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NUMERICAL EVALUATION OF MARINE ECOSYSTEMS PART 2. DYNAMICAL NUMERICAL MARINE ECOSYSTEM MODEL (DYNUMES III) FOR EVALUATION OF FISHERY RESOURCES

by
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August 1978

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest and Alaska Fisheries Center
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CONTENTS

Abstract

1. Introduction

2. Objectives, basic principles, and general outline of the DYNUMES model.

   2.1 Objectives

   2.2 Basic principles

   2.3 General outline

3. Basic data inputs

   3.1 Computational grid and environmental data

   3.2 Biological data

   3.3 Data on ecosystem processes

4. Formulas and computation procedures

   4.1 Predation by marine mammals and birds

   4.2 Simulation of plankton data

   4.3 Growth, mortality, and consumption of benthos

   4.4 Fish ecosystem

      4.4.1 Migration

      4.4.2 Growth of the biomass

      4.4.3 Feeding

      4.4.4 Mortalities

      4.4.5 Fishery

5. List of symbols

6. References

ABSTRACT

A method of numerical dynamical deterministic reproduction of a marine ecosystem with emphasis on applications to fisheries problems is presented. Although such simulations are location dependent--i.e. greatly determined by the nature of the specific ecosystem components present in the region and by the availability of local research and survey results as well as by the intensity and nature of the exploitation of marine resources by man in the given region--the method gives a general basic framework of one type of marine ecosystem simulation model. Objectives, principles, and major computational formulas of the model, which has been applied by NWAFC to the eastern Bering Sea and the area around Kodiak Island in the Gulf of Alaska, are also presented. More detailed discussions on the input of local knowledge, other specific data and their validity, results of model applications, and the computer program documentation are available in NWAFC Processed Reports.

1. INTRODUCTION

Environment-biota and interspecies interactions have long been recognized, however, attempts to quantify these interactions have been limited due to difficulties in obtaining direct quantitative observations of these processes and assessing their role in the ecosystem. Recent requirements of management of fishery resources require the consideration of the total marine ecosystem, i.e. not only the effects of the fishery on the target species must be known and projected in time, but also the effects on other species via interspecies interactions as well as the effects of environmental anomalies on the marine ecosystem must be considered. In addition to the pure fisheries management

questions, there are now some very complex environmental questions related to petroleum and fish and fish versus marine mammals, which demand models of the total marine ecosystem. Large-scale, numerical simulation models offer possibilities for quantitative studies of such processes and interactions and such approaches have been fruitful for interaction studies, e.g. in the atmosphere and elsewhere. The development of numerical marine ecosystem simulation models has, however, lagged, and this is partly due to the complexities of such models and the necessity of using the largest available computers for complete marine ecosystem simulations.

Some ecosystem modeling concepts originated in the 1940's when relatively simple quantitative explanations of plankton production and standing crop changes with time were attempted. Simple quantitative models connecting different trophic levels in the ecosystem via food requirements were also attempted. Though these attempts were necessary steps in the development of modeling concepts, they did not produce much in the way of applicable results, while diverse empirical research on different aspects of the ecosystem continued to produce knowledge that emphasized the complexity of processes in the ecosystem per se.

The development of single-species population dynamics models for various commercial fish was also intensified in the 1940's and especially in the mid-50's when also some basis for multispecies theory of fishing was initiated (Beverton and Holt 1957). The single-species population dynamics models provided some useful bases for single-species fisheries management decisions. More complex approaches would have been impossible as large computers were not available at this time. Several simplifications had to be made, such as assuming the natural mortality, which includes predation, to be constant.

The conventional fisheries production models considered environmental interactions only to the extent of assuming stability or long-term equilibrium in the environment. The validity of such assumptions is, of course, questionable and it is now realized that these models are insufficient to answer the complex questions of modern fisheries management. Clearly, the future development of fisheries management models must consider space-time variable interspecies interactions, such as predation and environmental effects, which are known to affect the productivity of various components of the ecosystem.

Several numerical two- and three-dimensional ecosystem models have been developed, which deal essentially with planktonic organisms as the basis for marine productivity. The nutrient-plankton-fish energy pathways are, however, greatly variable in space and time, with great lateral losses (e.g. losses into deep water, remineralization, etc.) that are not yet fully understood or accounted for quantitatively. There are also many textbook-style graphical and descriptive ecosystem models available in the literature. Although some of these are useful in provoking thought, few produce any verifiable quantitative results. The large-scale, intensive numerical modeling of the environment, especially the synoptic, numerical, analysis-forecasting models in meteorology and lately also in oceanography, have been developed, especially in the 1960's, and provide methods and approaches which are suitable for, but have not heretofore been applied to ecosystem modeling. Many simulation techniques that could be applied to ecosystem models have also been developed in other fields.

The first complete numerical marine ecosystem model with emphasis on fisheries problems has recently been developed in Denmark (Andersen and Ursin 1977). As no communication existed between the Danish scientists and us during the respective model developments, both evolved considerably differently, however, both contain some approaches which are quasi-identical and some approaches which are better developed in one than in the other model. The Andersen-Ursin model has a rather involved mathematical basis, whereby implicit approaches are predominantly used, however, their model lacks the spatial resolution developed in ours. There are plans for cooperative studies and it is hoped that many if not all aspects of these two models will be combined in the near future.

