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Utility of Holistic Ecosystem Simulation for Assessment of Stocks and Their Response to Fishing

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UTILITY OF HOLISTIC ECOSYSTEM SIMULATION FOR

ASSESSMENT OF STOCKS AND THEIR RESPONSE

TO FISHING

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ABSTRACT

Single species population dynamics are constrained by the implicit assumptions of independence of other species and the environment, and by the required explicit assumptions of stock and recruitment relationships, and the rate of natural mortality. Holistic ecosystem simulations based on empirically determined relationships and data can be used to determine interspecific relationships and the influence of a variable environment on the ecosystem. Predation is the largest component of natural mortality and is a major determinant of recruitment. Predation is calculated explicitly in holistic ecosystem simulations and thus alleviates the need for assumming a rate of natural mortality or a stock and recruitment relationship.

Resource assessment with holistic ecosystem simulations is accomplished with the computation of the long-term mean or equilibrium biomass, their reasonable bounds, and the magnitude and periods of their fluctuations. Effects of increased fishing on target and non-target species can be determined and resulting stock compositions portrayed. In closed, or semi-closed, systems the effects of different enhancement strategies (or species introductions) can be simulated for the enhanced and non-enhanced species.

Validation of the simulations is accomplished with verification of individual component processes, and with Monte Carlo error analyses. Direct comparisons of simulation results with field observations is desirable but not always possible.

INTRODUCTION

Marine and lake ecosystems are not stable over time; considerable fluctuations in the abundance and distribution of individual species occur even if the total carrying capacity varies little from year to year. The determination of the abundance, its fluctuations and the factors controlling these fluctuations continues to be a primary goal of fisheries scientists.

The methods and formulations proposed for resource assessment and yield prediction have traditionally been derived from a consideration of the dynamics of single species, but improvements in explaining the dynamics of single species have been slow in forthcoming. Comparatively recently, multispecies approaches to describing fishery dynamics have been proposed. These multispecies approaches offer significant advantages over the traditional single species approaches replacing the severely constraining assumptions of the latter with empirically derived relationships. In this paper we present a summary of the holistic ecosystem simulations derived at the Northwest and Alaska Fisheries Center, NWAFC, and their utility based on nine years of experience in their application.

General comparison of single species, multispecies, and ecosystem formulations.

Many properties and limitations of population dynamics methodology (models) are evident on close examination of their formulation; important assumptions include the lack of significance of features that are not included in addition to the form of features that are included. Single species models often consider a species as though it existed in a vacuum with no interactions with other species nor with the environment, even though such interactions are certain. A consequence of this approach is the stock and recruitment relationship which is modelled with any of a number of questionable formulae, none of which can

usually explain much of the variation in the stock and recruitment relationship. The simpler single species models include no spatial or temporal resolution and thus must assume that these are of little consequence. Thus natural mortality is considered invariant over the life history of the fish, to be affected neither by the age/size of the fish nor by its abundance relative to its predators and prey. When fishing is considered it is limited to its effects on the target species; secondary effects due to changes in the abundance of non-target species cannot be considered.

The few available multispecies approaches that include two or a few species usually must consider predation as a variable fixed in space and time. However, the entire ecosystem participates in predation processes which vary through space and time in an unpredictable fashion. Thus many of the limitations of single species approaches also apply to these constrained multispecies systems and the prediction of future fluctuations is limited to approximate those that have already been observed.

Holistic ecosystem simulations attempt to use all available pertinent knowledge to simulate the dominant processes in the ecosystem and their temporal and spatial fluctuations. These processes include availability dependent (or density dependent) predation mortality, the largest component of natural mortality, which is simulated as a function of both space and time. The simulation of interspecific predation enables the simulation of recruitment in quasi-realistic manner, as explained later. Effects of environmental anomalies on the system dynamics are also included. Enhancement or the introduction of new species into the ecosystem can be simulated as is described for cod enhancement in Balsfjord later in this paper. A consequence of including all available and pertinent information into the simulation is a loss of statistical precision, but this

lack of statistical precision is a realistic reflection of our knowledge of the system. More precise predictions are available from single species models but the validity of these predictions depend entirely on the validity of the underlying assumptions - as interspecific interactions change over time and the underlying assumptions are violated, incorrect predictions will be made with as much precision as correct ones.

PRINCIPLES OF ECOSYSTEM SIMULATION

Basic Principles.

Conventional food chain models (Fig. IA) start with an estimate of primary production and by applying conversion efficiencies move up the trophic ladder. Difficulties in this approach arise because of the variability in measurements of primary productivity and from a lack of knowledge of conversion efficiencies which may vary seasonally and with age as well as with species (Jones 1984). To circumvent these problems a "back down the food chain" approach was used at the NWAFC (Fig. IB). This approach starts with the apex predators, determines what biomass and composition of species is required to sustain them and, in turn, what biomass and species are required to sustain their prey. The food chain is descended in this manner until primary production is reached. In this manner minimum stock estimates and the minimum requirements for production are computed. This approach requires the diet and food requirements of the different species; data which are usually available from field sampling or the literature.

Several requirements have been found necessary for successful ecosystem simulations:

a) The ecosystem must be holistic, including all species and/or ecological groups and all essential processes affecting these.

CONVENTIONAL FOOD CHAIN MODEL
(based on production)

Energy   Nutrients

PHYTOPLANKTON
"conversion"

A
ZOOPLANKTON

FISH

APEX PREDATORS

Losses to   Losses in
bottom and   metabolism
regeneration

Principles: Estimation of transfer (conversion) of organic matter.

Main shortcomings: Primary production sampling incomplete.
Conversion efficiencies guessed at.
Magnitudes of "losses" unknown.
Proportioning between "levels" guessed at.

BACK DOWN THE FOOD CHAIN
(based on consumption)

APEX PREDATORS

PREY 1

B
PREY 2

PREY 3

PREY 4

Principles: Determine who eats what and how much and then determine
how much must be there to produce the eaten amounts.

Advantages: Lower bounds of the production (and standing stocks)
can be computed on all levels.
Amounts of noncommercial (and nonsampled) species can
be estimated.
Changes in one prey level are related to changes in
other prey levels.

Figure 1 A- Principles of conventional food chain model based on production

B- Principles of trophodynamic computations, based on consumption

b)   All major processes should be simulated with explicit, empirically derived, and/or tested formulae.

c)   The simulation must include diagnostic (i.e., to check input data) and prognostic phases.

d)   There must be sufficient space and time resolution.

e)   The simulation should not be conditionally stable (no ecosystem is stable!).

f)   Singular components (processes) must be independently verifiable.

Basic Formulae.

A numerical ecosystem simulation can be a voluminous computer programme. It usually contains much "bookkeeping" of various computed intermediate variables and outputs. Many simple and usually linear computations are used and many of the basic formulae are used repeatedly in each timestep and for each species/ecological group. The most important of these formulae is the biomass balance formula:

$$B_{i,t} = B_{i,t-1} \ e^{g-m} - C_{i,t-1} \qquad (1)$$

where $B_{i,t}$ is the biomass of species i in timestep t, $B_{i,t-1}$ its biomass in the previous timestep, and $C_{i,t-1}$ its losses due to predation in the previous timestep. Losses due to predation are computed according to equation (3). The growth (g) and non-predation natural mortality (m) coefficients are species specific and dependent on the length of the timestep. Weight at age data are used to compute g where annual increases in weight are weighted by the distribution of biomass with age to obtain the biomass growth rate. Recruitment to the exploitable part of the population is ultimately determined by predation (C) which in turn

affects the biomass distribution with age. Thus variations in recruitment will affect the biomass growth rate g. The growth coefficient is also made a function of temperature and food availability.

The non-predation mortality coefficient consists predominantly of spawning stress or senescent mortality and is relatively small in long-lived species but can be of great importance in determinate spawners (e.g., salmon or capelin). Spawning stress and senescent mortality will be reduced in a population where older members are removed by fishing and thus m will be influenced by fishing mortality (f). In conventional single species models predation (C) is included in natural mortality M, whereas in ecosystem simulations predation mortality is explicitly calculated and becomes variable over time and with the age and size of the fish.

The fishery yield (Y) is computed with a space and time variable fishing mortality coefficient (f):

$$Y_{i,t} = B_{i,t} - B_{i,t}\, e^{-f} \tag{2}$$

The consumption (predation) of species i in timestep t ($C_{i,t}$) is computed as a sum of predation of this species by all components of the ecosystem:

$$C_{i,t} = B_{i,t} q_i p_{i,i} + B_{j,t} q_j p_{i,j} + \ldots B_{n,t} q_n p_{i,n} \tag{3}$$

where $B_{i\ to\ n}$ are biomasses of species i to n, $q_{i\ to\ n}$ are food uptakes (requirements) of the individual species i to n--e.g., in terms of fractions of body weight daily and $p_{i,\ i\ to\ n}$ are the fractions of species i in the food of species i to n. The fraction of one species in the food of other species (p) varies in space (from one grid point to another) and also in time depending on the availability of suitable food. An initial average food composition is prescribed from food habits data.

This food composition table serves as a "suitability index". Examples of prescribed and computed food composition of flathead sole are shown in Table 1.

Food requirement for satiation (q) (expressed as percent body weight daily) is computed with two components.

$$q_{i,t} = a_i B_{i,t} + b_i G_{i,t} \tag{4}$$

where a_i is food requirement for maintenance of species i and b its food requirement for growth ($G_{i,t}$). Growth varies annually either as a harmonic function of time:

$$g_{i,t} = g_i^\circ + h_i (\cos \alpha t - \kappa_i) \tag{5a}$$

or as a function of temperature:

$$g_{i,t} = g_i^\circ e^{(\frac{1}{T_i^\circ} - \frac{1}{T})} \tag{5b}$$

Consequently the food requirement also varies in a seasonal rhythm.

If food requirements for satiation cannot be satisfied, partial starvation will occur (see Table 1). This starvation is assumed to influence growth:

$$g'_{i,t} = g_{i,t}((q_{i,t-1} - S_{i,t-1})/q_{i,t-1}) \tag{6}$$

The symbols in formulas 5a to 6 (which are not previously listed) are:
h_i - half amplitude of annual change of mean growth rate (g_i°); α phase speed (30° per month); κ_i phase lag; T_i° acclimation temperature; T actual temperature; $S_{i,t}$ missing proportion of food requirement for satiation.

