NORTHWEST & ALASKA FISHERIES CENTER PROCESSED REPORT

PRELIMINARY REPORT ON DYNAMICAL NUMERICAL MARINE ECOSYSTEM MODEL (DYNUMES II) FOR EASTERN BERING SEA

by
Taivo Laevastu and Felix Favorite

Environmental Assessment of the Alaskan Continental Shelf
Sponsored by
United States Department of Interior
Bureau of Land Management

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Northwest and Alaska Fisheries Center
2725 Montlake Boulevard East
Seattle, Washington 98112

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ABSTRACT

A second generation, four-dimensional Dynamic Numerical Marine Ecosystem model (DYNUMES II) has been programmed for the eastern Bering Sea. This model serves a number of purposes: for diagnostic evaluation of marine resources, for prognostic studies of the effects of exploitation, and for quantitative determination of the effects of offshore oil developments.

The logic and outline of the model is given together with formulas and computation procedures used. A brief summary of the sensitivity of the model to input variability is also presented. Values for essential parameters and coefficients are given in tabular form.

Selected outputs of the trophodynamics and time changes of abundance and distribution of major species and groups of species are presented, both to demonstrate the capability of the model, and to present conditions and processes of the marine ecosystem in the eastern Bering Sea that are of concern to oil developments.

The model shows that the patchy distribution of many species is caused mainly by space and time variability in feeding. The marine ecosystem is rather unstable and most species have long-period fluctuations in abundance. It appears that it will be difficult, if not impossible, to distinguish between any local, small-scale disturbances and fluctuations that may be caused by oil developments and naturally occurring fluctuations in the ecosystem. Any small-scale (1 = <50 km) disturbance in the marine ecosystem, caused e.g. by oil development, is relatively rapidly smoothed out due to the dynamics of the ecosystem.

The ecosystem internal consumption (predation and cannibalism) is high, resulting in a high annual turnover rate of most biomasses (0.86). The most sensitive part of the ecosystem is near the coastal boundaries (e.g., shallow water and beaches).

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I. INTRODUCTION

Ecologists and fishery scientists have long recognized the interaction among the components of an ecosystem, however, any attempts to quantify these phenomena were very limited until recently due to the unavailability of or limitations in computers vis a vis the volume and complexity of the numerical analyses required. Modern 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 were also attempted. These attempts and subsequent refinements are still continuing, especially in university research institutions. Though a necessary step in the development of modeling concepts, these earlier studies 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 process 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, and these studies provided some useful bases for single-species fisheries management decisions. Without exception, conventional fisheries production models consider environmental interactions only to the extent of assuming stability or long-term equilibria in the environment. The validity of such assumptions is, of course questionable and it is now realized that these models are insufficient for modern fisheries management. Clearly, the future development of fisheries management models must consider environmental effects and interspecies interactions.

Several numerical two- and three-dimensional ecosystem models have been developed, however, these deal with essentially planktonic organisms and are too simplistic if the total ecosystem is under consideration, and they do not consider the requirements of fisheries management schemes. The applied interests of man are focused on the upper end of the food web, where harvesting is profitable, rather than on the lower end (nutrients, phytoplankton, zooplankton). Furthermore, the nutrient-plankton-fish energy pathways are greatly variable, with great lateral losses 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 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 purpose of this study is to apply available simulation modeling techniques to the construction of a complete as possible ecosystem model that is tailored to man's needs from a scientific as well as applied points of view. The objectives of numerical ecosystem models can be grouped into three categories:
--Investigative and digestive, that permit quantitative biological resource evaluations, including:

- Synthesis of information, including quantification of descriptive data and quantitative summarization of exploratory and baseline studies.
- Simulation of the ecosystem with all of its essential interactions, including those between the ecosystem *per se* and the physical-chemical environment.

-Determination of the effects of environment and interspecies interactions and other natural fluctuations.

--General management guidance and effects of exploitation, including:

-Magnitude or status of the biological resources, their past and expected future fluctuations.

-Determination of effects of fishing intensity variations (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.

--Oil exploration/exploitation (developments) effects on marine ecosystem, including:

-Determination of the effects of oil "developments" on the ecosystem (and exploitable resources) as compared to natural fluctuations, including the determination of Contaminant Baselines - OCSEAP Tasks A and E.

-Quantitative determination (in space and time) of the possible ecosystem components susceptible to petroleum "development" - OCSEAP Task E.

-Quantitative determination (by means of numerical (model) simulation) of the effects the contaminants and other possible detrimental effects of petroleum "developments" on the marine ecosystem and its components - OCSEAP Task E.

In order to simulate the complex processes in the ecosystem, the numerical model becomes, by necessity, extensive and complex. In this report earlier results (e.g., Laevastu and Favorite 1976 a, b) are reviewed, the current model structure is described, and some initial assessments are discussed. A detailed description and program documentation will be compiled in a subsequent report.

II. THE DYNAMICAL NUMERICAL MARINE ECOSYSTEM (DYNUMES II) MODEL

A. THE BASIC PRINCIPLES, LOGIC AND OUTLINE OF THE MODEL

The accumulated knowledge on marine ecosystem and modeling/simulation experiences provides some of the basic principles related to a complete ecosystem model:

--An abundant species (and/or group of ecologically similar species) that interacts extensively with other species/groups of species should be selected as a reference species. This species should be subject to exploitation and past research so that reasonably reliable estimates of standing stocks of the exploitable part of the species biomass are available, and the general or specific nature of the interactions (e.g., predation) are known. An estimate of the "minimum sustainable biomass" - a biomass which is in quasi-equilibrium with growth and consumption within the ecosystem - of the reference species must be prescribed in the initiation of the model. The total biomass of a species, for which estimates of the exploitable biomass are available, can be computed, with some assumptions, by extrapolating from the exploitable portion (Laevastu and Favorite 1977a).

--The amounts of space-time distributions of the end consumers (i.e., the (highest) part of the "food chain", i.e., man, mammals and birds) must be prescribed (estimated) with the basic input into the model, and the consumption of other biomasses by these consumers must be computed.

--Analysis (determination of the initial state) is basic to all multi-dimensional dynamic models. Thus, the model must be started with estimated magnitudes of all species biomasses and their estimated distributions, obtained from available pertinent data. The iterative estimation of the magnitudes of the biomasses was an integral part of the initiation of DYNUMES, although a separate model (Bulk Biomass Model, BBM) was developed later (Laevastu and Favorite 1976b, 1977b) for this purpose. The basic principle of the BBM model is: $gB_t = G_t + F_t + M_t$, or in words: growth of biomass (B) in unit time t with growth rate g equals consumption (G) plus fishery catches (F) plus natural mortality (M) in the same unit time; g and F are known, M is relatively small and is estimated, and G is computed within the model with known data (composition of food and food coefficients). Thus, an estimate of B can be obtained with a relaxation method (Laevastu and Favorite 1977b).

--The trophodynamic computations (i.e., types and amounts of food consumed) in a given time step in the model commence with the computation of consumption by mammals, followed by computations of consumption by fish species and zooplankton and benthos. The simple food web (food pyramid) approach, so prevalent in the past, has been abandoned as unrealistic in light of the complex food relations (Figure 1).

--The model must account for all processes, including trophodynamic ones, in the ecosystem which affect the distribution and abundance of any component, such as migrations, environment effects, and biological functions (e.g., spawning). Dominant processes (Figure 2) must be quantitatively evaluated in time steps not exceeding one month. Obviously the smaller time steps for which adequate supporting data are available the more promising the result.

