Northwest and
Alaska
Fisheries Center

National Marine
Fisheries Service

U.S. DEPARTMENT OF COMMERCE

NWAFC PROCESSED REPORT 79-11

HOLISTIC SIMULATION MODELS OF SHELF SEAS ECOSYSTEMS

July 1979

This report does not constitute a publication and is for information only. All data herein are to be considered provisional.

NOTICE

This document is being made available in .PDF format for the convenience of users; however, the accuracy and correctness of the document can only be certified as was presented in the original hard copy format.

Inaccuracies in the OCR scanning process may influence text searches of the .PDF file. Light or faded ink in the original document may also affect the quality of the scanned document.

HOLISTIC SIMULATION MODELS OF SHELF SEAS ECOSYSTEMS

By

T. Laevastu and F. Favorite*

*Resource Ecology and Fisheries Management Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112

CONTENTS

1. OBJECTIVES AND PRINCIPLES OF NUMERICAL ECOSYSTEM SIMULATION.

2. MODELING DEVELOPMENTS LEADING TO HOLISTIC ECOSYSTEM SIMULATION.

3. BASIC COMPONENTS AND PROCESSES OF A MARINE ECOSYSTEM AND THEIR SIMULATION.

   3.1 Components and processes in a basic marine ecosystem simulation.

   3.2 Some basic mathematical formulations used in the simulations.

   3.3 Input data on the biota and biological processes.

   3.4 Environment and biota interactions and coupling of simulations.

4. SIMULATION OF EQUILIBRIUM BIOMASSES AND THEIR LONG-TERM FLUCTUATIONS.

5. EXAMPLES OF RESULTS FROM SOME HOLISTIC ECOSYSTEM MODELS.

6. VERIFICATION AND VALIDATION.

7. USE OF ECOSYSTEM SIMULATIONS IN RESEARCH GUIDANCE AND IN RESOURCE MANAGEMENT.

8. LIST OF SYMBOLS.

9. REFERENCES.

HOLISTIC SIMULATION MODELS OF SHELF SEAS ECOSYSTEM

T. Laevastu and F. Favorite
National Marine Fisheries Service
Northwest and Alaska Fisheries Center
Seattle, Washington 98112

I. OBJECTIVES AND PRINCIPLES OF NUMERICAL ECOSYSTEM SIMULATION

Man's scientific curiosity as well as his desire to exploit the food resources of the sea drive him to extend his knowledge of marine biology and processes within the marine ecosystem, to assess the abundance of marine resources, their behavior and distribution, and to ascertain the response of these resources to the fishery and possible environmental changes.

In order to obtain a coherent picture of the marine ecosystem we need to summarize the available information quantitatively and in a systematic manner. This task can be accomplished to a considerable extent by large ecosystem simulations on large computers.

Numerical ecosystem simulation is defined here as numerical reproduction of conditions and processes in the marine ecosystem, based on all available data and knowledge. It might be useful to differentiate between ecosystem models and ecosystem simulations although these terms have been used as synonyms. We usually consider a model to be an abstraction and simplification of a given condition and/or process, whereas a simulation is a reproduction of a system of conditions and processes based on available empirical data and may contain many tested models.

This paper describes a holistic simulation model in which the emphasis is given to the role of fish in the ecosystem. Ecosystem models which consider primarily plankton are not described here as several description of them are available in existing books (e.g. Kremer and Nixon, 1977). Rather than giving a general review of holistic ecosystem modeling, this paper describes and provides basic formulas of the Dynamical Numerical Marine Ecosystem (DYNUMES) simulation.

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

(1) Investigative and digestive (analytical) objectives, including basic ecological research, that permit quantitative determination of the state of the ecosystem, determination of the effects of environmental changes and interspecies interactions in space and time, and the establishment of research priorities.

(2) General management guidance, the assessment of fisheries resources, and the effects of exploitation.

The following basic principles are normally followed in ecosystem simulation.

—The ecosystem simulation must include all of the essential biological and environmental interactive components of the system.

—The ecosystem simulation should have proper space and time resolution, i.e. be three- to four-dimensional (two to three space and one time dimension), and must have a diagnostic and a prognostic phase.

—Theoretical conceptualizations should be avoided, unless they have been tested with expirical data and proven to be valid.

—Explicit approaches, free from mathematical artifacts, should be preferred, i.e. the mathematical formulas used in the model must reproduce known processes rather than assuming that a mathematical formula presents the behavior of a system.

—Biomass balance and trophodynamic computations should start with apex predators (including man); these can be treated as "forcing functions" of the system.

It has been amply demonstrated in the past that the start of trophodynamic computations from the lower end--i.e. basic organic production, does not lead to reliable quantitative results because the pathways of basic organic production to secondary and tertiary production are very variable in space and time and not fully known quantitatively. Many separate plankton production models exist, which try to alleviate these shortcomings.

2. MODELING DEVELOPMENTS LEADING TO HOLISTIC ECOSYSTEM SIMULATION

First attempts to develop mathematical models for fish and other animal populations were made between 1910 and 1925 by Ross, Kevdin, Baranov, and Alm. The models proposed and used by these early pioneers comprised predator-prey relations in some form.

Ecosystem modeling concepts originated in the 1940's when relatively simple quantitative explanations of plankton production were attempted by connecting different trophic levels in the ecosystem via food requirements. The development of single-species population dynamics models for commercial fish was also intensified in the mid-50's when also some basis for multispecies theory of fishing was initiated (Beverton and Holt, 1957). More complex ecosystem approaches would have been impossible as large computers were not available at this time.

Several numerical two- and three-dimensional ecosystem models have been developed in the recent past, which deal essentially with planktonic organisms as the basis for marine productivity, e.g. Kremer and Nixon, 1977. 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 accounted for quantitatively. The large-scale, numerical analysis-forecasting models in meteorology and oceanography developed in the 1960's, have provided methods and approaches which are suitable for, but were until now not applied, to ecosystem modeling.

New needs have recently arisen for ecosystem models. It has become clear that successful fisheries management requires the consideration of the total marine ecosystem because, for example, the fishery on one species affects the abundance and distribution of other species through interspecies interactions, such as predation.

A comprehensive quantitative marine ecosystem simulation model with emphasis on fish components of the ecosystem, has been developed recently in Denmark (Andersen and Ursin, 1977), that includes also primary production and phosphorus circulation. This model, as any extensive simulation model, seeks numerical solutions for established formulations. Various forms of their simulation use 14 to 81 entities of plants, animals, and nutritive matter, calling for simultaneous solution of from 42 to 308 differential equations.

The model emphasizes trophodynamics as does the simulation described in this chapter. Growth rates of all species in their model are also a

function of the season and availability of food. They have also partitioned natural mortality into various components such as predation mortality, spawning strain, starvation and disease mortalities.

The Andersen and Ursin model is number-based model and has no spatial resolution (i.e. a "box" model). The DYNUMES model described in this paper is a biomass-based model with spatial resolution (i.e. a "gridded" model).

The majority of available water quality management models ignore ecological interactions. The first multipurpose ecosystem model for larger estuaries for water quality management is the GEMBASE model (General Ecosystem Model for Bristol Channel and Severn Estuary, Longhurst 1978; Longhurst, Radford 1973), which was also designed as a tool for a variety of ecological studies. This model simulates the carbon and nitrogen flow between ecological state variables and seven geographical regions. The whole process requires about 150 equations with 225 parameter values. It uses hydrodynamical models for transfer of materials between adjacent geographical regions. Limited examples of this model are given in this paper.

3. BASIC COMPONENTS AND PROCESSES OF A MARINE ECOSYSTEM AND THEIR SIMULATION

3.1 Components and processes in a basic marine ecosystem simulation.

There are numerous and varied processes at work in the marine ecosystem, affecting its biological components in a variety of ways. Thus the quantitative computation of changes in the ecosystem requires the use of numerous explicit equations, each adapted to reproduce quantitatively a given process according to available empirical knowledge.

Generalized flow diagrams of ecosystem simulations illustrate some of the emphasis in and peculiarities of the simulations; the essential details are, however, given in computer programs and their documentations. The GEMBASE (Longhurst and Radford, 1978) flow diagram of the estuarine ecosystem is given in Figure 1. Figure 2 presents the principle processes which are emphasized in DYNUMES simulation. These two diagrams are obviously oversimplified presentations of the full models.

The numerical simulation of ecosystem in three-dimension spaces requires two-dimensional grids (see example of DYNUMES grid on Figure 3). All computations are carried out at each grid point and time step with prevailing conditions. The advection and migrations occur from grid point to grid point in u and v components. This grid can be repeated for several depth levels (e.g. near-surface layer and bottom). All space-dependent input data are digitized at each grid point, where all computations are carried out in each time step and outputs given in numerical form.

