Joanna S. Jaworska,[1] Thomas G. Hallam,[2] Shandelle M. Henson,[3] William R. McKinney,[4] and Ray R. Lassiter[5]

ECOTOXICOLOGY OF PREDATOR - PREY COMMUNITIES: AN INDIVIDUAL - BASED MODELING APPROACH

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ABSTRACT: Physiologically structured population models are used to study the effects of nonpolar narcotic chemicals on two predator-prey community models. The biological focus is on the individual, which allows a discussion of exposure and effects, two necessary attributes of ecological risk assessment. Exposure is represented here by an exchange model between the environment and the organism with two possible routes - food and environment. Quantitative structure activity relationships (QSARs) are used to assess both lethality and chronic effects such as reduction in growth. Densities of lipid, carbohydrate and structure, variables used to describe an individual, are compiled to describe population dynamics. Variation among individuals is entirely responsible for the response of the population to toxic stress. Direct and indirect effects of stress on the community level of organization are observed for two model predator-prey systems:

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[1] Graduate Research Associate, Environmental Toxicology Program, University of Tennessee, Knoxville, TN 37996-1300

[2] Professor, Department of Mathematics and Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37996-1300

[3] Graduate Research Associate, Department of Mathematics, University of Tennessee, Knoxville, TN 37996-1300

[4] Assistant Professor, Department of Mathematics, North Carolina State University, Raleigh, NC 27695-8205

[5] Research Ecologist, Biology Branch, Environmental Research Laboratory, Environmental Protection Agency, Athens, GA 30613

rainbow trout *(Oncorhynchus mykiss*) - *Daphnia* and *Tetrahymena pyriformis - Escherichia coli.* The direct effects include changes in the lipid, structure, age and size distributions of individuals in the populations. An example of an indirect effect is starvation of predators caused by death of prey in particular size classes.

KEY WORDS: aquatic toxicology, community models, ecological risk assessment, individual - based models, *Daphnia magna, Oncorhynchus mykiss, Tetrahymena pyriformis, Escherichia coli*

INTRODUCTION

Risk assessment at the community or ecosystem level is in a rudimentary state of development. Many approaches for investigating the dynamics of higher ecological organizational levels employ highly aggregated models that focus on average properties of individuals in the populations. Recent efforts to represent populations by utilizing an individual - based approach have led to new dynamic perspectives that reflect realistic individual variation in populations and allow chemical exposure to be adequately treated (Hallam et al. 1990a). Implementing extensions of these ideas at the community level results in a physiologically oriented, mechanistic approach to community risk assessment.

The basis of community dynamics is contained in the individuals that compose the community and the interactions of these individuals. When the feeding mechanism of an individual predator on a prey population is prescribed, growth of the individual predator is determined by the predator individual model and mortality caused by this predator on the prey population can be assessed. With the information coupling the predator and prey organisms, it is possible to construct a predator - prey community from population formulations for the prey and predator.

A general methodology for studying a stressed and an unstressed individual - based community requires development of the following components:

1. Formulation of an individual model for each species in the community.
2. Development of a toxicant exposure model and an effect model as well as linking them to the individual model.
3. Formulation of the population models incorporating a diverse group of individuals.
4. Coupling population models into a community model.

We now indicate how each part of the protocol is modeled for community risk assessment purposes.

ECOLOGICAL RISK ASSESSMENT MODULES

Individual Models

The individual model incorporates biological information in order to describe the physiology of the organism and toxicological stress in a realistic and mechanistic way. Physiological variables that are crucial for describing dynamics of growth and reproduction of an single organism, those which might get affected during stress and those that determine toxicant distribution in the body need to be included in the model. Here, the individual models utilize energy budget techniques much like those suggested by Kooijman and Metz (1984) and Kooijman (1986).

We focus on two individual - based predator - prey models, a microbial *Tetrahymena p. - E.coli* system and a *Daphnia* - rainbow trout *(Oncorhynchus mykiss)* system, and illustrate some effects of exposure to nonpolar narcotics. Individual models of *Daphnia* and fish have been described previously in detail (Hallam et al. 1990b; Lassiter et al. 1993) and the reader is referred to those articles for details. The models for trout and *Daphnia* are systems of ordinary differential equations that describe the dynamics of the physiological components. However, developments for the microbial system are new (Jaworska 1993) and are individually - oriented in that they are rule based. We briefly indicate the life history utilized in the microbial system models.