2. OBJECTIVES, BASIC PRINCIPLES, AND GENERAL OUTLINE OF THE DYNUMES MODEL

2.1 Objectives

The main purpose of simulation modeling of the marine ecosystems is: initially to reproduce quantitatively the important components and processes; subsequently, through analysis, insight, or new data to improve our knowledge of the system; and finally, to tailor the model to man's needs from a scientific as well as applied points of view.

The objectives of numerical ecosystem simulation models can be grouped into two main categories:

(A) Investigative and digestive (analytical) objectives that permit quantitative biological resource evaluations, including:

—Synthesis (analysis) of available information, such as quantification of descriptive data (e.g. migrations, feeding habits, etc.) and quantitative summarization of exploratory studies.

—Quantitative numerical simulation of the ecosystem with all essential distributions, processes, and interactions.

—Quantitative determination of the effects of environment and interspecies interactions and other natural fluctuations on the distributions and abundance of biotic components of the system.

(B) General management guidance and effects of exploitation objectives, including:

—Determination of the magnitude or status of the exploitable resources, their past and expected future fluctuations as response to ecosystem internal factors, such as reproductive capacity, or to external factors, such as fisheries.

—Determination of the effects of varying fishing intensity (including spatial and temporal changes in distribution of fishing effort) on the resources, and determination of the effects of proposed regulations.

—Establishment of research priorities, i.e. for obtaining of missing data or for better quantification of available essential information.

Among the initial scientific uses of the model have been the study of the quantitative effects of environmental anomalies (e.g. temperature--through the effects on growth, basic food availability, and partial population movements in relation to optimum environmental conditions) on the abundance and distribution of single species as well as on the changes of the ecosystem as a whole. Furthermore, the model has been used for determination of the "carrying capacities" of given regions and for the study of natural fluctuations of abundance of species as caused by various ecosystem internal factors (e.g. cannibalism).

Applied aspect studies include the quantitative determination of the effects of space and time variable fishery on a given species as well as its indirect effects (mainly via trophic relations) to other species, and simulation studies of quantitative effects of oil development on the site-surrounding marine ecosystem.

2.2 Basic principles

The following basic principles of our ecosystem simulation help explain the model and can serve as the bases for modeling approaches:

—The ecosystem model should include all of the essential biological and environmental components. This is essential for realistic depiction of all interactions in the system. However, practical considerations (e.g. computer core (size)) do not allow the inclusion of all species per se; therefore, ecologically similar species can be grouped into ecological groups using trophic factors, (feeding habits and food composition), living space (e.g. pelagic, coastal, etc.), and life span as criteria.

—It should have proper space and time resolution, i.e. be four-dimensional (three space and one time dimension), thus the model must have a two-dimensional computational grid, the third space dimension can be implicit (e.g. surface or bottom layer).

—It should have an initial diagnostic phase--i.e. analysis of initial conditions (analysis of distributions of species in space at a given initial time), and the model must be prognostic (predictive, time dependent) and capable of determining in four dimensions the state of the system when all the specified processes are active.

—It should work in time steps (maximum time step would be one month) and account for all essential processes at each grid point and time step which are active in the ecosystem and on which general, local, and/or special knowledge is available.

—Theoretical conceptualization should be avoided, unless it has been tested with empirical data and proven to be valid.

—Explicit approaches, free from mathematical artifacts, should be preferred and used. Thus available, proven modeling approaches, combined with new additional ones, should be used.

—Trophodynamic computations on biomass balance should start with apex predators at the upper end of the organic matter circulation, i.e. its removal by man (fishery) and by marine mammals and birds, followed by fish and other ecosystem biotic components. The start of the computations from the lower end--i.e. with basic organic production, does not lead to any reliable results, mainly because the pathways of basic organic production to secondary production are very variable in space and time and not fully known quantitatively. Furthermore, the simple food web (food pyramid) approach, so prevalently used in the past in attempts of marine fishery production evaluation, has been abandoned as unrealistic in light of the complex food relations.

—There should be open pathways into the model to enter actual and potential effects of man on the ecosystem (fishery, oil development effects, etc.) and there must be multiple verification possibilities.

2.3 General outline

No single or simple theory, and no simple primitive equation formulations are possible for the marine ecosystem. This system must be presented and simulated with a set of equations of considerable size, reproducing individual processes and distributions. However, three important processes dominate quantitatively, controlling the abundance and distribution of individual components--growth, predation, and migration. Each of these processes is in turn controlled by a relatively complex set of conditions. The above can be demonstrated in mathematical notation as follows:

The biomass of any given population is a function of time and location ($P = f\ (t,x,y,x)$). The individual time change of this population ($\frac{dP}{dt}$) is:

$$\frac{dP}{dt} = \frac{\partial P}{\partial t} + \frac{\partial P}{\partial x} V_x + \frac{\partial P}{\partial y} V_y + \frac{\partial P}{\partial z} V_z \qquad (1)$$

