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Equilibrium Procedures in SKEBUB: an Evaluation of Parameter Variations

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EQUILIBRIUM PROCEDURES IN SKEBUB:
AN EVALUATION OF PARAMETER VARIATIONS

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ABSTRACT

The equilibration process in SKEBUB, a multispecies biomass-based fisheries ecosystem model, was tested by varying selected input parameters in successive runs on the Burroughs 7800 at the Northwest and Alaska Fisheries Center. Simulation responses were related to the results of an extensive literature survey evaluating equilibria in natural and model ecosystems. This study indicated that varying the availability to predation or the growth rate parameter alone had little impact on the global equilibrium position selected by the simulation. Varying sea temperatures changed the shape of response surfaces of equilibrium-indicator output statistics, shifted the global equilibrium point towards different availability to predation and growth rate parameter values and inversely affected the mean annual biomasses at equilibrium. Changing the biomass iteration constant controlling convergence influenced the magnitude of equilibrium output biomasses as did increasing the initial group biomasses by a fixed percentage and simulating multiple equilibrium points at a constant temperature. Results of the literature survey indicate that although most natural systems are too complex to be fully described by equilibrium models, some assemblages have maintained a stable species composition for many years. Researchers may justify using equilibrium-based models to estimate the impact of human intervention in a particular system if they state their assumptions and interpret their results cautiously.

INTRODUCTION

SKEBUB (Skeletal Bulk Biomass Model) is a multispecies, biomass-based ecosimulation model without spatial resolution developed by N. Bax (1983;1985) as a simplification of the holistic ecosimulation models described in Laevastu and Larkins (1981). In 1984, J-E Eliasson of the University of Tromso together with N. Bax and T. Laevastu of the Northwest and Alaska Fisheries Center, Seattle, parameterized SKEBUB to study the impact of cod enhancement on the Balsfjord ecosystem in northern Norway. Eliasson's version, used in this report, simulates the dynamics of fourteen groups of marine organisms and their interactions.

The main purpose of this study is to validate equilibration processes in SKEBUB. Validating a simulation model aids other users in understanding the simulation's predictive limitations, identifies gaps in data or theory, and helps ascertain that the underlying model actually corresponds to the system of interest. To accomplish the latter, key mechanisms may be probed to check that their corresponding mathematical expressions are sound. Alternatively, validation involves continuous policing of the simulation output while it is running to pinpoint spurious results (Miller et. al.,1976). One way to validate SKEBUB is to test the properties of its global and local equilibria. Selected "baseline" input parameters that normally simulate an equilibrium state are replaced with a probability distribution. No attempt is made at this stage to quantify errors between runs; rather the distribution of results is visually compared to the baseline run and interpreted with respect to definitions of stability.

In addition to evaluating SKEBUB, this study first reviews some of the ecological literature on equilibria in natural systems for evidence either supporting or refuting the use of an equilibrium-based simulation in studying perturbations to a fisheries ecosystem. The review highlights uncertainties about the analytical and predictive powers of multispecies ecosystem models while illustrating the necessity of combining empirical and modelling approaches to maximize ecological understanding.

EQUILIBRIUM IN THE LITERATURE

Ideas about ecosystem structure in the 1950's through the early 1970's led by such eminent researchers as MacArthur (1955), Nicholson (1957), Slobodkin (1955,1967), and Ehrlich and Birch (1967) evolved from descriptions of nature into theories of ecosystems governed by a "balance of nature", equilibria, or steady state conditions (Colwell, 1985). Acceptance of equilibrium-based population interactions was widespread (Sousa, 1979) and models drawn from these ideas were developed and promulgated.

Despite the popularity of balanced nature theories and observations supporting these ideas (Table 1), how closely most natural systems approach equilibrium is a highly controversial topic (Wiens,1977). Beginning in the late 1960's, field ecologists began manipulating populations in order to uncover new information about community structure. These studies revealed populations as loosely connected, interactive units not forming a delicately balanced ecosystem but instead governed by chaos,

Table 1.--Evidence for stability

Author	Year	Comments
Connell & Sousa	1983	
McGowan & Walker	1985	Copepods Same rank abundances
Paine	1966	Invertebrates Rocky shores
Grossman	1982	Fish Rocky shores
Sherman et. al.	1982	Zooplankton N. Atlantic
Margelef	1969	Benthos More stable than plankton (?)
Tyler	1971	Fish African tropical communities
Murdoch	1969	
Hurd et. al.	1971	Old field vs. young field
Caddy & Gulland	1983	Whales Steady stock example
Thomson & Lehner	1976	Fish assemblages Rocky intertidal
Buchanan et. al.	1974	No. of spp.; biol. production Rel. stable over 4 yrs.
Schoener	1985	Lizards

disturbance and disequilibrium. Present ecosystem control hypotheses (Wiens, 1984) suggest that such systems persist from one disturbance to another; that the existence of some species assemblages is dependent on sporadic disturbances, that predation outweighs competition in structuring communities (Paine, 1966), and that climate and other factors may drive certain characteristic but non-equilibrial population cycles (Watt, 1969; Caddy and Gulland, 1983). Table 2 summarizes the reviewed papers that support a non-equilibrium view of natural systems.

Multiple stable states have been investigated with interest by some modellers and theoreticians (Lewontin, 1969; May et. al., 1979; Recknagel, 1985; Bax, 1985, this author). Some instances of alternate stable states have been reported in the field (Maguire, 1971; Sutherland, 1974; Sutherland and Karlson, 1977; Simenstad, 1978); although their existence has been criticized to be in the eyes and time scales of the beholders (Connell and Sousa, 1983; Peterson, 1984; Sousa and Connell, 1985). These studies reveal the importance of time scale in evaluating system stability, as over the short term even stochastic systems may appear deterministic. Using population member lifespans as a time gauge may help solve this problem.

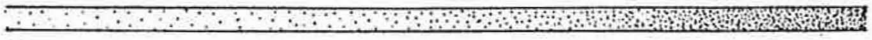
Most system models are based on the assumptions of global stability (Sutherland, 1974), yet the growing empirical evidence pushes for loosely bounded global indeterminism. Where then do theory and experience meet? Although SKEBUB and other holistic simulation models such as ECOPATH (Polovina and Ow, 1985), SALMO (Recknagel, 1985), the Lake Conway model (Ewel and Fontaine, 1982), and a Six Compartment Model (Miller et. al., 1976) are

Table 2.--Evidence for instability.

Author	Year	Comments
Preston	1969	Tilefish Nantucket
Caddy & Gulland	1983	Lobster, scallop
Hurd et. al.	1971	Consumers 2, 3 producers
Murdoch et. al.	1985	Pest populations maintained
Caswell	1978	References therein suggest long term instability
Wiens	1984	Birds foraging patterns Non-limiting environment
Sousa	1979	Marine boulder fields Diversity maintained by instability
Southward	1980	Fish communities English channel; climate influences
Watt	1969	Periodicities related to climate
Katz	1985	Snails Pred-prey interactions
Colwell	1985	New themes in ecology Disturbance forces
Paine	1969	Re: MacArthurian stability

potentially misleading if applied to non-deterministic systems, they may augment our understanding of other ecosystems or species assemblages. As Table 1 asserts, forms of ecosystem regulation do exist. Ursin (1982) maintains that recently too much attention has been paid to population imbalance and change; that in reality systems are stable. He cites examples from marine fisheries ecosystems such as density dependent mortality of juvenile fish, buffering mechanisms to the sizes of fish stocks and the differences between young, labile more opportunistic fish assemblages and older, more specialized systems. Unfortunately to what extent the mechanisms behind these equilibria are intrinsic, extrinsic, biological, or physical is still not well understood.

Another method for studying ecosystem stability is to give up trying to place systems into one of two camps. Instead, one allows for an ecosystem structure continuum as Wiens (1977; Fig. 1, this report) suggests, and looks for repeated patterns. Watt (1969) and Caddy and Gulland (1983), employing this method, have placed fluctuations of natural populations into several categories. Although Watt's (1969) community types range from microorganisms to land mammals, and Caddy and Gulland (1983) treat only marine species, their results are quite similar. The major difference is that Caddy and Gulland (1983) add a fourth pattern, "irregular production"; presumably this would be incorporated in Watt's graph of the pine looper (Watt, 1969, Fig.1, p.143). Recognizing a handful of community patterns may aid the management of environmentally and/or economically impor-



NONEQUILIBRIUM	*EQUILIBRIUM*
Biotic decoupling	Biotic coupling
Species independence	Competition
Unsaturated	Saturated
Abiotic limitation	Resource limitation
Density independence	Density dependence
Opportunism	Optimality
Large stochastic effects	Few stochastic effects
Loose patterns	Tight patterns

Fig. 1. Natural communities may be arrayed along a spectrum of states from equilibrium to non-equilibrium. At either extreme, several attributes of community structuring or dynamics can be anticipated, as shown (Wiens, Fig. 25.4, 1984).

tant animal and plant resources, such as commercial fisheries or marine mammals, in the face of few population-specific data.