The Life History Model of an Individual Tetrahymenid

The tetrahymenid model is related to the individual daphnid model (Hallam et al. 1990b) in that it represents *lipid* and *structure* (all nonlipid, noncarbohydrate dry mass, including protein and nucleic acids) dynamics but differs in several assumptions, some specific to the biology of the modeled organisms. In particular, due to importance of glycogen as a storage compartment, carbohydrate dynamics are also followed. Conversions between compartments are possible (i.e protein can be converted to lipid or carbohydrate). Ingested resource (carbohydrate, lipid, protein) is not necessarily assimilated to the corresponding compartment of the consumer or in special cases may not be assimilated at all. Feeding and reproduction are assumed to occur on discrete scales, while other processes like digestion and assimilation operate in a continuous manner. Energy requirements are computed based on the allometric relationship between the volume and the oxygen consumption of the individual. Amounts of lipid,carbohydrate and protein not used for energy purposes are assimilated. It is assumed that the growth of the protein compartment must be accompanied by proportional growth of the polar lipid compartment. Lipid not used to build structure is assimilated to the storage lipid compartment. Assimilation of carbohydrate is decoupled from lipid and protein assimilation in that it can only be assimilated to the carbohydrate compartment. The storage compartments, i.e neutral lipids and glycogen, also grow independently from each other but their growth is limited by the total mass of the organism.

Cell division into two identical daughter cells occurs in the model when the following three conditions are met simultaneously. First, the cell size is bigger than the reproductive size for a given food density; the reproductive size is a prescribed hyperbolic function of the food density. Second, the cell protein compartment is greater than a minimum size. Third, the nutritional status of the organism has to be sufficient to meet all energetic needs without utilization of the structure components, during the nonfeeding period prior to division. When all these conditions are met, the cell enters the reproductive mode. While in this mode, the organism does not feed but still can assimilate nutrients available in the storage vacuoles.

Sexual reproduction does not occur in cells such as *Tetrahymena p.* that have a micronucleus.

The Life History Model of Individual Bacterium, *E.coli*

The model is based on the developments of the biochemically structured model for *E.coli* formulated by Shuler and Domach (1983) and later simplified by Joshi and Palsson (1988). It expands the capabilities of their model by adding the process of starvation and a modification of the reproduction process. An individual bacterium is described by three pools: nucleic acids, proteins and cell envelop. Nucleic acids and protein form the proteinous part of the organism. The cell wall is composed of approximately 50% lipids and 50% complex carbohydrates. Cell geometry governs reproduction. The cell is cylindrical in shape with closed hemispherical ends. It grows in length and width in the cell cycle according to the growth of the pools. The reproduction process is initialized when the length of the organism reaches the reproductive length set by a hyperbolic function of the resource. From that time until division the cell does not elongate, rather it widens and builds a septum wall. At the moment when the length of the septum wall is equal to the diameter of the cell, separation of two daughter cells takes place.

Exposure Model

The exposure model coupled with the individual model is a modification of FGETS (Barber et al. 1988). This model, based upon a thermodynamic potential, represents the chemical exchange between an individual fish and its aqueous environment. This model assumes passive diffusion across gill membranes and across gut walls from ingestion of contaminated food. The model depends upon the total toxicant concentration in the organism, in the environment, and in the food and assumes immediate partitioning between the lipid, protein and aqueous phases of the organism. Internal instantaneous equilibration provides the worst case scenario for the chemical uptake because no more chemical can be allocated to compartments; however, it elicits a minimal depuration time (Lassiter and Hallam 1990).

Effects of Chemicals on Individuals

The basic ideas employed to assess the effects of chemicals on an individual and on a static population are given in (Hallam et al. 1990a; Lassiter and Hallam 1990). Quantitative structure activity relationships (QSARs) are used to assess acute effects such as mortality for fish (Veith et al. 1983) and *Daphnia* (Hermens et al. 1985) and chronic effects such as reduction in growth for *Tetrahymena* (Schultz et al. 1990) and *E.coli* (Jaworska and Schultz 1993). An effect is assumed to occur at the characteristic concentration in the reference phase, the aqueous portion of the organism (Lassiter and Hallam 1990). This representation allows for incorporation of both lethal and sublethal effects at the individual level. It is assumed that all individuals who reach a designated effect level, (for example, EC50 - the concentration where growth is reduced by 50%) in the reference phase, respond in an identical way as dictated by that effect. Morphology and body composition modify time to reach the threshold so that some individuals respond more quickly while others may escape the effect completely. The growth effects syndrome, when completely implemented, assumes that sublethal effects occur on a continuous scale and range from the no effect concentration through reduction in growth to the LC50 (the concentration that kills 50% of the exposed organisms) where mortality is assumed to occur. For narcosis effects, Lassiter (1991) indicates that r, the fractional reduction of enzyme sites that occurs through competitive inhibition, is a hyperbolic function in effect concentration and that the intercept of the quantitative dose-response representation is a continuous function of the reduction fraction r. This hyperbolic representation incorporates discrete empirical data such as the no observable effect, growth reduction, and mortality as depicted in Figure 1 for *Daphnia* in a continuous manner (Hallam et al. 1993) for a specific form of this hyperbolic function).