The first term on the right side ($\frac{\partial P}{\partial t}$) is the local time change and the following three terms represent migrations and advection. These migration terms comprise several processes, such as spawning and feeding migrations, dispersal and aggregation, migrations caused by unfavorable environmental conditions, and transport by currents. The migration terms determine largely the spatial distribution of most species/ecological groups. These terms never vanish; however, if we consider a large region (such as the Bering Sea), we may assume that the migrations into and out of this large region are negligible and that the migration term is 0. In this case individual change equals local time change. The local time change is largely a function of biomass growth (G) and its removal (R), the latter comprising mainly predation, mortality, and the fishery.

$$\frac{\partial P}{\partial t} = f(G,R) \tag{2}$$

If we consider that an equilibrium might exist (which, however, is very unlikely) in an ecosystem over one year, then $\frac{\partial P}{\partial t} = 0$ and

$$dG = dR \tag{3}$$

The above is the criterion for finding "equilibrium biomasses" with a deterministic Bulk Biomass Model (BBM) (Laevastu and Favorite 1978a).

Biomass growth of any given species is a function of the age of the species, time of the year (also in relation to e.g. spawning), food availability, and environmental conditions.

$$\frac{\partial G}{\partial t} = f(A_i, t, F, T) \tag{4}$$

The removal is a complex space-time function of many variables, such as food requirements of many components of the ecosystem, mortalities from various causes, etc.

$$\frac{\partial R}{\partial t} = f(t,x,y,z,q_1 \ldots q_n, m, s, k, f_f \ldots) \tag{5}$$

Thus it becomes apparent that quantitative computation of changes in the ecosystem requires the use of numerous explicit equations. Consequently the numerical ecosystem simulation becomes, to a large extent, the accountability of growth, removal (predation and mortalities), and the changing biomass imbalance in nature.

For such computations a special grid over a given area is required (see 3.1). First, some necessary auxiliary data are digitized in this grid, such as sea-land and statistical area tables and depths. Next, numerical values of monthly surface and bottom temperatures and apex predators (mammals, birds, etc.) are prescribed at each grid point. The initial distributions and abundances of species/ecological groups are also introduced with numerical values in the grid.

The grouping of ecologically similar species in the model is necessary in order to have a program of manageable size; on the other hand, provisions exist to consider individual species or even year classes for the special studies. These initial first guess values are usually obtained either from the BBM model or from extensive exploratory surveys. Numerous species specific coefficients (such as growth coefficients, food requirement, and fishing mortality coefficients, etc.) are introduced in the species computation subroutines. Then first guess fields of species/ecological groups are tuned to equilibrium state ($\frac{\partial P}{\partial t} = 0$) in the initial analytical phase of the model runs. In the prognostic phase of the model no equilibrium condition is imposed.

The schematic sequencing of the main body of the model is shown in Figure 1. The predation by apex predators is computed first. As the estimates of the numbers of apex predators is, in most cases rather uncertain, a steady-state condition is assumed.

The migrations (e.g. spawning and feeding migrations) of the species and resulting distributions are computed in each time step--weekly and/or monthly--in the species dynamics subroutines. In addition, the effects of the environment (e.g. temperature anomalies) and food availability during migrations are computed with relatively conservative assumptions.

Growth of biomasses, fishery losses, and mortalities are computed in each time step, using proper empirical coefficients. The monthly predation of the given species is taken from the summation of predation on this species in the previous month. Food composition is variable in space (from grid point to grid point) and in time, depending on the availability of food items. Food uptake as well as growth are influenced in the model by environmental factors with relatively conservative assumptions.