Studies that combine modelling and data collection on easily defineable systems should help clarify the importance of equilibria vs. random influences on natural systems. Recent tropical reef fish assemblage studies by Sale and others (Sale and Steele, 1986 and references therein) report that "a completely random pattern of successful recruitment of individual [reef fish] does not produce assemblages closely resembling those [found in nature]". In this case, modelling fish species distributions across patch reefs indicates that random colonization accounts for some, but not all, of the observed assemblage structure. Sale and Steele (1986) identify a group of reef fish, including several highly abundant species, whose distributions are determined by other factors. Such studies of partially bounded systems in nature (Sale and Steele, 1986; Schoener, 1985; and others) that couple simulation modelling with field experiments extend one step beyond laboratory experiments to elucidate ecological ordering mechanisms in natural systems. Open ocean system simulation will benefit, in turn, from the results of experiments on smaller systems. However, pelagic realm modelling results will take much longer to verify given the uneven data base that is currently available for testing them.

KEY CONCEPT DEFINITIONS

The latter half of this report describes a simulation study designed to improve methodology for investigating changes in large, oceanic or estuarine systems. Key concepts used in this study are defined below according to recent published literature. For those who crave a large dose of confusion, more expansive discussions of terminology may be found in Lewontin (1969), Preston (1969), Holling (1973), Sutherland (1974), Harrison (1979), Pimm (1984), Connell and Sousa (1983) and Katz (1985).

Equilibrium

Grossman (1982) and Caswell (1978), using slightly different terms, recognize the following two mechanisms governing the organization of multispecies assemblages: deterministic, or equilibrial, processes and stochastic, or non-equilibrial processes. The former assume that assemblages fluctuate around or eventually achieve a balanced state, an equilibrium. This may be a point, a set of points, or a limit cycle where births and immigrations equal deaths and emigrations (Schoener,1985). Laevastu and Larkins (1981) employ this definition in their simulation models. Such deterministically organized biological systems exhibit dynamic rather than static equilbria, as they continuously renew individuals and biomass (Preston,1969); Botkin and Sobel,1975; Kitching,1983). Systems organized in the latter (non-equilibrium) mode exhibit no particular trends, and elements of the system appear to fluctuate independently. For example, habitats can accommodate additional individuals, density independent population dynamics operate and opportunism is the common environmental exploitation strategy (Wiens,1984). As Wiens suggests, natural communities probably exist in a continuum between the two extremes (Fig. 1, reproduced from Wiens,1984).

In order for equilibrium to exist, system parameters must exhibit some form of stability at equilibrium points, yet few studies have successfully quantified stability in natural populations (Pimm,1984). Although a population that remains constant in numbers or biomass through time is most likely stable, temporally varying populations that oscillate around an underlying stable point may be impossible to distinguish from variable populations that operate far from equilibrium (Schoener, 1985). Part of the problem is that a rigorous test for stability among field populations requires monitoring population members for at least one complete turnover of individuals. (Connell and Sousa, 1983; Pimm,1984) and few research grants last long enough (Pielou,1981). In simulated multispecies systems this requirement is often satisfied by scaling the biomasses' convergence towards equilibrium to the lifespan(s) of the longest living species, as mentioned above (May et. al.,1979; Sutherland,1981).

Stability

Stability may be defined simplistically as the ability to weather a stress period, or perturbation (Harrison,1979; Schoener,1985). Perturbations are mortality agents potentially able to change community structure and may either be additions to or subtractions from the system (Sutherland,1981). Relative stability may be compared between equilibrium points by envisioning these points as topographic minima surrounded by a system of hills and valleys; their domains of attraction (Holling,1973; Peterman,1977). This approach, called Lyapunov neighborhood stability, deals only with the small local space around each equilibrium point and assumes that the equilibrium is stable if trajectories subsequent to perturbation tend toward that point (Lewontin,1969; Deakin,1975; Recknagel,1985; Katz,1985).

Three facets of systems stability relative to a hypothetical landscape are resilience, persistence and resistance (Margalef, 1969; Watt,1969; Sutherland,1974; Botkin and Sobel,1975; Gray,1977; Sousa,1979; Harrison,1979; Van Voris et.al.,1980; Sutherland,1981; Grossman,1982; Connell and Sousa,1983; Pimm,1984; Schoener,1985). Resilience stability, also termed adjustment stability or Lyapunov asymptotic stability (Recknagel,1985; Katz,1985) describes both the system's ability to return to equilibrium once it has been perturbed and the relative time to return. It is indicated by the steepness of the valley sides. Defined in this way, resilience stability need not be considered " incompatible with ecosystems that generate multiple stable states " (Recknagel,1985). Harrison (1979) further defines resilience as the system's response to perturbations of initial values of state variables (biomass, diversity, etc.). Persistence, the time duration of a particular assemblage or of a set of interesting properties of that assemblage, is related to the distance between valleys. It is a measure of the maximum variability observed around an equilibrium before a major change in system dynamics occurs. Resistance is the ability to avoid displacement from a particular equilibrium (Sutherland,1981; Katz, 1985) and describes the system's powers of adhesion to equilibrium during environmental perturbations (Harrison,1979; Connell and Sousa, 1983). In the hypothetical landscape, resistance is related both to valley steepness and width.

If a perturbation causes a movement a short way from an equilibrium point with return to that point, the system is locally stable. Return from a long distance or from all possible perturbations implies global stability (Sutherland,1981; Pimm, 1984; Schoener,1985). For the purposes of this study, potential local or global stable points were identified by plotting the relative between-year percent change in biomass obtained from a matrix of two sequentially varied input parameters. The usage of global and local here is similar to but does not strictly follow Lewontin (1969) in that each temperature regime potentially contains several (mutiple) local and one global equilibrium point. In addition, a stable point that encompasses all possible temperature regimes is identified.

METHODS

The holistic simulation model SKEBUB has been recently documented by Bax (1983;1985), Bax and Laevastu (in press) and Eliasson in prep.). A brief description of SKEBUB parameterized for the Balsfjord in northern Norway is presented here.

SKEBUB is consistent with recent evidence about the importance of predator limitation rather than resource limitation in structuring ecosystems (Pimm,1984). This version simulates predator-prey interactions between the major taxonomic groups inhabiting Balsfjord excluding parasites and microorganisms (Table 3). Baseline input biomass and food composition data reflect five years of research conducted at the University of

Table 3.--Group biomass compositions for Balsfjord SKEBUB.

Group No.	Species
2	0 Cod
3	1 Cod
4	2 Cod
5	Herring
6	Capelin
7	Flatfish
8	Other finfish
9	Prawns
10	Benthos
11	Copepods
12	Euphausiids
13	Other zooplankton

Tromso and will be fully presented by Eliasson in a subsequent publication (in prep.) SKEBUB is a "top-down" simulation; the energetics are based on the biomass of top predators in the system and their diets. Here the top predators are Atlantic cod, the main species of interest in the study. Biomasses of prey necessary to sustain the top predators are computed and their population dynamics represented by conventional fisheries growth and mortality functions as detailed in Bax and Laevastu (in press). The simulation itself thus determines most of the final group biomasses, minimizing the number of estimated parameters and thereby minimizing error. In cases where accurate seasonal data are sparse, group biomasses are prescribed and held constant. SKEBUB is designed to operate with (fishing) catch and one of the dominant group biomasses held constant; this prevents a trivial solution. The more biomasses or inputs such as apex predation and catch that are prescribed, the more distinct a solution to the equilibration process will occur.

The simulation runs in two modes as follows:

1. Equilibrium-searching mode: In this first stage of the simulation individuals grow, die, and consume each other according to consumption tables based on stomach data in twelve monthly time steps. After one year biomass growth increases for each group are compared with losses due to predation and fishing. The starting biomasses for the next year's cycle are adjusted, if necessary, via an iteration constant (AGA). Individual biomasses fluctuate from year to year, but eventually converge at a dynamic equilibrium within approximately 30 simulations of the same year. Equilibrium is defined here as the point (or points) where output

biomasses remain within 5% of the previous year's simulation results, i.e. where total annual growth minus non-predation mortality approximates total annual predation mortality. All of the simulations in this study are performed in this mode. Table 4 lists selected parameters used in this study.

2. Prognostic mode : Post equilibration, average biomasses remain steady, unless the system is perturbed. Selected input parameters such as fishing effort or temperature may then be varied in order to monitor the effects of such parameter perturbations on the species' biomass. Bax and Laevastu (in press) provide further uses and explanations of this mode.

