**Northwest and
Alaska Fisheries
Center**

National Marine
Fisheries Service

U.S. DEPARTMENT OF COMMERCE

NWAFC PROCESSED REPORT 86-09

AGE STRUCTURE—
Is it Necessary
in Biomass-Based Ecosystem
Simulations?

March 1986

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AGE STRUCTURE -- IS IT NECESSARY IN

BIOMASS-BASED ECOSYSTEM SIMULATIONS?

By

Nicholas J. Bax
Compass Systems Inc.
4640 Jewell St., #204
San Diego, CA 92109

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ABSTRACT

The SKEBUB-Balsfjorden simulation was compared with and without specific age structure for the cod. Substantial differences in equilibrium positions resulted, notably in biomass and growth rates. Although general system functioning was not affected, specific scenarios and quantitative assessments were affected by the change in representation of age structure. Age structure is not a feature that can be altered in these simulations without a complete reanalysis of system parameterization.

INTRODUCTION

Simulations of biological systems are only crude representations of the natural mechanisms involved. The resolution can range from below the level of the individual to, or above, the level of stock or population. Of interest in this study was the importance, or not, of including a specific age structure in the biomass-based simulations developed at the Northwest and Alaska Fisheries Center (Laevastu and Larkins 1981, Laevastu et al. 1982, Bax 1983).

The simulations under consideration are only gross caricatures of the fisheries ecosystems under study, but they are detailed to a level compatible with the data available. In many instances (e.g., the Gulf of Alaska) age-structured models are difficult to implement because of inadequate data on the age composition of the species present. For this reason this study utilized data collected by Norwegian fishery scientists, in particular data for Balsfjorden, a fjord in northern Norway.

Several methods for the implementation of age-structure have been tested in SKEBUB (Skeleton Bulk Biomass Model) parameterized to the Norwegian fishery ecosystem off Møre, and to Balsfjorden (Bax et al. 1984; Eliassen et al. in prep.). Initial implementation in NORFISK (Bax et al. 1984) described three age groups for each species or species group. Transfer from one age group to another was discontinuous occurring around spawning time each year. The proportion transferred was equal to the proportion of the total biomass in the age group contained in the oldest year class. This value was determined from long-term mean age structure information. Recruitment to the youngest age group was set at a fixed proportion of the mature biomass. This implementation of age structure was very difficult to stabilize (see

Sunnanå et al. 1985, for full details) because growth rates were discontinuous between age groups and large differences in absolute biomass growth accompanied the transfer of biomass through the age groups.

In the second implementation used in SKEBUB-Balsfjorden, only the cod were divided into three age groups. These three groups were treated as independent entities during initial equilabration procedures. After equilibrium was defined and the simulation was running in prognostic mode, any deviations from equilibrium biomass in the two younger age groups were transferred to the next oldest age class at year end. Biomass of the youngest age group was not dependent on adult biomass, but returned to the equilibrium value at year-end or a stochastic variation of that. This implementation was relatively easy to stabilize and has been used in this study. The methodology is readily transferable to the more detailed simulations at the Northwest and Alaska Fisheries Center.

METHODS

The SKEBUB simulation was parameterized to the Balsfjorden ecosystem in 1984 in cooperation with J.-E Eliassen of the University of Tromsø (Eliassen et al., in prep.). This parameterization included the division of cod into three age groups (0-1; 1-2; and 2+) to better understand the dynamics of enhancement of juvenile (0-1) cod. In 1985 a reparameterization of the simulation was undertaken to increase the flexibility in the feeding algorithm in order to simulate changes in the diet of cod associated with an influx of herring into the fjord (Eliassen and Grotnes 1985; Bax 1985c). This re-parameterization was used to compare the properties of the SKEBUB simulation when the cod were represented as 3 distinct groups, and when they were represented by one group only.

Pooling of Age Classes

The three age groups representing cod in the full SKEBUB-Balsfjorden simulation were pooled into one. This one group had an input biomass equal to the sum of the individual age groups. All other values - growth, food preferences, temperature preferences, etc. - for the pooled group were calculated as the mean of those values for the individual groups weighted by their input biomasses.

Definition of Equilibria

An iterative equilibrium searching routine was used to define the equilibrium points in the simulation. In this routine two parameters which operate on all species groups to the same degree are simultaneously and sequentially varied. The two parameters are the global adjustment to growth and the global adjustment

of availability to predation. These parameters have been previously identified as powerful modifiers of system behaviour (Bax 1985a,b).

SKEBUB-Balsfjorden was run through 30 year-long iterations for each combination of values for the two parameters. During these 30 iterations starting biomasses are systematically adjusted to move the simulation towards equilibrium. The two parameters were varied by 2.5% of their baseline value at each increment and covered a range of approximately 70% to 170% of the baseline value depending on model stability. This sequence resulted in approximately 1600 unique combinations of parameters. The following output variables were recorded for each combination and subsequently plotted as 3-dimensional figures:

la. Mean percent change in biomass of all species during the final year-long iteration.

lb. Mean percent change in biomass of all species weighted by final species biomass during the final year-long iteration.

2a. Mean percent of required food not obtained by all species during the final year-long iteration.

2b. 2a weighted by final species biomass.

3a. Mean percent consumption of each species during the final year-long iteration.

3b. 3a weighted by final species biomass.

4. Total final biomass of all fish species whose biomasses are adjusted in the equilibration process.

Equilibrium in the SKEBUB simulation is defined as the state where annual growth in biomass for each species equals (or closely approximates) its loss

in biomass due to predation, fishing, and natural mortality. In the context
of the equilibrium searching routine it is defined as the combination of the
global growth adjustment and the global adjustment of availability to predation
that produce the minimum value for the weighted mean percent change in biomass
of all species during the 30 year-long iteration (1b above). Previous
experience indicates that multiple equilibria may exist (Bax 1985a,b) and
thus the other outputs (1a, and 2a-4) are used to indicate which of these
equilibria approximate the current state of the ecosystem under study.

Analyses of Equilibria

Once the equilibria for the two versions of SKEBUB-Balsfjorden had been
defined they were more closely examined to compare their properties. Two
methods of comparison were used. The first method was simply a comparison
of the properties of the two versions at their respective equilibria.
Individual species biomass, percent of required food that was obtained, and
the percent of each biomass consumed were compared and contrasted.

The second method was an error analysis of the equilibria for the two
versions. A 2000 run Monte Carlo error analysis was performed on each version
of SKEBUB-Balsfjorden at its equilibrium position. A 15 percent coefficient
of variation was used with a normal error distribution to randomly perturb
each input parameter; input parameters were species specific. There were a
total of 69 input parameters in the pooled version, 85 input parameters in
the full version, and 33 and 39 output parameters in the two versions,
respectively. Output data from the error analyses were investigated using
principal components analysis (PCA). Full details are given in Bax (1985a).

Analysis of System Response after Equilibrium

Bax (1985c) investigated the response of SKEBUB-Balsfjorden under two scenarios chosen to represent the possible effects of the large influx of herring to the fjord as described by Eliassen and Grotnes (1985). In the first scenario herring were simulated to enter the fjord and their proportionate availability as a food source remained the same as in the baseline simulation; i.e., there was no switching by predators to herring beyond that in direct response to their increased abundance. In the second scenario as the herring were simulated to enter the fjord their availability as a food source also increased. This increase was arbitrarily set at the baseline value (which is approximately 80% of the net growth rate) plus approximately 80% of the immigration rate. In other words, the rate of immigration was considered as an external source of growth and the availability to predation set at a fixed percentage of the total "growth" rate of the population.

The two versions of SKEBUB-Balsfjorden were run for each scenario and the resulting biomass fluctuations compared and contrasted graphically.

RESULTS

Definition of Equilibria

Equilibrium searching routines of the pooled and full version of SKEBUB-Balsfjorden indicated no distinct equilibria (Figs. 1 and 2). Instead the simulations approached minimum values for biomass change at high levels of growth and low levels of availability to predation. However, these minima occurred immediately prior to gross model instability at the higher growth levels and were not reasonable in terms of overall system characteristics.

This is a very different result than that found in the original SKEBUB-Balsfjorden (Bax 1985a), i.e., when the prey switching algorithm had not yet been reparameterized to simulate the high variation in feeding habits noted by Eliassen and Grothnes (1985). A different approach to defining the equilibrium points is therefore required.

The difference between current and previous versions of SKEBUB-Balsfjorden was only the increased flexibility in prey switching. Evidently high variability in diet composition prevents a definite equilibrium from being obtained. It was decided therefore to prevent prey-switching in the equilibrium searching. This has the effect of putting more weight on the accuracy (or consistency) of the input food composition table. These input data are thus defined as the exact data for the system under study during the time that the biomass and growth data were collected. When, as in this instance, no seasonal food composition variability is defined, the input food composition table applies to all months of the year. Total food requirements would change as a function of temperature, however.

Equilibrium searching routines for both versions of SKEBUB-Balsfjorden were repeated with a fixed food composition. The simulation with pooled cod groups reached a definite equilibrium when the growth rates were 0.925 of the
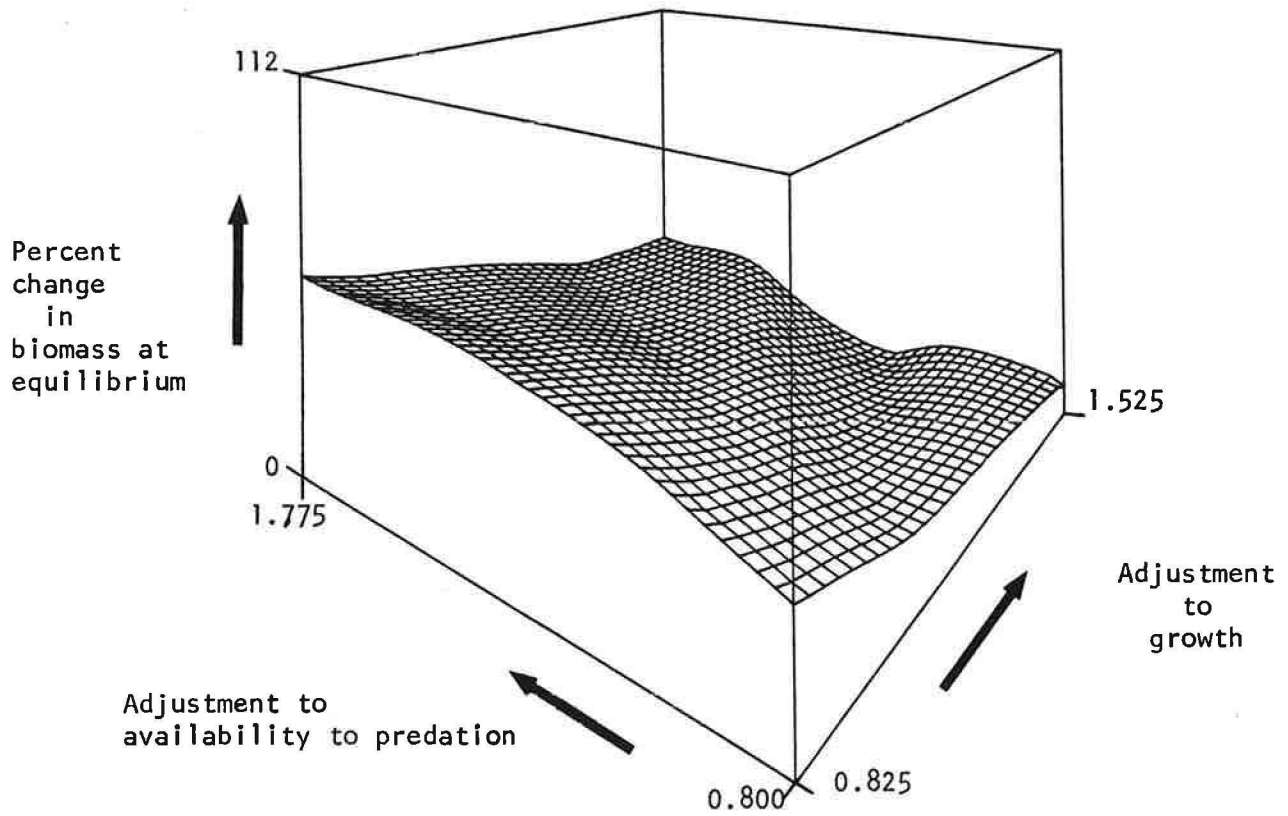
112