--There must be an open pathway into the model to enter actual and potential effects of man on the ecosystem (fishery, oil developments, etc.).

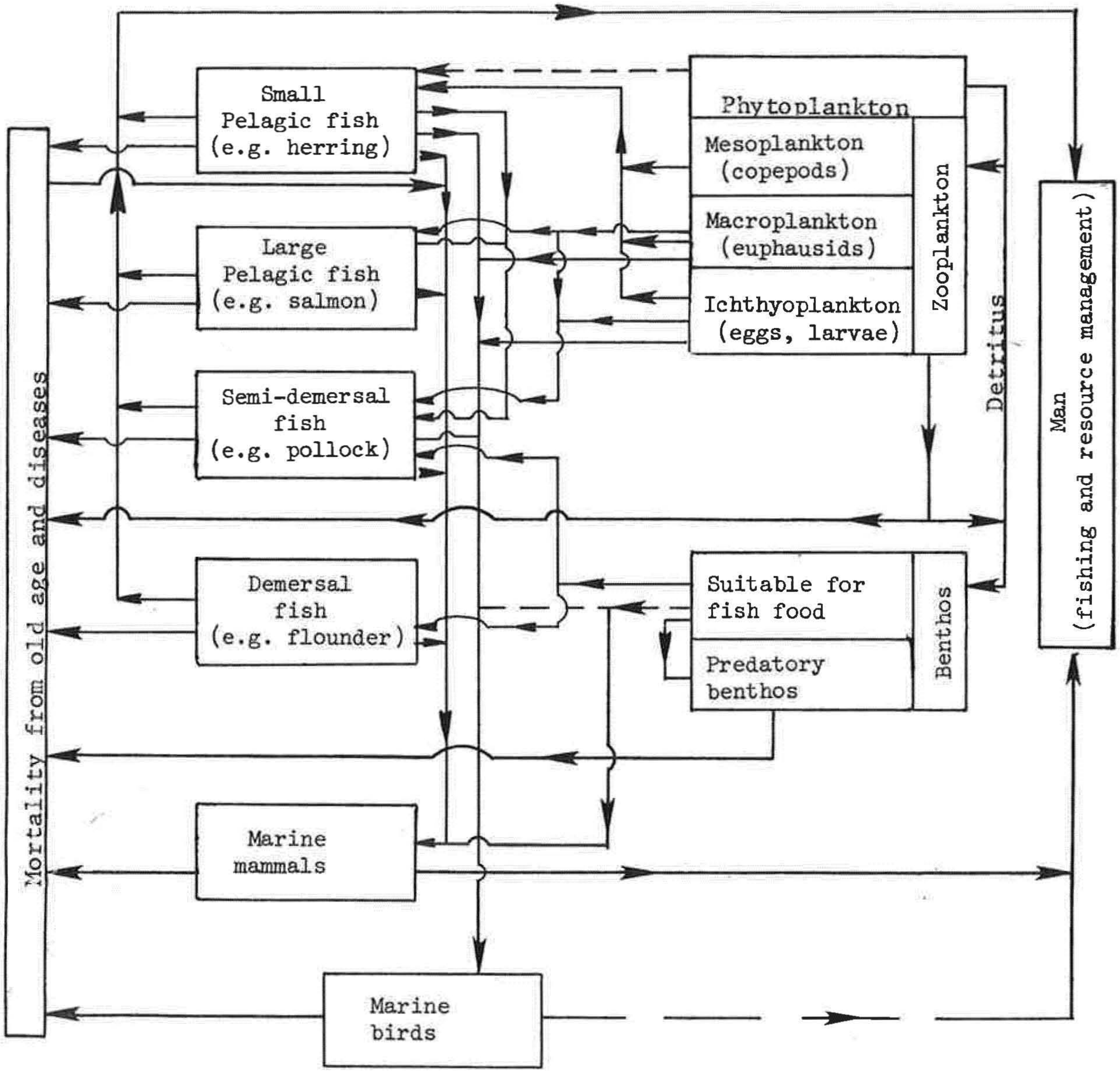

Figure 1. Generalized scheme of complex food relations in marine ecosystem.

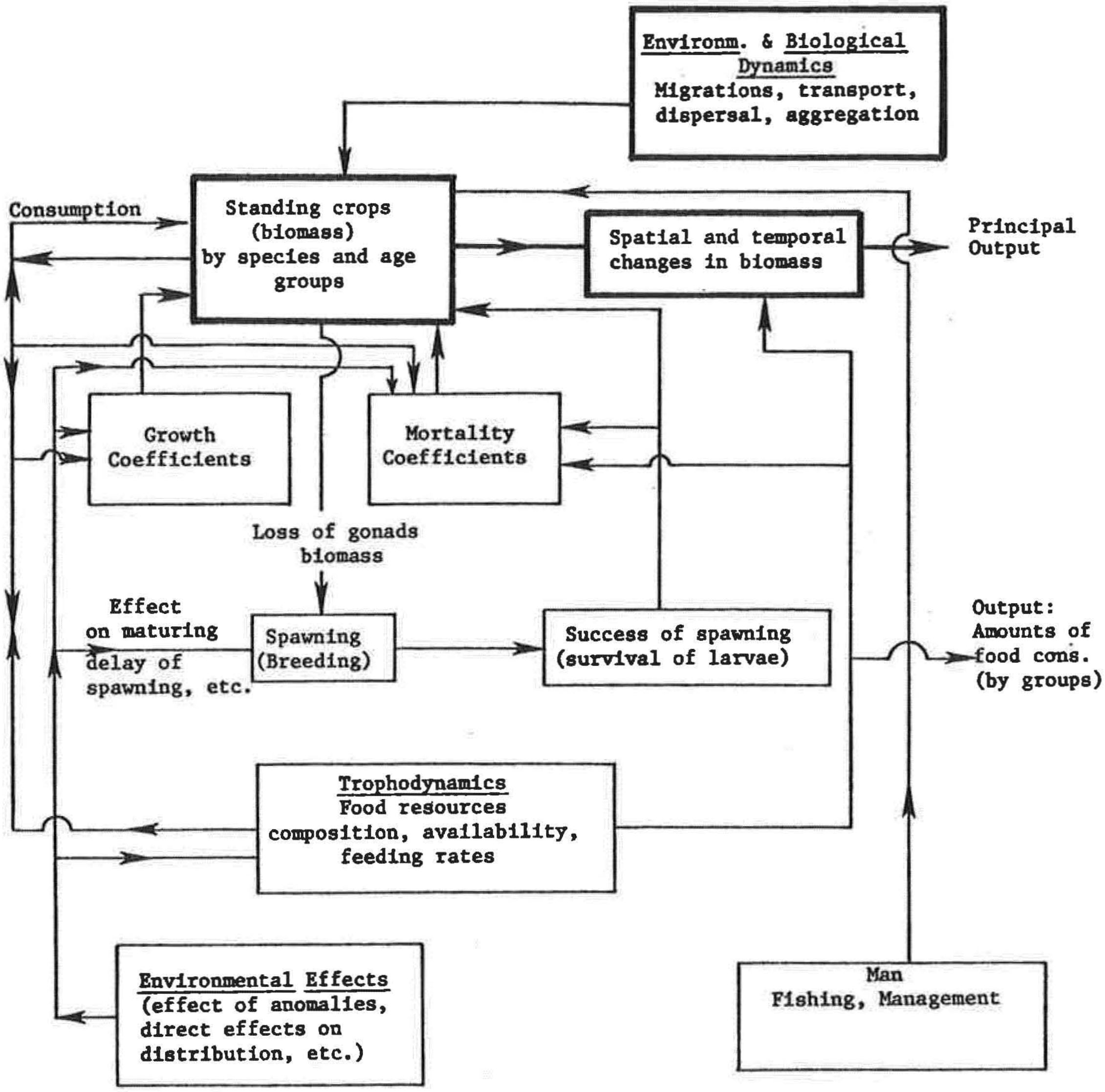

Figure 2. Scheme of principal processes and interactions in the marine ecosystem.

