Exxon Valdez Oil Spill
Restoration Project Annual Report

Toward a Mass-Balance-Based Dynamic Model of Alaska's Prince William Sound Ecosystem for the Post-Spill Period 1994-1996

Restoration Project 98330-2
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

Robert D. Powell
Stuart L. Pimm

Department of Ecology and Evolutionary Biology
University of Tennessee
569 Dabney Hall
Knoxville, TN 37996

June 1999

Toward a Mass-Balance-Based Dynamic Model
of Alaska's Prince William Sound Ecosystem
for the Post-Spill Period 1994-1996

Restoration Project 98330-2
Annual Report

Study History: This project was initiated in 1997 as part of the Restoration Project 98330 under the title A Trophic Mass-Balance Model of Prince William Sound. The lead organization is The Fisheries Centre of the University of British Columbia (UBC), where the Principal Investigator is Dr Daniel Pauly. The work reported in this publication was carried out under a subcontract at the University of Tennessee under the direction of Dr Stuart Pimm. Pauly's group is responsible for the static mass-balance model of Prince William Sound. This work was reported separately under the title *A Trophic Mass-Balance Model of Alaska's Prince William Sound for the Post-Spill Period 1994-1996.* Pimm's group is responsible for parameterizing a dynamic model using the UBC model as the point of departure. This report covers the first year's activity of Pimm's group. The project is currently in its second year of funding. A third year of funding is planned for closeout activities of the UBC group.

Abstract: A methodology was developed to parameterize dynamic models from static mass-balanced models. Dynamic models were constructed using four such static models supplied by our partners at the University of British Columbia. A number of simulations were built using a variety of approaches, including implicit and explicit detritus, constant effort and regulated fisheries, parametric variations in the amount of detritus in the system and several alternative approaches to parameterization. Eigenvalues were calculated for all the dynamic models and used to analyze the stability of the models. All the models were found to be unstable. The degree of instability was not great. Most species remain close to their equilibrium values, though oscillations are long-lived (>10 years). Under moderate perturbations most models hold together for more than ten years. Under more severe perturbations, some species undergo large oscillations and extinctions occur, sometimes within weeks of the perturbation. The most volatile species are the avian raptors, seabirds, invert-eating birds, orcas, small cetaceans, pinnipeds, and sea otters. It is noteworthy that these are all species greatly impacted by the *Exxon Valdez Oil Spill.* Difficulties with the models and the modelling process are discussed and recommendations are made for improving the models.

Key Words: dynamic models, Ecopath model, ecosystem modeling, *Exxon Valdez* oil spill, eigenvalue analysis, food webs, Lotka-Volterra model, mass-balance, system analysis.

Project Data: No field data was developed specifically for this project. See the UBC report for an account of the data gathering process that resulted in the static models.

Citation: Powell, R.D. and S.L. Pimm. 1999. Toward a mass-balance-based dynamic model of a Alaska's Prince William Sound ecosystem for the post-spill period 1994-1996, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98330), University of Tennessee, Knoxville, Tennessee.

Table of Contents

List of Figures

Executive Summary

This report relates the results of the second part of a two part effort to provide an overarching model that draws together the results of the many ecological studies conducted over the ten years since the *Exxon Valdez* oil spill. Most of these studies were sponsored by the *Exxon Valdez* Oil Spill Trustee Council as part of their restoration program. The main idea was to combine the Ecopath method of mass balancing food webs, developed by Pauly and various colleagues, with the ecosystem dynamics expertise of our group. The aim of the project was to obtain a comprehensive description of the Prince William Sound food web and a means of predicting the dynamic response of the system to perturbations.

ECOPATH — the software and the process that deduces the parameters — produces a mass-balanced model of an ecosystem. Given this static description, one can make sensible assumptions about the dynamic interactions between the ecosystem's components and so produce a dynamic ecosystem model. Dynamic models offer the possibility of answering major questions about permanent changes and transient shocks to an ecosystem. (Oil spills have features of both.)

This recipe is sequential: first ECOPATH, then dynamic modeling.

A key part of the model-building process, detailed in Pauly's annual report, was a collegial process of negotiation and data sharing over the course over the course of a year among a group of recognized domain experts. This led to the making of many models. In the process of refining the models, some were retracted by Dr. Pauly's group. Some were rejected in response to evaluations from the peer review group. Others we rejected as having impossible or implausible parameters from a dynamic point of view. This development and criticism of models is a natural and desirable part of the Ecopath process.

Our approach to dynamic modeling was to utilize the well-known Lotka-Volterra equations for a food web of predator-prey relationship. We developed the theory required to parameterize a dynamic using the Ecopath mass-balanced result as the description of the equilibrium condition. We demonstrated a dynamic simulation based on a preliminary Ecopath mode at an October 1998 workshop in Anchorage. Unfortunately, we did not receive the "final" Ecopath model of Prince William Sound until 17 February 1999, too late to complete a dynamic simulation and conduct an adequate analysis in time to meet the deadline for the annual report. Unfortunately, this has not been the only or even the major difficulty.

Ecopath, broadly defined, consists of several routines. They include those for assuring mass balance (Ecopath in the strict sense), a package for exploring alternative configurations within the range of parameter uncertainties (EcoRanger), a simulation package (EcoSim) and a spatially explicit simulation package (EcoSpace). We found that all these packages contained major software flaws — bugs — that prevented their use as advertised. Our experience of modeling complex dynamic systems led us to reject the two simulation packages from the outset. We circumvented other bugs by programming our own versions of Ecopath and EcoRanger.

We will show that even the "final" Ecopath model of Prince William Sound was flawed. It did not produce anywhere near enough detritus to satisfy the detritivores in the system. As published, the model would require a substantial input of detritus into the Sound just to balance it. There could be no bacteria in the system whatsoever and no accumulation of detritus on the bottom of the Sound. The detritivores would have to be 100% efficient at consuming fecal matter — including their own.

Subsequent to our pointing out these problems, we have an "adjusted" model that adequately addresses the detritus imbalance. The difference between this model and its predecessor, however, involves no mere tinkering. The change in flows *was on the order of the largest flow in the system.*

An additional difficulty affecting the stability of the system is that the adjusted model (indeed, all the Ecopath models) has large flows in and out of a small standing stock of detritus. This may be the case, but it leads to dramatic instabilities. We believe a more likely case is for there to be a large decaying detritus pool, such that flows in and out are relatively small. This makes the pool a "big slow" component, which tends to stabilize the system. Whatever the truth, we show that these different assumptions about detritus make large differences to many of the species' dynamics.

All the problems thus far are ones we believe to be systemic to Ecopath. However, this is not a report about Ecopath. It is a report about the dynamics of the ecosystem in Prince William Sound. Ecopath proposes models that are, in Pauly's words, “thermodynamically feasible.” Ecopath does not promise that any dynamic model derived from it will be dynamically stable. We have now parameterized four Ecopath models, including the final model and the adjusted model and *none* of them is stable. This restricts our ability to answer some, though not all, of the important questions about the Sound's food web dynamics.

If we have failed to properly describe the ecosystem in Prince William Sound, we have failed in an interesting way. We show in the sequel that while the present models contain unstable response modes, most of the modes are relatively benign under a wide range of perturbations. Even the unstable modes will often go for 10 years without producing any extinctions, though some of the oscillations are, to say the least, radical. Our simulations dealt with 44 living groups and 4 detritus groups. Most of these groups exhibited mild oscillations of periods of a few years varying between about 50% and 150% of their equilibrium values even in response to quite severe shocks.

The volatile species were a virtual role call of the species most severely impacted by the oil spill: the avian raptors, seabirds, invert-eating birds, orcas, small cetaceans, pinnipeds and sea otters. We believe this to be a significant result, arising as it does from a simple description of the food web with no *ad hoc* assumptions.

There are other difficulties in the dynamic models. These include unreasonably fast dynamics in some groups, including but not limited to the volatile groups mentioned above and a clearly deficient detritus model.

We believe that the plankton are cycling too fast, about once every five weeks. The literature suggests that twice a season is more likely. Several other groups show unreasonably fast dynamics, as well. In some simulations bird groups go extinct in as little as a month in response to perturbations that do not seem at all unrealistic. Orcas sometimes show astonishing growth rates, three- to ten-fold in less than 3 years. A reasonable value would be an increase in orca biomass of perhaps 10% even in a very rich environment. These anomalies may stem from inappropriate choices of Ecopath parameters or in erroneous assumptions of our dynamic models. Either way, we must modify our existing approach.

We discuss several suggestions for future work that may mitigate the speed with which these groups respond. They divide roughly into two themes. The first is that the static model will almost certainly have to be adjusted. The question is how. To that end, a series of parametric analyses using the dynamic model on subsets of the food web may shed light on which parameters are most influential in determining the time constants of the indicated response modes. The second theme is the search for behaviors such as prey switching and predator mobility that may not be susceptible to inclusion in the mass balance process.

It is clear to us that our treatment of the detritus is deficient. Part of the problem is destabilizing nature of the small standing stock of detritus posited by the Ecopath models. In addition, there is the fact that the detritus dynamics cannot be captured by Lotka-Volterra dynamics and that the detritus may be inherently unstable; *i.e.*, it continues to accumulate over any time frame reasonable for ecological investigations. These are modelling issues the resolution of which may require either a considerable expansion of modelling detail or a considerable simplification. Either way, there will be losses: in speed and transparency in the first instance and in resolution in the second.

We have some reservations about our treatment of the benthos. Results recently published in *Science* by Smith and Kaufmann showed almost no change in benthic activity at a northwest Pacific station despite a steady 7 year decline in the particulate organic carbon drifting down from the surface. It is impossible to say at this point how the observations reported by Smith and Kaufmann may be, but it suggests that there is an inertia in the benthos that we are not capturing in our model. We present a discussion of factors that may possibly bear on improving the model of the benthos and its relation to the detritus-modelling problem.

An unavoidable conclusion from our point of view is that the Ecopath software requires radical improvement. Our experience was that the software was so unreliable that we needed to rederive the Ecopath equations and do our own calculations whenever possible. Even so, an irreducible amount of Ecopath use was necessary in communicating the models between our groups. The power of the mass balance technique is undeniable, but its useful is currently swamped by its packaging.

A final comment on our results. As strange as it may seem from the foregoing talk of instabilities and modelling issues, the results we have achieved are surprisingly robust. We have looked at four different static models under a variety of assumptions (implicit versus explicit detritus modeling, parametric variation of the standing stock of detritus, constant effort and regulated fisheries, and four different approaches to parameterization. Yet the gross features of the simulation case runs show some striking similarities. Most notable among them are the composition of the stable and volatile groups. Under a wide variety of approaches and initial conditions the same groups show up as relatively unaffected and the same groups are heavily affected. This seems to indicate that the underlying system is very coherent and that we are close to achieving a satisfying description of it.

The optimists within us suggest that there is still hope for creating a credible dynamic model using Ecopath. That Dr. Pauly's team has sent us dozens of models in the last year demonstrates a willingness to address our concerns and to do so promptly. Dr. Pauly has openly admitted the software problems and is working to fix them. Both our teams recognize that the Prince William Sound model is the most complex ECOPATH project to date. No previous ECOPATH model has been as carefully scrutinized. The possibility remains that within the second year of our contract that we will find credible and robust solutions. Both teams are strongly committed to that goal.