Percent
change
in
biomass at
equilibrium

0

1.775

Adjustment to
availability to predation

1.525

Adjustment
to
growth

0.800   0.825

Fig. 1a.   Absolute mean percent change in biomass at equilibrum for all
variable species in SKEBUB-Balsfjorden, with pooled cod age
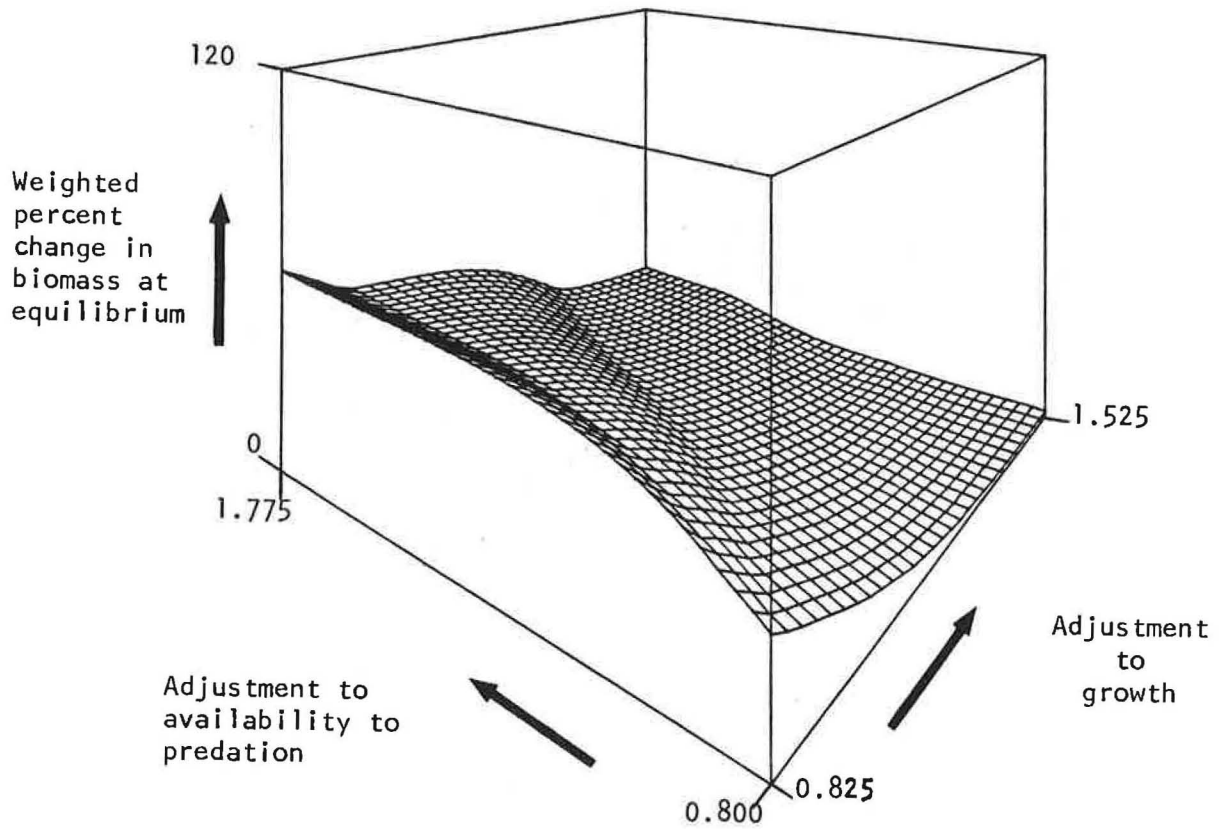groups and flexible food composition.

120

Weighted
percent
change in
biomass at
equilibrium

0

1.775

1.525

Adjustment to
availability to
predation

Adjustment
to
growth

0.825

0.800

Fib. 1b.   Absolute weighted mean percent change in biomass at equilibrium
for all variable species in SKEBUB-Balsfjorden, with pooled cod
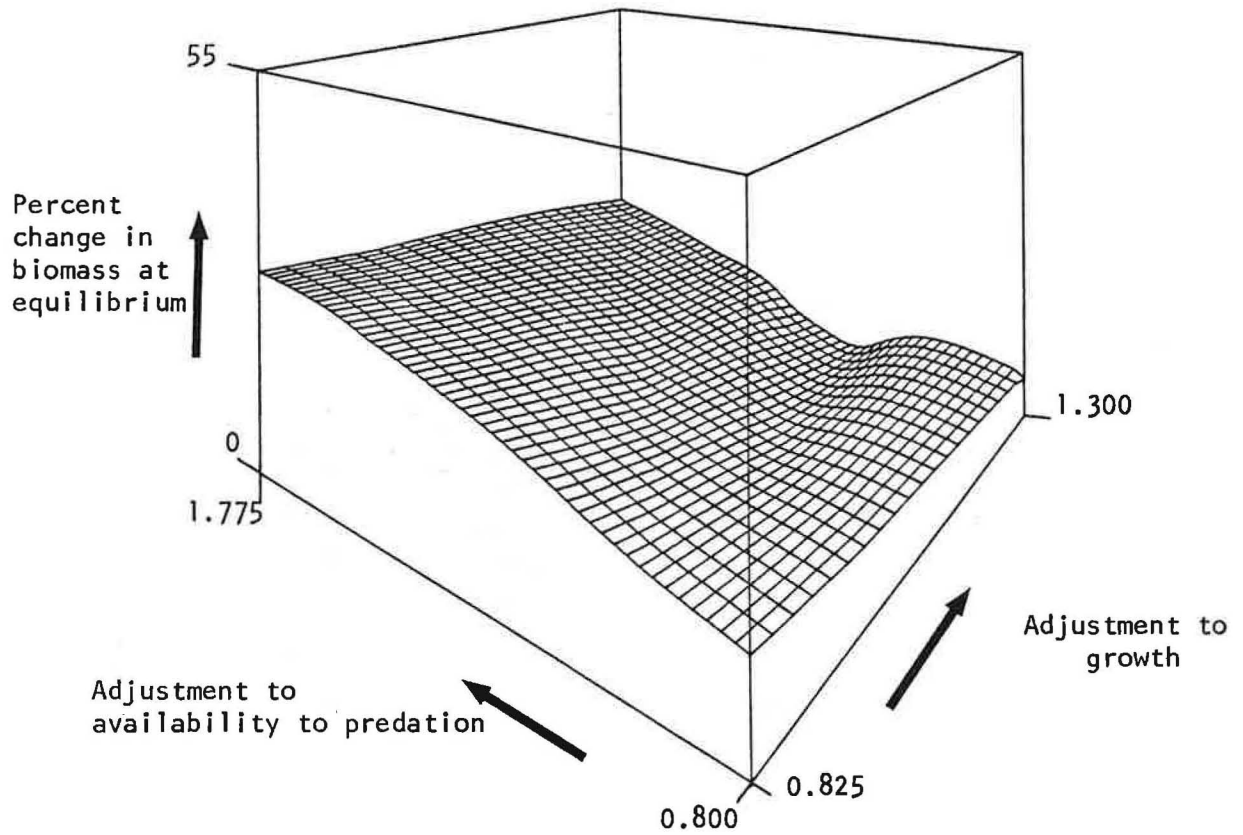age groups and flexible food composition.