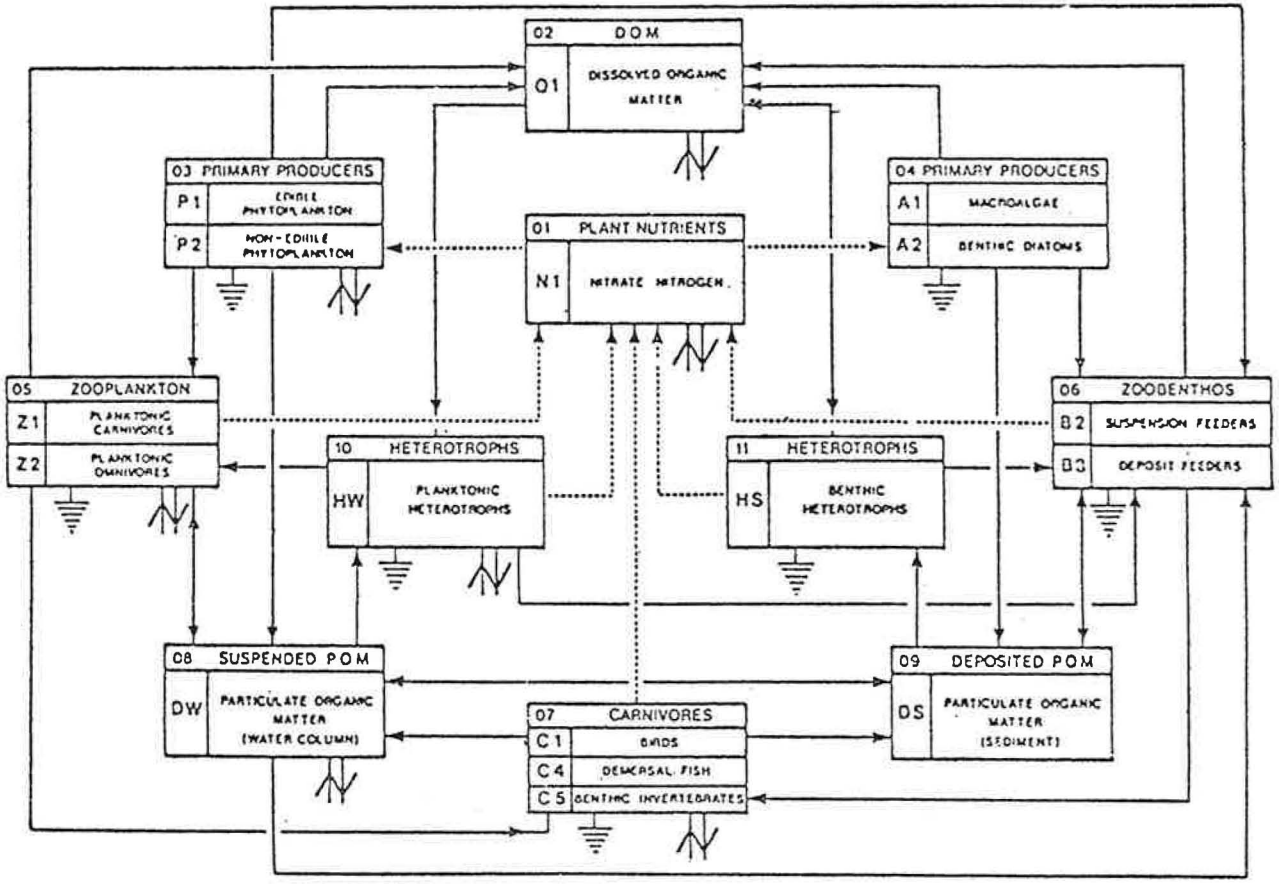

Figure 1.--Process flow diagram of a carbon-based holistic ecological model (GEMBASE) designed as a tool for understanding estuarine ecosystem function. (Longhurst and Radford, 1978)

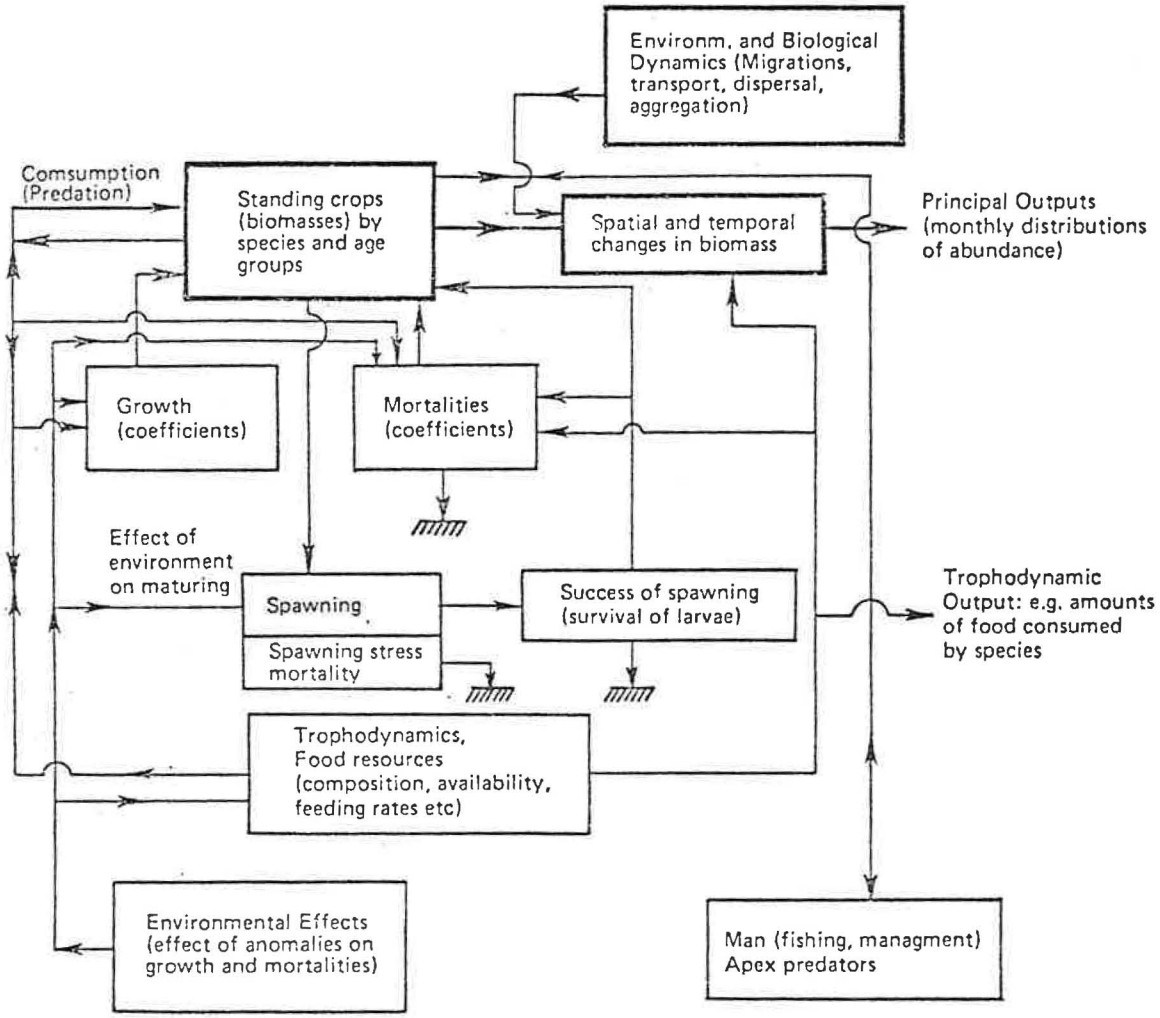

Figure 2.--Scheme of principal processes and interactions in the marine ecosystem.

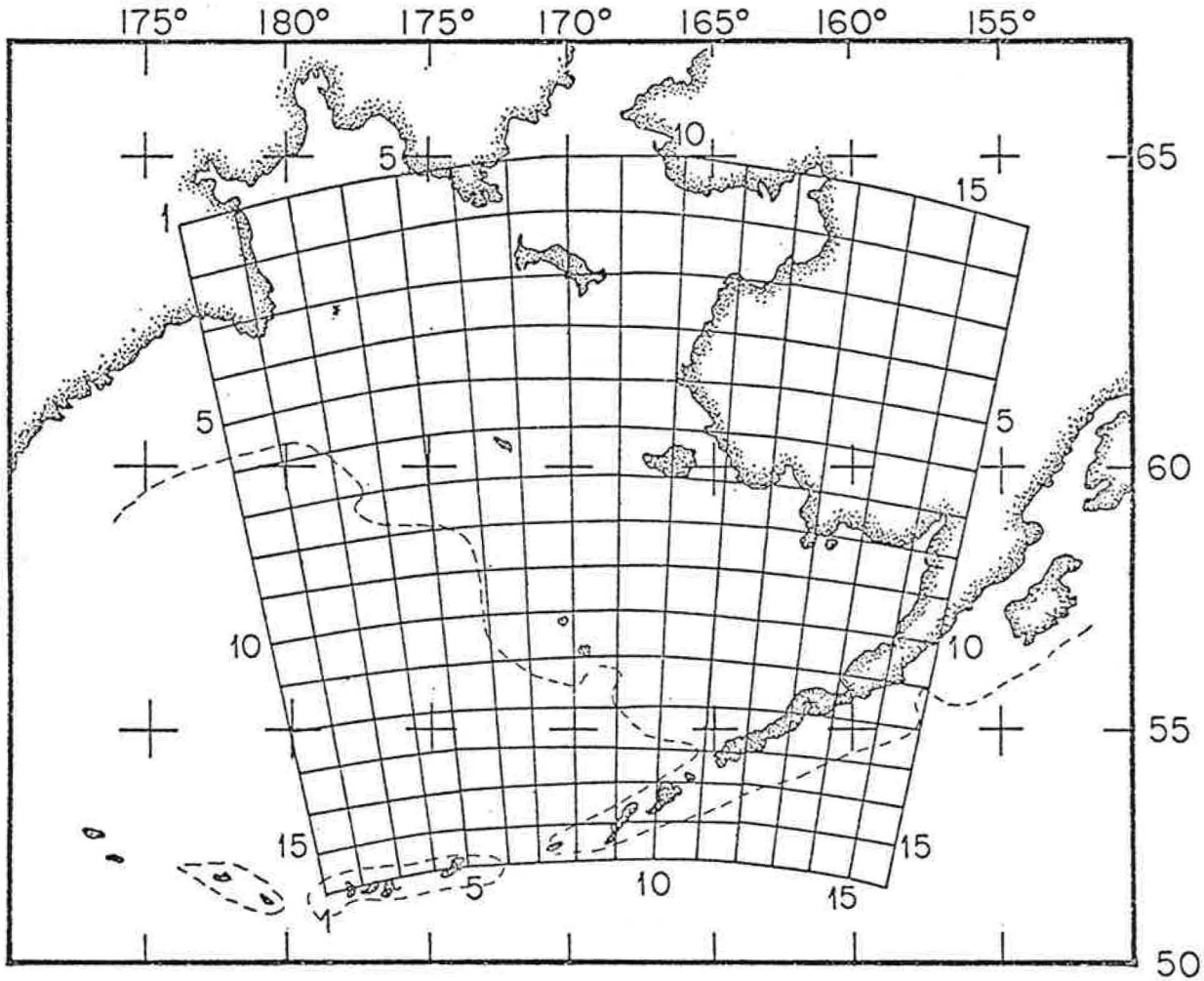

Figure 3.--DYNUMES III grid for eastern Bering Sea, drawn on Mercator projection.