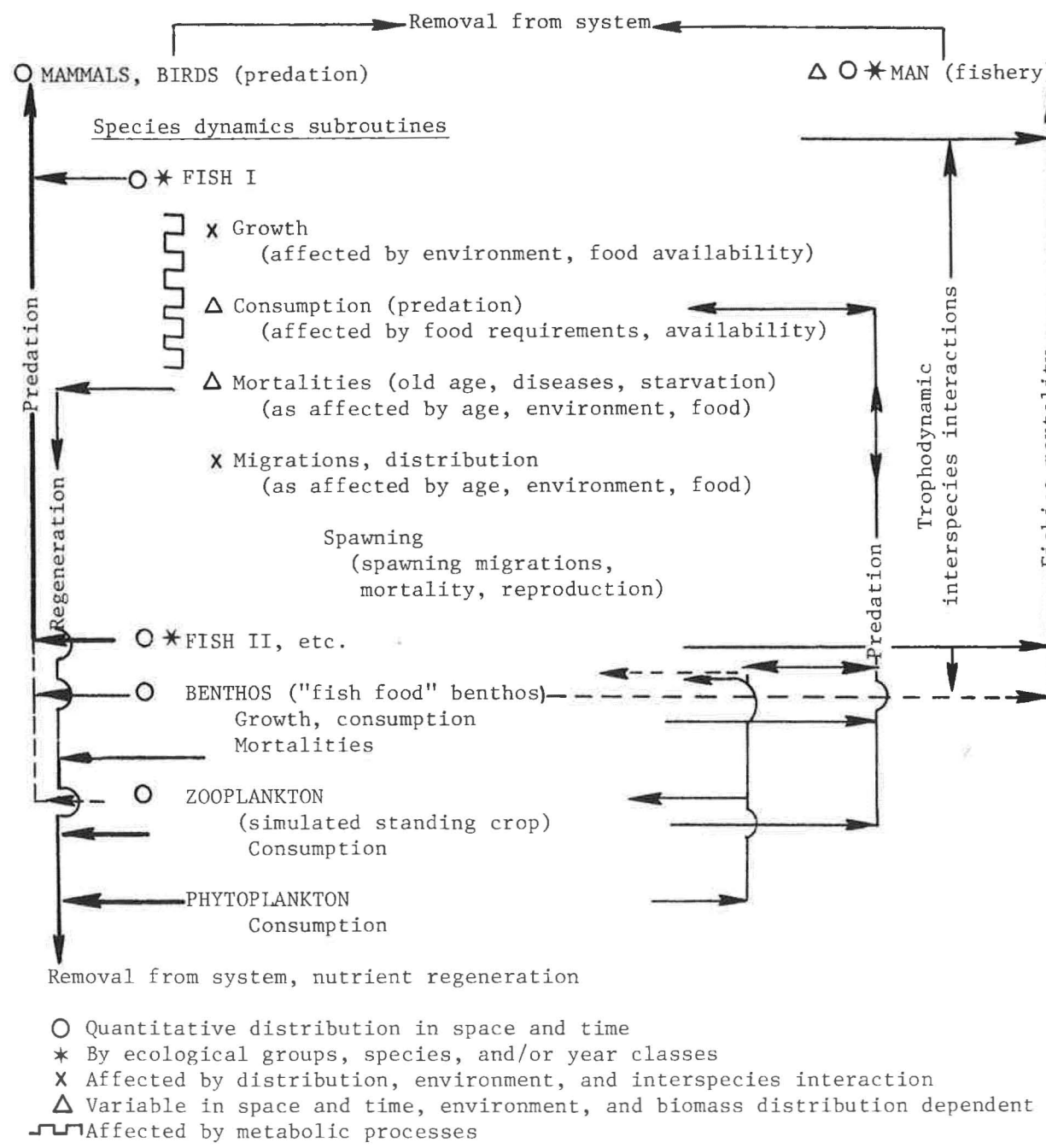

Figure 1.--Schematic outline of DYNUMES III

The standing stocks of plankton are simulated as functions of location and time. The results of these simulations have indicated that existing data are inadequate, thus plankton data are used only in a comparative manner, and do not restrict the computations of other biomasses. The quantitative knowledge of plankton and its space time variation are rather uncertain in most ocean areas. Computations of growth, grazing, and distribution of benthos are carried out only on that portion suitable as fish food; predatory benthos, about which the knowledge is scanty, is not taken into consideration in subsequent computations.

Great flexibility is allowed in the selection of model outputs, such as monthly distributions of individual species, results of processes, predation, species source and sink areas, etc.

3. BASIC DATA INPUTS

3.1 Computational grid and environmental data

The computational grid should be preferably designed on an equal area projection (e.g. polar stereographic) and should not exceed 1,000 grid points (re. computer core requirements). The boundaries of the computation area should preferably coincide with the boundaries of natural (or faunal) regions. A computation area with a small grid and several open boundaries, such as the one presented on Figure 2, would often require the specification of seasonal migration of many species through the boundaries.

The grid mesh length (grid size) selection is often dependent on the size of the region selected for the model. In past work, we have used mesh length from 18.5 km (Kodiak region on Figure 2) to 190 km (North Pacific salmon ecosystem model).