55

Percent
change in
biomass at
equilibrium

0

1.775

1.300

Adjustment to
availability to predation

Adjustment to
growth

0.825

0.800

Fig. 2a. Absolute mean percent change in biomass at equilibrium for all
variable species in SKEBUB-Balsfjorden, with distinct cod age
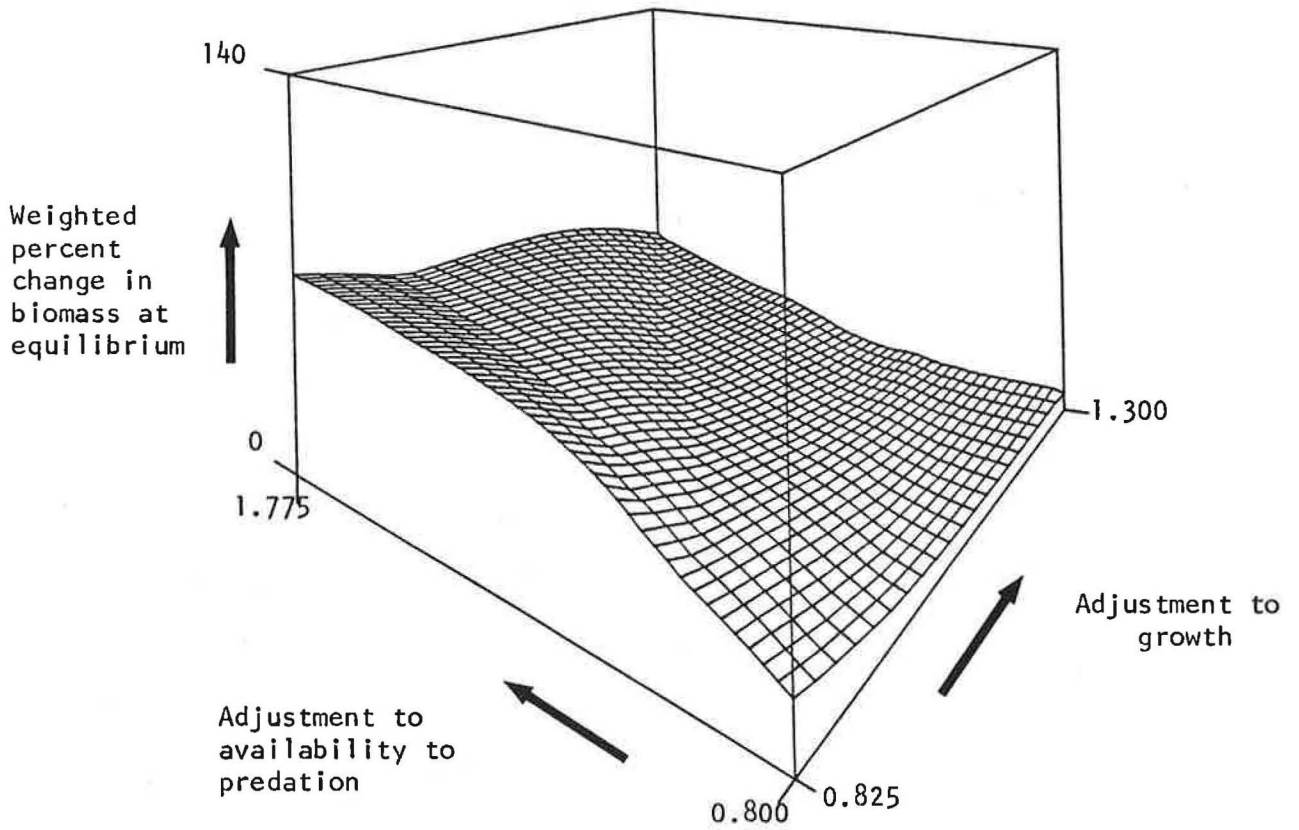groups and flexible food composition.

Fig. 2b. Absolute weighted mean percent change in biomass at equilibrium for
all variable species in SKEBUB-Balsfjorden, with distinct cod age
groups and flexible food composition.

empirically calculated values (Fig. 3). Availability to predation had no effect since this variable only influences prey switching. There was an equilibrium point for the simulation with distinct cod age groups when growth rates were between 1.35 and 1.5 times the input values (Fig. 4). This equilibrium was not as distinct as that for the simulation with pooled age classes and it is near, but not adjacent to, levels of growth which would produce gross system instability.

Analysis of Equilibria

Biomasses of all species and the percent consumption of each species in the two versions of SKEBUB-Balsfjorden were compared (Table 1). The version with distinct cod age groups had equilibrium biomasses similar to the input values (or initial estimates). Conversely the biomasses were, with the exception of cod, considerably larger than input values in the pooled version. These higher biomasses are a direct consequence of the lower growth rates in the pooled version - as growth rates decrease a higher biomass is required to sustain the relatively fixed loss of biomass to predators. Results from the equilibrium searching routine indicate this negative correlation between biomass and growth rate (Figs. 5 and 6).

Mean percent of biomass consumed was higher for the pooled version than for the version with distinct age classes, but this was due solely to the high percent consumption of phytoplankton - percent consumption of all other groups was lower for the pooled than for the version with distinct age classes. This is an expected result because the lower growth rates operating in the pooled version would be unable to sustain predation levels as high as that in the distinct-age groups version with its higher growth rates.
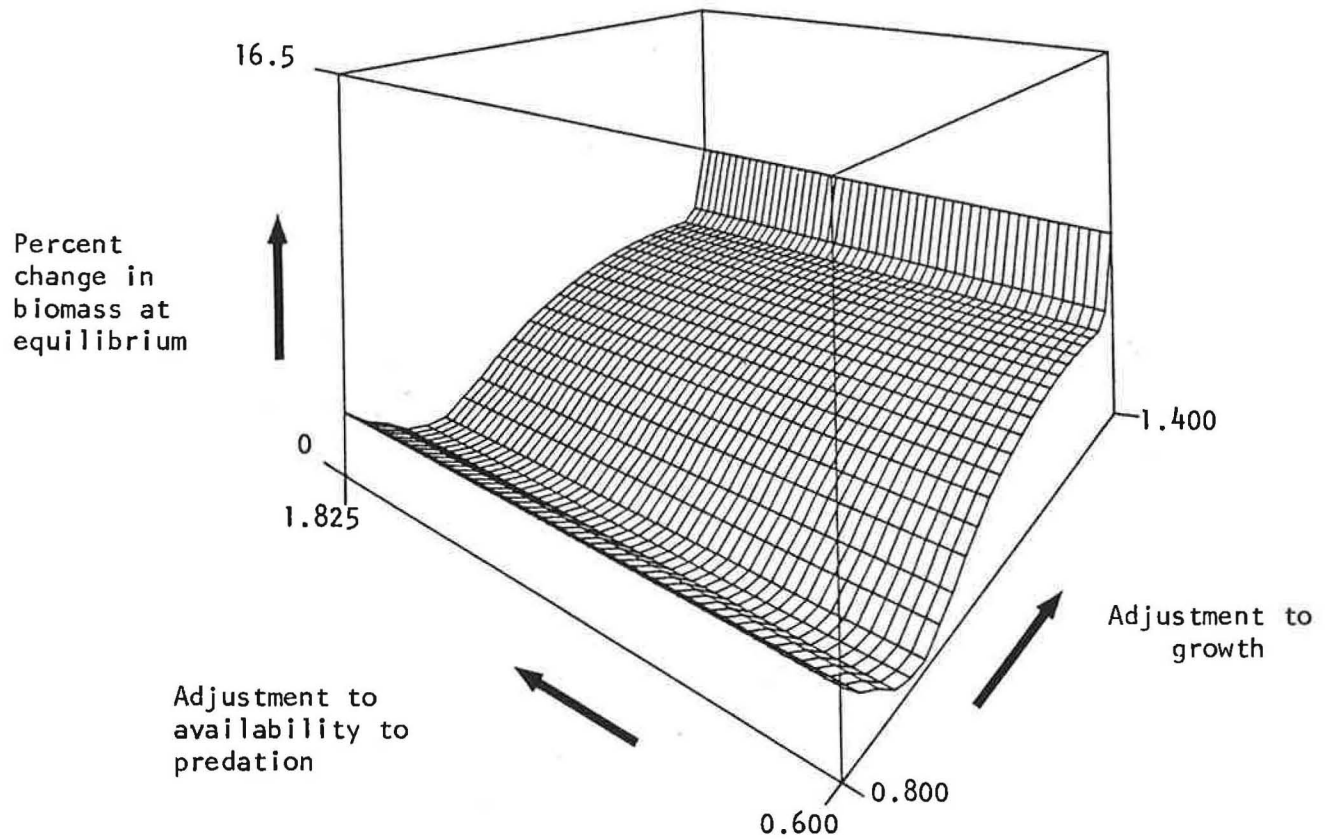
Fig. 3a.   Absolute mean percent change in biomass at equilibrium for all variable
species in SKEBUB-Balsfjorden, with pooled cod age groups and fixed
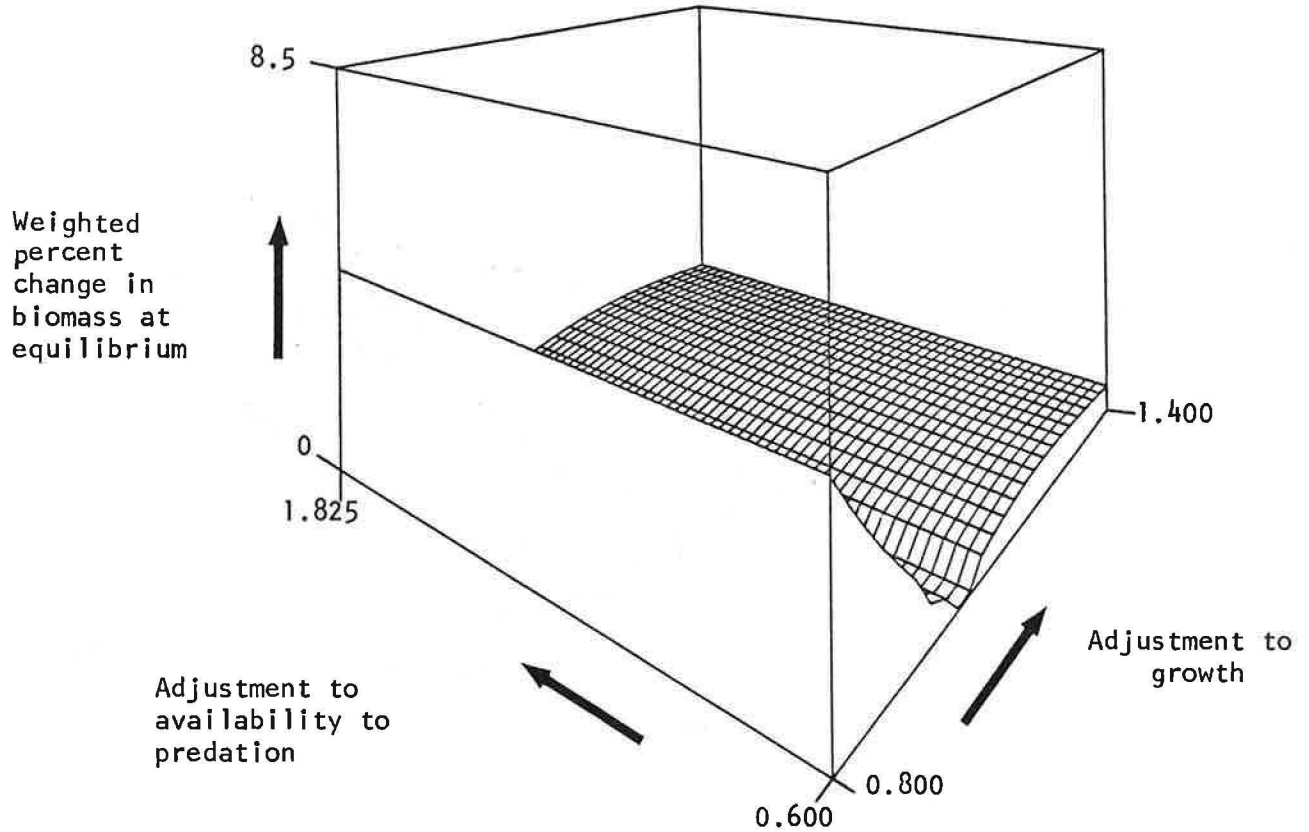food composition.