SKEBUB's equilibration process is a variant on relaxation procedures which are in turn an extension of the Gauss-Siedel iteration technique (Hornbeck,1975). At each step, input biomasses are replaced by the most recently adjusted values and the simulation is repeated. This is advantageous in that the system converges quickly. Originally, biomass-based ecosimulations designed by T. Laevastu selected a single, unique equilibrium point where total growth equaled total mortalities for each species or species group. In other words, the predators' diets were fixed. Later versions, including SKEBUB, allow limited interspecific prey switching. Consequently, while the simulation is running it may select one of several equilibria depending the value of allowable consumption (AC) which controls the level of predation on each species. AC is varied globally via the parameter APE in a number of the simulation runs as shown below (see Appendix).

Table 4.--Selected parameters in SKEBUB.

AGA	Biomass convergence factor
APE	Availability of a group to predation
GADJ	Growth adjustment parameter
DIFMAX	Maximum difference between successive iterations
TEMP	Temperature anomaly, deviation from baseline (°C)
AC	Allowable consumption
T, TA	Temperature, Acclimation temperature (°C)
B	Rate of prey switching
DMAX	Maximum amount of prey switching allowed

The first step in investigating SKEBUB's equilibrium-seeking mode is systematic variation of availability to predation (APE) and growth (GADJ). Simulation stable points (minima) are located by examining a series of statistics on the output data at one reference temperature and at six other temperatures selected from a range of known northern ocean temperature anomalies (Laevastu, 1984a;b). Three dimensional response surfaces illustrating the percent change in biomass at equilibrium (z-axis) as affected by different APE and GADJ (x- and y-axes, respectively) combinations for several different temperatures are plotted using a plotting program available on the Burroughs 7800 at the Northwest and Alaska Fisheries Center. Low points represent the potential equilibria. Resilience stability is evaluated at each equilibrium point by comparing slopes of the domains of attraction among plots and by comparing values of the percent biomass change at equilibrium. Second, the equilibrium convergence constant (AGA) is varied and species group biomasses compared. The simulation's resilience to data error is tested by adjusting several of the input biomasses upward or downward by between 10% and 30% of the initial biomasses. Finally, multiple stable points are investigated by comparing output biomasses from four pairs of APE and GADJ values producing separate minima in one temperature regime.

RESULTS AND DISCUSSION

Temperatures that deviate from baseline conditions alter the simulation solutions, the unique combinations of species biomasses at equilibrium that solve the biomass equations, in a number of different ways. Table 5 summarizes the stability trends at seven different temperature anomalies, and Figures 2-7 display the domains of attraction surrounding locally stable (APE,GADJ) points for four positive anomalies (note the scale variations of x- y- and z- axes). Increasing the temperature from ambient (Fig. 2) to an anomaly of +2.0° C (Fig. 7) shows that at high temperatures, the system as a whole is less stable. This is indicated by high values for percent change of biomass (z-axis) along the array borders in Figs. 6 and 7, and in Table 5 (at maximum instability). However, the between-year percent change in biomass for the global solution is relatively low (Table 5); its lowest value occurs at an anomaly of 1.5° C. In other words, the global solution is more stable at higher (Fig. 5) than at lower (Fig. 3 and Table 5) temperatures, but it is very dependent on APE and GADJ. Thus it has a narrow domain of attraction. At lower temperatures, more solutions to the biomass equations produce relatively low percent changes in biomass. This results in a flat response surface (wide domain of attraction) with several solutions, none of which are as distinct as the global high temperature solution. This is consistent with work by Laevastu (1984a) where he finds that fish populations respond with detectable biomass changes to temperature anomalies of +1.5° C or greater but not to less than +1.5°C.

Results from this simulation identify a global solution to the biomass equations at each temperature anomaly (Table 5) and point out additional characteristics for further study. Six globally stable (APE,GADJ) points for six temperature anomalies produced the series of mean annual equilibrium biomasses shown in

Table 5. Global equilibrium and maximum instability values of % change in biomass, proportion of baseline level for availability to predation (APE) and proportion of baseline level for growth (GADJ) in SKEBUB parameterized to Balsfjord, Norway, at seven different temperature anomalies.

Temperature Anomaly °C	GLOBAL EQUILIBRIUM % Change in Biomass	APE	GADJ	MAXIMUM INSTABILITY % Change in Biomass	APE	GADJ
-1.5	12	1.2	1.44	23.4	1.15	1.08
-1	10.5	1.13	1.44	35.9	1.23	1.08
-0.5	7.5	1.23	1.44	27.4	1.23	1.08
0.5	3.1	1.18	1.38	29.3	0.88	1.44
1	1.6	1.13	1.34	40.7	0.88	1.44
1.5	0.6	1.1	1.31	233.6	0.88	1.41
2	2.2	1.08	1.31	9569.4	1	1.44

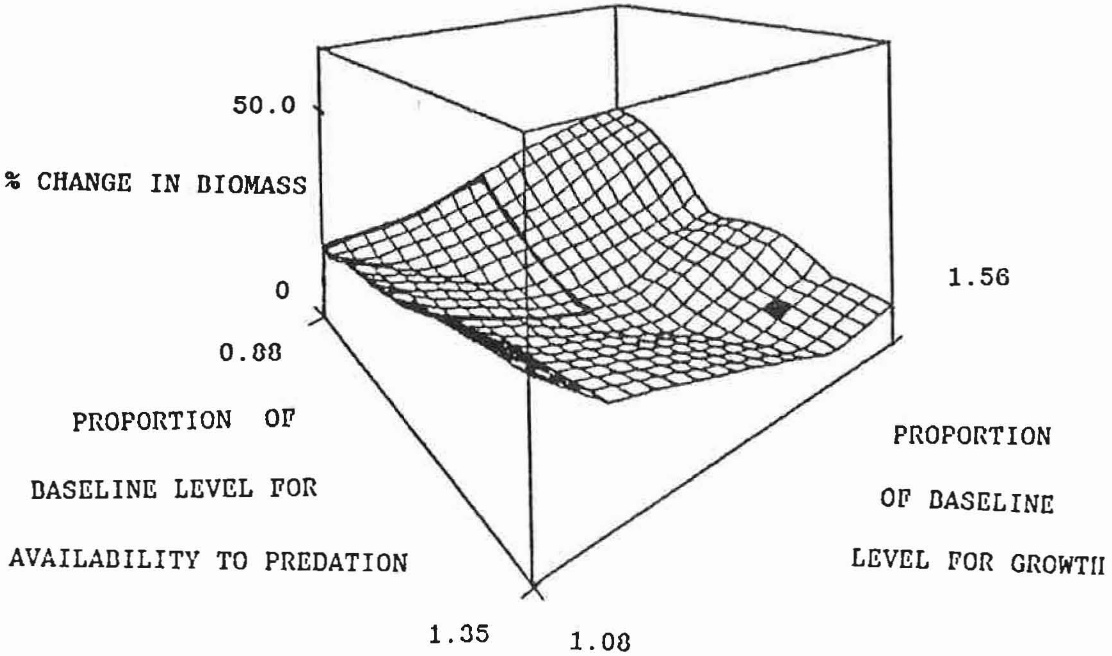


Fig. 2. Response surface of the percent change in biomass at equilibrium (absolute values) when the temperature anomaly is 0.5 °C. Blackened square denotes the (APE,GADJ) equilbrium point.

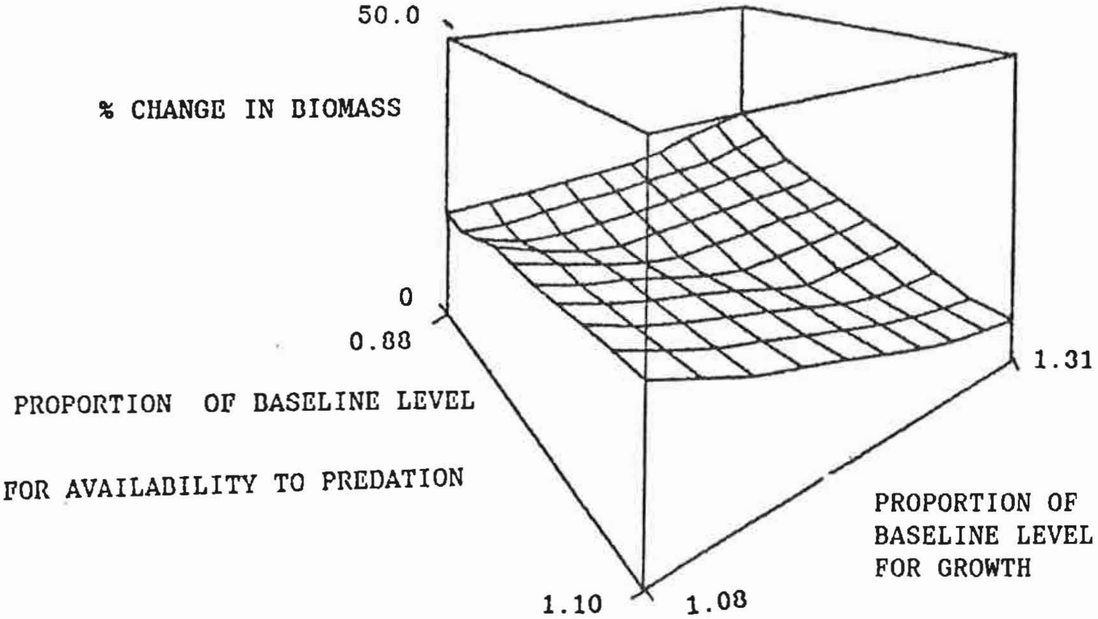


Fig. 3. 10x10 section of fig. 2 (outlined square).