Introduction

Scope

At 0008 on 24 March 1989 the tanker Exxon Valdez ran hard aground on Bligh Reef and immediately began leaking oil. Before it was all over 11,000,000 gallons of Alaska crude were discharged into the waters of Prince William Sound setting off a train of ecological, economic and psychosocial ramifications which still reverberate around Alaska 10 years later.

The question that the media loves to ask is "To what extent has the Sound recovered." The *Exxon Valdez* Oil Spill Trustee Council is continually challenged to answer this question, especially in this tenth anniversary year. The official answer is that of 28 species that were listed as severely impacted, only two (river otters and bald eagles) have "recovered". An additional 18 species are termed "recovering." Finally 8 species are listed as "not recovering."

This is a simplistic answer to a simplistic and artificial question, yet important political and economic questions depend on the answer. In making these important categorizations, the EVOSTC depends on the results of a large number of studies of various aspects of the Prince William Sound ecosystem, most of them funded through the Trustee Council's restoration program.

Almost all of these studies have concentrated on one or a few species over a comparatively short time frame (3-5 years). This reflects common practice in the field (Pimm, 1991). A great deal of information has been collected in this way and there have been thoughtful analyses on the larger conclusions to be drawn from the mass of data that has been generated (Spies,*et al.*, 1996). Still, there is a need for an overarching expression of our knowledge of the ecosystem of Prince William Sound. This project is a way of doing that and the work summarized in this report is our contribution to that.

Models and Data

The goal of this project is to synthesize the accumulated knowledge of the Prince William Sound ecosystem in a model that clearly displays the interrelationships among its constituent parts and has the capability of analyzing the response of the system to shocks to the system. In an ideal world, we would actually have made two models, one representing the pre-spill Sound and one representing the post-spill Sound. Unfortunately, before the events of 24 March 1989 made Prince William Sound a household name there were comparatively few studies of the ecology of this relatively isolated and pristine area, far too few to provide even a speculative model of the pre-spill community there. Data in sufficient detail did not become available until the research funded by the Trustee Council and others began to pay off. For this reason, it was decided that the time frame 1994-1996 would be used for our modelling efforts.

All models rely on data from other sources, usually multiple sources. It is a major task to bring all the data together in such a way that it presents a coherent picture. Our partners, Dr. Daniel Pauly's group at the Fisheries Centre at the University of British Columbia, took the lead in this area. A large group of participants was assembled, each member of which is an acknowledged expert in his or her particular domain. Through a process of iterative negotiation a mutually acceptable food web for Prince William Sound was pieced together in a way that every participant could sign up to. Then the Ecopath technique was used to balance the production and consumption and biomass values for each member of the food web.

Ecopath is the name of a software package developed under Pauly's direction with input from many fisheries experts and marine ecologists around the world (Pauly and Christenson, 1993). The Ecopath mass balance method is recapitulated in the UBC annual report on this project (Okey and Pauly, 1999). The basic idea is that in a system at equilibrium all the mass of production must be balanced by mortality and other losses such as harvests and emigration. This leads to a system of linear algebraic equations that expresses this balance. If the production, consumption and biomass parameters are consistent with certain constraints (ecotrophic efficiency < 1, positive respiration, etc), then the system is at least "thermodynamically feasible," in Pauly's terms.

Dynamic models must proceed from the static models. The general form of ecosystem models has been known for many years (Pimm, 1991). The models always contain parameters such as carrying capacity and growth ratio which are often not available directly from ecological studies. The limited availability of data is the bane of the dynamic modeller. However, the fully parameterized food webs produced by the mass balance give a complete picture of the behavior of the system at equilibrium, where the rate of change of the biomass of the system components is zero. From our experience as dynamic modellers, we believed that this powerful relationship would be sufficient for us to evaluate all the parameters we needed to build a dynamic model of the food web.

We were indeed able to solve all the theoretical problems involved in parameterizing a dynamic model. In fact, we built several models based on four different Ecopath models and embodying a variety of approaches to sensitive issues. This work was hampered by difficulties we found with the Ecopath software. As powerful as the mass balance idea is, the software in which it is realized is riddled with bugs. In most of our work, we eventually decided that it was easier and quicker and more reliable to develop our own calculations rather than rely on Ecopath.

Principal Results

Most of our principal results so far are negative. We found that the Ecopath model given by Okey and Pauly in their annual report (Okey and Pauly, 1999) were fundamentally flawed in that much more detritus was consumed than produced by the system. An adjusted model was produced which provides a quick fix to this problem. Unfortunately, this was only the start of our difficulties.

We have now produced dynamic models based on four Ecopath mass-balanced models. All of them are unstable. All of the models have four unstable eigenvalues each. The unstable eigenvalues are small and produce instabilities that are not always immediately evident. In fact, the first of these models we produced (and demonstrated at the October 98 workshop in Anchorage) we believed to be stable until we subjected it to eigenvalue analysis after finding the instabilities in subsequent models.

The real parts of the unstable eigenvalues are small. For small perturbations, the system holds together for more than ten years. For larger perturbations, we have large excursions in all the groups characterized by low p/q ratios: Avian raptors, invert-eating birds, orcas, pinnipeds, small cetaceans, etc. The system is particularly sensitive to large perturbations in the macroalgae. A 50% pulse in the macroalgae leads to the loss of the invert-eating birds in a matter of weeks, with the avian raptors following not long after. In addition, there are large swings in the orcas and others, some not apparent for 4-6 years. In some simulations, the orcas increase their biomass by factors of 2 to 8 over only three or four years.

The dynamics of several groups are much faster than they should be. The phytoplankton response has a time constant on the order of few weeks, whereas the literature suggests it should be on the order of months. Inspection of the eigenvectors shows that the benthos reacts very strongly to changes in the primary producers. Smith and Kaufmann, writing in Science (14 May 99, p 1174), show results that indicate that the activity in the benthos stayed almost constant over seven years despite a steady decline in the food supply drifting down from the surface. There is obviously a lot of inertia in the benthos that we are missing entirely.

The picture is not entirely bleak, however. The whole midsection of the food web is gratifyingly stable. These groups typically respond in modes that are associated with eigenvalues clustered near the origin. These result in lightly damped oscillations with small amplitudes and low frequencies. Oscillations set in motion by various shocks to the system tend to be rather mild even if they last a long time. Most groups are more or less impervious to the wild oscillations of the problem groups.

The problem groups themselves are almost a role call of the species most severely affected by the oil spill. Furthermore, their behavior is consistent with the observation that many years may pass with little or no indication of "recovery." We are obviously in the right neighborhood, we just need to get those eigenvalues a little further to the left.

We are not yet able to say with certainty where these erroneous results stem from. There is considerable discussion of this question in the sequel. It seems clear that the static model needs to be adjusted. In fact, our partners have already modified the model contained in their annual report as a first cut at solving the detritus discrepancy. Unfortunately, it is difficult to know at this point just how the model needs to be changed, though it is clear that the most serious problems lie with the groups where the p/q ratio is very low. We probably need to do a set of case runs here varying some parameters to see how the system is affected. In electrical systems you can change the resistance, capacitance and the inductance in a circuit to change its performance. We need to find the analogous parameters in this model. We are set up now to do this but have not yet begun to run specific cases.

We also need to be sure of our methodology on the dynamic side. We have already started that process. After looking at four alternative formulations of the differential equations, we still have confidence in the present formulation (which is also the original). It has the virtues that its parts are intuitively meaningful and that it spontaneously produces zero derivatives at the equilibrium point to within the resolution of the Ecopath model. However, we must not be too quick to dismiss the possibility that we have made an error.

We need to examine the problems with the excessively fast dynamics, the detritus and the benthos with a few to finding mechanisms that may not be susceptible to the mass balance technique. These may include prey switching and the use of the mobility of some groups to mitigate their situations in times of scarcity.

As a final observation, we would make the claim that our results are actually pretty robust. We have tried a number of alternative approaches (implicit and explicit treatments of the detritus, constant effort and regulated fisheries, different approaches to parameterization, etc) and the results are not greatly different. Stable groups stay stable and the composition of volatile groups does not vary much from one approach to the next. We would be much more concerned if we got very divergent results with relatively small changes in the simulation model. Moreover, in having looked at four Ecopath models in depth, we see pretty much the same responses in all of them.

An old physics professor of mine once observed that it is entirely possible to have a system that is statically balanced but dynamically unstable. As the number of degrees of freedom increase the possibilities multiply. We are dealing with a huge system here, probably one of the biggest models of its kind ever built. Perhaps it should not surprise us that the first attempt has not been completely successful. Indeed, we may have done an extremely good job in that the model holds together as well as it does. From the beginning, we feared that our first attempts might well produce wholesale extinctions producing several more or less independent food webs. That hasn't happened and the fact that it hasn't happened is encouraging.

Method

Overview

Dynamic food web studies depend very heavily on the Lotka-Volterra formulations of the dynamic relationships between the components of the food webs (Pimm, 1982). The Lotka-Volterra equations have been known since the twenties and have been thoroughly debated and explored. The advantages and disadvantages of the technique are well-known. We have chosen to use a straightforward form of this technique for two reasons. First, simpler formulations are transparent. They allow ready interpretation of the results and provide the analyst with clear insight into the character of the system. Second, more complicated systems require more data, much of which is not generally available. Making such models usually requires the estimation of important parameters, which introduces more and more uncertainty that the results are products of the behavior of the system and due to the imprecision of the estimates.

Having decided on the formulation of the system equations, we are left with the problem of determining the system parameters. For this we rely on the work of our partners at the University of British Columbia. Using the Ecopath technique (Pauly and Christenson, 1993), a comprehensive static model has been proposed which describes the mass balance of various components of the Prince William Sound ecosystem (Okey and Pauly, 1999). Using this description, we are able to calculate the parameters necessary to parameterize the dynamic model.

The Lotka-Volterra Equations

The multispecies Lotka-Volterra model depends on the recognition that the dynamics of species *i* is governed by two kinds of reactions. First, there are factors which depend only on the amount of the species *i* in the system. (We speak of *amount* rather than number because the currency of the Ecopath technique is biomass rather than population. Although most of the population dynamics literature uses number, there is no loss of generality adopting biomass as the measure of the population.) Effects that depend only on the amount of species *i* include factors such as the amount of species *i* that is removed from the system by fisheries, the net migration of the species, the amount of respiration and the contribution of dead bodies to the detritus. Second, there are reactions that depend both on the amount of species *i* and the amounts of the other species in the systems. These interactions are similar to mass action terms in chemistry and capture the effects of feeding activity. Species *i* adds biomass from eating other members of the system and gives up biomass to groups that prey on it. All of these feeding interactions depend on the amount of the predator in the system and the amount of the prey.

In view of these observations, we can write a differential equation for each species *i* as follows:

$$\dot{x}_i = x_i\left(b_i + \sum_{j=1}^{N} A_{ij} x_j\right)$$

where N is the number of living components of the system. The system is completely described by the set of N equations of this form, one for each Ecopath group.

We summarize the dynamics of the whole system by using the "state space" technique of control theory, which relies on matrix notation. We do this in order to take advantage of powerful techniques in stability analysis which are greatly facilitated by this approach. In keeping with the conventions of control theory, we define the *state vector,* x, as column vector whose elements are the biomasses of the system components. Thus, the ith component of x is the biomass of group i of the Ecopath model. We define b and A similarly. For instance, A is an N x N matrix whose elements are the A_{ij} of the equations above. Note that we do not bother with subscripts. An unsubscripted quantity is assumed to be a vector or matrix of the appropriate dimensions.