Weighted
percent
change in
biomass at
equilibrium

8.5

0

1.825

Adjustment to
availability to
predation

0.600

0.800

1.400

Adjustment to
growth

Fig. 3b. Absolute weighted mean percent change in biomass at equilibrium for
all variable species in SKEBUB-Balsfjorden, with pooled cod age groups
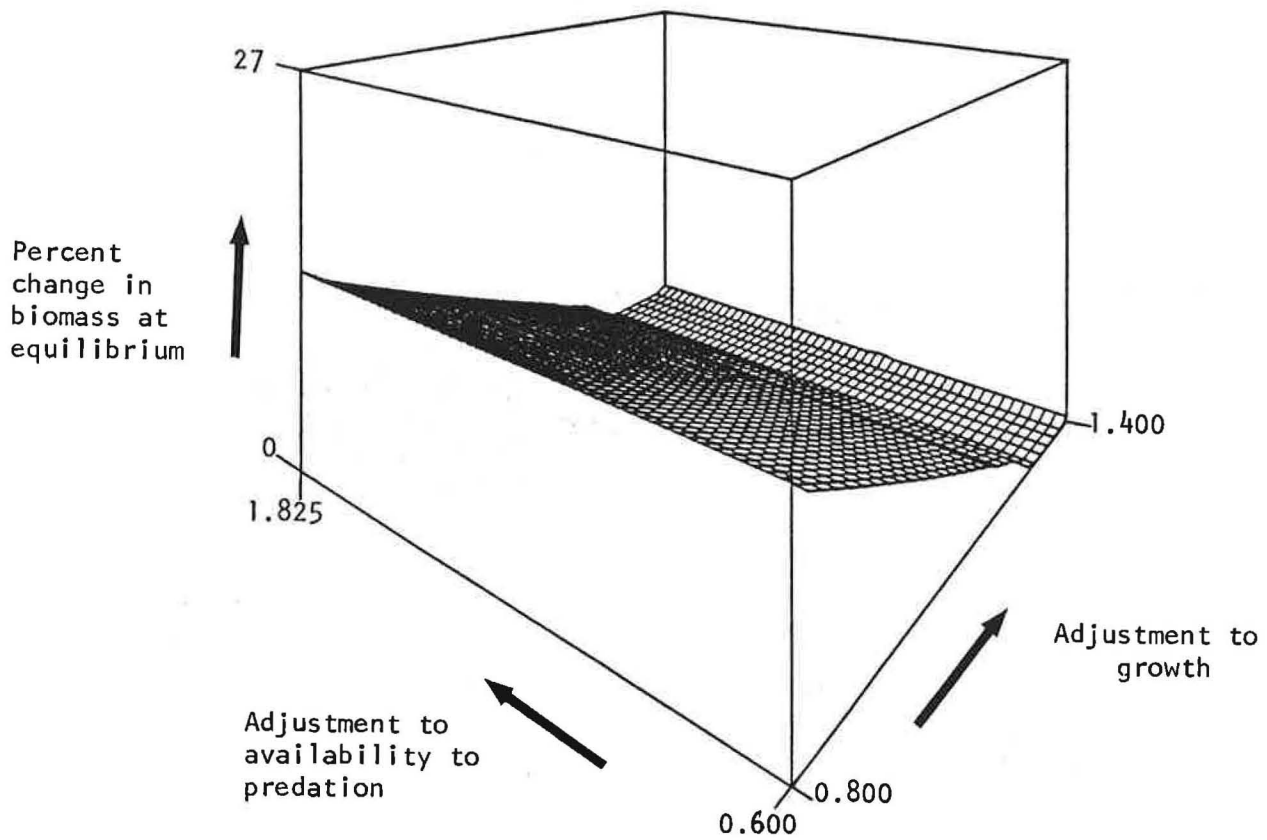and fixed food composition.

Fig. 4a. Absolute mean percent change in biomass at equilibrium for all
variable species in SKEBUB-Balsfjorden, with distinct cod age
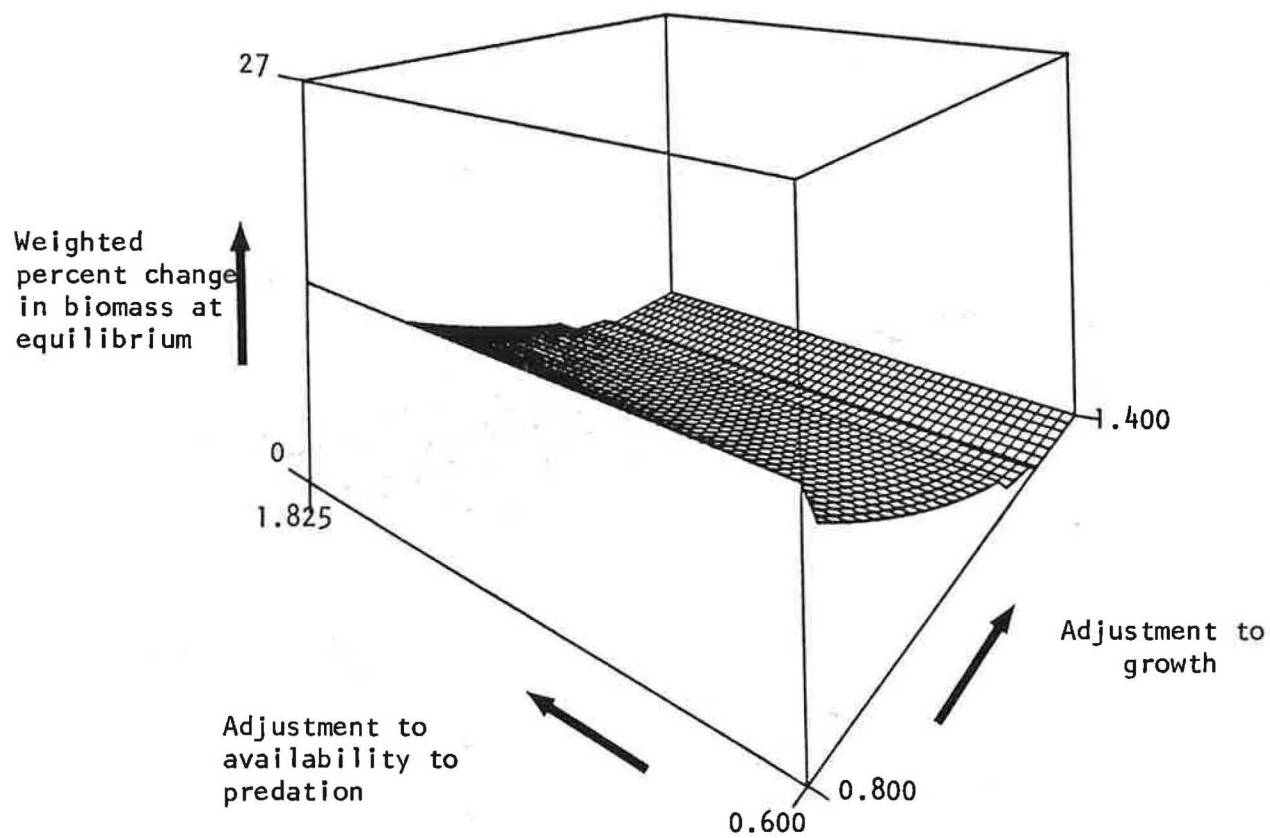groups and fixed food composition.

Fig. 4b.   Absolute weighted mean percent change in biomass at equilibrium
           for all variable species in SKEBUB-Balsfjorden, with distinct
           cod age groups and fixed food composition.

Table 1.--Comparison of characteristics of equilibria indicated by SKEBUB-Balsfjorden with and without pooling of the cod age groups.

| Species | Input biomass | Equilibrium Biomass (proportion of input) | | Annual Proportion of Biomass Consumed | |
		Cod groups pooled	Cod groups distinct	Cod groups pooled	Cod groups distinct
Cod 0-1	453		460 (1.02)		1.28
Cod 1-2	636		530 (0.83)		0.63
Cod 2+	3027	2158 (0.52)	2963 (0.98)	0.26	0.29
Herring	1764	3295 (1.87)	1957 (1.11)	0.20	0.34
Capelin	8348	11824 (1.42)	8024 (0.96)	0.23	0.41
Flatfish	269	463 (1.72)	273 (1.01)	0.36	0.61
Other fish	958	1654 (1.73)	969 (1.01)	0.26	0.44
Prawns	2802	3745 (1.74)	2850 (1.02)	0.87	1.38
Benthos	72500	Fixed	Fixed	0.64	0.69
Copepods	91068	388250 (4.26)	151693 (1.67)	0.36	0.63
Euphausids	58783	251438 (4.28)	98823 (1.68)	0.32	0.58
Other zooplankton	33526	Fixed	Fixed	1.23	1.32
Phytoplankton	212772	Fixed	Fixed	13.62	6.02
Total fish biomass	18257	23139 (1.27)	18026 (0.99)		
Mean proportion of biomass consumed				1.67	1.12