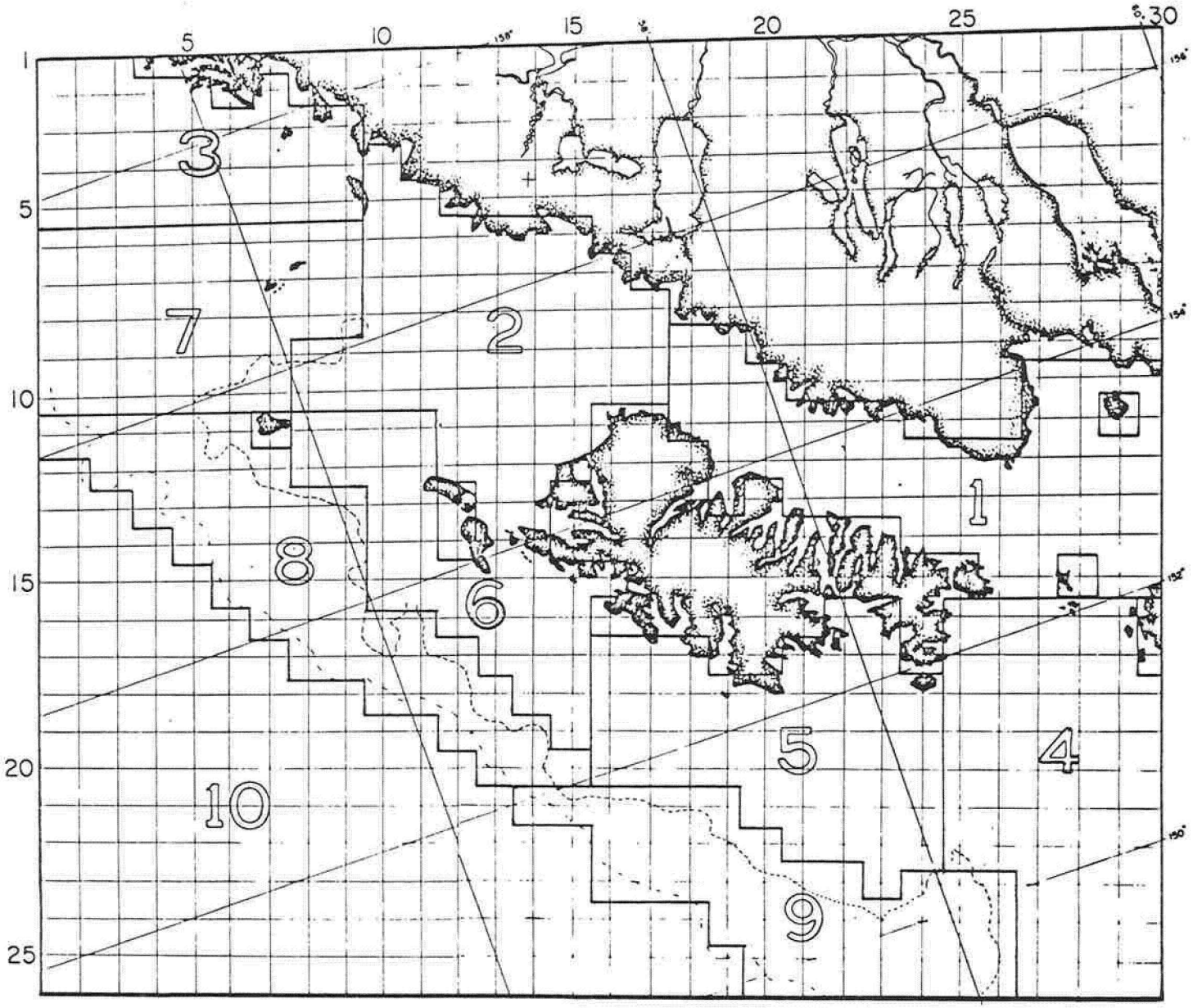

Figure 2.--Computational grid with subregions for Kodiak and in the Gulf of Alaska.

The normal computational time step is one month. However, some computational stability considerations require shorter time steps, especially in migration subroutines. The migration stability criterion is dependent on the grid length (ℓ) and the maximum migration speed component (V_{max}):

$$\Delta t \leq \frac{\ell}{|V_{max}|} \tag{6}$$

It is advantageous to divide the computation region into subregions. A digitized index field is prepared and input into the program, in which the grid points over land are designed 0 and over the ocean 1 or the actual subregion number at these gridpoints falling into designed subregion (see Figure 2).

At each grid point the digitized depth (in meters), monthly long-term mean surface and bottom temperatures are also required. Temperature anomalies are introduced by changing the digitized long-term monthly mean temperatures at desired grid points and/or subregions.

3.2 Biological data

The inputs of biological data are considerably dependent on the region under consideration and on the availability of original data. Thus, only a few general notes on this subject are given below.

Seasonal numbers of apex predators (marine mammals, birds, and sharks) are estimated for each subregion from available data. These seasonal data are interpolated to months, the numbers converted to weights, and the resulting biomasses computed for grid points in the subregions.

The inputs of first guess fields of fish species/ecological groups (for e.g. January) originate from preanalysis with the BBM model or from extensive exploratory surveys. The data from the latter must be corrected using catchability coefficients and recomputed to total biomass (i.e. including juveniles). The distribution of biomasses between juveniles and the exploitable part of the biomass is obtained from another model (Laevastu and Favorite 1978b).

The phyto- and zooplankton biomasses are simulated in the model and tuned to available empirical data. No further use is made of these biomasses in the computations, except at a later stage for evaluation of their utilization by the rest of the ecosystem.

The fish food benthos biomass is simulated on the basis of empirical knowledge of standing crops of this benthos component in respect to depth, distance from the coast, and type of bottom. The predatory benthos is usually not included in the model because it can be considered an apex predator of benthos, its influence on the rest of the ecosystem is small, and quantitative knowledge on this benthos component is usually inadequate.

3.3 Data on ecosystem processes

The migration speeds of individual species/ecological groups must be digitized at the grid points as u and v components in km/day. These speeds are deduced from empirical knowledge about the seasonal occurrence and migrations (including feeding and spawning migrations). The migrations due to unfavorable temperature and/or scarcity of food are simulated within the model.

Many species-specific coefficients are needed in the model. The biomass growth coefficient varies with age and its derivation from empirical data requires the knowledge of the distribution of biomass with age, which is computed in an auxiliary model (Laevastu and Favorite 1978b). The growth coefficient must be adjusted to computational time step, e.g. percent per month.