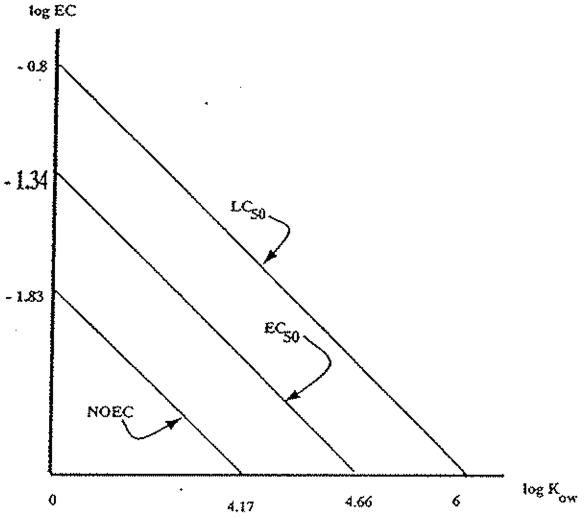

Figure 1. QSARs for 3 endpoints: LC50, the concentration that kills 50% of the exposed individuals; EC50, the 50% growth reduction concentration; NOEC, the no observed effect concentration. All bioassays are for *Daphnia magna*. The horizontal axis is the logarithm of the 1-octanol/ water partition coefficient. The vertical axis is the effect concentration in the environment (Lassiter and Hallam 1990). Data from Hermens et al. (1985).

If the time of exposure is equal to or less than a generation time then fractional reduction in growth of the population is equivalent to the same fractional reduction of growth of individuals in this population. However , the QSARs used in the microbial model study employ multigeneration endpoint, such as 48-h 50% growth inhibition for *Tetrahymena* or 10-h 50% growth inhibition for bacteria. In order to determine how growth of the average individual is reduced to produce known reduction in the population biomass, we have simulated both populations separately by reducing the food uptake function. We found an interesting nonlinear relationship between population and individual effects, which is best described by Figure 2.

The choice of the uptake function as the one reduced in the model is arbitrary. We reduced other physiological variables (e. g. assimilation rate) and obtained a similar effect.

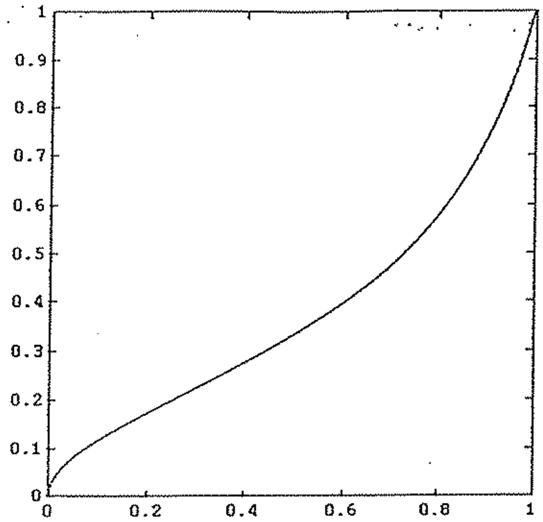

Figure 2. The relationship between reduction in biomass of the *E. coli* population and reduction in growth of the individuals. The horizontal axis is the population biomass reduction effect and the vertical axis is the individual growth reduction effect.

