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Sensitivity Analyses of the Equilibrium State in SKEBUB

A biomass-based fisheries ecosystem simulation model

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Sensitivity Analyses of the Equilibrium State in SKEBUB - A Biomass-Based Fisheries Ecosystem Simulation Model

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ABSTRACT

Sensitivity analyses have been performed on the biomass-based fisheries ecosystem simulation, SKEBUB, developed at the Northwest and Alaska Fisheries Center. This simulation contains an equilibration routine that forces it to an equilibrium state by adjusting the species biomasses. Sensitivity analyses were performed at this equilibrium state. Preliminary analyses indicated a GH'Biplot of Monte Carlo error analysis data to be more useful than a fractional factorial analysis of variance, because the Biplot simultaneously analyzes all output variables. Response surfaces of sensitive output variables were generated to study nonlinearities in response.

The biomass at equilibrium and the predation/biomass ratio were the most sensitive output variables, and their sensitivities were species-specific. The consumption/biomass ratio was not a sensitive output variable in this simulation. The simulation was most sensitive to the following input variables: growth, the food requirement for growth and maintenance, the availability to predation, percent contribution to other species diets, and the rate of prey switching by predators. Again the sensitivities of the different species to these parameters was species-specific. In general, variability in input parameters was increased by approximately an order of magnitude in the output variables. This increased variability would be reduced if simulations in the sensitivity analyses were required to reach an equilibrium state at least as stable as that of the baseline run. Response surfaces had limited applicability because of the many variables and interactions excluded; however, they did show the presence of multiple equilibria in the silver hake and flatfish groups. The particular equilibrium state which is chosen as the baseline for the

sensitivity studies is anticipated to influence the outcome of the sensitivity analyses. Sensitivity analyses will thus be specific to both the simulation model and the data input to that model.

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INTRODUCTION

The sensitivity analysis of large ecosystem models is complex and time consuming because of the panoply of variables to be considered, but it is this complexity, added to the tendency of simulation models to magnify input errors, that makes sensitivity analyses a necessity. The aims and types of sensitivity analyses are as varied as the models and the aims of the researchers in constructing them. They can be used as the final testing of a model to indicate significant sources of error and their consequence (e.g., Gardner et al. 1981) or as part of an ongoing procedure to improve system representation by the model (Miller et al. 1976).

Sensitivity analyses can be divided into methods which perturb input parameters and measure the resulting variation in output (also called error analysis), and methods which take the partial derivatives of the model equations with respect to each input parameter. This second method is constrained by the necessary rigorous assumptions and is not applicable to models where there are either significant nonlinearities in response, or parameter interactions (although see Behrens 1978), and applies only to small deviations of the parameters from their mean value (Gardner et al. 1981). The former method is generally more applicable to large ecosystem models, with its one major drawback, high computer usage, becoming less of a constraint to its effective implementation.

The many forms of error analysis are limited only by the statistical tools available and computer time involved; however, the form of the error distribution assigned to the input parameters can limit the level of interpretation possible. If there is little or no information on the error distribution associated with each input parameter, then the researcher is constrained to a study of model sensitivity, but if additional information is available then it is possible to estimate the importance of the error associated with each input parameter and its effect on the predictions output from the simulation. There is realistically no compromise between these levels of interpretation; assigning incorrect error ranges to even a few parameters can produce at best erroneous, and at worst misleading, results.

Once error distributions and ranges have been assigned and the output variables of interest determined, many procedures are possible. These range from individual parameter perturbation (IPP) to many multivariate analyses. IPP provides detailed information on the shape of the response curve and can be used to detect nonlinearity in response (e.g., Livingston 1983), but gives no information on parameter interactions. Multivariate methods such as fractional factorial analysis of variance (systematic and simultaneous perturbation of parameters) or Monte Carlo methods (random and simultaneous perturbation of parameters) can provide information on the effects of each parameter and their interaction on the chosen output variable (Rose 1983, Gardner et al. 1981), but model instability can result from the simultaneous perturbation of many parameters if their reaslistic error ranges are large. Huson (1982) extended the analysis of Monte Carlo results by using a modification of the GH'Biplot technique (Gabriel 1971) which simultaneously estimates the effects of the parameter perturbations on all measured output variables, producing a complete multivariate approach to sensitivity analyses. The most suitable method in any instance is determined by the model to be analyzed and the intended goals of the analysis, but several techniques are needed to gain an overall picture of model response (Huson 1982, Rose 1983).

The time during a simulation run at which output is measured can affect the results of a sensitivity analysis and measurements taken at a single time may poorly represent model performance in general (O'Neill et al. 1980). This can occur when a simulation is not in equilibrium or is displaying cyclical (e.g., seasonal) dynamics. In these instances the results from the sensitivity analysis can be considered valid for only that time in the simulation at which the variables were measured.

In this paper I present the results from sensitivity analyses on an abbreviated fisheries ecosystem simulation model (SKEBUB) developed at the Northwest and Alaska Fisheries Center (Bax 1983). It is derived from the biomass-based simulation models of the Bering Sea - PROBUB and DYNUMES (Laevastu and Larkins 1981). It differs from these models mainly in its lack of spatial resolution. These simulation models (PROBUB and SKEBUB) contain an equilibration function which forces the simulation to an equilibrium position, defined as the point where the annual growth equals the annual mortalities for each species or species grouping (c.f. May 1971). Equilibrium is attained by adjusting the biomasses of the individual species, although at least one species must be self-regulating (c.f. Deakin 1975, May 1973). This technique is a variant on relaxation procedures, in turn an extension of the Gauss-Siedel iteration technique, and facilitates the sensitivity analysis by providing a stable simulation for analysis.

METHODS

The Simulation

The simulation model SKEBUB was set up to be broadly representative of the Georges Bank ecosystem as reported by researchers at the Northeast Fisheries Center (NEFC); however, this paper is not an analysis of that ecosytem and the simulation has not been sufficiently parameterized to enable such an analysis. The data used from the published works of the scientists at the NEFC or their personal communication, include the diet compositions of the species or species groupings, production biomass ratios (which were assumed proportional to biomass growth rates), input biomass values (data from 1964 to 1966 resource assessment surveys and mean zooplankton values), and mean temperature data.

Each run of the simulation model proceeded for 30, year-long iterations. The beginning biomass for each iteration was adjusted to move the simulation closer to an equilibrium position. With baseline values for input parameters, a stable equilibrium (i.e. no further changes in beginning biomasses) was reached after 20 iterations, and at this point all annual percent changes in biomasses were less than 5%. When the input parameters are perturbed during the sensitivity analyses, annual percent changes will be greater.

Sensitivity Analyses

Preliminary studies were conducted where the same parameter perturbation was made to all species groups and the output variables were summed over all species groups. Subsequent analyses were designed to study the species-specific effects of the parameters.

Two multivariate methods were used in the preliminary analyses; fractional factorial analysis of variance (ANOVA) and Monte Carlo error analysis, using a modified GH'Biplot to analyze the output. The basis of a fractional factorial ANOVA is a fully factorized design with (usually) two categories, or levels, for each parameter, and one measurement for each possible combination of parameters. The fractional factorial design assumes that higher order interaction effects are negligible and confounds, or aliases, a new parameter with the distinct sequence of upper and lower measurement levels associated with one of these higher order interactions. When this design is then analyzed as a standard ANOVA, the effect of the added parameter will be recorded as the interaction effect with which it is confounded. There are numerous designs for fractional factorial ANOVA's (e.g. National Bureau of Standards 1957), the designs varying in the number of parameters in the basic design (and therefore the number of combinations of parameters to be measured), and the number of additional parameters that are to be confounded with the higher order interactions. The design used in this study used the computer programs written by Rose (1983) and was a six-way ANOVA with parameters measured at two levels. This design requires 64 (2^6) runs and additional parameters can be confounded with the three-way and five-way interaction effects, enabling the simultaneous analysis of up to 32 parameters.

The GH'Biplot technique has been described by Gabriel (1971) and Everitt (1978), and its modification for sensitivity analyses described by Huson (1982). The following summary is taken from Huson (1982):

> "The Biplot is a graphical display of multivariate data, based, where necessary, on a rank two approximation of the original data matrix. The plot is formed from two sets of coordinates, one of which represents the rows of the original data matrix, and the other the columns. The rows of the matrix [representing individual simulation runs and denoted as points] are plotted so that increasing deviation of a row from the mean is shown as increasing distance from the origin of the Biplot.... The columns of the matrix [representing individual variables and denoted as line vectors] are represented as projections which have lengths proportional to the variance of the column they represent. The correlation between columns is approximated by the cosine of the angle between column projections."

In most instances ecological models will require the original sensitivity matrix, which is the ratio of the data value to the baseline value for that variable, to be approximated as a rank two matrix. This approximation, derived from the latent roots and vectors of the variance/covariance matrix of the sensitivity data is dominated by the most sensitive parameters or variables; parameters of lesser sensitivity can be misrepresented. This can present a problem in large ecosimulation models where the variability associated with output variables can be an order of magnitude greater than that associated with the input variables (O'Neill et al. 1980). In this analysis the deviation of each output variable from its mean was reduced by a factor of 10, before generating the variance/covariance matrix. This improved representation of the input parameters.