Biomass at
equilibrium
10^3kg/km^2

2 600

0

1.825

1.400

Adjustment to
growth

Adjustment to
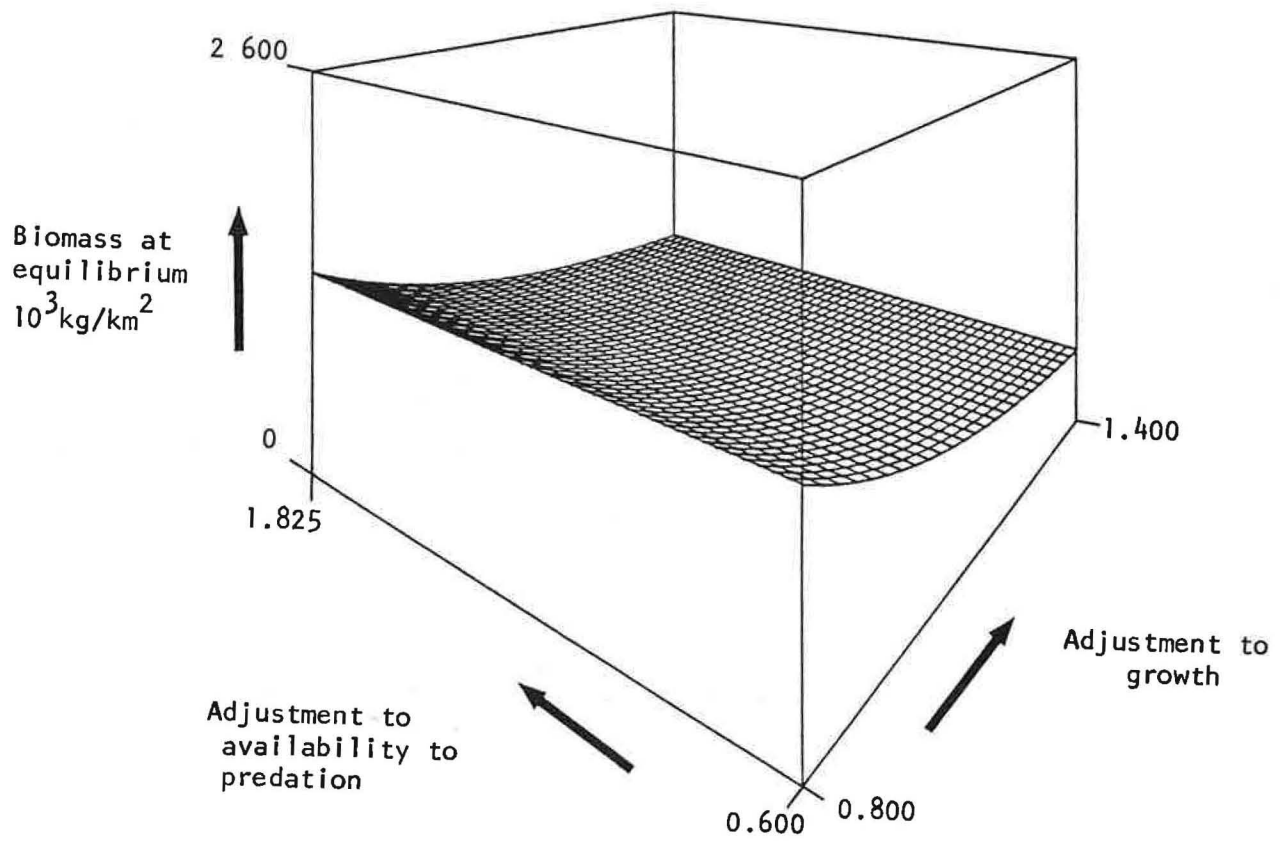availability to
predation

0.600   0.800

Fig. 5. Total biomass at equilibrium for all variable species in
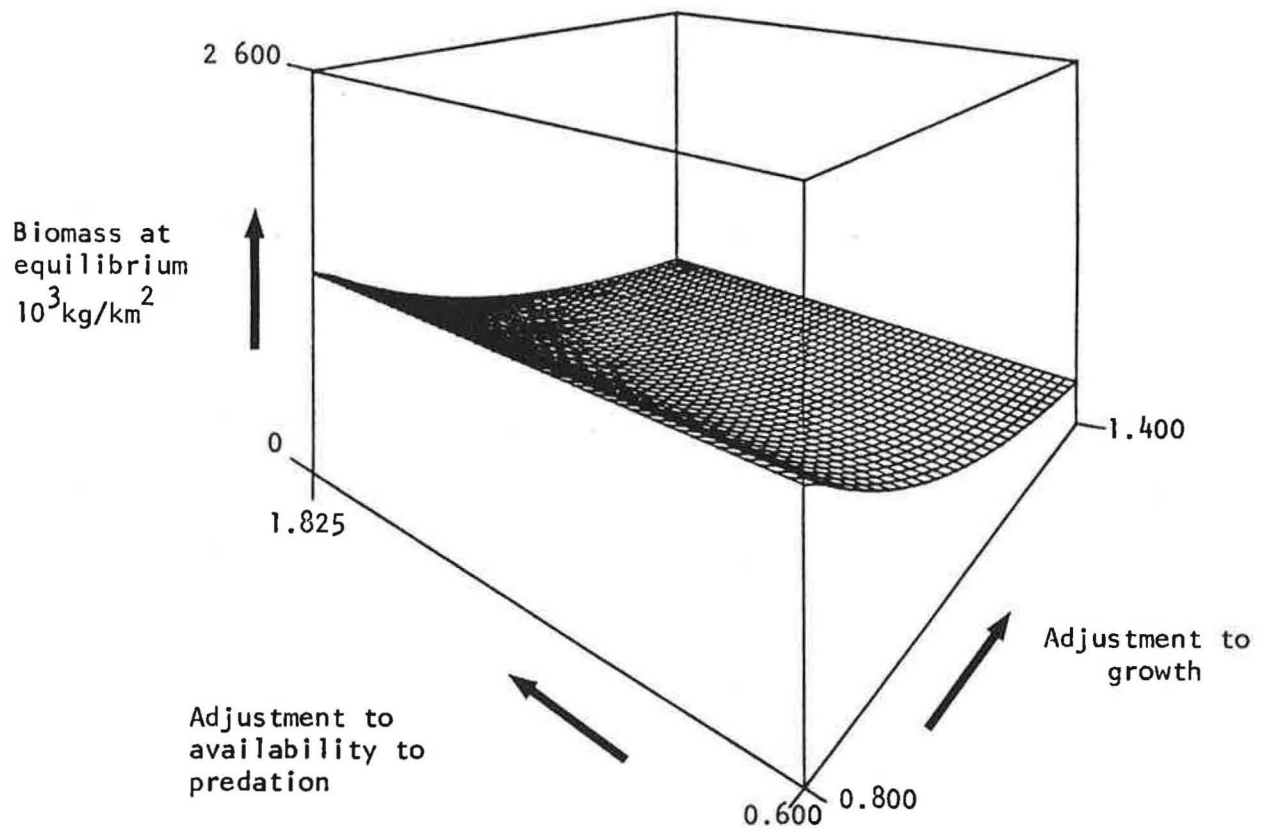SKEBUB-Balsfjorden with cod age groups pooled and food
composition fixed.

Fig. 6. Total biomass at equilibrium for all variable species in SKEBUB-Balsfjorden with cod age groups distinct and food composition fixed.

Error analyses of the equilibria for the two versions indicated sensitivities to similar parameters. The dominant factor in both instances was associated with overall fish biomass (Tables 3 and 4), and was chiefly influenced by the growth rates, food requirements, and food composition of cod. A major difference between the two versions is the increased dominance of the cod groups in explaining system variability in the version of SKEBUB-Balsfjorden with distinct age groups. Cod contribute heavily to the variance explained by the second factor for this version, as compared to the version with pooled cod age classes where cod loaded heavily on the seventh factor. The second and seventh factor explained 12 and 6 percent, respectively, of the total system variance for the two versions.

There were seven remaining factors indicated as important (i.e., explaining more of the total variance than that explained by an individual output variable) for each version. Each factor was associated with an individual species group. On each factor the percent consumption and the percent of required food not obtained were negatively associated with the species final biomass. Temperature was indicated to be important. Higher temperatures, or lower acclimation temperatures for the species, were negatively correlated with final biomass. As temperature increases growth rates also increase thus enabling a higher percentage consumption from a smaller biomass than at lower temperatures.

In summary the equilibria indicated by the two versions of SKEBUB-Balsfjorden, although indicating quite different final biomasses, did not appear appreciably different in their response to input parameter variation. Cod were indicated as contributing more to system variance when they were represented as distinct groups rather than as a pooled group.

Table 2.--List of input parameters, biomass groups, output variables used in the Monte Carlo error analysis, and their abbreviations.[1]

	INPUT PARAMETERS		BIOMASS GROUPS
AP	Availability to predation	COD	Cod
CFT	Occurrence in predators diets	HERR	Herring
V	Starting biomass	CAP	Capelin
G	Growth coefficient	FLAT	Flatfish
FRG	Food requirement for growth	OTHR	Other finfish
FRM	Food requirement for maintenance	PRWN	Prawns
TA	Acclimation temperature	BEN	Benthos
B	Rate of prey switching	COP	Copepods
DMAX	Maximum prey switching	EUPH	Euphausiids
TTU	Temperature in upper layers	ZOO	Other zooplankton
TT	Temperature in bottom layers	PHYT	Phytoplankton
	OUTPUT VARIABLES		
PC	Percent of equilibrium biomass consumed by others		
SC	Required food not obtained expressed as percent of equilibrium biomass		
BB	Equilibrium biomass		
FP	Total catch		

1/ Parameters and variables (except B, DMAX, TTU, and TT) are species specific and are identified by both parameter/variable name and a biomass name, e.g. APCOD.

Table 3. Principal components analysis of a 2000 run error analysis of SKEBUB - Balsfjd, with cod groups pooled.

Factor Description	1 Biomass	2 Copepods	3 Euphausids	4 Other Fish	5 Herring	6 Capelin	7 Cod	8 Flatfish	9 Prawns
Output[1] variables with positive factor loadings	BBPRWN BBCOD BBFLAT BBCAP bboth bbherr pcben pczoo bbeuph	BBCOP PCPHYT pczoo bbeuph	PCEUPH SCEUPH	PCOTHR SCOTHR	PCHERR SCHERR	PCCAP SCCAP	PCCOD SCCOD	PCFLAT scflat	PCPRWN SCPRWN
Input[2] parameters positively correlated with factor	FRMCOD cfcod	TACOP	TTU GEUPH frmeuph	GOTHR FRMOTHR ttu	FRMHERR GHERR ttu	FRMCAP GCAP ttu	FRMCOD GCOD tt	GFLAT FRMFLAT tt	GPRWN FRMPRWN tt
Output variables with negative factor loadings		PCCOP SCOP pceuph pccap	BBEUPH pcphyt pczoo bbcop	bbothr	bbherr	bbcap		bbflat	bbprwn
Input parameters negatively correlated with factor	GCOD cfeuph	TTU gcop	TAEUPH	TAOTHR	TAHERR	TACAP	TACOD	TAFLAT	TAPRWN
Proportion of variance explained by factor	0.15	0.14	0.11	0.07	0.07	0.07	0.06	0.06	0.06
Coefficient of determination	0.63	0.79	0.82	0.85	0.86	0.83	0.82	0.88	0.89

1/ Loadings >0.70 uppercase; 0.25-0.70 lowercase

2/ Partial correlation coefficient >0.20 uppercase; 0.05-0.20 lowercase

Table 4. Principal components analysis of a 2000 run error analysis of SKEBUB - Balsfjd with cod groups distinct.

