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Alaska
Fisheries Center**

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SUMMARY REPORT

**Workshop on Ecosystem Models for
Fisheries Assessment and
Management**

16 April to 11 May 1979

**Northwest and Alaska Fisheries Center
Seattle, Washington**

July 1979

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National Oceanic and Atmospheric Administration
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2725 Montlake Boulevard East
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1. INTRODUCTION AND GENERAL DISCUSSIONS

The Ecosystem Models Workshop was held in the Northwest and Alaska Fisheries Center in Seattle from 16 April to 11 May 1979. The main purposes and objectives of this workshop were:

- 1) To review the present state of the art of multispecies and ecosystem models for fisheries assessment and management.
- 2) To compare two existing models (Andersen and Ursin model - The Danish model, and the Laevastu and Favorite model - the NWAFC model).
- 3) To review all subject matter pertaining to fisheries ecosystem simulation and to suggest which processes are of primary importance to be included in the simulation models.

The main participants of the workshop (called collectively hereafter "the workshop") were: E. Ursin (Danish Fisheries and Marine Research), N. Daan (Netherlands Institute for Fisheries Investigation), T. Laevastu and P. Livingston (NWAFC, Seattle), E. Henderson and E. Cohen (NEFC, Woods Hole), and J. Burdine (Marine Mammals Laboratory, Seattle). In addition, other scientists from NWAFC (F. Favorite and others) participated in the sessions of various subject matters.

It was recognized by the workshop that the conventional single species population dynamics models are no longer adequate for solving many present problems of stock assessment and fisheries management. The single species models lack the interspecies interactions (mainly through food dependence). On the other hand, the multispecies and ecosystem models take the trophodynamics quantitatively into consideration. Furthermore, it was recognized that the terms models and simulations, as well as multispecies models and simulation models, can be considered as synonyms.

It was also suggested that multispecies models should not entirely replace the single species models. The latter often provide input data for the former. If a given problem can be solved with single species consideration, then the single species model should be used, provided that proper evaluation of adequacy is made and the limitations recorded.

The workshop noticed that the number of ecosystem models is increasing and that it is difficult to follow all of them in detail. It was considered preferable to document the essentials of the models in somewhat simplified form to enhance the review and evaluation. Therefore, the skeleton forms of both models (the Danish and the NWAFC Bulk Biomass model (BBM)) were prepared and given in the appendices of this report.

The major part of the workshop time was spent in detailed scrutiny of the BBM model and its scientific background, suggesting possible modifications for future testing. The DYNUMES and Danish models were dealt with only in a comparative manner, in hopes of studying their details in future workshops

As trophodynamics play a central role in the ecosystem models, recommendations for proper fish food studies were made. Furthermore, different numerical experiments with size dependent feeding were recommended.

The ecosystem models require a great variety of data, some of which are scarce in the literature. Furthermore, emphasis is often put on some data which were not considered essential in past fisheries research. It was, therefore, suggested that the reorientation of fisheries data needs could be discussed in a larger meeting of fisheries scientists in the future.

The workshop considered a follow up of the present workshop essential, both for furthering the science and technology of the subject matter, and for promoting the application of the models in research guidance and in fisheries management. Dr. Daan promised to explore the possibilities of holding the next ecosystem models workshop in the Netherlands.

2. DISCUSSIONS OF BASIC PROCESSES IN THE ECOSYSTEM MODELS

The energy based ecosystem models were considered not fully adequate as the necessary conversions to numbers and/or biomass is quite uncertain due to lack of proper data on caloric values. The number based models (e.g. the Danish model) follow to a large extent the conventional single species approaches and the outputs are easy to understand with conventional thinking. Furthermore, these models usually have a strictly defined mathematical background. On the other hand, the biomass based models (e.g. the NWAFC models) require some rethinking in different terms than customary in the past (e.g. the presentation of recruitment). They are mathematically less rigorous, requiring local simulations and considerable personal interactions, and are difficult to describe in mathematical terms (except in discrete, time stepping finite difference forms). The multi-habitat, multi-layer approach is essential in both types of models (the Danish and NWAFC models).

All existing ecosystem models require simplifications in presentation (description) to make them understandable and acceptable to a wider circle of users.

2.1 Growth

Growth rates are computed from empirical weight-age data. However, these data on juveniles, specially in the first and second years of life, are scarce and/or deficient in all species. Considerable year-to-year variations in growth rate could occur. Thus it is desirable to obtain better empirical data on this subject.

In biomass based models the growth coefficient of the biomass of any species is dependent on growth rate at any given age interval and the relative abundance (fraction) of biomass in this age interval. Thus the growth coefficient should vary (with trophic and environmental effects) also with the variation of recruitment and fishery

(i.e. with factors affecting the age distribution of biomass). Thus it is desirable to account for the age distribution change either by dividing the species into several age groups or by computing the age distribution with another model (or subroutine). This problem is of interest to some management approaches due to changes resulting from rejuvenation of populations (re. Dementjeva) due to fishery.

The empirical knowledge of distribution of numbers (and/or biomass) of fish in prefishery juveniles is lacking in all species. This applies also to age variable mortality rates at these younger ages. Thus any studies which provide knowledge in these areas (i.e. changes of numbers and mortalities in prefishery juveniles) are most desirable.

The effects of water temperature on growth are treated in the models according to best available knowledge. However, there is very little empirical data available on acclimatization of different species to different temperature ranges.

The effects of the availability of food and related partial starvation on growth is treated in a manner consistent with available knowledge. However, no special studies (using model outputs) have been conducted on this matter. It was suggested that this matter be discussed further in the next workshop.

In some species the seasonal changes of growth are not fully in phase with temperature and/or availability of food. In these cases it was suggested to simulate the known seasonal variation with a harmonic formula (see Appendices 2 and 3).

2.2 Trophodynamics

Although both models can partition the food requirement (and utilization) between growth and maintenance, it was considered that additional data (and research) would be desirable on the seasonal change of feeding rates, specially in pelagic species.

Although the temporal dependence of feeding rate (and food uptake) on food density is simulated in the Danish and NWAFC's BBM models, the simulation of the spatial food density dependence is possible only in gridded models such as the DYNUMES model.

The size-dependent feeding must be used in all realistic fishery-oriented ecosystem simulation models. It was suggested that attempts be made to introduce a vulnerability index into biomass based models instead of food preference indices (via mean food composition).

The fundamental differences between single species models and ecosystem models is that predation (and trophodynamics in general) is included in the latter, thus quantitatively connecting the dynamics of all species in the ecosystem. Trophodynamics forms a basis for modern fish stock assessment methods. However, good quantitative fish food and feeding habit studies are rare (example of an excellent study is the cod study by Daan). It was recommended that good quantitative fish food studies be promoted in all areas.

2.3 Distribution of biomass with age

Detailed, direct knowledge (and evidence) of the distribution of numbers (and biomasses) of prefishery juveniles is lacking in all species. The models with age-constant mortality coefficients were considered unrealistic for computation of the number distributions of juveniles. It was recommended that any direct and indirect means be explored for furthering knowledge on the number and biomass distribution in prefishery juveniles and on the age-dependent mortalities.

Changes in relative age and size composition occur in all species, from a variety of causes (e.g. variation in recruitment, fishery, etc.) which in return induce other changes in the ecosystem and its dynamics (e.g. with reference to size-dependent feeding). It is imperative that the models compute the biomass

and/or number distribution as caused by a variety of known factors. It was suggested that this subject (together with results from prospective studies of the dynamics and consequences of time dependent changes in age composition of species biomasses) be discussed more fully during the next workshop.

The effects of different spatial distribution of juveniles and adults on e.g. predation can be simulated only in gridded models such as DYNUMES.

The turnover rates of most fish biomasses can be computed with BBM (and other) models. However, more data (empirical or theoretical) on annual turnover rates of zooplankton and benthos would be highly desirable from ecologically different locations (regions). These latter data are especially needed for more accurate determination of carrying capacities of different regions.

2.4 Effects of fishery

The fishery causes changes in age composition of the target species. These changes are computed directly in the Danish model where all species are divided into a number of age groups. In NWAFC models only one or two species at a time are at present divided into different age groups. In non-divided species, the changes in age composition must be depicted in a number of parameters, notably in biomass growth rate. These age (size) composition dependent changes must also be depicted in trophodynamics (re. size dependent feeding, composition of food, etc.).

In the species where schooling is pronounced, the fishery should be computed as constant catch in time (i.e. the fishing mortality coefficient must be adjusted each time step). This approach could also be used to demonstrate quantitatively the manner of "crash" (collapse) of pelagic stocks.

It was considered desirable to investigate numerically the effects of seasonally varying fishery on the biomass of the target species. During the workshop it was demonstrated numerically that the annual difference in catches is not proportional to the difference in the change of biomass of the species, but the latter can be

many times greater (e.g. 400 kg/km^2 annual increase of yield might result in 1200 kg/km^2 decrease of biomass).

Spawning stress mortality was first introduced into Danish model and is now used in the NWAFC models. There is a nonlinear interaction between fishing mortality—constant over fully exploited year classes, and spawning stress mortality—increasing ca 10% per year. Thus it was felt that it would be desirable to compute numerical examples of the interactions of fishery and spawning stress mortalities for different species with different number of year classes in exploitable stock.

It was furthermore felt that the present and future data from commercial catch sampling (e.g. length-age-frequency data) might not be fully comparable with data from earlier years when fishery was less regulated than at present.

2.5 Mortalities

Several recent investigations show an age dependent spawning stress mortality, without providing absolute proof of it. This age dependent mortality may also be thought as being caused by decreased vulnerability to gear in larger fish and/or emigration of larger (older) fish into deeper water. It was found desirable that more basic research be conducted on spawning stress mortality (and/or age dependent senescent mortality) in a variety of species; specially observations on spawning grounds would be especially desirable.

Mean (natural) mortality coefficient was considered unrealistic for any species. The greatest component of the "natural mortality" in juveniles is the predation mortality. Both models compute it at least partially as age (size) dependent predation mortality (re. size dependent predation). However, it was felt that there is a further need to study and describe age dependent mortality in all species by various means (drafts of two related studies were available to the workshop).

Exceptionally cold winters are known to cause additional mortality in many species. Furthermore, severe starvation might be expected to cause additional mortality in fish. It was found desirable to summarize all quantitative observations in these subjects.

The predation mortality must be quantitatively limited (density dependent) when the density of prey becomes low. In the Danish model it is limited indirectly via vulnerability coefficient. In the NWAFC biomass based model it is limited by two factors: a) a prescribed monthly maximum percent of biomass allowed to be consumed, and b) with a predation level factor (\bar{B}/B_t - equilibrium biomass/actual biomass).

The effects of spatially and seasonally changing predator-prey distributions on the predation rates can be included (and studied) only in models with spatial resolution (such as DYNUMES).

It was found desirable to summarize all available quantitative observations on disease mortalities. Furthermore, the possible range of errors in mortality coefficients should be studied (and reported on in the next workshop).

3. DISCUSSIONS OF FULLY MODEL DEPENDENT SUBJECTS

3.1 Types of grids and initial analysis

The gridded models such as DYNUMES have several advantages, allowing the presentation of space resolution, migrations, differences in space and time of predator-prey relations, etc. On the other hand, these gridded models are expensive in set up and in computer core and time requirements. The "box models" (e.g. Danish model and NWAFC's BBM and PROBUB models) are sufficient for many fisheries research and management problems. The computations in these models are done either in mass and/or number units per unit area or per total box area.

Whereas the Danish model takes initial input from various available assessments, the DYNAMES model needs the initial analysis of input biomasses. This initial analysis consists of computing a unique solution to the biomass equations with predetermined food composition and food requirements using BBM or PROBUB models. With this approach the mean carrying capacity (and/or equilibrium biomasses) can be computed.

The ecosystem models require that all the components of its biota be presented quantitatively in the simulation. This presentation is not always possible by species, but by groups of species. Feeding habits and food composition are recommended as the main criteria for grouping of species.

Use can be made of quantitative exploratory fishery survey data in biomass based models for initial input (spatial analysis). However, these survey data must be first converted to total biomass. For this conversion vulnerability (to gear) coefficients and availability coefficients are needed.

It was suggested that the types of outputs taken from the models be presented in the form similar to conventional fisheries data in order to make comparison easier. Obviously there is no limitation of taking (outputting) of any specific data pertinent to special studies.

3.2 Data inputs

The input data for the Danish model and for the NWAFC models are considerably different. These differences are partly dependent on the type of model, but initially (in the model designing stage) caused by the differences in availability of data. This pertains also to derived (indirect) data, such as various coefficients and rates. Due to differences in the ecosystems per se, different geographic locations, and especially due to the nature (emphasis) and intensity of past fisheries research, the ecosystems simulations must often be designed differently depending on available data. However, it was felt that wherever possible some conversion factors and methods should be derived for making general fisheries data quantitatively comparable.