Population Model

Once the dynamic model of an individual is known, it can be incorporated into a population model via an extended McKendrick - von Foerster partial differential equation (Hallam et al. 1993); the details of incorporating the individual dynamics into a population are indicated in (Hallam et al. 1990a). This equation represents transport processes based upon a conservation law and is a hyperbolic partial differential equation of the form

$$\rho_t + \rho_a + \Sigma_i (\rho g_i)_{m_i} = - \mu\rho \qquad (1)$$

where the subscripts t, a, and m_i indicate partial derivatives with respect to that subscripted variable. In (1) , t represents time, a represents age, and m_i represents the physiological variables used to describe the individual. The sum in (1) ranges from i= 1, 2,...,n where n is the number of physiological variables used to structure the model of the individual. The physiological variables, m_i, are often determined by the particular problem being investigated. Two natural candidates for these variables in almost any population modeling endeavor are some measure of size and lipid. Size is a determining factor for some physiological processes such as ingestion and maintenance. Size of individuals is important at the community level because prey selection by a predator is often size dependent and the size of the predator determines the size of prey it can eat. Lipid is important for many aspects of energetics and reproduction. Our original interest in these variational structured problems was from the ecotoxicological perspective where many toxicological effects relate to the fraction of lipid present in the chemically stressed organism. The function g_i is the growth rate of the physiological variable m_i in a model that represents the individual organism. The dependent variable $\rho = \rho(t,a,m_1,m_2,\ldots,m_n)$ is the population density function, and μ represents the mortality rate function of the population.

In order for the problem to make sense biologically and for the mathematical problem to be well posed, it is necessary to prescribe initial and boundary conditions for the population. The initial distribution

$$\rho(0,a,m_1,m_2,\ldots,m_n) = \varphi(a,m_1,m_2,\ldots m_n)$$

describes the population at time $t = 0.$ A boundary condition, often called the renewal equation, indicates the birth process of the population. In structured models this can have numerous forms. For example, one form is

$$\rho(t,0,m_1(0),m_2(0),\ldots,m_n(0)) =$$

$$\int\ldots\int\beta(t,a,m_{10},m_{20},\ldots,m_{n0},m_1,m_2,\ldots,m_n)\rho(t,a,m_1,m_2,\ldots,m_n)da\,dm_1dm_2\ldots dm_n,$$

where β is the fertility rate function that describes the number of eggs with the initial physiological dimensions $m_{i0} = m_i(0),\ \ i = 1,2,\ldots,n$ produced by a organism of age a and physiological state $m_1,\ldots,m_n$ at time t. The function β is determined by the individual model in that the allocation to eggs must be represented at the times of reproduction for each organism.

For fish and *Daphnia* the boundary condition is required to describe the birth process. The functions g_i describe the individual dynamics of the lipid and protein compartments.The equations for *Tetrahymena* and *E.coli* dynamics do not require a boundary condition due to the reproductive scheme of these organisms (Metz and Diekmann 1986; Sinko and Streifer, 1971). This modeling approach together with the technique for solving it (the method of characteristics) is advantageous because it allows for incorporation of both individual and toxicant dynamics at the population level.

The Predator - Prey Model

To create a community from the population approach described above we first consider a trout - *Daphnia* example. We need only specify how each of the individuals in the fish population feeds upon the *Daphnia* population and how subsequent mortality due to predation is assessed in the *Daphnia* population. An individual fish has a prey window, a range in the size of prey that it can eat, whose boundaries are determined by linear functions of the predator length. The individual fish is assumed to have access to the entire prey population (to minimize computations, the prey population is scaled for a particular subset of the lake) and, according to the density of daphnids it encounters, captures, and grows from the daphnids in its prey window.

In the microbial food chain model, ciliates feed on bacteria without size selection and have access to the entire prey population. In addition, *Tetrahymena* excrete by-products, called autochtonous substances, of metabolism which are excellent nutrients for bacteria (Sambanis 1985). Their exact composition is not known but included are amino acids and carbohydrates. The model assumes that the amount of these substances generated is proportional to the biomass of tetrahymenids with the carbohydrates to amino acids amount always being in a fixed ratio. This creates an interesting feedback in the system.

The two communities, trout - *Daphnia* and *Tetrahymena* - *E.coli* have different resource dynamics. The first is a continuous culture with constant concentrations of algae serving as a sources of food for different ecotypes of *Daphnia.* The second is a batch setting where nutrients are depleted. Both models focus on physiological processes and reference fixed nominal environmental conditions.

RESULTS AND DISCUSSION

Both predator - prey systems are investigated numerically with the nominal, unstressed simulations compared to simulations with toxicant stress. We report results of two toxicant releases. The first stress is near the starting time of the simulation when the community is not well organized. The second is in the middle of the simulation, after the community was given more time to organize. The relationship between toxic stress and extinction is also discussed.