We also introduce at this point a special convention to allow us to use a notation in keeping with the powerful array manipulation features of modern computer software. Conventionally, matrix multiplication is defined in the following way:

$$Ax = \sum A_{ij} x_j$$

This method arises from its usefulness in mathematics and physics for describing linear transformations and certain important physical phenomena. However, in other contexts, particularly in nonlinear dynamics, it is often necessary to deal with *element-by-element* multiplications and divisions by arrays. Modern software packages implement these operations under various names (e.g., *array formulas* in Excel, *array manipulations* in MatLab). Here we will use the term *element-by-element operations,* hoping to gain in clarity what may be lost in elegance. We use the symbol "$\circ$" to denote such an operation. Thus for two matrices G and H, we define

$$(G \circ H)_{ij} = G_{ij} H_{ij}$$

This terminology is used frequently in the development of the theory behind the simulation and we have developed an algebra to aid us. The full details will be included in an appendix in the final report.

Using these definitions we can now write the state space description of the system in the following form:

$$\dot{x} = x \circ (b + Ax)$$

Note that up to now we have made no assumptions that limit the applicability of this description. That is about to change.

The Parameterization of the Equations

The Ecopath model describes the equilibrium state of the system. At equilibrium, the rate of change of all the states must be zero. We then have

$$\dot{x} = x^* \circ (b + Ax^*) = 0,$$

where x^* denotes the vector of the equilibrium biomasses from the Ecopath model.

Obviously, one of the factors must be zero. The solution $x^* = 0$ is not true since we have the results of the Ecopath model. Interesting solutions can arise only if

$(b + Ax^*) = 0$. We use this fact to find the necessary values of b and A. This process is described briefly in the following sections.

The A Matrix

There are three types of groups in the Prince William Sound system that require distinctly different handling. Animal groups live by consuming other members of the food web. If *i* consumes *j*, there will be nonzero terms for both A_{ij} and A_{ji}. Plant groups differ from animal groups in that they exhibit logistic growth in the absence of predation. This must be provided for in special terms on the diagonal. Finally, detritus groups differ fundamentally from the living groups in that they do not grow, reproduce, or respire. In fact, it is not at all clear that the detritus groups are actually in equilibrium with the living groups since sediments often accumulate. In any event, detritus groups require special handling.

Living Groups. The *A* matrix expresses all the feeding behavior. The interaction between two groups *i* and *j* is embodied in term $A_{ij}x_ix_j$. The Lotka-Volterra convention is that the coefficient expresses the effect that *j* has on *i*. If *j* eats *i* then A_{ij} must represent the loss of *i's* biomass to *j*. Conversely, if *i* eats *j* then A_{ij} must represent the gain in *i*'s biomass due to the assimilation of the biomass of *j* that *i* has ingested. The Ecopath model gives us the data we need to evaluate these quantities at equilibrium.

Let us define some quantities, all available from the Ecopath model.

p	Production per unit biomass
q	Consumption per unit biomass
D	The diet composition matrix. D_{ij} is the proportion of *j*'s diet comprised of *i*
S	The proportion of the diet that is not assimilated. Referred to in the Ecopath literature as "unassimilated consumption" and referred to here as the "fecal fraction"
E	The ecotrophic efficiency, defined as the proportion of production that flows up the food web or to the harvest
H	The harvest
N	The net migration. In keeping with the Ecopath convention, immigration is negative and emigration is positive

Now we can express the relationships between feeding and the A matrix. If *j* feeds on *i*, *i* experiences a loss of its biomass equal to the amount consumed by *j*. This means that

$$-D_{ij}q_jx_j^* = A_{ij}x_i^*x_j^*$$

where the minus sign indicates the loss in biomass. Thus

$$A_{ij} = -\frac{D_{ij}q_j}{x_i^*}$$

If we have the reverse situation, i.e., i eats j, i recruits the amount eaten discounted by the fecal fraction.

$$D_{ji}q_i x_i^*(1-S_i) = A_{ij}x_i^* x_j^*$$

which leads to

$$A_{ij} = \frac{D_{ji}q_i(1-S_i)}{x_j^*}$$

Usually if D_{ij} is nonzero, then $D_{ji} = 0$ and vice versa. That is to say, the usual state of affairs is that if j eats i then i doesn't eat j. There are cases of mutual feeding and cannibalism in the Ecopath model primarily due to aggregation of species and age cohorts into a manageable number of groups. We handle this by simply adding the two effects, giving the net effect. In mutual feeding, the group that feeds the most gets a net gain; the other group gets a net loss. Cannibalism allows results in a net loss. These points are discussed in more detail in the full report. The result is that we can state with generality that the components of the A are given by

$$A_{ij} = \frac{D_{ji}q_i(1-S_i)}{x_j^*} - \frac{D_{ij}q_j}{x_i^*}$$

Plant Groups. In addition to the elements described above, plant groups require elements on the diagonal which will provide logistic growth in the absence of predation. If k is the index of a plant group, then $b_k + A_{kk}x_k$ must be chosen in such a way as to insure that in the absence of predation, the biomass of k rises to a carrying capacity and stays there. These parameters can be found by the method of isoclines from the equilibrium conditions. The process is too lengthy to be included here, but will be given in the full report. Suffice it to say at this point that for plants, we must have

$$b_k = \frac{1}{x_k^*}\left(d_k + \sum_{j=1}^{N} D_{kj}q_j x_j\right)$$

and

$$A_{kk} = -\frac{d_k}{\left(x_k^*\right)^2}$$

where d_k is the detritus produced by k.

Detritus Groups. Detritus groups are not amenable to description by Lotka-Volterra type equations because of the asymmetric operation of the mass action terms. Loss of detritus technically depends on the both the amount of detritus present and the number of detritus feeders, but the accumulation of detritus depends only on the contribution of the living groups and not on the amount of detritus that is already present. Furthermore, there are a number of reasons to consider the amount of detritus constant; that is, there will always be enough to satisfy the needs of the detritus feeders. We have investigated both approaches, implicit (essentially infinite) detritus and explicitly tracking the detritus accounts. While there are distinct differences in the results, we have doubts about the ability of the Ecopath methodology to support a detailed detritus model. The result is a model that is more complicated but not necessarily more illuminating. This is dealt with in more detail in the discussion session. The full report will contain a complete exposition of the detritus issues, including the derivation of the explicit detritus model.

The b Vector

Overview

The b vector contains all of the elements that are not density dependent (i.e., not mass action terms).

The Food Value of Detritus

In the implicit detritus formulation, the detritus is not density dependent and we assume that there is always enough to satisfy the needs of the detritivores. Thus the food value of detritus must be accounted for in the b vector. The food value of detritus has the effect of increasing the biomass of the component that consumes it. It is calculated by multiplying together the total consumption, the proportion of the diet that is composed of detritus and the assimilation efficiency. Let S be the set of the indices of the detritus groups. Then the proportion of the diet of component i that is made up of detritus is

$$D_d = \sum_{j \in S} dc_{ji}$$

Thus the food value of detritus is given by

$$f_d = q \circ D_d \circ (1 - S) \circ x$$

Respiration

Respiration is the difference between the assimilated consumption and the production. It is the fate of the biomass that is consumed but neither excreted or put into production. Clearly, respiration is a function only of the consumer and does not depend on the standing stock of the prey.

The respiration is calculated by

$$R_i = Q_i - S_i - P_i$$

Using the fecal fraction and substituting the specific consumption and production, this is

$$R_i = q_i x_i (1 - S_i) - p_i x_i$$

or

$$R_i = x_i\left[q_i\left(1-S_i\right)-p_i\right]$$

In element-by-element array multiplication notation, we have

$$R = x \circ \left(q \circ \left(1-S\right)-p\right)$$

The Harvest and the Migration

The harvest and the migration are inputs; that is, they do not arise naturally as a consequence of the mass balance process. They must be specified by the analyst on a case by case basis. The specification is actually valid only for the equilibrium condition. For the migration there is no difficulty in extending this to a *pro rata* extrapolation for off-equilibrium conditions. This is because migration is clearly a function which varies directly with the population. If there is a larger population, there will be a larger number of migrating individuals and *vice versa.* To a first approximation then, the migrating biomass is the equilibrium migration per unit biomass times the current biomass, or

$$M = \frac{M^*}{x^*}x$$

The harvest is treated similarly

$$H = \frac{H^*}{x^*}x$$

There are questions about this approach that require comment. This formulation is essentially equivalent to a constant effort fishery. If the fishery is regulated, the harvest will usually be exactly the regulated value regardless of the standing stock. That is to say, the harvest will be independent of the state of the system. A constant harvest is inconsistent with the Lotka-Volterra formulation. The equilibrium condition is no longer synonymous with $b + Ax = 0$. Although the eigenvalues of the system remain the same, the new equilibrium conditions arising from a change in the harvest (the "press experiment") can no longer be found by simply inverting the A matrix. Instead, one must solve a large set of simultaneous quadratic equations. That is a task of a wholly different magnitude. At this point, we are not convinced that the added insight would be worth the effort. Consequently, we have chosen to restrict our inquiries to constant effort fisheries.

The Expression for b

We now have expressions for all of the relevant terms. They line up like this:

Increase biomass

food value of detritus

$$f_d = q \circ D_d \circ (1 - S) \circ x$$

Decrease biomass

Harvest $(H^*/x^*) \circ x$

Migration $(M^* . x^*) \circ x$

Respiration $(q \circ (1 - S) - p) \circ x$

Flow to detr $p \circ (1 - E) \circ x$

We factor out the x and do some algebra and get

$$b = p \circ E - q \circ (1 - S) \circ (1 - D_d) - (H^* + M^*)/x^*$$

Growth-Limited Elements

Elements that feed on unlimited resources (*e.g.,* sunlight) must be constrained to logistic growth or they will spiral out of control. This limitation is imposed in the b vector since it is not density dependent. If k is the index of a plant component, then b_k is given by

$$b_k = (d_k + C_k)/x_k^*$$

where C_k is the total amount of component k consumed by other members of the system.

We have also consider a similar term for the detritivores. Under the assumption of the implicit detritus formulation, it could be argued that the benthos needs a similar term to limit their growth. Thus far, the results to not substantiate the need, but it is a consideration we need to bear in mind.

Summary

For all living groups

$$A_{ij} = \frac{D_{ji} q_i (1 - S_i)}{x_j^*} - \frac{D_{ij} q_j}{x_i^*}$$

In addition, for plant groups

$$A_{kk} = -\frac{d_k}{(x_k^*)^2}$$

For animal groups, the elements of the b vector are

$$b = p \circ E - q \circ (1 - S) \circ (1 - D_d) - (H^* + M^*)/x^*$$

For plant groups

$$b_k = (d_k + C_k) / x_k^*$$

Limitations

To this point, we still have made no assumptions regarding the size of variations that can be considered. Thus, we need not limit ourselves to small perturbations from the equilibrium condition. On the other hand, the parameterization depends entirely on the Ecopath values of equilibrium parameters, such as *p* and *q*. These parameters should be constant over a wide range of conditions, but this is not necessarily true for extreme excursions from equilibrium. The same may be true for the migration, which for some species may well depend nonlinearly on the actual level of the population .

Eigenvalue Analysis

Assessing the stability of a system is best done through eigenvalue analysis. The subject can be very abstruse and there is a considerable body of literature on it. A reasonable level of understanding of the eigenvalue problem as it applies to food webs can be achieved by reading Pimm's exposition in his books (Pimm, 1982, 1991). For our purposes, it is sufficient to recapitulate the main points.