Initial inputs of the DYNUMES model are: depth, sea-land table, surface and bottom temperature, and nature of the bottom. The initial distribution and abundance of species/ecological groups are also given at each grid point as first guess fields.

Numerous species specific coefficients (such as growth coefficients, food requirement, and fishing mortality coefficients, etc.) are introduced in the species computation subroutines. Most of the coefficients in the model, the majority of which present rates of changes, are influenced by a number of factors at each grid point and time step and are thus correspondingly recomputed on the bases of empirical knowledge of their behavior. Thus the model becomes a process oriented model with rate variables which determine the state variables.

Growth of biomasses, fishery yields, mortalities, consumptions (predation), and migrations are also computed in each time step. The monthly consumption of the given species, which is necessary for the computation of actual month biomass balance, is taken from the summation of predation of this species in the previous month. 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.

3.2 Some basic mathematical formulations used in the simulations.

There is usually a lack of reliable quantitative data on marine mammals, birds, and other apex predators present in any given region. Therefore, it is not possible to compute their growth and mortality, but only predation by them, which becomes one of the forcing functions of the model. (Symbols and abbreviations see subchapter 8):

$$F_{a(t,n,m)} = B_{a(t,n,m)}\, q_a \cdot t_d \qquad (1)$$

The consumption of species i by apex predator a is:

$$C_{i,a(t,n,m)} = F_{a(t,n,m)}\, P_{i,a} \qquad (2)$$

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

$$C_{i,A(t,n,m)} = \sum_a C_{i,a(t,n,m)} \qquad (3)$$

The migrations of individual biomasses are computed with predetermined migration speed components (u,v) either on whole or portion of the biomass, using an "upcurrent interpolation and direct advection" formulation which is mass conserving. This computation is done in two steps; first the linear gradient of biomass in the "upcurrent" direction is determined:

$$\text{U positive: } UT_{(n,m)} = (B_{n,m} - B_{n,m-1}(\,/\ell \qquad (4)$$

$$\text{U negative: } UT_{(n,m)} = (B_{n,m} - B_{n,m+1})\,/\ell \qquad (5)$$

(The V gradient (VT) is computed in an analog manner.)

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

$$B_{(t,n,m)} = B_{(t-1,n,m)} - (t_d|U_{(t,n,m)}|UT_{(n,m)}) - (t_d|V_{(t,n,m)}|VT_{(n,m)}) \qquad (6)$$

After migration computations, a smoothing (diffusion) operation is performed (which can be considered a random movement of fish).

$$B_{(n,m)} = \alpha B_{(n,m)} + \beta\,(B_{n-1,m} + B_{n+1,m} + B_{n,m-1} + B_{n,m+1}) \qquad (7)$$

The migrations due to unfavorable environmental conditions or due to scarcity of food are computed by testing the gradients of surrounding points in respect to predescribed criterion and a portion of the biomass at unfavorable grid points is moved towards more favorable conditions:

$$B_{i(n,m)} = B_{i(n,m)} - k_o B_{i(n,m)} \qquad (8)$$

$$B_{i(n\pm1,m\pm1)} = B_{i(n\pm1,m\pm1)} + k_s B_{i(n,m)} \qquad (9)$$

The coefficient k_o depends on the amount the grid point values of environmental parameters or food availability 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).

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

$$B_{i(t,n,m)} = B_{i(t-1,n,m)} \; (2 - e^{-g}) \tag{10}$$

The time step in the model is sufficiently short so that second order terms can be neglected. In some species the growth is made a function of time (i.e. seasonal variations in the growth coefficient):

$$g = g_o + A_g \cos (\alpha_1 t - \kappa_g) \tag{11}$$

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

$$g = k_t g_o e^{\frac{-1}{T(n,m)}} \tag{12}$$

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

$$g = g_o - \frac{S_{i(n,m)}}{F_{i(n,m)}} \; g_o \tag{13}$$

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 ($S_{i(n,m)}$) are computed in the model at each grid point and time step.

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

$$B_{i(n,nm)} = B_{i(t-1,n,m)}(2-e^{-g})\ e^{-m} - C_{i(t-1,n,m)} \tag{14}$$

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

$$F_{i(t,n,m)} = B_{i(t,n,m)}(1-e^{-g})\ r_i + q_i B_{i(t,n,m)} \tag{15}$$

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 (i.e. no spatial and temporal variations) the consumption would be:

$$C_{i(t,n,m)} = F_{i(t,n,m)}p_{i,i} + F_{j(t,n,m)}p_{i,j} + \ldots F_{n(t,n,m)}p_{i,n} \tag{16}$$

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:

$$F_{i,j(t,n,m)} = F_{i(t,n,m)}p_{i,j}a_{j(t,n,m)} + F_{i(t,n,m)}p_{i,j}b_{m(t,n,m)} + F_{i(t,n,m)}p_{i,j}c_{j(t,n,m)} \tag{17}$$

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. The factor a_j is a function of the fraction of the biomass of species j consumed at this location in previous time step. The second term presents the amount of species j consumed on the bases of starvation array requirements (i.e. substitution of more abundant food item).

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. Thus, the computed biomasses can be food availability limited via growth and are also greatly affected by predation.

The biomass mortality from diseases and "old age" is computed with the conventional formula by multiplying biomass with e^{-m} (Formula 14). Furthermore, a spawning stress mortality is computed on some species during the months of spawning. Consequently the resultant state variables are all determined by rate variables.

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

$$P_{u,i(t,n,m)} = B_{i(t,n,m)} - B_{i(t,n,m)} e^{-f_{i(t,n,m)}} \qquad (18)$$

The standing crops of phyto- and zooplankton are simulated with a harmonic formula, which is tuned to available empirical data.

$$P_{s(t,n,m)} = P_{r,o} + A_{1,r} \cos(\alpha_1 t - \kappa_1) + A_{2,r} \cos(\alpha_2 t - \kappa_2) \qquad (19)$$

The annual mean standing stocks for given subregions ($P_{r,o}$), the half-range of primary and secondary annual "peaks" ($A_{1,r}$ and $A_{2,r}$) and their phase lags (κ_1 and κ_2) must be obtained from available quantitative empirical data, or computed with a plankton submodel. The other two holistic ecosystem models (GEMBASE, Longhurst and Radford, 1978 and Andersen and Ursin, 1977) include detailed phytoplankton simulation approaches.

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. The growth, mortality, and consumption of the benthos biomass is computed in each time step with Formula 14.

3.3 Input data on the biota and biological processes

The availability, quality, and accuracy of basic input data for the simulation can vary considerably from one region to another. Therefore, only some generalities of input data are considered below.

Estimates of the numbers of marine mammals and birds present in any area are associated with some uncertainties. As marine mammals and birds are consumers only, and their amounts are not large in most areas, the errors introduced by their inaccurate estimates affect the computation of the final biomasses relatively little.

The initial estimates of biomasses of fish species/groups of species are introduced into the program as inputs. A grouping into ecologically and trophically similar groups has been found necessary due to computer limitations--e.g. semidemersal fish (cod, hake), demersal flatfish (e.g. turbot, halibut), etc. However, some single, dominant species can be treated as single species (e.g. herring, pollock, etc.) and, if desired, divided into age groups.

The recruitment in the biomass-based model such as the DYNUMES simulation model is largely regulated by changes in growth rate and predation pressure, which simulate the regulatory mechanisms which are considered to occur in unexploited natural populations (Ware, 1975). Obviously changes in the recruitment can also be caused by other factors which can be introduced into the model if so desired. The biomass growth changes with age. Thus the computation of the growth rate of a given species biomass requires the knowledge of the distribution of biomass with age within the species, which is computed in an auxiliary model (Laevastu and Favorite, 1978).

The growth coefficient must be adjusted to computational time step (e.g. percent per month). Environmental variables, such as temperature, modify growth. One of the effects of climatic variability can thus be introduced via temperature variability.

The migration speeds of species/groups of species are deduced from empirical knowledge about the seasonal occurrence and migrations (including feeding and spawning migrations) and are prescribed in the model. The migrations due to unfavorable temperature and/or scarcity of food are simulated within the model.

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. This food composition is changed in computations, considering the availability and suitability of food items.

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 these coefficients vary from species to species, depending on activity, growth rates, and normal environmental temperature (re. metabolism). Data for food requirements for growth, maintenance, and reproduction are scarce in the literature, although for some species (gadids) excellent information is available (e.g. Jones, 1978, Daan, 1973), which can be generalized to other species. If an overall food intake coefficient is used (without separation of growth and maintenance requirements), the food coefficient is usually between 0.7% and 1.8% of body weight daily. The food coefficient has seasonal change in higher latitudes, which is approximated by a harmonic curve in the present model.

The uncertainties and errors introduced by trophic coefficients normally do not induce an error in excess of 20% in the final biomass computation according to preliminary experimental determination with the model.

The true natural mortality from old age (senescent mortality) and diseases and possible spawning stress and "starvation" mortalities are small in exploited populations compared to fishing and predation mortalities. Fishing mortality is computed outside the model from fisheries statistics; and predation mortality, which is the largest component of "natural mortality", is directly computed within the model. In unexploited and in short-lived species, such as squids, the senescent mortality can, however, be large. The possible errors made in the estimates of fishing and senescent mortality coefficients do not normally cause errors in biomass estimates in excess of 10% in careful work according to preliminary test results with model in which coefficients were changed in reasonable limits.

3.4 Environment and biota interactions and coupling of simulations.

Most of the pronounced environment-biota interactions must be included in the ecosystem simulations in order to reproduce the ecosystem in a realistic manner. Some fixed environmental data, such as depth, are used directly as a criterion for seasonal migrations of flatfish, abundance of benthos, and in other distribution determinations.

Current as transport mechanism and migrations affect the distribution of most species. The distributional changes in turn affect the predator-prey relations and availability of proper food, thus affecting largely the

interspecies interactions. Trophodynamics (feeding relations) and growth variations have been recognized as probably the most important aspects of interspecies interactions in the marine ecosystem (e.g. Andersen and Ursin, 1977). The interactions between growth and predation determine largely the source and sink areas of a given species. In the source area, growth exceeds predation and mortality; and, in sink areas, predation and mortality exceed growth. Examples of these effects are shown in subchapter 5. The temperature affects concurrently the growth, uptake of food, and activity, including migration. Recent work of Jones and Hislop (1978) has provided new data on the effects of food availability and intake on growth and the effect of temperature on metabolic rate.