There are conclusions drawn from the analysis of the individual - based predator - prey system that agree with conclusions obtained from classical predator - prey models. There is a community threshold of persistence; when the mortality scale factor is below this threshold, there is ultimate extinction of the fish population. This extinction can occur through two obvious avenues. One is that the fish are not the appropriate size to eat available daphnids. In this case they can find nothing to eat, the fish population starves and goes to extinction, and the *Daphnia* population survives. A second extinction behavior is that the fish eat all available daphnids, the *Daphnia* population crashes, the fish population then goes to extinction and, consequently, the complete community goes to extinction. The threshold is clearly a function of the scale factors associated with each of the populations and the physiological size structures in the population.

Figure 3 consists of graphs representing the age structures of the *Daphnia* and trout populations in a stressed simulation of the dynamical community model. The simulation is initiated by putting the two populations together and letting the predators initiate feeding on the prey. There is an organizational period for the community, followed by the dynamics of the mature community. Here, the chemical stressor is applied after the community is organized. Young fish with small lipid storages are affected. The stressed *Daphnia* population becomes more diverse in age than occurs in the nominal run, probably due to a release in predation pressure coupled with the toxic effects. This diversity in age structure has also been observed for the *Daphnia* population under chronic, sublethal stress but without predation (Hallam et al. 1993). As illustrated in Figure 3, the diversity in age is even more than in the healthy community. The undisturbed portion of this figure before the toxic stress occurs may be used for comparison with the dynamics of Figure 4 where the effects of the nonpolar narcotic chemical release occurs early in the community organizational stage. The most prominent effects are on the younger fish and as well as the entire *Daphnia* population where community organization is delayed.

This structured predator - prey system allows investigation of the processes and mechanisms of interactions between two populations. We tend to look for features of the system that are fundamental to the understanding of the nature of predation. This requires finding basic attributes of populations and determining what changes ensue when the two populations involved in the predator - prey interaction are coupled. The intrinsic oscillatory frequencies present in population dynamics represent population markers that might be affected by coupling the populations. There are longer term *Daphnia* frequencies (50 - 250 days) that are of a similar order as the reproductive frequency of the fish (1 year). Consequently, it might be expected that these frequencies could be modified by the interactions of individuals. We have found this to be the case. Different numerical simulations show that the long term frequency of the prey, *Daphnia,* and the reproductive period of the predator, trout, can be altered through community interactions. Other changes due to community interactions and perturbations caused by toxicant stress are currently under investigation.

Because of the second model's totally different resource setting - a batch culture - in which environmental conditions constantly change, it is important to follow the amount of organic material circulating in the environment such as dead organisms and feces. As time progresses more and more toxicant is bound to this organic material, thus providing a buffer of protection for the living species. During mild stress, it is possible that toxicant is not available in sufficient concentration at the end of the simulation to cause any adverse effect although initially there were effects. The dynamics of such a community is generally only slightly perturbed, in that it takes longer for the community to organize, compared to the nominal behavior. With initial predation at low levels, the bacterial population is not depleted as fast as in the nominal run and the massive death of ciliates occurs later. This causes the shift of the ciliate "dip" in time (Figure 5). Figure 5 demonstrates the effects of a toxic chemical on the *Tetrahymena - E.coli* community. Here, the dynamic lipid

