Modeling Population and Ecosystem Response to Sublethal Toxicant Exposure

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LONG TERM GOALS

The ecological effects of environmental stress occur within complex communities and ecosystems. Prior to the current award, the PIs formulated and tested general dynamic energy budget models characterizing the response of individual organisms to toxicants, and developed methodology for using these models to predict population dynamics. They also developed new theory describing the trophic dynamics of open systems. They now propose to use these advances as the basis of research to test the predictive power and limitations of an individual-based approach to understanding the impact of pollutants on the dynamics of marine communities and ecosystems with multiple trophic levels.

OBJECTIVES

The research has three main components:

a) Models of the acclimation of individual organisms to changes in their environment.
b) Development of simple models of marine organisms in open populations competing for a single resource in a polluted environment. Tests against data on estuarine fish experiencing environmental gradients.
c) Development of simple ecosystem models with primary producers, competing herbivores and explicit incorporation of microbial dynamics. Tests of the models using experimental data on polluted benthic microcosms obtained by Dr. Kevin Carman (Louisiana State University). Use of the models to interpret field data on infauna near point sources of pollution.

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APPROACH

Underpinning all the research are *dynamic energy budget* (DEB) models of individuals. We use simple DEB-based *individual-based models* to describe changes in structure and biomass of populations, with mechanistic descriptions of competition included where appropriate. We are developing ecosystem models that describe the flow of elemental matter in a way that is consistent with the DEB models of individuals.

Dynamic energy budget models

Toxic compounds may reduce the fecundity, development rate, and/or survival probability of *individual organisms*. These changes can be modeled using dynamic energy budget (DEB) models incorporating information on the physiology of individuals (Kooijman 1993, 2000; Nisbet et al., *in press*). DEB models use differential equations to describe the rates at which individual organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment, (food density, temperature, toxicant levels, etc.). Solutions of the model equations represent the life history of individual organisms in a potentially variable environment.

Individual-based models of populations

Individual based models (IBMs) treat a population as a collection of individuals, each growing, reproducing and dying in response to its physiological state and to the local environment. We use IBMs in which the physiology of individuals is described by a DEB model. Previous research on zooplankton dynamics (Nisbet et al. 1997), and related research on microbial populations (Kooijman 1993, 2000) has established that in a wide range of situations, we can successfully predict biomass changes using simple ordinary differential equations, derived by making special assumptions that simplify our DEB models. Where possible, such simplified descriptions are used in the current work.

Community dynamics

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. 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 use recent competition theory for “open” benthic systems, originally developed through previous ONR funding (Wilson et al. 1999), and extended as part of the present research (Richards et al. 2000; see also report to ONR for FY 1999). This theory exploits the biomass-based approach described above, our criterion for two species to “coexist” being that each can grow in the presence of the other. Our most recent work (FY 2000, detailed below), involves consideration of source-sink dynamics, and uses some variants of the more traditional models.

Modeling ecosystems

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. Ross et al., 1993a; Gurney and Nisbet, 1998; chapter 7) make a convincing case that ecosystems do truly have dynamics that can be described by relatively simple, general, models. Our research exploits one important property of DEB-based ecosystem models: the capability to link the description of biological and chemical phenomena. The development of appropriate methodology is part of the on-going research (see section d below); as a starting point we use a model developed by Kooijman and Nisbet (2000) 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.** We have found that considerable simplification of the Kooijman-Nisbet approach is essential if practical models are to be achieved. This is reported in the first section of "Results" (below).