Initial inputs of food composition are of necessity mean values from many samples and are dependent on the species composition available to the predator immediately prior to sampling. An adjustment is required to reflect changing abundances of prey species and to prevent the over consumption of a prey species with decreased biomass. Such overconsumption is prevented by defining a maximum

Table 1.--Examples of food composition changes in flathead sole in two subregions in the eastern Bering Sea and Gulf of Alaska in March.

Food item (group)	Food composition in %		
	Initial annual mean	Subregion 3	Subregion 7
Infauna	3	3.7	3.5
Epifauna	22	8.6	13.4
Euphausids	45	56.0	52.8
Cottids and other demersal	9	4.0	3.3
Cod	4	2.7	2.7
Crab	1	0.4	1.2
Shrimp	2	2.5	2.3
Pollock	8	10.0	9.0
Other flatfish	2	2.5	2.3
Capelin and other pelagic	2	1.1	1.2
Rockfish	2	1.2	2.3
Starvation		7.3	6.0

annual consumption proportional to a species annual growth rate in biomass (minus senescent and reasonable fishing mortality), and at the same time substituting other prey items which have traditionally occurred in the predator's diet and are now at an elevated biomass level.

The standing stock of plankton is usually simulated with a harmonic function and the biomass of benthos is made a function of depth, bottom substrata, and season.

A simplified scheme of computations in simulations is shown in Figure 2. Figure 3 summarizes the factors affecting the biomass dynamics.

Equilibrium biomasses in an ecosystem.

Equilibrium biomass is defined as a biomass in a dynamic ecosystem which does not change from one year to next, i.e., if in biomass balance formula:

$$B_{i,t} = B_{i,t-1} \, e^{(g_{i,t} - z_{i,t})}$$

$g_{i,t} = z_{i,t}$; meaning growth equals removals (total mortality, Z). This condition can be iterated in an ecosystem simulation with the assumption that g (growth rate) is correctly determined from empirical data, but that the initial input biomass is an estimate only. Thus we must increase and/or decrease the biomasses until an equilibrium (unique solution) is reached. This requires numerous iterations (in the order of 300 or more), using an iteration constant k which decreases as the number of iterations increase:

$$B_{i,o}^{'} = B_{i,o} - (B_{i,12} - B_{i,o})/k \tag{7}$$

i.e., a fraction of the difference between the initial estimate of biomass $(B_{i,o})$ and the biomass after 12 months $(B_{i,12})$ is subtracted from the initial estimate to give the second estimate of biomass $(B_{i,o}^{'})$.
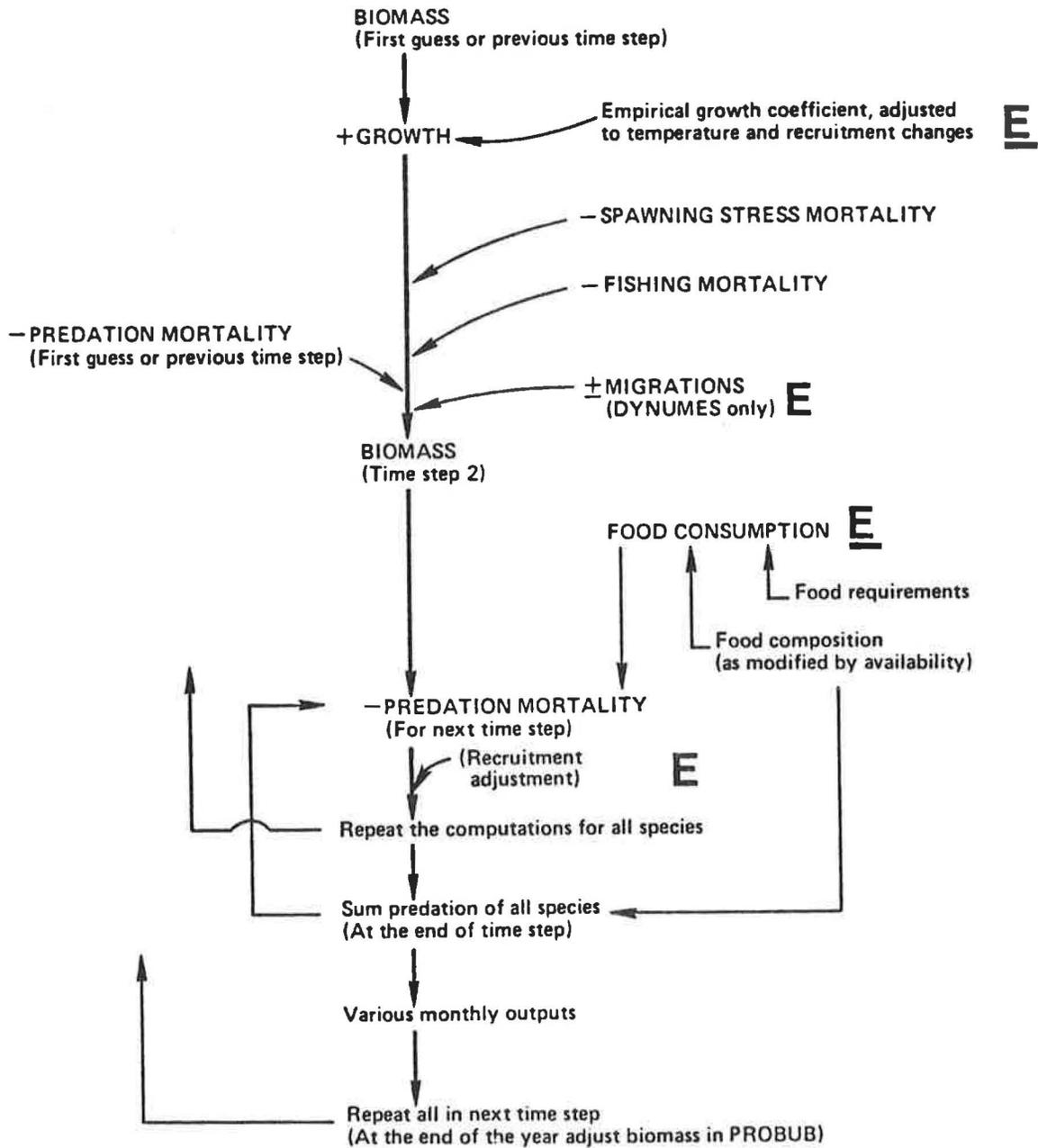
BIOMASS
(First guess or previous time step)

+GROWTH ← Empirical growth coefficient, adjusted to temperature and recruitment changes **E**

− SPAWNING STRESS MORTALITY

− FISHING MORTALITY

−PREDATION MORTALITY
(First guess or previous time step)

±MIGRATIONS
(DYNUMES only) **E**

BIOMASS
(Time step 2)

FOOD CONSUMPTION **E**

Food requirements

Food composition
(as modified by availability)

−PREDATION MORTALITY
(For next time step)

(Recruitment adjustment)   **E**

Repeat the computations for all species

Sum predation of all species
(At the end of time step)

Various monthly outputs

Repeat all in next time step
(At the end of the year adjust biomass in PROBUB)

Figure 2.--Simplified scheme of computation of processes and state variables
in ecosystem simulation. The processes marked with E include
environmental influences. In the model used in present study,
only growth and food consumption were affected by temperature.

FISH BIOMASS DYNAMICS
and factors affecting it

$$\text{BIOMASS}_{i,t} = \text{Biomass}_{i,t-1} + \text{Growth} - \text{Mortalities} - \text{Emigration (immigration)}$$

i species
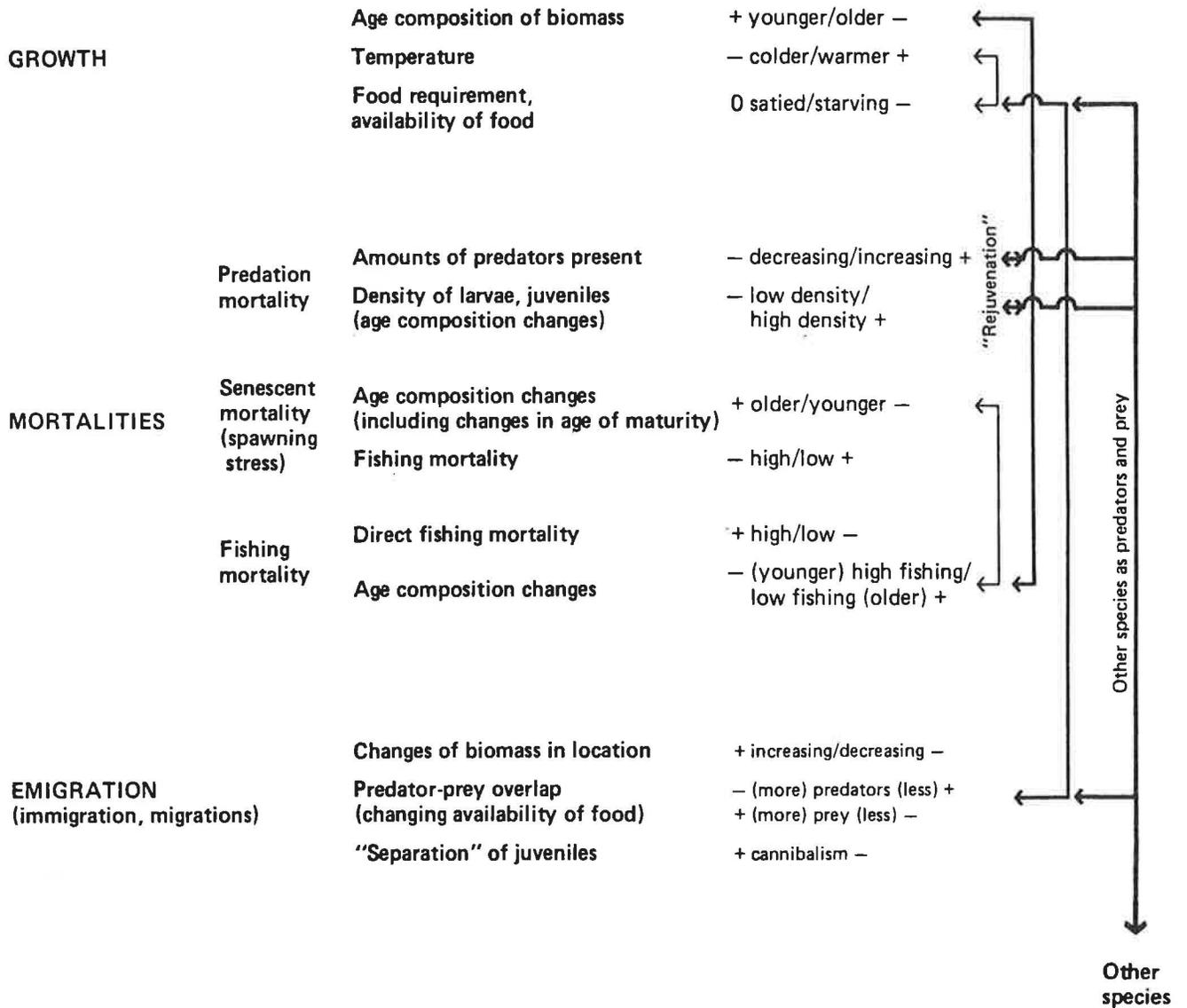t time (month)
+ increase
− decrease