Everitt (1978) presents several measures of goodness of fit between the Biplot and either the variance/covariance matrix or the original data. The goodness of fit between the Biplot and the variance/covariance matrix is the sum of the first two latent roots divided by the sum of all latent roots. As the number of runs in an analysis increases, this goodness of fit measure decreases implying that it is weighted towards the representation of individual runs rather than towards individual parameters, which one would expect to be better represented as the number of observations increases.

Four series of 64 runs were analyzed with the fractional factorial ANOVA. In these series the two levels for each parameter were its baseline value and one of -20%, -10%, +10%, +20% of baseline value, with the same level applying to all parameters in any one run. Many input parameters to the simulation were not estimated with great accuracy and confidence limits were not available. Any attempts to define precise error ranges would have been futile, instead a maximum error range of ±10% was assigned for the Monte Carlo analysis, with a triangular error distribution.

In the final sensitivity analyses the number of input parameters to be independently perturbed was increased by making most parameter changes species specific; it was considered that the pooling of parameter perturbations and output variables over different species could produce misleading results by averaging out dominant, but opposing, relationships. Similarly, output variables were measured for the individual species. This extension to the analysis resulted in 117 input and output variables. The effects of perturbations to the fishing coefficient and the effects of parameter perturbations on total catch were not analyzed in this final sensitivity analysis. There were 117 input and output variables studied (Table 1). The species groupings are listed in Table 2. Maximum perturbations were again set at ±10% of the mean value for the Monte Carlo error analysis. The fractional factorial ANOVA was not used in this final analysis.

A cautionary note is necessary regarding the preparation of data for the sensitivity matrix. The sensitivity matrix suggested by Huson (1982) computes each value as the proportion of its baseline value. This works well for input parameters when the error distribution is described as a proportion of the mean value, but can prove troublesome for output variables. To provide compatibility in scales between predation and starvation, the predation on each biomass, and the amount of food obtained by each biomass (an indirect measure of starvation) were recorded as proportions of each biomass. This also removed the strong dependency of predation and food obtained on the actual biomass. Another output variable, percent change in biomass at equilibrium, could not be realistically analyzed using this variant of the GH'Biplot procedure. The equilibration procedure adjusts the biomasses in the simulations until close to zero annual change is recorded during baseline runs; any slight absolute deviation from the equilibrium obtained in the baseline run would be proportionately enormous. The change in biomasses at equilibrium will be analyzed separately using IPP methods.

RESULTS

Preliminary Sensitivity Analyses

The fractional factorial ANOVA and the GH'Biplot produced similar results, ranking the input parameters, coefficient of growth, availability to predation, and food requirement for growth and maintenance as the parameters exerting most effect on the measured simulation outputs. There were differences in ranking between the methods but the differences were no more than those between the ANOVA with different percent parameter perturbations. There were differences in parameter rankings between the ANOVA's when different dependent variables were used as a measure of change in the simulation; the GH'Biplot considers all dependent variables simultaneously.

Two conclusions from these preliminary analyses were that the indicated sensitivity of the input parameters was clearly dependent on the output variable measured, and that the amount of perturbation of the input parameters influenced the results. The fractional factorial ANOVA and the GH'Biplot gave qualitatively similar rankings of the relative effect of perturbations of the input parameters.

Main Sensitivity Analyses

The GH'Biplot was used in the main sensitivity analyses, because it enables the simultaneous analysis of all perturbed input parameters and output variables. The differences in the ranking of parameter sensitivities when the fractional factorial ANOVA was run with different percent perturbations to the input parameters indicated that non-linearities in response might be occurring and the plotting of response surfaces was planned to investigate this.

The GH'Biplot was applied to data sets generated from 200 and 550 simulations. The parameters and variables which showed the greatest sensitivity did not vary between applications, but the properties of the parameters and variables of lesser sensitivity were more distinct in the results from the larger data set.

The goodness of fit of the GH'Biplot to the variance/covariance matrix was 11%, indicating a poor fit. When the data from the 550 run simulation were subsampled to give data sets of 200 and then 50 runs, this goodness of fit measure increased to 14% and 22%, respectively. Although the goodness of fit measure seems weighted to be more representative of the individual model runs than of the individual variables, the indicated fit is sufficiently low to treat these results with caution. It is likely that the parameters of lesser sensitivity may be poorly represented.

There are too many variables to be plotted on one figure, and they were thus subdivided into either variables or species. I emphasize that all the GH'Biplot figures result from the one analysis and the figures can thus be directly compared.

The input parameters producing greatest sensitivity in simulation output were growth, the food requirement for growth and maintenance, the availability of the species to predation, the percent contribution to other species diets, and the rate of prey switching (Figs. 1-5, respectively). The input biomasses and the acclimation temperature (which determines seasonal changes in growth) did not exert as great an effect on simulation output; maximum deviations from the origin were 0.37 and 0.35, respectively.

The three output variables showed markedly differing sensitivities. Equilibrium biomass was the most sensitive variable (Fig. 6), which is not surprising given the equilibration technique used. A more significant contrast is that between the predation/biomass ratio (proportion of each biomass) consumed and the consumption/biomass ratio (food obtained by each biomass). The predation/biomass ratio was a very sensitive variable, considering the tenfold reduction in deviations from the mean during data preparation (Fig. 7). The consumption/biomass ratio was a far less sensitive variable (maximum deviation from mean 0.09).

Additional information is obtained by comparing the orientation of the vectors. The predation/biomass ratio shows a strong positive correlation with the equilibrium biomass. This is again a result of the equilibration procedure which increases a species biomass, and thus its absolute amount of growth, if the total mortalities operating on it increase. In general, growth is negatively correlated with the equilibrium biomass, also as a consequence of the equilibration procedure. The availability of a species to predation, and the food requirements for growth and maintenance are in general positively correlated with the predation/biomass ratio and equilibrium biomass although this is apparent only for the more sensitive species. The different sensitivities of the different species to these variables emphasize the importance of considering each species individually. The greater sensitivity of the predation/biomass ratio compared to the consumption/biomass ratio indicates the importance of prey switching in this simulation. The sensitivity to the rate of prey switching coefficient substantiates this and this high sensitivity is surprising when it is considered that this parameter was set at the same value for each species, and is thus the sum of potentially opposing influences.

The second output from the Biplot is the deviation of each row of the sensitivity data matrix, that is of each run, from the mean. In the analysis of a system that was dominated by one or two variables or species, a distinct pattern would develop (e.g., Huson 1982). In this analysis there was little asymmetry in the plot, indicating a lack of extreme sensitivity to changes in any individual parameter by any variable (Fig. 8).

In the preceding plots (Figs. 1-7) two species groupings, the flatfish and silver hake were noticeable for the high sensitivity to their input parameters. Figures 9 and 10 are the same data rearranged to facilitate a more detailed examination of the parameters of these two species. The biomass of the flatfish was particularly sensitive to its growth rate and amount available for consumption by other species (Fig. 9). Simulation outputs are not sensitive to the percentage representation of the flatfish in the diets of other species, indicating that in this simulation the predation on the flatfish biomass was limited by its availability to predators and not by their preference for it. The flatfish biomass is comparatively small and thus unable to withstand a large predation pressure; the high sensitivity to its growth rate was negatively correlated with its equilibrium biomass and with increased predation.

The parameters which produced the largest changes in the silver hake biomass were its growth rate, its food requirement for growth and maintenance, and its proportional representation in the diet of predators (Fig. 10). It was not as sensitive to its availability to predators, indicating the predation on the silver hake biomass was controlled by the preference of the predators for it, not by its availability. Silver hake has a piscivorous diet and the high sensitivity to its food requirements may result from a sensitivity of the system as a whole to increased predation rather than solely a sensitivity of its own biomass.

The plots for these two species illustrate the different sensitivities to their parameters. There is high correlation between principal parameter vectors (either negative or positive) for each species as indicated by the grouping of the principal parameter vectors within a narrow angle, but between the two species parameter vectors are at approximately 90 degrees illustrating minimal correlation between groups.

The GH'Biplot indicates which input parameters produce greatest sensitivity in output variables and their general relations. For a more detailed examination of the effects of individual or pairs of parameter response surfaces of output variables can be generated; however, examination of individual parameter effects in isolation from the other parameters in the model can provide only a limited view of system sensitivity. The two parameters which produced the greatest sensitivities for the flatfish group (growth and prey availability), and in a separate simulation the parameters which produced the greatest sensitivities for the silver hake group (growth and the food requirement for growth and maintenance), were sequentially perturbed and response surfaces of the annual change in biomass, consumption to biomass ratio, predation to biomass ratio, and the biomass at equilibrium generated for each species.