Ecosystem models require more and different data than conventional single species models. Thus there will be a reorientation of fisheries data collection in the future, when ecosystem models come more into use. Thus the fisheries data collection reorientation should be discussed in larger groups with diverse fisheries research backgrounds.

The use of environmental data (and anomalies) in the ecosystem model was discussed and emphasized in the areas where seasonal anomalies can be large (e.g. in the Bering Sea).

3.3 Migrations

The migrations in box models can be described as "boundary values" - i.e. the fluxes through the boundaries. Growths and mortalities outside the boxes cannot be computed. The migrations are treated in detail in gridded models, provided some prior information on migrations is available. Furthermore, the dispersal, aggregation, and passive transport by currents is computed in gridded models such as DYNUMES.

The workshop considered that it would be desirable to develop special migration submodels which can be fitted to existing ecosystem models. It was suggested that the problems of migration be discussed in greater detail in another workshop.

3.4 Reproduction, recruitment

The accuracy of the prognoses of the fisheries resources is largely dependent on recruitment. However, the processes controlling the recruitment are quantitatively poorly known. Considerable time and effort of the workshop was spent in discussing recruitment problems and the modeling of this process.

In the Danish number based model the spawning products are released in a given month of spawning. The number of larvae surviving is controlled by an empirical formulation which allows lower survival at high number of spawners and high survival at low number of spawners.

In the present NWAFC biomass based model the recruitment is a function of biomass size and of the growth coefficient of the biomass. If a given species under special study is divided into a number of age groups, then the recruitment is a function of the biomass of the older (sexually mature) age group. Although discrete spawning season can be simulated in biomass based models, it has been found convenient to consider recruitment as a continuous process, as the spawning of most species in the Bering Sea covers a period of three to five months. Furthermore, the eggs when released are considered as a part of the zooplankton and they (and the larvae) are consumed during the first few months at the same rate as zooplankton. The early recruitment to the biomass of the species is assumed to occur at the age of four to six months. Thereafter the recruitment is largely controlled by predation by other ecosystem components as well. The recruitment level is controlled by modifying growth coefficient, making it inversely proportional to biomass level (B_t/\bar{B} -- actual biomass/equilibrium biomass; and $\sqrt{B_t/\bar{B}}$).

Several suggestions were made for experimentation with recruitment modeling, which included the separation of each biomass into two age groups.

It was generally concluded that the recruitment (in all prefishery age levels) remains one of the important problems to be solved in fisheries research. It was also felt that the year class strengths might be determined by predation on larvae and juveniles rather than by early survival of larvae.

4. PLANKTON AND BENTHOS IN FISHERIES ECOSYSTEMS

Several ecosystem models deal exclusively with plankton production. The attempts to compute fishery production exclusively from plankton production have, however, not been successful in the past, mainly because the pathways of

plankton utilization are diverse and greatly variable in space and time. One of the main tasks of the fisheries oriented ecosystem models is to determine quantitatively the species composition of the ecosystem and the resulting utilization of available food resources. Consequently the fisheries oriented ecosystem models also need as input the standing crops and/or production of plankton and benthos.

The standing crop data of zooplankton is simulated on the basis of available empirical data. The consumption of zooplankton is computed in detail in the ecosystem models. However, there is in general a lack of data on turnover rates of zooplankton, which is needed for determination of carrying capacity.

Furthermore, the workshop concluded that there is a lack of quantitative data on the predators in the zooplankton, such as jellyfish, ctenophores, and chaetognaths which might be important competitors and even predators on small fish larvae. Furthermore, little is known on squids as predators of zooplankton and fish larvae.

Standing crop of benthos is usually simulated in ecosystem models as a function of depth and type of bottom. The knowledge on the turnover rate (re production) of benthos is also poor.

5. VERIFICATION AND VALIDATION

The sensitivity analysis, verification, and validation of large ecosystem models pose many problems which have not been attacked by conventional means in the past. First, it was suggested that the ecosystem models be described in the manner and form in which they would be understandable to a wider group of fellow scientists. This would enhance the verification of the models. Beginning of this task is made with the skeleton models given in the appendices of this report. Detailed descriptions and documentations of the computerized models should be available upon request.

The error limits of the outputs can be estimated, in some cases, by considering the possible error limits in the input data and the formulas used in the model where these inputs are used as parameters. This will also lead to verification of the results of individual processes.

It was considered desirable to estimate the accuracy and confidence limits of various outputs by different means. Furthermore, special numerical studies could be made of some new approaches used in the models, such as dampening of errors in recruitment.

It was specially recommended that some of the model output be tailored to produce data which can be validated with conventional fisheries data. Obviously new research approaches must also be designed to validate several aspects of ecosystem processes and results thereof.

Appendix 1

A Multispecies Fish Stock Assessment Model

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Abstract. The basic framework of the Danish multispecies model (the North Sea model) is described in mathematical terms with emphasis on why these terms were chosen. The full model (Andersen and Ursin, Meddr Danm. Fisk.- og Havunders., NS, 7: 319-435) is complicated and difficult to take in during a single lecture. When computerized, the basic structure described in the lecture behaves like a 'generalized' sea with four species behaving too rigidly to be identified with any particular animal species.

Introduction

=====

The model is primarily a multispecies extension to the Beverton and Holt (1957) fishery model. When complete it also describes primary production as a function of sunlight and nutrient concentration in the water. It keeps account of nutrient transfer from water to plant to animal; from one animal to another; from animal to dead organic matter; from animal and dead organic matter back into inorganic nutrient in the water. It also traces biomass transfer in such a way that consumption equals predation.

The model can be implemented as a closed box or with an exchange of matter with the surrounding environment (the ocean, rivers). It can be set up as a simple box or as a set of two or more boxes with migrations across box borders.

The model is basically analytical, but some empirical relations had to be introduced to cover problems for which no analytical solution can be offered. The advantage of the analytical model above the purely empirical one is that you can make use of not quantifiable information whereas the empirical model utilizes one particular set of data. For instance, if all you know about the food of herring is that it has been ascertained in an extensive investigation that 50 pct of adult herring's food is crustacean plankton weighing less than 2 mg, then you can adjust the appropriate parameter values of an analytical model in such a way that the herring of the model feed in accordance with this information. An awkward effect of this is that the number of degrees of freedom for parameter estimation is not defined. The parameters can be counted, but the number of observations is a misty quantity. You have in fact included your own indefinable 'fund of knowledge of marine life'.

An impressive example of the purely empirical approach is the paper by Lett and Kohler (1976) on herring and mackerel interaction in the Gulf of St. Lawrence. Such an approach is good when the data are good. Most data sets on marine fish stocks are defective because of excessive variance and a multitude of bias.

The entire model (Andersen and Ursin, 1977) with all its details and embroilings is quite complicated. However, the first draft of the model which was distributed privately in 1971 is simple and remained the basic framework of the final model. It was used by Beyer and Lassen (1975) and Lasser (1978) to describe in general terms the biological effects of synthetic pollutants in the North Sea and is referred to by Andersen and Ursin (1977, paragraph 5) as 'a reduced model for rapid computation'.

This skeleton model can be compared to a picture of a man drawn with such bold and simple strokes that anyone can see that it is a man, but not which one. This is a picture of a sea with some species in it. Nobody knows which sea or which species. It was not published in 1971 because the authors feared adding to the pile of ecosystem models which never reach the stage of applic-

ation to practical problems.

Model Structure =====

Species Interaction and Beverton and Holt -----

We shall first specify the problem by writing the three basic differential equations of the Beverton and Holt singlespecies assessment model upon which most advice on fishery regulation in Europe is based today. These equations describe mortality, growth and yield, respectively.

Let t be time, w the body weight, N the number of fish in one year class, Y the accumulating yield, and F and M the fishing and natural mortality coefficients:-

$$dN/dt = - (F + M) N(t) \quad (1)$$

$$dw/dt = H w(t)^{2/3} - k w(t) \quad (2)$$

$$dY/dt = F N(t) w(t) \quad (3)$$

F , M , H and k (and the powers of weight) are parameters. N , w and Y are variables. They are functions of time. We want to put species indices on all these quantities and to establish species interaction by introducing a functional relationship between the mortality and food consumption because consumed animals and plants die. The actual parameters involved are the natural mortality parameter M , and the coefficient H of the positive term of the growth equation. For H to be positive there must be something to consume. H must therefore be developed as a function of food consumption, and so must M .

To achieve the goal we introduce a fourth differential equation describing the food consumption of an individual fish. Let R be the accumulating food consumed:-

$$dR/dt = f(t) h w(t)^{2/3} \quad 0 \leq f \leq 1 \quad (4)$$

The similarity with the first term of the growth equation is deliberate. The coefficient h is a parameter. The coefficient f is called the feeding level and is a variable. If the fish gets everything it can eat we put $f = 1$. If it gets a fraction of what it can eat, the fraction is f . If it gets nothing at all we have $f = 0$. As shown below, the feeding level is not a function of time only, but also of all the N 's and w 's in the system. Assume now that only the fraction v of the food consumed is actually assimilated and available for growth and basic metabolism. This fraction is the positive term of the growth equation, eq (2). In other words:-

$$H = v f(t) h \quad (5)$$

The Feeding Level -----

The next problem is to determine f as a function of available food, ϕ . (The notation of Andersen and Ursin, 1977, is adopted except that greek letters are spelled out for technical reasons). we choose a simple hyperbolic expression:-

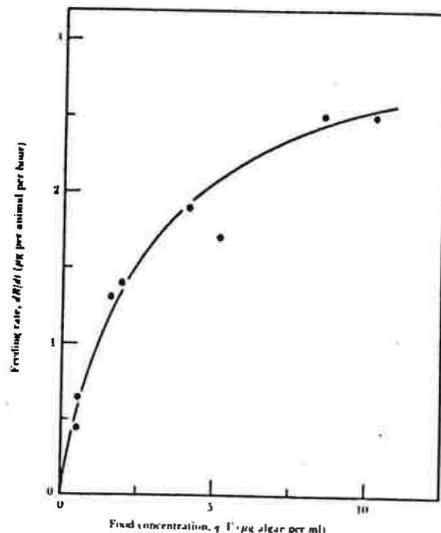


Fig 1

$$f := \phi / (\phi + Q)$$

(6)

where Q is a parameter of the 'half saturation constant' type. Note that Q is a large quantity because eq (6) is not divided through by the volume of the sea investigated. By this formulation we express that the feeding level increases with increasing food concentration, rapidly at low concentrations and towards an asymptote of $f = 1$ for high concentrations. An application to data for a cladoceran is illustrated in Fig 1. This curve can be derived analytically, based on assumptions on the rate of search for food and the rate of food consumption (Andersen and Ursin, 1977).

So far so good, but we must also describe the available food, ϕ . To a first approximation ϕ can be the biomass of all animals and plants in the sea. Let the index i indicate the predator and the index j the prey. Brackets in the expression below indicate, that this is not the final formulation. The contribution of each category of prey becomes $(\phi_{i,j}) = N_j w_j$ and we get:-

$$(\phi_i) = \sum_j (\phi_{i,j}) = \sum_j N_j w_j$$

But this will not do. Suppose that i (the predators) are one year old herring and j (the prey) three years old cod. Three years old cod are not food for one year old herring. They are too big. It is necessary to introduce a coefficient g indicating the suitability of j as food for i :-

$$\phi_{i,j} := g_{ij} N_j w_j$$

$$\phi_i = \sum_j \phi_{i,j} = \sum_j g_{ij} N_j w_j \quad 0 \leq g \leq 1 \quad (7)$$

For $g = 1$ we count all of j 's biomass as food for i . For $g = 0$ we count j out entirely. Else, we count the fraction g of j 's biomass as food available to i .

Another coefficient could be introduced to ascertain for instance, that pelagic animals eat other pelagic animals only, but such embroiderings are not our purpose in this short overview.

Predator/Prey Size Ratio

The solution of one problem creates the next. We must describe g as a function of predator size and prey size. When the model was formulated in 1971 very little was known about prey size preferences of fish or other marine animals. We made the assumptions (1) that there exists a preferred prey size, (2) that the ratio predator/prey weight remains the same through a predator's lifetime and, (3) that a prey twice the preferred size is as acceptable as a prey half the preferred size.

