An Ecosystem Model Evaluation: The Importance of Fish Food Habits Data

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ABSTRACT—Sensitivity analysis of an ecosystem model for the Gulf of Alaska revealed the importance of fish food composition parameters in determining model outputs. Since food habits parameters are important to most multispecies models which have predation as the main source of species interaction, the parameters should be estimated as accurately as possible. Unfortunately, collection of data on fish feeding habits in the North Pacific has been sporadic, and the estimation of model predation parameters from the data is thus subject to a great deal of error. The importance of developing a standardized data base on fish food habits is emphasized in conjunction with the use of the data base to improve ecosystem model reliability. A four-stage process is described for data base development and recommendations are made for future food habits research.

An important aspect of model evaluation is validation—that is, the process of confirming that model behavior corresponds to reality. Model results can be validated by comparison with field data, but this technique limits the validation to a particular set of field conditions (Miller, 1974). A less restrictive method is sensitivity analysis: Model runs in which input parameters are perturbed one at a time and compared with a base model run using the best estimates of input parameters. This type of sensitivity analysis is called individual parameter perturbation (IPP). If the input parameters are perturbed by an amount equal to their range of error, the sensitivity analysis gives an indication of the amount of error in model outputs.

Sensitivity analysis also yields other information that can be of use to the modeler, some of which is suggested by Waide and Webster (1976). One use of sensitivity analysis is in resource management, where manageable parameters can be identified and their effect on the system can be evaluated. The analysis can also pinpoint those particular input parameters that cause the most change in model outputs, thereby directing research effort toward obtaining more precise estimates of these parameters (Wiens and Innis, 1974). The sensitivity analysis reported here was performed for such research effort allocation, to describe model behavior when input parameters are changed, and to identify parameters which are most important in determining model output values.

The Model

The Bulk Biomass Model (BBM), developed by Taivo Laevastu at the NMFS Northwest and Alaska Fisheries Center (NWAFC), Seattle, Wash., estimates the equilibrium biomasses of fish and invertebrate groups in a given marine region (Livingston, 1980). The region in this particular adaption of BBM is the Gulf of Alaska (Fig. 1). The region is divided into five geographical areas with three different habitats in each: Coastal, slope, and offshore. The model consists of a set of equations which describe the biomass of species or species groups of fish and invertebrates in terms of species-specific

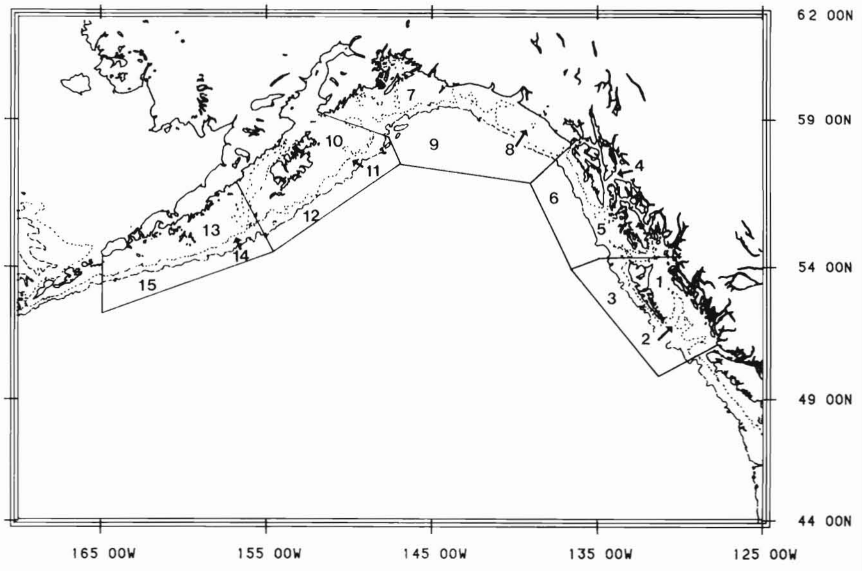

Figure 1.—The Gulf of Alaska region covered by the model and the location of computational subregions.