The response surfaces of annual biomass change were similar for both species and indicate that there is a series of combinations of parameters that produce stable equilibrium conditions (Figs. 11 and 12). The response surface for the flatfish has several local minima; the response surface for the silver hake does not. In a fully parameterized simulation it would be important to analyze the response surfaces for the different species to detect any local minima for equilibrium conditions. The presence of such local minima and the potential for movement between them would have important consequences for the results from this simulation model.

The remaining response surfaces were linear (curvilinear for biomass) functions of the perturbed variables with no local minima. The most sensitive variable was the equilibrium biomass as indicated by the GH'Biplot, and it showed the same positive correlation with availability to predation and the food requirement for growth and maintenance, and the same negative correlation with the growth coefficient. One conclusion of the GH'Biplot was the lack of sensitivity of the consumption/biomass ratio in the simulation. The response surfaces for the flatfish and silver hake did not indicate this; rather for the silver hake the response surfaces indicated the consumption/biomass ratio to be more sensitive to both the growth coefficient and the food requirement for growth and maintenance than was the predation/biomass ratio. The flatfish response surfaces indicated comparable sensitivity to growth and less sensitivity to availability to predation for the consumption/biomass ratio when compared with the predation/biomass ratio. It is not clear whether these differences between analyses are a consequence of the poor goodness of fit estimated for the GH'Biplot or a consequence of the differences between univariate and multivariate analyses.

To investigate this question the input parameters directly affecting the silver hake and the output variables for silver hake were reanalyzed. The data used for the previous GH'Biplot were used again. These data were analyzed using simple correlation analysis and partial correlation analysis controlling for all other parameters and variables. The parameters and variables were ranked according to the sensitivity indicated by each analysis (Table 3).

The consumption/biomass ratio was indicated to be the most sensitive variable in the simple correlation analysis. This was not the case however in either the partial correlation analysis or the GH'Biplot, where equilibrium biomass was again found to be the most sensitive variable. This indicates the limitations of the IPP methods which can produce results with high definition of nonlinear responses but are limited in applicability to define system behavior as a whole. The results of the GH'Biplot and the partial correlation analysis are also not in accordance. A closer examination of the results from these two methods indicated good correspondence for the input parameters and output variables to which the system was most sensitive, but less correspondence for the parameters and variables to which the system was less sensitive. This is a function of the approximation process used to generate a rank two matrix for the GH'Biplot, but at the same time the distinction drawn between IPP and partial correlation applies. That is, partial correlation analysis can produce statistically precise results but is unable to synthesize the large amounts of information that the GH'Biplot can. Thus, the results from the partial correlation analysis will be limited to the particular conditions or variables under which they were taken. The GH'Biplot can summarize, and present in an easily assimilable format, the results from large sets of data, but the results are approximations and can indicate with reasonable confidence only the parameters, variables, and interactions to which the system is most sensitive.

DISCUSSION

The preceding analyses indicate the complex nature of the sensitivity analysis of large simulation models. None of the methods applied was ideal, each making a compromise between definition and generality. This is an extension of the views of Beck (1981) who, comparing large and small models, concluded that a large model might be able to predict the "correct" future with little precision, whereas a small model might predict, albeit with high precision, an incorrect future. Sensitivity analyses which are limited in their scope, for example, a straightforward comparison of the simulation output with expected values, are also limited in their usefulness. Tyler et al. (1982) found that various combinations of input parameters could produce the expected result for a stock assessment model; such ambiguities have given rise to criticism of the usefulness of simulation models in general.

One approach to the problem of generating reasonable results from spurious data is to restrain from tuning the data input to the simulation, relying instead on only the best empirical estimates (Sissenwine 1977). Even so, because the simulation in many ways repeats the same assumptions that were employed in the empirical data preparation, there are no guarantees that reasonable outputs necessarily result from reasonable inputs and a reasonable simulation. When simulation models are constructed with data requirements which are impossible to fulfill using only empirical estimates, some tuning of the simulation will be required. In these instances a complete multivariate sensitivity analysis is necessary. Although this can result in a lack of precision in estimating the sensitivities of the simulation to the individual parameters it is a more realistic representation of the degree of precision which is attainable with the simulation under consideration.

Certain general conclusions are evident from the sensitivity analyses of SKEBUB. The simulation was most sensitive to the parameter of growth and those parameters affecting interspecific predation. Similar parameters were the most sensitive ones in an abbreviated version of the Andersen and Ursin multispecies model (Livingston 1983). The parameter defining prey switching has a considerable impact on the simulation and it is likely that it is an important factor in system stability (Murdoch 1969). In the SKEBUB simulation, the biomass growth functions include the effects of recruitment; the model's sensitivity to the growth parameter reflects the importance of this factor.

In the GH'Biplot the deviations of the output variables from their baseline value were reduced by a factor of 10. With this reduction, the variances of the input parameters and output variables were comparable, suggesting that errors in input parameters were magnified approximately tenfold in the output variables. O'Neill et al. (1980) found that the coefficients of variation of input parameters were up to an order of magnitude less than the coefficients of variation of the output variables in a two-variable non-linear model. One method that O'Neill et al. (1980) utilized to reduce these large coefficients of variation in output variables, was to define acceptable limits of model behavior at particular times in the simulation, thus effectively limiting the allowed error ranges of the input parameters. The assumption here, of course, is that the simulation is an accurate representation of the system and that the acceptable limits of the output variables can be well defined. Although this method did reduce the total error, the authors did not consider it to be the optimal method as there was no guarantee that the output at other times in the simulation would be reasonable. In SKEBUB the equilibration procedure can be used to reduce the total permissable output variability by constraining the acceptable percent annual change in biomass at equilibrium. Figures 11 and 12 indicate the increase in percent annual change at equilibrium for the silver hake and flatfish groups as a function of two variables. The reduction in output variability would be dependent on the allowed annual change in biomass at equilibrium. Fully 70% of the Monte Carlo simulations had annual percent changes in biomass greater than those of the baseline run (highest percentage for baseline run was 0.7%). Thus, if the percent change in biomass obtained from the baseline was used as the criterion, a substantial reduction in output variability would result. This does not imply that our simulation has become any more accurate, but only that we are willing to place more confidence in the assumption of a long-term equilibrium than we are in the largely undetermined error ranges of the input parameters.

The conclusions on the sensitivities of simulation outputs to input parameter perturbations are drawn from an analysis of the simulation stabilized at a particular point in the parameter space; response surfaces indicate the presence of multiple equilibria and the conclusions at different equilibria would most likely be different. This is especially likely in the case of the consumption/biomass ratio which was indicated to be of lesser sensitivity than the predation/biomass ratio in the multivariate analyses. The sensitivities of the variables are not just a function of the formulations within the model but of the input data themselves; this is well demonstrated by the differing parameter sensitivities of the different species.

Sensitivity analyses often begin with the important, and often untested, assumption that there is a correct data source with which to either compare results or with which to ascribe reasonable error bounds. The results of the sensitivity analyses are then often presented in terms of the model, without regard for the fact that the simulation model is just one in a series of models which started with initial assumptions at the time of data collection (e.g., associated normal, lognormal, or other probability distribution), and ended with the assumptions involved in the sensitivity analyses themselves. This series of models needs to be taken into account when interpreting the results from sensitivity analyses; the results from sensitivity analyses can represent the hypotheses and assumptions of the scientists involved in researching the entire system.

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Table 1.--Parameters and variables used in the sensitivity analyses.

Abbreviation	Full name
	Input parameters
G1/	Growth coefficient
FRGM1/	Food requirement for growth and maintenance
CF1/	Percent contribution in diet of other fish
AP1/	Availability to predation
INBIOM1/	Input biomass
DMAX	Maximum allowed change in percent food composition
B	Rate of change of percent food composition
PS	Predation by sharks
PM	Predation by mammals
PB	Predation by birds
T	Mean annual temperature
TA1/	Acclimation temperature
	Output variables
C/B1/	Consumption/biomass ratio
P/B1/	Predation/biomass ratio
BIOM1/	Equilibrium biomass

1/ Species specific values

Table 2.--List of species or species groups represented in SKEBUB simulation.

Number	Group
1.	Dogfish
2.	Flatfish
3.	Haddock
4.	Demersal "others"
5.	Cod
6.	Silver hake
7.	Pelagic "others"
8.	Herring
9.	Mackerel
10.	Squids
11.	Shellfish (commercially exploited)
12.	Benthos
13.	Zooplankton
14.	Phytoplankton

Table 3.--Ranking of parameters and variables associated with the silver hake group according to their sensitivity as indicated by different analyses.

	Simple correlation[1/]	Partial correlation[1/]	GH'Biplot
1.	C/B	BIOM	BIOM
2.	P/B	G	FRGM
3.	G	P/B	G
4.	FRGM	FRGM	CF
5.	BIOM	C/B	B
6.	CF	CF	P/B
7.	AP	INBIOM	INBIOM
8.	INBIOM	TA	DMAX
9.	DMAX	T	PM
10.	B	AP	T
11.	PS	B	AP
12.	PM	PB	PS
13.	PB	PM	PB
14.	T	PS	TA
15.	TA	DMAX	D/B

[1/] Ranking ordered on sum of squared correlation coefficients.