These assumptions lead to the conclusion that values of the coefficient g are log normally distributed about the logarithm η of the preferred predator/prey size ratio. Except for one thing: we want to adjust the curve to a maximum value of one instead of adjusting to an area one under the curve. We are therefore not dealing with probabilities of a log normal distribution. Denoting the standard deviation by σ we have:-

$$g_{ij} = \exp\left(-\frac{(\ln(w_i/w_j) - \eta)^2}{2\sigma^2}\right)$$

$$= \exp(-\gamma(\ln w_i - \ln w_j - \eta)^2) \quad (8)$$

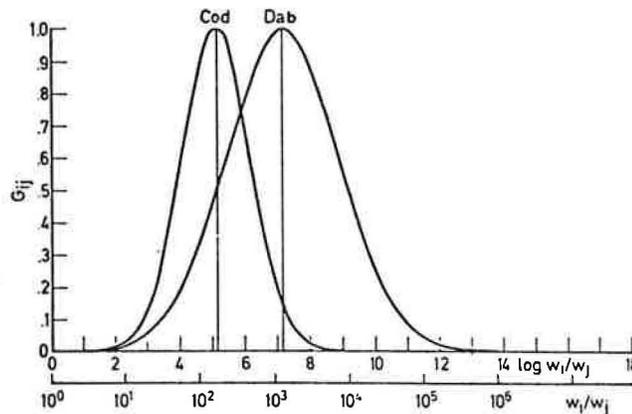


Fig 2

where the parameter γ is introduced to simplify the expression. In the present skeleton model η and σ are, unrealistically, treated as universal constants. The parameters were estimated for two fish species (Ursin, 1973) and there was found a fair agreement with available data which were - and remain - few. The shapes of the curves are shown in Fig 2. Fenchel (1975) independently developed a similar model for the food item selection of proscobranchs of the genus *Hydrobia*. Discrepancies from the expected curve are discussed by Ursin (1973) and Agger and Ursin (1977), but the hypothesis is retained so far.

The Relation of Consumption to Mortality

This brings us to the end of the description of food consumption and we realize that the total consumption by all animals in the ecosystem is:-

$$\sum_i N_i \frac{dR_i}{dt} = \sum_i N_i f_i h_i w_i^{2/3}$$

and that this is the quantity which must be expressed differently to describe predation mortality. Introducing a predation mortality coefficient M_2 we must have, in order to retain the mass balance within the system:-

$$\sum_j M_2 N_j w_j = \sum_i N_i f_i h_i w_i^{2/3} \quad (9)$$

That is, the total predation mortality of all prey j equals the total consumption by all predators i . What is needed is an expression for the individual predation mortality coefficient M_2 of prey j as developed below.

Mortality in General

The original expression, eq (1), for the change in numbers is:-

$$dN/dt = - (F + M) N(t).$$

M must be partitioned into predation mortality M_2 and residual natural mortality M_1 so that we have:-

$$dN/dt = - (F + M_1 + M_2) N(t).$$

One kind of residual mortality namely, the density dependent mortality of young fish, is here dealt with in a different way, by transferring it to the moment of hatching (see below). The remaining M_1 mortality, whichever its causes, is treated as a constant: M_1 remains a parameter just like the M (for adult fish) of Beverton and Holt, whereas density dependent mortality and predation mortality must be developed as functions of some new parameters. This warrants the more detailed treatment of these mortalities below.

Predation Mortality

The coefficient M_2 of predation mortality is the limit of the ratio of the amount consumed (in a time interval) over biomass when the time interval decreases towards zero. To find the amount consumed we write first the sum of everything consumed by all predators i :-

$$\sum_i (dR_i/dt) N_i.$$

The food available to each predator is defined above in eq (5) and denoted ϕ_i . One part, ϕ_{ij} , of ϕ_i consists of the prey j in which we are interested. The fraction of j in the food available to i is ϕ_{ij}/ϕ_i . The predator i is eating indiscriminately out of its available food resources because the discrimination is already accounted for by the factors g in the expression for available food. The consumed food of i contains the same fraction of j as the available food. Therefore, j 's losses due to all kinds of predation are:-

$$\sum_i (\phi_{ij}/\phi_i) N_i dR_i/dt.$$

Dividing by the biomass of j we have M_2 directly because using infinitesimal notation it is not necessary to bother about limiting values:-

$$M2_j = \sum_i ((\rho h_{i,j} / \rho h_{i,i}) N_i \alpha R_i / dt) / (N_j w_j) \quad (10)$$

Summing over j gives the identity formulated in the previous paragraph, eq (8). Perhaps it ought to be mentioned that i and j were used differently by Andersen and Ursin (1977).

Density Dependent Mortality

Density dependent mortality of young fish is necessary in the model. With recruitment proportional to mature biomass the model is not stable: numbers increase continually, feeding levels decrease and mean weights of age groups decrease accordingly.

The simplest way of introducing density dependent mortality is by letting it reduce egg numbers. Eggs are hatched immediately in the model. With E the number of eggs spawned we express the number E1 of hatched eggs as:-

$$E1 = E (C / (C + E)) \quad (11)$$

where C is a species specific parameter and C/(C + E) is the fraction hatched. The expression can be derived from the model described in paragraph 6.1.4 of Beverton and Holt (1957) by putting density independent mortality to zero, but it can also be considered an empirical relationship with the effect of making the probability of hatching inversely related to egg production.

The expression stabilizes the model so that, eventually, a stationary solution is reached. In the steady state the same stock composition is observed every year on the same date. Which steady state is reached depends upon the choice of parameter values and is independent of the starting values of numbers and body weights.

This simple model of density dependent mortality gives an unrealistic description of the food consumption of fish larvae because too many are killed before they start feeding. As pointed out by Jones (1978) the larval food consumption amounts to a considerable fraction of the total food consumption of the stock. To describe this realistically, a more elaborate model of density dependent mortality is called for (Andersen and Ursin, 1977, Appendix).

Spawning

In order to retain the age group concept of Beverton and Holt it is necessary to introduce momentaneous spawning at fixed time intervals at which the mature age groups loose a fraction pi of their weight. This biomass is divided by the weight omega of one egg to give the egg number E from which the number hatched, E1, is calculated as described above. The E1 larvae form the youngest age group. The older groups move one step up the age group ladder. The oldest age group contains after spawning the same animals as before, but with members of the oldest-but-one added. Body weight of the oldest age group is recalculated accordingly, see below.

The Model Set-Up

=====

Species Structure and Starting Values

The model is here described with 4 species a, b, c and d, and with halfyearly discontinuity points to permit spawning. The system is open for introduction of matter through species a of which a constant amount is added at the beginning of each halfyear. Exit from the system is through faeces, metabolism (combustion), unspecified M1 mortality, density dependent egg mortality and fishing.

Species a does not eat, does not metabolize and does not propagate. It is of no consequence how much is left at the end of a halfyear: the losses in that halfyear are replaced at the beginning of the next. This simulates an annual phytoplankton or zooplankton cycle with a spring maximum and an autumn maximum.

Species b, c and d eat, are eaten, metabolize, die from unspecified (M1) causes and propagate at the discontinuity points, with a density dependent egg mortality.

Species b spawns twice every year, beginning when one year old. It is a small animal as for instance a euphausiid. Species c spawns in the autumn, beginning when two years old. It can be visualized as a small clupeid. Species d spawns in the spring and begins when three years old. It can be visualized as a medium sized gadoid fish.

We start the computation in the autumn when species c has just spawned, and use the initial data set (state vector of numbers and body weights) listed in Table 1. Note the 'empty' entities nos. 6, 9, 11 and 13 for species c and c which spawn only once a year. Yields are put to zero at the beginning of the computation (and at every discontinuity point) and therefore do not figure in Table 1.

Parameter Values

Some parameters are handled as universal constants. They are:-

1. the fraction assimilated of food ingested. The v of eq (5); $\approx .4$
2. the prey size preference parameters of eq (8): $\eta = \sigma = \ln 100 = 4.60517$ from which $\gamma = .10857$;
3. the half saturation constant of eq (6): $Q = 50\ 000$;
4. the fraction of mature biomass spawned: $\rho = .2$;
5. the residual natural mortality: $M1 = .1$.

Other parameters must be handled as species specific, or the model would not make sense. Their purpose is to create animals of different body size and different stock size. They are the coefficient of food consumption h , eq (4), the coefficient k of the negative term of the growth equation, eq (2), the egg size ω , and the recruitment parameter C of eq (11). The values used are listed in Table 2. For species a there are two parameters only, the constant body size, $w = .001$ g, and the input at

the beginning of each halfyear, $N = 1\ 000\ 000\ 000$.

Table 1. Initial arbitrary data set.

Species and entity	Age years	h	k	ω grams
a	1	0	1 000 000 000	.001
b	2	0	40 000	.01
	3	.5	10 000	.25
	4	1.0+	10 000	1.00
c	5	0	1 000 000	.02
	6	.5	none	
	7	1.0	100	25.00
	8	1.5+	100	40.00
d	9	0	none	
	10	.5	1 000	3.00
	11	1.0	none	
	12	1.5	2	42.50
	13	2.0	none	
	14	2.5+	1	250.00

Table 2. Species specific parameter values.

Species	h 1/year	k 1/year	ω grams	C
b	10	2.50	.01	2 000 000
c	18	1.75	.02	10 000
d	35	.40	.05	2

Eggs are made very big in order to speed up the numerical integration which has to be performed in short steps for small values of w . The relative growth rates of very young animals are unrealistically high in the growth equation used.

The fishing mortality coefficients are as follows:-

$$F_1 = F_2 = \dots = F_{12} = 0$$

$$F_3 = F_7 = 1 \quad \text{Heavy 'young clupeid' fishery.}$$

$$F_9 = .2 \quad \text{Modest 'adult clupeid' fishery.}$$

$$F_4 = F_{10} = \dots = F_{12} = 0$$

$$F_{14} = .5 \quad \text{Medium fishery for 'adult gadoids'.$$

The Differential Equations

The task is to integrate the following equations:-

$$dN_i/dt = - (M1 + M2_i + F_i) N_i \quad i = 1, \dots, 14$$

$$dw_i/dt = v f_i h_i w_i^{2/3} - k_i w_i \quad i = 2, \dots, 14$$

$$dY_i/dt = F_i N_i w_i \quad i = 1, \dots, 14$$

Not counting the 'empty' index numbers this amounts to the simultaneous numerical integration of 28 first order differential equations. At first sight the task is extremely simple, but for each step it is necessary to evaluate f_i and $M2_i$ according to the descriptions in eqs 4, 6, 7, 8, and 10, which is a time consuming process.

The integration can be performed by simply adding to current values of N , w and Y the values of the differential quotients as evaluated for, e. g., one week at a time. A fourth order Runge-Kutta procedure obtains the same accuracy faster.

The Discontinuity Points

The processes of spawning and moving the age groups one step up the ladder are exemplified below by species b (indices 2, 3 and 4). We designate by $N(2,bef)$ and $N(2,aft)$ the numbers in entity 2 before and after spawning, and similarly for the other entities and for weights.

The number of eggs is the biomass times the fraction spawned, divided by egg size:-

$$E = p_i (N(4,bef) w(4,bef))/\omega$$

$$N(2,aft) = (E C)/(E + C) \quad \text{(the number of eggs hatched)}$$

$$N(3,aft) = N(2,bef)$$

$$N(4,aft) = N(3,bef) + N(4,bef).$$

For the body weights we have:-

$$w(2, \text{aft}) = \text{omeqa}$$

$$w(3, \text{aft}) = w(2, \text{bef})$$

Calculating $w(4, \text{aft})$ is more complicated. After spawning the weight $w(4, \text{bef})$ is reduced by the fraction pi . We want a weighted mean of this and the so far unchanged $w(3, \text{bef})$, the weighting factors being the numbers $N(4, \text{bef})$ and $N(3, \text{bef})$. Thus:-

$$w(4, \text{aft}) = \frac{(1 - \text{pi}) w(4, \text{bef}) N(4, \text{bef}) + w(3, \text{bef}) N(3, \text{bef})}{N(4, \text{bef}) + N(3, \text{bef})}$$

The similar calculations for species c and d, spawning only once a year, are described in Andersen and Ursin (1977, p. 384) and it should not be necessary to go into them here.

Calculation Results

Someone might want to write a program in order to visualize the functioning of the model in which case it is desirable to check the output. Hence Table 3 which shows the contents of the state vector of numbers and body weights after the first and second halfyears, before and after spawning. Similarly, Table 4 shows the stationary solution achieved after about 30 years, depending on steplength, starting values and the number of significant digits.

Table 3. Trial runs. State vector of numbers and body weights after one and two halfyears, before and after spawning. To 4 significant digits.