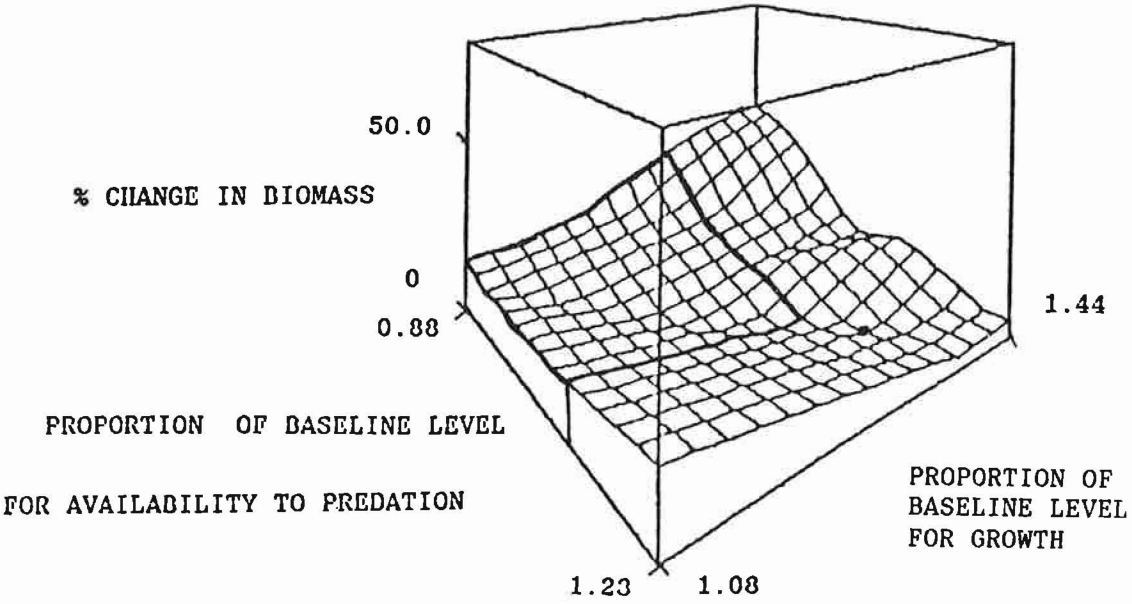


Fig. 4. Response surface of the percent change in biomass at equilibrium at a temperature anomaly of 1.0° C. Black dot denotes equilibrium point.

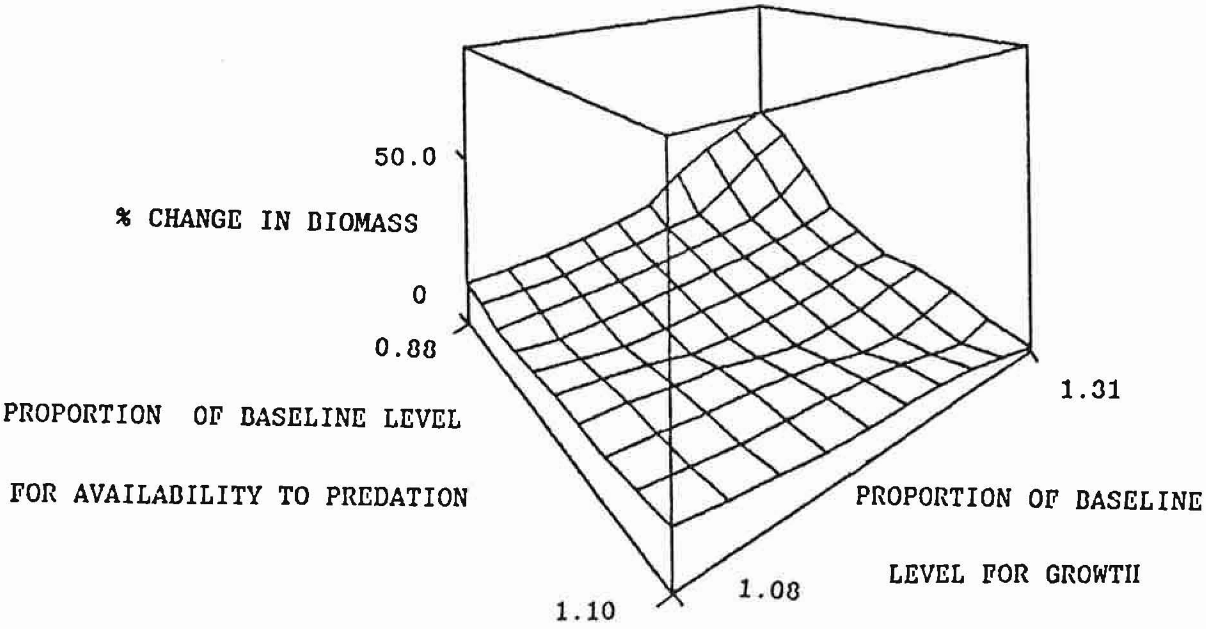


Fig. 5. Response surface of the percent change in biomass at equilibrium at a temperature anomaly of 1.5°C.

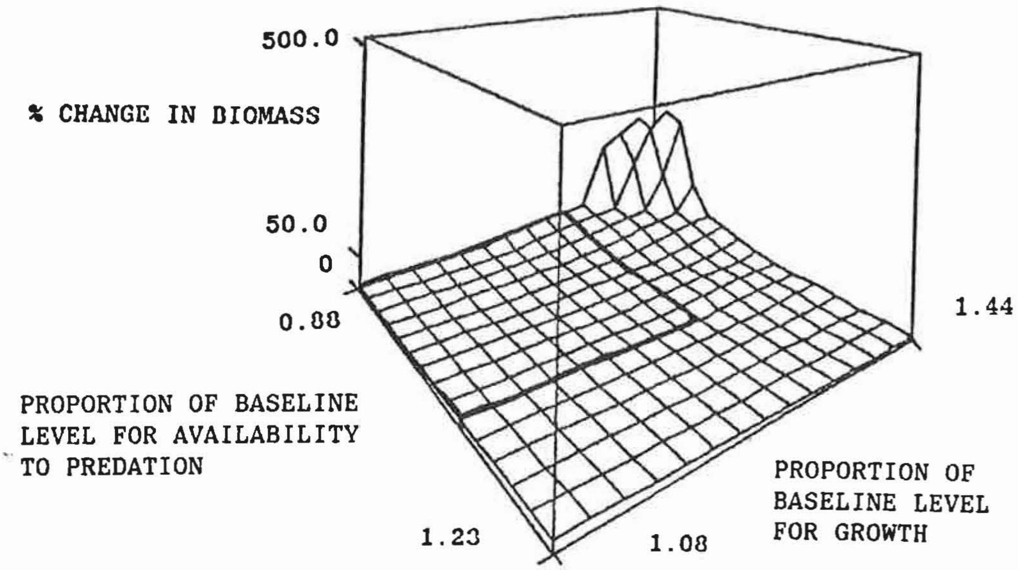


Fig. 6. A 15 X 15 plot of Fig. 5 (1.5°C), for comparison. Note peaks at high growth (GADJ) values.