The preceding six principles require the following general logic to be the basis of the model development:

-The ecosystem simulation is, to a large extent, a bookkeeping of changing balance (imbalance) in nature.

-The model must be based on available basic knowledge and must provide multiple checking (verification) possibilities. Unsubstantiated assumptions and beliefs, such as the widely held belief that the number of spawners determines largely the year class strength in all species, have been avoided. To the contrary, the early model results indicate that predation on 0+ and 1+ year classes determines largely the exploitable year class strength of most species.

-The grouping of similar species in the model must be possible in order to have a program of manageable size. On the other hand, provision must exist to consider single species or even year classes, if so desired.

The schematic sequencing of the main body of the program is presented (Figure 3) and a more detailed outline is also given (Figure 4). A few additional explanations are listed below:

(1) Inputs, initiation

Grid - equal area two dimensional grid, grid size 95.25 km. Third dimension (depth) either implied and/or used in zoomed areas.

Fixed data - depth, monthly mean environmental conditions (ice, temperature, etc., for anomaly computation), sea-land and special subregion tables.

Coefficients - e.g., food requirement, growth, fishing intensity, etc., coefficients, some specific for species, some specific for area and time (detailed data given in discussions on specific species).

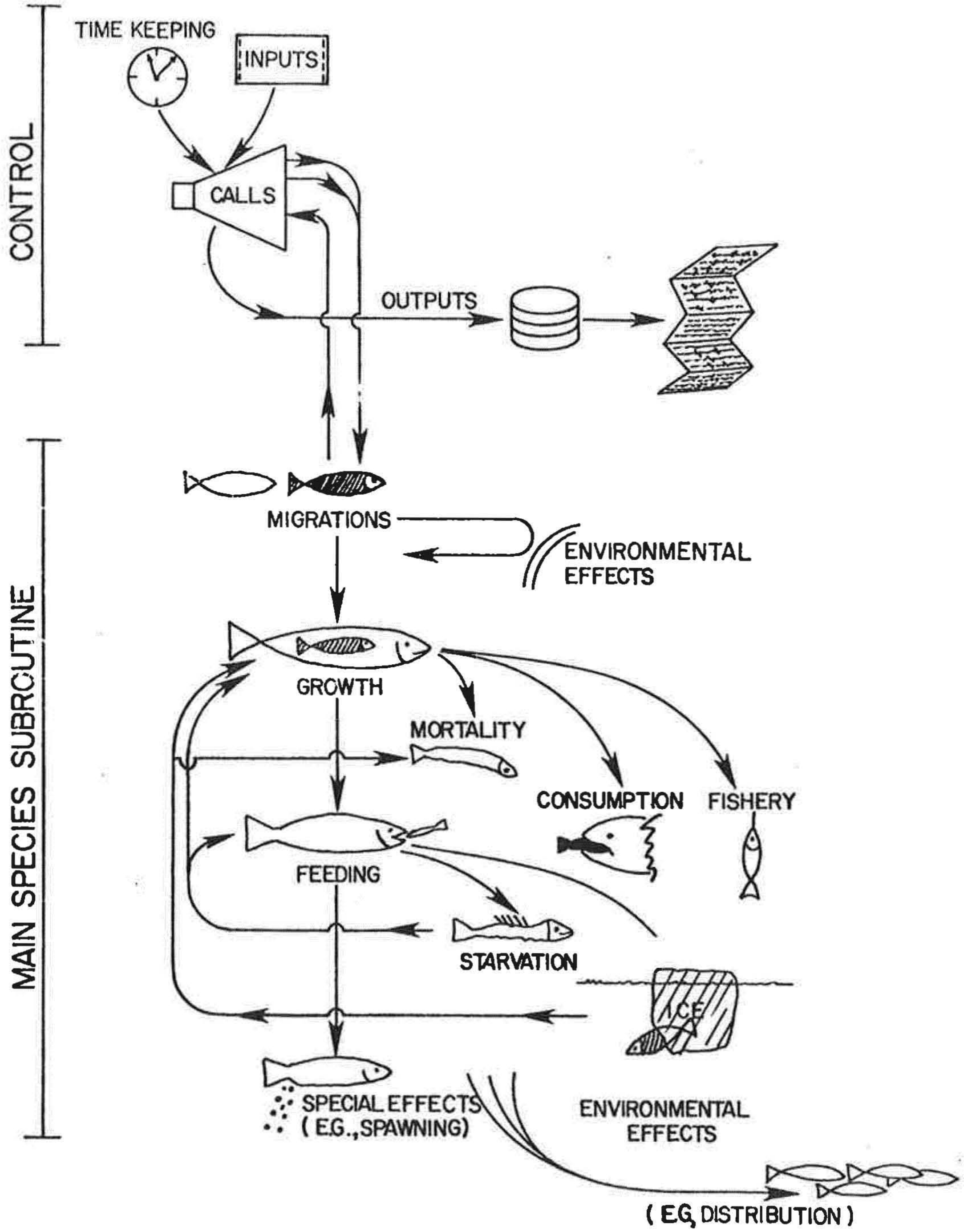

Figure 3. Schematic sequencing in species subroutines.

Control

Input of basic data

Timekeeping

Calls to species subroutine

Outputs of multi-subroutine fields

Species dynamics subroutines (fish, mammals, birds)

Migrations, distributions

Environmental effects

Growth, mortality, consumption, fishery

Feeding, starvation

Feedbacks

Food availability, selectivity

Environmental effects

Specific processes/effects (spawning)

Feedbacks

Outputs: time series quantitative distributions

"Organic production" subroutines

Phytoplankton consumption

Zooplankton standing crop simulation

Zooplankton consumption

Benthos, growth, consumption

Special manipulation/output subroutines

Zooms (area, time)

Graphing

Special outputs (special investigations)

Figure 4.-Schematic outline of the DYNUMES II model.

Biological (species) data - initial quantitative distributions of fish, division of "important" species into age (size) groups; monthly distribution of mammals and birds.

(2) Control program

The control program includes timekeeping, calling of subroutines, and month-end outputs of fields which are computed in several subroutines. Inputs are also done with the control program which also prints the input fields and other data for verification purposes.

(3) Species dynamics subroutines (fish)

The migrations of the species and resulting distribution is computed in each time step (weekly or monthly). The effects of environment (e.g., ice, temperature, depth, nature of the bottom) on migration will be incorporated in version III of DYNUMES model.

Growth, consumption (grazing), fishery, and natural mortality is computed using the monthly consumption of the given species from the previous time step. The food consumption (for growth and maintenance) is computed with constant coefficients and composition, however, the DYNUMES III will have time and space varying composition of food (adjusted to availability and preference) and the food uptake, as well as growth, as influenced by environment (temperature).

(4) Mammal and bird subroutines

Monthly quantitative distributions of mammals and birds is prescribed. As these estimates have certain margins of error, it is not rewarding at this time to compute growth and mortality of mammals and birds, but only consumptions (grazing) by them.