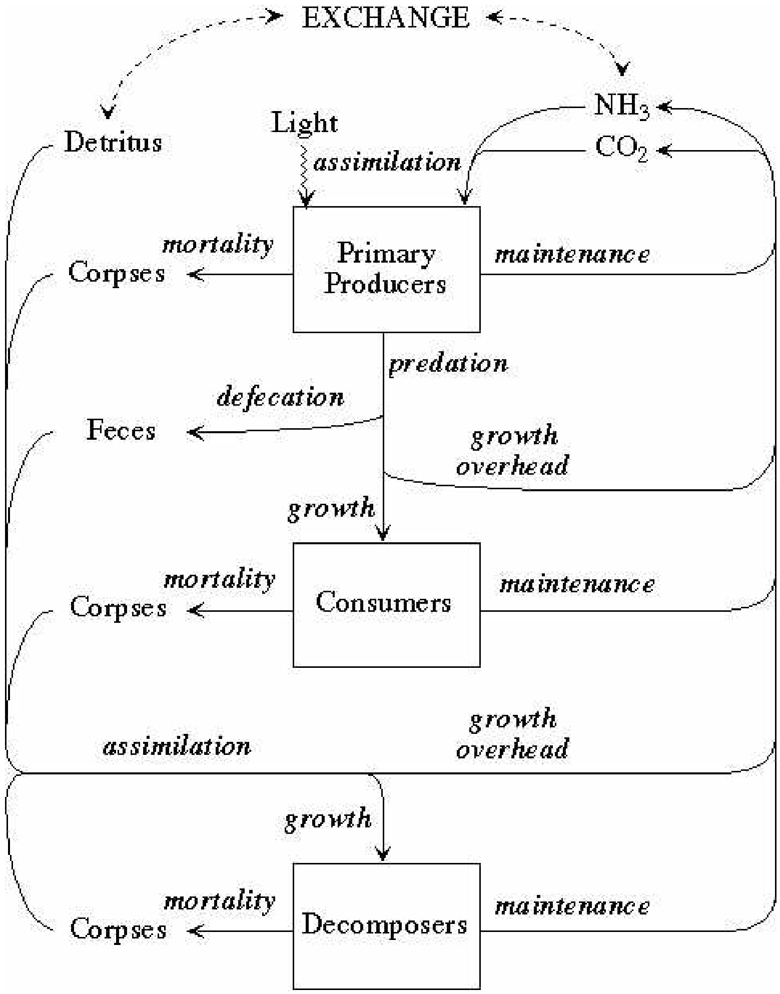
WORK COMPLETED

Highlights of FY 00 include:

- Development of ecosystem models with simultaneous energy flow and recycling of elemental matter.
- Formulation of population models that explicitly recognize herbivore stoichiometry.
- Modeling the trade off between dispersal ability and competitive strength.
- Tests of a simple model of experiments by Dr. Kevin Carman on polluted benthic microcosms.

RESULTS

Ecosystem models with simultaneous energy flow and recycling of elemental matter



We have developed a simple DEB-based ecosystem model with three trophic levels, primary producers, grazers and decomposers (see figure above). Primary producers grow with any of light, carbon dioxide and/or nutrient limitation. Consumer growth is energy limited, and decomposers may experience either or both of energy or nutrient limitation. Primary producers, consumers and decomposers all have stoichiometric constraints that specify remineralization fluxes due to assimilation and growth overheads and maintenance processes. In initial model testing, we assumed a system that is open with respect to energy and carbon (light and carbon dioxide can come in, heat and carbon dioxide can go out) and closed with respect to nutrients and biota, but the model is much more widely applicable.

Many previous models of consumer-resource systems ignore microbial dynamics and do not fully specify all processes that are needed to construct elemental mass balances. A common observation with such models is that enrichment of the system tends to destabilize the dynamic, with the amplitude of fluctuations in producer and consumer densities increasing with increasing nutrient loads. However, the dynamics of real populations are much more stable (e.g. Murdoch et al. 1998). We have found that, with realistic parameter values from aquatic systems and tidal mudflats, decomposers have a stabilizing effect on producer and consumer dynamics, since adding the level of decomposers implies adding a delay in the remineralization of nutrients from feces and corpses. However, the stabilizing effect is not sufficient to bring the dynamics of model organisms in accordance with those of real populations. We have also investigated how toxicants may affect the stability of the system. If the toxicant effect is primarily an increase in the mortality of either primary producers or consumers, the dynamics of the system tend to stabilize.

Population Models with herbivore stoichiometry

C:N and C:P ratios vary greatly in algae as a result of their capacity to store nutrients. There is typically much less variability in the stoichiometry of grazers; furthermore grazers commonly have carbon to nutrient ratios lower than that of photosynthsizing algae. A consequence is the possibility of nutrient limited control of grazer growth. Some simple models of this situation were modeled by Andersen (1997) in the context of phosphorus limitation of the growth of freshwater zooplankton. We have generalized this work, in simple models where the concept of the synthesizing unit (SU) described by Kooijman (2000) allows a mechanistic representation of multiple limitations. Details are in Muller *et al.* (*submitted*).

Modeling the trade off between dispersal ability and competitive strength.

Our previous work on competing marine consumers (reported in FY 1999) focused on the effects of open recruitment. The models we developed are appropriate to studies in a single locality, where feedback to the "source(s)" of the open population is unimportant. Working in collaboration with Dr. P. Amarasekare (NCEAS), we have extended this work by studying metapopulation models that consider explicitly the interaction between competition and dispersal. We showed that a dispersal-competition tradde-off can only lead to local coexistence of both species in a single locality when there are patches in the landscape that the superior competitor cannot colonize. If such refuges for the inferior competitor do not exist, and the environment is otherwise spatially homogeneous, a dispersal-competition trade-off cannot lead to local or regional coexistence. If biotic or abiotic factors create spatial heterogeneity in competitive rankings across the landscape, then local coexistence can occur even in the absence of a dispersal-competition trade-off. Co-existence involves source-sink dynamics. Details of this work are reported in Amarasekare and Nisbet (*submitted*).