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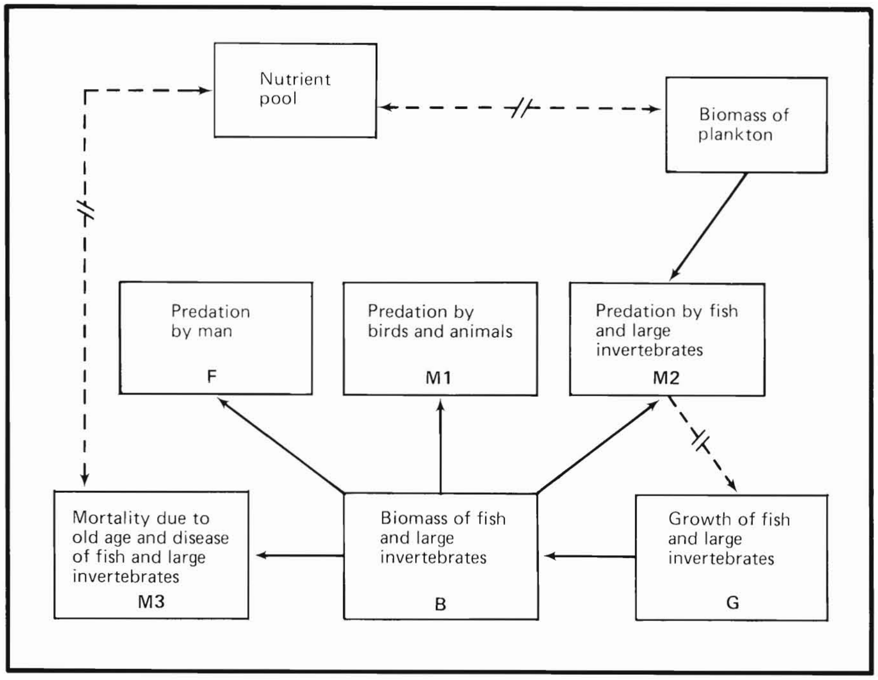

Figure 2. – Simplified view of biomass flow in the Bulk Biomass Model (dashed line = not modeled).

biomass growth (G_o) and removal (Fig. 2). There are four sources of removal input as constants or calculated in the model:

1) Predation by man through fishing (F);
2) Predation by birds and mammals ($M1$);
3) Predation by fish and invertebrates ($M2$); and
4) Old age and disease mortality ($M3$).

Fishing mortality (F) and old age and disease mortality ($M3$) are species specific constants. Bird and mammal predation ($M1$) is calculated in the model given:

1) Bird and mammal biomass (B_{mam});
2) the rate of bird and mammal food consumption (K_{mam}) in terms of percent body weight consumed per month; and
3) the fraction of each fish and invertebrate group in the diet of each bird and mammal group.

Predation of fish and invertebrates ($M2$), which provides the link between fish and invertebrate groups, is calculated in a manner similar to bird and mammal predation. Each fish and invertebrate group has given food requirements for growth and maintenance, K_g and K_m, defined in terms of percent body weight consumed per month. It also has a prescribed diet defined in terms of the proportion by weight of each prey fish and invertebrate group, i, in the total food for each predator fish and invertebrate group, j, designated as $\rho_{i,j}$.

A general set of $\rho_{i,j}$'s for each predator species group was first derived from a survey of the literature on the food habits of North Pacific fishes (Livingston and Goiney, 1984). Since the literature often does not contain information on spatial variations in fish feeding habits, each group's general diet was then modified, based on empirical knowledge of the distribution of prey species, to produce a different diet for each habitat: Coastal, slope, and offshore. Lastly, a biomass estimate was made for each group to calculate group food requirements.

With the exception of some base groups whose biomasses are well known, the model estimates equilibrium biomass of each fish and invertebrate group. An initial guess of each group's biomass obtained from resource assessment data, $B_{i,1}$, is input into the model. Then an iterative procedure is used which continually readjusts these initial estimates, using the biomass growth and removal parameters discussed above, until each group's biomass is in equilibrium. Thus, the estimates of growth and removal parameters set up the determination of the fish and invertebrate group's equilibrium biomass level.