GROWTH

Age composition of biomass	+ younger/older −
Temperature	− colder/warmer +
Food requirement, availability of food	0 satied/starving −

MORTALITIES

Predation mortality
Amounts of predators present	− decreasing/increasing +
Density of larvae, juveniles (age composition changes)	− low density/ high density +

Senescent mortality (spawning stress)
Age composition changes (including changes in age of maturity)	+ older/younger −
Fishing mortality	− high/low +

Fishing mortality
Direct fishing mortality	+ high/low −
Age composition changes	− (younger) high fishing/ low fishing (older) +

EMIGRATION (immigration, migrations)

Changes of biomass in location	+ increasing/decreasing −
Predator-prey overlap (changing availability of food)	− (more) predators (less) + / + (more) prey (less) −
"Separation" of juveniles	+ cannibalism −

"Rejuvenation"

Other species as predators and prey

Other species

Figure 3. Fish biomass dynamics and factors affecting it.

In order to achieve convergence of the equation system in the simulation it is necessary to "fix" one of the major fish biomasses (i.e., assume that it is known with sufficient accuracy). On the other hand, if apex predation (e.g., by mammals) is large and is "fixed" (i.e., computed with system independent formulas that are independent of biomass levels), or the fishery on most species is of considerable magnitude, convergence can also be achieved.

Equilibrium in the context of this simulation is envisaged as the long-term (i.e., 20 or more years) mean biomass values for the different groups. In its initial stages equilibrium searching highlights inconsistencies in input data; for example, where predation of species A on species B calculated from stomach contents is larger than that available from species B as indicated by survey data. In its final stages the concept of equilibrium provides a stable, and replicable, position from which to study perturbations to the system.

Data requirements for simulations.

The ecosystem simulation uses general knowledge as well as location specific data, If there is a lack of specific and local data, simulations can still be programmed, using estimates based on general comparative data from similar regions and from similar ecological species/species groups. The data needs can be grouped into three categories: basic inputs, initial estimates, and derived (indirect) data.

The main (basic) input data are: Growth rate of the biomass (g), computed from age specific growth rate and biomass distribution with age. A special auxiliary programme (BIODIS) is used for this computation. Food requirement (q) for maintenance (a) and for growth (b) is estimated from data usually available in literature. A combined food requirement (in terms of percent body weight daily) can also be used. Senescent mortality (spawning stress mortality) is

usually a relatively small mortality coefficient (m in Formula 1) and is estimated either in BIODIS model or with consideration of life span in non-commercial species. Fishing mortality (f) is computed from catch data. Apex predation (by birds and mammals) is usually computed from available data, and when fixed for one year will not change in subsequent computations.

Among initial estimates (which are modified within the computations) are the estimated biomass and average food composition. The latter is obtained from empirical data, but need often to be modified in consideration of the amounts and types of food of juveniles. It should also be noted that all species/biological groups occur as prey items. If a region for the simulation has open boundaries, the immigration/emigration through these boundaries need to be estimated.

Derived (indirect) data include some "control parameters" such as the maximum allowable consumption of a species which limits overconsumption at low biomass levels. It is set equal to potential growth minus mortality other than predation. Two factors associated with maximum allowable consumption are the rate of availability dependent prey switching by a predator and its maximum amount. These factors are adjusted so that the simulated prey consumption by predators is similar to that derived empirically.

Comparison of age-structured, number-based models with non age-structured, biomass-based models.

Most conventional population dynamics models have been number-based, requiring a complete description of age structure. If not formulated on a yield per recruit basis these models have usually required an explicit stock and relation-ships. Ecosystem simulations of Andersen and Ursin (1977) have extended these

approaches. The present authors considered the dominating influence of the spawner-recruit relationship and the high loss (in numbers) of larval and juvenile fish, both of which are poorly understood processes, to be a limiting factor in these approaches. Consequently, the ecosystem simulations developed at the Northwest and Alaska Fisheries Center have been biomass-based with each species or ecological group pooled over age class. Where necessary for detailed studies (e.g., of cannibalism in Bering Sea pollock, or of enhancement of juvenile cod in Balsfjord) biomasses have been divided into (usually) 3 age groups, which also permits direct inclusion of larval and juvenile survival functions to simulate variable year class strength. Changes in recruitment through the biomass are effected through changes in predation on the different biomasses and/or through competition for food.

USE OF ECOSYSTEM SIMULATION IN RESOURCE
ASSESSMENT AND YIELD PREDICTION

The ecosystem simulation can serve a multitude of purposes. Its objectives can be grouped into two categories:

1 - <u>Investigative and digestive</u>, that permit quantitative

biological resource evaluations which include:

—<u>Synthesis of information</u>, including quantification of

descriptive data and quantitative summarization of

exploratory and baseline studies.

—<u>Simulation of the ecosystem proper</u> with all of its essential

interactions, including those between the ecosystem <u>per</u> <u>se</u>

and the physical-chemical environment.

—<u>Determination of the effects of environment and inter-

species interactions and other natural fluctuations.</u>

2 - <u>General management guidance and effects of exploitation</u>,

including:

—<u>Determine magnitude or status of the biological resources</u>,

their past and expected fluctuations.

—<u>Determination of effects of fishing</u> intensity variations

(including spatial and temporal changes in distribution

or fishing effort) on the resources, and determination

of the effects of proposed regulations.

—<u>Establishment of research priorities</u>.

<u>Resource assessment</u>.

Resource assessment with ecosystem simulations is largely accomplished with
the computation of equilibrium biomasses in defined conditions (i.e., finding
the unique solution to the numerical system). These computations also give
the carrying capacity of the defined ecosystem of a given ocean region or a
lake. Bounds can be computed for the equilibrium biomasses. The minimum
carrying capacity (or minimum equilibrium biomasses) can be obtained by
specifying highest plausible biomass growth rates and lowest plausible food
requirements. Both parameters can be obtained from empirical data. Corresponding
maximum equilibrium biomasses can be computed with lowest possible growth rates
and highest possible food requirements.

Example of computed maximum and minimum biomasses and mean exploitable
biomasses in the eastern Bering Sea is given in Table 2.

<u>Fluctuations of stocks</u>.

Aquatic ecosystems are not stable, but fluctuate along all time scales.
The study and prediction of these fluctuations is one of the main tasks of
fisheries biologists. Some of the factors causing the fluctuations in marine
ecosystem are listed in Table 3.

Table 2.--Maximum equilibrium biomasses of species and ecological groups
in the eastern Bering Sea (in 1,000 tons). (Estimated minimum
equilibrium biomasses and mean exploitable biomasses are given
for comparison.)

Species/ecological group designation	Maximum equilibrium biomass	Estimated minimum equilibrium biomass	Mean exploitable biomass
Halibut	585	400	220
Flathead sole	875	650	380
Yellowfin sole	1,660	1,100	510
Other flatfish	1,160	850	245
Cottids	4,438	4,000	−
Cod	1,468	1,000	745
Sablefish	183	120	51
Pollock	15,165	8,000	6,450
Rockfish	1,825	1,000	485
Herring	2,327	1,500	590
Capelin	5,149	3,500	(1,000)**
Mackerel	1,438	1,100	520
Salmon	(73)	(50)	−
Squid	2,310	1,200	(500)**
Crab	1,225	800	(300)**
Shrimp	1,792	900	(600)**
Predatory benthos	818	700	−
Infauna	24,219	20,000	−
Epifauna	20,947	15,000	−
Zooplankton	58,430*	35,000	−

* − 500 mg/m^3; 100 m.

** − Includes species which are not exploited at present.

Table 3.--External and internal factors causing fluctuations in marine ecosystem.

Factors	Affects
External	
Temperature anomalies	Affect metabolic rate in turn affecting growth rate and food uptake, thus predation rate of prey
	Affect migration and thus spatio-temporal overlap of predator and prey
Fishing	Affects abundance of older biomass, thus affecting predation, cannibalism, and therefore recruitment to exploitable stock
	Affects total biomass (including spawning biomass)
Internal	
Predation (including cannibalism)	Affects recruitment to exploitable biomass; main mechanism in interspecies interaction in predator-prey system
Competition	Interspecies interaction in predator-prey system; can also affect starvation, which in turn affects growth
Migration	Affects predator-prey system by changing predator-prey overlap (local density)
	Affects prey availability (thus predation) in space and time

Ecosystem fluctuations can be computed with the simulations after the computation of equilibrium biomasses has been completed. In these subsequent computations the equilibrization computations are bypassed, the mean food composition derived at equilibrium point is used and the food composition changes are simulated with the "density dependance" (i.e., with the factor of prey biomass change $-\sqrt{B_{i,t}/B_{i,e}}$, where $B_{i,e}$ is the biomass at equilibrium and $B_{i,t}$ is the actual biomass). Small changes of growth rates are also computed, as affected by temperature anomalies and changes in the relative amounts of juveniles and adults (the rejuvenation effects) caused by fishing and/or changes in predation. Past studies with the simulations indicate that the total biomass of finfish remains relatively stable - while some species increase, others decrease. Examples of the computed fluctuations of some biomasses in the Bering Sea are shown in Figures 4 and 5.