The ecosystem simulation thus provides a long-sought means of evaluating the environment-biota interactions and the effects of environmental anomalies in all space and time scales, including the study of the effects of climatic changes.

Complete environmental models such as hydrodynamical-numerical models require large computer core and considerable computer time. Thus, it is difficult to run these environmental models simultaneously with ecosystem models. The environmental data fields must either be prescribed (forced) in digital form from preanalyzed data (e.g. monthly means) or environmental models must be run separately, storing their outputs on tapes or on discs from where they are read into ecosystem models in desired time steps.

Coupling of different simulations can also be done in biological subjects, such as coupling marine mammal and bird models and/or separate plankton and benthos dynamics simulation models with holistic ecosystem

simulation which emphasize nekton ecosystems. The main coupling in this case is via predation. Properly constructed dynamical, time-dependent ecosystem models can use existing single-process and/or single species models or parts of them as adapted, integral parts of holistic simulation models. Exceptions from the above role occur in these holistic models which do not have a diagnostic phase (initial analysis), such as GEMBASE. In the latter models the results from single-process models are used as initial inputs for definition of the initial state and must thus be "harmonized" (dynamically balanced) with the main model.

4. SIMULATION OF EQUILIBRIUM BIOMASSES AND THEIR LONG-TERM FLUCTUATIONS IN MARINE ECOSYSTEMS.

Several methods are in use for assessment of marine fishery resources, such as direct surveys, virtual population analyses using catch and age composition data, etc. None of the past available methods are fully sufficient *per se* for resource evaluation and none of them give the biomasses of all species and/or ecological groups present, nor the productivity of their biomasses per unit time and/or area. The evaluation of total production, starting with primary production, has not been successful either as the pathways of organic matter transfer are greatly variable in space and time and not known quantitatively, and the concept of distinct trophic levels has been abandoned as unrealistic over-simplification for quantitative resource assessment.

If we, however, apply available empirical knowledge of food requirements of all species, composition of food, and computed growth as affected by a multitude of factors, we can apply an iterative method to find solution

to the total utilization of available food resources in the marine ecosystem. The main objectives of such simplified, essentially trophodynamic, bulk biomass models, are:

1) To determine the abundance of species and/or ecological groups in a given region with available diverse food resources (i.e. determine the carrying capacities and "equilibrium biomasses" - see definition below - in respect to given species and regions.

2. To determine quantitatively the trophic couplings between different species or groups of species, and to evaluate the marine ecosystem stability.

The equilibrium biomass is defined as the level of the biomass of a given species, or an ecological group of species, which with a given plausible growth rate and plausible ecosystem internal consumption (i.e. lowest plausible food requirements), does neither decline nor increase within the course of a year; seasonal fluctuations are, however, allowed. Mathematically this means that we find a unique solution of a set of equations (Formulas 14 and 15) if one species is predetermined.

Equilibrium biomasses in a given region are computed with the approaches and formulas given in previous subchapter (Formulas 14 and 15). The basic differences are that only one region rather than each grid point is computed (i.e. no space resolution and no migrations), and that equilibrium conditions are assumed (i.e. growth equals removal by predation, fishery, and other mortalities). Among other limitations of this method are that food composition cannot vary in space and time, and that the obtained equilibrium biomasses are also to some extent dependent on the error in the initial estimate of one or more "ascertained biomasses".

Relaxation methods (Shaw 1953) can be used to solve the equilibrium of ecosystem equation complex; however, a logical (for the particular problem adapted) iteration procedure for the adjustment of biomasses in each January that makes use of the two following criteria, is employed:

$$B_{cg} = B_g - \left[(B_{1,1} - B_{2,1}) / k_c\right] \quad (20)$$

$$B_{cf} = \left[(C_1 + B_g) / B_{gg}\right] B_g \quad (21)$$

where k_c is an iteration constant (3.5 to 10) and

$$B_{gg} = B_g \ (2 - \exp^{-g}) \exp^{-m} \quad (22)$$

A mean of the above two is formed as the new adjusted biomass:

$$B_c = (B_{cg} + B_{cf}) / 2 \quad (23)$$

In most cases, 50 years and more computations in real time are required for convergence to a unique solution.

The biomass of one or more species which have been empirically ascertained (e.g. by extensive surveys of spawning biomass, sonar surveys, extensive exploratory fishery, etc.) ("ascertained biomasses") must be kept constant (i.e. are not passed through the iterative adjustment procedure); all other biomasses which were introduced as first guesses are changed in the iteration for a unique solution.

After achieving satisfactory convergence, the model can be run in a predictive mode for various investigations--e.g. long-term and cyclic changes in the ecosystem caused by the fishery and other factors, such as climatic changes. In the predictive mode, density (food availability) dependent feeding must also be used.

Some of the advantages of the bulk biomass model, as compared to some other models, such as virtual population analyses (see Ulltang, 1977), are:

1) It is possible to determine the equilibrium biomasses in little exploited, unexploited (virgin), and extensively exploited stocks with a known fishing mortality.

2) The total ecosystem in a given region is considered, with large-scale quantitative interspecies interactions. Thus it is possible to examine the effects of changing fishing intensity on target species as well as the indirect effects of such fisheries on species that are unfished or little fished, but are trophically related to target species.

3) A detailed, direct computation of predation mortality (i.e. direct determination of largest component of natural mortality) is made.

4) The time variable growth computation allows the simulation of large-scale effects of environmental anomalies via effects on growth.

In contrast to gridded models such as DYNUMES, the bulk biomass models do not allow any spatial resolution. The model is heavily dependent on good, reliable estimates of the quantitative composition of food of species and/or ecological groups.

5. EXAMPLES OF RESULTS FROM SOME HOLISTIC ECOSYSTEM SIMULATIONS.

The marine ecosystem simulations and results from such simulations are location-dependent. Therefore, only a few examples of the results are given below.

An example of outputs from a bulk biomass ecosystem model simulation of equilibrium biomasses (carrying capacity) in the Kodiak Island area in the Gulf of Alaska is given in Table 1. The fish biomasses in this table include also prefishery juveniles (the exploitable portion of biomass varies from species to species, e.g. herring 30%, yellowfin

Table 1.--Mean biomasses of ecological groups, their consumption and turnover rates in Kodiak area in the Gulf of Alaska as determinated within an ecosystem simulation (all values in tons/km^2, except turnover rate).

Species/ecological group and/or other subjects	Coastal areas and continental shelf	Continental slope (150 to 500 m)	Off continental slope (>500 m)
Mean biomasses			
Herring	8.92	3.29	1.60
Other pelagic fish	15.56	13.39	6.97
Squids	3.11	2.53	1.35
Salmon	0.44	0.40	0.37
Rockfish	2.68	1.74	0.49
Gadids	7.55	5.10	1.32
Flatfish	3.96	1.99	0.43
Other demersal fish	4.91	3.55	0.66
Crustaceans (of commercial value)	9.03	3.82	1.32
Benthos ("fish food" benthos)	46.91	20.57	3.50
Total finfish	44.02	29.46	11.84
Turnover rates			
Finfish	0.87	0.83	0.75
Crustaceans (of commercial value)	1.17	1.12	1.12
Benthos ("fish food" benthos)	0.85	0.87	0.75
Annual phytoplankton production	1,500	1,350	1,000
Mean phytoplankton standing crop	200	180	135
Annual zooplankton production	200	175	190
Mean zooplankton standing stock	42	35	40
Zooplankton consumption by nekton	165	125	53

sole 46%, pollock 71% of the total biomass). The fish biomass decreases from coastal areas to offshore as expected. The turnover rates (consumption plus other mortality within a year divided by mean standing stock) varies from species to species (0.4 to 1.2), and is in average 0.82 for fish in this region.

The basic organic production in the Kodiak area has been conservatively assumed moderate (100 to 150 $gC/m^2/year$). The zooplankton production on the continental shelf in the Kodiak area is about 13% of the phytoplankton production. This is in general agreement with Polyakova and Fedorov (1975) who found that zooplankton production in the White Sea was 5.6 to 15% of primary production.

The requirements of zooplankton as food by nekton communities are high in coastal and continental shelf regions. Two additional factors contribute to this apparently high demand of zooplankton. First, the zooplankton production estimates in the present model were conservative and may be too low. Secondly, the high zooplankton consumption and availability in coastal and slope areas relative to local production may be caused by shoreward transport of zooplankton in deeper layers from the open ocean by the upwelling type circulation that occurs in summer in this area. In addition meroplankton on the continental shelf that obtain part of their food from the surface of the sediment (Gammarids, Mysids, and Harpacticoid Copepods), has been included in the benthos. Considering the above it seems plausible that plankton production can sustain the equilibrium biomasses of other marine ecological groups as computed in this model. Furthermore, it is apparent from the lack and uncertainty of plankton data that basic organic and plankton production cannot be used as a reliable sole basis for fish and other biomass production estimates and modeling.

Some additional observations can be made on the bases of data in Table 1. First, the nektonic biomasses are greatly dependent upon each other (i.e. feeding upon each other) whereby the younger, juvenile stages provide the greatest contribution. The benthos on the continental shelf is another important food source for fish ecosystem. Advection of zooplankton from deep ocean by upwelling type circulation might contribute to the standing stock of zooplankton on many shelf areas. On the other hand, many pelagic fish and juveniles of semidemersal fish (e.g. pollock, hake), who depend on euphausids as food, spend part of their life feeding in offshore locations where euphausids are plentiful.

The four-dimensional DYNUMES simulation can produce a great variety of outputs. A somewhat smoothed distribution of Pacific herring in the eastern Bering Sea during February, computed with DYNUMES simulation, is given in Figure 4A. The model estimates of equilibrium biomass of herring in the eastern Bering Sea is 2.75 million tons; the magnitude of annual fluctuation of this biomass is about 0.3 million tons. Shaboneev (1965) found the biomass of wintering herring north and northwest of the Pribiloffs to be 2.16 million tons, which compares favorably with our model results. For comparison, the biomass of the herring in the North Sea has been estimated by Andersen and Ursin (1977) to be 1.8 million tons at the end of 1959.