(5) "Organic production" subroutines

Phytoplankton and zooplankton consumptions are computed throughout the model even though present knowledge of phytoplankton production is too scanty for meaningful simulation. Zooplankton standing crop is simulated as a function of location, latitude and time (season). Benthos computations (growth, grazing, distribution) are carried out only on the portion of benthos which is suitable as fish food; no predatory benthos, about which the knowledge is scanty, is taken into consideration.

(6) Special manipulation/output subroutines

Special graphing subroutines and printout subroutines are incorporated and special ancilliary graphic programs are available externally. DYNUMES III will contain a zooming subroutine, which will allow detailed computations with small mesh; the boundary conditions for zooming subroutine being extracted from regular model run.

B. FORMULAS AND COMPUTATION PROCEDURES

Because of large computer core and intermediate storage requirements, the model makes extensive use of random access mass storage. Although in the initial modeling stages many of the input fields were created in the program (e.g., bearded seal distribution field in relation to ice edge), without additional cores it will be necessary in subsequent versions to punch these fields after creation on cards and read these into storage in the initiation of the program. The "minimum sustainable biomass" of each species was initially also established by model outputs. Now a separate model (Bulk Biomass Model, BBM) is used for this purpose.

In the following paragraphs only some essential formulas and computation procedures are presented. Extensive use is made in the program of a variety of "restrained functions"; these are best explained in program documentation, which is in preparation.

(1) Migration speed

The migration speed (u and v components) is simulated within the program for each species or is prescribed with input fields. The migration, including diffusion and "smoothing" is computed in weekly time steps (shorter time steps in zoomed models) with the following finite difference formula:

$$B_{t,n,m} = B_{t-1,n,m} - C_1 B_{t-1,n,m} + C_2\ (B_{t-1,n-1,m} + B_{t-1,n+1,m}$$
$$+ B_{t-1,n,m-1} + B_{t-1,n,m+1} - 4B_{t-1,n,m}) - T_d\ C_3\ C_4$$
$$- T_d C_5 C_6 + C_2\ (B_{t-1,n-1,m-1} + B_{t-1,n-1,m+1} + B_{t-1,n+1,m-1}$$
$$+ B_{t-1,n+1,m\_1})\ /4$$

Where:

$C_1 = 2T_d A/L$

$C_2 = T_d A/L$

$C_3 = u$

$C_4 = (B_{t-1,n,m} - B_{t-1,n,m+1})\ /L$ (u neg)

$C_4 = (B_{t-1,n,m} - B_{t-1,n,m-1})\ /L$ (u pos)

$C_5 = v$

$C_6 = (B_{t-1,n,m} - B_{t-1,n-1,m})\ /L$ (v neg)

$C_6 = (B_{t-1,n,m} - B_{t-1,n+1,m})\ /L$ (v pos)

Symbols:

A - "smoothing coefficient" (time step and grid size dependent) = 0.5 in present model

B - biomass

C_4C_6 - "upstream interpolation"

L - grid length (km)

n,m - grid point designations

T_d - time step (days)

t - time step designator (t - current, t-1 - previous)

u,v - migration speed components

Although the above migration formula is conservative, some minor loss of biomass can occur near open boundaries. This can be corrected by the following approach.

$$B_{t,n,m} = B_{t-1,n,m} \frac{B_{t-1(tot)}}{B_{(tot)}}$$

where $B_{(tot)}$ indicates total biomass over the area (t-1 in previous time step and t in present time step).

The aggregation at boundaries (e.g., the spawning of herring and capelin near the coast) will be simulated with restrained functions in DYNUMES III.

(2) Growth of biomass

The growth of biomass is computed with a formula similar to those used in conventional population dynamics approaches:

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

g is growth coefficient for a given species. It changes with the age of the species. Therefore, it is necessary to know the mean age of the biomass (see Section II-D below). In this model version (II) the growth coefficient is either constant in some species or changing harmonically throughout the year. In DYNUMES III the growth coefficient will be a function of environment (temperature) and food availability (starvation).

(3) Fishing and mortality losses

Fishing and (natural) mortality (from old age and diseases) losses are also computed by an exponential function:

$$B_{t,n,m} = B_{t-1,n,m}\ e^{-f}$$

f is a fishing intensity coefficient, which is prescribed as a monthly field in some intensely exploited species (e.g., pollock), or applied to all species biomass at each grid point in some other species. It is tuned to a value which yields quantities corresponding to available catch data. In mortality computations f is replaced with a relatively low mortality coefficient. In DYNUMES III the latter coefficient will be made a function of unfavorable environment (e.g., temperatures below 0.5°C) and of availability of food (starvation).

The total biomass balance formula thus becomes

$$B_{t,n,m} = B_{t-1,n,m}\ (2-e^{-g})\ e^{-(f+m)} - C_{t-1,n,m}$$

where C is the consumption (grazing) in the previous month (see below).

(4) Trophodynamics

The trophodynamic formulas compute the food uptake (and requirements) and effect the bookkeeping of the consumption (grazing).

Food requirement formula:

$$F_{i,t} = B_{i,t-1}\ (2-e^{-g_t})\ K_{i,g} + B_{i,t}\ K_{i,m}$$

Food proportioning formula:

$$C_{i,j,t} = F_{i,t}\,\rho_{i,j}$$

$$C_{i,k,t} = F_{i,t}\,\rho_{i,k} \qquad \text{--etc.}$$

$$C_{i,t} = C_{j,i,t} + C_{k,i,t} + \ldots C_{n,i,t}$$

The symbols in the above equations are:

$B_{i,t}$ - biomass of ecological groups i in months t,

$g_{i,t}$ - growth coefficient (approximately growth in % per month),

$F_{i,t}$ - food requirement for growth and maintenance,

K_g - food coefficient for growth (e.g., 1:2 - 2 kg of food biomass gives 1 kg of growth),

K_m - food coefficient for maintenance (in terms of body (biomass) weight per time step),

$C_{i,t}$ - total amount of ecological groups consumed by other groups in unit time (months),

$\rho_{i,j}$ - proportion of ecological group in the food of group i,

i,j,k,n - ecological groups.

The ecosystem internal grazing is unevenly distributed over different ages (year classes) of the species, but in DYNUMES III there will be a provision for partitioning several biomasses into juveniles and adults and consequently obtaining separate growth and consumption computations. DYNUMES II has this provision only for pollock. DYNUMES III will also permit a space and time variable composition of food, depending on its availability, as well as bookkeeping of partial starvation, which in turn will modify growth and mortality rates.

(5) Special effects

Among special effect formulas, which have been described in previous reports (e.g., Laevastu, Favorite and McAlister 1976) the following could be listed: conversion between geographic and model grid coordinates, boundary treatment, general analysis program and graphing program, the last two being external to the model.

Zooplankton standing crop simulation formula can serve as an example for simulation of similar and/or related fields in the program:

$$Z_{t,n,m} = P_1 + C_1 \cos(\alpha T_d - \kappa_1) + C_k \cos(\beta T_d - \kappa_2)$$

Z - is zooplankton standing crop (e.g., in mg/m^3)

P_1 - is a latitude and location (subarea) dependent annual mean zooplankton standing crop

C_1 - is the half-magnitude of annual change of zooplankton standing crop (function of latitude and specific location)

C_k - is a "modifying magnitude" (e.g., for reproduction of autumn "bloom"

α and β are phase speeds (time step dependent, 30^o and 60^o respectively for monthly time step)

κ_1 and κ_2 are phase lags

T_d - is time (in month)

Other specific formulas and procedures used in the model will be described in DYNUMES III documentation.