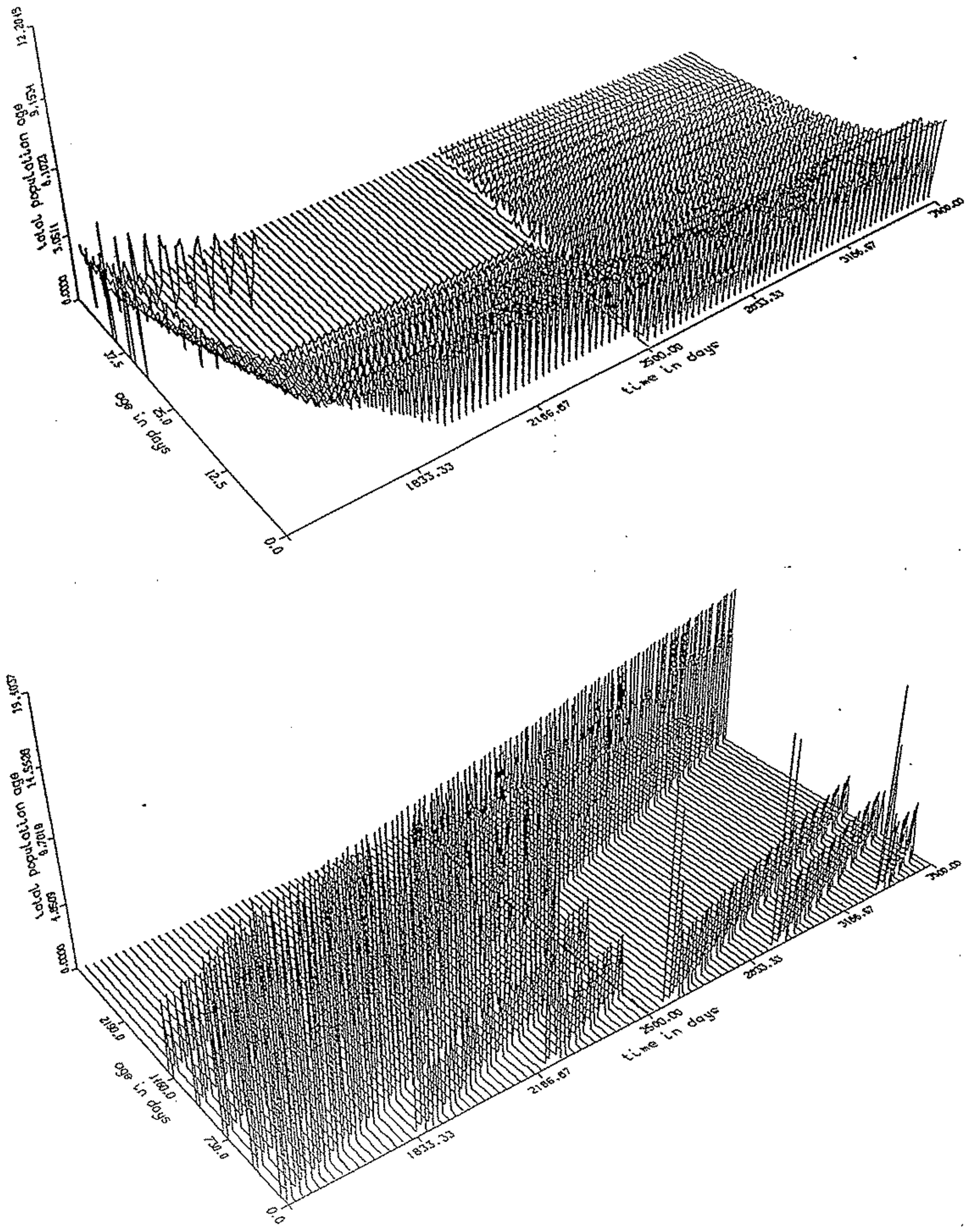

Figure 3. The distribution of age in the *Daphnia* and trout populations as a function of time. The graphs of the simulation are for 1500 - 3500 days and the community was exposed to a toxicant from 2503 - 2505.3 days. The right horizontal axis is the time axis. The left horizontal axis is the age of the individual. The vertical axis is the log of the number of individuals with a given age. Top: *Daphnia magna*; Bottom: *Oncorhynchus mykiss.*