The dominant component of natural mortality--predation, is computed in detail within the model itself (see 4.4). The mortalities from old age and diseases are small in exploited populations as compared to predation and fishing mortalities. These mortalities can be estimated subjectively or by the use of the abovementioned auxiliary model, which gives the total mortality in different age groups, from which predation and fishing mortalities are subtracted, leaving the rest as old age and disease mortality. Starvation mortality is estimated in the model by increasing the old age mortality slightly in proportion to the degree of starvation at the times and grid points where food availability computations so indicate.

Seasonal or annual mean composition of food (in percent) must be prescribed for each species/ecological group, using available data and by considering size dependent feeding and change of food composition with the age (size) of the species. The food composition tables are used as guidance in the model. The actual composition of food can vary from grid point to grid point, depending on relative abundance of food items. The trophic interspecies interactions in the model are largely dependent on the relative species composition of the food of all species.

The food requirement coefficient is divided into two parts in the present model: food requirement for growth and food requirement for maintenance. The values of the coefficients vary from species to species, depending on activity, growth rates, and normal environmental temperature (re. metabolism). The food requirement for growth is given as the ratio growth/food required--and this ratio varies between 1:1.25 and 1:2. The food requirement for maintenance is given as percent body weight daily (varying between 0.6 and 1%).

There are, in addition, a number of auxiliary coefficients which are briefly discussed in the following section together with the formulas where these coefficients are used.

4. FORMULAS AND COMPUTATION PROCEDURES

4.1 Predation by marine mammals and birds

Due to uncertainties in the estimates of marine mammals, birds, and other apex predators present in any given region, it is not necessary to compute their growth and mortality (except in special studies emphasizing the apex predator aspects of ecosystems). Thus, only predation by apex predators is computed in the present model:

$$F_{a(t,n,m)} = B_{a(t,n,m)}\, q_a\, t_d \qquad (7)$$

The consumption of species i by predator a is:

$$C_{i,a(t,n,m)} = C_{a(t,n,m)}\, p_{i,a} \qquad (8)$$

Consumption of species i by all apex predators is the sum:

$$C_{i,A(t,n,m)} = C_{i,a(t,n,m)} + C_{i,b(t,n,m)} + \ldots C_{i,n(t,n,m)} \qquad (9)$$

The coefficients p and q are from empirical data, $p_{i,a}$ is the fraction of species i in the food of species a and is taken from the prescribed food composition for the given species, and q_a is the food requirement in terms of fraction of body weight daily. This varies from one mammal species to another (4 to 8% body weight daily) and for birds it is 12 to 20% body weight daily.

4.2 Simulation of plankton data

The standing crops of phyto- and zooplankton is simulated with a harmonic formula, which can be tuned to reproduce the known seasonal cycles:

$$P_{s(t,n,m)} = P_{r,o} + A_{1,r}\cos(\alpha_1 t - \mathcal{H}_1) + A_{2,r}\cos(\alpha_2 t - \mathcal{H}_2) \qquad (10)$$

The annual mean standing stocks for given subregions ($P_{r,o}$), the half-ranges of primary and secondary annual "peaks" ($A_{1,r}$ and $A_{2,r}$) and their phase lags ($\mathcal{H}_1$ and $\mathcal{H}_2$) must be obtained from available measurements.

4.3 Growth, mortality, and consumption of benthos

The initial standing stock of benthic fish food is prescribed (digitized) at each grid point. It is assumed to be a function of depth, bottom type, distance from the coast, and the prevailing bottom temperature

$$B_{ob(n,m)} = f\ (D, B_s, L_c, T_b) \qquad (11)$$

The growth mortality and consumption of the benthos biomass is computed in each time step.

$$B_{b(t,n,m)} = B_{b(t-1,n,m)} \ (2 - e^{-g}) \ e^{-m} - C_{b(t-1,n,m)} \qquad (12)$$

Growth coefficient (g) and mortality coefficient (m) are estimated from available empirical data (ca 10 and 3% monthly) and consumption (C_b) is computed in the model.

4.4 Fish ecosystem

4.4.1 Migrations

There are several reasons for fish migrations (feeding, spawning, temperature/depth preferences, etc.) and consequently the nature of the migration process can be different. In some cases only a portion of the biomass undertakes the migration (e.g. seasonal depth migrations of flatfish, spawning migrations). In each case, the portion of biomass involved in the migration must be estimated and separated quantitatively from the rest during computation of migrations.

The U and V components of migration speeds are determined from empirical data. An "upcurrent interpolation and direct advection" quantitative migration computation has been found mass conserving and applicable in our model. This computation is done in two steps, first the linear gradient of biomass in the "upcurrent" is determined.