Species and Entity		Before spawning		After spawning	
		N	W	N	W
After first halfyear					
a	1	19 940	.0010	1 000 000 000	.0010
	2	76.32	.0600	71 960	.0100
b	3	1 358	.3490	76.32	.0600
	4	3 890	.9596	5 248	.6593
	5	130 700	.4682		
c	6			130 700	.4682
	7	54.69	25.46		
	8	83.05	36.06	137.7	31.85
	9			1.997	.0500
	10	871.9	29.35		
d	11			871.9	29.35
	12	1.876	115.5		
	13			1.876	115.5
	14	.7392	389.2	.7392	311.4
After second halfyear					
a	1	418 600 000	.0010	1 000 000 000	.0010
	2	6 509	.2649	19 280	.0100
b	3	7.688	.4338	6 509	.2649
	4	839.3	1.160	847.0	.9231
	5			7 066	.0200
c	6	16 620	3.049		
	7			16 620	3.049
	8	89.19	27.01	89.19	21.60
	9	.5433	9.516		
	10			.5433	9.516
d	11	709.7	79.44		
	12			709.7	79.44
	13	1.707	216.9		
	14	.5398	473.3	2.247	278.5

Table 4. Continuation of the trial run of Table 3: steady state achieved after 30 years.

Species and Entity	Before spawning		After spawning	
	N	w	N	w
After any first halfyear				
a 1	97 550 000	.0010	1 000 000 000	.0010
2	142 100	.2296	859 800	.0100
b 3	53 540	.6462	142 100	.2296
4	63 140	1.194	116 700	.8155
5	3 664	1.258	none	
c 6	none		.3 664	1.258
7	769.0	8.243	none	
8	1 346	17.61	2 115	14.21
9	none		1.999	.0500
d 10	1.140	54.72	none	
11	none		1.140	54.72
12	1.004	294.6	none	
13	none		1.004	294.6
14	1.548	1 146	1.548	917.0
After any second halfyear				
a 1	102 800 000	.0010	1 000 000 000	.0010
2	136 000	.2301	848 000	.0100
b 3	52 990	.6461	136 000	.2301
4	61 630	1.195	114 600	.8125
5	none		9 674	.0200
c 6	1 551	4.324	none	
7	none		1 551	4.324
8	1 683	17.65	1 683	14.12
9	1.261	10.44	none	
d 10	none		1.261	10.44
11	1.065	148.3	none	
12	none		1.065	148.3
13	.9499	490.5	none	
14	1.145	1 195	2.095	875.8

Appendix 2

Mathematical background of Laevastu-Favorite

Bulk Biomass Model in "skeleton" form

by

N. Daan and T. Laevastu

Contents

Abstract

1. Introduction
2. The basic biomass equations
3. Trophodynamic equations
4. Recruitment in biomass based models
5. Model inputs and the unique solution as equilibrium biomasses
6. Symbols for constants, calculated parameters, and state vectors
7. References

ABSTRACT

The basic formulas of Laevastu-Favorite Bulk Biomass Model (BBM) are given in simplest possible (skeleton) form in terms which are similar to those used in conventional fisheries population dynamics. Although the formulas have been used in ecosystem model, they can be applied with some modifications to a succession of year classes, leading to a biomass based multispecies cohort analysis. The BBM model uses a discrete time stepping procedure with one month time step.

When at least one biomass is well known and the mean food composition is assumed to remain constant, there exists an unique solution ("equilibrium biomasses") for the set of biomass equations for all species in the ecosystem, provided they are connected to each other via trophic relations. This solution can be obtained with iterative methods as outlined in this report.

The recruitment control in biomasses based models is effected via the change of the growth rates of individual species.

1. INTRODUCTION

The Bulk Biomass Model (BBM) of Laevastu and Favorite (1978a) has been described in technical report and programme documentation which present the programme formulation mainly in finite difference form. The mathematical background of the skeleton (basic) BBM model is described in this paper, using abbreviations which are conventional to many single species population dynamics formulations.

The equations presented here can be applied to any fish species. The formulations and treatment of plankton and mammal (apex predator) are excluded. The biomass and trophodynamic equations can also be applied, with some modifications, to a single cohort of any species. The numerical behavior of the individual formulas is well known and thus not described here. Of the numerous "auxiliary" computation formulas, which are used in the Prognostic Bulk Biomass Model (PROBUB), only a few are presented in the text.

The skeleton BBM model is the simplest multispecies ecosystem model. It is a biomass based model (in contrast to conventional number based models). The biomass growth and mortality is computed in discrete time steps. The biomass growth rate is computed from empirical data of annual growth rates and distribution of biomass with age. The latter is obtained from the age frequency distribution for exploitable part of the population and for the prefishery juveniles it is computed with an age-dependent mortality rate (mainly predation mortality) (Laevastu and Favorite 1978b). Examples of these two data sets required for computation of the mean biomass growth rate are given in Figures 1 and 2. The mean biomass growth rate (γ_i) is $\gamma_i = \sum \gamma_a * B_a$, where γ_a is the growth rate of a given age group (cohort) and B_a is the fraction of total biomass in this age group.

The major component of the "natural mortality", i.e. the predation mortality (or ecosystem internal consumption), is computed in detail with the model as an age (and time) dependent parameter.

2. THE BASIC BIOMASS EQUATIONS

The biomass (B) of a cohort, species or group of species (i) at the end of a given time step (t) (monthly time step is normally used) is computed with a well-known formula (1), using biomass from previous time step (t-1) and growth rate (coefficient) (g) minus total mortality rate (Z) for this time step (for symbols see Chapter 6).

$$B_{i,t} = B_{i,t-1} * e^{g_i(t) - Z_i(t)} \quad (1)$$

The yield (Y) is computed with a prescribed fishing mortality coefficient ϕ_i . It should be noted that all the instantaneous coefficients (growth, mortality, fishery) are different than the corresponding conventional coefficient for number based models which use annual time step. Thus all these coefficients have to be computed on biomass base and for the time step used in the model.

$$Y_{i,t} = B_{i,t} * e^{-\phi_i(t)} \quad (2)$$

As relatively short time step is used in the computation, the second order terms, such as nonlinearities in growth and mortality during the time step, can be neglected. Furthermore, the fishing mortality (fishing intensity) coefficient must be adjusted to the mean biomass present. If the biomass changes considerably during the course of the computation and a predetermined yield per unit time is required, the fishing mortality coefficient must be multiplied by a factor of mean (base) biomass divided by actual biomass ($\phi_{i,t} = \phi_i^0 * (\bar{B}_i / B_{i,t})$).

The growth coefficient is computed in each time step, accounting for the effects of starvation in the previous time step:

$$g_i(t) = g_i^0 * ((R_{i,t-1} - S_{i,t-1})/R_{i,t-1}) \quad (3)$$

If there was no starvation in previous time step ($S_{i,t-1} = 0$), the rate of growth ($g_i(t)$) will take the prescribed value g_i^0 , but if the species was not able to get all the food required for maximum growth rate ($R_{i(t)}$), the prescribed growth rate will be reduced by the ratio of the amount of food which the species was not able to get during the previous time step ($S_{i,t-1}$) over the total amount of food required by the biomass to grow under unlimited conditions ($R_{i,t-1}$). Both values are available from previous time step and the possible error caused by this necessary backstepping choice is again minimized by the use of short time step in the computations.

The initial (prescribed) growth rate is presented in past BBM models as a harmonic function over time to take account of seasonal differences in growth ($g_i^0 = \gamma_i + \sigma_i * \cos(\alpha_i t - \kappa_i)$) where γ_i is the annual mean growth coefficient, σ_i is half of the magnitude of its annual change, α_i is the phase speed and κ is the time lag to reach the maximum. Furthermore, in full BBM models the growth rate is made a function of either surface or bottom temperature. Growth rate is also a recruitment parameter in biomass based models (see Chapter 4 below).

The mortality rate ($Z_{i(t)}$) is the addition of all negative rates of changes representing thus the total mortality rate:

$$Z_{i(t)} = \phi_{i(t)} + \mu_i + \beta_{i,t-1} \quad (4)$$

All rates of change are presented as instantaneous coefficients and are therefore additive. Fishing mortality ($\phi_{i(t)}$) and natural mortality from old age and diseases, including also spawning stress mortality (μ_i) are prescribed, but

the predation mortality coefficient ($\beta_{i,t-1}$) is computed trophodynamically in previous time step from the ratio of consumption of the species over its biomass ($\beta_{i,t-1} = \ln(1 - (C_{i,t-1}/B_{i,t-1}))$).

The general time dependent scheme of computations is given in Figure 3.

3. TROPHODYNAMIC EQUATIONS

The amount of food eaten by a species i ($R_{i(t)}$) with unlimited food availability is:

$$R_{i(t)} = B_{i,t} * r_i * \tau \quad (5)$$

where r_i is the prescribed daily ration (in fraction of body weight daily) and τ is the length of time step in days. If the growth rate (g_i^0) is made a harmonic function over the year, r_i must also be made a harmonic function

$$(r_i = \rho_i + \delta_i * \cos(\alpha_i t - \kappa_i)).$$

If the food supply of all food items for a given species would be unlimited, we could compute the consumption of each food item (e.g. the consumption of species j by species i ($C_{j,i}$)) from the food requirement (R_i) and the fraction of species j (prey) in the food of species i (predator) ($\pi_{i,j}$):

$$C_{j,i} = R_{i,t} * \pi_{i,j} \quad (6)$$

In this case the total consumption of species i would be:

$$C_i = \sum_j C_{i,j} \quad (7)$$

and the starvation would be zero. However, some food might be in limited supply and only part of the biomass of a prey is usually accessible as suitable food (re size dependent feeding). The vulnerability of one species (prey) to another species (predator) is prescribed by average composition of the food of predator. Therefore the fraction of the each species which is allowed to be consumed in each time step is prescribed in BBM model (p_j), considering mainly the size composition of the biomasses of individual species. Furthermore, substitution of low-availability food items with high-availability items must be used. However, conditions can arise

where full substitution is unrealistic and partial starvation will occur.

There are various ways of computing the actual consumption with the above described limitations. The following serves as an example. First, the fraction of biomass of a given species consumed in previous time step (month) (p_a) is compared to the allowable fraction (p_j). If the actually consumed fraction exceeds the allowable fraction, then the prescribed mean fraction of this species in the food of the species under consideration is decreased ($\pi_{i,j} = p_j/p_a * \pi_{i,j}$). The new food composition for the species i is summed and the missing fraction of food requirement is divided between these food items which had an ample supply in proportion of their occurrence in the mean food composition (prescribed at the start of the computations). However, if the missing fraction is large (e.g. in excess of 40% of food requirements), part of this missing fraction is recorded as starvation. The latter part of this approach requires thus several subjective decisions and can require a lengthy computer program.

4. RECRUITMENT IN BIOMASS BASED MODELS

The recruitment is usually depicted in number based models as a time dependent discontinuity, relating it to discrete spawning period. In the biomass based model the spawning can be treated as a continuous process. This consideration is more acceptable if we think in terms of size groups rather than age groups, a long spawning period and consider variations in growth of individuals belonging otherwise to the same age group.

Considering a continuous recruitment to all size groups and assuming (a) that there are no exceptionally strong or weak year classes of postlarval juveniles, the recruitment would be proportional to the biomass present. The variations in postlarval recruitment would be depicted in biomass based model by the variations of growth coefficient in the species biomass (if the species is treated as one unit). This is shown in Figures 1 and 2, where high growth rate

in postlarval juveniles (dotted line in Figure 1) and an increase in biomass of these postlarval juveniles (dotted curve in Figure 2), would result in increased overall (mean) growth coefficient for the species. (A strong year class of older fish would lower the mean growth coefficient.)

On the other hand, large spawning biomasses are known to produce proportionally smaller year classes and small spawning biomasses are known to produce proportionally large recruitment (year classes). Therefore, the recruitment could be regulated (controlled) in biomass based models, making the growth coefficient inversely proportional to biomass present.

$$g_c^o = g_i^o \times B_i^E / B_{i,t-1}$$

where B_i^E is the equilibrium or mean biomass of species i . This computation can be done in the models in prognostic mode after the determination of the equilibrium biomasses.

The factor $B_i^E / B_{i,t-1}$ dampens the possible fluctuations of recruitment rather heavily so that the much above or below average recruitment does not appear. It has been found somewhat more acceptable to use the term $\sqrt{B_i^E / B_{i,t-1}}$ instead. It could be generally noted that in contrast to number based models, the biomass models are not oversensitive to errors in recruitment computation.