C. INPUTS AND OUTPUTS

The following is a list of two-dimensional field arrays which are either read (direct input) from cards (marked with i) or created in the program. If the species/group of species can be consider "indigenous" to the area, only the initial field is read (created). However, where considerable migrations through the boundaries occur, monthly distribution fields have been read from cards (marked im in the following list). Seasonal distributions are marked with s; whereas im, c indicates fields which were initially created with the model but are at present read from cards.

(1) Environment and model operation fields:

Sea-land table (depths in DYNUMES III) (i)

Special indices (subareas) (i)

Ice (im)

Bottom temperature (is) } (DYNUMES III only)
Surface temperature (is) }

Surface currents (is) (DYNUMES III) only)

Actual temperature and current anomalies (im) (DYNUMES III only)

Operation fields (40) (Space in main core; output and intermediate fields on disc not accounted, the latter exceed 700 at present)

(2) Ecological groups and major single species:

Mammals

1. Fur seal (im)
2. Sea lion (im)
3. Bearded seal (im,c)
4. Ringed and ribbon seals (im,c)
5. Harbor seals (im,c)
6. Baleen (true) whales (im,c)
7. Toothed whales (including porpoises, dolphins (im,c)
8. Walrus (im,c)

Birds

9. Murres (im,c)
10. Shearwaters (im,c)
11. Other marine birds ("lumped" group) (im,c)

Fish

12-15. Pollock (3 age groups) (c) total (i)

16. Other gadids ("lumped") (i)

17. Herring (i)

18. Other pelagic fish (capelin, smelts, etc.) (i)

19. Yellowfin (i)

20. Other flatfish (i)

21. Other demersal fish (sculpins, etc.) (i)

Plankton, benthos

22. Benthos ("fish food" benthos) (i,c)

23. Squids (i)

24. Euphausids (c)

25. Copepods (c)

26. Total zooplankton (c)

27. Phytoplankton (consumption only) (c)

For most of the above species/ecological groups, monthly consumption fields, migration speed fields, and "starvation" fields are created in the program. As the number of fields (arrays) to be operated on, exceeds 700 at present, and as the program is in excess of 6000 cards, it is obvious that a larger computer is required and that the program must be optimized in a multitude of way.

The outputs are in the form of field printouts and various tables and graphs. Most of the routine outputs are two-dimensional field printouts of monthly quantitative distributions and consumption. Special outputs are tailored to the problems and questions to be solved and usually include time series outputs at selected locations. Examples of outputs are found in the following Sections, (mainly in Section III).

D. SENSITIVITY OF THE MODEL TO INPUT VARIABILITY

The sensitivities of various aspects of the model, especially the linear and quasi-linear interactions of growths and mortalities, were investigated during the model design/programming and tuning stages using, among others, special outputs from runs with assumed (e.g., plausible minimum/maximum values) of input variables. Details of these more qualitative than quantitative sensitivity tests would require voluminous reports, which would have a limited audience. However, one of the main tasks, and also objectives, of the model is to study the sensitivity of the ecosystem and interactions within it to various changes and influences, internal as well as external to the system. These are studied with special investigative/production runs and will be reported separately as they are made and when a final model structure is arrived at. One example of such studies is found in the report on dynamics of pollock biomass in the eastern Bering Sea (Laevastu and Favorite 1976c).

The greatest sensitivity of the model to input parameters is in the nonlinear parts of the model, where exponential functions are used (e.g., growth and mortality computations). New scientific as well as applied questions and problems have arisen in the formulation and tuning of these parts of the model, which have required special studies and developments. This is illustrated below with an example of determining a mean growth coefficient for Pacific herring. The weight growth coefficients decrease with age of the species (Figure 5). Thus, for the computation of the biomass distribution for any given time it is necessary to know the age composition of the biomass of a species/ecological group. This composition can be computed using available data and some assumptions. First, the age distribution of the exploitable part of the biomass can be obtained by summarizing the distribution of year classes in the catches (Figure 6) and determining from this summary a mean age composition of catch (Figure 7). Next, a more subjective estimation of the consumption of the fish of different size (and age) must be performed (Figure 8). This estimation is first done by size categories, using knowledge of the size of prey (from stomach analyses), relative amounts of predators, and turnover rates. The estimates of the last two parameters are guided by the ecosystem model outputs (these estimates are given in Figure 9 on a linear age scale).

Next, iterative extrapolations of the numbers and biomass are carried through juvenile year-classes by taking into account that the biomass of the previous year class must deliver the biomass of the next year class with the experimentally (by measurement) determined growth rate (Figure 5) plus the biomass consumed within this year (Figure 9). This computing procedure is reported in another report (Laevastu and Favorite 1977a). The resulting biomass and number distribution of Pacific herring in the Bering Sea is given (Figure 10) which also indicates that only 30% of the biomass of this species is under exploitation and 70% is in the juvenile stage. The bulk of the biomass of many species is in juvenile stages, which explains the necessity of the use of relatively high growth coefficients in the model. Considering the formula for growth (see previous Section) it becomes obvious that the total biomass and its fluctuations are sensitive to the selection of a proper growth coefficient and its change. In DYNUMES III, the growth coefficient is a function of environment (temperature) and availability of food.

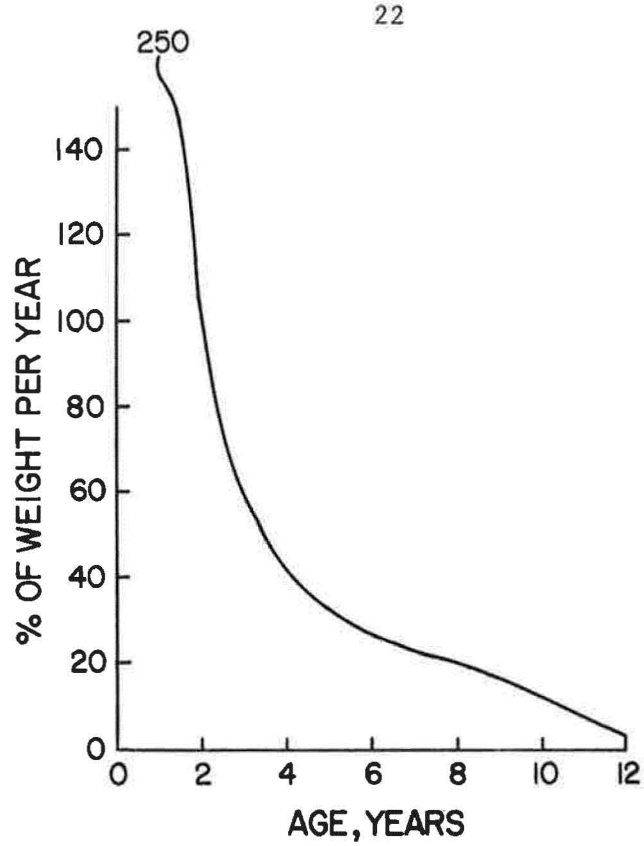

Figure 5. Growth of weight of Pacific herring in the Bering Sea (% per year).