Yield predictions.

Fishing affects not only the target species but also other species via interspecific interactions, mainly predation. In order to investigate changes in the ecosystem caused by different levels of fishing, the ecosystem simulation is run with different fishing intensity and the ecosystem composition is reviewed after each run. In some cases moderate fishing can even cause the biomass of a target species to increase through compensatory effects, such as a decreased senescent mortality, increased growth rate, and decreased predation (the latter occurs in cases of extensive cannibalism).

When the fishing intensity reaches a higher level (which varies from species to species and region to region) "stock collapse" will occur. Specific applications of ecosystem simulations for yield prediction are provided in the next section.
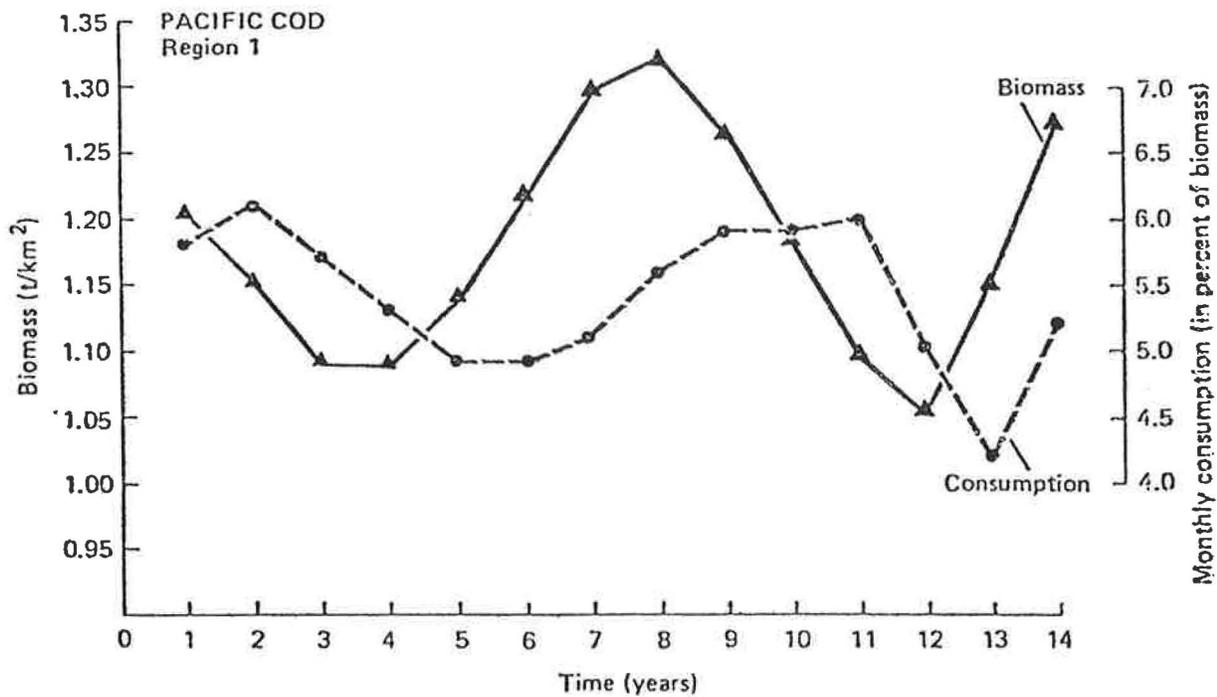
Figure 4. Fluctuations of Pacific cod biomass in Region 1 of the Bering Sea and the consumption of cod (in % of biomass) by the ecosystem.
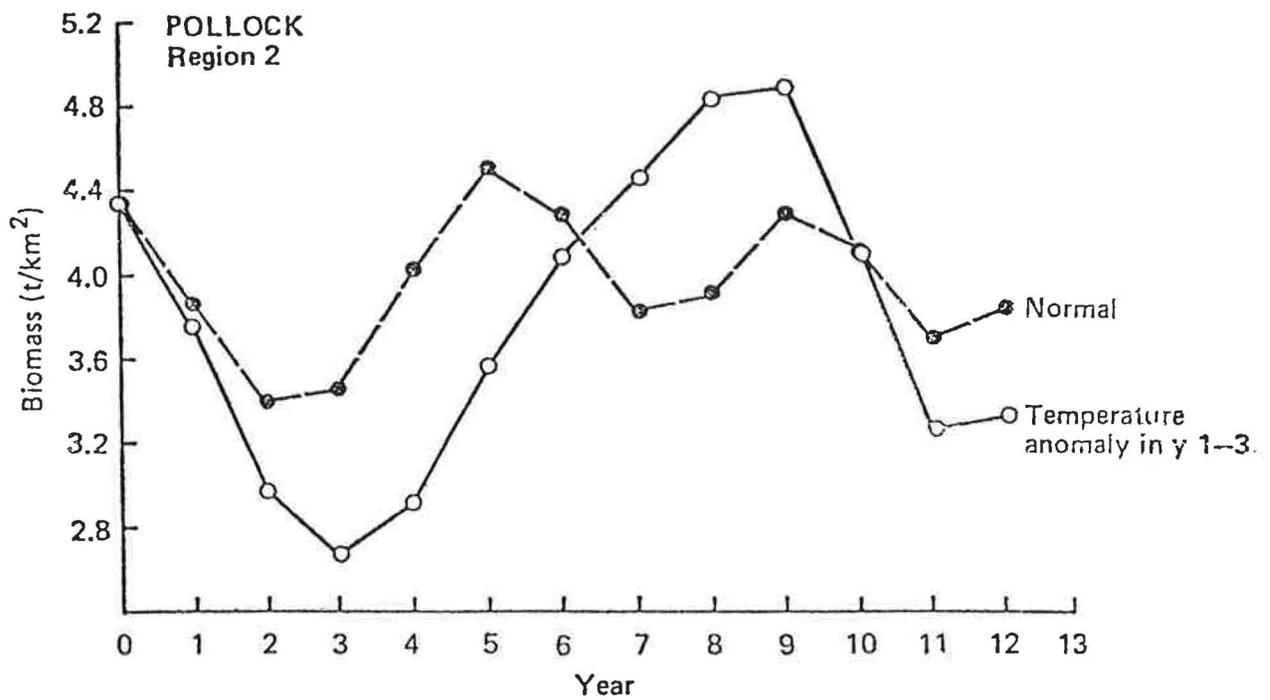
Figure 5. Changes of pollock biomass (in t/km^2) with time in Region 2 of the Bering Sea in normal conditions and with temperature anomaly in years 1 to 3 (-1.5; -2.5; -1.5^{0}C, respectively)

SOME APPLICATIONS OF ECOSYSTEM SIMULATIONS

The ecosystem simulations PROBUB, SKEBUB and DYNUMES have been applied in the past to a number of regions in the Pacific and Atlantic oceans. Some examples from these applications have been given in previous chapters. In addition, some examples of applications of PROBUB to the eastern Bering Sea and western Gulf of Alaska will be given below, demonstrating the effects of a changing fishery. Furthermore, brief results of application of SKEBUB on a semi-closed fjord in Norway pertaining to enhancement of coastal cod are also given.

A question was raised by the northwest U.S. fishing industry as to whether the stocks of cod and pollock in the Bering Sea and Gulf of Alaska could tolerate increased exploitation. The simulation was run with present catches; examples of the fluctuations of cod in Bristol Bay and in western Gulf of Alaska with this fishing effort are shown in Fig. 6. Fishing was increased considerably in the next simulation run (Bering Sea from 50K tonnes to 97K tonnes and Gulf of Alaska from 17K tonnes to 78K tonnes). These increased catches caused only a slight lowering of cod biomass in the Bering Sea (Bristol Bay), but caused the cod stock in Gulf of Alaska to collapse in six years (Fig. 7). When the catch was decreased to 58K tonnes in the Gulf of Alaska, about a 40% lowering of the cod stock occurred, but no stock collapse was apparent (Fig. 8).