The ecosystem internal consumption of herring, as computed within the simulation, is shown on Figure 4B. Comparison of Figures 4A and B indicates that predation intensity is not necessarily a function of the density of prey, thus the source and sink areas of herring would be different than its distribution.

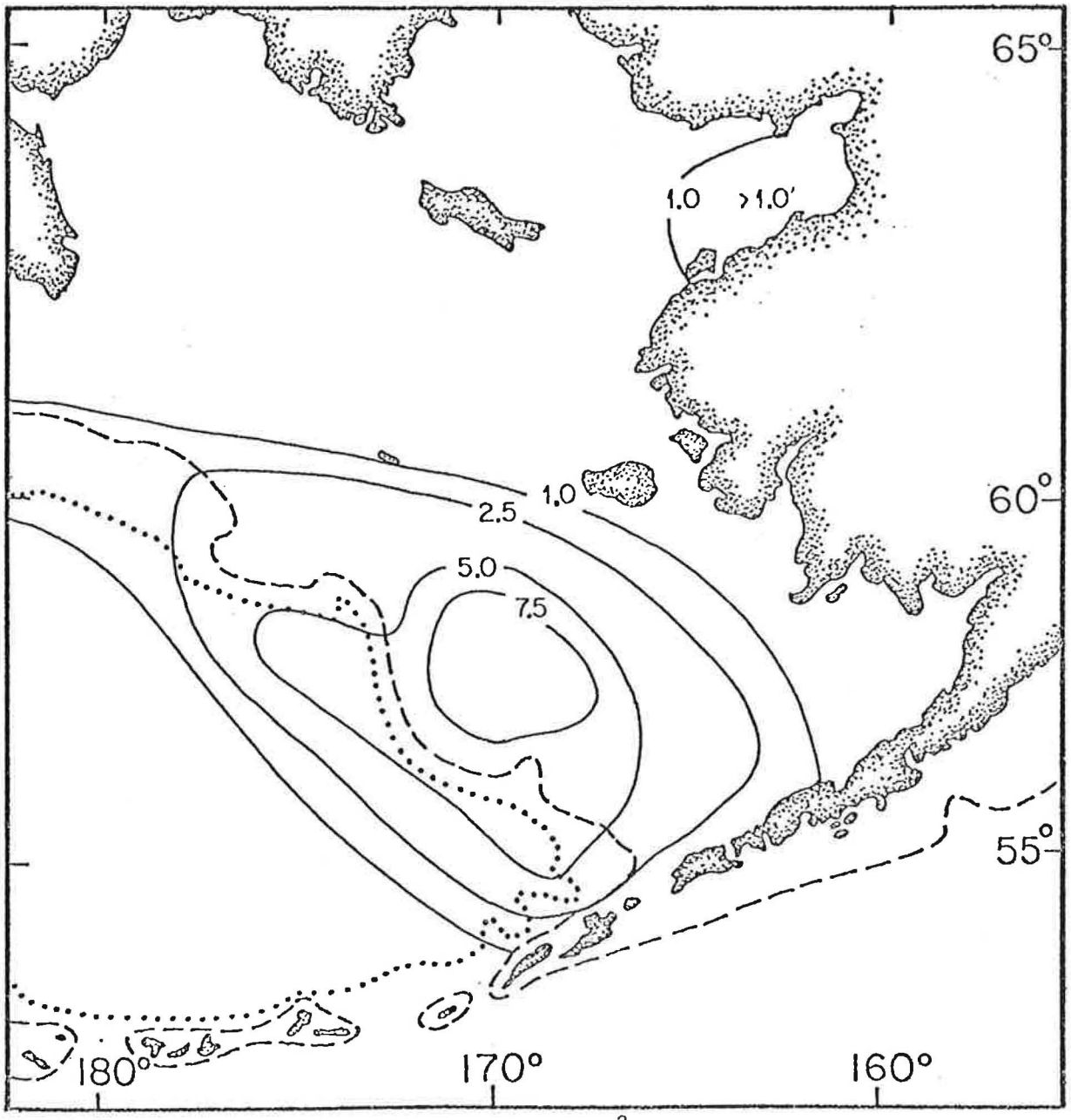

Figure 4A.--Distribution of herring (tons/km^2) in February (equilibrium biomass (EB), 2.75 million tons).

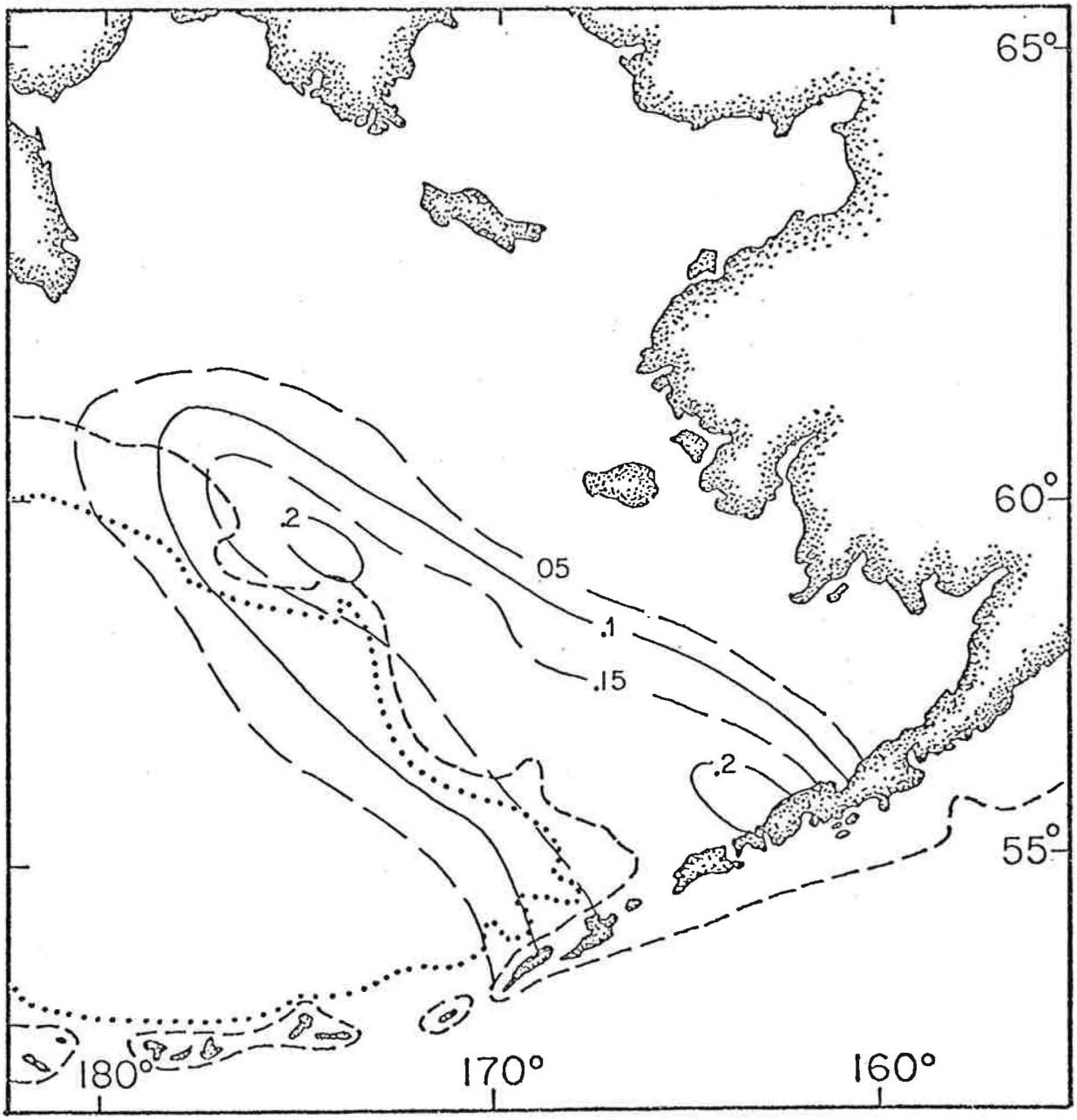

Figure 4B.--Consumption of herring (tons/km^2) in February (EB, 2.75 million tons).

The spatial and temporal source-sink mapping provides useful information on many scientific as well as practical fisheries management considerations. Sources and sinks of herring in the eastern Bering Sea in February are presented on Figure 5A. During the winter months losses of herring biomass exceed increases, except in a small source (increase) area in the southern part of the Bering Sea near the continental slope.

The effects of temperature anomalies in the eastern Bering Sea on the changes of biomass of pelagic fish were investigated with the DYNUMES simulation, using the effect of temperatures on growth. In one of the model runs, a +1.5^{o}C temperature anomaly in the surface layers during three winter months was prescribed. The sources and sinks of the herring biomass during February with +1.5^{o}C positive temperature anomaly is shown on Figure 5B which depicts rather pronounced changes from normal conditions (see Figure 5A). The magnitude of the effect of the temperature anomaly on the biomass changes (via physiological processes) appeared to be considerably more significant than expected before computations and might explain a great part of the relatively large fluctuations of fish stocks observed in other high latitude areas. These effects can be studied with ecosystem simulation models.

The monthly mean zooplankton biomass (standing stock) rather than production is simulated in the DYNUMES model. Figure 6 shows the percentage of mean zooplankton standing stock consumed as food by fish, mammals, and birds in the eastern Bering Sea ecosystem in February. The utilization of zooplankton in the northern part of the Bering Sea as well as over deep water, is relatively low, whereas in some parts over the shelf the utilization exceeds 40% of the mean monthly standing stock.