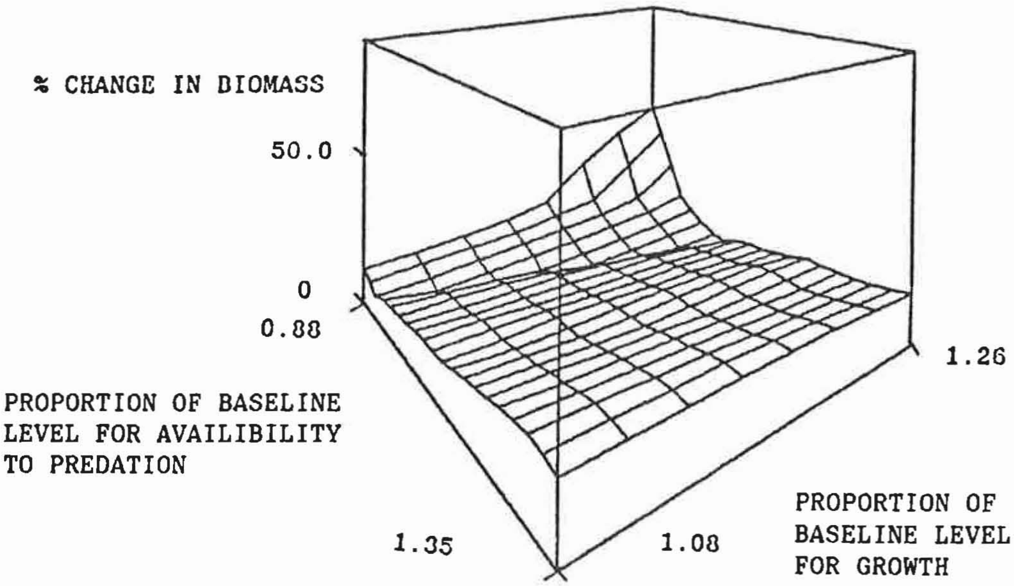


Fig. 7. 20X8 response surface of the percent change in biomass at equilibrium at the temperature anomaly of 2.0°C. Note peak at highest growth values.

Fig. 8. Within the range tested, increasing temperature decreases species biomasses, except for flatfish and prawns. This is because an increase in temperature stimulates growth rate in this simulation (see Appendix) and higher growth rates increase system productivity, requiring lower biomasses to sustain the predation. Negative temperature anomalies destabilize the Balsfjord system more than positive temperatures, just as they did in a PROBUB study of the Bering Sea (Laevastu, 1984a).

Varying the rate of biomass convergence to equilibrium (AGA), affects each group's equilibrium biomass differently (Fig. 9 & Table 6). When AGA is increased by 50% at a given temperature, herring, capelin, and other finfish biomasses decline, flatfish and cod remain steady, and prawn biomass increases. Decreasing AGA by 50% reverses the above trends and decreases cod biomass slightly. Any 50% change in AGA may produce between a 1% and 29% change in output biomasses, with a trend towards greater percentage change for decreased AGA than for increased AGA. Adjusting AGA up or down produces total mean annual biomasses at equilibrium that are not very different from those of the original reference run. SKEBUB thus displays relative resilience to AGA perturbations.

Varying the input biomasses of several species groups at a constant temperature to simulate data error has a variety of effects on output biomasses depending on the nature of the trophic link between the species varied and the rest of the system. In the preliminary runs of the Balsfjord SKEBUB, increasing or decreasing some of the input biomasses by 20% produced nearly

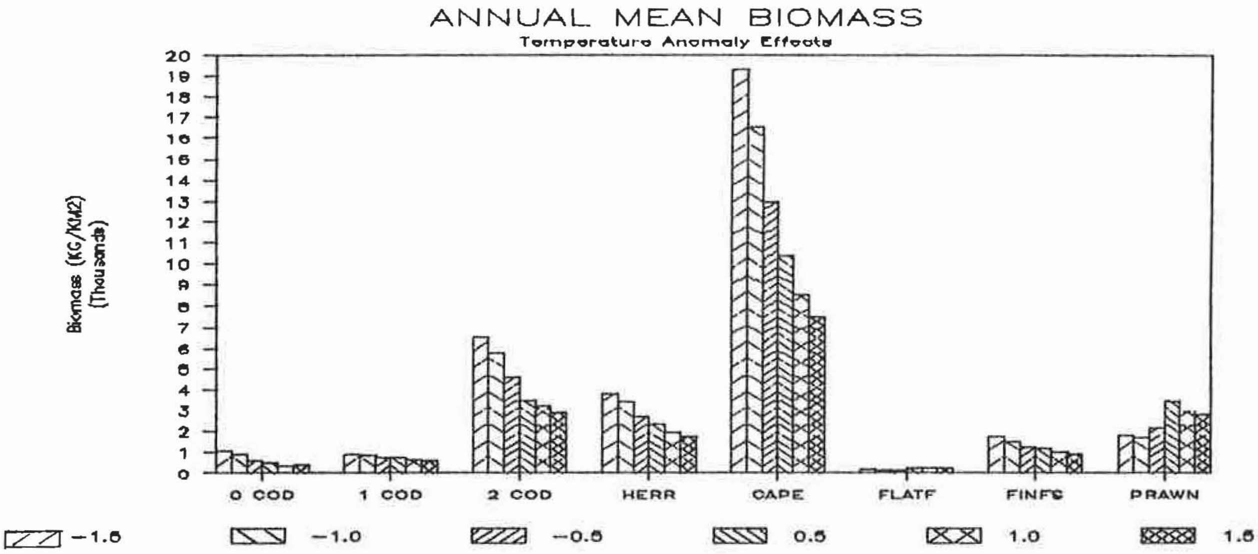


Fig. 8. The effect of temperature on annual mean biomass at equilibrium. Legend shows°C deviations from baseline values.

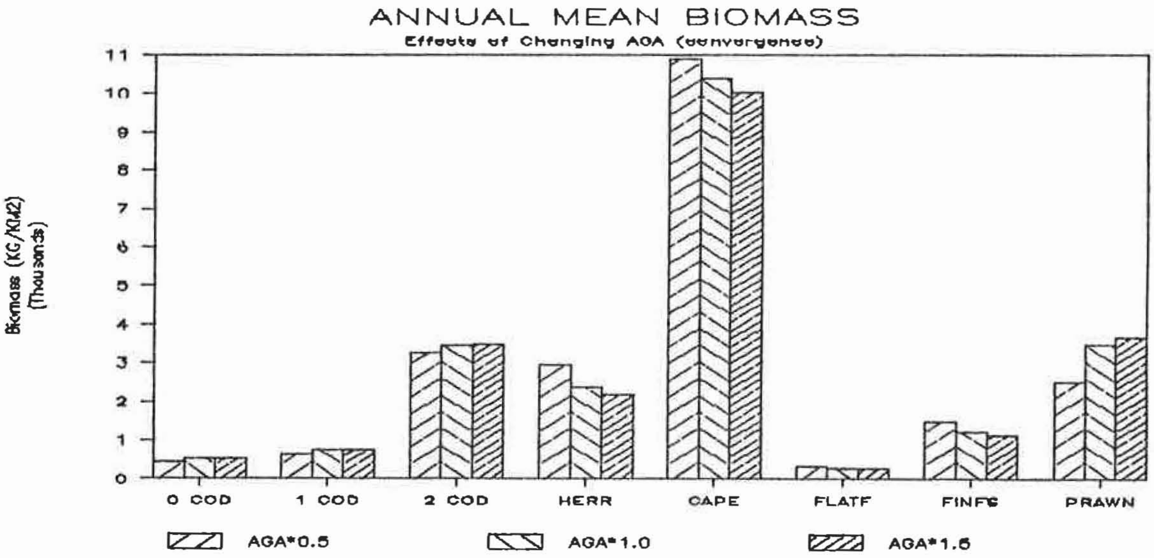


Fig. 9. The effects of changing AGA on output biomasses. Baseline value of AGA is multiplied by factors shown.