U positive:

$$UT_{(n,m)} = (B_{n,m} - B_{n,m-1}) \ / \ell \qquad (13)$$

U negative:

$$UT_{(n,m)} = (B_{n,m} - B_{n,m+1}) \ / \ell \qquad (14)$$

V positive:

$$VT_{(n,m)} = (B_{n,m} - B_{n-1,m}) \ / \ell \qquad (15)$$

V negative:

$$VT_{(n,m)} = (B_{n,m} - B_{n+1,m}) \ / \ell \qquad (16)$$

Thereafter the gradient is advected to the grid point under consideration:

$$B_{(t,n,m)} = B_{(t-1,n,m)} - (t_d|U_{(t,n,m)}|UT_{(n,m)}) - (t_d|V_{(t,n,m)}|VT_{(n,m)}) \quad (17)$$

If a species is transported by current, the same method is used for computation of advection, except the U and V are current speed components. This calculation (17) also has a stability criterion, see (6).

After migration computations a smoothing (diffusion) operation is performed. "Diffusive migrations" are assumed to occur also on fishing and feeding grounds and after spawning, and this smoothing operation is applied several times in the computations:

$$B_{(n,m)} = \alpha B_{(n,m)} + \beta\ (B_{n-1,m} + B_{n+1,m} + B_{n,m-1} + B_{n,m+1}) \quad (18)$$

α is a diffusion coefficient (0.80 to 0.96) and β is $(1-\alpha)/4$.

Fish are migrating in search for food and are forced to alter paths if environmental conditions get unfavorable (e.g. too cold or too warm). These migrations are treated in the model in the following manner: Each species is assigned upper and lower limits of optimum temperature and lower food concentration (density) limits for the most important food items. Tests are made at each grid point and time step of these criteria. If the criteria are exceeded, the gradients of surrounding points are tested and a portion of the biomass at unfavorable grid points is moved towards more favorable conditions:

$$B_{i(n,m)} = B_{i(n,m)} - k_o B_{i(n,m)} \quad (19)$$

$$B_{i(n\pm1,m\pm1)} = B_{i(n\pm1,m\pm1)} + k_s B_{i(n,m)} \quad (20)$$

The coefficient k_o depends on the amount values exceed the prescribed criterion and on the number of computational passes (ca 0.03 in two-pass operation). Coefficient k_s depends in addition on the number of favorable surrounding points (two-pass value is ca 0.008 to 0.03).

4.4.2 Growth of the biomass

The biomass growth can be computed with a formula similar to compound interest computation:

$$B_{i(t,n,m)} = B_{i(t-1,n,m)} \ (2 - e^{-g}) \tag{21}$$

The time step in the model is sufficiently short so that second order terms can be neglected. The growth coefficient is obtained from empirical data and must correspond to the time step used in the model. This growth factor is variable (species and region dependent) and changed due to factors affecting the growth. In some species it is made a function of time (i.e. seasonal variations in growth).

$$g = g_o + A_g \cos (\alpha t - \mathcal{H}_g) \tag{22}$$

In other "temperature sensitive" species the growth is made a function of either surface or bottom temperatures.

$$g - k_t g_o e^{\frac{-1}{T(n,m)}} \tag{23}$$

Temperature (T) is restrained between 1 and 18°C and the coefficient k_t is slightly larger than 1 and is species dependent. Furthermore, the growth is dependent on the degree of starvation.

$$g = g_o - \frac{S_{i,f(n,m)}}{F_{i(n,m)}} \ g_o \tag{24}$$

The food needed by the biomass of species i in a given location ($F_{i(n,m)}$) and the shortage of food to satisfy the food requirement of the species ($S_{i,f(n,m)}$) are computed in the model.

The biomass change formula (growth, mortality, and predation) excluding fishery is:

$$B_{i(t,nm)} = B_{i(t-1,n,m)} \ (2-e^{-g}) \ e^{-m} - C_{i(t-1,n,m)} \qquad (25)$$

The mortality (m) and consumption (predation) (C_i) computations are discussed below.

4.4.3 Feeding

The amount of food required by species i is composed of food requirement for growth and food requirement for maintenance:

$$F_{i(t,n,m)} = B_{i(t,n,m)} \ (1-e^{-g}) \ r_i + q_i - B_{i(t,n,m)} \qquad (26)$$

The consumption of a species (C_i) is the sum of the consumption of this species by all other components of the ecosystem. With "fixed" food composition the consumption would be:

$$C_{i(t,n,m)} = F_{i(t,n,m)}p_{i,i} + F_{j(t,n,m)}p_{i,j} + \ldots F_{n(t,nm)}p_{i,n} \qquad (27)$$

The feeding is food density (availability) dependent. Thus, the fractional composition of food can vary from grid point to grid point and from one time step to another. Furthermore, partial starvation can occur. The food requirement of species i with respect to species j as a food item consists of three terms:

$$F_{i,j(t,n,m)} = F_{i(t,n,m)}p_{i,j}a_{j(t,nm)} + F_{i(t,n,m)}p_{i,j}b_{j(t,n,m)} + F_{i(t,n,m)}p_{i,j}C_{j(t,n,m)} \qquad (28)$$

The first term at the right hand side is the amount of species j taken as food. This is controlled by availability factor of species j at given grid point (a_j). This factor is a function of the fraction of the biomass of species j consumed at this location in previous time step. This factor

varies from species to species and simulates partly size dependent feeding (e.g. for fish the fraction consumed the previous month is restrained between 0.22 and 0.1 and the corresponding value for a_j varies from 0.1 to 1.0). The second term presents the amount of species j consumed on the bases of starvation array requirements. This consumption is controlled by constant b_j which is dependent on the amount in the starvation array of the given species (i), location, and time-step, and the fraction of biomass of species j consumed in the given location.