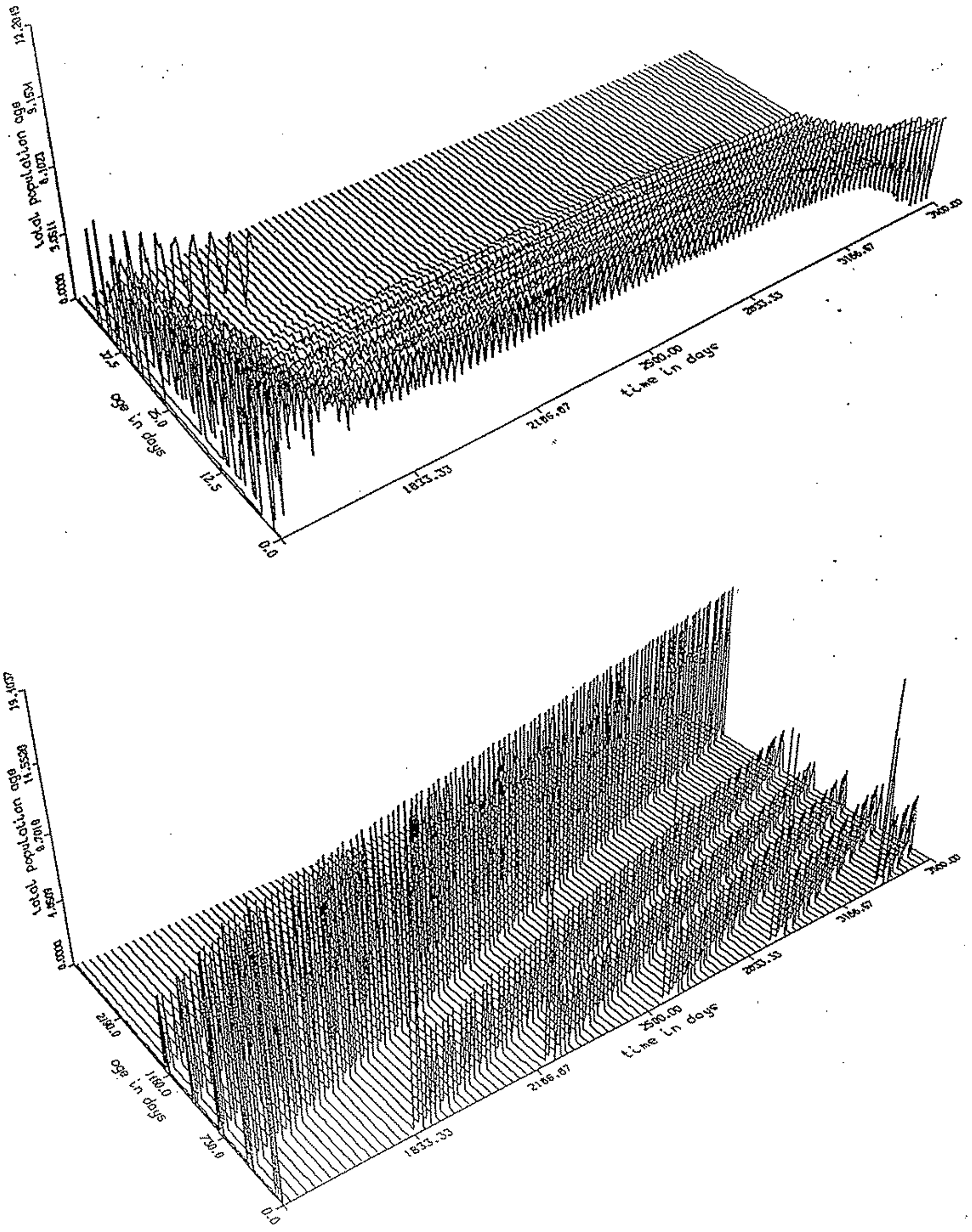

Figure 4. The distribution of age in the *Daphnia* and trout populations as a function of time. The graphs of the simulation are for 1500 - 3500 days and the community was exposed to a toxicant from 1503 - 1505.3 days. The right horizontal axis is the time axis. The left horizontal axis is the age of the individual. The vertical axis is the log of the number of individuals with a given age. Top: *Daphnia magna*; Bottom: *Oncorhynchus mykiss*.

