Coupled Biological-Physical Models:
Physical Transport vs. Stochastic Forcing

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Abstract. The variability in records of biological quantities may be due to physical phenomena or the inherent variability in biological processes. A program of model studies employing simple biological formulations can address this issue. The biological models, though simple, contain important elements of the complexity thought to characterize marine systems. Preliminary results depend on the details of both the biological and physical models. They suggest that both physical transports and stochastic forcing may give agreement with observations. Recommendations for future studies are sketched.

1. Introduction

How do organisms in the sea change over space and time? This broad question occupies most biological oceanographers. More precisely, how do the numbers, or concentrations, of marine organisms vary spatially and temporally? This restricts the investigators to those interested in the population and community ecology of marine biota—broadly defined, however. For example, this might include geochemists, because biota play central roles in biogeochemical cycling in the sea (Fasham, 1984; Wollast et al., 1993). Moreover, physical oceanographers participate in the large, multidisciplinary investigations (e.g., JGOFS, GLOBEC, CoOP) that increasingly involve a large fraction of the U.S. oceanographic community. One reason for the need to couple knowledge of the physical phenomena to biological research in the sea is the crucial role that transport may play in budgets for nutrients and interacting organisms (McGillicuddy et al., 1995a,b). Indeed, advective contributions may dominate the expressions that arise for the time and space derivatives of biological and geochemical quantities (Powell, 1989), that is, physical processes may control the spatial and temporal variability of, for example, biological quantities.

Let me make these considerations more precise. Consider a control volume of fluid in the sea, depicted by the rectangular box in Figure 1. Let one construct a budget for some quantity, $Q$, within the control volume. $Q$ could be any conserved quantity, like energy, or the mass of a nutrient, or even organisms, themselves. Input and output fluxes, $F_i$ and $F_o$, respectively, transport the quantity into and out of the box. Within the control volume itself, $Q$ may be produced or consumed, and one calls the rate of production $P$, and the rate of consumption, $C$. Thus within the control volume,

$$\frac{dQ}{dt} = (P - C) + (F_i - F_o) \quad (1)$$

![Figure 1. Control volume used to construct a budget for a quantity, $Q$, in the sea. $F_i(F_o)$ is an input (output) flux of $Q$. $P(C)$ is internal production (consumption) of $Q$. See equation 1.](image)

The $(P - C)$ terms are the traditional concerns of biology, geochemistry, etc. $(F_i - F_o)$ is "the physics"; in this case the net transport into the control volume. As noted above, the $(F_i - F_o)$ terms often dominate such budgets. So, in biological investigations, judicious coupling of physical processes to biological phenomena is crucial to observational programs (GLOBEC 1992, GLOBEC 1996), analysis of data, and modeling studies (Eckman, 1994).

Here I address one of a large number of questions that can arise in coupled biological-physical models. Using equation (1) as a template, assume that expressions exist for $(P - C)$, i.e., a biological model exists. (The variety of organisms in the sea is great. Accordingly, a very large number of ecological models exist that attempt to describe marine populations and communities. No small number of references can suffice. Nonetheless, one might enter this vast literature through Hofmann and Ambler, (1988); Wrablewski and Hofmann, (1989); Fasham et al., (1990); Denman and Gargett,
Finally, there are two reasons why this year’s ‘Aha Huliko’a proceedings is a natural place for this contribution. First, the coupled biological-physical models have intrinsic interest for physical oceanographers and applied mathematicians—as well as biologists. The coupled problem introduces new spatial and temporal scales—regimes determined by a new set of non-dimensional numbers. Perhaps the best analogy might be to a chemically reacting fluid (Hill, 1976). Here two “new” non-dimensional numbers arise from time scales set by the rates of chemical reactions (they are called the Damköhler groups). They determine the regimes in which different phenomena in the chemically reacting fluid are observed. Second, the nature of the stochastic forcing that should be applied is far from clear. Perhaps techniques may be profitably borrowed from physics for performing this coupling. Perhaps some of the other contributions to these proceedings may have direct bearing on this question. I point, for example, to the chapter of R. Adler.