The stability of a system described by a set of *N* simultaneous differential equations $\dot{x} = f(x)$ is governed by the Jacobian, which is defined as the *N* x *N* matrix whose elements J_{ij} are given by

$$J_{ij} = \frac{d\dot{x}_i}{dx_j}$$

The Jacobian is just a way of describing how the derivatives change with changes in the state variables. By examining the behavior of the Jacobian around an equilibrium, one can obtain a large amount of information about the characteristic responses of the system to perturbations. In particular, it is possible to deduce whether the system is stable.

For a Lotka-Volterra system it is very easy to show that the Jacobian is just

$$J = x \circ A$$

Exactly the same information can be obtained by *linearizing* the equations in the vicinity of the equilibrium point. In this approach we consider a small perturbation ξ from the equilibrium state x^*. By substituting $x^* + \xi$ into the equations, using the equilibrium condition and neglecting second order terms in the small quantity ξ, we can obtain a linear differential equation for ξ. Either way, we are led to the eigenvalue problem.

The solutions to the eigenvalue problem are *N* values λ_i. In general finding the eigenvalues requires finding the zeroes of a polynomial of order N. This used to be a daunting task but modern math packages such as MatLab solve for eigenvalues very efficiently.

Associated with each eigenvalue is an eigenvector which describes a characteristic mode of the system. The eigenvector varies in time according to $e^{c\lambda t}$. Any trajectory of the system can be described as a linear combination of the characteristic motions of the system.

The eigenvalues are either real numbers or occur in complex conjugate pairs. In the latter case, they have the form

$$\lambda = r \pm i\omega$$

That means that the solutions are in the form

$$x = Ce^{c(r+i\omega)t}$$

There is a common identity from calculus that says

$$e^{i\theta} = \cos\theta + i\sin\theta$$

It is not hard to show that by proper choice of the constants C and c, the complex conjugate roots can be shown to give rise a real solution of the form

$$x = Ae^{rt}\cos(\omega t + \varphi)$$

A and φ are called the *amplitude* and the *phase angle*, respectively, and are constants determined from the initial conditions.

Inspection of this equation shows that it is made up of a superimposition of an exponential and an oscillation. The oscillation is characterized by an amplitude A and a frequency ω. If r is zero, the system oscillates at this frequency forever. That is *neutral stability.* If r is not zero, the oscillations will eventually die out (r negative) or will increase without bound (r positive). Clearly, in the first instance the system is stable. If disturbed, it tends to return to the equilibrium condition. In the second instance, the system is unstable. If disturbed, it tends to diverge further and further from the equilibrium position.

From this it can be seen that the stability of the system can be deduced from the form of the eigenvalues. If the real part of the eigenvalue is negative, then the associated eigenvector gives rise to a stable mode. If the real part is positive, the associated eigenvector gives rise to an unstable mode. If the real part is zero, the associated eigenvector gives rise to a neutrally stable mode.

As part of the evaluation of the system, it is a common practice to draw an eigenvalue map, like the one in Figure 1 below. For a stable system, we want all the eigenvalues to lie in the left half-plane. In addition, there is information available about the characteristic modes. For instance, eigenvalues that lie on the real axis give rise to characteristic modes which have no oscillatory component; they either decrease to zero or grow without bound. Similarly, an eigenvalue located on the imaginary axis produces pure oscillatory motion that never decays.

For other eigenvalues, the farther left the point lies, the faster the mode returns to equilibrium. The greater the separation of the complex conjugate pairs, the higher is the frequency of the oscillation. Furthermore, it is possible to draw two lines from the origin that constitute the locus of points that correspond to *critically damped* modes. A critically damped mode returns to equilibrium in the shortest possible time without overshooting. Pairs of eigenvalues that lie outside these lines are *underdamped,* that is, they overshoot the equilibrium, usually several times, before settling down to the equilibrium condition. An underdamped system is said to "ring," because of its similarity to the motion of a bell. Pairs of eigenvalues that lie inside the lines are said to be *overdamped* and approach the equilibrium condition slowly.

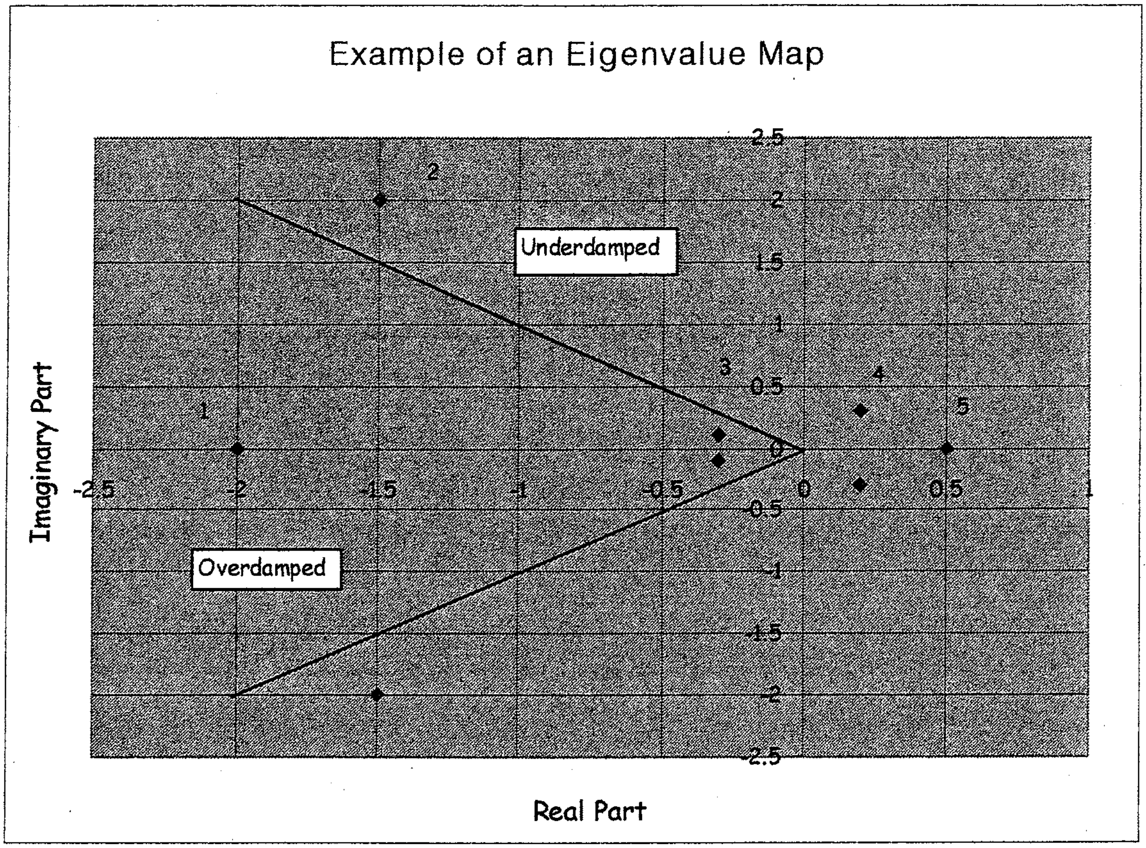

Figure 1. Example of an eigenvalue map. These sample eigenvalues correspond to the following kinds of response modes. 1. A non-oscillatory, strongly damped mode. 2. A high frequency, underdamped oscillatory mode. 3. A low-frequency, overdamped mode. 4. An unstable mode with growing oscillations. 5. A non-oscillatory mode with exponential growth.

The Simulation Technique

We integrated the state equations by implementing an Adams-Bashforth one step method in an Excel spreadsheet. We are indebted to Carl Walters of UBC, who suggested this method. The Adams-Bashforth one step method uses the derivatives of the previous two-steps as does the more common improved Euler method, but it is more stable and accumulates round-off error more slowly. Tests showed that errors on the order of 10^{-7} were being accumulated after 10,000 iterations. Greater accruacy can be achieved with Runge-Kutta or predictor-corrector methods, but these are much harder to implement in a spreadsheet. In view of the fact that the resolution of the Ecopath model is only on the order of 10^{-3}, we elected to keep the flexibility and visibility of the spreadsheet.

The resolution of the Ecopath model is appropriate to the static balance objective. Indeed, it is questionable whether the input data is even that precise. However, a precision of 10^{-3} is too coarse for an integration of many steps. Accordingly, during the parameterization process, we calculated the value of $b + Ax^*$, which was generally on the order of 10^{-3} (as expected) and added a correction to the b vector to reduce the error in the equilibrium value of this quantity to 10^{-10} or smaller.

We also conducted tests to select a time step that provided a good compromise between stability and run time. A time step of 0.01 years showed anomalies that disappeared when the time step was reduced to 0.001 years. A further reduction to 0.0001 years produced trajectories that were identical to those produced by the 0.001 time step, so we adopted that value. This required 10,000 iterations to produce a 10 year projection. Excel was able to do this for a 44-group model in a few minutes on a 450 MHz Windows NT machine with 384 MB of RAM.

An extinction trap was incorporated. Any species whose biomass decreases to less than 1 kg/km^2 is zeroed out for the remainder of the simulation. This is necessary for two reasons. First, it is not unusual in these simulations for species to decrease to very small numbers (much less than the biomass of a single organism) and remain that way for years, then spring back to life when conditions change. Second, it is even less unusual for the simulation to step across to negative biomass. This invariably leads to very strange anomalies in the trajectories.

After integration, the trajectories were winnowed to 1,000 points in order to reduce file size and redraw time for charts. We also tried using only 100 points. Although the charts looked good, some of the characteristic modes were too fast for this time scale and produced aliasing. Comparison of charts using 1,000 points and all 10,000 showed no differences.

Results

History and Organization

The work of this project was carried out by our group and the Fisheries Centre at the University of British Columbia. The Fisheries Centre group were charged with providing the Ecopath software, carrying out the collegial process of gathering the necessary data from recognized authorities in the specialist fields, and constructing a balanced model of the static equilibrium condition of Prince William Sound. The task of our group was to develop the necessary methodology for parameterizing a dynamic model from the Ecopath static model, to build a simulation of the Prince William Sound ecosystem and to analyze its principal features, particularly its stability.

In the course of the project we received and inspected over a hundred Ecopath models. We examined about of dozen of these in detail and fed back comments on disecrepancies we found. We developed the methodology mostly on the UBC Ocean Test model. The Ocean Test Model has only eleven groups and is much easier to work with than the PWS models, which run to more than forty groups.

We made about two dozen simulations from various PWS static models which we have used to run over a hundred cases. The first of the dynamic simulations was based on the UBC PWSim10 model. The PWSim10 model and our simulation based on it were presented at the October 98 workshop in Anchorage. We used the PWSim23 static model to develop our Monte Carlo analysis methodology but did not build a simulation based on this model until after we began to get results from the PWSim28 model.

The PWSim28 model was to have been the "final" model of the project. This is the model that was presented in the UBC annual report (Okey and Pauly, 1999) and was the basis of a paper given at the Anchorage meeting on the 10th Anniversary of the *Exxon Valdez* oil spill (Okey, *et al.*, 1999). Most of our simulations and analysis have been performed on this model.

We discovered two disturbing anomalies in this model. First, the model had a detritus discrepancy on the order of the largest number in the system. The amount of detritus being consumed in the system exceeded the amount being produced by about 1000 tons/km^2/yr. Second, the model contained unstable eigenvalues.