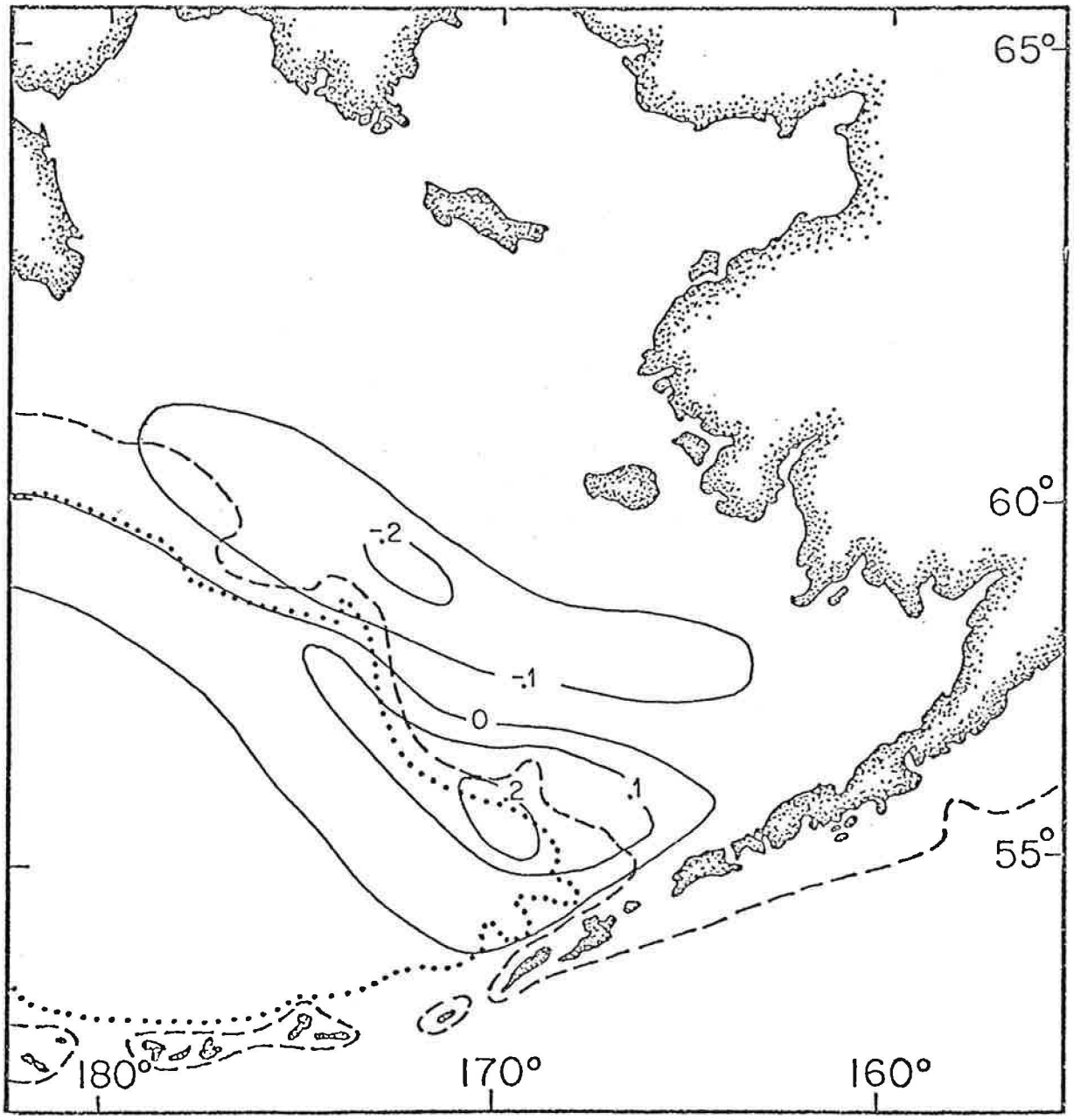

Figure 5A.--Herring sources and sinks (tons/km^2) in February.

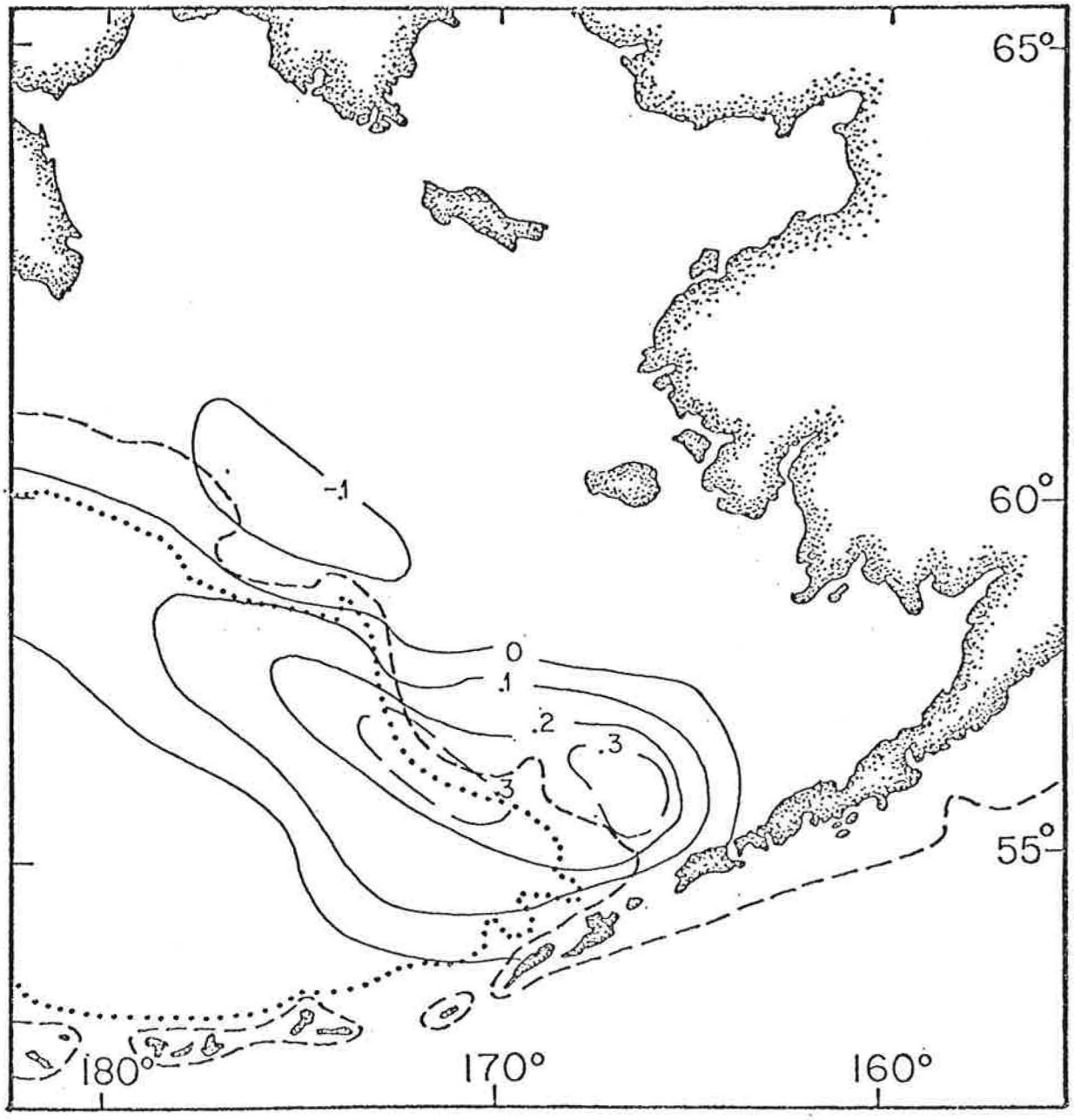

Figure 5B.--Herring sources and sinks (tons/km^2) in February (1.5°C positive anomaly).

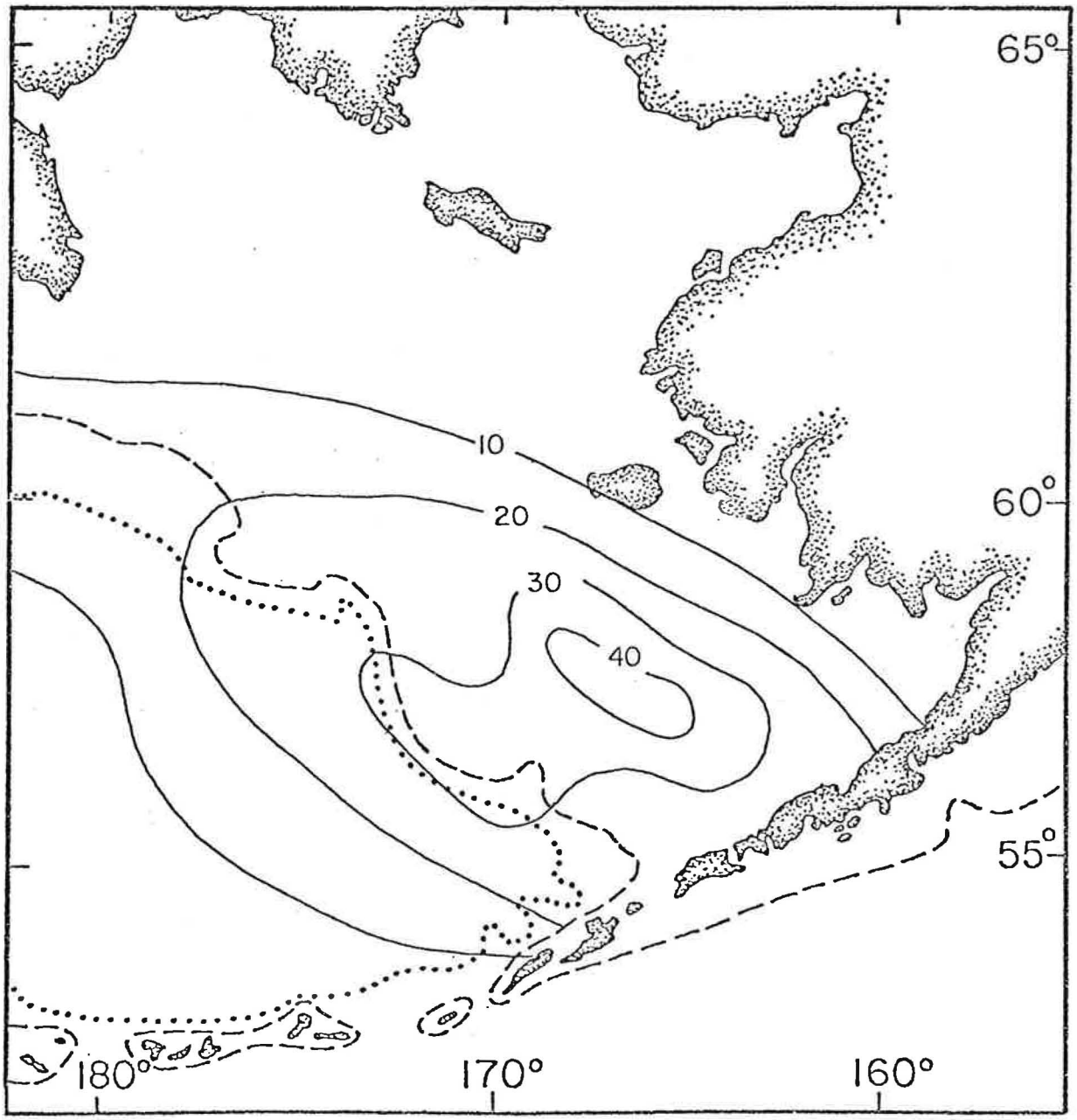

Figure 6.--Percentage of mean zooplankton standing stock consumed in February.