2. Simple Formulations

2.1. Overview

All realistic food webs are complex. Figure 3 shows a common diagram with a large number of species (boxes) and a very large number of links (arrows) between species. Some of the “species” within each box, are not species at all, but aggregates of related species, like ”phytoplankton”, or ”amphipods.” If an equation like (1) were written for each box, in terms of the many (surely) nonlinear connections between boxes, the set of equations would be numerous—unmanageably so, and contain a very large number of potentially poorly known constants. Tentative generalizations about the temporal behavior of such a large, nonlinear system would be greeted with skepticism—and justifiably so. The only approach to such a system is numerical simulation, with the caveat that another set of parameters, initial conditions, etc., could be expected to lead to entirely different results.

Most oceanographic models have turned from elaborate schemes that might contain tens to hundreds of equations, to more manageable formulations that contain of order five boxes (equations). Figure 4 taken from Fasham et al. (1990) shows a popular 7-box ecosystem model on which a great deal of effort has been expended. Such models, stemming from pioneering work of Riley (1947), Riley et al. (1949), and elaborated upon by Steele (1974), fall under the general rubric of N-P-Z models—boxes for nutrients (N), phytoplankton (P), and zooplankton (Z). Figure 4 contains additional boxes necessary to represent other processes, especially recycling, but the general theme of this model differs little from that discussed by Steele (1974).
Figure 3. An Antarctic food web.
Most would agree that two additional elements of real food web structure/processes in the sea are essential for any model. The first is saturation. Consider the link (arrow) between boxes P and Z in Figure 4. The arrow represents the consumption rate of phytoplankton by zooplankton, i.e., grazing. A graph of per capita grazing vs. P (phytoplankton concentration) would approach an asymptote for large values of P; i.e., there is a maximum number of phytoplankton that a single zooplankter can graze per unit time. Hence, the curve describing the grazing response of zooplankton to phytoplankton is nonlinear. The second element is complex life history. Whenever trophic levels “above” phytoplankton are important, i.e., grazers on phytoplankton, like microzooplankton and mesozooplankton (Frost, 1987), must be included, the modeler must address the large number of life stages—termed age-, or stage-structure—that are necessary to describe accurately zooplankton population dynamics. For example, the most numerous of the marine mesozooplankton, calanoid copepods, have twelve life stages (microzooplankton are known to be voracious consumers of phytoplankton, but little is known about the details of their life history). In Steele’s (1974) studies, the life cycle of North Sea copepods was incorporated by adding a box to represent zooplankton weight. The model zooplankton populations were allowed to reproduce until individuals had reached a certain weight, i.e., had become reproductively competent adults. Landry (1976) constructed a generalization of Steele’s (1974) model that avoided the earlier artificial approach to copepod life histories.

The three simple models discussed here incorporate some form of saturation. However, only one of the three incorporates age-, stage-structure for the zooplankton predators. The aim of the authors of the models was to show that even with very simple models—and the models are nearly as simple as one could possibly conceive—quite complicated behavior results for realistic parameter choices. To add age-, stage-structure to the two models that do not contain it would only make the calculated behavior more complicated. Moreover, the addition of age-, stage-structure might distract the reader from the straightforward points that the authors were attempting to establish.