Consultation with our UBC partners produced a modified model which we are calling "PWSim28 adjusted." This model doubled the fecal fraction for all the benthic groups and resolved the first difficulty. The second remains and will be discussed in the next section.

Following the discovery of the detritus discrepancy and the unstable eigenvalues, we went back to the PWS10 and PWS23 models and found the same problems to a lesser degree in both of those as well.

The Static Models

The PWSim10 model contained 46 living groups and 2 detritus groups. Following the Oct 98 workshop, this model was extensively reworked based on the input of workshop participants. This resulted eventually in PWSim23 which reorganized the living groups, lumping some and splitting others, with the net effect that the number of living groups was reduced to 44. The number of detritus groups remained at two.

PWSim23 was subsequently refined to produce PWSim28. The number of groups remained the same, but some fairly exensive changes were made to the diet composition matrix. Some of these changes had significant repercussions for the dynamic model and we found it necessary to perform some modifications on our models to accommodate them.

The Dynamic Models

As mentioned above, some modifications to the static models were necessary in the process of synthesizing the dynamic models. A summary follows.

Transient Spawners

First, we had to account for the feeding behavior of the species such as adult salmon that transit the system to spawn but feeding only sparingly. The Ecopath model handles this by retaining the normal production and consumption parameters and reducing the elements of the diet composition matrix so that the consumption while in the system comes out right. Under this procedure, the column sums of the diet composition matrix add to something less than 1.000.

The dynamic model uses the diet composition elements to parameterize the A matrix. This process requires the column sums to equal 1.000. In order to make this so, we calculated the total consumption while in the system and derived an effective consumption parameter, then normalized the affected diet composition elements so as to make the column sum precisely 1.000

Fisheries Discard Feeders

The PWSim28 model contained a diet category called "fisheries discards." This category, consisting primarily of discarded by-catch was fed on by several groups, most notably sharks. However, there was no explicit provision in the model for where the fisheries discards came from. We solved this problem by creating a new detritus group. called appropriately enough "Fisheries Discards." We calculated the amount of fisheries discards consumed at equilibrium and made this the equilibrium value of the new detritus group.

In the explicit detritus models we also calculated the proportion of the total equilibrium harvest that went to fisheries discards and modeled the flow to fisheries discards as this proportion of the harvest at each time step. We also considered the fisheries discards as an ephemeral resource. At the end of each time step, the stock of fisheries discards is exported to offshore detritus

Dead Salmon Feeders

A significant source of food for eagles and gulls is dead salmon. However, the Ecopath disposition of dead salmon was to assign them to nearshore detritus. This put the avian raptors and the seabirds in competition with the shallow benthos. Since all of the birds are very sensitive, we decide to create a new detritus category called "dead salmon ." The flow to this category was a pro-rated portion of the salmon die-off at equilibrium. This category was also considered ephemeral. At the end of each time step, remaining dead salmon were exported to nearshore detritus.

Summary

The modifications resulted in a model with 44 living groups and four detritus groups.

Significant Results

The System Possesses Unstable Eigenvalues

This result is presented out of the sequence in which we actually did the analysis because it informs all the rest of the results. Actually, we ran a large number of cases before doing the eigenvalue analysis, partly to test the integration methodology and partly out of simple curiosity.

The eigenvalue analysis was performed using MatLab on the Jacobian matrix developed in accordance with the procedure outlined in the previous section. This was first done for the PWSim28 model, but we looked at the eigenvalues of all four of the major models. All of them showed four eigenvalues with positive real parts. The real parts are small. All of the systems will hold equilibrium for at least ten years with very little deviation from the nominal state. Even with small perturbations, the system will often hold together for ten years. With larger perturbations, however, we begin see big swings in some species and a certain number of extinctions. These are discussed in more detail below.

The eigenvalue maps (see Figures 2, 3, 4, and 5) are instructive. Each of these shows one or two eigenvalues on the real axis. These correspond to modes that decay without any oscillations. There are also two pairs of eigenvalues with very negative real parts and large imaginary parts. These correspond to high frequency modes that decay rapidly. We have not yet done an extensive eigenvector analysis on any of these models, but from our observations on case runs, it would appear that these modes are dominated by the phytoplankton. The rest of the stable eigenvalues are clustered near the origin. Note the disparity of scale between the real and imaginary axes. This obscures the fact that the imaginary parts are generally an order of magnitude greater than real parts. This means that the resulting modes are very oscillatory and, because the real parts have a small magnitude, the modes are only very lightly damped. Finally, there are two unstable oscillatory modes in each model. Note that in Figure 3 there are four eigenvalues on the positive real axis. These correspond to the behavior of the four detritus groups, which were made deliberately unstable to allow for the accumulation of sediments.

The Unstable Groups are Those Most Severely Harmed by the Oil Spill

Most of our case runs have been made with initial conditions that model shocks to the system. We usually reduce one (occasionally several) low trophic level groups to a fraction (usually half) of the equilibrium value. This tends to excite most or all of the modes to varying degrees. Figures 6, 7, and 8 illustrate typical reactions over a ten-year time horizon. These figures plot normalized biomass versus time. Normalized biomass is the biomass divided by the equilibrium biomass. Thus, all the unperturbed groups start at 1.0 and should tend to return to 1.0. Note that macroalgae shocks produce responses that are much more volatile than shocks in either of the phytoplankton groups.

The common feature of these runs is a core list of species that invariably react very strongly. These include orcas, small cetaceans, pinnipeds, avian predators, seabirds, and invert-eating birds. The bird groups often go extinct within ten years and the others exhibit growing oscillations. In addition to these species, we sometimes see strong reactions in adult salmon and adult herring. It is significant that all of the

Most Groups are Solidly Stable

With the exceptions noted above, the rest of the food web exhibits very stable behavior under almost all the shocks we have thus far subjected the system to. The sole exception is a massive shock where we reduced all the benthos to 50% of their equilibrium values. This can also be seen in Figures 6, 7, and 8, all of which show that most groups never deviate much from the equilibrium condition. In keeping with our observations on the eigenvalue map, all of the oscillations are long-lived, but the amplitude of the oscillations are small, usually not more than about 25% from the equilibrium condition and only 50% or so in the most severe shocks. This is a comforting result in that it shows that the core of the system is very resilient. Perhaps this is what the Exxon scientists mean when they claim that there is "a healthy, robust ecosystem" in Prince William Sound today.

The Dynamics of Many Critical Species are too Fast

There are three areas of concern here in which the simulated system differs sharply from observed behavior. These are the speed of the plankton cycles, the speed with which some groups go extinct and the unrealistic rates of growth exhibited by some groups.

Phytoplankton Cycles

Figures 9 and 10 illustrate the behavior of the system during the first year under the effect, respectively, of shocks in the offshore phytoplankton and the nearshore phytoplankton. Note that the offshore phytoplankton cycles in about 30 days and that the herbivorous zooplankton closely track the phytoplankton with a time lag of about five days. The cycle times for the nearshore phytoplankton and the nearshore herbivorous zooplankton are slightly longer. The literature (Longhurst, 1996) suggests that the cycle time for the plankton should be on the order of 2-4 months and that the lag in the zooplankton should be more like a couple of weeks, rather than a few days. On the other hand, Okey (pers comm) cites conversations with members of our collegial group that indicate that in the colder waters of Prince William Sound, the turnover may be much faster.

It is worthy of noting here an interesting aspect of multivariable dynamic behavior. When the phytoplankton shock is applied, it excites all of the eigenvectors. The degree to which any eigenvector is excited depends on whether the phytoplankton has a significant magnitude in it. Here, there is clearly an eigenvector which encapsulates almost all of the plankton behavior. It is characterized by a high frequency, strongly damped oscillation. Other eigenvectors are also excited. The interesting aspect is that the effects of these other eigenvectors are still reverberating through the system long after the initial perturbation has died out.

The Speed of Extinctions

Figure 11 shows the case of a 50% macroalgae shock. Note that the invert-eating birds (sea ducks) go extinct after only two months and the sea otters follow about six months later. This is in response to relatively small decreases in the shallow benthos. This response is out of all proportion to the perturbation. It may be that the input data may be in error and it is also possible that there are sources of error in the simulation methodology, but even in a worst-case scenario it is highly doubtful that these factors could account for all the error. Clearly, there is some very basic mechanism that protects these species from big swings like this that cannot be captured in the mass-balance methodology.

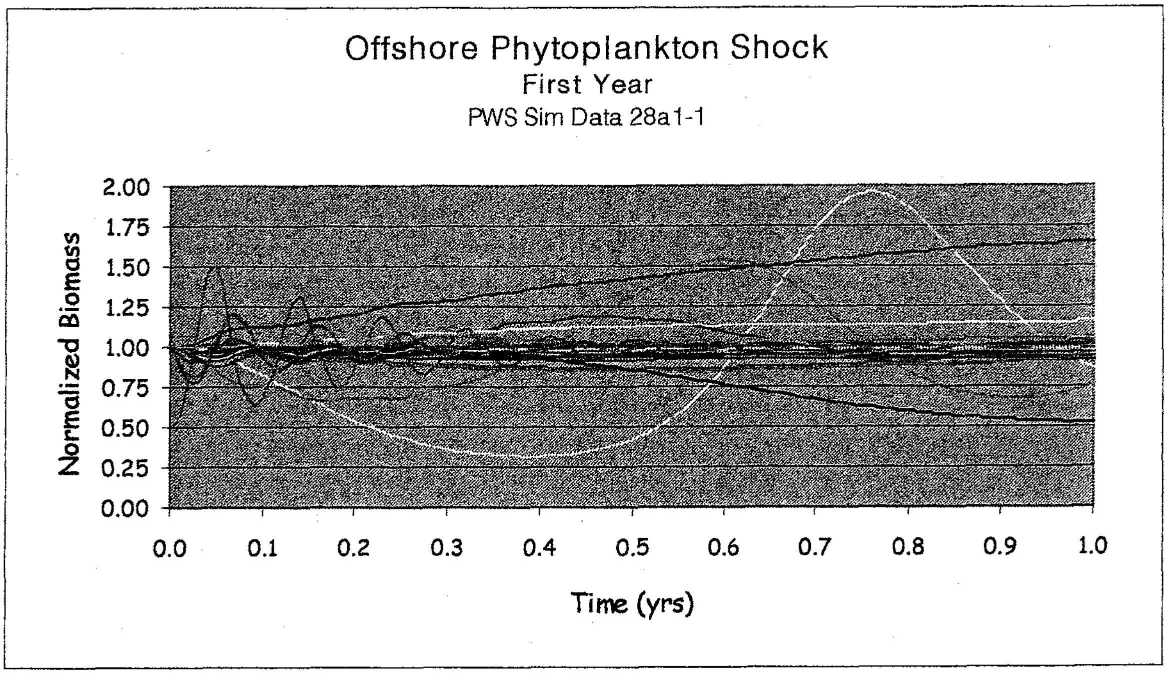

Figure 9. First year transients in offshore phytoplankton shock. The response of the phytoplankton is much faster than reported in the literature.