The last term on the right hand side presents the requirement of species j as food for the species i, which cannot be satisfied from available biomass at given location and time, and is added to the starvation array.

4.4.4 Mortalities

The mortality coefficient for old age and diseases is estimated as described earlier and the biomass mortality is computed with the conventional formula:

$$B_{i(t,n,m)} = B_{i(t-1,n,m)} \, e^{-m} \qquad (29)$$

In some species the mortality coefficient is slightly increased at the grid points where severe starvation is computed. Furthermore, a very small spawning mortality is computed experimentally on some species during the months of spawning. It is emphasized that the mortality coefficient "m" does not represent the past conventional "natural mortality", but is about one order of magnitude smaller. The past conventional natural mortality included predation mortality, the latter is being computed in our model separately and in detail.

4.4.5 Fishery

The fish catches are computed using a time and space variable fishing mortality coefficient:

$$P_{u,i(t,n,m)} = B_{i(t,n,m)} - B_{i(t,n,m)} e^{-f_{i(t,n,m)}} \qquad (30)$$

In some species only a time variable fishing mortality coefficient is available. The fishing mortality coefficient used in this model is not the corresponding past conventional fishing mortality coefficient, but a coefficient which is computed and tuned to time step, catches and biomass of the species present.

Many additional details of the model are found in the FORTRAN code of the program (Laevastu 1978). Further details of the outputs and results of the model applications are available in other NWAFC processed reports (Laevastu and Favorite 1977, Alton, Laevastu and Livingston 1978).

5. LIST OF SYMBOLS

A_i - age of species i.

A_g - half of the annual range of growth coefficient change.

$A_{1,r}$ - half-range of annual main (spring) plankton maximum.

$A_{2,r}$ - half-range of annual secondary (fall) plankton maximum.

a_j - fraction of species j requirement as food satisfied (taken from available biomass.

B - biomass.

B_a - biomass of apex predator a.

B_b - fish food benthos biomass.

B_{ob} - initial fish food benthos biomass.

B_s - type of the bottom substrata

b_j - fraction of the species j requirement as food taken on the bases of starvation array requirements.

C_b - consumption (predation) of fish food benthos.

C_i - consumption of species i.

$C_{i,a}$ - consumption of species i by apex predator a.

$C_{i,A}$ - consumption of species i by all apex predators.

$C_{i,j}$ - consumption of species i by species j.

C_j - fraction of the requirement for species j as food, which cannot be satisfied due to low food concentration in given location, and is added to starvation array.

D - depth.

è - base of natural logarithms.

F - food availability

F_a - consumption of an apex predator

F_i - amount of food required by species i.

$F_{i,j}$ - amount of species j (required) in the food of species i.

f_f - fishing mortality.

$f_{i(t,n,m)}$ - time and space dependent fishing mortality coefficient.

G - biomass growth.

g - growth coefficient.

g_o - basic growth coefficient.

k - spawning mortality.

k_o - fraction of biomass leaving "unfavorable" grid point.

k_s - fraction of biomass arriving at given grid point from neighboring "unfavorable" grid point.

k_t - coefficient.

L_c - distance from coast.

ℓ - grid length, km.

m - mortality coefficient (from old age and diseases).

m - mortality coefficient (general).

M - space coordinate.

n - space coordinate.

P - population (biomass).

$P_{i,a}$ - decimal fraction of species i in the food of apex species a.

$P_{i,j}$ - fraction of species j in the food of species i.

$P_{r,o}$ - annual mean of plankton standing stock in subregion.

P_s - plankton standing stock.

P_u - catch (fishery)

q_a - food requirement of apex predator a (in % of body weight daily).

q_i - food requirement of species i (in % of body weight daily).

$q_i \ldots q_n$ - food requirements of species i to n.

R - biomass removal (predation, mortality, and fishery).

r_i - ratio of growth to food required for growth.

$S_{i,t}$ - shortage of food of species i ("starvation").

s - starvation mortality.

T - temperature.

T_b - bottom temperature.

t - time.

t_d - time in days.

U - u component of migration speed.

UT - "upcurrent" (upmigration) gradient of biomass (u component)

V - v component of migration speed.

V_{max} - maximum migration speed component.

VT - "upcurrent" (upmigration) gradient of biomass (v component).

V_x - speed (migration) in x direction.

x, y, z - space coordinates.

Δt - time step (days).

$\frac{dP}{dt}$ - individual change of population biomass.

$\frac{\partial P}{\partial x}$ - gradient of P (in x direction).

α - smoothing coefficient (horizontal diffusion coefficient).

α_1, α_2 - phase speed (e.g., degrees per month).

β - $(1-\alpha)/4$ (secondary smoothing coefficient).

$\mathcal{H}_g$ - phase lag of annual growth coefficient change.

$\mathcal{H}_1, \mathcal{H}_2$ - phase lag (month of annual maximum).

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