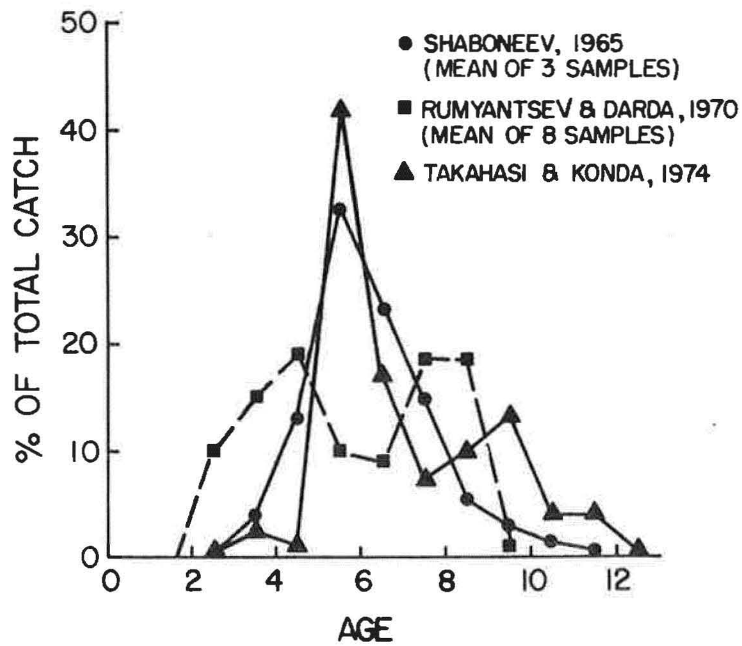

Figure 6. Age composition of catch of Pacific herring in the Bering Sea as reported by different investigators.

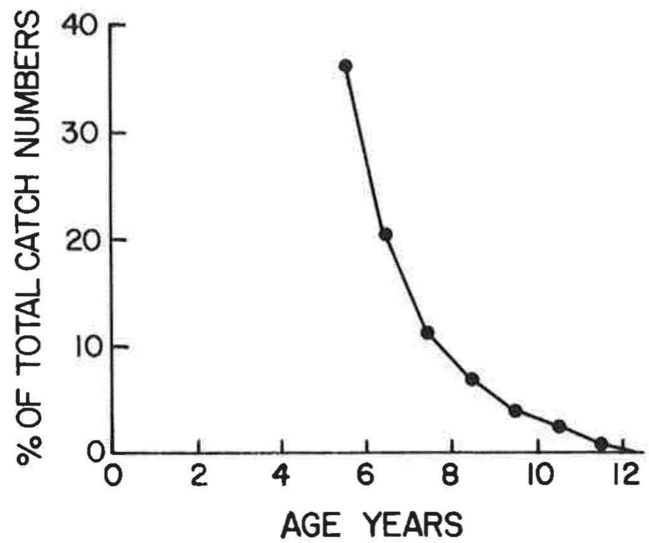

Figure 7. Estimated mean age composition of Pacific herring in the Bering Sea.

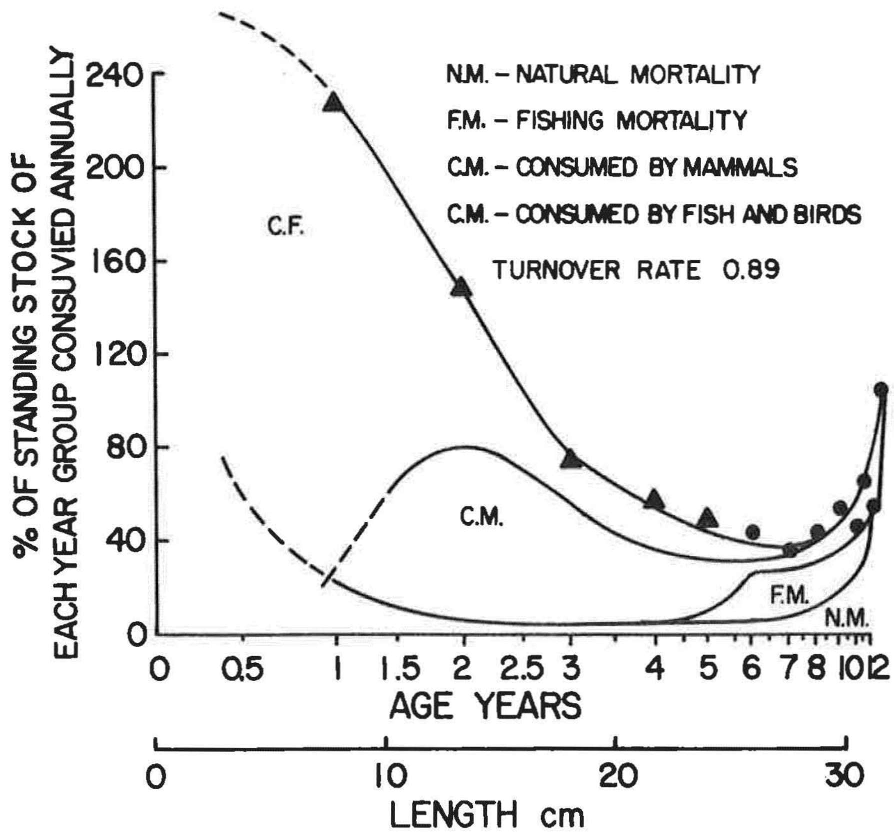

Figure 8. Percent of biomass consumed annually of different size (and age) groups of Pacific herring in the Bering Sea.

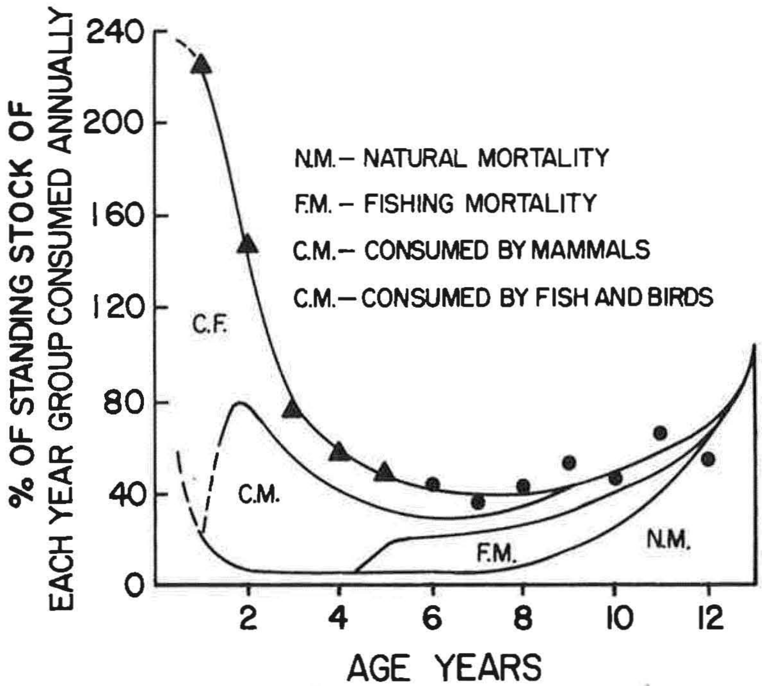

Figure 9. Percent of total biomass of each year class of Pacific herring consumed annually in the Bering Sea.