DYNUMES model runs over several year-spans show that marine ecosystems are unstable and sensitive to changes in growth rates, relative distribution, and abundance of predators/prey, and changes of composition of food. Due to the multiple interactions in the ecosystem, the abundance and distribution of most species show quasi-cyclic variations. An example of changes of biomasses of three different size groups of pollock in the eastern Bering Sea with 1.2 million tons of "present" fishery and half of this fishery over four and one-half years, is shown on Figure 7. Medium-size and large pollock (>45 cm length) are cannibalistic (ca 50% food consists of younger pollock). When the fishery removes the older, cannibalistic fish, predation pressure on juveniles is relieved. As the growth in juveniles is high, a higher pollock biomass results.

An example of outputs from Andersen and Ursin (1977) model for the North Sea is shown in Table 2, where the North Sea was also run in a virgin state (i.e. no fishery, column C). Comparing the virgin state with the states of ecosystem in 1959 and 1970 (columns A and B) shows that after the cessation of fishing, control passed from man to cod, which, with a biomass of 4 million tons, exerted a predation pressure upon most other species with approximately the same effect as the fishing mortality in 1970. The biomass of plaice alone was too large to be effectively controlled by cod.

According to Longhurst (1978), the GEMBASE has produced conceptually realistic simulations of the ecology of the estuary. It has not been systematically exploited as a research tool as yet. However, during model development it has become apparent that it can be used to investigate a variety of ecological questions including theories on ecological relationships. An example of GEMBASE output is given in Figure 8.

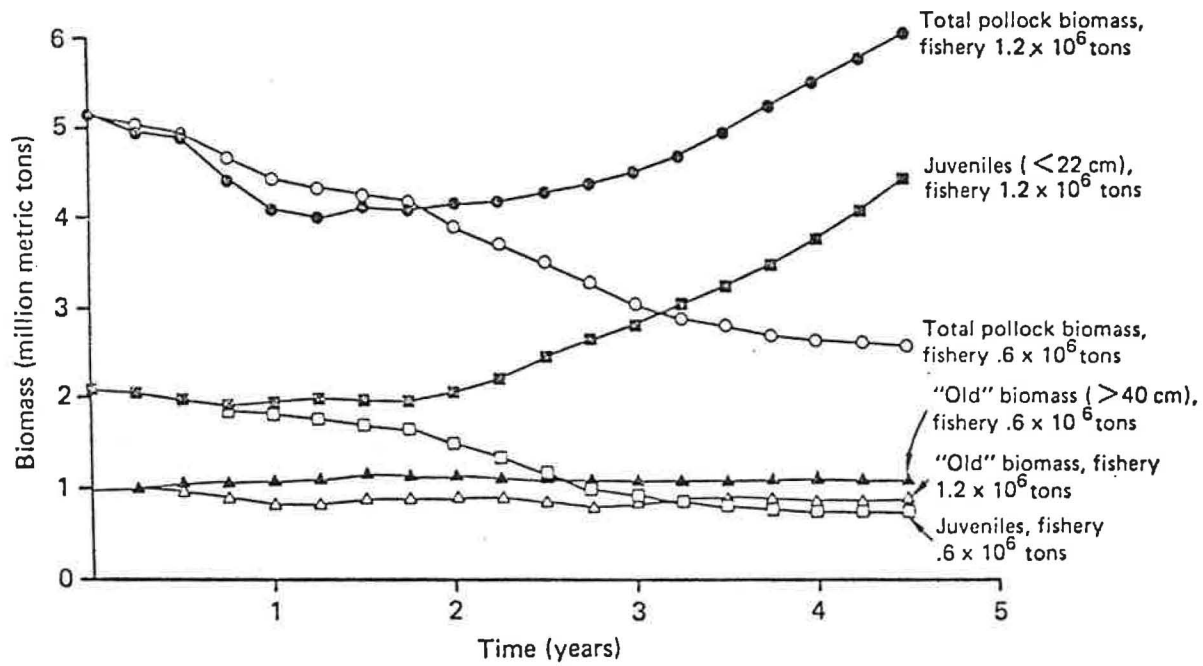

Figure 7.--Change of biomass of juvenile, old and total walleye pollock in the eastern Bering Sea with simulated present fishing intensity and half present intensity (DYNUMES submodel).

Table 2.--Estimated biomass at the end of the year in 1959, in 1970, and for the almost virgin population (i.e. after 11 years without fishing) in the North Sea. Unit: 1 million tons. Zero means less than 50,000 tons. (From Andersen and Ursin 1977.)

	Realistic fishing effort A 1959	B 1970	No fishing C
Plaice	.3	.4	2.2
Dab	.3	.4	.6
Long rough dab	.1	.1	.2
Saithe	.1	.6	.4
Cod	.2	.4	4.2
Haddock	.1	.3	.5
Whiting	.1	.1	.3
Norway pout	.1	.3	1.0
Mackerel	2.6	.6	.2
Herring	1.8	1.0	.9
Sandeels	.2	.5	1.1
Benthos A	5.7	4.8	4.4
Benthos B	6.6	9.7	8.6
Benthos C	1.6	2.0	1.4
Zooplankton A	.0	.2	.0
Zooplankton B	2.4	1.5	2.1
Zooplankton C	2.0	1.9	2.1
Algae, pelagic	.5	.7	.6
Algae, demersal	.2	.2	.2
Detritus (demersal)	.1	.1	.1
Carcass (demersal)	.1	.1	.1
Fish in all	5.8	4.8	11.6
Benthos in all	14.0	16.5	14.3
Zooplankton in all	4.5	3.6	4.2
Animals in all	24.2	24.9	30.2
Total	25.1	26.0	31.2

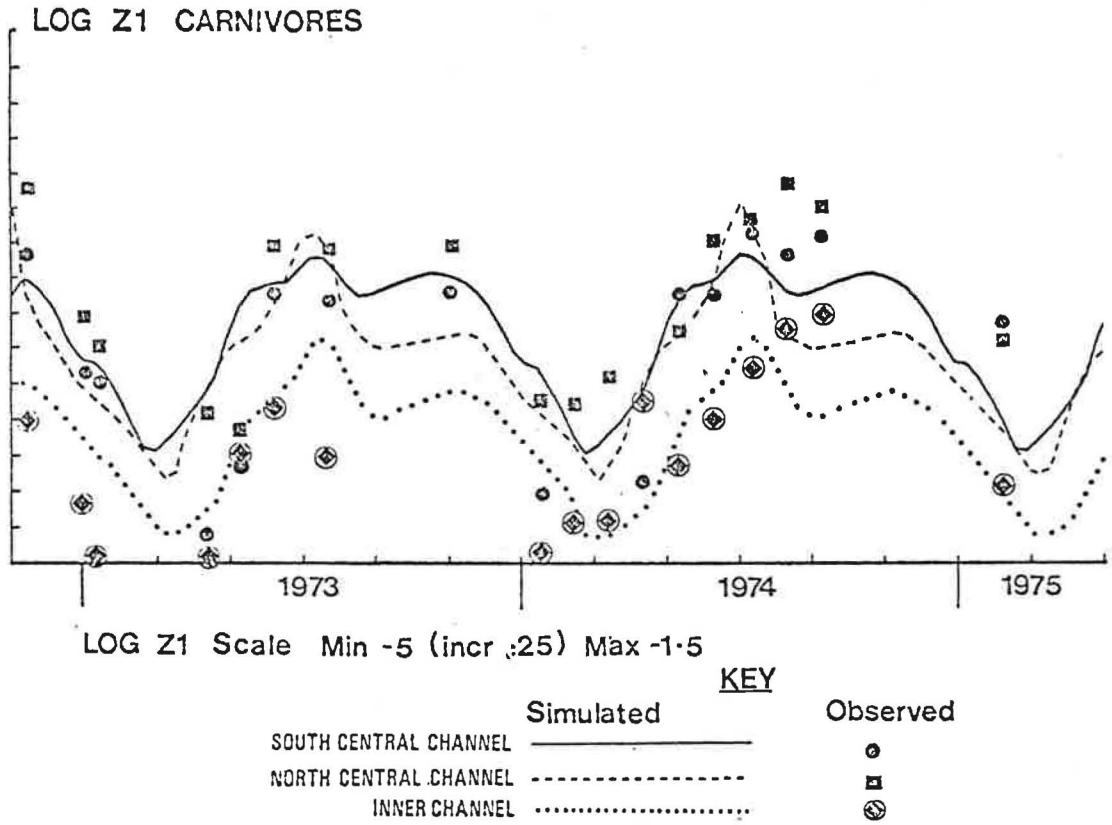

Figure 8.--Example of validation of GEMBASE model (Longhust and Radford, 1978).

6. VERIFICATION AND VALIDATION.

It is necessary to differentiate between verification and validation in large ecosystem simulations. Verification refers to checking of logic and the correctness of individual models and formulas used in the simulation. The models and formulas are verified with available empirical data. Verification includes also the testing of the simulation at large, using various impulses as input, whereby the expected response of the ecosystem to the impulse must be at least qualitatively known. The effect of water temperature on growth in the DYNUMES model was formulated on bases of some earlier available knowledge on the subject, notably Krogh's metabolic curve. When an excellent paper by Jones and Hislop (1978) appeared later, dealing parly with the subject, verification and additional tuning was provided. Further empirical evidence on the effect of temperature on herring abundance was provided by Grainger (1978).