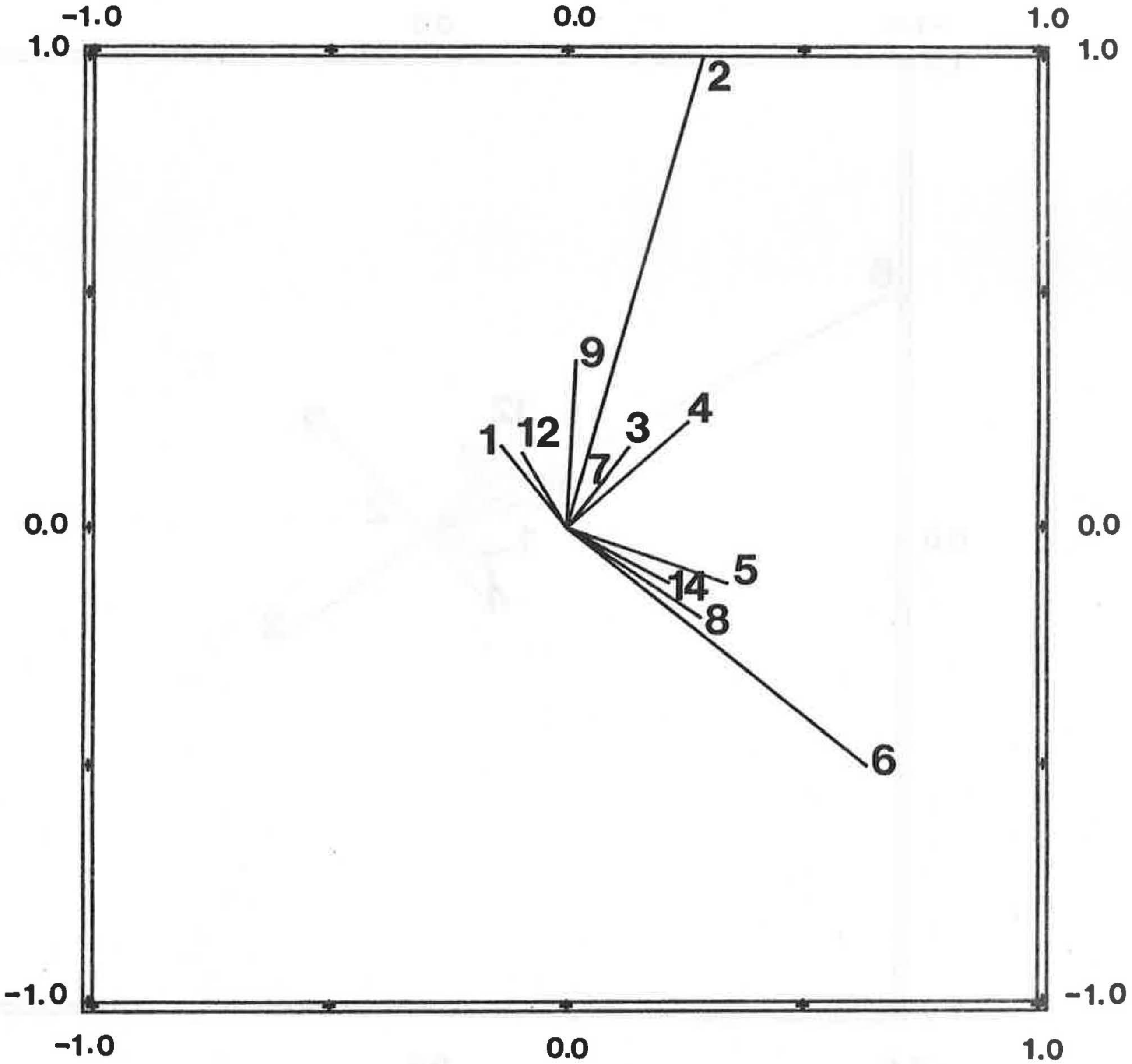

Figure 1.--Sensitivities of SKEBUB simulation to species specific growth coefficients.

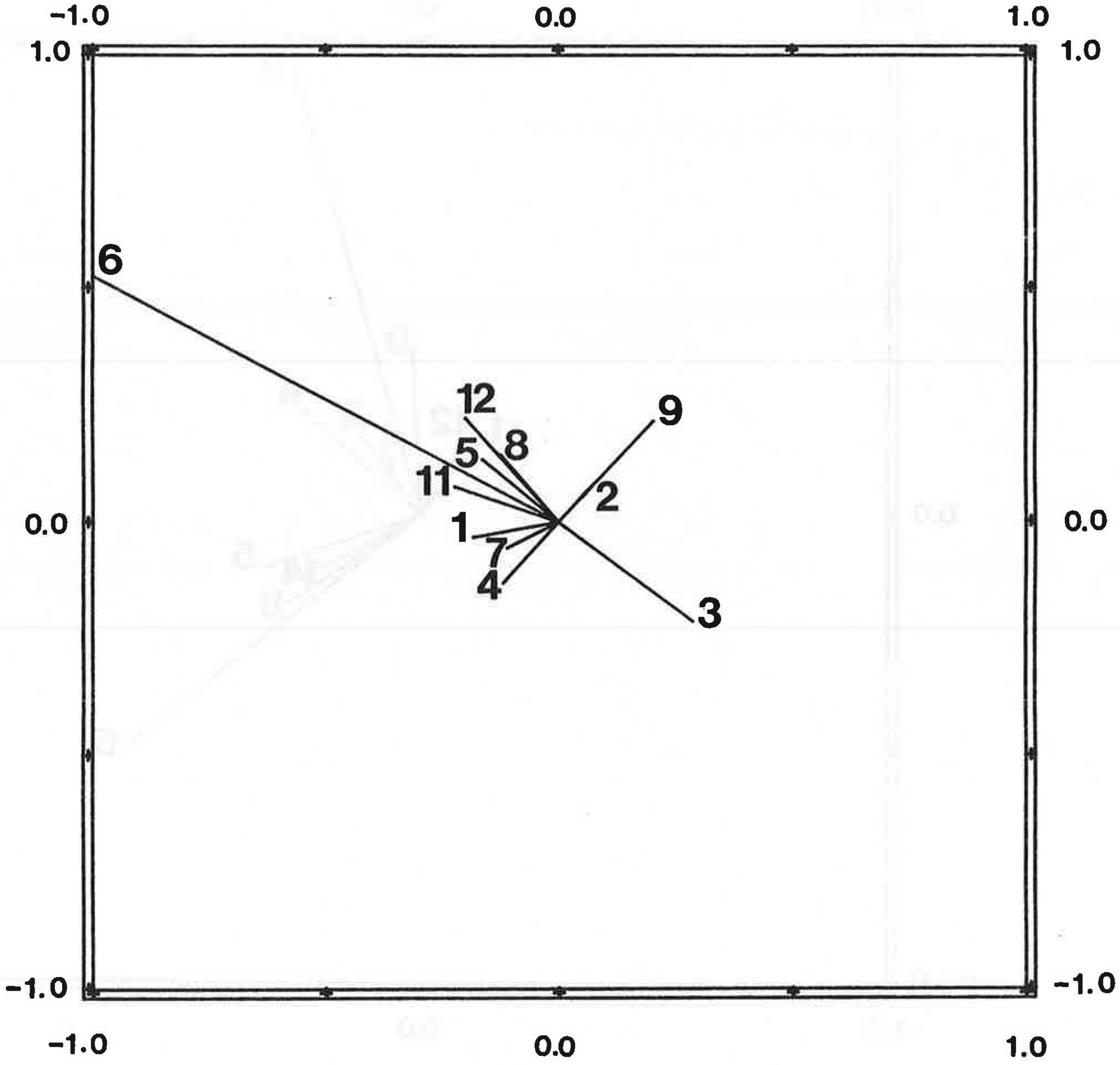

Figure 2.--Sensitivities of SKEBUB simulation to species specific food requirements for growth and maintenance.