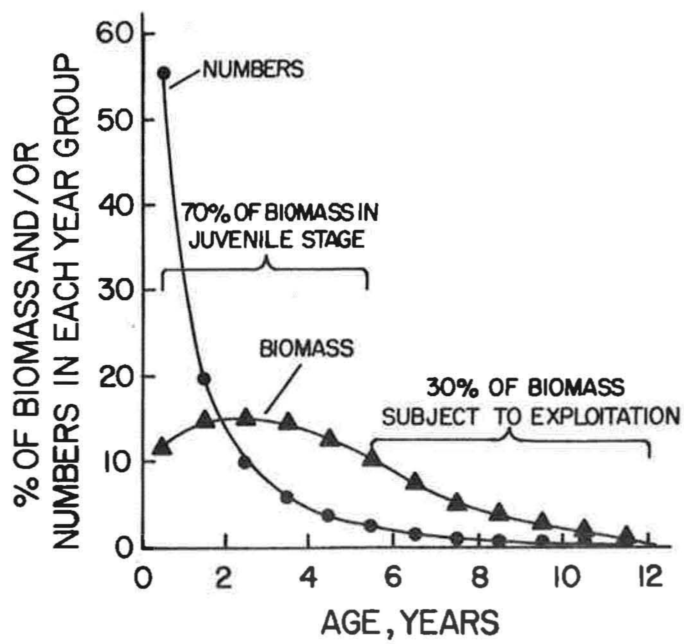

Figure 10. Distribution of biomass and numbers with age of Pacific herring in the Bering Sea.

III. QUANTITATIVE RELATIONS IN THE ECOSYSTEM OF THE EASTERN BERING SEA

A. GROWTH AND FOOD COEFFICIENTS AND COMPOSITION OF FOOD

The prognostic results from the model are greatly dependent upon the validity of the initial inputs, primarily the various coefficients and food compositions. The initial guess of the abundance of a given species and/or ecological group is determined by the Bulk Biomass Model (BBM) (Laevastu and Favorite 1976b) and the distribution of the given species is determined empirically from knowledge extracted from the rather extensive literature. The final adjusted distributions will be described in detail in a report on DYNUMES III. It has been observed in the course of using the model that the initial, relatively smooth, prescribed distributions are modified after about a 6 month computation period, resulting partly in somewhat patchy distributions (which is a known normal condition with most species), and in partial separation of the centers of bulk distribution of species into more than one cluster in some species. This is also a normal, known condition in the sea, where the bulk of the catches in some areas in medium and higher latitudes consist of one or two species, which are replaced in other not too distant locations by other species. Examples of patches and distributions are given later in this report.

The growth coefficients (Table 1) are empirically derived from available data. If the species is not divided into size (age) groups, the distribution of biomass with age must be used for computation of growth coefficients. Experiments with seasonal and area variable growth coefficients were carried out (in DYNUMES III growth coefficients will be functions of temperature and food availability at each grid point and at each time step).

Table 1

Growth and mortality coefficients
(% per month)

Species/ecological group	Growth coefficient	Natural mortality coefficient	Fishing mortality coefficient
Pollock, group 1	13.0	0.3	-
Pollock, group 2	5.0	0.3	}Time & space
Pollock, group 3	1.5	1.5	}variable
Herring	9.0	0.4	2.0 (4 months)
Other pelagic fish	12.0	0.5	-
Yellowfin	7.0	0.09	0.7
Other flatfish	8.0	0.07	0.7
Other gadids	11.0	0.3	0.3
Other demersal fish	10.0	0.3	0.35
Squid	12.0	3.0	-
Benthos ("fish food benthos")	12.0	3.0	0.05

Note: 1. Natural mortality refers to mortality from disease and old age only.

2. Fishing mortality does not reflect in all species present catches, but also potential catches.

The fishing mortality coefficients (Table 1) are, in most cases derived by tuning (adjustments) so that the computed results represent the present catch. Runs have also been made with "potential catch" coefficients. Where the time and space distribution of fishing intensity is known (e.g., with pollock), it has been prescribed with input.

The natural mortality coefficient refers to mortalities caused by diseases and "old age" only. It has been estimated by considering also the average life length of the species and fishery (if any).

The consumption (grazing) is computed within the model. It depends on food requirements and composition of food (preferred food items) of all model components. In addition, the size of the food item has been taken into consideration by adjusting the composition of food of a given species.

The food coefficients are given (Table 2) without discussion at this time. It could be pointed out here that the food coefficients are considerably lower than conventionally used and found in the literature. This is partly due to the model results which have led us to believe that the relatively few experimentally determined food coefficients are somewhat too high, having been determined in tanks and in fish culture ponds.

The composition of the food of different species and ecological groups (Table 3) are based on considerable literature review and synthesis of relatively scattered and variable notes on this subject. It has become apparent that the composition of food of any given species varies within relatively wide limits, not only with the age of the species, but also with the location and the season. Therefore, the food composition in DYNUMES III will be made variable in space and time, depending largely upon the availability of preferred and suitable food items.

Table 2

Food coefficients

Species/ecological group	Food for maintenance (% body weight daily)	Food for growth (ratio, growth/food)
Pinnipeds		
Fur seal	5	
Bearded seal	5	
Sea lion	5	
Harbor seal	5	
Ringed/ribbon seal	5	
Walrus	5	
Whales & ecologically related species		
Baleen whales	4	
Toothed whales, porpoises	3.3	
Birds		
Shearwaters	12	
Murres	12	
Other birds	12	
Fish		
Pollock, group 1	0.75	1.7
Pollock, group 2	0.65	1.4
Pollock, group 3	0.5	1.4
Herring	0.8	1.8
Other pelagic fish	0.75	1.8
Yellowfin	0.8	
Other flatfish	0.8	
Other gadids	1.0	
Other demersal fish	1.0	
Other ecological groups		
Squid	0.5	1.5
Benthos ("fish food benthos")	0.8	

Table 3

Composition of food (percentage)

PINNIPEDS

Fur seal

Pollock	73
Other gadids	6
Herring	5
Salmon	2
Other pelagic	2
Benthos	2
"Others"	10

Sea lion

Pollock	65
Salmon	8
Other gadids	7
Herring	6
Other pelagic	4
"Others"	10

Bearded seal

Benthos	61
Pollock	10
Squids	8
Herring	5
Other flatfish	5
Other gadids	3
Other pelagic	3
Salmon	1
"Others"	4

Ringed/ribbon seals

Pollock	28
Other pelagic	18
Benthos	14
Squids	12
Herring	12
Other gadids	10
Other flatfish	2
Salmon	1
"Others"	3

Walrus

Benthos	95
Pollock	2
Other flatfish	1.5
Salmon	0.5
"Others"	1

Harbor seals

Benthos	23.5
Pollock	20
Squids	20
Other gadids	15
Other pelagic	7
Herring	3
Other flatfish	2
Salmon	1.5
"Others"	8

WHALES, DOLPHINS, PORPOISES

Baleen whales

Euphausids	80
Squids	9
Copepods	6
Other pelagic	2
Herring	1.5
Pollock	1
Other gadids	0.5

Toothed whales, dolphins

Other pelagic	30
Pollock	25
Herring	17
Other gadids	5
Other flatfish	5
"Others"	18

Table 3 - Cont'd.