Factor Description	1 Biomass	2 Cod	3 Copepods	4 Euphausids	5 Other Fish	6 Herring	7 Capelin	8 Prawns	9 Flatfish
Output[1] variables with positive factor loadings	BBCOD2 BBCOD3 BBPRWN BBFLAT BBCAP BBOTHR pczoo bbherr bbeuph pcben pcphyt sccod2	SCCOD3 PCCOD2 SCCOD2 SCCOD1 pccodl	PCCOP SCCOP pceuph pcherr pccap	PCEUPH SCEUPH pccodl	PCOTHR SCOTHR	SCHERR PCHERR	SCCAP PCCAP	PCPRWN SCPRWN	PCFLAT SCFLAT
Input[2] parameters positively correlated with factor	FRMCOD2 CFCOD2	GCOD1 FRMCOD2 tt	TTU GCOP	TTU GEUPH	GOTHR TTU FRMOTHR	GHERR FRMHERR ttu	FRMCAP GCAP ttu	GPRWN FRMPRWN tt	no analysis
Output variables with negative factor loadings	pccodl		BBCOP pcphyt pczoo bbeuph	BBEUPH pcphyt pczoo bbcop	bbothr	bbherr	bbcap		bbflat
Input parameters negatively correlated with factor	GCOD3 cfeuph	TACOD2	TACOP	TAEUPH	taothr	TAHERR	TACAP	taprwn	
Proportion of variance explained by factor	0.22	0.12	0.11	0.09	0.06	0.06	0.06	0.05	0.05
Coefficient of determination	0.76	0.85	0.82	0.78	0.84	0.84	0.80	0.87	

1/ Loadings >0.70 uppercase; 0.25-0.70 lowercase

2/ Partial correlation coefficient >0.20 uppercase; 0.05-0.20 lowercase

Analysis of System Response after Equilibrium

In the first scenario, where an immigration of herring to the fjord was simulated and their proportionate availability to predation kept constant, the two versions of SKEBUB-Balsfjorden reacted similarly (Figs. 7 and 8). An asymptotic increase in herring biomass from years 35 to 39 in the simulation was followed by a decline to original levels once immigration stopped in year 40. All other groups reacted negatively to the increase in herring biomass, and following their subsequent reduction some overcompensation was indicated. The biomass changes were more pronounced in the version of SKEBUB-Balsfjorden with cod age groups pooled than in the version with them distinct.

The second scenario produced contrasting results for the two versions of the simulation. With the age classes of cod pooled the response was identical to that elicited by the first scenario, despite the availability of herring being made proportional to growth plus immigration (Figs. 9 and 10). This difference between the two versions of the simulation results from the higher biomass of herring and the lower biomass of cod indicated by the equilibrium for the pooled version. Thus the ratio of total cod biomass to total herring biomass was 0.65 in the pooled version but 2.02 in the distinct version.
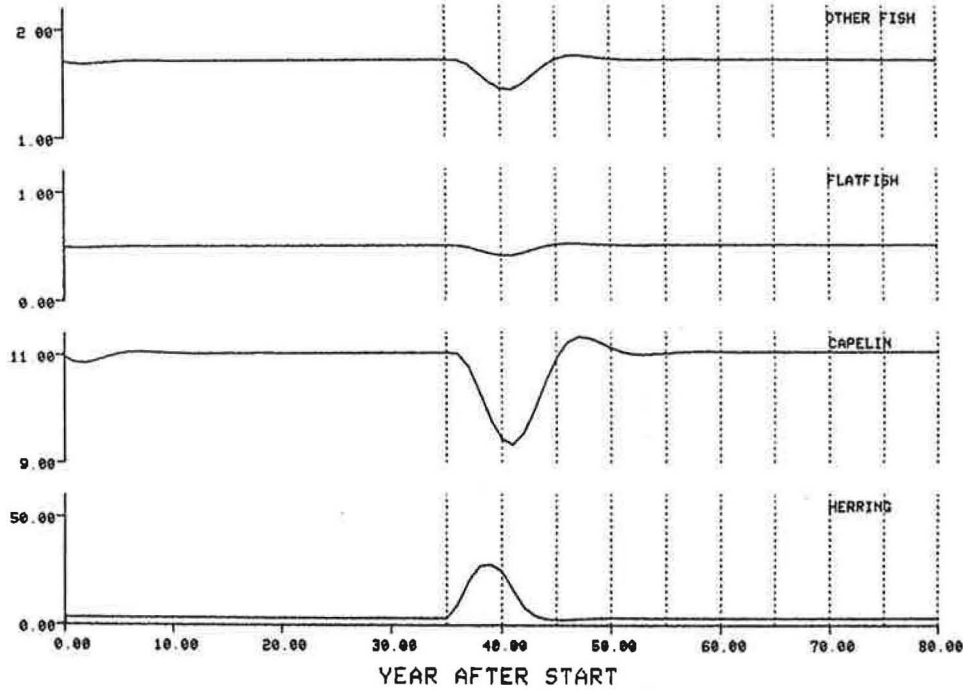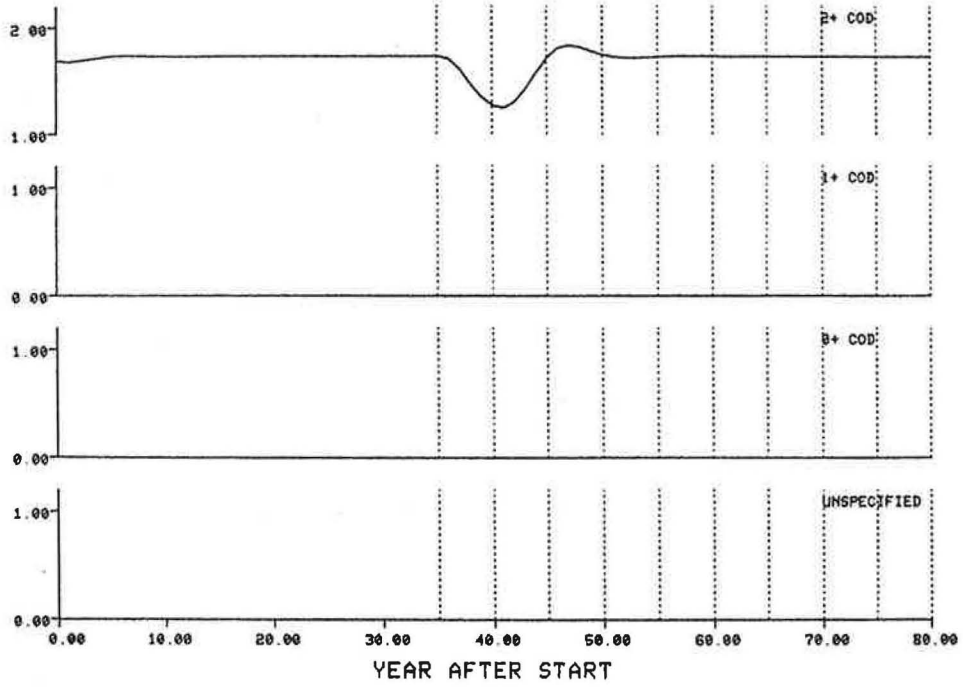
Fig. 7. Biomass (10^3 kg/km^2) of species in SKEBUB-Balsfjorden
responding to an influx of herring in years 35-39.
Cod age groups were pooled and availability of herring
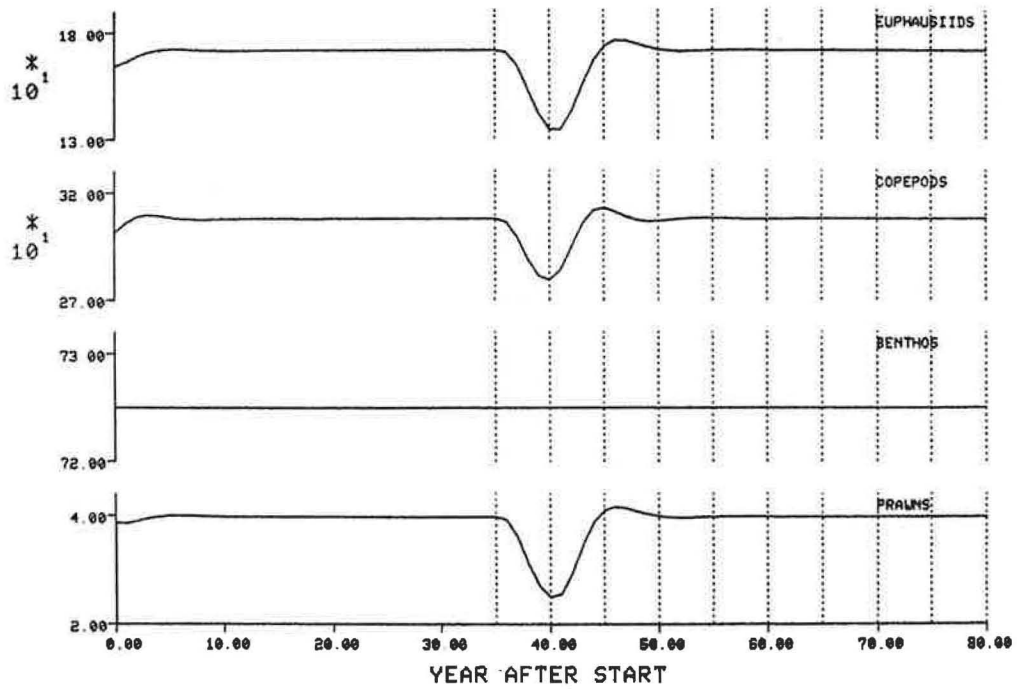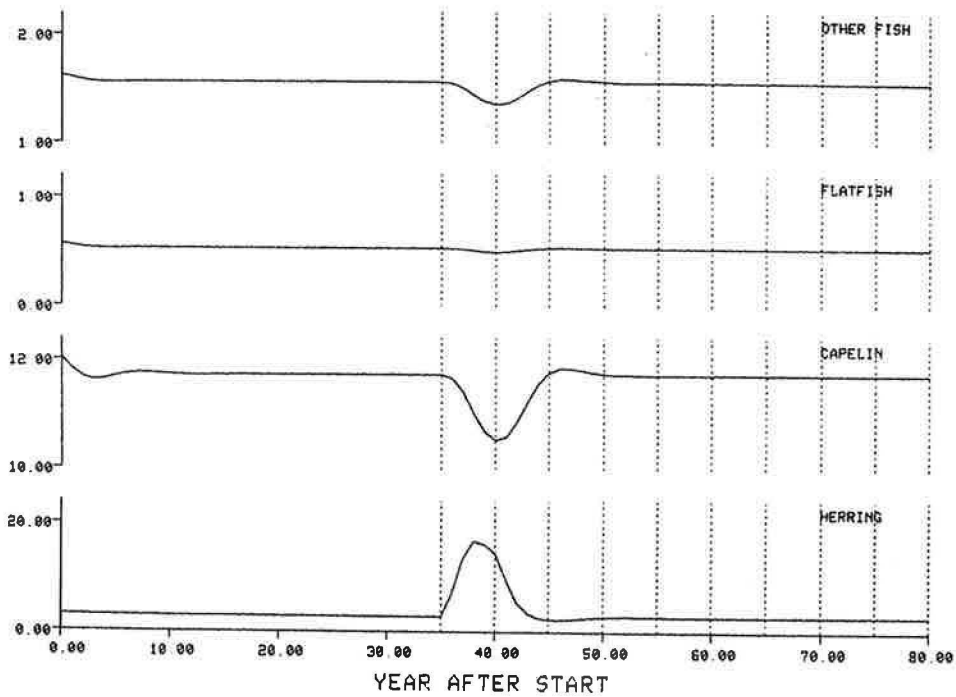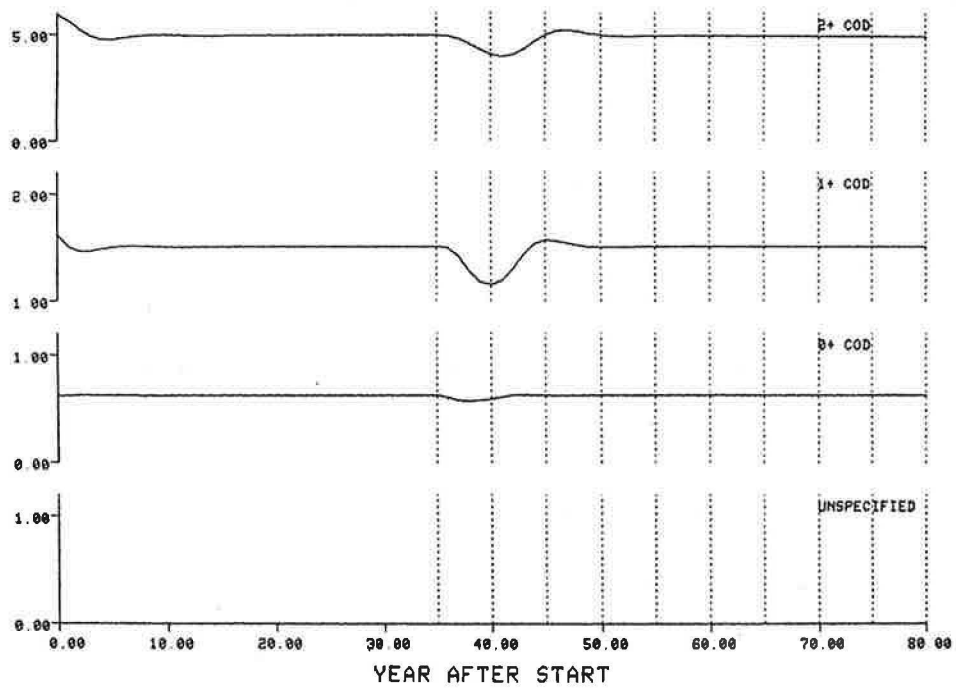to predation fixed.