A concentrated change of the stocks of rockfishes occurred in both regions, resulting in a slow increase in biomass of long-lived rockfishes due to decreased predation by cod (and pollock) on the pelagic juveniles of these species (compare Figs. 9 and 10).
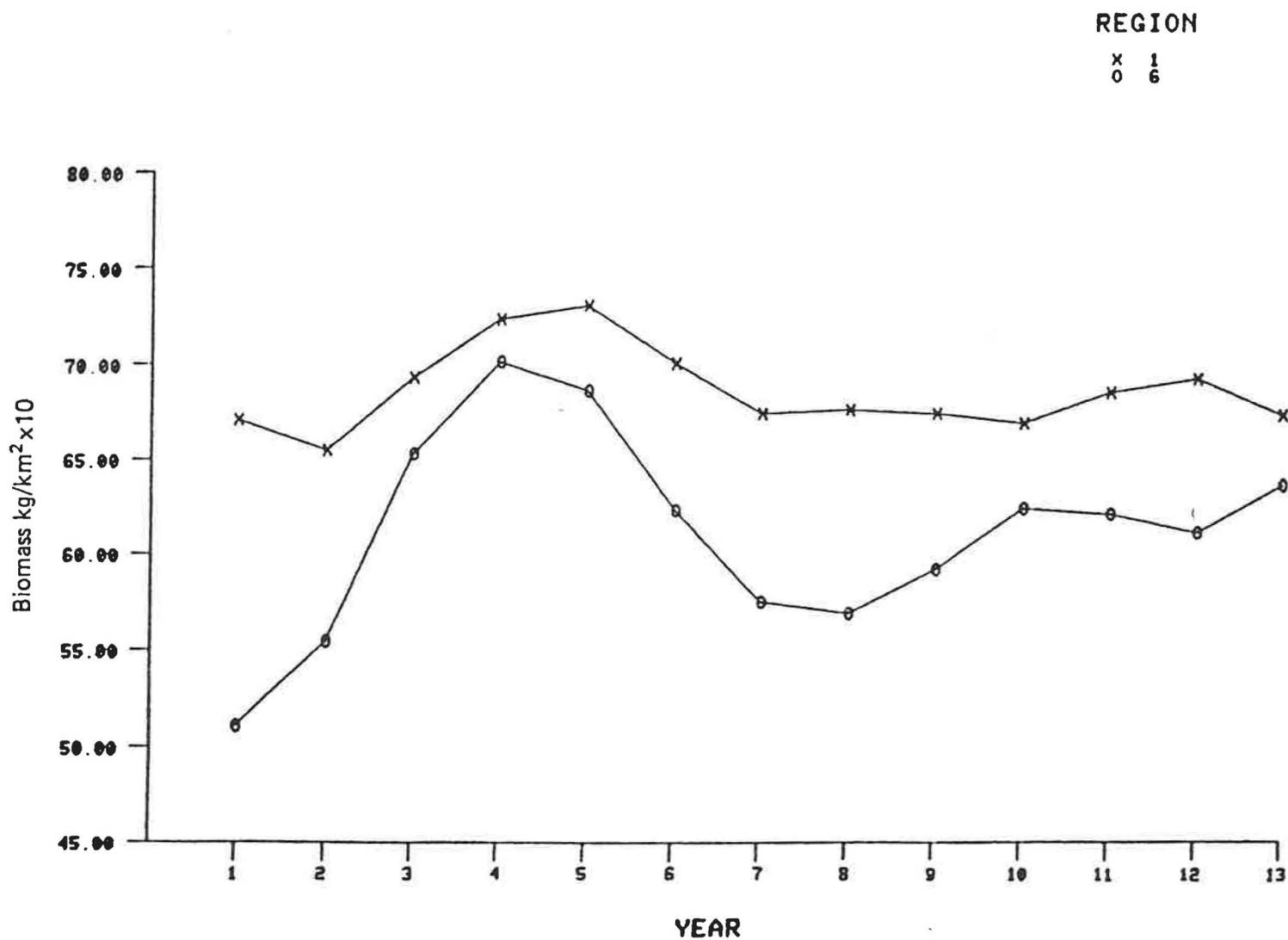
Figure 6.--Changes of cod biomasses with time in Bristol Bay (Region 1) and in western Gulf of Alaska (Region 6) (kg/km^2). (Initial catches 50K tonnes from the eastern Bering Sea and 17K tonnes from the Gulf of Alaska).
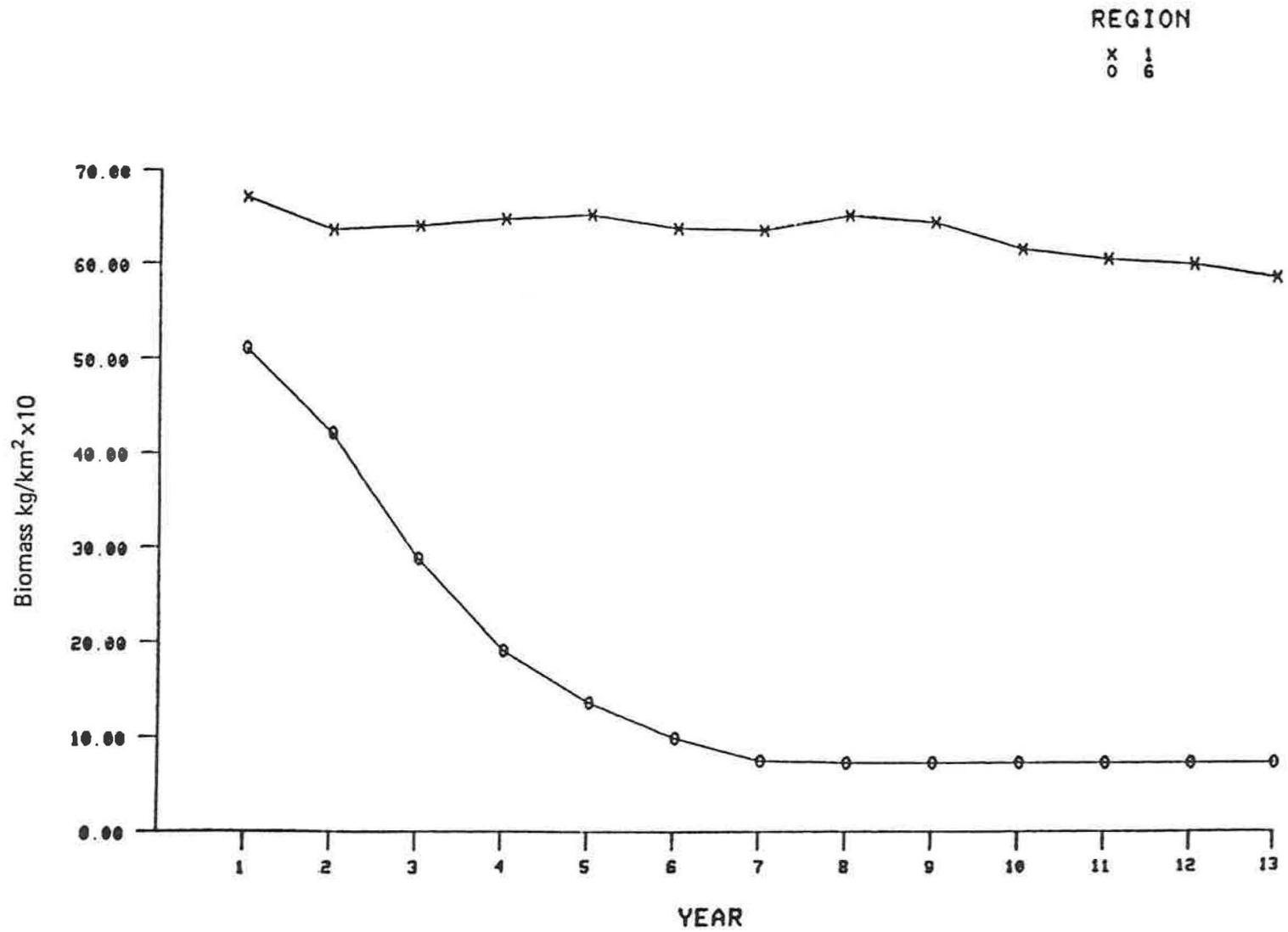
Figure 7.--Same as Figure 6 except initial catches of 97K and 78K tonnes, respectively.
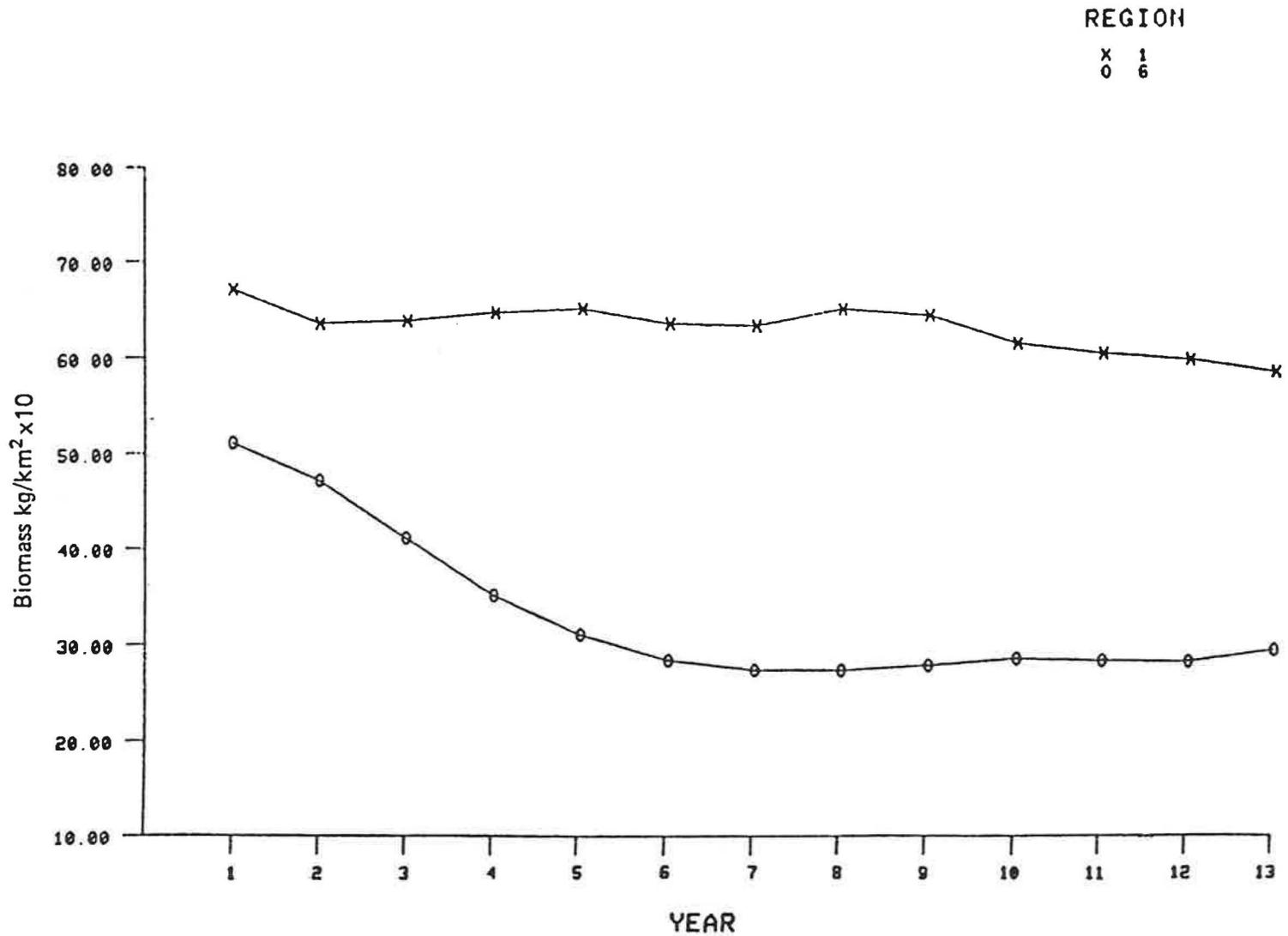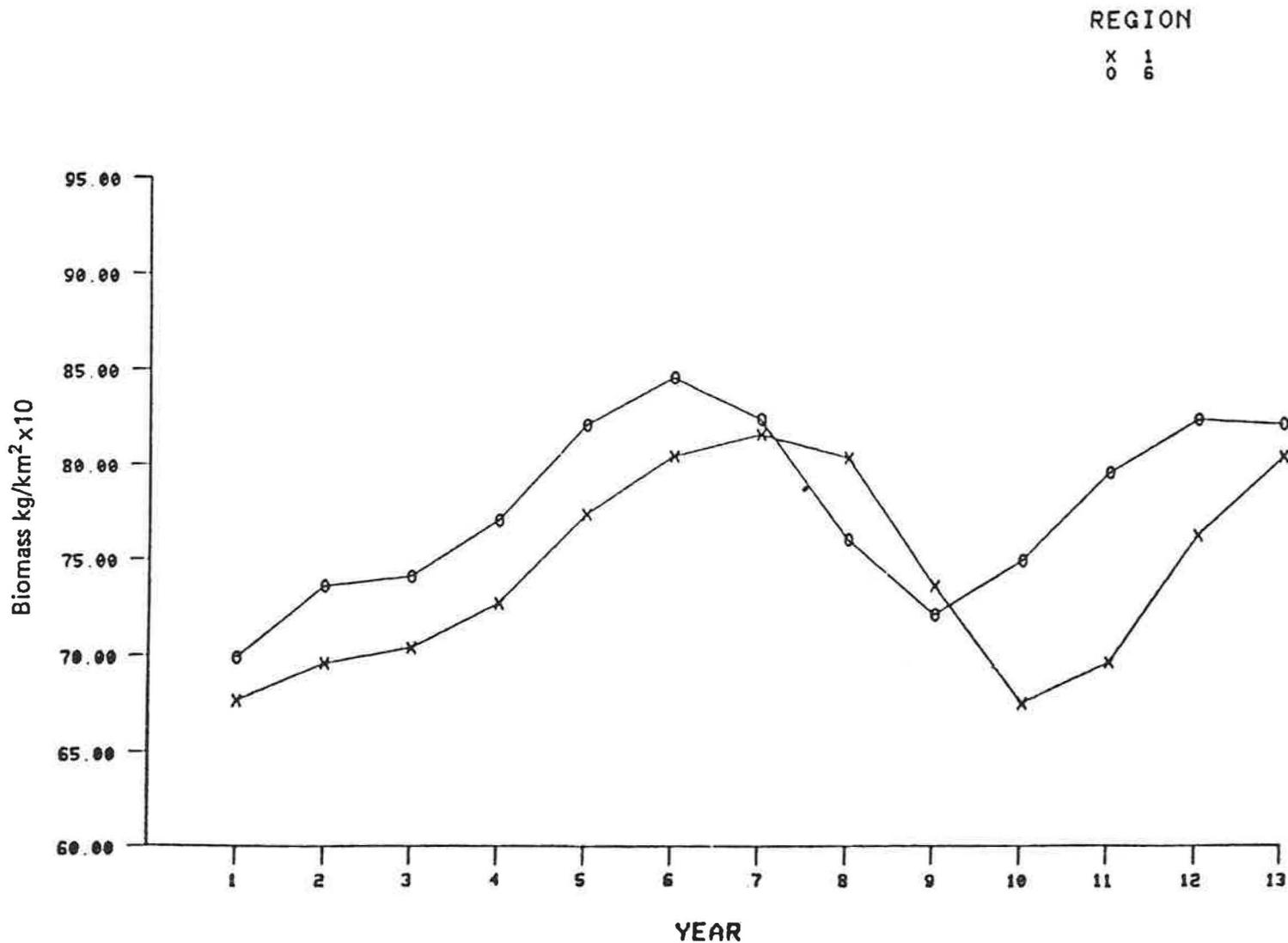
Figure 8.--Changes of cod biomasses with time in Bristol Bay (Region 1) and in western Gulf of Alaska (Region 6) (kg/km^2). (Initial catches 97K tonnes from the eastern Bering Sea and 58K tonnes from the Gulf of Alaska.)

