Mathematical Models Relating Effects of Xenobiotic Substances on Individuals and Populations

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LONG TERM GOALS

The research involves the development of mathematical models suitable for relating the effects of xenobiotic substances on individuals and populations of benthic marine organisms. This goal recognizes that the ecological effects of contaminants occur within complex ecological communities, but that the response of the constituent populations to environmental stress is difficult and/or very expensive to measure. Thus it is important to extract as much insight as possible from the large body of experimental information quantifying the impact of toxicants on the individual organisms within impacted, or potentially impacted populations.

OBJECTIVES

The research has two main parts: (i) modeling the consequences for individuals of toxicant-induced changes in the rates of energy acquisition and utilization by individual organisms, and (ii) using individual-based population models to predict the implications of these changes on the abundance and spatial distribution of organisms.

APPROACH

Our research makes use of two types of models. In modeling the response of individuals to toxicants, we use dynamic energy budget (DEB) models to describe the rules by which individual

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organisms assimilate and utilize energy from food. They incorporate feeding and assimilation rates dependent on the state of the individual and the environment, together with rules for energy allocation to maintenance, growth and reproduction (including priorities for energy allocation when food is scarce). Thus DEB models constitute a natural context within which to model the mechanisms whereby vital biological rates (growth, reproduction, respiration) are influenced by exposure to contaminants. In particular, DEB models offer a systematic conceptual framework within which to identify general principles from the large body of information relating to specific toxicants and/or impacted genus, species, or even life stage. Model development is largely the responsibility of the PI (Nisbet) working in collaboration with Dr. Erik Muller (UCSB), and Dr. Konstadia Lika (UCSB; recently appointed to the University of Crete). Model tests have made extensive use of data collected by co-PI Schmitt.

In modeling spatially explicit populations, we use individual-based population models. Individual organisms are distributed over a two-dimensional grid, and interact with each other and with the environment in accordance with rules that are a simplified version of the rules describing individual energetics, supplemented with assumptions on mortality. This approach allows a rigorous implementation of individual behavior and physiology at the population level, and also allows for dynamic change in the spatial distribution of interacting organisms. This work has been performed by Nisbet and co-PI Wilson. Recent work has emphasized models of competing herbivores using data on marine snails collected by co-PI Schmitt.

In the past year, we have performed some very preliminary work on ecosystem models based on DEB representations of individuals. These models are capable of describing simultaneous flows of energy and elemental matter.

WORK COMPLETED

Highlights of FY98 include:

- Formulation of a new, general DEB model.
- Detailed study of predictions of one DEB model for organisms experiencing a variable environment. This is the first stage of a study of models describing acclimation of organisms to environmental stress.
- Development of general models of competing herbivores.
- Preliminary studies of ecosystem models with simultaneous energy flow and recycling of elemental matter.

RESULTS

New DEB Model

All our previous models of toxicant action are based on the theory of Kooijman (1993; see also Kooijman and Bedaux 1996 and references therein). We used Kooijman's theory for two reasons: the generality of the model formulation so as to cover a wide spectrum of organisms and environments, and its previous successes in modeling standardized toxicity tests. There is a second family of DEB models known as "net production models" that differ from Kooijman's model in the assumptions made on priorities for energy use. These models are commonly used in fisheries studies, but have also been applied to marine mussels (e.g. Ross and Nisbet 1990; van Haren and Kooijman 1993). Previous work (Nisbet et al. 1996) has suggested that, while the differences between the predictions from the two types of model are commonly (though not invariably) unimportant in a constant environment, they may be substantial in variable environments and for organisms experiencing acute stress. Yet there was no systematic recipe for writing down net production models in a way that ensures mathematical consistency in a variable environment, and such systematic formulation is vital if model predictions are to be based on the underlying biology rather than mathematical artifacts. Lika and Nisbet (submitted) have now developed the required formalism, which will be used, along with Kooijman's, in future modeling efforts.

DEB Models of Individuals in a Varying Environment

A prerequisite to understanding the population level consequences of energy acquisition and use is a detailed investigation of the DEB model predictions for individual organisms experiencing temporal variation in their environment. In most natural environments, organisms need to cope with temporary shortages of food. Toxicants aggravate the condition of starving organisms, and may accelerate death due to starvation.

Our default DEB model (that of Kooijman – see above) assumes that an organism dies when it cannot fulfill its maintenance demands, which happens when energy is released from reserves at an insufficiently rapid rate. We have conducted a few simulation studies of mussels experiencing fluctuations in both food availability and water temperature. The model predicts a high likelihood of 100% mortality in apparent contradiction to the robustness of many observed populations. We are studying modifications of the model that make different assumptions concerning energy use when food is scarce or if toxicant concentration is high, and are modeling starvation behavior in an environment where food and/or toxicant level fluctuates randomly. We find that model organisms in a stochastically variable environment are more vulnerable than organisms in a periodic environment, and predict that they will thus be more conservative in their utilization of reserves.