2.2. Three-level food chain

Hastings and Powell (1991) [hereafter HP] analyzed a three-level food chain that was designed to mimic a simple phytoplankton-microzooplankton-mesozooplankton interaction. Constants were chosen from information collected in the subarctic North Pacific, i.e., the SUPER collaboration (Miller, 1993). The non-dimensional equations used by HP are

\[
\frac{dx}{dt} = x(1 - x) - f_1(x)y \\
\frac{dy}{dt} = f_1(x)y - f_2(y)z - d_1y \\
\frac{dz}{dt} = f_2(y)z - d_2z
\]

where \(f_1(u) = a_1u/(1 + b_1u); a_i, b_i, d_i \) are constants and \(x\) can be considered an autotroph, \(y\) an herbivore population, and \(z\) a carnivore population. Figure 5a shows the behavior of one of the populations \((x)\); Figure 5b shows the three-dimensional inverted “teacup-like” attractor in the phase space of the three populations. Figure 5c shows the sensitivity-to-initial conditions that this system exhibits for this choice of parameter values. That is, the system is chaotic.

HP suggested that the chaotic behavior arose because of the natural tendency of predator-prey systems to oscillate. That is, \(x\) and \(y\) are undergoing predator-prey oscillations; and \(y\) and \(z\) are also experiencing predator-prey oscillations, but with a different frequency. Note that the two oscillators are (nonlinearly) coupled via \(y\); i.e., \(y\) is the predator in one oscillator and the prey in the other. When the two frequencies are incommensurate (i.e., not multiples of one another) then one might expect chaos to ensue just as in the case of periodically forced oscillations. Because food webs are a complex system of interacting producers and consumers (see Figure 3) one might expect oscillatory behavior to be common. And some of the oscillations are likely to be chaotic.

The reason to focus on this simple model is that it is just one example of the result that the general coupled biological-physical system will involve physical forcing of a subsystem with (potentially) chaotic behavior—the biological model. Thus, the general program depicted in Figure 2 should allow a “biota box” with

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**Figure 4.** A schematic showing a 7-box model of plankton dynamics based on transfers of nitrogen between compartments. After Fasham et al. (1990).
sufficient complexity for chaos. Whether the physical forcing in Figure 2 employs the “usual” transport equations, or stochastic forcing, the investigator should be prepared for extremely complicated results—even from very simple-looking models.

2.3. Two age-class, two patch model

Hastings (1992) [hereafter H92] developed a model for a single population with two age classes (e.g., juveniles and adults) existing in two patches. Organisms were allowed to disperse between patches, but the dispersal rate depended upon the age class of the dispersers. Moreover, the fecundity of the adults (i.e., the rate at which juveniles are produced) depended in nonlinear, saturating, fashion upon both the number of juveniles and adults—termed density dependence. Figure 6 shows a schematic of this two age-class, two patch model; details of the actual difference equations, including the simple, saturating functional forms, and constants used in the discrete-space, discrete-time calculations can be found in H92.

Figure 5. a. \( x(t) \) vs. \( t \)—the “autotroph”. Note the close-to-periodic appearance. b. The inverted teacup attractor in the 3-dimensional phase space of the three populations \( x, y, \) and \( z \). c. Sensitivity-to-initial conditions, i.e., chaos. \( x(0) \) for the dotted curve was changed by approximately 1\( \sigma \) from that of the graph of a. \( y(0) \) and \( z(0) \) were unchanged.

Figure 6. Schematic of the two-stage, two-patch model, with density dependent fecundity (reproduction) H92.
and spatially varying growth rate for the prey along a single space dimension. P93 allows both prey and predator to diffuse (Fickian diffusion in one dimension with the same diffusion coefficient, \(d\)). The two non-dimensional equations used by P93 are

\[
\begin{align*}
\frac{\partial p}{\partial t} &= r_x p(1 - p) - (a ph)/(1 + bp) \\
&+ d(\partial^2 p/\partial x^2) \quad (3a) \\
\frac{\partial h}{\partial t} &= (aph)/(1 + bp) + d(\partial^2 h/\partial x^2) \quad (3b)
\end{align*}
\]

where \(p\) is the prey concentration and \(h\) is the predator concentration, \(a\) and \(b\) are constants, and \(r_x\) is a spatially varying growth (taken as a linear function of \(x\) by P93). Note the similarity to equations 2. Note also that, in contrast to HP and H92, equations (3) are partial differential equations in two dimensions, time \((t)\), and space \((x)\). Moreover, equations (3) allow consumer and producer to interact, in contrast to H92. Further, Fickian diffusion is a more realistic approximation to dispersion in the sea than that used by H92. The constants used by P93 were selected to approximate those that are thought to characterize phytoplankton and zooplankton transported by turbulence in the sea.