Table 6. Percent change in output equilibrium biomass when AGA is varied by +/- 50% from baseline values.
TEMP = 0.5°C BENTHOS = CONSTANT

GROUP	NUMBER	INPUT CHANGE IN AGA	OUTPUT BIOMASS CHANGE	INPUT CHANGE IN AGA	OUTPUT BIOMASS CHANGE
0 COD	2	-50.0%	-16.0%	50.0%	-2.9%
1 COD	3	-50.0%	-12.8%	50.0%	1.6%
2+ COD	4	-50.0%	-5.4%	50.0%	0.9%
HERRING	5	-50.0%	25.0%	50.0%	-8.0%
CAPELIN	6	-50.0%	4.9%	50.0%	-3.5%
FLATFISH	7	-50.0%	13.5%	50.0%	-3.1%
FINFISH	8	-50.0%	22.4%	50.0%	-7.2%
PRAWNS	9	-50.0%	-27.6%	50.0%	5.3%
BENTHOS	10	-50.0%	0.0%	50.0%	0.0%

identical output biomass changes at equilibrium. Generally, if and when an input biomass is changed, corresponding adjustments should have been made in the food composition of the species. Thus in order to investigate the unexpected model behavior, three different food composition tables were tested at each of three different sets of values for the rate of prey switching (B) and the maximum amount of prey switching (DMAX) in this system (Laevastu, pers. comm.). Table 7 evaluates the resilience of the simulation to input biomass changes at the most reasonable combination of food compostion and prey switching parameter values, for different biomass inputs. While most of the species groups' equilibrium output biomasses deviate only slightly from baseline levels when perturbed, indicating system resilience, a few, namely herring, flatfish and occasionally 0 cod, directly reflect the percentage of input biomass change. This illustrates the weak linkages that exist between herring or flatfish and the other species groups. In this version of SKEBUB, herring and flatfish depend mainly on zooplankton and benthos for sustenance. The available quantities of these food groups are so large that they are effectively inexhaustable, rendering their predators relatively independent from perturbations occurring in the rest of the system. The effect of weak linkages will be studied further when SKEBUB is applied to other ecosystems. Table 7 also shows simulation results obtained when 2+ cod are held constant versus when they are allowed to fluctuate. The constant 2+ cod runs exhibit slightly more stable equilibria than the variable 2+ cod runs, evidenced by the relative percent changes (Table 7) and by outputs of between year percent changes in the equilibrium-

Table 7. The relative percent change in output biomass compared with the baseline run, for the indicated % change in input biomass at one temperature. A modified food composition table was used. B,DMAX = 1.2, TEMP = 0.5.

SPECIES GROUP	NUMBER	INPUT BIOMASS CHANGE	OUTPUT BIOMASS CHANGE	
			VARYING 2+ COD	CONSTANT 2+ COD
0 COD	2	0.0%	-3.5%	-3.1%
1 COD	3	20.0%	4.0%	2.1%
2+ COD	4	0.0%	-2.5%	0.0%
HERRING	5	-20.0%	-20.7%	-20.7%
CAPELIN	6	0.0%	-1.0%	-1.0%
FLATFISH	7	-20.0%	-19.7%	-19.7%
FINFISH	8	0.0%	-1.3%	-1.0%
PRAWNS	9	20.0%	-1.5%	-1.2%
BENTHOS	10	0.0%	0.0%	0.0%
0 COD	2	15.0%	32.4%	32.0%
1 COD	3	0.0%	-2.0%	1.2%
2+ COD	4	0.0%	-11.7%	0.0%
HERRING	5	-25.0%	-18.5%	-19.1%
CAPELIN	6	25.0%	15.5%	12.1%
FLATFISH	7	0.0%	3.2%	3.7%
FINFISH	8	-15.0%	-12.9%	-12.4%
PRAWNS	9	0.0%	6.1%	7.9%
BENTHOS	10	0.0%	0.0%	0.0%
0 COD	2	-10.0%	-2.9%	-4.6%
1 COD	3	0.0%	6.0%	4.4%
2+ COD	4	0.0%	8.2%	0.0%
HERRING	5	25.0%	29.5%	28.8%
CAPELIN	6	0.0%	4.6%	3.9%
FLATFISH	7	-15.0%	-12.6%	-13.0%
FINFISH	8	25.0%	28.8%	27.8%
PRAWNS	9	0.0%	7.5%	4.9%
BENTHOS	10	0.0%	0.0%	0.0%
0 COD	2	0.0%	-6.6%	-7.4%
1 COD	3	10.0%	8.5%	1.9%
2+ COD	4	0.0%	14.8%	0.0%
HERRING	5	0.0%	-5.5%	-5.7%
CAPELIN	6	-15.0%	-18.7%	-14.6%
FLATFISH	7	0.0%	-0.9%	-1.6%
FINFISH	8	15.0%	14.5%	13.8%
PRAWNS	9	0.0%	0.1%	-4.0%
BENTHOS	10	0.0%	0.0%	0.0%

seeking mode.

Other tests showed that the exact percentage change in output biomass changes slightly with temperature. Higher temperatures result in more moderate changes in output for a given level of input change (Fig. 10). Temperature affects output biomasses by influencing the growth rates and food requirements of each species group.

The influence of global versus local equilibria on the magnitude and stability of output biomasses are examined at two temperature anomalies (Figures 11, 12 and Table 8). At +0.5 °C, 0 cod and prawns express the highest percent change to different availability to predation and growth parameters while at +1.5° C, 2+ cod vary the most. At +0.5°C, local equilibria are spaced further apart and resultant output biomasses differ more in magnitude than at +1.5°C. These results suggest that a single, stable equilibrium exists at +1.5°C while at +0.5° C similar, less stable, multiple equilibria are possible.

SUMMARY AND CONCLUSIONS

The equilibration procedure in SKEBUB parameterized for Balsfjord, Norway, was evaluated with respect to its response to environmental and biotic perturbations. Equilibrium output species group biomass exhibited globally stable behavior when perturbed by positive temperature anomalies within a two degree range, growth coefficient parameters, availability to predation, and biomass convergence factor. Increases or decreases in input

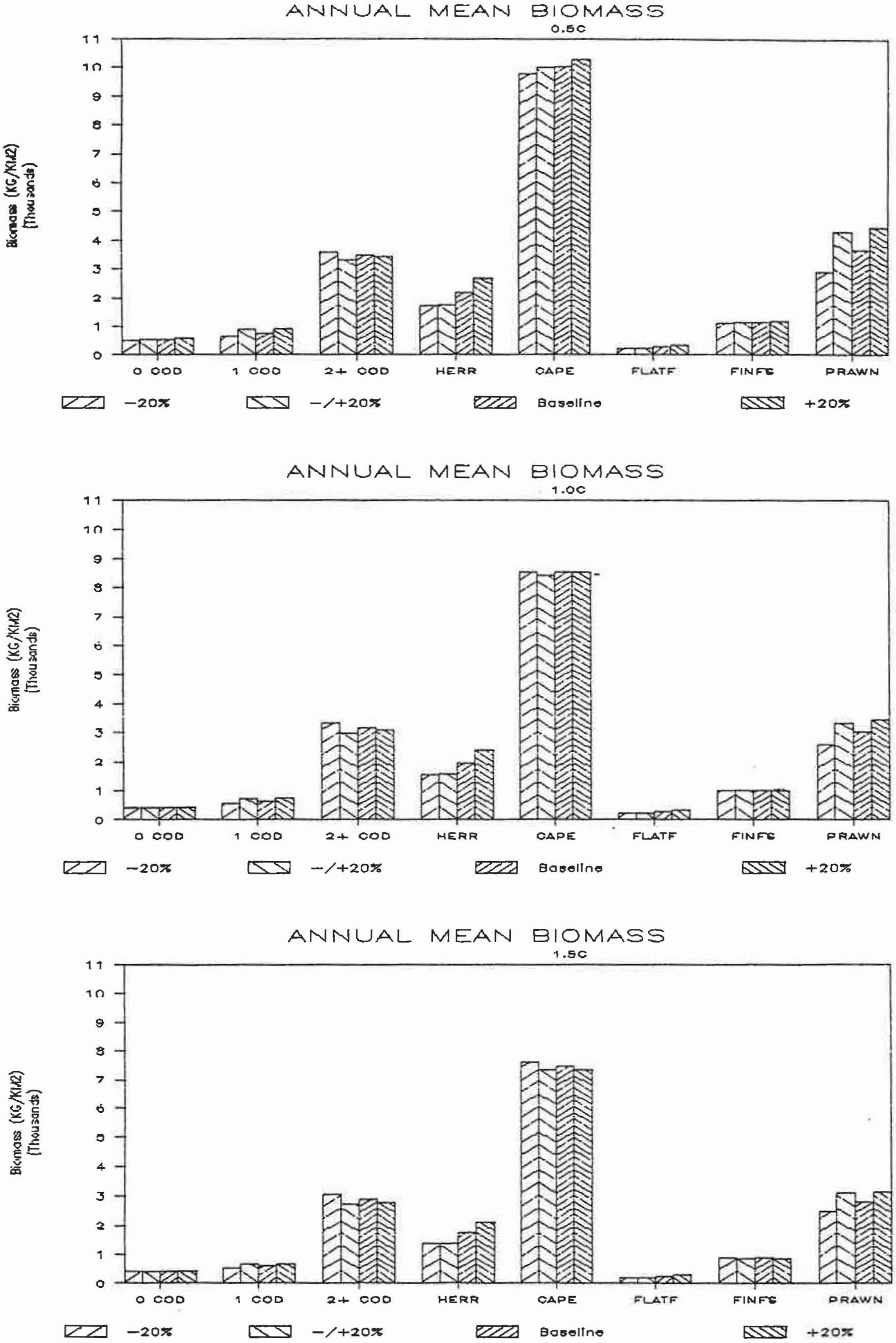


Fig. 10. The effects on output biomass at equilibrium of changing several input group biomasses by +20% and/or -20% compared with the baseline conditions, at three different temperature anomalies.