5. MODEL INPUTS AND THE UNIQUE SOLUTION AS EQUILIBRIUM BIOMASSES

If the biomasses of all species in the ecosystem do not change over a year (i.e. previous January biomass is the same as actual January biomass), then we can say that the biomasses are in equilibrium. This implies that the growth of the biomass equals its removal by mortalities (specially by predation). If we want to achieve this equilibrium, we can change either growth rate, mortality rate, or biomass level itself. The growth rate is determined by empirical data

and the other factors, such as temperature, are assumed in the equilibrium case to be the same from one year to another (although seasonal changes can occur). Fishing and other mortality rates are also assumed to remain the same from one year to another. The predation mortality (consumption) must then balance (together with other mortalities which remain unchanged) the growth rate. This balancing can be achieved if the biomass levels of the predators are adjusted at the end of each year so that at the end of the iterations biomass of one January is the same as in the next January. This adjustment can be done by finding a unique solution to the biomass equations of all species (or groups of species) in the ecosystem. This unique solution exists when one of the biomasses and the consumption by that biomass is predetermined (assumed to be known and fixed). In this case an iterative solution can be applied to adjust the biomasses of other species once after each year's computation:

$$B_{i,t12,0} = B_{i,t12,a} + \frac{(B_{i,b} - B_{i,a})}{k}$$

where $B_{i,t12,0}$ is the new (adjusted) biomass for December, $B_{i,t12,a}$ is the previous December biomass, $B_{i,b}$ is the biomass of previous January (computed as next step from $B_{i,t12,a}$), $B_{i,a}$ is the computed biomass in January one year later and k is an iteration constant (3.5 to 10, depending on the state of convergence). Forty years or more of computation is needed before the solution converges to a unique (equilibrium) solution. The speed of convergence is among others dependent how close to equilibrium values were the initial guess biomasses at the start of computation.

The model requires as input a number of species specific constants (see Chapter 6). Besides these, the biomass of at least one species must be prescribed as known (i.e. not altered in iterative adjustment). The biomasses of other species must be initially prescribed as the best first guesses. The first guess values of the consumption (C) can be computed by assuming C_i to be eight percent of B_i per month.

In order to determine the carrying capacities of given ocean regions with the model and to obtain realistic equilibrium biomasses, the model must include all species. Computer capacity as well as basic information available does not usually allow the specification of all species separately, but many species must be grouped into ecological groups, where the composition of food and feeding habits are the main criteria for grouping.

6. SYMBOLS FOR CONSTANTS, CALCULATED PARAMETERS, AND STATE VECTORS

Constants

- α_i - phase speed, time step dependent (e.g. 30 degrees per month, radians)
- γ_i - annual average instantaneous growth rate
- ϕ_i - instantaneous fishing mortality coefficient
- ∂_i - half amplitude of annual change of food requirement (fraction of body weight daily)
- σ_i - half amplitude of annual change of growth rate
- ρ_i - annual average food requirement (fraction of body weight daily)
- κ_i - phase lag (in radians)
- μ_i - instantaneous rate of mortality (other than predation mortality)
- $\pi_{i,j}$ - fraction composition of prey j in the food of predator i
- p_j - fraction of biomass j allowed to be taken in one time step (month)
- r_i - prescribed rate of food requirement (fraction of body weight daily)
- g_i^0 - prescribed instantaneous growth rate

Note: The latter two parameters (r_i and g_i^0 can also be computed if γ_i and ρ_i and related constants are prescribed).

Dynamically calculated parameters

- $g_{i,(t)}$ - calculated instantaneous growth rate
 $Z_{i(t)}$ - calculated total instantaneous total mortality rate
 B_i^E - equilibrium biomass

State vectors

- $B_{i,t}$ - biomass of species i at time t
 $C_{i(t)}$ - consumption of species i (predation) during time step t
 $R_{i(t)}$ - food requirements
 $S_{i(t)}$ - starvation (the amount of food missing from the full food requirement $R_{i(t)}$)
 $Y_{i(t)}$ - yield
 $C_{j,i}$ - consumption of species j by predator i

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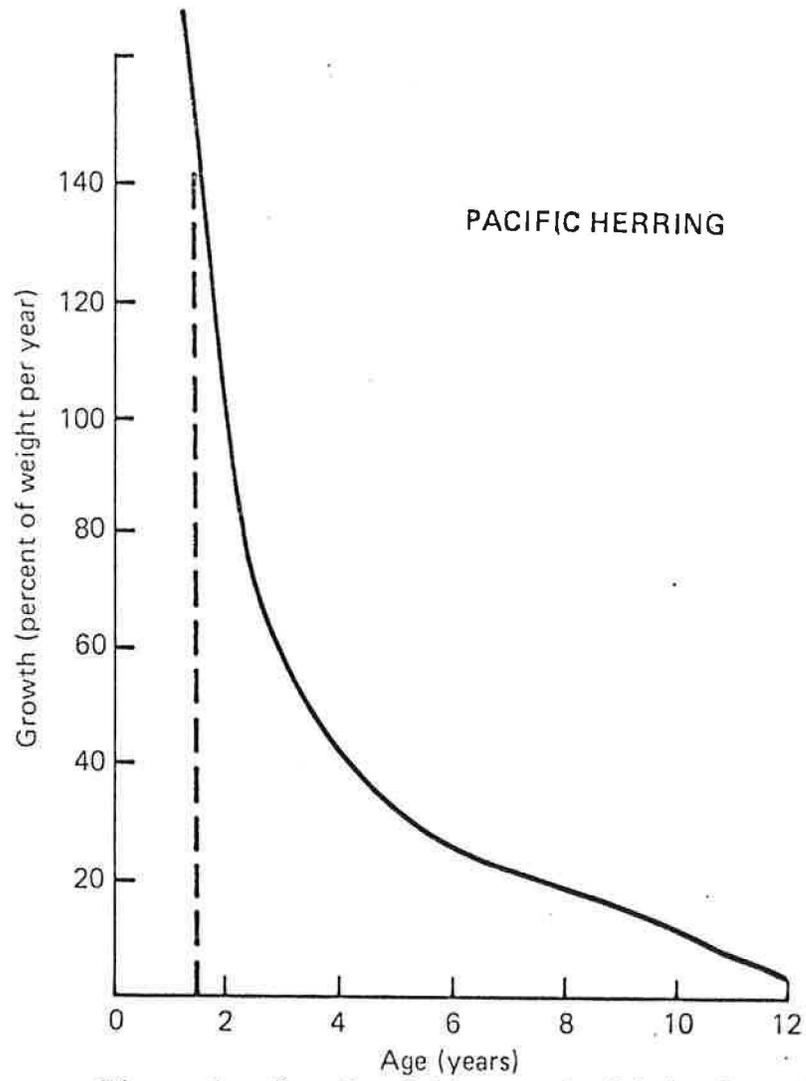


Figure 1.--Growth of biomass (weight) of Pacific herring at different ages, as percent per year.

Skeleton Bulk Biomass Model

SKEBUB

by

T. Laevastu

CONTENTS

1. Purpose of the model
2. Sequence of computations and brief outline of the programme.
3. List of symbols.
4. Programme listing with annotations.

1. PURPOSE OF THE MODEL

Biomass based ecosystem simulation models must be adapted to available data from given regions. Thus no ecosystem model is universally applicable without considerable reprogramming. Some basic approaches and formulas are, however, used in all biomass based ecosystem models. The following skeleton bulk biomass model (SKEBUB) is an example of the simple bulk biomass ecosystem simulation model and shows also the method of iterative solution to equilibrium biomasses. Furthermore, it serves to explain the working of discrete time stepping ecosystem models in general.

2. SEQUENCE OF COMPUTATIONS AND OUTLINE OF THE PROGRAMME

The enclosed example programme contains only five species/groups of species: herring (and other pelagic fish), pollock in two age groups, flatfishes, and "fish food benthos". Marine mammals are lumped in one group and consumption by them is used as a "forcing function". Zooplankton standing stock is simulated with a harmonic formula.

The DATA statement introduces the main growth rates, their harmonic constants, food requirement coefficients and their harmonic constants, monthly mean pollock (group 2) biomass (if there is a desire to keep it constant), mean composition of food, and maximum allowable consumption of the species per time step (month).

After setting the zooplankton constants and zeroing the arrays, the initial biomasses and their initial consumptions are introduced.

The computations start with the simulation of zooplankton standing crop, whereafter the consumption by mammals is computed.

The computation of growth, mortalities, and consumption of the fish species and benthos follows species by species. Within these computations the feeding subroutine FOCONS is called which also recomputes the composition of food according to availability, as well as possible starvation.

The "month end computations" include the computation of fraction of biomass consumed, transfer of fraction of juvenile pollock ("pollock one") to adult pollock ("pollock two"), and outputs.

The iteration of equilibrium biomasses is carried out with variable iteration constant. A "recruitment control" is computed before increasing the month account. Subroutine PRIFLD is called for printing of outputs and subroutine FOCONS is called in species computations for recomputing of food composition, for computing of consumption (predation), and for estimation of possible starvation. Additional comments can be found in the enclosed programme.

3. LIST OF SYMBOLS

AGA - iteration constant
AL - (not used)
ALP - phase speed (30 deg)

BE - benthos biomass

BEC - consumption of benthos

BEE - "equilibrium" biomass of benthos

BEI - "adjusted" biomass of benthos

BEJ - monthly mean consumption of benthos

BEM - annual mean biomass of benthos

BEP - percent consumption of benthos (per month)

BK - phase lag of maximum food requirement

BM - biomass of marine mammals

BP - annual mean food requirement (% body weight daily)

BR - half of annual range of food requirement change

C - intermediate (instantaneous coefficient of predation mortality)

CO - percentual composition of food

D - intermediate (in FOCONS)

D1 - intermediate (in FOCONS)

DIF - difference in biomass in two adjacent Januaries (year apart)

FBM - total food consumption by mammals

FC - fractional food composition of flatfish

FF - flatfish biomass

FFC - consumption of flatfish

FFE - equilibrium biomass of flatfish

FFI - "adjusted" biomass of flatfish

FFJ - monthly mean consumption of flatfish

FFM - annual mean biomass of flatfish

FFP - percent consumption of flatfish (monthly)

FFS - starvation of flatfish

FL - yield (catch)
FM - fishing mortality coefficient
FOOD - total food consumption
G - annual mean growth coefficient
GB - storage array for mean growth coefficient
GG - growth coefficient (intermediate)
GIK - phase lag of maximum growth
GK - phase lag for maximum growth coefficient
GR - half of the annual range of growth coefficient change
HC - fractional food composition for herring
HE - herring biomass
HEC - consumption of herring
HEE - equilibrium biomass of herring
HEI - "adjusted" biomass of herring
HEJ - monthly mean consumption of herring
HEM - annual mean biomass of herring
HEP - percent consumption of herring
HES - starvation of herring
I - counter
IS - species number
J - counter
K - month
KIK - maximum number of years computed
L - year
LAL - year when equilibrium biomasses are expected
LL - year count (in PRIFLD)

LR - number of experiment (run)
N - counter (in FOCONS)
NP - previous month
P - maximum percent biomass allowed to be consumed
PCO - percent consumption (in PRIFLD)
PC - fractional food composition of "adult" pollock
PIM - phase lag of maximum mammal standing stock
PIP - consumption divided by biomass
PIZ - converted phase lag in zooplankton
PV - (not used) (monthly mean biomass of adult pollock, if kept constant)
PW - food requirement (computed)
P1 - juvenile pollock biomass ("pollock one")
P1C - consumption of juvenile pollock
P1E - equilibrium biomass of juvenile pollock
P1I - "adjusted" biomass of juvenile pollock
P1J - monthly mean consumption of juvenile pollock
P1M - annual mean biomass of juvenile pollock
P1P - percent consumption of juvenile pollock
P1S - starvation of juvenile pollock
P2 - adult pollock biomass ("pollock two")
P2C - consumption of adult pollock
P2E - equilibrium biomass of adult pollock
P2I - "adjusted" biomass of adult pollock
P2J - monthly mean consumption of adult pollock
P2M - annual mean biomass of adult pollock
P2P - percent consumption of adult pollock
P2S - starvation of adult pollock

R - intermediate for percent of consumption of biomass
RAC - factor for conversion of degrees to radians
S - starvation mortality coefficient
SC - sum of unchanged fraction of total
SD - sum of fractions of food missing
SM - mortality coefficient (from old age and diseases)
SMA - starvation, amount of food missing (in FOCONS)
SP - species biomass (intermediate)
SS - starvation (in percent of food missing)
SU - sum (intermediate)
T - month (intermediate)
UC - fractional food composition of juvenile pollock
Z - coefficient, growth minus mortalities
ZK - phase lag of maximum zooplankton standing stock
ZO - zooplankton standing stock
ZOC - consumption of zooplankton
ZOM - annual mean zooplankton standing stock
ZOP - percent of zooplankton biomass consumed
ZR - half annual range of zooplankton change