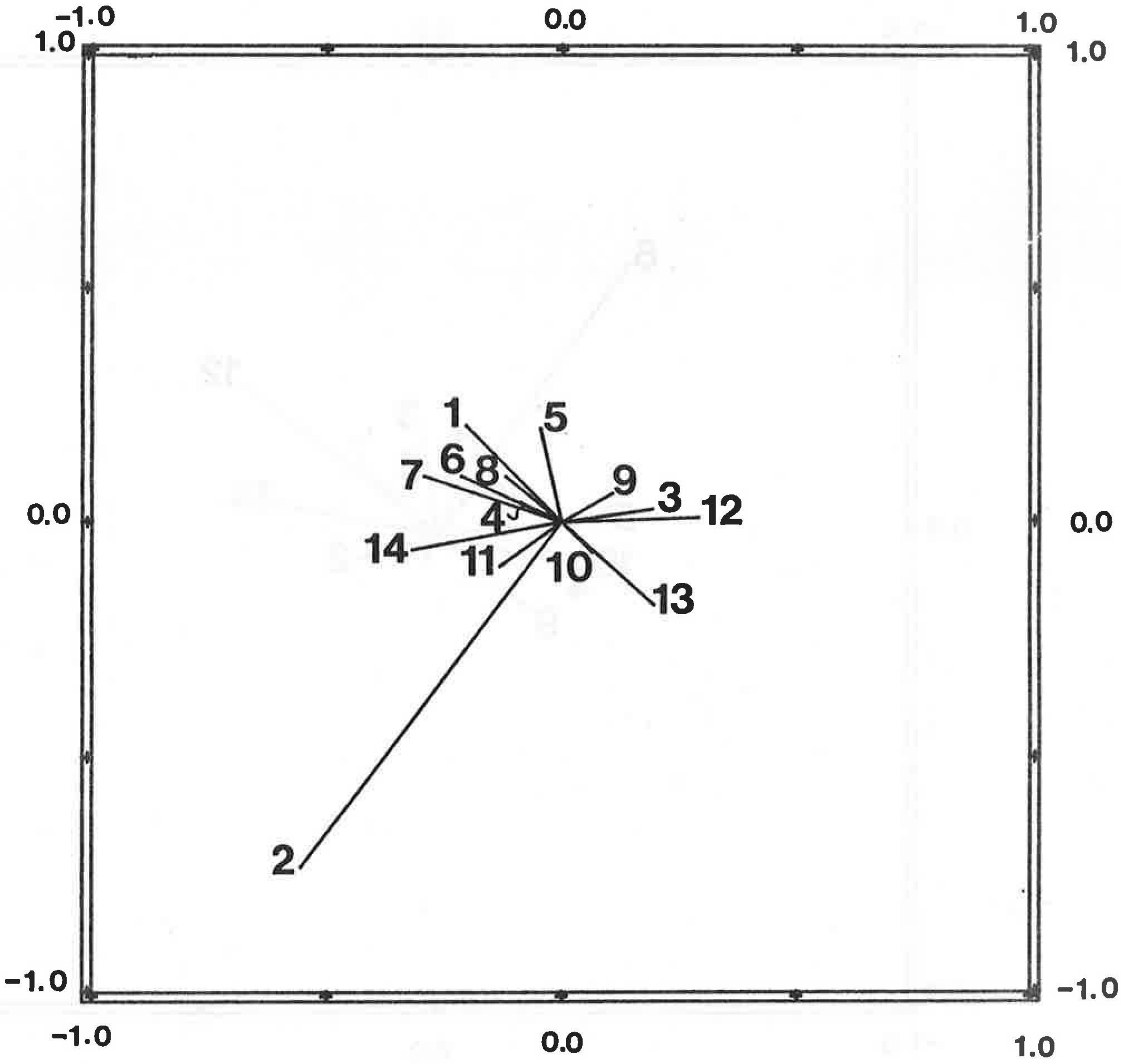

Figure 3.--Sensitivities of SKEBUB simulation to species specific availability to predation.

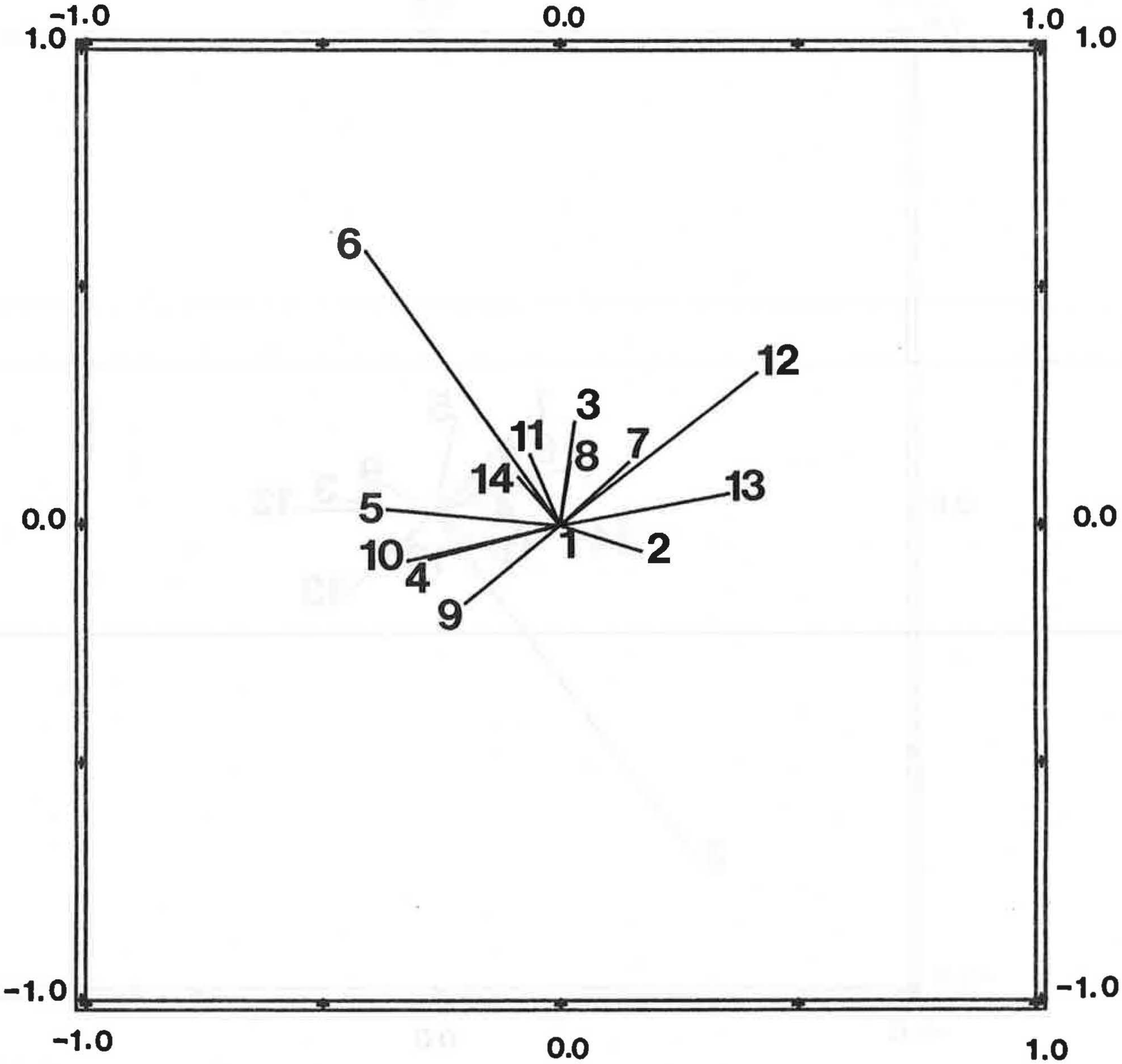

Figure 4.--Sensitivities of SKEBUB simulation to species specific percent contribution to the diets of predators.