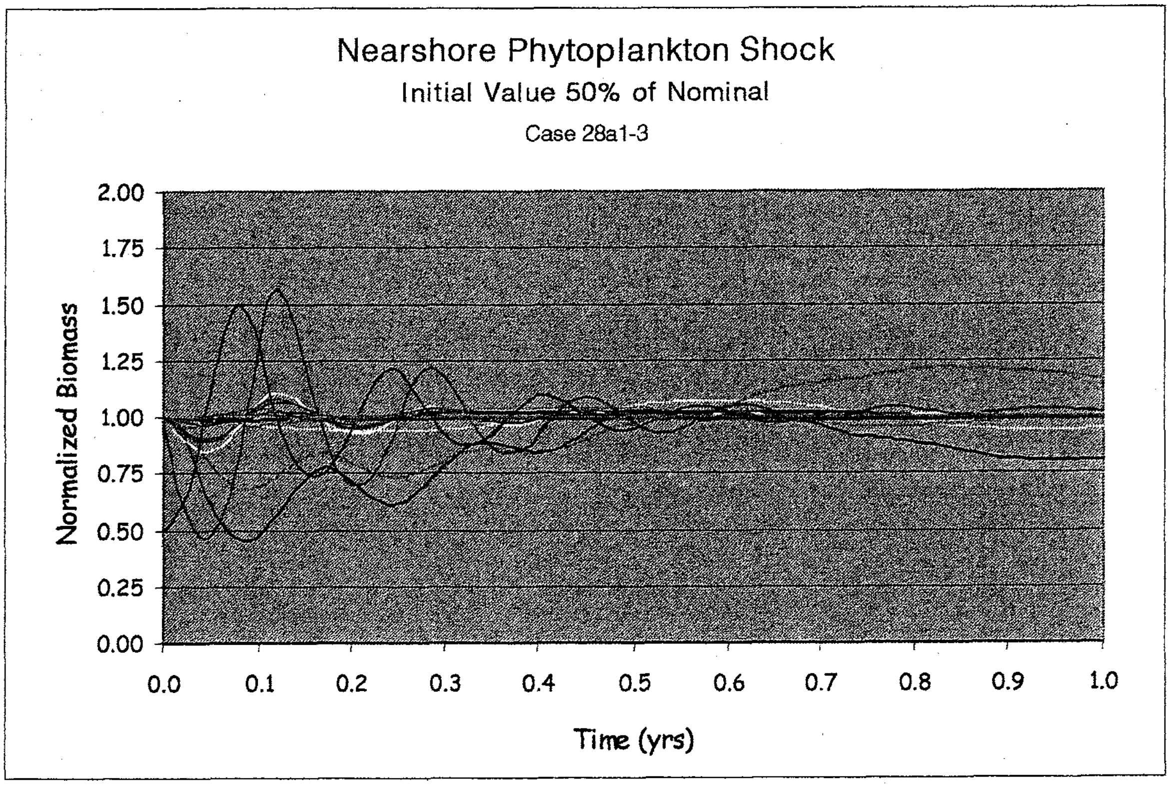

Figure 10. First year transients in nearshore phytoplankton. The response is similar to that of the offshore phytoplankton.

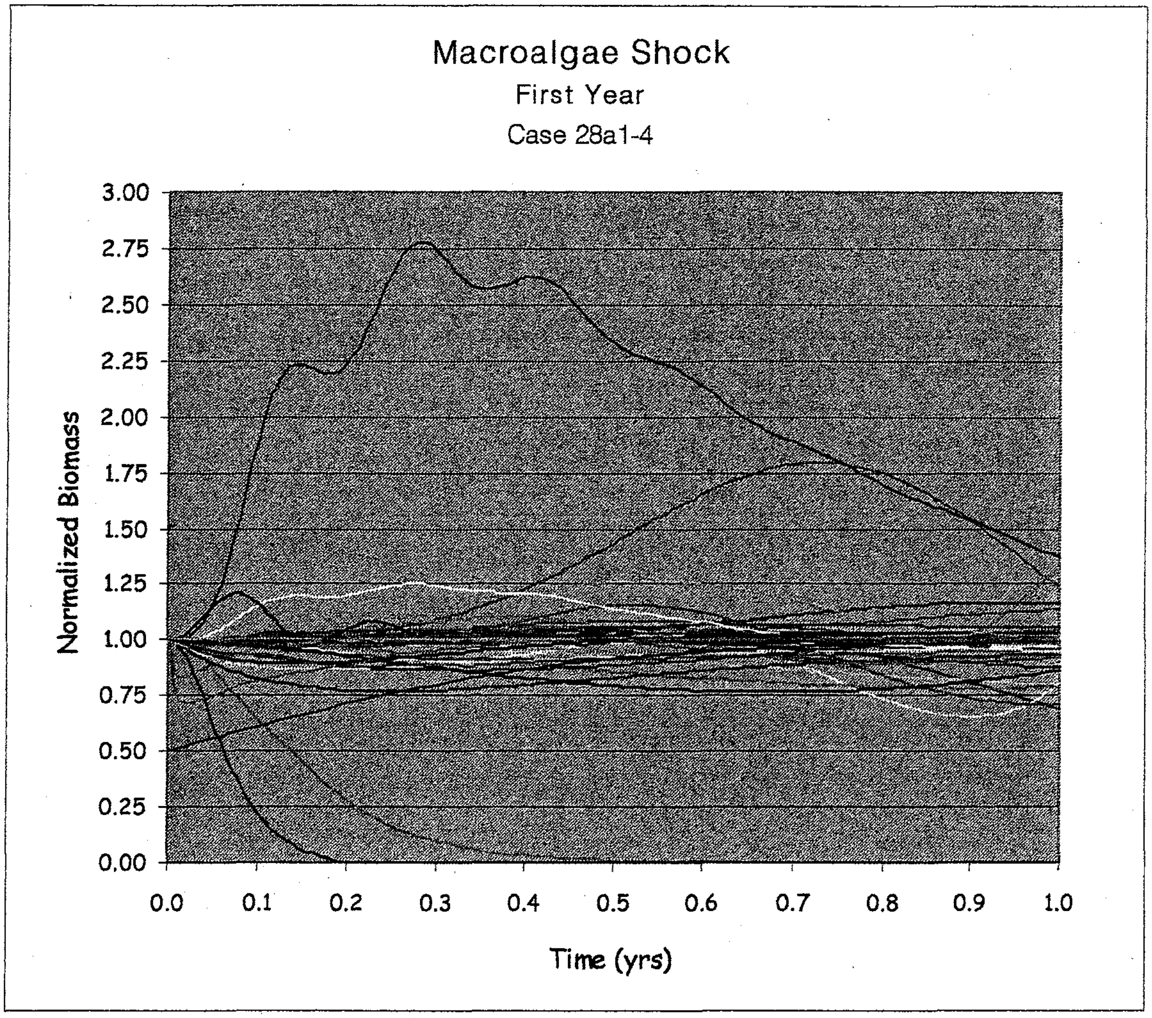

Figure 11. First year transients in a macroalgae shock. Note how the invert-eating birds and the sea otters go extinct unrealistically quickly.

Unrealistic Growth Rates

The most egregious example of this defect is the behavior of the orcas. Figure 8 shows the behavior of the full model (with explicit detritus tracking) responding to a 50% macroalgae shock. Beginning four years after the shock, the orcas begin a sharp increase that balloons them to 10 times their equilibrium biomass in less than two years. Clearly, this is due to a convergence of increases in groups that comprise their diet, but it is inconceivable that such a big predator could possibly increase so fast regardless of how rich their resources might be.

This is not an isolated phenomenon, *i.e.*, it is not that we have made an error in the orcas. The same effect shows up in all the groups characterized by very small p/q ratios. Figure 12 is an excerpt from the same case as the orcas which highlights the behavior of the avian raptors and the seabirds. The behavior of the avian raptors is particularly dramatic with sharp spikes to 15 or 20 times their equilibrium biomasses over a few months. These spikes are obviously linked to the adult salmon. Adult salmon produce dead salmon, one of the principal diet components of both bird groups. One would expect the birds to track the salmon, but as in the case of the orcas, the response is far out of proportion to the perturbation.

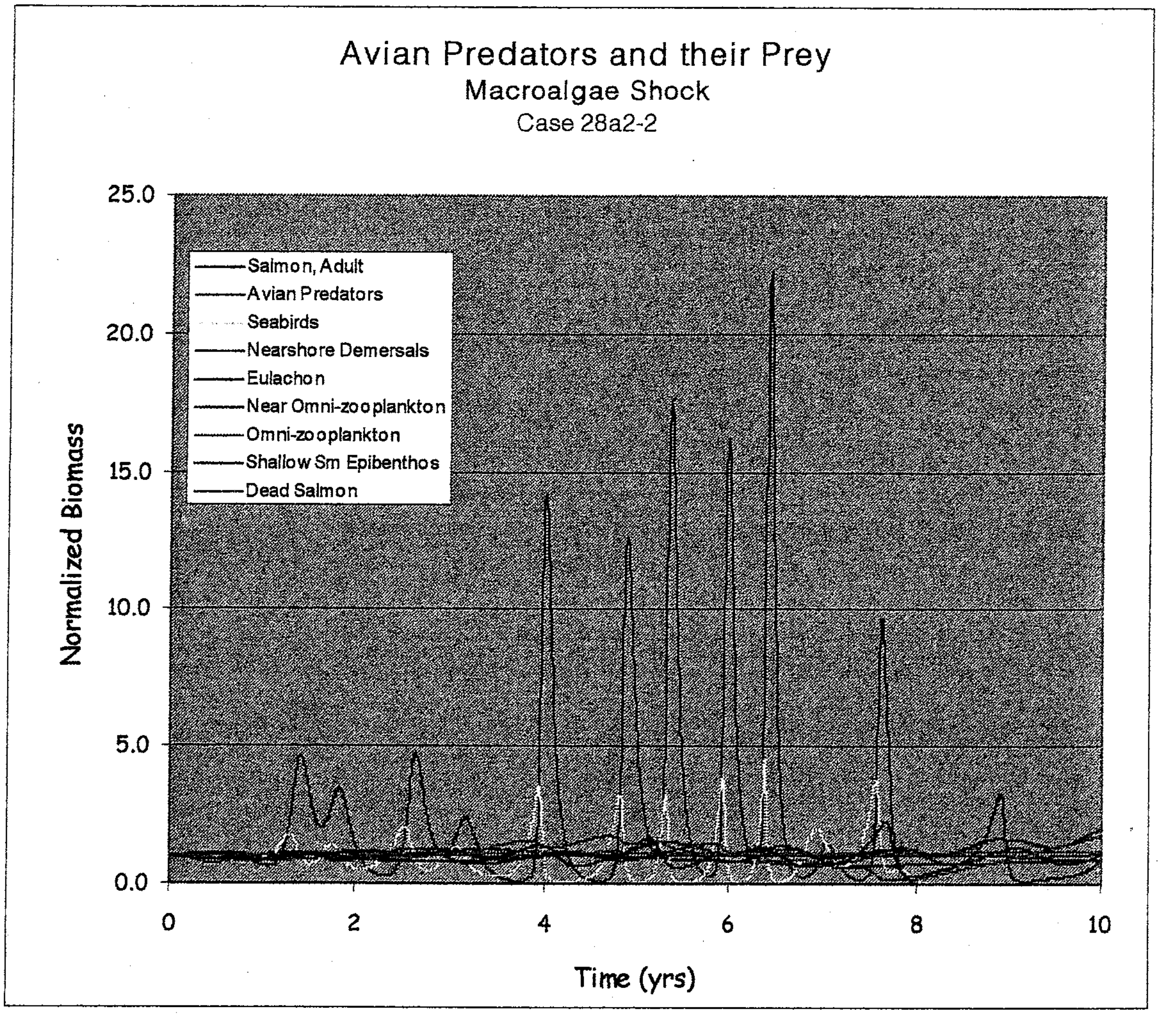

Figure 12. Behavior of avian predators and seabirds in response to macroalgae shocks, showing unreasonably fast variations in biomass.