PROGRAM NSSKEL

73/74

OPT=1

ETN 4.7+476

07/10/79 08.29.44

```

PROGRAM NSSKEL (INPUT, OUTPUT, TAPE5=INPUT)
REAL K, N, M1, N1, M2
INTEGER STEPS, HALFYR
DIMENSION H(14), K(14), OMEGA(4), C(4),
* N(14), W(14), F(14), WLOG(14), PHI(14,14), G(14,14),
* FI(14), ORDT(14), M2(14), Y(14), GLDW(14), OLDW(14)
READ(5,10) V, ETA, GAMMA, Q, PI, M1
10 FORMAT(3F8.5, F8.0, 2F8.5)
PRINT 20, V, ETA, GAMMA, Q, PI, M1
20 FORMAT(1X, #V #, F8.5, # ETA #, F8.5, # GAMMA #,
* F8.5, # Q #, F8.0, # PI #, F8.5, # M1 #, F8.5)
READ(5,30) H, K
30 FORMAT(7F7.3)
PRINT 40, H, K
40 FORMAT(1X, #H= #, 14F7.3/1X, #K= #, 14F7.3)
READ(5,50) OMEGA
READ(5,50) C
50 FORMAT(7L9.2)
PRINT 60, OMEGA, C
60 FORMAT(1X, #OMEGA= #, 4F7.3, 10X, #C= #, 4F11.2)
READ(5,30) F
PRINT 70, F
70 FORMAT(1X, #F= #, 14F7.3)
READ(5,90) N, W
PRINT 80, N, W
80 FORMAT(1X, #N= #, 14E9.2/1X, #W= #, 14E9.2)
READ(5,90) STEPS, HALFYR
90 FORMAT(2I4)
PRINT 100, STEPS, HALFYR
100 FORMAT(1X, #STEPS PER HALFEAR #, I4,
* 5X, #NU. OF HALFEARS#, I4)
C***** INITIALIZATION
N1=N(1)
L=1
DELTA=1./(STEPS*2.)
DELTA=DELTA/16.
N1STEPS=STEPS*16.
N(1)=N1
GLDW(1)=W(1)
DO 114 I=1,14
DO 114 J=1,14
114 G(I,J)=0.
C***** BEGIN HALFEAR
115 DO 120 I=1,14
120 Y(I)=0.
DO 190 NT=1, NSTEPS
DO 130 I=1,14
Y(I)=Y(I)+F(I)*N(I)*W(I)*DELTA
WLOG(I)=0.
130 IF(W(I).GT.0.)WLOG(I)=ALOG(W(I))
DO 150 I=1,14
FI(I)=0.
DO 150 J=1,14
G(I,J)=EXP(-GAMMA*(WLOG(I)-WLOG(J)-ETA)**2.)
PHI(I,J)=G(I,J)*N(J)*W(J)
150 FI(I)=FI(I)+PHI(I,J)
SAME1=0. $ SAME2=0.

```

PROGRAM N5SKE1

73/74

OPT=1

FTN 4.7+47b

07/10/79 08.29.44

```

SUM1=0.
DIFF=0.
DO 160 I=1,14
  CLDW(I)=W(I)
  FEEDLV=F1(I)/(F1(I)+Q)
  TWQ3=2.73.
  DRDT(I)=FEEDLV*H(I)*(W(I)**TWQ3)*DELTA
  SAME1=SAME1+N(I)*DRDT(I)
  DWDT=V*DRDT(I)-K(I)*W(I)*DELTA
  W(I)=W(I)+DWDT
160 SUM1=SUM1+N(I)*DWDT
  DO 180 J=1,14
    CLDN(J)=N(J)
    M2(J)=0.
    IF(N(J).EQ.0.)GO TO 180
    DO 170 I=1,14
      IF(N(I).EQ.0.)GO TO 170
      M2(J)=M2(J)+G(I,J)*DRDT(I)*N(I)/F1(I)
170 CONTINUE
    QNDT=-((F(J)+M1)*DELTA+M2(J))*N(J)
    N(J)=N(J)+QNDT
    SUM1=SUM1+CLDW(J)*QNDT
    DIFF=DIFF+N(J)*W(J)-CLDN(J)*CLDW(J)
    SAME2=SAME2+M2(J)*CLDN(J)*CLDW(J)
180 CONTINUE
190 CONTINUE
  SAMQUU=SAME1/SAME2
  PRINT 185,NT,SAME1,SAME2,SAMQUU
185 FORMAT(1X,*,CHECK:*,5X,I4,5X,2E15.6,15X,E15.6)
  QUU1=SUM1/DIFF
  PRINT 186,DIFF,SUM1,QUU1
186 FORMAT(15X,3E15.6,9X,E12.6)
C****STEP - LOOP ENDS
C
C$$$SPAWNING
DO 195 I=1,14
  CLDN(I)=N(I)
195 CLDW(I)=W(I)
  E=PI*N(4)*W(4)/OMEGA(2)
  E1=E*C(2)/(C(2)+E)
  W(4)=((1.-PI)*W(4)*N(4)+W(3)*N(3))/(N(4)+N(3))
  W(3)=W(2)
  W(2)=OMEGA(2)
  N(4)=N(4)+N(3)
  N(3)=N(2)
  N(2)=E1
  IF(L/2*.EQ.L)GO TO 230
C$$$SPECIES C DOES NOT SPAWN
  W(8)=(W(6)*N(8)+W(7)*N(7))/(N(8)+N(7))
  N(8)=N(8)+N(7)
  DO 210 I=1,2
    J=8-I
    W(J)=W(J-1)
210 N(J)=N(J-1)
  W(5)=0.
  N(5)=0.
C****SPECIES D SPAWNS

```

RUGKAM NSSKEL 73/74 OPT=1

FIN 4.7+476

07/10/79 08.29.44

```

E=PI*N(14)*W(14)/OMEGA(4)
E1=E*C(4)/(C(4)+E)
W(14)=(1.-PI)*W(14)
DO 220 I=1,4
  J=14-I
  W(J)=W(J-1)
220 N(J)=N(J-1)
  W(9)=OMEGA(4)
  N(9)=E1
  GO TO 200
C***END OF ODD HALFYEAR SPAWNING
C***EVEN HALFYEAR SPAWNING
C
C**SPECIES C SPAWNS
230 E=PI*N(8)*W(8)/CMEGA(3)
  E1=E*C(3)/(C(3)+E)
  W(8)=(1.-PI)*W(8)
  DO 240 I=1,2
    J=8-I
    W(J)=W(J-1)
240 N(J)=N(J-1)
  W(5)=CMEGA(3)
  N(5)=E1
C****SPECIES D DOES NOT SPAWN
  W(14)=(W(14)*N(14)+W(13)*N(13))/(N(14)+N(13))
  N(14)=N(13)+N(14)
  DO 250 I=1,4
    J=14-I
    W(J)=W(J-1)
250 N(J)=N(J-1)
  W(9)=0.
  N(9)=0.
C****CUTPOINT AFTER HALFYEAR
260 N(1)=N1
  PRINT 300,L
300 FORMAT(//,A AFTER#,I3,A HALFYEAR#//1X,
  *#ENTITY#,23X,#BEFORE#,37X,#AFTER#/
  *18X,#N#,16X,#W#,21X,#N#,16X,#W#/)
  DO 310 I=1,14
310 PRINT 320,OLDN(I),OLDW(I),N(I),W(I)
320 FORMAT(1X,I4,2F16.4,5X,2F16.4)
C** READY FOR NEXT HALFYEAR
  IF(L.EQ. HALFYR) STOP
  L=L+1
  DELTA=DELTA1
  NSTEPS=STEPS
  GO TO 115
END

```

V .40000 RIA 4.0017 GAMMA .14457 Q 50000. FT .20000 MI .10000
H= 0.000 10.000 10.000 10.000 18.000 18.000 18.000 18.000 35.000 35.000 35.000 35.000 35.000 35.000
K= 0.000 2.000 2.000 2.000 1.750 1.750 1.750 1.750 400 400 400 400 400 400
MEGA= .001 .010 .020 .050 C= 0.00 2000000.00 10000.00 2.00
F= 0.000 0.000 0.000 0.000 0.000 1.000 1.000 1.000 0.000 0.000 0.000 0.000 0.000 0.000
M= .10E+10 .00E+00 .14E+06 .12E+06 .97E+04 0. .16E+04 .17E+04 0. .13E+01 0. .11E+01 0. .21E+01
N= .10E-06 .00E-04 .00E+00 .00E+00 .20E-01 0. .43E+01 .14E+02 0. .10E+02 0. .15E+03 0. .00E+03
STEPS PER HALFYEAR 64 NO. OF HALFYEARS 30
CHECK: 1022 .000441E+03 .004401E+03 .100003E+01
-.000431E+03 -.000355E+03 .999669E+00

AFTER 1 HALFYEAR

ENTITY	BEFORE		AFTER	
	N	W	N	W
1	97048047.0074	.0010	1000000000.0000	.0010
2	141000.0000	.2274	80422.3420	.0100
3	5522.7097	.0400	14100.2203	.2294
4	3300.0374	.1430	110901.4071	.8135
5	3004.7014	1.2552	0.0000	0.0000
6	0.0000	0.0000	3029.7014	1.2562
7	700.0401	8.2391	0.0000	0.0000
8	1343.4700	17.3440	0.0000	14.1897
9	0.0000	0.0000	1.9494	.0500
10	1.1391	7.942742	0.0000	0.0000
11	0.0000	0.0000	1.1391	54.5442
12	.9407	294.2314	0.0000	0.0000
13	0.0000	0.0000	.9407	294.2314
14	1.2440	1140.4700	1.2440	917.1812
CHECK:	00	.973424E+04	.973017E+04	.100042E+01
		-.944300E+04	-.942295E+04	.597792E+00

AFTER 2 HALFYEAR

ENTITY	BEFORE		AFTER	
	N	W	N	W
1	103022374.7744	.0010	1000000000.0000	.0010
2	132020.4740	.2270	851450.2140	.0100
3	32044.0000	.0400	132020.4740	.2270
4	31004.7174	1.2003	114400.4474	.8159
5	0.0000	0.0000	4073.0419	.0200
6	1234.7130	4.3207	0.0000	0.0000
7	0.0000	0.0000	1234.7130	4.3207
8	1000.0070	17.0330	1600.0070	14.1070
9	1.2340	9.0439	0.0000	0.0000
10	0.0000	0.0000	1.2340	9.8409
11	1.0041	147.3047	0.0000	0.0000
12	0.0000	0.0000	1.0041	147.3649
13	.9401	409.3500	0.0000	0.0000
14	1.1410	1140.1430	2.0000	875.4549
CHECK:	00	.100270E+05	.100225E+05	.100045E+01
		-.900541E+04	-.903323E+04	.997703E+00

AFTER 29 HALFYEAR

ENTITY	BEFORE		AFTER	
	N	W	N	W
1	97355672.1828	.0010	1000000000.0000	.0010
2	140900.5711	.2267	868982.4495	.0100
3	52980.3851	.6446	140900.5711	.2265
4	63827.8788	1.2037	118808.0639	.8187
5	3605.4955	1.2244	0.0000	0.0000
6	0.0000	0.0000	3605.4955	1.2244
7	751.1619	8.1912	0.0000	0.0000
8	1324.0634	17.6029	2075.2254	14.1962
9	0.0000	0.0000	1.9994	.0500
10	1.1204	22.4959	0.0000	0.0000
11	0.0000	0.0000	1.1204	22.4959
12	.9862	287.1203	0.0000	0.0000
13	0.0000	0.0000	.9862	287.1503
14	1.5181	1132.2937	1.5181	905.8349
CHECK:	00	.973621E+04	.973208E+04	.100042E+01
		-.945027E+04	-.942945E+04	.997797E+00

AFTER 30 HALFYEAR

ENTITY	BEFORE		AFTER	
	N	W	N	W
1	102010294.3934	.0010	1000000000.0000	.0010
2	134393.8596	.2267	856781.8470	.0100
3	52597.0889	.6445	134393.6596	.2267
4	62259.1253	1.2038	114856.2453	.8172
5	0.0000	0.0000	9668.7049	.0200
6	1518.1852	4.2712	0.0000	0.0000
7	0.0000	0.0000	1518.1852	4.2712
8	1653.8406	17.6465	1653.8406	14.1172
9	1.2409	9.8264	0.0000	0.0000
10	0.0000	0.0000	1.2409	9.8564
11	1.0467	143.5900	0.0000	0.0000
12	0.0000	0.0000	1.0467	143.5900
13	.9334	480.3159	0.0000	0.0000
14	1.1218	1182.6138	2.0552	803.8620

4. PROGRAMME LISTING WITH ANNOTATIONS

////////////////////////////////////

PROGRAM SKEBUB 73/74 OPT=1 FTN 4.7+476 07/10/79 03.22.40

```

PROGRAM SKEBUB (INPUT,OUTPUT)
COMMON /LINE/ ZD(13),ZDC(13),ZUP(13),BE(13),BEC(13),BEP(13),
ZHE(13),HEC(13),HEP(13),HES(13),P1(13),P1C(13),P1P(13),P1S(13),
3PZ(13),P2C(13),P2P(13),P2S(13),FF(13),FFC(13),FFP(13),FFS(13),
4G(6),GR(6),GK(6),BP(6),BK(6),BK(6),FM(6),SM(6),PV(13),
ZK,L,IS,ZOM,ZR,ZK,BEE,BEI,BEJ,HEE,HEI,HEJ,P1E,P1I,P1J,
OPZE,PZI,PZJ,FFE,FFI,FFJ,SM
7,HC(6),UC(6),PC(6),FC(6),P(6),R(6),CD(6),GB(6)

```

C
C

```

DATA G/O.,0.14,0.090,0.125,0.054,0.058/,
2GR/C.,0.06,0.0425,0.0575,0.025,0.024/,
3GK/210.,210.,240.,210.,210.,240./,
4BP/O.,0.,0.0082,0.009,0.0022,0.0046/,
5BR/O.,0.,0.006,0.007,0.00325,0.00225/,
6BK/210.,210.,240.,210.,210.,240./,
1FM/C.,0.,0.006,0.002,0.015,0.008/,
2SM/O.,0.003,0.002,0.002,0.003,0.0025/,
3,PV/13*1750./
4,HC/94.,0.8,2.,2.,1.,0.2/,
5UC/81.,2.,10.,4.,2.,1./,
6PC/40.,10.,15.,29.,1.,5./,
7FC/8.,77.5,2.,6.,0.5,6./,
8P/40.,11.,8.,9.,5.,6./

```

} Data input

C** HC,UC,PC,FC - PERCENT COMPOSITION OF FOOD
C** P - MAX. CONS. ALLOWED

C 11 SPECIES 5 CHANGING, MAMMAL CONS. CONSTANT

```

ZOM=430.
ZR=240.
ZK=210.