P93 found that as the diffusion coefficient was reduced, the otherwise periodic system (i.e., predator-prey oscillations) became chaotic. Figure 8 shows evidence for the sensitivity-to-initial conditions found in the P93 calculations. One concludes that the spatial dimension (i.e., transport) may lead to temporally complex behavior in the sea. Further, careful investigation may discover that spatial patterns in the sea could be related to the generation of spatially-induced chaos. Finally, one is struck by the similarities of the conclusions

**Figure 7.** a. Juveniles in patch 1 vs. time \(D_0 = 0.5\); b. Juveniles in patch 1 vs. time \(D_0 = 0.15\); c. Juveniles in patch 1 vs. time \(D_0 = 0.005\).

**Figure 8.** Sensitivity-to-initial conditions, i.e., chaos, in equations (3). At a fixed position \((x)\), the two curves represent two different initial conditions for \(p\) and \(h\). The initial values differ by approximately 1\(\sigma\); all other quantities in equations (3) are identical for the two curves.
drawn by H92 and P93—the existence of dispersion (diffusion) in space, with low dispersion (diffusion) coefficients, can lead to chaotic behavior in two very different models.

The conclusions from the three models—HP, H92, and P93—are consistent. When working to carry out the program depicted in Figure 2, expect that the “biota box” may exhibit chaos, and be prepared to interpret results from any model coupling physical transports to biological processes—usual fluid transports or stochastic forcing—in terms of the possible chaotic, oscillatory behavior. Intuitively observers often surmise that physical variability—“unpredictable” waves, winds, tides, currents, mixing, etc.—are the agents that give biological records the appearance of unpredictability. This may not be the case. Rather, the chaotic behavior of biological phenomena may be the cause of the difficulty in explaining variability. Even the simplest models may lead to extremely complex behavior.

4. Partial Successes

Though the program of Figure 2 has not been carried out for any of the three models considered in the previous section, some progress has been made. Models that capture some of the flavor of both the “physical forcing” and “stochastic forcing” paths have been coupled to biological models. The results obtained with these efforts provide signposts for future, more ambitious endeavors that will attempt to capture a larger amount of the essence of Figure 2’s program.

4.1. Physical Transport

Powell and Okubo (1994) [hereafter PO] coupled a predator-prey model to a model for turbulent flows. The predator-prey formulation, the classic Lotka-Volterra model, reminds one of Pascaul’s (1993) phytoplankton-zooplankton model but does not contain the important saturating responses. The turbulence model, a diffusion approximation, has the proper spatial and temporal scale dependence for small scales [i.e., in the 3-dimensional inertial sub-range (Tennekes and Lumley, 1972; McComb, 1991) and large scales (i.e., 2-dimensional, “enstrophy” regime). PO obtained analytical results for the coupled system if the (nonlinear) Lotka-Volterra forms were linearized about their mean values.

Focusing on general characteristics of the resulting spatial patterns, PO asked what were the contributions that biological interactions (i.e., the “biota box” in Figure 2) made to the spatial distribution of variability? More precisely, PO compared wave-number spectra obtained for interacting organism patterns in the coupled system to spectra obtained for organisms acting merely as passive tracers, i.e., noninteracting. The interacting and noninteracting model systems showed very different behavior. However, depending upon the turbulence regime, one could find more variability at small spatial scales (a “whiter” spectrum), or more variability at larger scales (a “redder” spectrum). No immediate generalizations about how “biology” might affect the spatial pattern in a coupled biological-physical system emerged from this study. This lack of a simple generalization has been mirrored in another similar theoretical investigation directed toward terrestrial systems (Roughgarden, 1978). Apparently, small details in the model formulation can, and do, make a big difference. It does not seem productive to pursue the comparison between PO’s results and those that might be obtained from a stochastically forced, linearized Lotka-Volterra system. The neglected non-linear interactions may be simply too important in this case.