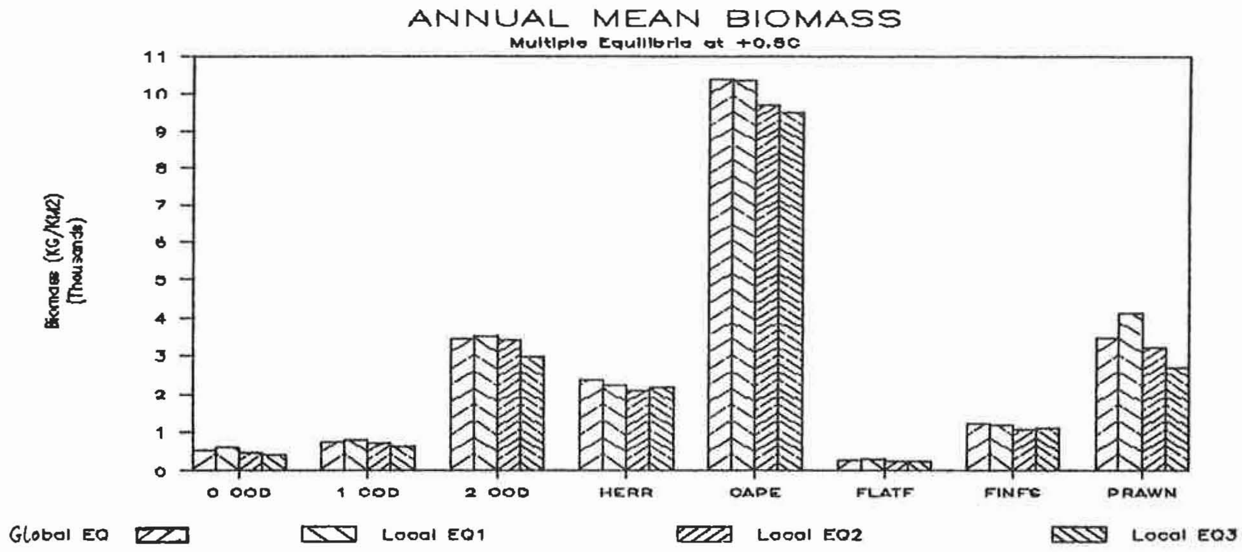


Fig. 11. A comparison of output biomasses produced by one global and three local equilibria at a temperature anomaly of 0.5 °C.

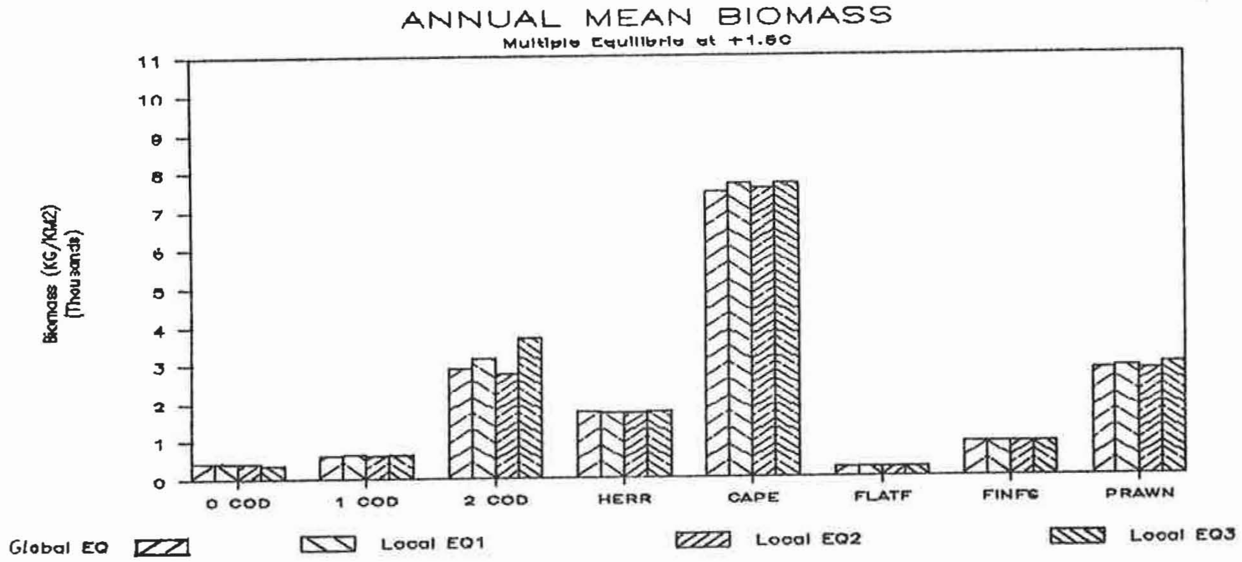


Fig. 12. A comparison of output biomasses produced by one global and three local equilibria at a temperature anomaly of 1.5 °C.

Table 8. Percent changes in output equilibrium biomass at three local equilibrium growth values compared with the global equilibrium.
TEMP = 0.5 BENTHOS = CONSTANT

		LOCAL EQUILIBRIUM NO. 1		LOCAL EQUILIBRIUM NO. 2		LOCAL EQUILIBRIUM NO. 3		
GROUP	NUMBER	INPUT CHANGE IN GADJ	OUTPUT BIOMASS CHANGE	INPUT CHANGE IN GADJ	OUTPUT BIOMASS CHANGE	INPUT CHANGE IN GADJ	INPUT CHANGE IN APE	OUTPUT BIOMASS CHANGE
0 COD	2	2.2%	-7.2%	-1.4%	-14.4%	4.3%	1.7%	-20.9%
1 COD	3	2.2%	-3.1%	-1.4%	6.5%	4.3%	1.7%	-12.4%
2+ COD	4	2.2%	-0.8%	-1.4%	2.8%	4.3%	1.7%	-14.0%
HERRING	5	2.2%	-10.9%	-1.4%	-4.9%	4.3%	1.7%	-7.4%
CAPELIN	6	2.2%	-6.6%	-1.4%	-0.2%	4.3%	1.7%	-8.7%
FLATFISH	7	2.2%	-10.4%	-1.4%	4.2%	4.3%	1.7%	-12.5%
FINFISH	8	2.2%	-11.1%	-1.4%	-3.1%	4.3%	1.7%	-9.1%
PRAWNS	9	2.2%	-6.7%	-1.4%	18.9%	4.3%	1.7%	-22.2%
BENTHOS	10	2.2%	0.0%	-1.4%	0.0%	4.3%	1.7%	0.0%

biomasses produced output equilibrium biomasses within a reasonable error range, although weak linkages between some species groups lowered the abilities of those species to respond to input biomass anomalies. Negative temperature anomalies evoked greater simulation instability. Temperature effects on different species groups agreed only partially with Laevastu (1984a). Some of the differences are attributed to the fact that he evaluated interseasonal anomalies while this study used interannual anomalies, and to the different ecosystems modelled. Balsfjord may be more starvation controlled while the North Pacific is more predation controlled (Bax, pers. comm.). Additional research using SKEBUB seeks to incorporate data from other coastal and pelagic systems such as African upwelling systems and the Barents Sea.