```

} Zooplankton constants

AL=0.0235

C SAVE ORIGINAL GROWTH COEFFICIENT

```

DO 601 I=1,6
GB(I)=G(I)

```

601 CONTINUE

C LR - NUMBER OF EXPERIMENT

```

LR=21
PRINT 500,LR

```

300 FORMAT(//5X,6HRUN NO,I6//)

C DO LOOPS 1 AND 2 - ZERO ARRAYS

```

DO 1 I=1,13
ZD(I)=ZUP(I)=HEP(I)=HES(I)=0.
BEP(I)=P1P(I)=P1S(I)=P2P(I)=P2S(I)=0.
FFP(I)=FFS(I)=0.
1 CONTINUE
DO 2 I=1,13
ZDC(I)=BE(I)=BEC(I)=HE(I)=HEC(I)=0.
P1(I)=P1C(I)=P2(I)=P2C(I)=0.
FF(I)=FFC(I)=0.
2 CONTINUE

```

C ENTER INITIAL GUESS FIELDS

C COMPUTE INITIAL (GUESS) CONSUMPTION

```

BE(12)=BEI=BEE=3800.
BEC(12)=BEJ=BE(12)*0.10
HE(12)=HEI=HEE=4200.
HEC(12)=HEJ=HE(12)*0.08
P1(12)=P1I=P1E=4100.

```

PROGRAM SKRUBB 7/74 OPT=1 ETN 4.7+476 07/10/79 08.22.40

P1C(12)=P1J=P1(12)*0.090
P2(12)=P2i=P2f=1750.
P2C(12)=P2J=P2(12)*0.10
FF(12)=Ffi=FFE=3000.
FFC(12)=FFJ=FF(12)*0.05

C*****

C*****

DU 421 I=1,6 Transfer of allowable consumption
K(I)=P(I) into permanent array

421 CONTINUE

C ZLLPLANKTON SIMULATION

K=1 I=K

KAC=0.0174533

ALP=30.*KAC

PiZ=ZK*KAC

20 Z0(K)=Z0M+ZR*COS(ALP*I-PiZ)

ZC(K)=Z0(K)*60.

K=K+1

T=K

IF(K-1)20,20,21

21 PRINT 22,(Z0(I),I=1,12)

22 FORMAT(//5X,13H200PL. KG/KM2,12F8.0/)

C MAMMALS

C K - MONTH L - YEAR

K=1

C LAL - NUMBER OF YEARS FOR EQUILIBRIUM ITERATION

C KIK - TOTAL NUMBER OF YEARS OF COMPUTATIONS

LAL=40

KIK=48

L=1

PRINT 206,L

206 FORMAT(//5X,4HYEAR,16/)

23 T=K

C CONSUMPTION BY ANIMALS

C THIS IS THE ONLY PRESCRIBED AND FIXED BIOMASS AND CONSUMPTION

420 PIM=210.*KAC

BM=(2.8+1.0*COS(ALP*T-PIM))*100.

FBM=BM*0.05*30.

Z0C(K)=FBM*0.12

BEC(K)=FBM*0.15

HEC(K)=FBM*0.18

P1C(K)=FBM*0.29

P2C(K)=FBM*0.10

FFC(K)=FBM*0.10

IF(L-LAL)208,207,208

207 PRINT 19,K,BM

19 FORMAT(//5X,18HMAMMAL BIOMASS, M=,16,F8.0/)

PRINT 24,(Z0C(K),BEC(K),HEC(K),P1C(K),P2C(K),FFC(K))

24 FORMAT(//5X,14HCONS. BY MAMM.,6F8.0/)

C BENTHOS

208 IS=2

NP=K-1 Setting of "previous month" index

IF(NP)25,25,26

25 NP=12

26 GG=G(IS)

PIP=3EC(NP)/BE(NP)

IF(PIP*100.-2.*P(IS))410,410,411

411 PIP=2.*P(IS)*0.01

410 C=ALOG(1.-PIP)

Z=GG-SM(IS)+C

BE(K)=BE(NP)*EXP(Z)

C HERRING

IS=3

Species number

IF(HE(NP))60,60,52

52 PIP=HEC(NP)/HE(NP)

IF(PIP*100.-2.*P(IS))412,412,413

413 PIP=2.*P(IS)*0.01

412 C=ALOG(1.-PIP)

S=ALOG(1.-HEC(NP)/HE(NP))

IF(L-LAL)51,51,53

51 GG=G(IS)

GO TO 55

53 GIK=GK(IS)*RAC

GG=G(IS)+GK(IS)*COS(ALP*T-GIK)

55 Z=GG-SM(IS)+C+S*0.5

HE(K)=HE(NP)*EXP(Z)

SP=HE(K)

HE(K)=HE(K)*EXP(-FM(IS))

FL=SP-HE(K)

IF(L-LAL)31,209,209

209 PRINT 30,K,FL

30 FORMAT(//5X,14HHEK. CATCH, M=,I0,F8.0/)

31 IF(L-LAL)33,33,34

34 GIK=BK(IS)*RAC

PW=BP(IS)+BR(IS)*COS(ALP*T-GIK)

CG(1)=HC(1)

CG(2)=HC(2)*BE(NP)/BEE

CG(3)=HC(3)*HE(NP)/HEE

CG(4)=HC(4)*P1(NP)/P1E

CG(5)=HC(5)*P2(NP)/P2E

CG(6)=HC(6)*FF(NP)/FFE

SU=0.

DO 56 I=1,6

SU=SU+CG(I)

56 CONTINUE

DO 57 I=1,6

CC(I)=CG(I)*100./SU

57 CONTINUE

GO TO 35

35 PW=BP(IS)

DO 310 I=1,6

CG(I)=HC(I)

310 CONTINUE

35 CALL FDCUNS(K,PW,SS,HE,CG,P,R,ZUG,BEC,HEC,P1C,P2C,FFC,L,LAL) Feeding subroutine call
Herring starvation (relocation)

HEC(K)=SS

GO TO 201

60 HE(K)=1.

C FLOCK ONE

201 IS=4

IF(P1(NP))70,70,62

62 PIP=P1C(NP)/P1(NP)

IF(PIP*100.-2.*P(IS))414,414,415

415 PIP=2.*P(IS)*0.01

414 C=ALOG(1.-PIP)

} Conversion of consumption to instantaneous coefficient.

} Recomputation of growth coefficient

} Total "biomass change" coefficient
Herring biomass

} Fishery (yield)

} Food requirement coefficient computation

} Recomputation of food composition

} Other species computations follow the same sequence as herring above

S=ALOG(1.-P1S(NP)/P1(NP))

IF(L-LAL)61,61,63

01 GG=G(IS)

GD TO 04

03 GIK=GK(IS)*RAC

GG=G(IS)+GR(IS)*COS(ALP*T-GIK)

04 Z=GG-SM(IS)+C+S*0.5

P1(K)=P1(NP)*EXP(Z)

SP=P1(K)

P1(K)=P1(K)*EXP(-FM(IS))

FL=SP-P1(K)

IF(L-LAL)102,210,210

210 PRINT 05,K,FL

02 FORMAT(/,5X,15HPDL,1 CAT, H, M=,I6,F8.0/)

102 IF(L-LAL)09,69,68

08 GIK=BK(IS)*RAC

Pw=BP(IS)+BK(IS)*COS(ALP*T-GIK)

CO(1)=UC(1)

CO(2)=UC(2)*BE(NP)/BEE

CO(3)=UC(3)*HE(NP)/HEE

CO(4)=UC(4)*P1(NP)/P1E

CO(5)=UC(5)*P2(NP)/P2E

CO(6)=UC(6)*FF(NP)/FFE

SU=0.

DO 66 I=1,6

SU=SU+CO(I)

06 CONTINUE

DO 67 I=1,6

CO(I)=CO(I)*100./SU

67 CONTINUE

GD TO 36

09 FW=BP(IS)

DO 311 I=1,6

CL(I)=UC(I)

311 CONTINUE

30 CALL FDCJNS(K,PW,SS,P1,CL,P,R,ZUC,BEC,HEC,P1C,P2C,FFC,L,LAL)

FIS(K)=SS

GO TO 202

70 P1(K)=1.

C PCLLUCK FWD

202 IS=5

401 IF(P2(NP))00,80,72

72 PIP=P2C(NP)/P2(NP)

IF(PIP*100.-2.*P(IS))410,410,417

417 PIP=2.*P(IS)*0.01

416 C=ALOG(1.-PIP)

S=ALOG(1.-P2S(NP)/P2(NP))

IF(L-LAL)71,71,73

71 GG=G(IS)

GD TO 75

73 GIK=GK(IS)*RAC

GG=G(IS)+GR(IS)*COS(ALP*T-GIK)

75 Z=GG-SM(IS)+C+S*0.5

P2(K)=P2(NP)*EXP(Z)

GL TO 403

402 P2(K)=PV(K)

P2E=P2(K)