Nonetheless, one can draw some conclusions from PO’s calculations that may have broader applicability. First, a spatial pattern set up by physical forcing alone can be altered substantially by biological interactions. Second, how such alterations will manifest themselves is dependent upon the details of the specific model. Indeed, Powell and Okubo found situations where biological interactions led to more variance at both small and large scales. Finally, the PO calculations could be carried out for the full (nonlinear) Lotka-Volterra model. In this case the calculations would have to be performed numerically; PO linearized the biological equations in order to obtain analytical results. If the stochastic forcing calculations were also performed on the the nonlinear system, this could provide a test for the program of Figure 2.

4.2. Stochastic forcing

In a recent paper Higgins et al. (1997) [hereafter H97] forced a simple age-structured model of the Dungeness crab on the west coast of the U.S. with stochastic forcing. The model is similar in structure to that of Hastings (1992)—including the saturating responses—but allows more age classes. H97 does not contain spatial structure, i.e., no patches. The model was fitted to 42 years of data from eight separate locations extending over one thousand miles in Washington, Oregon, and Northern California. The predictions agree well with the observed crab catch data.

For some years there has been interest in the role that physical transports play in controlling the variability of the Dungeness crab catch along the west coast of North America (e.g., Johnson et al., 1986). It is also thought that spatial structure is important in controlling the dynamics of the crab populations (Hastings and Higgins, 1994). For these reasons, and the commercial importance of the Dungeness crab, it seems likely that physical transport models will soon be coupled to H97. This
could provide the first test of the full program depicted in Figure 2.

5. Recommendations

I make two recommendations for future work. They follow closely upon my previous discussion of the five models—three “simple formulations” (HP, H92, and P93) and two “partial successes” (PO and H97).

First, the program of Figure 2 should be completed. That is, all five biological models should be coupled to, and driven by, a physical transport model and stochastic forcing. There is much to be said for an incremental approach—small steps; so the initial tasks should focus on the partially successful work of PO and H97. A sketchy prescription of how one might proceed in both cases was given in the previous section. One can be optimistic about “greater successes” in a timely fashion with this approach. Minor modifications must be made to H92 and P93 to pursue this path further. That is, more realistic dispersion (diffusion) algorithms must be substituted for the present, simpler calculations. This task is straightforward, however. Indeed, my colleagues and I have started on this activity for the P93 model. No modifications seem necessary for coupling HP to a physical transport/stochastic forcing model, however.

Second, some careful attention must be directed to the formulation of the stochastic forcing model. It is far from clear how the “statistical fluctuations” should be applied to the biological models, Through uncertainty in model constants? “Noise” added to the calculated quantities at specified intervals? And what is the statistical distribution of the fluctuations? The attack on these and other similar questions can profit from insights developed by physicists—some of whom have contributed to this ‘Aha Huliloko’a volume.

In conclusion, the program of Figure 2 can be successfully completed for the five “manageable” models described above. It promises to provide a basis for future studies. In particular, for the model systems, the program can suggest mechanistic answers to questions like, how much of the variability seen in biological records is due to the variability caused by physical forcing? How much is due to the inherent variability found in biological phenomena?

Finally, the program of Figure 2 is timely. The rapid increase in computational resources attracts modellers to full-scale simulations of systems like that shown in Figure 3 or to considerable elaborations of Figure 4. Coupled simulations of such complex systems will “soon” be performed, and may become common. We are not likely to understand the results of such presently daunting computations, except from some platform of experience developed from studies of simpler systems—which is the program of Figure 2 applied to models like the five I have discussed here.

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