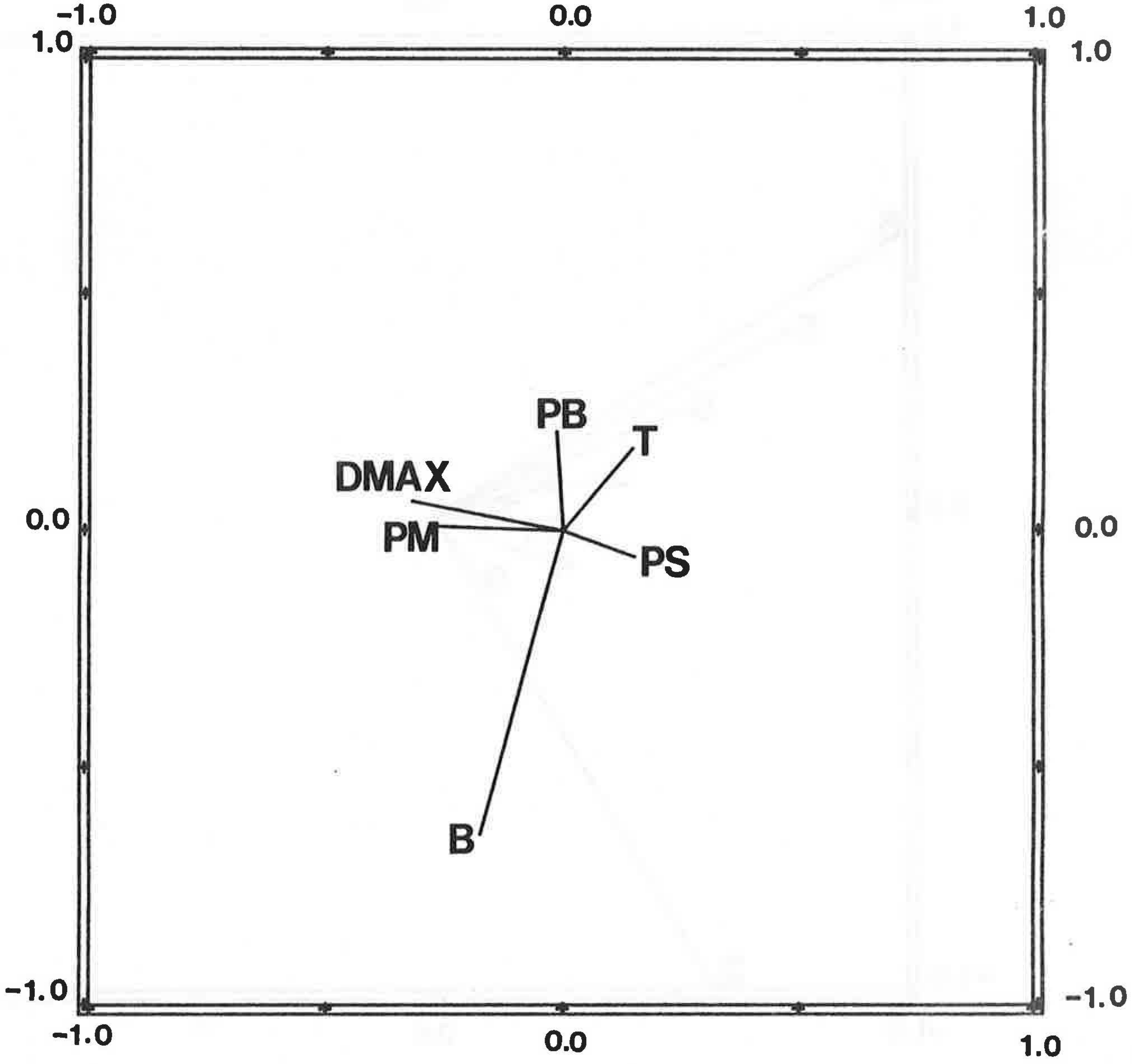

Figure 5.--Sensitivities of SKEBUB simulation to global parameters (see Table 1 for definitions).

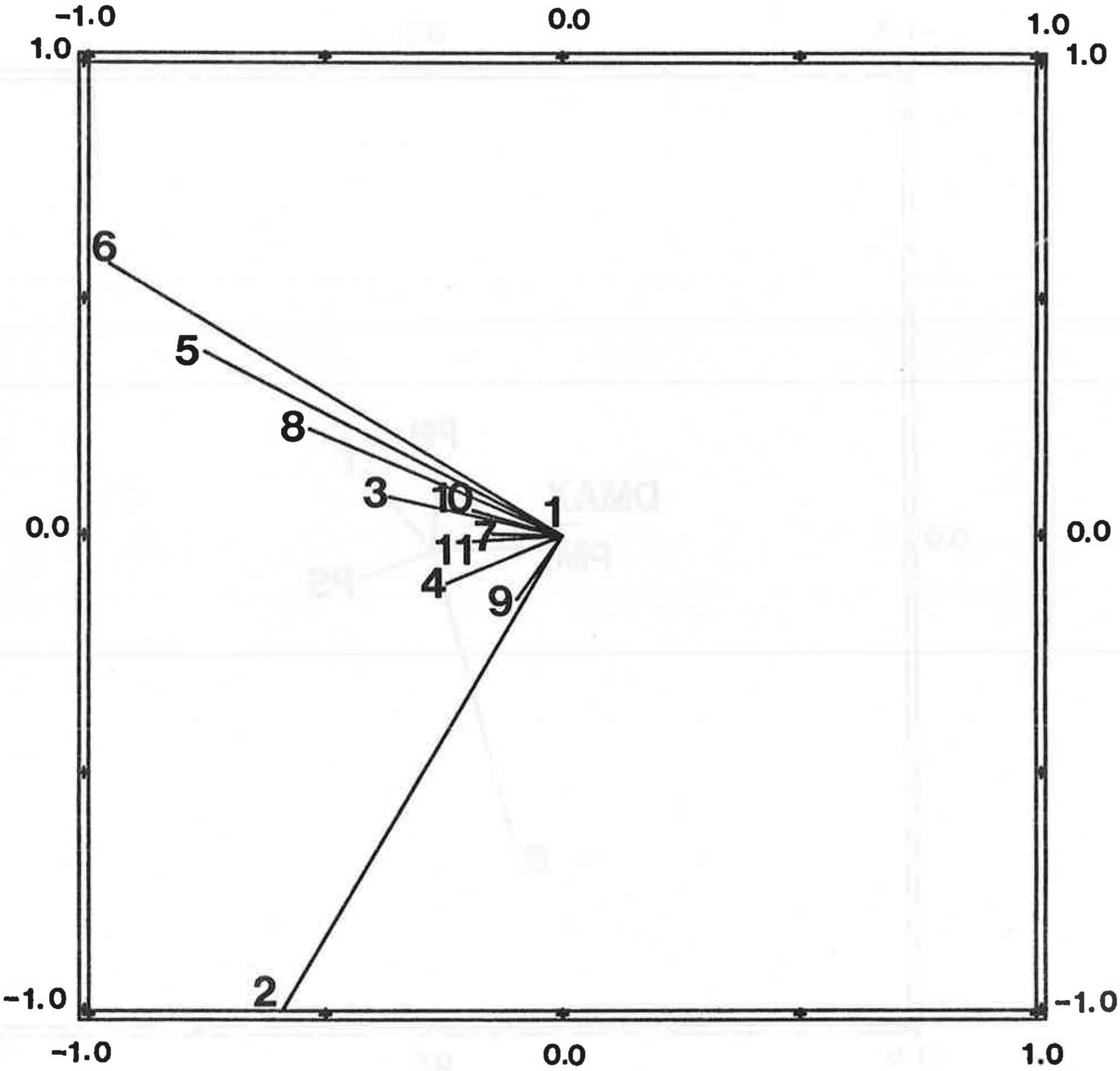

Figure 6.--Sensitivities of species specific equilibrium biomasses in SKEBUB simulation.

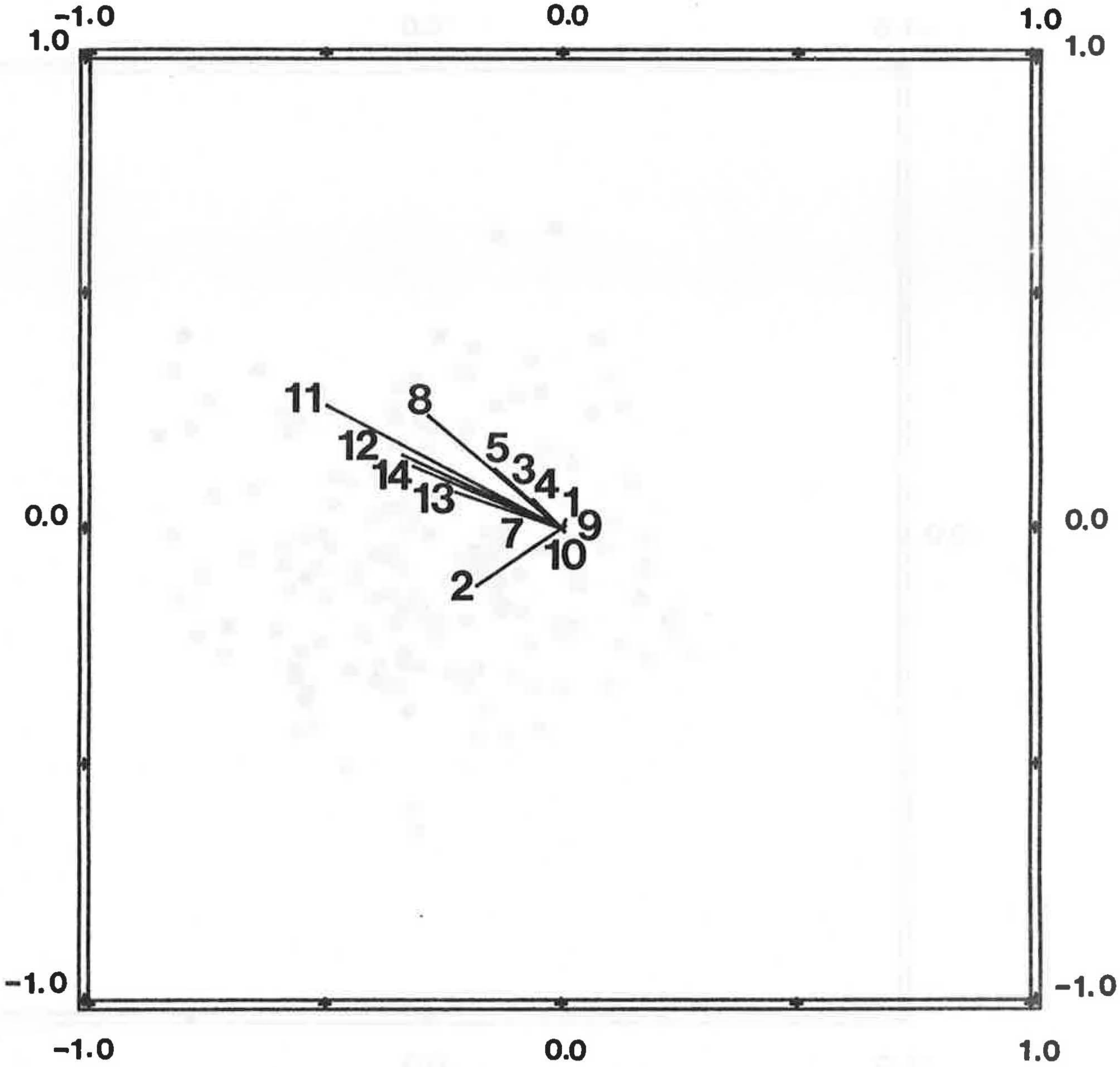

Figure 7.--Sensitivities of species specific predation/biomass ratios in SKEBUB simulation.