Sensitivity Analysis of the BBM

The sensitivity analysis requires estimates of the absolute standard error, E, in model input parameters G_o, ($F + M3$), K_g, and K_m, mammal and bird biomasses (B_{mam}), and the proportion of prey i in the diets of predators j ($\rho_{i,j}$). These figures were derived from a survey of the literature. Since it was not possible to assign a specific error to each $\rho_{i,j}$, the error was determined to be derived from the process of estimating a different diet for each subregion. A series of model runs was made in which each set of parameters was increased and then decreased by its estimated error (Table 1). Only one run (run 15) was made to test the effect of error in the food habits parameters $\rho_{i,j}$. For that run, each species' diet in each subregion was entered as the original literature-derived general diet for that species, which did not consider possible changes in prey availability in coastal, slope, and offshore subregion types.

For the remaining runs (1-14) the perturbed value, P'_i of a parameter P_i, is:

$$P'_i = P_i (1 \pm E')$$

where E' is the fractional error ($E' =$

Table 1.—BBM sensitivity model runs and parameter changes.

Run no.	Parameter		Parameter change
1	G_o	Monthly growth coefficients for each fish and invertebrate group	−10%
2	G_o		+10%
3	$(F + M3)$	Monthly fishing and natural mortality coefficients for each fish and invertebrate group	−15%
4	$(F + M3)$		+15%
5	K_g and K_m	Monthly food requirement for growth and maintenance for each fish and invertebrate group	−20%
6	K_g and K_m		+20%
7	B_{mam}	Biomasses of each bird and mammal group	−50%
8	B_{mam}		+50%
9	$B_{i,1}$	Initial biomasses for all fish and invertebrate groups	−50%
10	$B_{i,1}$		+50%
11	$B_{i,1}$	Initial biomasses for base fish and invertebrate groups only	−50%
12	$B_{i,1}$		+50%
13	$B_{i,1}$	Initial biomasses for all fish and invertebrate groups except base groups	−50%
14	$B_{i,1}$		+50%
15	$\rho_{i,j}$	Same fish and invertebrate food composition for all subregions	

Table 2.—Range of percent change, S'_i, in dependent variables, B_i and $(M1_i + M2_i)$, over model subregions for sensitivity runs 1-15.

		Range of S'_i	
Run	Test	B_i	$(M1_i + M2_i)$
1	$-G_o$	62.4, 83.7	35.1, 54.2
2	$+G_o$	−28.0, −33.4	−15.5, −22.4
3	$-(F + M3)$	−21.0, −25.3	−12.9, −17.2
4	$+(F + M3)$	34.2, 47.0	20.6, 31.2
5	$-K_g$, $-K_m$	−42.5, −48.0	−40.1, −47.1
6	$+K_g$, $+K_m$	71.6, 87.9	66.6, 84.8
7	$-B_{mam}$	−1.0, −17.4	−1.0, −17.9
8	$+B_{mam}$	1.0, 17.4	1.1, 17.9
9	−all $B_{i,1}$	−32.6, −49.0	−32.1, −48.9
10	+all $B_{i,1}$	32.6, 49.0	32.1, 49.0
11	−base $B_{i,1}$	−31.9, −48.7	−31.7, −48.8
12	+base $B_{i,1}$	31.9, 48.7	31.7, 48.8
13	$-B_{i,1}$ except base	−0.8, −1.0	−0.1, −0.6
14	$+B_{i,1}$ except base	0.2, 1.0	0.2, 0.6
15	$\rho_{i,j}$ same food composition for all subregions	0.0, 126.8	0.0, 122.5

E/P). This method of sensitivity analysis, called individual parameter perturbation (IPP), assumes that interaction effects among parameters are not significant. This may not be true for some complex models (Rose, 1981). In this study, fish and invertebrate equilibrium biomasses, B_i, and their annual mortality rates $(M1_i + M2_i)$/year due to predation were measured for sensitivity to parameter changes.