Model of Carman's microcosms

We completed a rigorous qualitative analysis of a large family of models of polluted benthic microcosms, motivated by experiments of Dr. K. Carman and co-workers (Louisiana State University), who investigated the effects of diesel fuel contamination of a benthic, estuarine, food-web, using microcosms. The model uses three differential equations describing changes in utilizable nitrogen, biomass density of algae, and biomass (or carbon) density of grazers. Nitrogen becomes available at a fixed rate, and is absorbed by benthic microalgae (BMA), whose growth rate depends on light and available nitrogen. Gazers gain carbon by eating algae and lose carbon through respiration and mortality. We previously showed that in a linear chain model, the equilibrium density of BMA is unaffected by an increase in the input flux of nitrogen, but will increase in response to increased loss rates for grazers. We have extended these analyses to include the effects of recycling of nitrogen within the system

We have derived an almost complete set of model parameters that will allow quantitative tests of the models against Carman's data. The one unresolved parameter relates to an apparent inconsistency in remineralization fluxes measured by different methods. A paper on this work will be submitted in the near future.

IMPACT/APPLICATIONS

Our DEB modeling work aims to unify theory describing the effects of environmental stress on diverse range of organisms. A key component is the emphasis on model testing; insight gained here will be applicable in other contexts. 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.

RELATED PROJECTS

PI Nisbet led, and co-PI Muller particpated in a working group at the National Center for Ecological Analysis and Synthesis (NCEAS) on the theme "Population level effects of toxicants". The working group met twice in FY 2000.

REFERENCES

Andersen, T. (1997). *Pelagic Nutrient Cycles*. Springer-Verlag.

Kooijman, S.A.L.M. (1986) Population dynamics on basis of energy budgets. The Dynamics of Physiologically Structured Populations (eds. J.A.J. Metz & O. Diekmann), pp. 266-297. Springer-Verlag, Berlin.

Kooijman, S.A.L.M. (1993). *Dynamic Energy Budgets in Biology*. Cambridge University Press.

Kooijman, S.A.L.M. (2000). *Dynamic Mass and Energy Budgets in Biology*. Cambridge University Press.

Kooijman, S.A.L.M. and Nisbet, R.M. (2000). How light and nutrients affect life in a closed bottle *In*: Jorgensen, S.E. & Kay, J.J. (Eds) *Thermodynamics and Ecology*. Lewis Publ.

Lika, K. and Nisbet, R.M. (in press). A dynamic energy budget model based on partitioning of net production. *Journal of Mathematical Biology*.

Muller, E.B., Nisbet, R.M., Kooijman, S.A.L.M., Elser, J.J., and McCauley, E. Multiple growth limitations in herbivores. Submitted to *Ecology Letters*.

Murdoch, W.W., Nisbet, R.M., Mccauley, E., DeRoos, A.M. and Gurney, W.S.C. (1998) "Plankton abundance across nutrient levels: tests of hypotheses". Ecology 79(4) 1339-1356.

Nisbet, R.M., Mccauley, E., Gurney, W.S.C., Murdoch, W.W. & deRoos, A.M. (1997) Simple representations of biomass dynamics in structured populations. Case studies in mathematical modeling--ecology, physiology, and cell biology (eds. H.G. Othmer, F.R. Adler, M.A. Lewis & J.C. Dallon), pp. 61-79. Pretice Hall,, Upper Saddle River, New Jersey.

Nisbet, R.M., Muller, E.B., Lika, K. & Kooijman, S.A.L.M. (2000) From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, in press.

Wilson, W.G., Osenberg, C.W., Schmitt, R.J., and Nisbet, R.M. (1999). Complementary foraging behavior allows co-existence of two grazers. *Ecology* **80**: 2358-2372.

PUBLICATIONS

Amarasekare, P. and Nisbet, R.M. Spatial heterogeneity, source-sink dynamics, and the coexistence of competing species, Submitted to *American Naturalist*.

Kooijman, S.A.L.M. and Nisbet, R.M. (2000). How light and nutrients affect life in a closed bottle *In*: Jorgensen, S.E. (Editor) *Thermodynamics and Ecology*. Lewis Publishers.

Lika, K. and Nisbet, R.M. A dynamic energy budget model based on partitioning of net production. *Journal of Mathematical Biology,* in press.

Muller, E. B., Nisbet, R. M. Survival and production in variable environments. *Bulletin of Mathematical Biology*, in press.

Muller, E.B., Nisbet, R.M., Kooijman, S.A.L.M., Elser, J.J., and McCauley, E. Multiple growth limitations in herbivores. Submitted to *Ecology Letters*.

Nisbet, R.M., Muller, E.B., Lika, K, and S.A.L.M. Kooijman. From molecules to ecosystems with dynamic energy budget models. *Journal of Animal Ecology*, in press.

Richards, S. A., Nisbet, R. M., Wilson, W. G., Possingham, H. P. (2000) “Grazers and diggers: competition and coexistence among foragers with different feeding strategies on a single resource”. *American Naturalist,* 155:266-279.