Figure 9 .--Changes of rockfish biomasses with time in Bristol Bay (Region 1) and in western Gulf of Alaska (Region 6) (kg/km^2). Initial catches of pollock 512 K and 139 K tonnes respectively

REGION

X 1
O 6
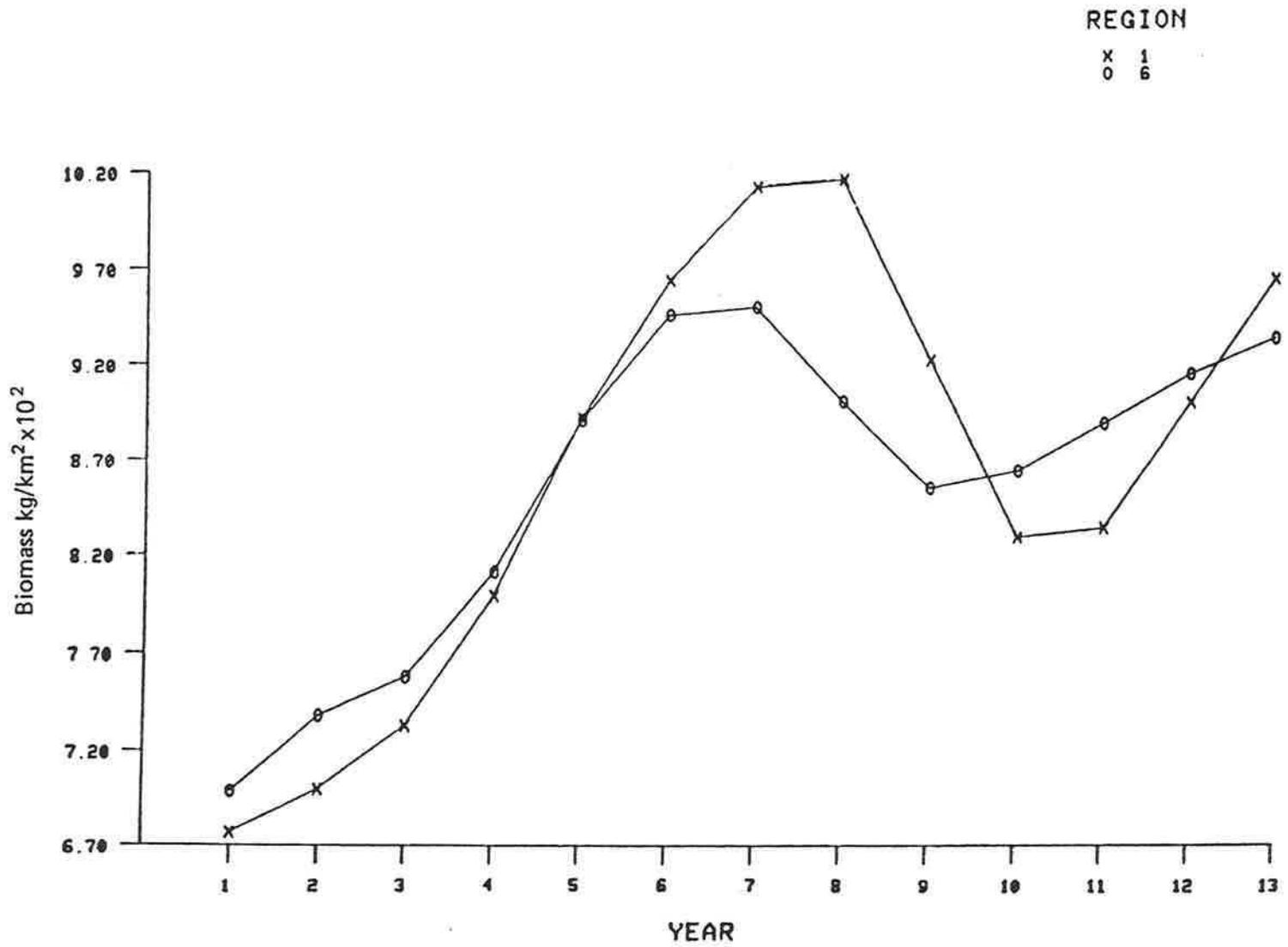
Figure 10.--Same as Figure 9 except increased catches of pollock (1,729 K and 493 K tonnes respectively.

The study of cod enhancement in Balsfjord, a semi-closed fjord in northern
Norway, is an ongoing cooperative project with the University of Tromsø. Some
preliminary results are available. For this simplified simulation (no spatial
resolution) the cod biomass was divided into three age groups (0, 1, and 2+).
Once stabilization was reached cod enhancement at the rate of 50% of the stable
zero cod biomass was introduced (year 35 in accompanying figures). Enhancement
led to an initial rapid increase of the adult cod population followed by a
decrease as prey populations decreased (Figs. 11 and 12). Yield from the
enhanced stock (the coefficient of fishing mortality was kept constant) was
increased by 18% under the deterministic solution and by 22% when a random
survival function was imposed on the unenhanced zero cod. Yields were increased
almost as much when the cod were enhanced for only 50% of the years (Table 4).

VERIFICATION AND VALIDATION OF SIMULATIONS

Ecosystem simulations are complex systems consisting of a number of
empirically derived formulas. These formulas are used to compute a number of
dependent variables in interlocking time steps, creating a nonlinear system.
The verification of the simulation is done by testing the individual formulas
against empirical data, checking the logical flow of the computations, and,
above all, with the use of sensitivity analysis.