Our Detritus Model is Deficient

This is an area that has concerned us from the beginning. At the Mar 98 meeting, we presented our concerns about the difficulty of modelling the detritus. The detritus does not fit into the Lotka-Volterra formulation. Our basic intuition was that there is an awful lot of detritus around and that it was a reasonable assumption that there would always be enough to satisfy the requirements of the detritivores. That would justify making the detritus constant. On the other hand, there was the fear that the detritivores would take over the system if they were essentially given all the food they wanted. Not being able to decide which way was right, we decided to do it both ways.

We built “implicit detritus” models that considered the detritus constant and “explicit detritus” models that specifically tracked all the detritus accounts. At this point it is difficult to judge which is best. We can, however, present some data that indicates that it makes a difference. Compare Figure 8 with Figure 13. The former is the result of an implicit detritus model. The latter is a “heavy detritus” model, an explicit detritus model with the equilibrium masses of the detritus multiplied by a factor of 100. Note that the orca hump is reduced from 10 to about 3. On the other hand, the spikes in the avian predator biomasses *decrease* by a factor of two.

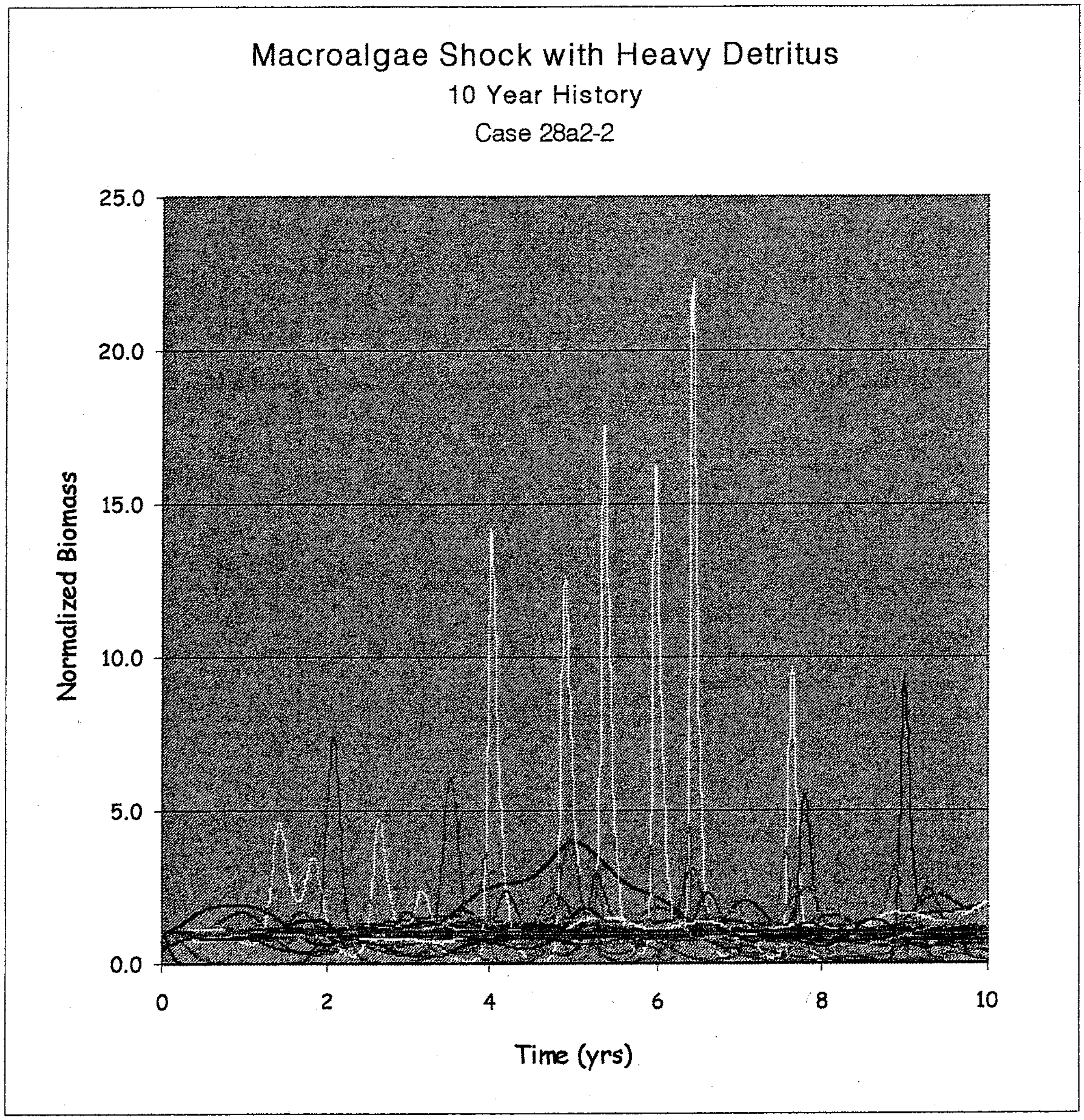

Figure 13. Macroalgae shock with "heavy" detritus. The initial conditions are the same as in Figure 8 but the standing stock of detritus is increased by a factor of 100. There are dramatic differences, but not always in the same direction.

We have also tried a simulation holding the benthos constant; *i.e.*, cutting the detritus out of the loop entirely. The results are shown in Figure 14. Note that many of the troublesome oscillations are considerably smoothed out, but that we still lose the avian raptors at about the eight year point.

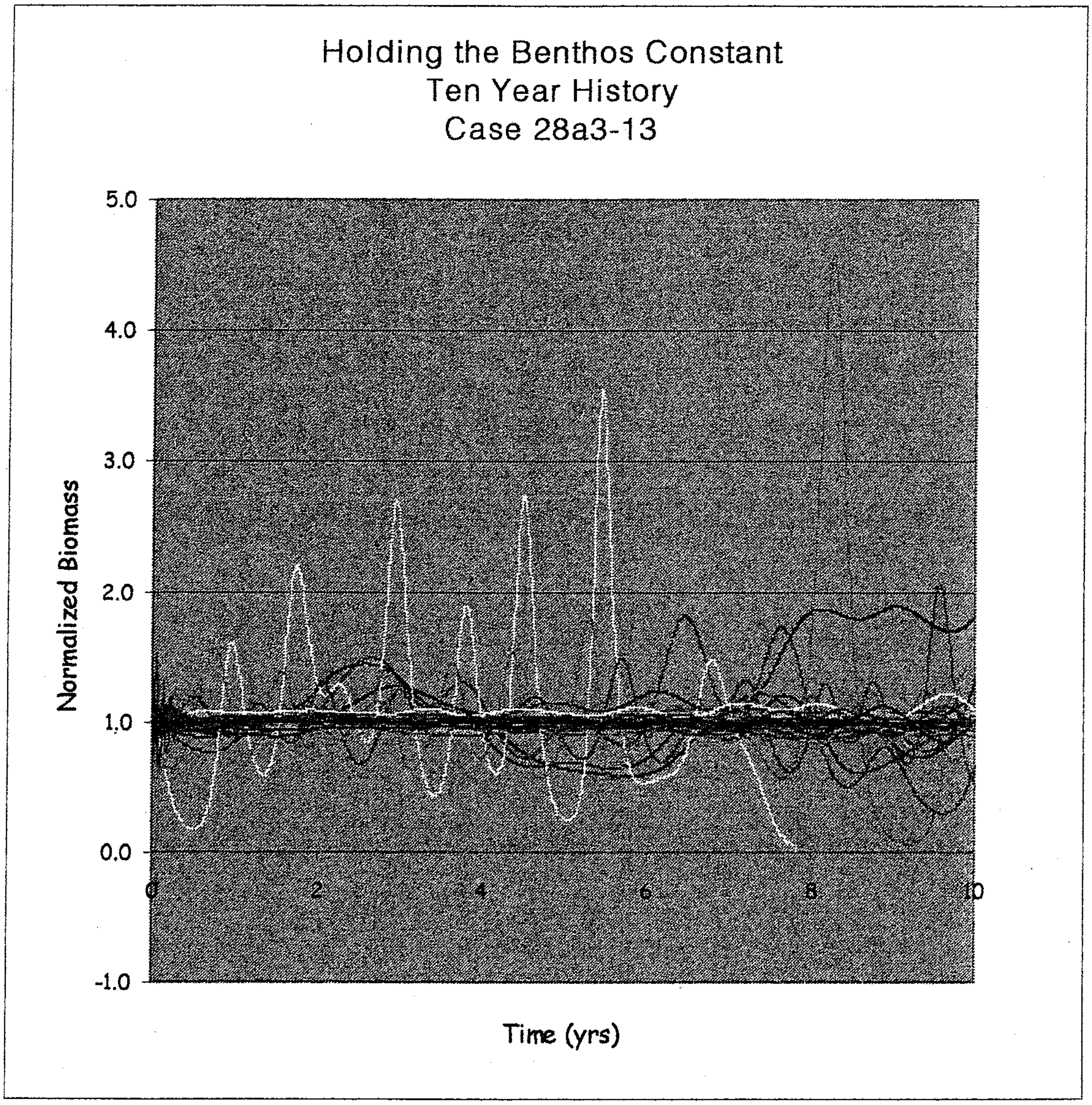

Figure 14. Macroalgae shock with the benthos held constant. Many responses are much smoother, but note that the avian predators are still lost at about year 8.

We have at present no way to choose among these models. It is not at all clear that one is "better" than the other. The only conclusion we can draw is that it makes an important difference. We return to this point in the discussion section.

Our Results are Robust

The results are not very *consistent*, but they are pretty robust from one formulation to another. We have tried a number of alternative approaches (implicit and explicit treatment of detritus, constant effort and regulated fisheries, and a variety of approaches to parameterization, all applied to four different static models) and the results are not greatly different in a structural sense. Stable groups stay stable and the composition of volatile groups does not vary much from one approach to another. This engenders a certain amount of confidence in the basic approach and indicates that the system itself is very coherent.

Discussion

This is not the report we wanted to write. Up to this point it dwells more on the difficulties we have encountered in making the models and less on what we have learned about marine ecology in general and Prince William Sound in particular. Yet the picture is not entirely bleak. Despite the obvious failings in our models, there are some significant points that bear on the ecology of the Sound and its reaction in the wake of the spill. Here is our assessment of the results thus far.

Stability and Instability

The fact that the model has some unstable eigenvalues is a major disappointment. Whatever else it may be, Prince William Sound is manifestly stable. The history of the post-spill ecosystem is notable for its slowness to change. Otherwise, we would have seen more species classified "recovered" or we would have seen species go extinct.

Our disappointment is partially offset by the fact that the unstable eigenvectors describe the dynamics of precisely those species that were most severely impacted by the oil spill. This result arises out of a simple description of the food web without any additional assumptions or caveats. Furthermore, the behaviors predicted by the model are consistent with the observation that many years may pass with little or no indication of "recovery." We are obviously in the right neighborhood, we just need to move those eigenvalues a little further to the left.