PROGRAM SKEPUB

73/74

DPI=1

FIN 4.7+476

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```

403 SP=P2(K)
    P2(K)=P2(K)*EXP(-FM(IS))
    FL=SP-P2(K)
    IF(L-LAL)92,211,211
211 PRINT 86,K,FL
    88 FURMAT(//2X,15HPQL,2 CATCH, M=,16,F8.0/)
    92 IF(L-LAL)79,79,78
    78 GIK=BK(IS)*RAC
    PW=BP(IS)+BR(IS)*COS(ALP*T-GIK)
    CU(1)=PC(1)
    CU(2)=PC(2)*BE(NP)/BEE
    CU(3)=PC(3)*HE(NP)/HEE
    CU(4)=PC(4)*P1(NP)/PIE
    CU(5)=PC(5)*P2(NP)/P2E
    CU(6)=PC(6)*FF(NP)/FFE
    SU=0.
    DO 76 I=1,6
    SU=SU+CU(I)
76 CONTINUE
    DO 77 I=1,6
    CG(1)=CU(I)*100./SU
77 CONTINUE
    GO TO 37
79 PW=BP(I,S)
    DO 312 I=1,6
    CG(1)=PC(I)
312 CONTINUE
37 CALL FUCGNS (K,PW,SS,P2,CG,P,R,ZUG,BEC,HEC,PIE,P2C,FFC,L,LAL)
    P2S(K)=SS
    GO TO 203
80 P2(K)=1.
C FLATFISHES
203 IS=6
    IF(FF(NP))90,90,82
82 PIP=FFC(NP)/FF(NP)
    IF(PIP*100.-2.*P(IS))418,418,419
419 PIP=2.*P(IS)*0.01
418 C=ALOG(1.-PIP)
    S=ALOG(1.-FFS(NP)/FF(NP))
    IF(L-LAL)81,81,83
81 GG=G(IS)
    GO TO 85
85 GIK=GK(IS)*RAC
    GG=G(is)+GK(IS)*COS(ALP*T-GIK)
85 Z=GG-SM(IS)+C+S*0.5
    FF(K)=FF(NP)*EXP(Z)
    SP=FF(K)
    FF(K)=FF(K)*EXP(-FM(IS))
    FL=SP-FF(K)
    IF(L-LAL)137,212,212
212 PRINT 133,K,FL
133 FURMAT(//2X,16HFLATF. CATCH, M=,16,F8.0/)
137 IF(L-LAL)84,84,84
84 GIK=BK(IS)*RAC
    PW=BP(IS)+BR(IS)*COS(ALP*T-GIK)
    CU(1)=FC(1)
    CU(2)=FC(2)*BE(NP)/BEE

```

PROGRAM SKEBUB

73/74

OPT=1

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CU(3)=FC(3)*HE(NP)/HEE

CU(4)=FC(4)*P1(NP)/P1E

CU(5)=FC(5)*P2(NP)/P2E

CU(6)=FC(6)*FF(NP)/FFE

SU=0.

DO 86 I=1,6

SU=SU+CU(I)

86 CONTINUE

DO 87 I=1,6

CG(I)=CG(I)*100./SU

87 CONTINUE

GO TO 38

89 FW=BP(1S)

DO 313 I=1,6

CU(I)=FC(I)

313 CONTINUE

38 CALL FDCUNS(K,PW,SS,FF,CL,P,R,ZUC,BEC,HEC,P1C,P2C,FFC,L,LAL)

FFS(K)=SS

GO TO 213

90 FF(K)=1.

C MONTH END COMPUTATIONS

213 CONTINUE

203 CONTINUE

204 ZUP(K)=(ZUC(K)/ZQ(K))*100.

111 BEP(K)=(BEC(K)/BE(K))*100.

113 HEP(K)=(HEC(K)/HE(K))*100.

115 F1P(K)=(P1C(K)/P1(K))*100.

117 P2P(K)=(P2C(K)/P2(K))*100.

119 FFP(K)=(FFC(K)/FF(K))*100.

Computation of percent biomass consumed

C*****

C TRANSFER

P1(K)=P1(K)-0.023*P1(K)

Transfer of fraction of pollock 1 to pollock 2

P2(K)=P2(K)+0.023*P1(K)

C*****

K(1)=ZUP(K)

K(2)=BEP(K)

K(3)=HEP(K)

K(4)=F1P(K)

K(5)=P2P(K)

K(6)=FFP(K)

Transfer of percent consumption into operational arrays

121 K=K+1

Augmentation of month count

IF(K-13)23,23,165

165 CALL PRIFLD(L,BE,BEC,BEP,2)

CALL PRIFLD(L,HE,HEC,HEP,3)

CALL PRIFLD(L,P1,P1C,P1P,4)

CALL PRIFLD(L,P2,P2C,P2P,5)

CALL PRIFLD(L,FF,FFC,FFP,6)

Year end printout

IF(L-LAL)166,178,190

Start of year end iteration for unique solution

166 IF(L-8)168,168,167

167 IF(L-16)169,169,170

168 AGA=3.0

GO TO 171

169 AGA=5.0

GO TO 171

Setting of iteration constant

170 IF(L-26)93,93,94

93 AGA=0.0

GO TO 171

```

94 AGA=7.0
171 DIF=BE(13)-BE(1)
    BEI=BE(1)-DIF/AGA
    BE(12)=BEI
    BEE=BEI
    BEC(13)=0.
    DO 172 I=1,12
172 BEC(13)=BEC(13)+BEC(I)
    BEJ=BEC(13)/12.
    BEC(12)=BEJ
    DIF=HE(13)-HE(1)
    HEI=HE(1)-DIF/AGA
    HE(12)=HEI
    HEE=HEI
    HEC(13)=0.
    DO 173 I=1,12
173 HEC(13)=HEC(13)+HEC(I)
    HEJ=HEC(13)/12.
    HEC(12)=HEJ
    DIF=P1(13)-P1(1)
    P1I=P1(1)-DIF/AGA
    P1(12)=P1I
    P1E=P1I
    P1C(13)=0.
    DO 174 I=1,12
174 P1C(13)=P1C(13)+P1C(I)
    P1J=P1C(13)/12.
    P1C(12)=P1J
    DIF=P2(13)-P2(1)
    P2I=P2(1)-DIF/AGA
    P2(12)=P2I
    P2E=P2I
    P2C(13)=0.
    DO 175 I=1,12
175 P2C(13)=P2C(13)+P2C(I)
    P2J=P2C(13)/12.
    P2C(12)=P2J
305 DIF=FF(13)-FF(1)
    FFI=FF(1)-DIF/AGA
    FF(12)=FFI
    FFE=FFI
    FFC(13)=0.
    DO 176 I=1,12
176 FFC(13)=FFC(13)+FFC(I)
    FFJ=FFC(13)/12.
    FFC(12)=FFJ
    DO 177 I=1,13
    HES(I)=P1S(I)=P2S(I)=FFS(I)=0.
177 CONTINUE
    GO TO 000
178 DO 179 I=1,13
179 HES(I)=P1S(I)=P2S(I)=FFS(I)=0.
    BE(13)=HE(13)=P1(13)=P2(13)=FF(13)=0.
    DO 180 I=1,12
    BE(13)=BE(13)+BE(I)
    HE(13)=HE(13)+HE(I)
    P1(13)=P1(13)+P1(I)

```

} Adjustment of benthos biomass

} Other biomass adjustment are similar and follow below

} Computation of annual mean biomass

PROGRAM SKEBUB 73/74 PFI=1 FTN 4.7+476 07/10/79 08.22.40

P2(13)=P2(13)+P2(I)
FF(13)=FF(13)+FF(I)

180 CONTINUE
BEE=BE(13)/12.
HEE=HE(13)/12.
PIE=P1(13)/12.
P2E=P2(13)/12.
FFE=FF(13)/12.

C ADD EXPERIMENT HERE
C*****

GO TO 600
190 DO 422 I=1,13
HES(I)=PIS(I)=P2S(I)=FFS(I)=0.

422 CONTINUE
BE(13)=HE(13)=P1(13)=P2(13)=FF(13)=0.
DO 191 I=1,12.

BE(13)=BE(13)+BE(I)
HE(13)=HE(13)+HE(I)
P1(13)=P1(13)+P1(I)
P2(13)=P2(13)+P2(I)
FF(13)=FF(13)+FF(I)

191 CONTINUE
BEM=BE(13)/12.
HEM=HE(13)/12.
P1M=P1(13)/12.
P2M=P2(13)/12.
FFM=FF(13)/12.

C RECRUITMENT CONTROL IN BIOMASS MODEL

G(2)=GB(2)*(BEE/BEM)
G(3)=GB(3)*SQRT(HEE/HEM)
G(4)=GB(4)*SQRT(PIE/P1M)
G(5)=GB(5)*SQRT(P2E/P2M)
G(6)=GB(6)*SQRT(FFE/FFM)

600 K=1

L=L+1

Augmentation of year count

PRINT 206,L

IF (L-K) 23, 23, 200

200 STOP

END

SUBROUTINE FOCONS(K,PW,SS,SP,CU,P,R,ZOC,BEC,HEC,PIC,P2C,FFC,L,LAL)

DIMENSION SP(13),CU(6),P(6),R(6),ZOC(13),BEC(13),

* HEC(13),PIC(13),P2C(13),FFC(13),N(6)

C SP - SPECIES

C CU - PERCENT COMPOSITION OF FOOD; INITIALLY PRESCRIBED

C P - PERCENT OF BIOMASS ALLOWED TO BE CONSUMED OF EACH FOOD ITEM

C K - PERCENT CONSUMED IN PREVIOUS MONTH

C S - STARVATION, PERCENT FOOD MISSING

C SMA - STARVATION, AMOUNT OF FOOD MISSING

C SS - PERCENT STARVATION

C SD - SUM OF PERCENT FOOD MISSING

C SC - SUM OF UNCHANGED PERCENTAGE OF FOOD

C K - MONTH

DO 1 I=1,6

N(I)=0

SC=SD=S=0.

SS=0.

IF(L-LAL)30,30,31

31 DO 2 I=1,6

F(R(I))4,4,2

5 IF(P(I)/R(I)-1.)3,4,4

3 D=CU(I)

CO(1)=P(I)/R(I)*CO(I)

O1=D-CO(1)

SD=SD+O1

N(I)=1

GO TO 2

4 SC=SC+CO(1)

2 CONTINUE

IF(SC-100.)19,30,30

19 IF(SC-40.)21,21,20

20 DO 18 I=1,6

IF(N(I))18,0,18

6 CU(I)=CU(I)+(CO(I)/SC)*SD

10 CONTINUE

GO TO 30

21 IF(25.-SD)23,22,22

22 DO 17 I=1,6

IF(N(I))17,7,17

7 CU(I)=CU(I)+0.65*(CO(I)/SC)*SD

17 CONTINUE

S=0.35*SD

GO TO 30

23 DO 16 I=1,6

IF(N(I))16,8,16

8 CU(I)=CU(I)+0.40*(CO(I)/SC)*SD

16 CONTINUE

S=0.60*SD

30 FOOD=PW*30.*SP(K)

ZLC(K)=ZOC(K)+FOOD*CO(1)*0.01

BEC(K)=BEC(K)+FOOD*CO(2)*0.01

HEC(K)=HEC(K)+FOOD*CO(3)*0.01

PIC(K)=PIC(K)+FOOD*CO(4)*0.01

P2C(K)=P2C(K)+FOOD*CO(5)*0.01

FFC(K)=FFC(K)+FOOD*CO(6)*0.01

SMA=FLDL*S*0.01

SS=SMA/FOOD

RETURN

END

Readjustment of food composition of "overconsumed" species and computation of changed and unchanged fractions

Readjustment of food composition of "fully" available food items and determination of starvation

Total food uptake

Partitioning of food uptake (consumption) between food items

SUBROUTINE PRIFLO 73/74 OPT=1 FIN 4.7+476 07/10/79 08.22.40

```
SUBROUTINE PRIFLO (LL,SP,CO,PCU,IS)
C LL - YEAR
C SP - SPECIES
C CO - CONSUMPTION
C PCU - PERCENT CONSUMPTION
C IS - SPECIES NUMBER
DIMENSION SP(13),CO(13),PCU(12)
PRINT 1,IS,LL,(SP(I),I=1,12)
1 FORMAT(//5X,16HBIOMASS, SPECIES,I4,4HYEAR,I4,12F7.0/)
CO(13)=0.
DO 2 I=1,12
CO(13)=CO(13)+CO(I)
2 CONTINUE
PRINT 3,IS,LL,(CO(I),I=1,13)
3 FORMAT(//5X,16HCONSUMPTION, SP.,I4,4HYEAR,I4,13F6.0/)
PRINT 4,IS,LL,(PCU(I),I=1,12)
4 FORMAT(//5X,17HPERCENT CUNS. SP.,I4,4HYEAR,I4,12F6.1/)
RETURN
END
```

BIOMASS, SPECIES 2YEAR 41 2024. 2152. 2313. 2427. 2560. 2600. 2506. 2571. 2548. 2555. 2598. 2643.

CONSUMPTION, SP. 2YEAR 41 141. 143. 170. 225. 293. 346. 354. 450. 420. 289. 250. 197. 3067.

PERCENT CONS. SP. 2YEAR 41 7.0 6.6 7.4 9.1 11.4 13.3 13.3 13.6 12.6 11.3 9.6 7.3

BIOMASS, SPECIES 3YEAR 41 2038. 2044. 2053. 2002. 2069. 2068. 2089. 2114. 2141. 2159. 2167. 2166.

CONSUMPTION, SP. 3YEAR 41 73. 82. 112. 156. 203. 213. 222. 213. 193. 163. 127. 90. 1849.

PERCENT CONS. SP. 3YEAR 41 3.6 4.0 5.5 7.6 9.8 10.3 10.6 10.1 9.0 7.5 5.9 4.1

BIOMASS, SPECIES 4YEAR 41 1990. 1975. 1995. 2041. 2103. 2105. 2231. 2276. 2287. 2249. 2203. 2140.

CONSUMPTION, SP. 4YEAR 41 107. 114. 143. 188. 236. 254. 267. 201. 248. 203. 164. 123. 2297.

PERCENT CONS. SP. 4YEAR 41 5.2 5.6 7.0 9.0 10.9 11.5 11.7 11.2 10.2 8.8 7.3 5.6

BIOMASS, SPECIES 5YEAR 41 727. 736. 740. 750. 764. 774. 796. 811. 819. 816. 807. 804.

CONSUMPTION, SP. 5YEAR 41 46. 51. 62. 77. 90. 100. 104. 101. 91. 77. 63. 52. 914.

PERCENT CONS. SP. 5YEAR 41 6.8 7.3 8.8 10.8 12.6 13.7 14.0 13.3 11.9 10.1 8.3 6.9

BIOMASS, SPECIES 6YEAR 41 1505. 1501. 1500. 1503. 1510. 1521. 1528. 1541. 1552. 1540. 1544. 1542.

CONSUMPTION, SP. 6YEAR 41 40. 40. 49. 63. 77. 94. 93. 92. 101. 67. 55. 43. 815.

PERCENT CONS. SP. 6YEAR 41 2.6 2.7 3.3 4.2 5.1 6.2 6.1 6.0 6.5 4.4 3.6 2.8

YEAR 42

Example of output