U.S. GLOBEC NEWS

Models, Physics and Predictive Biological Oceanography: KNOW Your Organism

by Marc Mangel

From its inception the U.S. GLOBEC program has rightly recognized that modeling should be an inherent conceptual component, particularly if we want to connect biological and physical oceanography. In fact, there is considerable merit to the argument that the harder it is to get the data, the more important it is to do the modeling. Michael Sissenwine (1983), considering the Convention for the Conservation of Antarctic Marine Living Resources, wrote,

> Modeling should be an integral part of research on Antarctic marine living resources. It is the process of formalizing thought. Mathematical models express ideas in concise and universal language...Like thinking, modeling is an ongoing process which is stimulated by observations (i.e., data). Models in turn stimulate additional data collection, usually followed by modeling. The process of modeling forces consistent thinking. This process is particularly important for multi-disciplinary, multi-national situations where observations are made and ideas evolve independently. A model is a synthesis of these observations and ideas.

Simply put: before spending lots of time at sea, we should think carefully about the kinds of data that should be collected and what they can tell us; here models can play an enormously important role.

But, what kinds of models should be used? I differentiate between models based in "physical mathematics" and those based in "biological mathematics." The former are essentially rooted in classical mechanics, and assume large numbers of identical individuals. The latter differ most importantly in recognizing the role of natural selection in shaping organisms and, particularly, that organisms can facultatively respond to their environments, often in unanticipated ways.

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In its early stages, our field benefited greatly from the use of "physical" mathematics (ordinary and partial differential equations) to describe biological settings. For example, the Lotka-Volterra predator prey equations illustrate how purely biological interactions between predators and prey can lead to oscillations in population numbers. Similarly, the Lotka-Volterra two-species competition equations show how competitors might either co-exist or not, depending upon the strength of inter- and intra-specific interactions. Nonlinear reaction-diffusion equations show how species-specific interactions such as predation or competition, melded with diffusion, can lead to spatial pattern. However, such models

are difficult to use as predictive tools if they involve parameters that are fit from the data series which are being modeled (as is often the case). They do not provide a means for predicting how the parameters, and thus the dynamics, will change in changed circumstances. An exception could be the situation in which organisms are transported by passive diffusion or currents (so that we understand the transport parameters very well), but even simple organisms can behave in complex ways and modify their transport.

Physical mathematics is especially limiting, for two reasons, if we want to predict the response of organisms to changed environments. First, the historical emphasis of physical mathematics has lead to what might be called "backward hypotheses": workers often formulate a "null" hypothesis that is exactly contrary to what would be concluded by careful thinking about the biological situation. For example, the inappropriate assumption that the experimental subject and observer share the same perceptions of the environment causes one to assume global information as a null hypothesis when, in fact, exactly the opposite should often be the underlying assumption. To illustrate this, a common assumption is that predators in a spatially distributed system will aggregate in regions having highest prey densities. This idea is based on the assumption that the predators "know" the global distribution of prey and are wide ranging. When organisms demonstrate such global environmental knowledge, the phenomenon needs to be explained, but it is not the starting point. This is particularly important if we want to use models of organisms to help identify the correct scales of measurement for physical studies. Second, because of the enormous numbers of particles usually studied in physics, diversity is not important. But one of the great attractions of biology is the enormous variation of living organisms. In fact, R. J. Berry (1989)

has said, "Variation is the core of biology." Removing diversity from biological descriptions renders those descriptions nearly devoid of meaning.

To include such diversity and develop means for predicting the parameters in the equations of population dynamics, we must adopt the principle "KNOW Your Organism" as a guidepost for biological modeling, and for coupling of biological and physical models in the U.S. GLOBEC program. The principle asserts that organisms can display a wide range of behaviors in response to their environments and that we must thoroughly and deeply understand the particular organism before constructing a quantitatively predictive model. Approaches that focus on the state of the organism (Mangel and Clark, 1988; Mangel and Ludwig, 1992) allow this to be done. Furthermore, by considering the state, we link physics and biology in a natural way since physical factors such as temperature, photoperiod, and flows generally affect and constrain (because of physical and chemical laws) the physiological condition of organisms. Physical mathematics underlies these couplings.

The principle "Know Your Organism" is almost antithetical to what guides us in physics. After all, the laws governing ocean physics are the same in the California or Benguela Currents, or in the Antarctic or at the Equator. And it is true enough that biological organisms must obey the laws of physics. But these laws merely act as a constraint on the main law of natural selection that governs organisms. "Know Your Organism" means that, in general, we will not be able to develop highly predictive and general "zooplankton" or "fish" models, although we should be able to develop qualitative models which provide insight by using physical mathematics. Highly predictive models must treat the organisms as ones which can behave and respond to changed environments in novel ways, and it is here that biological mathematics is needed. In general, the challenge still awaits us.

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