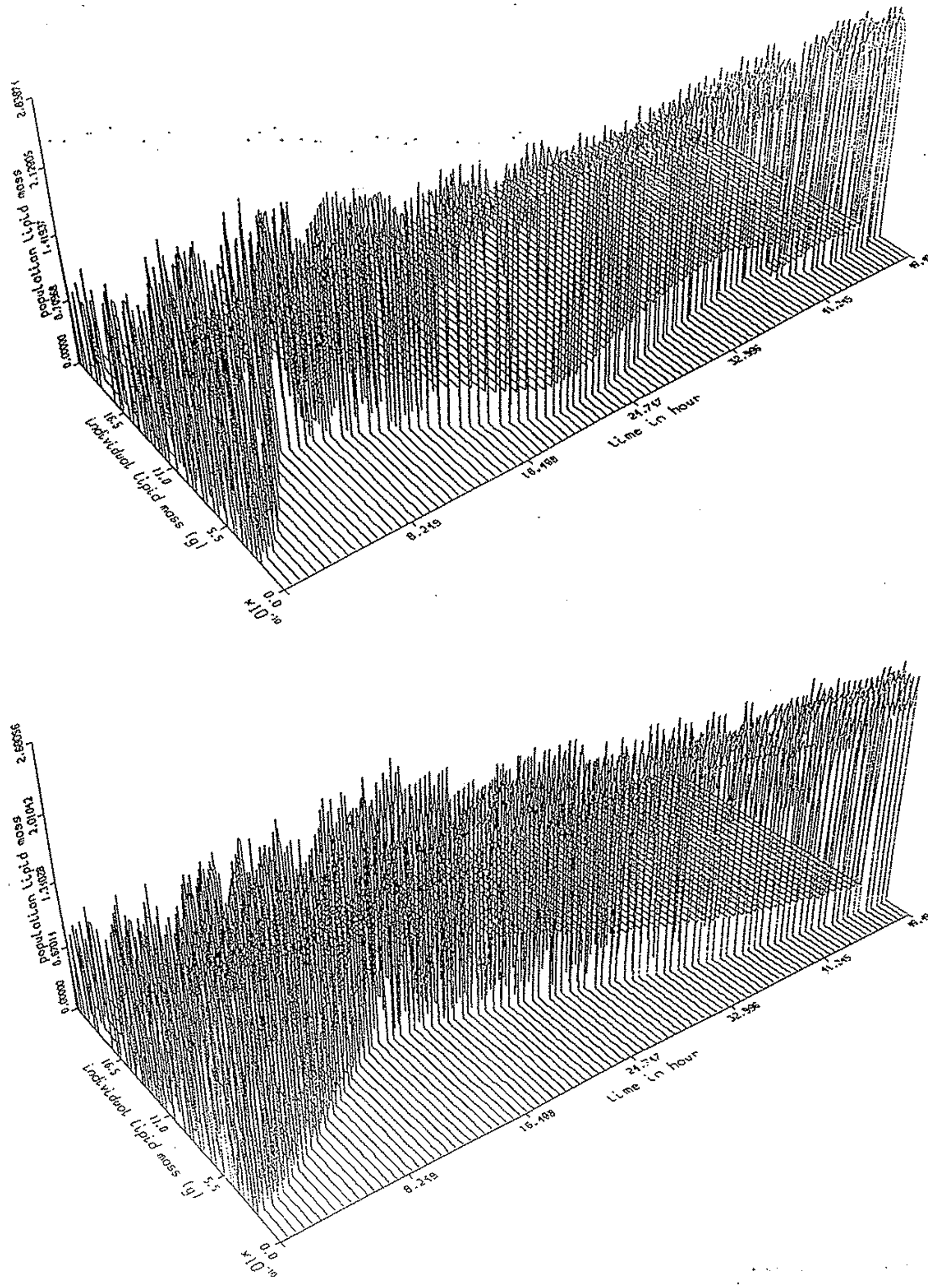

Figure 5. The distribution of lipid in the *Tetrahymena pyriformis* population as a function of time. The graphs of the simulation are for 0 to 50 hours. The right horizontal axis is the time axis. The left horizontal axis is the lipid content of the individual. The vertical axis is the log of the number of individuals with a given lipid content. Top: Unstressed simulation. Bottom: The community was exposed to a toxicant from 0 - 50 hours.

distribution is shown for the stressed and unstressed *Tetrahymena* population. Lipid distributions are examined because of their importance during toxic stress by lipophilic chemicals. Note the delay in development that is expected because the growth rate of the tetrahymenids is reduced by the stressor.

Another important feature of this community is that ciliates and bacteria are not equally susceptible to the toxicant. This becomes apparent under severe stress. Based on QSARs analysis, bacteria are less sensitive than ciliates. Therefore, it is common to observe that only one population - the ciliates - is adversely affected. This lowers the predation pressure on the bacteria population which escape the control and, subsequently, bloom. The exploding bacteria population provides excellent food conditions for the ciliates. However, the remaining predators are unable to fully utilize the resource because of toxic stress reflected as reduced food uptake, cessation of growth, or ultimately, starvation. If the decreased uptake of food does not meet energy requirements, tetrahymenids have to utilize their storage. In the situation where this continues for a sufficiently long period, starvation ensues. Such behavior of bacterial dominance is well documented in the wastewater literature. Depending on the water quality, different organisms dominate, with bacteria surviving in the most contaminated waters.

When both populations are affected, there are two types of outcomes. First, the stress has to be very toxic to the ciliate population in order to have an impact on the bacterial population. Then, the ciliates die off quickly, the bacteria are released from predation but do not bloom as before because their growth is reduced by toxicant stress. The case when both populations die off is the least interesting; here, extinction of ciliates proceeds extinction of bacteria.

Comparison of toxicant response to both systems reveals that despite dramatic differences such as continuous versus batch culture, acute versus sublethal stress, temporary presence of the toxicant versus continuous presence we can find some commonalities. In particular, stress in the middle of the simulation produces different effects in both communities than stress during the community organizational period. It is hypothesized that as communities evolve over time and ultimately reach a more organized state where initial transient behavior has damped, certain toxic stresses have less disrupting effects. In the *Daphnia* and fish population models, as time progresses, there is an ecotype that dominates population dynamics, a behavior called "survival of the fittest". In both predator - prey models, reduction in diversity from the initial distribution is noted in the predator population. Relatively small size individuals predominate in stressed environments. On the other hand, initial diversity of prey population tends to remain.

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