The validation of ecosystem simulation is in essence the study of the
behavior of the system. Validation of the results could be made against the
resource survey data, if the latter were reliable. However, survey results
often have a very low accuracy. It is thought, however, that ecosystem
simulations could be validated more completely for lake ecosystems, where the
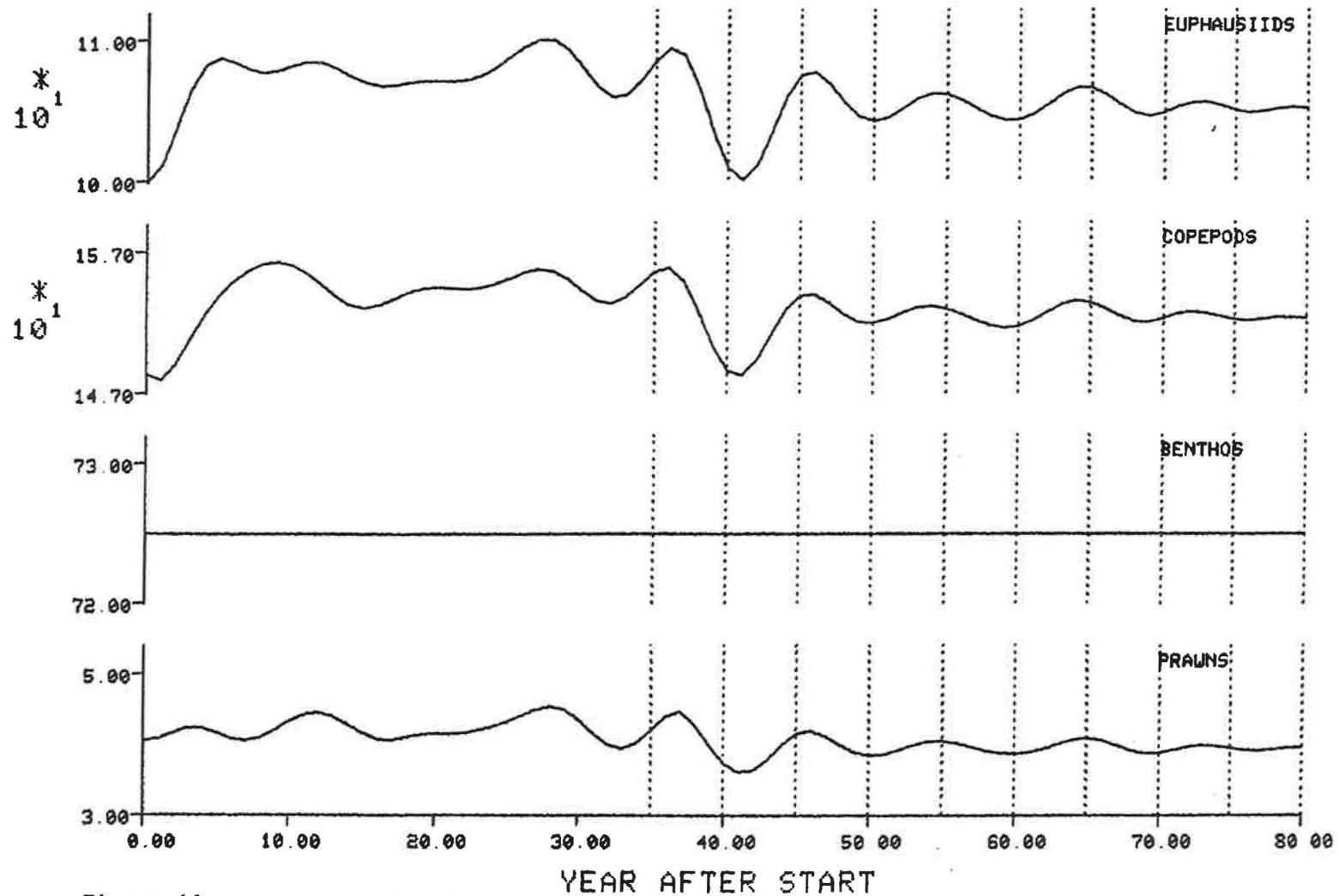pertinent data are often considerably better than for the oceans.

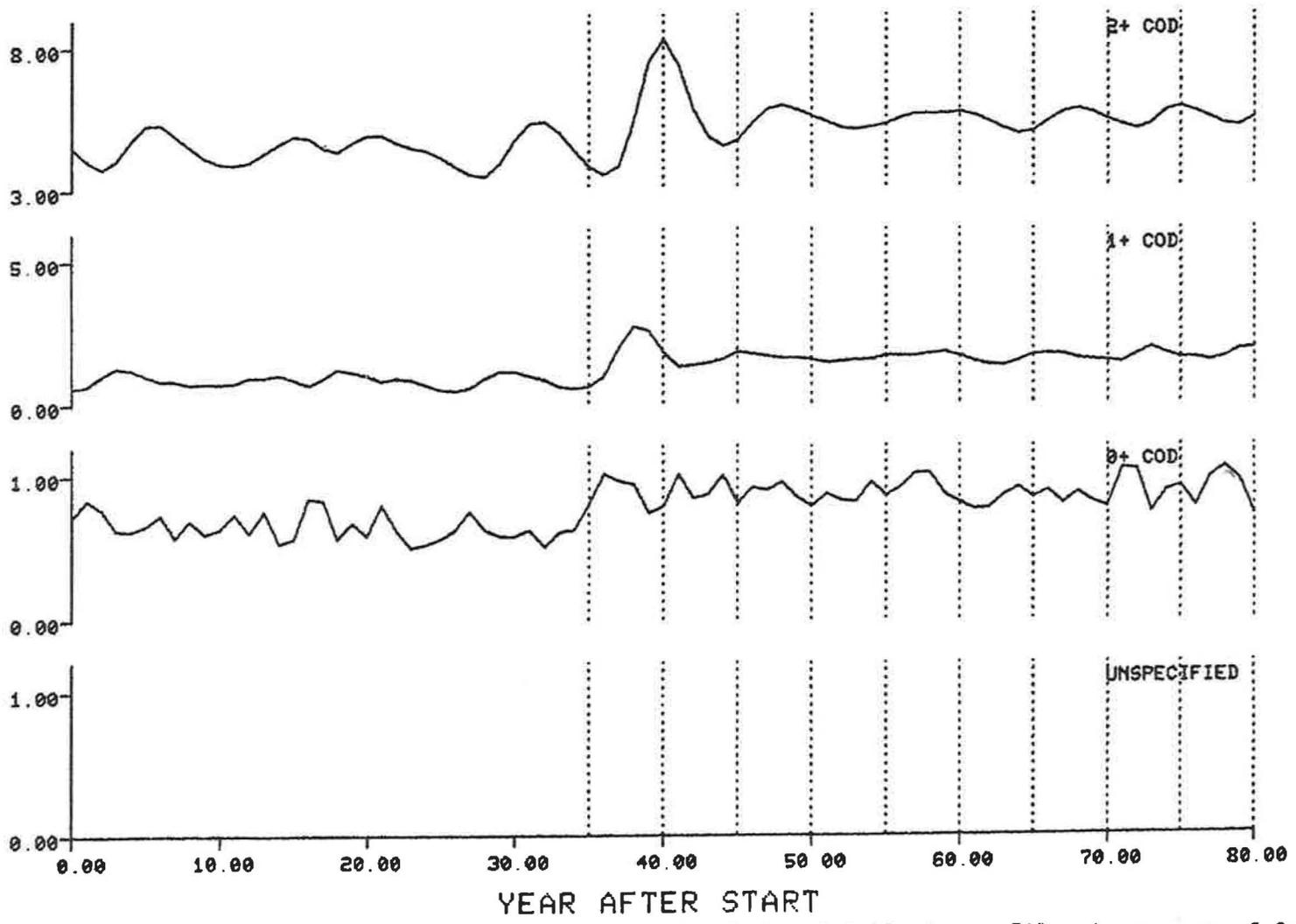Figure 11.--Response of cod population in Balsfjord to a 50% enhancement of 0+ cod in year 35.

Figure 12.--Response of some prey populations in Balsfjord following a 50% enhancement of 0+ cod in year 35.

Table 4.--Increased yield of cod to the fishery as proportion of initial
yield under different enhancement strategies for Balsfjord, Norway.
Enhancement set at 50% of initial zero cod biomass.

	Enhancement Strategy				
	Continuous	1/1*	2/2	5/5	10/10
Random recruitment	1.22	1.11	1.18	1.18	1.12
Constant recruitment	1.18	1.10	1.14	1.14	1.08

* years of recruitment/no recruitment

Sensitivity analysis.

Monte Carlo error analyses have been used to analyze the sensitivity of the ecosystem simulations to the input data. Individual species-specific parameters are perturbed randomly through a $\pm$ 10% triangular probability distribution and species-specific output variables recorded. In even the simplest ecosystem simulation over 100 input parameters and 50 output variables need to be studied. Principal components analyses have been used to reduce the analyses of output variables. When a good proportion of the total variance is explained by the first two principal components a GH' Biplot has been used to display sensitivity analysis results (Figs. 13 and 14) [1]. In these figures the length of each vector is proportional to the variance of the variable it describes (in principal component space) and the cosine of the angle between two vectors approximates the covariance of the variables they represent. In the sensitivity analysis of the Georges Bank ecosystem which is partially presented in Figs. 13 and 14, the first principal component represents the silver hake biomass and its predation on the rest of the ecosystem. The silver hake play a dominant role in this ecosystem.