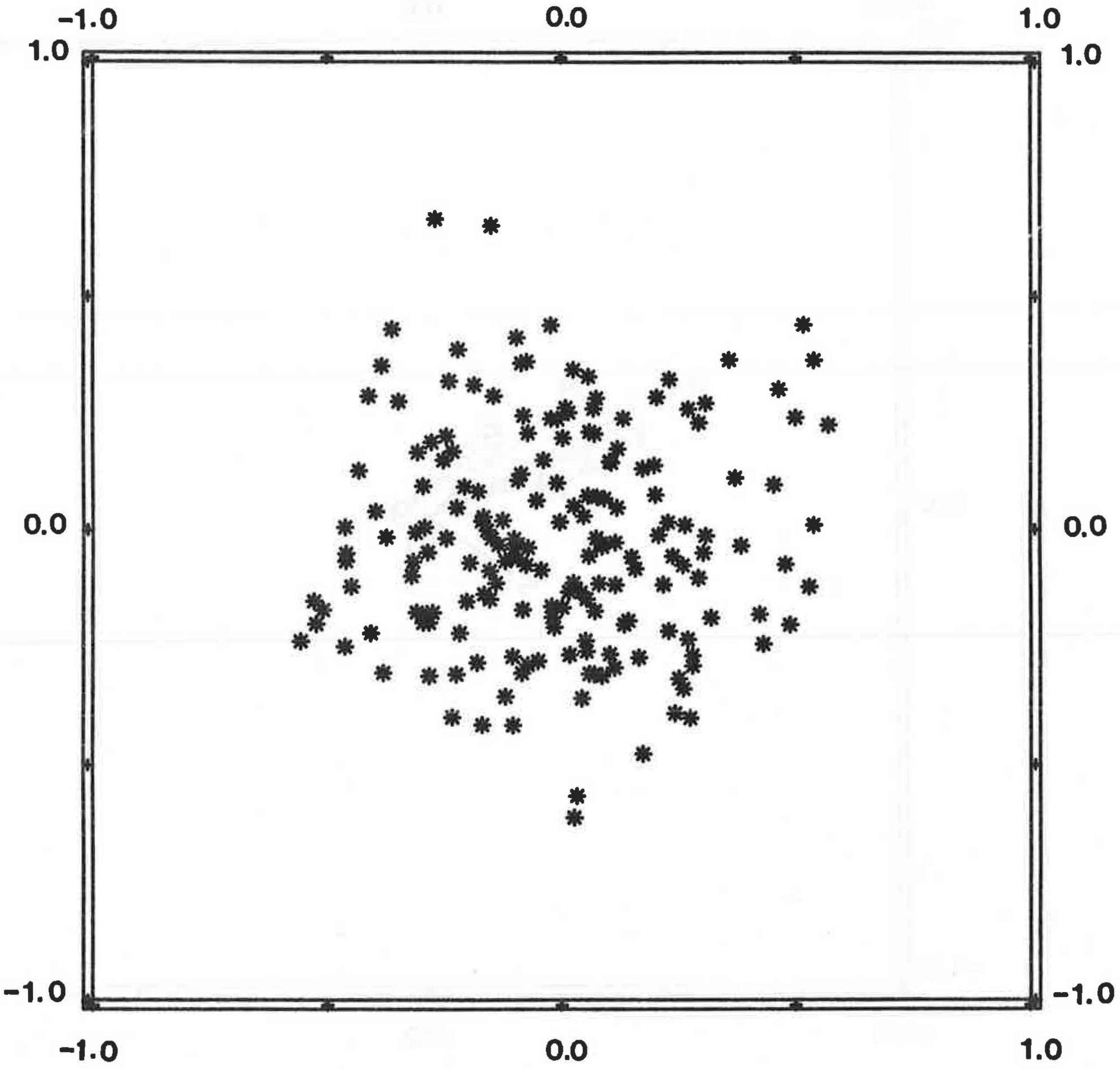

Figure 8.--Sensitivities of individual model runs of SKEBUB simulation.

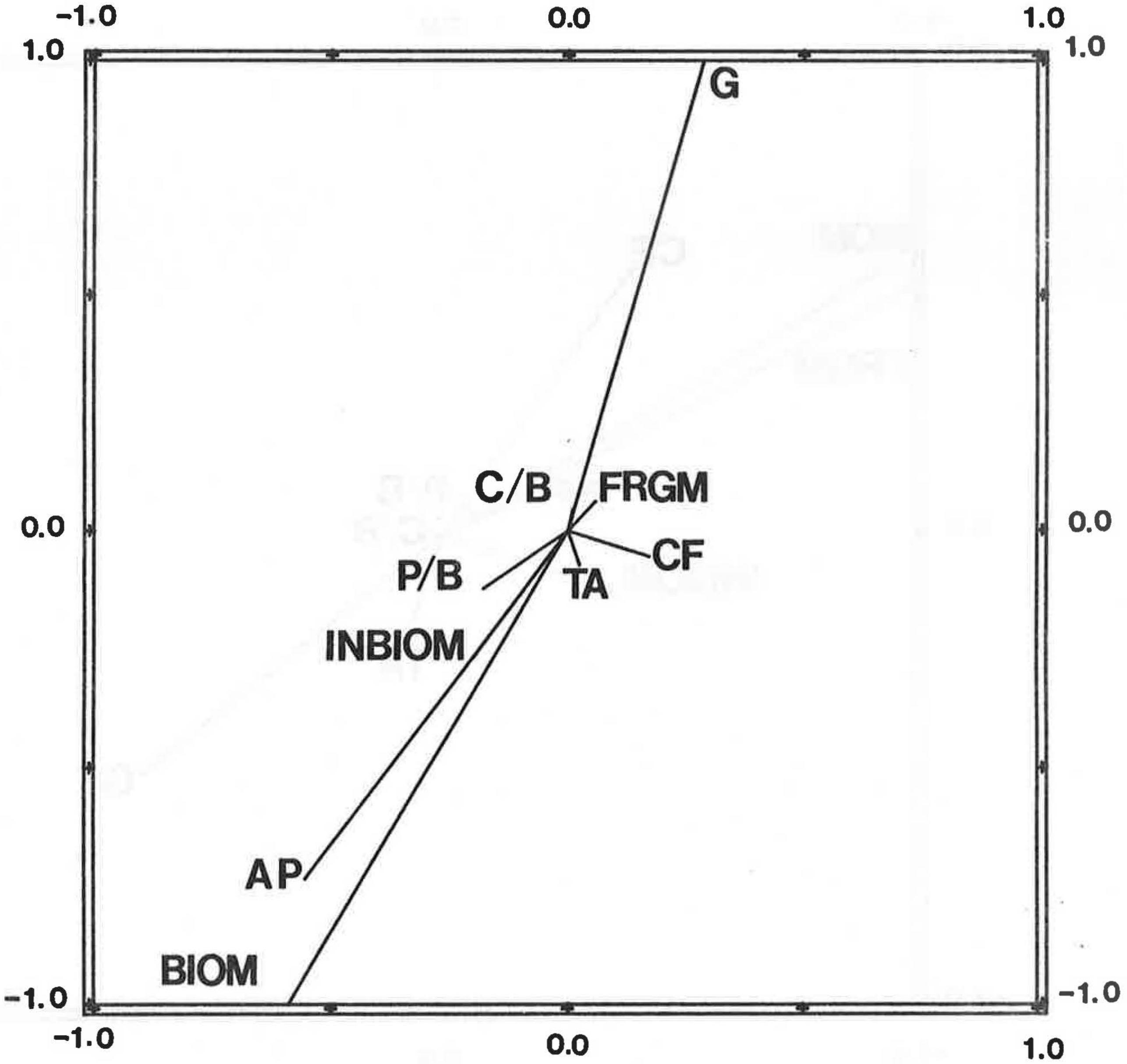

Figure 9.--Sensitivities of input and output variables directly relating to the flatfish species grouping.