Fig. 7 cont'd.

Fig. 8. Biomasses (10^3 kg/km^2) of species in SKEBUB-Balsfjorden responding to an influx of herring in years 35-39. Cod age groups were distinct and availability of herring to predation fixed.
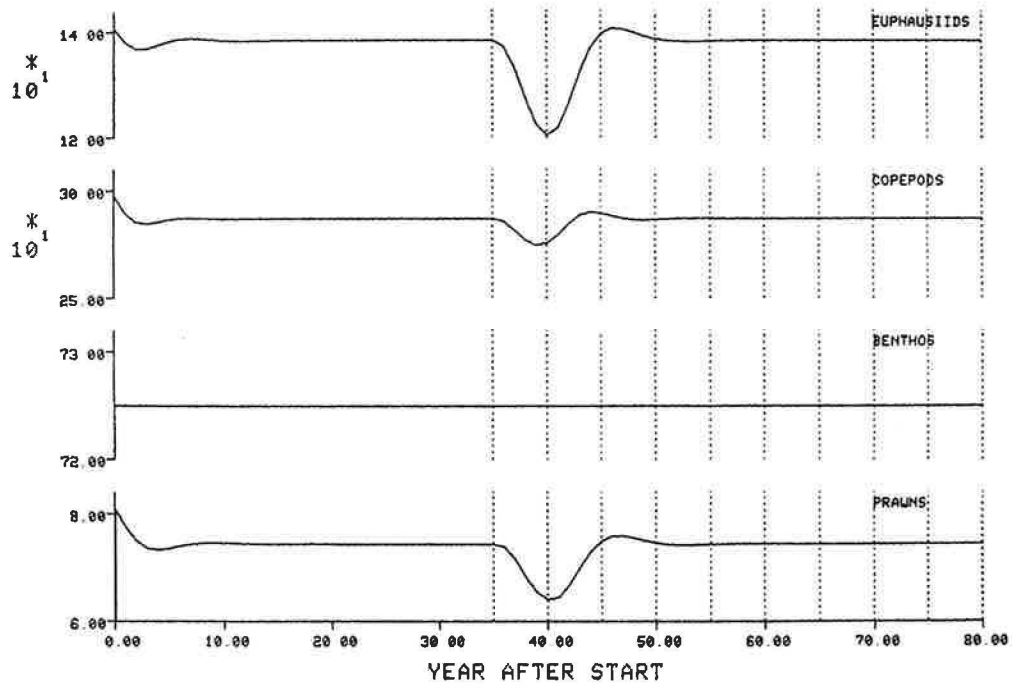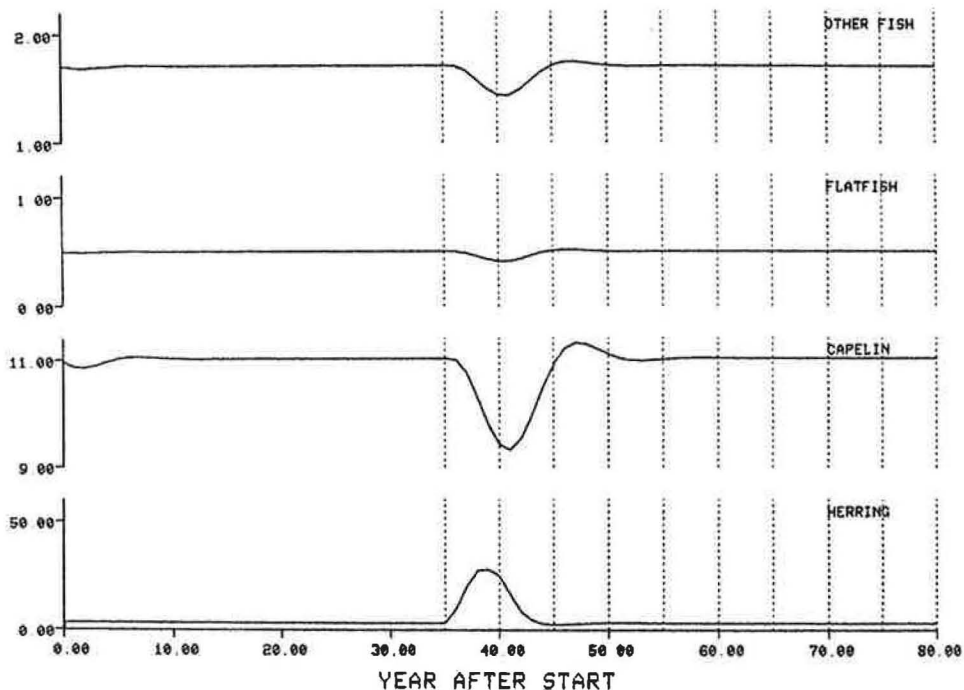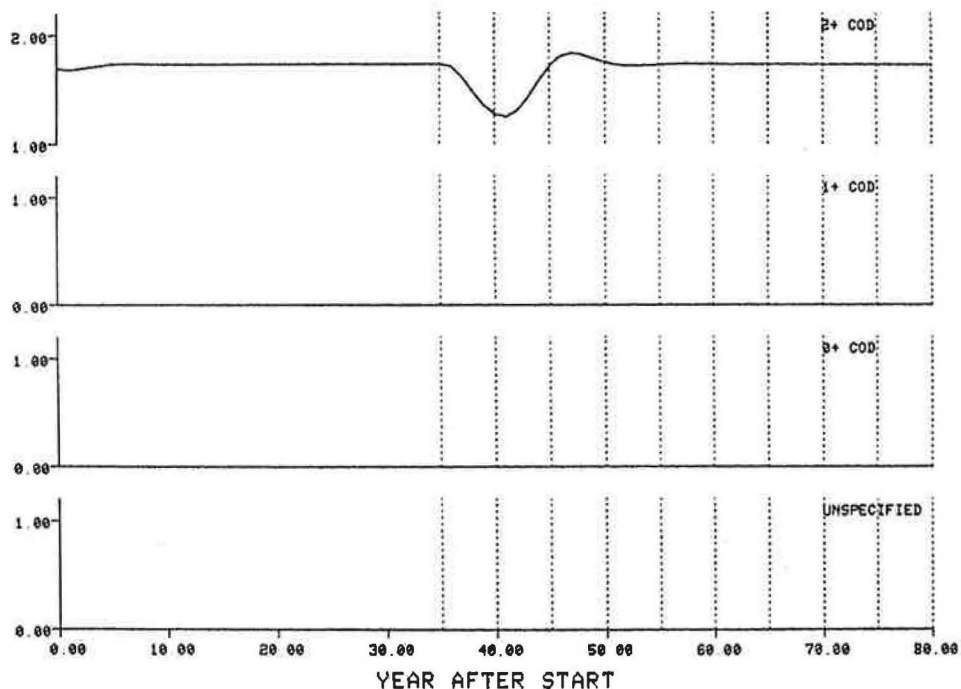
Fig. 8 cont'd.