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```
      DO 600 IT=4,4                                                     CC
      DO 600 IG=1,20                                                    0C
      DO 600 IAP=1,20                                                   CC
C                                                                       0C
C                                                                       0C
C********READ ALL DATA VARIABLES*****************************************CC
C                                                                       CC
C         GLOBAL GROWTH ADJUSTMENT,EQUM YEAR,FINAL YEAR,AP ADJUST,      0C
C         FEEDING EQUATION SLOPE AND MAXIMUM,OUTPUT DETERMINANT,RUN NO..CC
  455 READ(66,/)GADJ,LAL,MIK,APE,E,DMAX,INT,NUM                         0C
      0L2:002D:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEME
      IF (ITEST.EQ.0)GO TO 456                                          0C
      APE=APE-0.25+0.025*FLOAT(IAP)                                     0C
      GADJ(1)=GADJ(1)-0.25+0.025*FLOAT(IG)                              C
C                                                                       CC
C         INDIVIDUAL ALLOWABLE CONSUMPTN.                               CC
C                                                                       CC
C         PERCENTAGE FOOD COMPOSITION TABLE                             CC
  456 READ(66,/)((CF(J,I),J=1,14),I=1,14)                               C
      0L2:004E:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
C                                                                       C
C         FISHING CONSTANT,FOOD REQUIREMENT MAINTENANCE AND GROWTH      C
      READ(66,/)((FK(I),I=1,14),(FRM(I),I=1, 14),(FRG(I),I=1,14))       C
      0L2:006E:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
C                                                                       C
C         GROWTH,SENESCENT MORTALITY                                    C
      READ(66,/)((G(I),I=1,14),(SM(I),I=1,14))                          C
      0L2:0086:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
C                                                                       C
C         ACCLIM TEMP, MONTHLY TEMP(2 LVLS),DEPTH, INPUT BIOMASSES      C
      READ(66,/)((TA(I),I=1,14),(TM(I),I=1,12),                         C
     +(TMU(I),I=1,12),(IDEEP(I),I=1,14),(V(I),I=1,14))                  C
      0L2:00BE:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
      IF(ITEST .EQ. 0)IT=1                                              C
      DO 97 I=1,12                                                      C
      TM(I)=TM(I)-0.5+0.5*FLOAT(IT)                                     C
      TMU(I)=TMU(I)-0.5+0.5*FLOAT(IT)                                   C
      TMU(I)=TMU(I)-1.0                                                 C
   97 CONTINUE                                                          C
C                                                                       C
C         MONTHLY BIOMASSES - COPEPODS,EUPHAUSIIDS,ZOOPL.,PHYTO.        C
C           SKIP COPEPODS AND EUPHASIIDS                                C
      READ(66,/)(BB(13,K),K=1,12)                                       C
      0L2:00DA:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
      READ(66,/)(BB(13,K),K=1,12)                                       C
      0L2:00EA:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
      READ(66,/)((BB(N,K),K=1,12),N=13,14)                              C
      0L2:00FF:3  IS THE LOCATION FOR EXCEPTIONAL ACTION ON THE I/O STATEM
C                                                                       C
C     SMOOTH ON MOVING AVERAGE OF 3                                     C
C                                                                       C
      DO 452 N=13,13                                                    C
      DO 454 K=1,12                                                     C
      BE(1,K)=0                                                         C
      DO 454 IJ=1,3                                                     C
      KJ=K+IJ-2                                                         C
      IF(KJ.LE.0)KJ=12                                                  C
      IF(KJ.GT.12)KJ=1                                                  C
      BE(1,K)=BB(1,K)+BB(N,KJ)/3                                        C
  454 CONTINUE                                                          C
```

APPENDIX

```
C
    3 ICOUNT=0
      MICOUN=1
      COUNT=0.
      MCOUNT=1.
      TI(1)=1
      TIU(1)=1.
C
C
C*********FROM INPUT MAXIMUM FOOD COMPOSITION ADJUSTMENT,*****************
C          AND RATE OF ADJUSTMENT  COMPUTE THE ALLOWABLE
C          PERCENTAGE COMPOSITION AS A FRACTION OF SPECIE
C          GROWTH.  VALUES FOR BENTHOS, ZOOPLANKTON, AND
C          PHYTOPLANKTON ARE INPUT SEPERATELY.
C          ** NOTE: CALCULATE AP BEFORE RANDOM ADJUSTMENT TO
C                   GROWTH IN SENSITIVITY ANALYSIS, SO THAT DO
C                   NOT GET MULTICOLLINEARITY.
C
      DO 33 N=2,12
      GS(N,13)=0.
      DO 32 K=1,12
      TMF=TM(K)
      IF(IDEEP(N).EQ.0)TMF=TMU(K)
      ETN=1./TA(N)-(1./TMF)
      IF(IDEEP(N).EQ.0)ETN=ETN*6.
      IF(N.GE.11)ETN=ETN*2.
      GS(N,K)=G(N)*EXP(ETN)
      GS(N,13)=GS(N,13)+GS(N,K)/12.
   32 CONTINUE
      AP(N)=100.*(EXP(GS(N,13))-1.)
      AP(N)=AP(N)*APE
   33 CONTINUE
      AP(13)=100.*APE*(EXP(G(13))-1.)
      AP(14)=100.*APE*(EXP(G(14))-1.)
      DO 34 N=1,14
   34 CONTINUE
C
      A=(DMAX(1)-1.)/EXP(-B(1))
      IF(INNOUT .EQ. 0)GO TO 8
      CALL INOUT(CF,V,NUM,A,B,DMAX)
      CALL INOUT2(AP,G,FRM)
      CALL INOUT3(FRG,SM,TM)
      CALL INOUT4(TMU,TA,IDEEP)
    8 IF(NRUNS.EQ.1)GO TO 12
      IF(NDONE.EQ.1)GO TO 12
C
C
C*********MAKE RANDOM ADJUSTMENTS TO PARAMETERS WHEN*****************
C          RUNNING SENSITIVITY ANALYSES.
C
      CALL SENSA(G,ISHAPE(1),DLTAMX(1),14,1,DSEED,SEED)
      CALL SENSA(B,ISHAPE(2),DLTAMX(2),1,2,DSEED,SEED)
      CALL SENSA(DMAX,ISHAPE(3),DLTAMX(3),1,3,DSEED,SEED)
      CALL SENSA(TTU,ISHAPE(4),DLTAMX(4),1,4,DSEED,SEED)
      CALL SENSA(FRM,ISHAPE(5),DLTAMX(5),14,5,DSEED,SEED)
      CALL SENSA(FRG,ISHAPE(6),DLTAMX(6),14,6,DSEED,SEED)
      CALL SENSA(AP,ISHAPE(7),DLTAMX(7),14,7,DSEED,SEED)
      CALL SENSA(FK,ISHAPE(8),DLTAMX(8),14,8,DSEED,SEED)
      CALL SENSA(SM,ISHAPE(10),DLTAMX(10),14,10,DSEED,SEED)
      CALL SENSA(TA,ISHAPE(11),DLTAMX(11),14,11,DSEED,SEED)
```

```
      CALL SENSA(TT,ISHAPE(12),DLTAMX(12),1, 12,DSEED,SEED)
      CALL SENSA(V,ISHAPE(13),DLTAMX(13),14, 13,DSEED,SEED)
      CALL SENSM(CF,ISHAPE(14),DLTAMX(14),14,14,14,DSEED,SEED)
C
      DO 14 I=2,13
      TA(I)=TM(I)*TT(1)
      TAU(I)=TMU(I)*TTU(1)
   14 CONTINUE
   13 IF(NDONE .GT. 4)GO TO 12
      WRITE(6,5)GADJ(1),B(1),CMAX(1),TTU(1),TT
    5 FORMAT(/,6(5X,F10.4))
      WRITE(6,6)((G(I),I=1,14),(AP(I),I=1,14),(FK(I),I=1,14),
     1(FRM(I),I=1,14),(FRG(I),I=1,14),(SM(I),I=1, 14),(TA(I),I=1,14),
     2(V(I),I=1,14),((CF(I,J),J=1,14),I=1,14))
    6 FORMAT(/14(1X,F8.2))
      WRITE(6,7)(ISHAPE(I),I=1,NPAMS)
    7 FORMAT(/16(5X,I2),////)
C
C*********INITIALIZE VARIABLES ***************** ******
C
   12 DO 15 I=2,14
      DO 15 J=2,13
      FF(I,J)=0.
      GFS(I,J)=0.
      GS(I,J)=0.
      DAR(I,J)=0.
   15 CONTINUE
      L=1
      K=1
C
C
C*********FOR FIRST MONTHS COMPUTATIONS ONLY CONSUMPTION IS************ **
C         SET AT 80% OF ALLOWABLE CONSUMPTION.   INITIAL
C         BIOMASSES ARE SET EQUAL TO INPUT DATA FOR ALL SPECIES
C         STARVATION IS SET TO ZERO FOR THIS FIRST MONTH.
C         INITIALIZE ARRAYS THAT ARE TO BE REUSED.
C         GLOBAL GROWTH COEFFICIENT ADJUSTMENT IS MADE.
C
   22 DO 58 N=2,14
      G(N)=G(N)*GADJ(1)
      SO(N)=0.
   59 IF(N-12)56,56,57
   56 BE(N,12)=V(N)
      BESTOR(N)=V(N)
   57 CO(N,12)=BE(N,12)*0.01*AP(N)*0.8
   58 CONTINUE
C
C
C
C
C**************************************************************************
C*********ENTRY POINT FOR SIMULATION - ALL MONTHS AND YEARS****************
C**************************************************************************
C
C         NE IS INDEX FOR PREVIOUS MONTHS VALUES.
C         IF K =1 (JANUARY), NE IS SET EQUAL TO 12 (DECEMBER)
C         COMPUTE MONTHLY CHANGE IN BIOMASS FOR ALL SPECIES
C         NOT DESCRIBED BY FIXED MONTHLY BIOMASSES.
C         WHEN ICOUNT = 0, PREVIOUS MONTHS VALUES FOR
C         CONSUMPTION AND STARVATION ARE USED.
```