresholds. In this case, extinction can also result from a lethal chemical dose to one of the populations.
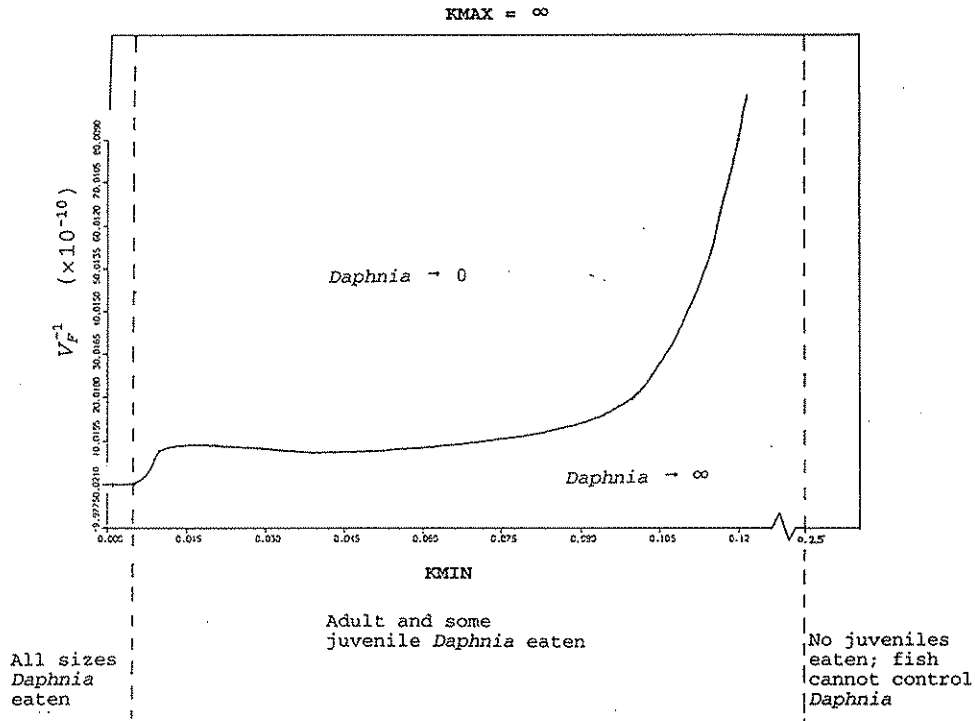
KMAX = ∞

Daphnia → 0

Daphnia → ∞

KMIN

Adult and some
juvenile *Daphnia* eaten

All sizes
Daphnia
eaten

No juveniles
eaten; fish
cannot control
Daphnia

Fig. 5. Extinction threshold as a function of k_{min} when $k_{max} = \infty$.

4. Acknowledgements

5. References

1. T. G. Hallam, R. R. Lassiter, J. Li, and W. McKinney, *Env. Tox. Chem.* **9** (1990) 597-621.
2. T. G. Hallam, R. R. Lassiter, and S. M. Henson, Modelling fish population dynamics: a physiologically based perspective, to appear (1994).
3. T. G. Hallam, R. R. Lassiter, J. Li, and L. A. Suarez, *Ecology* **71** (1990) 938-954.
4. T. G. Hallam, R. R. Lassiter, J. Jaworska, and W. McKinney, in *Recent Trends in Differential Equations*, ed. R. P. Agarwal (WSSAA 1, Singapore, 1992).
5. J. S. Jaworska, T. G. Hallam, S. M. Henson, W. R. McKinney, and R. R. Lassiter, in *Environmental Toxicology and Risk Assessment - Third Volume*, eds. J. S. Hughes, et al. (ASTM STP 1218, Philadelphia, (1995) 157-172.