These studies of model performance in a variable environment will allow us to study acclimation of organisms to the presence of toxicants. Our models contain two types of parameter. *Physiological* parameters take values that reflect biochemical or thermodynamic constraints on organism performance, and cannot readily change their values without major changes in the organisms properties (e.g. a shift from aerobic to anaerobic metabolism). By contrast, life history parameters representing, for example, strategic choices about energy allocation and the critical size for changing a life stage are likely to be *adaptive*. Given sufficient genetic diversity, natural selection can lead to significant changes in the values of adaptive parameters over a few generations. We have completed some work on adaptation in DEB models (Lika and Nisbet, submitted), and are planning to extend this to include variable environments during year 1. This will enable us to predict adaptations in fluctuating, but chronically polluted, environments.

Models of competing herbivores

The cornerstone of traditional ecological theory of competition is the competitive exclusion principle, which asserts that two or more species cannot coexist on a single resource. Exploration of the limitations of this "principle", and identification of mechanisms that promote co-existence has become a growth industry among theoretical ecologists. However, the scope of much of this theory is restricted by the assumption of "closed" populations, where recruits are the offspring of existing members of the population and the effects of immigration and emigration are negligible. We recently developed competition theory for "open" benthic systems with individuals recruited from the open ocean at rates determined by external factors and not by local population size (Wilson et al. in press). In the open system context, our criterion for two species to "coexist" is that each can grow in the presence of the other. We find that coexistence is possible if the species exploit the algal substratum in different ways: "diggers" move slowly but remove fully exploit their location, while "grazers" move fast and skim the surface. The model successfully predicted the outcome of competition between two species of marine snail studied by Schmitt (1996).

During the past year, we have developed a more general model of competing open populations. The new model abandons the very crude caricature of the algal resource in the model of Wilson et al., which is inadequate for modeling situations where a toxicant affects the depth of substrate accessible to either competitor. The model confirms the robustness of some of the previous results, notably the possibility of co-existence of grazers and diggers, but reveals subtle dependence of the co-existence conditions on the resource renewal dynamics. The model is now ready for application to study the efficacy of different grazing strategies in stressed environments. This work is of interest in its own right, but is also a prerequisite for modeling ecosytems where the outcome of competition among herbivore species may be critical to the long-term fate of the system.

Ecosystem models

In ecosystems, the state variables no longer relate to populations, but to functional groups of populations (e.g. decomposers, primary producers and herbivores) or to the chemical make-up of the constituent populations and the environment. The full potential of DEB models for marine ecosystem modeling remains an open issue, but existing models of the flow of energy and elements (e.g. Gurney and Nisbet, 1998; chapter 7 and references therein) make a convincing case that ecosystems do truly have dynamics that can be described by relatively simple, general, models.

One, largely unexploited, strength of DEB-based ecosystem models is the capability to link the description of biological and chemical phenomena. Thus, Kooijman and Nisbet (in press) have developed a DEB model of mass and energy turnover in a closed ecosystem with primary producers, herbivores and decomposers. Individuals at each trophic level grow and reproduce in accordance with a DEB model. Assumptions on stoichiometry enable calculation of the fate of up to 16 compounds. Important quantities predicted include carbon dioxide production, oxygen consumption and ammonia production.

IMPACT/APPLICATIONS

Our DEB modeling work, taken with that of Kooijman and Bedaux (1996), represents the first attempt to develop general theory characterizing the effects of environmental stress on diverse range of organisms. The study of competing herbivores takes a very original approach, and opens the possibility of using energetic-based models to relate the outcome of competition to environmental change. The new ecosystem models will link our research to the large body of empirical and theoretical work on the cycling of elemental matter in stressed environments.

TRANSITIONS

The research is not yet at a point to move from research into the Navy fleet or to industry. It has been used in a project related to off-shore oil production (see below).

RELATED PROJECTS

- The work on dynamics energy budget modeling has proceeded in parallel with a project, funded by the Southern California Educational Initiative of the Minerals Management Service, which involved modeling the effects of produced water on growth and reproduction of mussels. In particular, Dr. E.B. Muller, a post-doctoral researcher employed with that support, has made vital contributions to the present work.
- PI Nisbet has support from the National Center for Ecological Analysis and Synthesis (NCEAS) for sabbatical research in academic year 1998-9 and for a working group on the theme "Population level effects of toxicants". The working group will bring together for four one-week meetings researchers using different approaches to the problem of relating the effects of toxicants on individuals, populations and ecosystems. This should lead to improved methodology in future ONR-funded research.

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