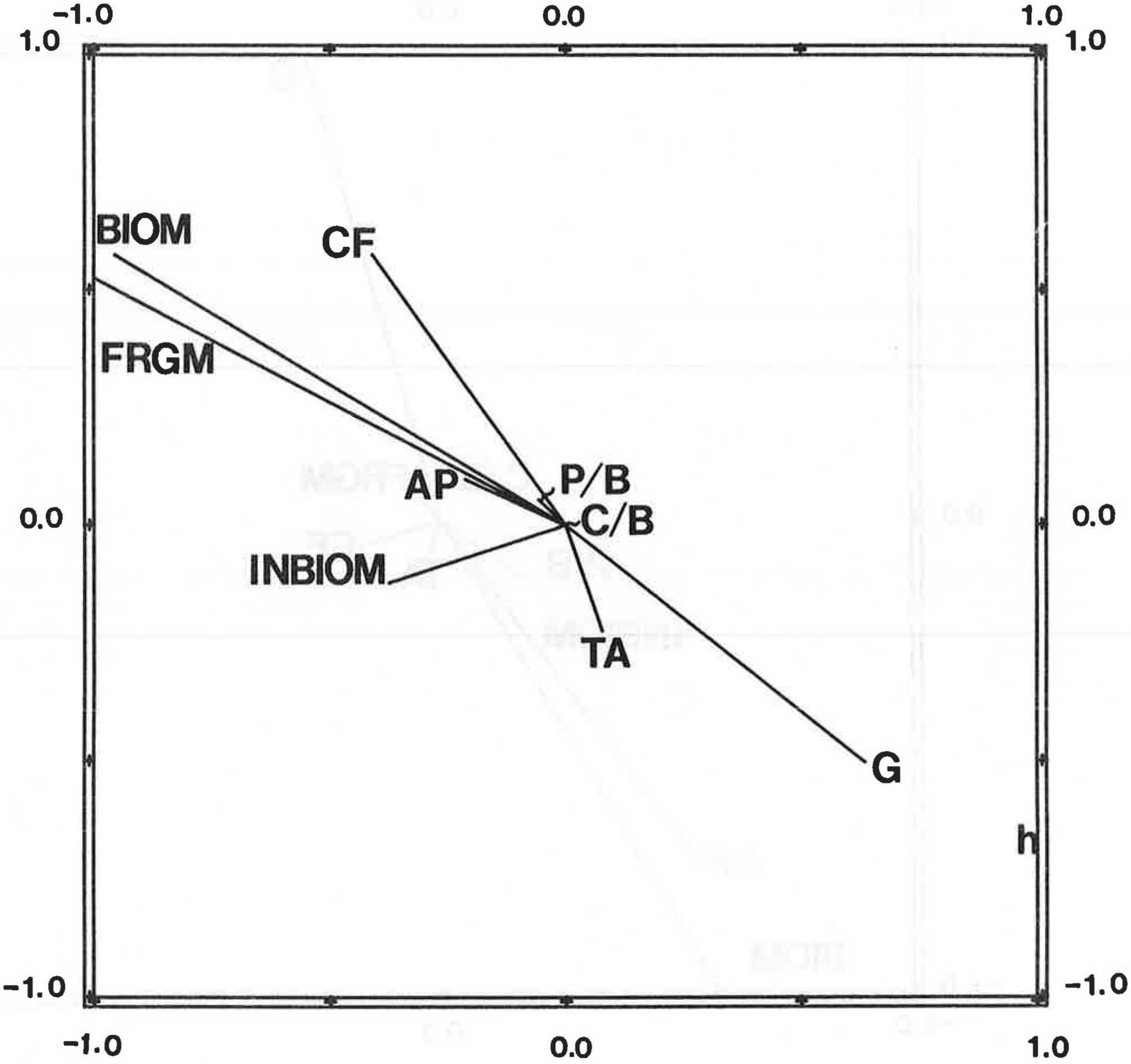

Figure 10.--Sensitivities of input and output variables directly relating to the silver hake.

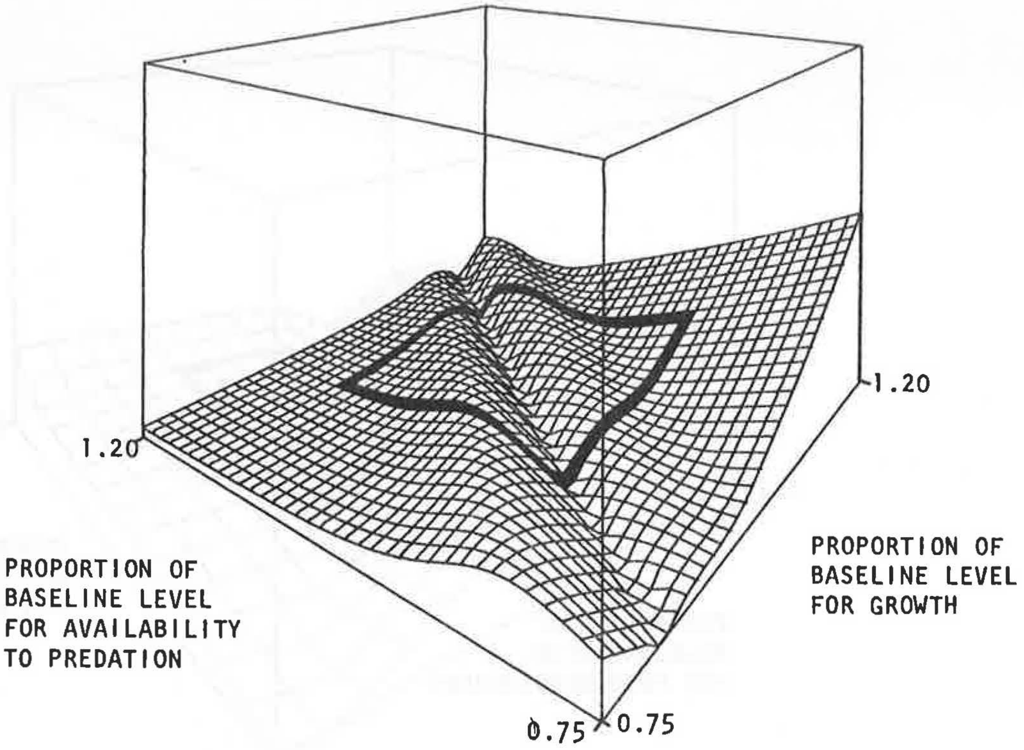

Figure 11.--Response surface of percent annual change in biomass at equilibrium for the flatfish species grouping (absolute values). Outlined area indicates parameter range in sensitivity analyses.

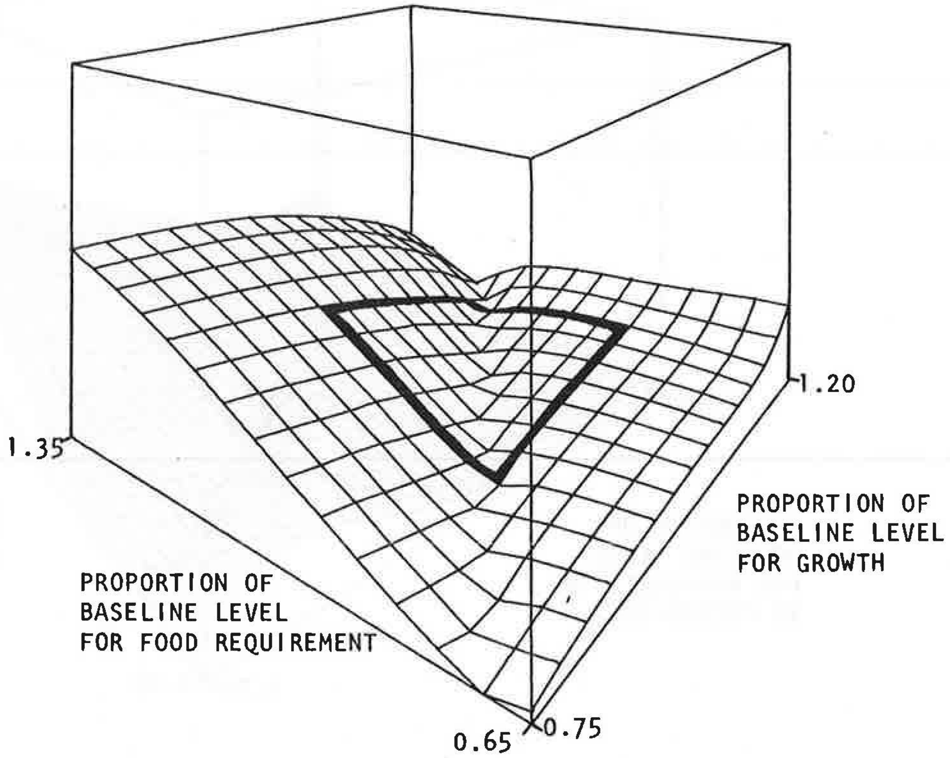

Figure 12.--Response surface of percent annual change in biomass at equilibrium for the silver hake (absolute values). Outlined area indicates parameter range in sensitivity analyses.