It is encouraging, too, that the whole midsection of the food web is gratifyingly stable. Oscillations among these groups tend to be rather mild, though they are long-lasting. Most groups seem impervious to the wild swings of the problem groups. This may offer a way of coming to grips with the unstable groups. If the dynamics of the groups in the middle of the food web are benign, it may be possible to lump many of them. This will provide deeper insight into the unstable groups and make it easier to do parametric studies on them to determine how their behavior varies with changes in the input parameters.

Every physics student learns that it is entirely possible for a system to be statically balanced but dynamically unstable. As the number of degrees of freedom increases, the number ways this can occur multiply. We are dealing with a huge system here, probably one of the biggest models of its kind ever built. It should not surprise us that our first attempt has not been completely successful. Indeed, we may have done an extremely good job in that the model holds together as well as it does. From the beginning, Pimm feared that our first attempts might well produce wholesale extinctions producing several small food webs more or less independent of one another. That hasn't happened and the fact that it hasn't happened is encouraging.

Slowing Down the System Responses

There can be no question that the system is reacting too quickly in many important loops. These include the phytoplankton , the benthos and all the groups characterized by low p/q ratios:. The birds, orcas, small cetaceans, pinnipeds, etc. There are almost certainly several different modelling problems involved. Here are some of the things that we believe must be considered

- The plankton dynamics need to be investigated parametrically to determine which parameters determine the time constant of their responses. Then we must coordinate with our panel to see whether the parameters can be adjusted so as to match observations. The dynamics of plankton may be faster in colder waters, but we need to find the data that establish this.
- Steep downside behavior is probably mitigated by prey switching in times of need. Again, we need to indicate that this is so and the extent to which it occurs before we can build it into the models. This is an example of a mechanism unlikely to be captured by the mass balance technique.
- Dealing in biomass may be misleading. and that the time delays necessary to produce the numbers equivalent to the increased biomass will mitigate the steep upside behavior. In times of plenty, there may not be enough individuals to consume all of the available food. New individuals need to be created and that takes time
- The low p/q groups are in general highly mobile and very opportunistic. When faced with a shortage of food, they may well simply go somewhere where the pickings are better. Similarly, in times of plenty, organisms from outside the system may entered in large numbers so that the biomass does indeed increase as predicted by the models. In this sense, the results of our simulations may be thought of as the system quickly generating the capacity to support large numbers of these species. This approach is only feasible if it can be shown that neighboring pools of these organisms do in fact exist and can react on this time scale.
- The inertia of the benthos may be a great deal higher than our model suggests. Smith and Kaufmann (1999) show results that indicate that activity in the benthos remained relatively constant over seven years despite as steady decline in the food supply drifting down from the surface.
- The function of the detritus in the dynamics of the lower trophic levels is clearly important and complicated . See the discussion below

As powerful as the mass balance method is, it is doubtful that any of these factors can be treated successfully except for the first.

Benthos Modelling Issues

The results of Smith and Kaufmann (1999) indicate that the behavior in the benthos may seem to be independent of the surface activity over significant time periods. As shown in figure 3-13, this would have the effect of smoothing out the dynamics of a large part of the system. This suggests that perhaps we should improve our treatment of the benthos. Unfortunately, this appears to be a nontrivial prospect.

Introducing more verisimilitude into the model of the benthos would probably require an explicit treatment of the microbial loop. Perhaps as many as three such loops would be required: one in the water column, one in the sediments and one at the interface between the water and the sediments (Parsons, *et al.,* 1984). The bioturbation layer would certainly be important (Wildish and Kristmanson, 1997), as that is where much of the microbial enrichment takes place. Furthermore, bioturbation can cause resuspension, which feeds back to the epifauna, and redeposition, which feeds back into the infauna. Finally, the effectiveness of the feedback loops depends on hydrodynamic flow rates.

A model of the benthos that captured all these features would add a great deal of complexity to the present model. In fact, it is quite likely that such a model would be as big as or bigger than all the rest of the model. Perhaps the answer lies in the opposite direction. Moreover, it is not at all clear that the data exists to build so complex a model (Druffel and Robison, 1999)

Suppose we reason that whatever happens in the benthos happens on a time scale slow in comparison to the rest of the system (as suggested by the results of Smith and Kaufmann) and that we can actually assume that it is constant with respect ot events inf the higher trophic levels. We could then run a set of cases designed to look at the behavior of the higher trophic levels. If necessary we can then reverse the procedure and look at the behavior of the benthos assuming that all other groups react instantaneously. This is a well known technique in aerodynamics called singular perturbations, where events in the free stream and the boundary layer occur on vastly different time scales. It has also been used in control engineering. It is an example of thinking that can yield useful results by simplifying the problem rather than by complicating it.

Detritus Modelling Issues

The current model of the detritus is clearly inadequate. We have shown that the results depend in a nonsimple way not only on the detritus flows, but also on the standing stock of detritus. In the current Ecopath model the "equilibrium" values of the nearshore detritus and the offshore detritus are respectively 3.5 and 4.0 tons/km^2. Then flows to detritus and the consumption of detritus in the system are three orders of magnitude greater than this. This is analogous to a tiny pool into and out of which there are huge flows. It is easy to understand that this leads to a highly volatile situation. A standing stock that is large compared to the inflows and outflows would create a buffering effect that would smooth out the response and slow it down. Unfortunately, as things stand now we do not have sufficient data to structure such an approach.

A Word of Caution

The most common response of modelmakers when confronted with problems like these is to add new modules to the model. Improving the model does not necessarily mean making it more complicated. In fact, we should be wary of making the model too complicated. It increases the number of things that can go wrong, requires more data, costs more, increases run times and storage requirements, makes the model less transparent and harder to debug, and makes the results more difficult to interpret. We must hold in check our impulse to fix things until we are sure we know what to fix. In the next section we present some recommendations on how to go about this.

Conclusions and Recommendations

We have not yet achieved the objective

The model as it now stands has very basic flaws. It will take a significant effort on the part of both partners to rectify these.

We have gained some valuable insights

The collegial process of bringing together the domain experts and hammering out a mutually acceptable set of food web parameters has been a great success. It is very encouraging that this set of parameters, properly mass balanced, spontaneously identifies as most volatile precisely those species that are in the gravest trouble in Prince William Sound. No *ad hoc* tampering with the dynamics was necessary to achieve this. We didn't begin with any identification of especially endangered species; they just popped out of the numbers. Similarly, the finding that most species respond rather moderately to perturbations in the system is equally encouraging.

The static model needs to be adjusted.

The static model published by our partners must be withdrawn. Indeed, they have already modified it in response to our pointing out the detritus deficiency. Simply increasing the fecal fraction for the benthos has not provided the stability that is needed. We believe that the basic parameters probably need to be adjusted. Unfortunately, it is difficult to know just how at this point, though it is clear that the most serious problems lie with the groups where the p/q ratio is very low. We need to do a set of case runs here varying some parameters to see how the system is affected so that we can make intelligent suggestions to our partners on where to look for answers. In electrical systems you can change the resistance, capacitance and the inductance in a circuit to change its performance. We need to find the analogous parameters in this model. Of course, any alteration in the agreed-upon parameters will require consulation with our panel of domain experts. We are set up now to do parametric analysis but have not yet begun to run specific cases.

We need to be sure of our methodology at this end.

We cannot neglect the possibility that we have overlooked some important factor in parameterizing the dynamic model. We have already started the process of carefully considering other approaches. After looking at four alternative formulations of the differential equations, we are still very confident that we have got it right. The present formulation (which is also the original) has the virtues that its constituent parts are intuitively meaningful and that it spontaneously produces zero derivatives at the equilibrium point to within the resolution of the Ecopath model. We would nevertheless be glad to submit it to peer review. In addition, we believe a program of parametric case runs for well defined subsets of the food web can shed a lot of light on this.

We need to look for effects that may not be susceptible to mass balance analysis

A number of possible factors were suggested in the discussion that one would not expect to be found in an analysis based strictly on the static parameters of the food web. These include, but may not be limited to, climatic factors in the plankton dynamics, mitigating behaviors among the groups with low p/q ratios, and the intricacies of the interactions between the detritus and the benthos. Each of these may develop into major research areas that would need to involve the domain experts.

The Ecopath software needs radical improvement

The idea of mass-balancing food webs is immensely powerful and has the undeniable ring of truth. On the other hand, the Ecopath software has been a constant source of frustration for us. We have conveyed our experience in broad terms to our sponsors and in detail to our partners. It is probably not appropriate to rehash all of the Ecopath problems here. Suffice it to say that our experience was such that we eventually found it necessary to rederive the mass balance equations and do our own calculations whenever possible.

We recommend, on the basis of a certain amount of software development experience, that the Ecopath establishment retrench and concentrate on producing a bombproof package that simply does the basic mass balance and includes all the usual Windows methods (file handling, cut and paste, export in ASCII and/or spreadsheet format, etc). This package should continue to be available in a standalone form, regardless of the state of development of other modules. Other functionality may be developed in a separate stream. The software development process of proceeding through alpha and beta releases can be carried on, but software quality assurance methods must be put into place to insure that the basic module is not corrupted. Finally, fallback positions must be allowed to exist. A package that works should not be removed from circulation while there is any question whatsoever about the functionality of a new release.

Acknowledgements

The authors express their gratitude to the Trustee Council for their support of this project. Special thanks go to Bob Spies, Chief Scientist of the restoration program and Andy Gunther, Assistant Chief Scientist, for their encouragement and particularly for their patience when the project fell behind schedule. Our thanks are also due to our colleagues Daniel Pauly and Tom Okey at the University of British Columbia for their adroit management of the collegial process by which the data were assembled and for their readiness to deal with our questions and complaints in a friendly and professional way. Finally, we are very grateful for the enthusiasm and dedication of the many domain experts who contributed to the project. Their names are all inscribed in the report of our colleagues. Data is the mother's mild of the modeller and it has seldom flowed so freely as on this project.

Literature Cited

Druffel, E.R.M. and B.H. Robison. 1999. Is the deep sea on a diet? Science 284:1139.

Longhurst, A. 1996. Seasonal cycles of pelagic production and consumption. Prog. Oceanog. 36:77

Okey, T.A. and D. Pauly. 1999. Trophic mass-balance model of Alaska's Prince William Sound ecosystem for the post-spill period 1994-1996, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98330), The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.

Pauly, D. and V Christensen. 1993. Stratified models of large marine ecosystem: a general aproach and an application to the South China Sea, p. 148-174. *In:* K. Sherman, L.M. Alexander and B.D. Gold (eds.). Large marine ecosystems: stress, mitigation, and sustainability. AAAS Symposium. AAAS Press, Washington, DC.

Pimm, S.L. 1982. Food webs. Chapman and Hall, New York, NY.

Pimm, S.L. 1991. The balance of nature? University of Chicago Press, Chicago, IL.

Smith, K.L. and R.S. Kaufmann. 1999. Long-term discrepancy between food supply and demand in the deep eastern north Pacific. Science 284:1174

Spies, R.B., S.D. Rice, D.A. Wolfe, and B.A. Wright. 1996. The effects of the *Exxon Valdez* oil spill on the Alaskan coastal environment. p. 1-16. *In:* Rice, S.D., R.B. Spies, D.A. Wolfe, and B.A. Wright (eds.). Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society Symposium 18, Bethesda, MD.

Wildish, D. and D Kristmanson. 1997. Benthic suspension feeders and flow. Cambridge University Press, Cambridge, UK