An important part of the verification is the sensitivity analyses. Sensitivity analyses indicates where the influence of possible flaws in the available knowledge has major consequences, thus sensitivity analysis acts also as guidance for further research.

In the past sensitivity analysis in simple, few-parameter models was done by changing one constant (vice parameter) at a time. This method is not applicable to large ecosystem models as the number of simulations required is prohibitively large. Behrens (1978) has outlined an analytical method for sensitivity analyses for models consisting of ordinary first order differential equations.

In these ecosystem models which rely heavily on various input parameters for determination of the initial state and for satisfying the parameterized equations in the model, such as GEMBASE, the verification would include the testing of accuracy and reliability of such inputs which are obtained from a multitude of sources.

As both the bulk biomass and the DYNUMES models are deterministic, conventional sensitivity analyses are neither necessary nor possible. In deterministic models, sensitivity analyses become studies of specific responses of the systems to expected changes of parameters (see example in previous subchapter and Figure 7). The variations in results of deterministic models depend also on accuracy and reliability of the input data, but to a lesser degree than the "parameterized" models.

Validation of simulation refers to comparison of principal results from simulation with direct observations in the field. Usually these results present either abundance and/or distribution changes of given species if and when a causative factor for these changes has been introduced in the simulation model. Special research projects usually provide validation of the various rate parameters.

One of the basic validation procedures is to compare observed data, e.g. from exploratory surveys with simulation results. Table 3 presents example of such validation in respect to simulation results in Table 1 and survey results from the same area by Ronholt, Shippen, and Brown (1978). Besides errors and uncertainties in interpretation of survey results themselves, additional difficulties arise especially in the use of a catchability coefficient, which is variable in space and time and not well known. Despite these difficulties, the mean equilibrium biomasses

Table 3.--Comparison of total biomass of some groups of species in Kodiak area as computed with Bulk Biomass (BB) model (Table 1) and survey data (Ronholt et al., 1978) as adjusted with catchability coefficient and converted to total biomass.

Group of species	Exploitable biomass, catchability coefficient = 1, Ronholt et al. 1978.			Adjusted catchability coefficient	Percent exploitable biomass of total biomass	Adjusted mean biomass (surveys)	Mean biomass from BB model (Table 1)
	1960 decade	1970 decade	Mean				
Flatfish	3.4	3.6	3.5	0.75	60	7.78	4.0
Roundfish	1.9	5.3	3.6	0.55	70	9.35	7.6
Rockfish	0.7	0.2	0.45	0.40	50	2.25	2.7
Invertebrates (mainly crustaceans)	2.7	1.6	2.15	0.50	35	12.29	9.0

computed with the bulk biomass model are in reasonable agreement with mean biomasses of survey results, as adjusted by catchability coefficient and total biomass conversion factors. The largest discrepancy occurs in flatfishes.

Figure 8 presents partial results of GEMBASE model validation with observed data (Longhurst and Radford, 1978). Some indirect validation of simulation output at large in respect to zooplankton utilization and carrying capacity evaluation, were described in subchapter 5.

7. USE OF ECOSYSTEM SIMULATIONS IN RESEARCH GUIDANCE AND IN RESOURCE MANAGEMENT.

The compilation (designing) of the ecosystem simulation serves already as general research guidance, indicating missing data and other shortcomings in data and knowledge. The simulation models serve also as indicators of priorities of research, by suggesting processes of greater importance in terms of greater "sensitivity" to resultants of larger processes and those of lesser concern and influence. Some of the guidances, in respect to need for new emphasis and direction of research, are local, but many are universal and promote diversity of research as well. Among the examples of new thrust in fisheries research caused by the ecosystem approach is the realization of shortcomings in single species approaches which lack trophodynamic interactions between the species. However, one of the most important links in interspecies interactions in ecosystem models is the food relations affecting growth and abundance; another example is the realization of the necessity to deal with age/size dependent mortalities, to ascertain the predation mortalities as well as spawning stress mortalities in ecosytem models.

Quantitative numerical ecosystem simulations bring out processes and resulting changes in the ecosystem which have not been easily observed in the past and permit ecological experiments which would be impossible to conduct in nature.

Among the initial scientific uses of the holistic simulations have been the study of the quantitative effects of environmental anomalies, pollutants, and the fishery on the biotic components of the ecosystem. Furthermore, the determination of the "carrying capacities" of given regions and the study of fluctuations of abundance of species as caused by various ecosystem internal factors (e.g. cannibalism) using ecosystem simulations has been successfully demonstrated.

The marine ecosystem simulations with emphasis on fish ecosystems provide new powerful tools for fisheries management. These simulations not only allow the determination of magnitudes of the resources and their distributions, but also the simulation of variable space and time responses to any desired and/or prescribed fishery, on target species, as well as indirectly on other species as well, via interspecies interactions. The ecosystem simulations have shown the importance of the determination of the magnitudes and periods of large-scale "natural fluctuations" in the marine ecosystem which can occur without the influence of fishery but can be caused by fishery as well. Without proper evaluation of these fluctuations, the effects of the fishery on the abundance and distribution of the species cannot be evaluated either (see example of the fluctuations of pollock biomass in subchapter 5).

The applications of ecosystem simulations are indeed numerous and far from being fully explored and utilized. We might visualize these seemingly unlimited possibilities if we consider that in essence we attempt to simulate nature (i.e. the ecosystem) and its functioning quantitatively in computers and can review the whole system of the nature on our desk.

8. LIST OF SYMBOLS

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).

$B,(B_i)$ - biomass (of species i).

B_a - biomass of apex predator a.

B_c - adjusted biomass in January.

B_{cg} - adjusted biomass due to biomass change within a year.

B_{cf} - adjusted biomass due to consumption (predation).

B_g - adjusted biomass from previous year.

B_{gg} - resultant biomass from growth and mortality.

$B_{1,1}$ - biomass in January, previous year.

$B_{2,1}$ - biomass in January, actual year.

b_m - fraction of food substitution.

C_c - "constant consumption" for prescriped "ascertained" biomasses.

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.

C_1 - predation (consumption).

e - base of natural logarithms.

F_a - amount of food consumed by an apex predator a.

F_i - amount of food required by species i.

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

f_i - time and space dependent fishing mortality coefficient.

g - growth coefficient.

g_o - basic mean growth coefficient.

k_c - iteration constant.

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 - grid length (km).

m - mortality coefficient (from old age and diseases); also space coordinate.

n - space coordinate.

$P_{i,a}$ - 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 a 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 (also food requirement for maintenance in % of body weight daily).

$q_{i,j}$	- fraction (decimal) of species i in food of species j.
r_i	- ratio of growth to food required for growth.
S_i	- shortage of food of species i ("starvation").
t (t_d)	- time, time step.
T	- temperature.
U	- u component of migration speed.
UT	- "upcurrent" (upmigration) gradient of biomass (u component).
V	- v component of migration speed.
VT	- "upcurrent" (upmigration) gradient of biomass (v component).
α	- smoothing coefficient (horizontal diffusion coefficient).
$\alpha_1(\alpha_2)$	- phase speed (e.g., degrees per month).
β	- $(1-\alpha)/4$ (secondary smoothing coefficient).
κ	- phase lag of annual growth coefficient change.
κ_1,κ_2	- pase lag (month of annual maximum).

9. REFERENCES

Andersen, K.P. and E. Ursin.

1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Meddr. Danm. Fisk.-og Havunders. N.S. 7:319-435.

Behrens, J. Chr.

1978. A semi-analytical sensitivity analysis of non-linear systems. Inst. of Mathem. Stat. and Oper. Res., Techn. Univ. Denmark, Res. Rpt. 4/1978:29 pp.

Beverton, R.J.H. and S. T. Holt.

1957. On the dynamics of exploited fish populations. Min. Agr. Fish. and Food, Fish. Invest. London. Ser. 2 19:1-533.

Daan, N.

1973. A quantitative analysis of the food intake of North Sea cod, Gadus morhua. Netherlands J. of Sea Res. 6(4):479-517.

Grainger, R.J.R.

1978. Herring abundance off the west of Ireland in relation to oceanographic variation. J. Cons. int. Explor. Mer. 38(2):180-188.

Jones, R.

1978. Estimates of the food consumption of haddock (Melanogrammus aeglefinus) and cod (Gadus morhua). J. Cons. int. Explor. Mer., 38(1):18-27.

Jones, R. and J.R.G. Hislop.

1978. Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. int. Explor. Mer. 38(2): 244-251.

Kremer, T.N. and S.W. Nixon.

1977. A coastal marine ecosystem. Simulation and analysis. Springer-Verlag, N.Y. 217 pp.

Laevastu, T. and F. Favorite.

1978. Fish biomass parameter estimations. NWAFC Proc. Rpt., 16 pp.

Longhurst, A.R.

1978. Ecological models in estuarine management. Ocean Management 4 (1978):287-302.

Longhurst, A.R. and P.J. Radford.

1975. GEMBASE I. Internal documents, Inst. for Mar. Env. Res., Plymouth.

Polyakova, T.P. and V.D. Fedorov.

1975. Production of individual links in the food chain in the White Sea. Okeanologia 15 (5):881-885.

Ronholt, L.L., H.H. Shippen, and E.S. Brown.

1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948-1976 (A historical review). Northwest and Alaska Fisheries Center, Processed Report, August 1978.

Shaboneev, I.E.

1965. O biologii i promysle sel'di vostochnoi chasti Beringova morya (Biology and Fishing of herring in the eastern part of the Bering Sea). Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 58 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 53): 139-154. In Russian. (Transl. by Israel Prog. Sci. Transl., 1968, p. 130-146 in P.A. Moiseev (ed.), Soviet fisheries investigations in the northeast Pacific, Pt. 4, avail. Natl. Tech. Inf. Serv., Springfield, Va. as TT 67-51206.)

Shaw, F.S.

1953. An introduction to relaxation methods. Dover Pub., N.Y. 396 p.

Ulltang, Ø.

1977. Sources of errors in and limitations of Virtual Population Analysis (Cohort Analysis). J. Cons. int. Explor. Mer., 37(3):249-260.

Ware, D.M.

1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board, Can. 32:2503-2512.