The sensitivity results can be expressed in terms of percent change of a dependent variable, X, from the base run, as suggested by Orth (1979). This sensitivity indicator, S'_i, is simply

$$S'_i = \frac{X_i - X_b}{X_b} \cdot 100$$

where X_i is the value of the dependent variable X when the ith parameter is perturbed and X_b is the value of X in the base run of the model which contains best estimates of all the parameters. Table 2 summarizes the range of these sensitivity coefficients, S'_i, over model subregions for all sensitivity runs, including the food composition run. Total equilibrium standing stock biomass (B_i) and mortality/year $[(M1_i + M2_i)]$ in each subregion are the dependent variables. Food composition changes (run 15) not only produced the widest range of sensitivity values but also the highest values. Decrease of growth coefficients (run 1) and increase of food coefficients, K_g and K_m, (run 6) also showed high sensitivity values with some variation between subregions. The sensitivities from the other runs were not as high or as variable as runs 1, 6, and 15.

Thus, the model proved most sensitive to changes in food composition, growth rates, and food coefficients. These three parameters, along with fishing and old age mortality, determine directly or indirectly how much food is eaten and of what kind. Changes in these parameters most affected the heavily preyed upon groups—benthos, crustaceans, and other pelagics. The relative amount of each group's equilibrium standing stock biomass in the model therefore depends primarily on the model definition of predation processes.

Implications of Sensitivity Results

The sensitivity of model results to the model's rigid definition of predation suggests that expressing predation merely in terms of fixed percentages by weight of each prey item in a predator's diet may not be the best method for modeling predation processes. Development of an alternate structure which allows for feedback between system components might increase model realism. In fact, Gardner et al. (1980) found that more complex and realistic feeding terms for predator populations resulted in smaller within-model variances for their predator population estimates. The development of a functional relationship between predator and prey, for instance size dependent feeding, would thus provide the model with a better feedback structure for defining changes in size (age) composition of fish stocks due to predation. Such size composition information is necessary for management purposes.

These results pinpoint two problems in developing multispecies models: 1) There is a lack of useful data on the feeding habits of the fishes being modeled and 2) the functional form of the feeding portion of some models may be too deterministic. It follows that there are also two solutions to these problems: 1) To improve the quantity and quality of diet information collected on fish in the North Pacific and 2) to utilize this data and specific experiments to formulate a more mechanistic description of prey selection by fishes. For example, the results of the present study spurred the development of a flexible, prey availability-dependent representation of feeding in the largest ecosystem model called DYNUMES (Laevastu and Larkins, 1981) at NWAFC. Implementation of both of these improvements would reduce the error in the model, both through more reliable input data and through better use of the data. Specifically, the data should

FOUR STAGE PROCESS IN PRODUCING A FISH FOOD HABITS DATA BASE

I Planning	II Field sampling	III Laboratory analysis	IV Data analysis
Identify 1 Geographic area 2 Species to be sampled a. major commercial species (fish eaters) b. noncommercial species (fish eaters) 3. Number of samples to be taken according to: a. subregions within sampling area b. species size groups c. time of year	Collect required number of stomachs and label and preserve individually Record 1 Station data 2 Lengths and sex of fish sampled 3. Stomach type a. containing food b. empty c. regurgitated	Identify for each stomach 1 Prey items to species level, if possible 2 Weights, numbers and lengths of prey items	1 Code, keypunch and edit predator-prey information from lab analysis and associate it with the station data 2. Run programs to summarize, compute statistics and produce graphic output of data

Figure 3. — Description of a four-step process in producing a data base for information on fish food habits.

be used to define not just what a fish will eat, because in many fishes this may be extremely variable, but, more importantly, it should be used to quantify why fish eat what they do. For instance, a predator may select certain prey because they are of the appropriate size; to quantify this kind of relationship, we need a data base which includes measurements of individual prey sizes.

The procedure for developing the data base should involve detailed organization in the following four areas (Fig. 3):

1) Planning, in terms of identifying the specific geographic areas, fish species, and number of stomach samples;
2) field sampling of stomachs;
3) laboratory analysis of stomach contents; and
4) data analysis.

The goal is to produce a data base on food habits of uniform quality and format which can be easily accessed and summarized by computer. It would then be available in a readily usable form to those who wish to parameterize ecosystem models or to those who need basic information on feeding habits of fishes. The data base would provide a strong link between basic research and the theoretical models which require research data. The utilization of such data in ecosystem models would provide a quantitative view of species interactions and enable us to make more informed decisions on multispecies management.

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