When the principal components analysis fails to distinguish an appreciable proportion of the total variance onto the first two components, more components than can be represented by a GH' Biplot must be considered. This was the case for the Balsfjord simulation where many species had important, but independent, effects in the ecosystem (Table 5). In this instance the principal components were regressed against input parameters to determine those parameters with the greatest influence. Whereas analysis of individual species had indicated predation to be the most important process structuring individual species response, the principal components analysis grouped the starvation of many

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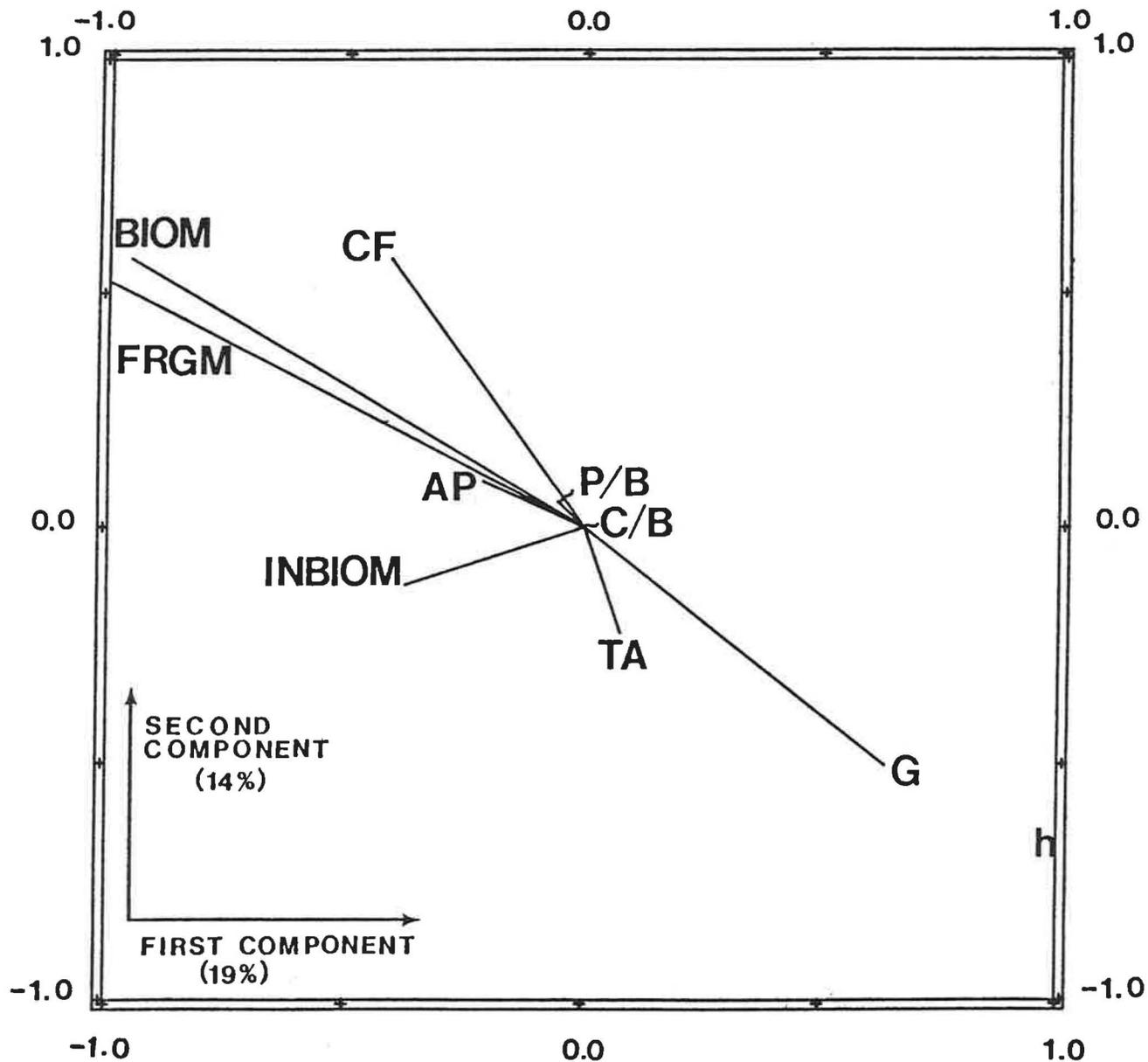[1] A list of variable names is provided in Table 6.

Figure 13.--Biplot of the sensitivity of silver hake output variables on the first two principal components of simulation output and of input parameters to which they were most sensitive. Parameters are defined in Table 6. Vector length is relative sensitivity, cosine of angle between vectors approximates their correlation.
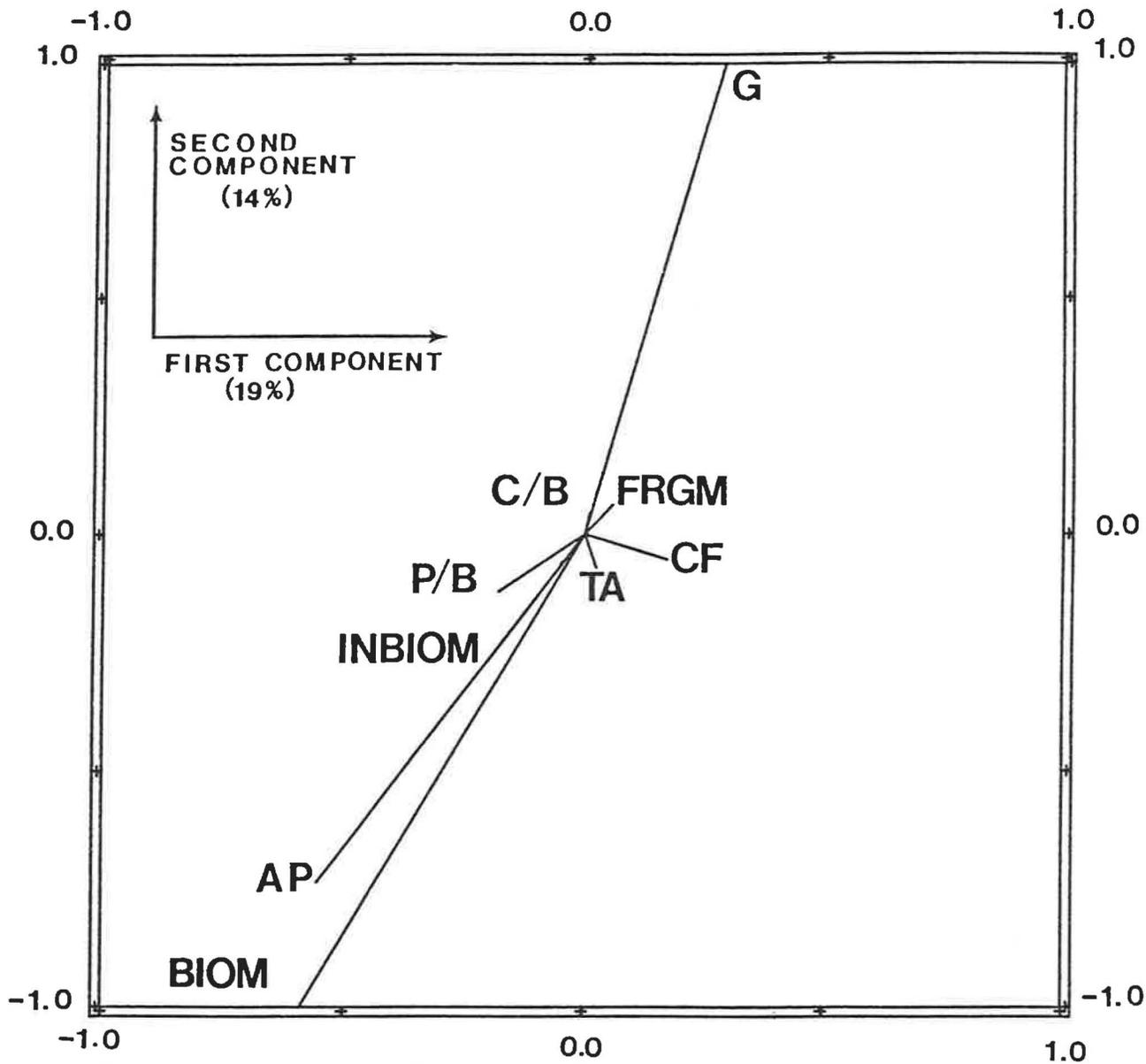
Figure 14.--Biplot of the sensitivities of flatfish group output variables on the first two principal components of simulation output and of input parameters to which they were most sensitive. Parameters are defined in Table 6. Vector length is relative sensitivity, cosine of angle between vectors approximates their correlation.

Table 5.--Principal components of a 2500 run error analysis of SKEBUB-Balsfjord. a) Output variables with largest loadings on each component, and b) input parameters with largest partial correlation from stepwise regression analysis.

Factor Description	1 Starvation	2 Copepods	3 Euphausiids/predation	4 Cod	5 Herring	6 Flatfish	7 Other fish
a) FACTOR LOADINGS OF OUTPUT VARIABLES							
Positive loadings[1]/	SCCAP SCHERR SCOTH SCPRWN SCFLAT bbeuph pcphyt	BBCOP PCPHYT scprwn	PCPRWN PCEUPH SCEUPH PCCAP BBCOD pcben pczoo bbprwn	SCCOD PCCOD bbeuph pcphyt	PCHERR BBHERR bbeuph	BBFLAT PCFLAT	PCOTH BBOTH
Negative loadings	PCZOO BBCAP BBCOD BBPRWN bbherr pcben pceuph sceuph bboth pccod	PCCOP SCCOP pcben pceuph	BBEUPH pcherr pcphyt scoth		bbcod pccap sceuph pceuph		
Proportion of variance explained by factor	0.24	0.14	0.13	0.08	0.07	0.06	0.06
b) ASSOCIATED INPUT PARAMETERS							
Positive independent variables [2]/	TAEUPH gcap apprwn apeuph gprwn frmflat tt	TACOP	TTU APPRWN geuph gcap tacop taherr vben	TACOD APCOD apprwn	TAHERR APPRWN APHERR gcod	APFLAT TAFLAT	APOTH TAOTH gprwn
Negative independent variables	tacap geuph taoth	TTU gcop taeuph frmcop	TAEUPH tacap gcod	GCOD ttu tacop	gherr ttu tacop gprwn	gflat tt	goth ttu
Coefficient of determination	0.49	0.88	0.75	0.84	0.79	0.93	0.88

1/ Loadings: uppercase > 0.50; lower case > 0.25

2/ Partial correlation coefficient: underlined > 0.50; uppercase > 0.10; lower case > 0.01,

Table 6.--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.

species onto the first principal component, indicating that from an ecosystem perspective starvation was the more important process. Reinforcing this conclusion was the sensitivity of the measured output variables to the temperature effects on growth (an important consideration in the northern latitudes where Balsfjord is located). The importance of multispecies analyses of these ecosystem simulations suggests the importance of multispecies analyses in investigating actual fishery ecosystems.

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