Fig. 9. Biomasses (10^3kg/km^2) of species in SKEBUB-Balsfjorden responding to an influx of herring in years 35-39. Cod age groups were pooled and availability of herring proportional to growth and immigration.
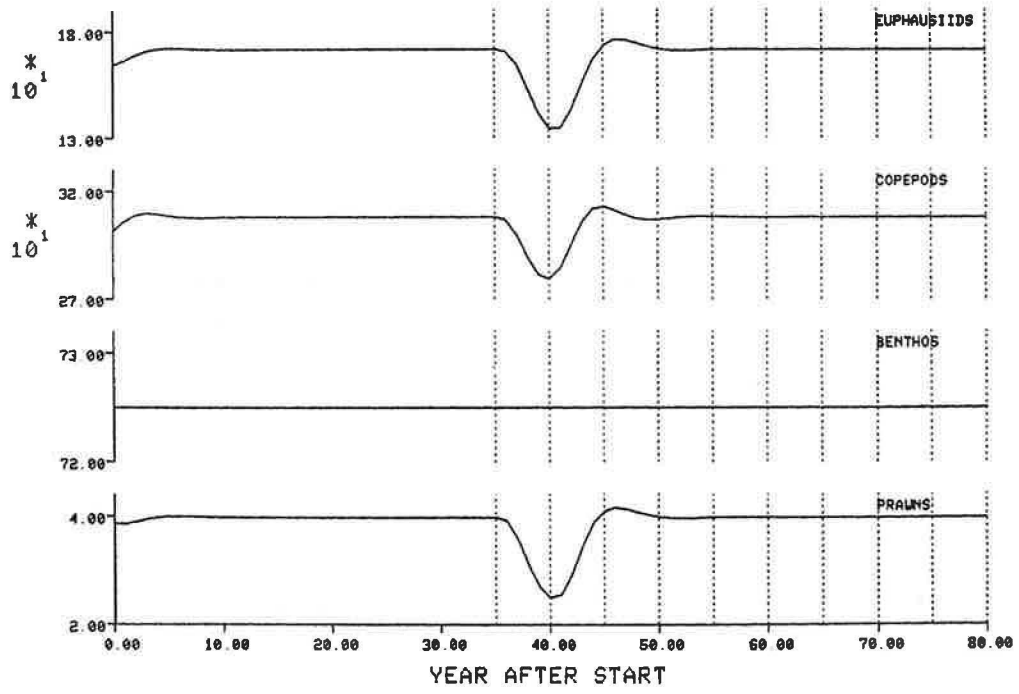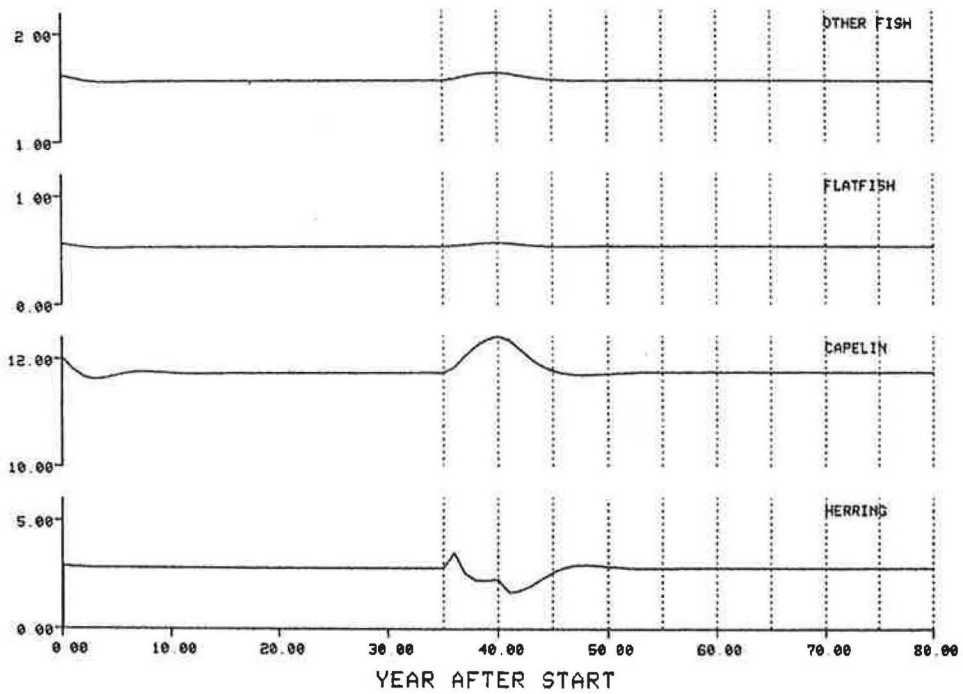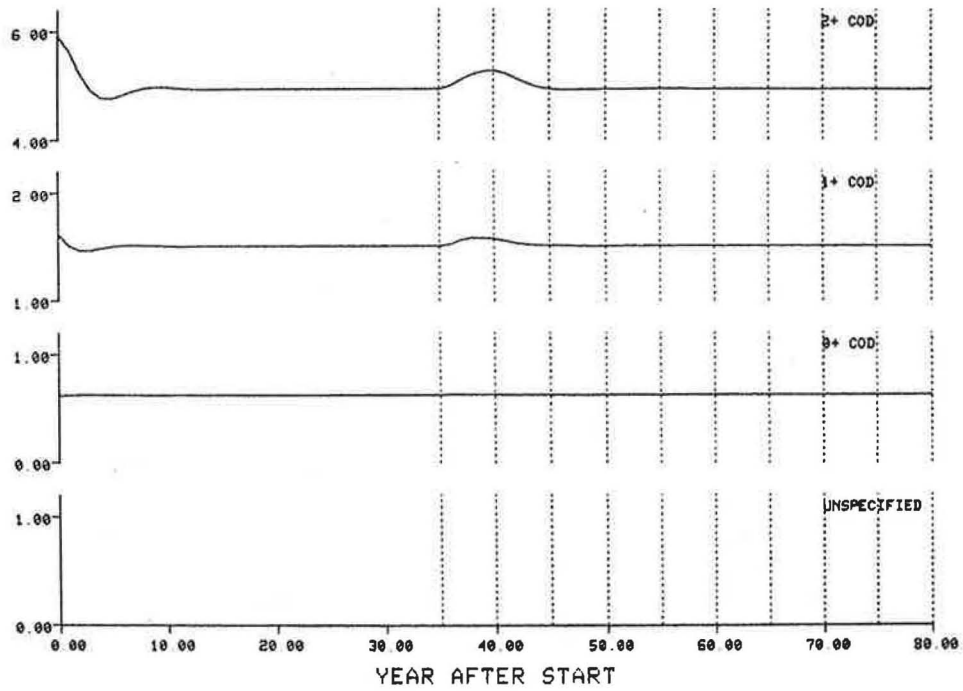
Fig. 9 cont'd.

Fig. 10. Biomasses (10^3kg/km^2) of species in SKEBUB-Balsfjorden responding to an influx of herring in years 35-39. Cod age groups were distinct and availability of herring proportional to growth and immigration.
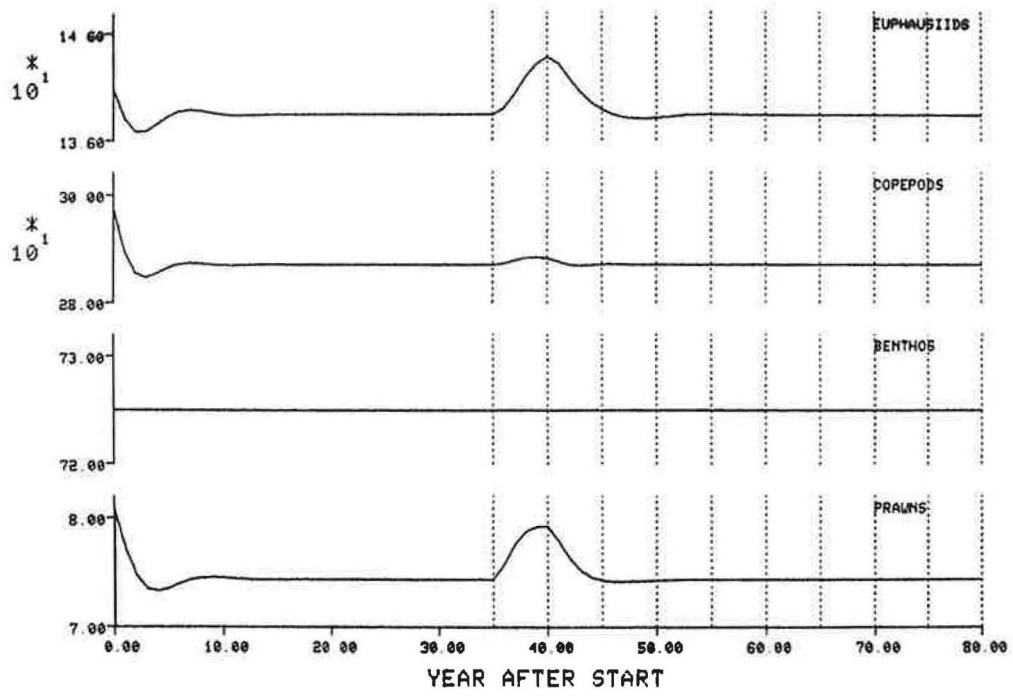
Fig. 10 cont'd.

DISCUSSION

There were distinct differences and distinct similarities between the two versions of SKEBUB-Balsfjorden. The major differences occurred because of the lower growth rate (and higher biomasses) that the simulation stabilized at once the cod groups had been pooled. This affected response to the herring influx scenarios, but not to the overall simulation processes as indicated by the error analyses.

Neither equilibrium was entirely consistent with the available data. Biomasses were too high in the pooled version, although growth rates were approximately equal to input levels. Conversely in the distinct version although biomasses were consistent with those estimated from survey data, growth rates were considerably higher than empirical estimates. Although each simulation departed from the available information in different ways they both had the same effect: either growth rates or biomass had to be higher to prevent starvation in the system. In the original simulation food composition was not fixed before equilibrium, and not all of the required food was obtained. With food composition fixed no starvation was possible (as this would have affected the food composition) and thus higher productivity is required in the system. Two remedies spring readily to one's mind -- both limit food consumption. In the first it is assumed that not all of the required food is obtained, i.e. there is some starvation, and this would then reduce the predation demand in the system. In the second it is assumed that there is more seasonal variability in the food requirements. There is evidence for some marine fish species e.g., plaice (Basimi and Grove 1985) that food consumption drops markedly during the winter months. Often in the

available data daily rations of fish are presented without regard to seasonal variability. More information is required on the feeding and metabolism of fish during the colder months of the year.

As to the question of whether age structure affects the functioning of the simulation, it is evident from these results that it does. Furthermore it is evident that it affects the entire simulation and not just the species to which it is applied (Table 1). Surprisingly the overall properties of the simulation remained similar in both versions, indicating that qualitative projections of the simulation and its interactions are remarkably consistent. Is age structure necessary? The answer depends on the specific circumstance being analyzed. It appears to be more important for specific perturbations to the system which are age dependent than to general analyses. It is certain however that the simulation must be designed from the beginning with a clear conception of the degree of age structure to be explicitly represented. It is not something that can be routinely modified at a later time without substantial reparameterization.

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