BIRDS

Murres		Other birds	
Pollock	27	Euphausids	40
Other pelagic	27	Other pelagic	20
Euphausids	14	Squids	8
Squids	7	Benthos	8
Herring	7	Copepods	8
Other flatfish	2	Herring	4
Salmon	1	"Others"	12
"Others"	15		

Shearwaters	
Euphausids	80
Other pelagic	10
Herring	5
Squids	5

FISH

Herring		Other pelagic fish	
Copepods	68	Copepods	45
Euphausids	19	Euphausids	35
Phytoplankton	3	Phytoplankton	10
Other pelagic	3	Other pelagic	4
Squids	1	Squids	3
Pollock	0.5	Pollock	2
Other gadids	0.3	Other gadids	0.5
Yellowfin	0.3	Herring	0.5
Other flatfish	0.3		
"Others"	4.6		

Pollock	Group 1	Group 2	Group 3
Copepods	68	22	6
Euphausids	28	56	29
Pollock, Gr. 1		5	13
Pollock, Gr. 2			4
Herring	0.5	2	8
Other pelagic	1	2	5
Other gadids			3
Other demersal	2	3	5
Squids		1	8
Benthos	0.5	9	17
Yellowfin			1.5
Other flatfish			0.5

Table 3 - Cont'd.

Yellowfin	
Benthos	50
Euphausids	20
Other demersal	10
Pollock	8
Other flatfish	7
Squids	3
Other gadids	2

Other gadids	
Benthos	28
Euphausids	20
Copepods	14
Other demersal	10
Pollock	9
Other pelagic	8
Herring	4
Other flatfish	4
Yellowfin	3

Other flatfish	
Benthos	65
Euphausids	10
Pollock	10
Yellowfin	2
Other flatfish	2
Other pelagic	2
Other gadids	2
Other demersal	2
"Others"	5

Other demersal fish	
Benthos	37
Euphausids	22
Copepods	12
Other flatfish	9
Other gadids	6
Pollock	4.5
Yellowfin	4
Other pelagic	3.5
Herring	2

OTHER ECOLOGICAL GROUPS

Benthos ("fish food benthos")	
Phytoplankton (detritus)	75
Benthos	11
Copepods	7
Euphausids	4
Other demersal	1
Other flatfish	0.5
Yellowfin	0.3
"Others"	1.2

Squids	
Other pelagic	30
Euphausids	25
Pollock	15
Copepods	15
Herring	10
Other gadids	5

As the consumption is one of the more important factors (in fact quantitatively considerably higher than the intensive fishery) determining the dynamics and abundance of species, and as feeding depends on the space and time variable food composition of most species in an ecosystem, only large, multi-component, relatively complete ecosystem models such as DYNUMES II can simulate realistically marine ecosystem. The list of main consumers of different species and/or ecological groups (Table 4) demonstrates the complexity of food relations.

The subsequent discussions in this Section indicate only a few salient points of the distributions and interactions in the Bering Sea ecosystem and a few other poorly known facts about the populations in this area. However, there are several conditions and processes in the Bering Sea that must be ascertained by further field studies before the model results on these conditions can be considered fully valid. Among these problems the following are listed as examples:

- How large a part of the population of a given species remains under the ice? (Most of the fish species in the Baltic survive under the ice. However, the Baltic does not have any really cold bottom temperatures such as those occurring in the Bering Sea).
- Are the cold (subzero) bottom temperatures lethal to some species in the Bering Sea, and to what extent?
- What are the major spawning areas and times of the fish species in the Bering Sea (this information is still scant for many major species)?
- What is the biomass of some of the species which are indicated to be abundant forage fish such as capelin and smelt?

Table 4

Main consumers of various species and ecological groups in the eastern Bering Sea

Species/group of species	Consumers (minor consumers in parenthesis)
Pollock	Fur seal, sea lion, ringed/ribbon seals, harbor seals, (bearded seal, walrus); toothed whales; murres; pollock, other gadids, other flatfish, squids, yellowfin, other demersal
Herring	Sea lion, fur seal, ringed/ribbon seals, bearded seal (harbor seals); toothed whales, murres, shear-waters, other birds (baleen whales); pollock, other gadids, other demersal, squids, other pelagic
Other pelagic fish	Ringed/ribbon seals, harbor seals, sea lion, bearded seal, (fur seal); toothed whales (baleen whales); murres, other birds, (shearwaters); pollock, other gadids, other demersal, squids, other pelagic
Yellowfin	Pollock, other gadids, other demersal, other flatfish, (benthos)
Other flatfish	Bearded seal, harbor seals, ringed/ribbon seals, walrus; toothed whales; murres; pollock, other flatfish, other gadids, other demersal, yellowfin
Other gadids	Sea lion, fur seal, harbor seals, bearded seal, ringed/ribbon seals; toothed whales; pollock, other flatfish, other demersal, squids, (herring, other pelagic)
Other demersal fish	Pollock, yellowfin, other flatfish, benthos, other gadids
Squids	Harbor seals, bearded seal, ringed/ribbon seals; baleen whales; murres, shearwaters, other birds; pollock, herring, other pelagic
Benthos	Bearded seal, walrus, ringed/ribbon seals, harbor seals, yellowfin, other flatfish, other gadids, other demersal, benthos, pollock
Salmon	Sea lion, harbor seal, fur seal, bearded seal, (walrus); (toothed whales); (murres); (pollock, other gadids)

Table 4 - Cont'd.

Euphausids	Baleen whales; murres, shearwaters, other birds; herring, other pelagic, pollock, other gadids, other demersal, squids, yellowfin, (benthos)
Copepods	(Baleen whales); other birds; herring, other pelagic, pollock, other gadids, other demersal, squids, benthos.
Phytoplankton	Herring, other pelagic, benthos (as detritus)
"Others"	Fur seal, bearded seal; toothed whales; murres, other birds; herring, other flatfish, benthos

B. CONSUMPTION OF FISH BY MARINE MAMMALS AND BIRDS

The Bering Sea is a major feeding ground for whales in the North Pacific Ocean. Three species of the baleen whale are found there during the summer (Table 5), but only one species (Bowhead) remains there during the winter. Three species of the toothed whales also feed in the Bering Sea only during the summer. The conservatively estimated number of whales (Table 5) has been converted in the model into weight (Figure 11) and distributed in the area according to available information. The main food for baleen whales is euphausids; other food items, such as squids and 0 and 1 age group of mainly pelagic fish, are taken as "incidentals" during essentially "filtering" feeding process. Baleen whales consume about 1.2 million tons of euphausids (Table 6). If this amount of euphausid were consumed by fish, it would produce about 400,000 tons of fish biomass.

Toothed whales consume mainly "adult" (larger) fish and compete directly with man in the harvest of fishery resources. The total annual consumption of finfish by toothed whales is about 1.2 million tons, i.e., more than half of the total commercial catch.

The estimated numbers of pinnipeds in the eastern Bering Sea are also conservative (compare Figures 12 and 13 with data in McAlister and Perez 1976). The pinnipeds in the Bering Sea can be grouped into three groups by seasonal occurrence and migrations. Some species are associated with the ice edge and migrate to the Arctic Ocean with the retrogradation of ice to the north (e.g., bearded seal, walrus). In the behaviorally opposite group are species which migrate into the Bering Sea during the summer for feeding and spend the winter at lower latitudes (e.g., sea lion and fur seal). The third group consists of species which are found in the area year around (ringed and ribbon seals, harbor seals).

Table 5

Estimated number of whales and porpoises in the Bering Sea

Species	Average weight tons	Estimated Number Summer	Winter
Baleen whales			
Fin	50	5,000	-
Gray	40	5,000	-
Mink	9	2,000	-
Bowhead	10	2,000	2,000
Toothed whales			
Sperm	40	20,000	-
Humpback	10	300	-
Giant bottlenose	10	2,000	-
Killer	12	800	800
Beluga	3	2,000	2,000
Porpoises	0.1	5,000	5,000

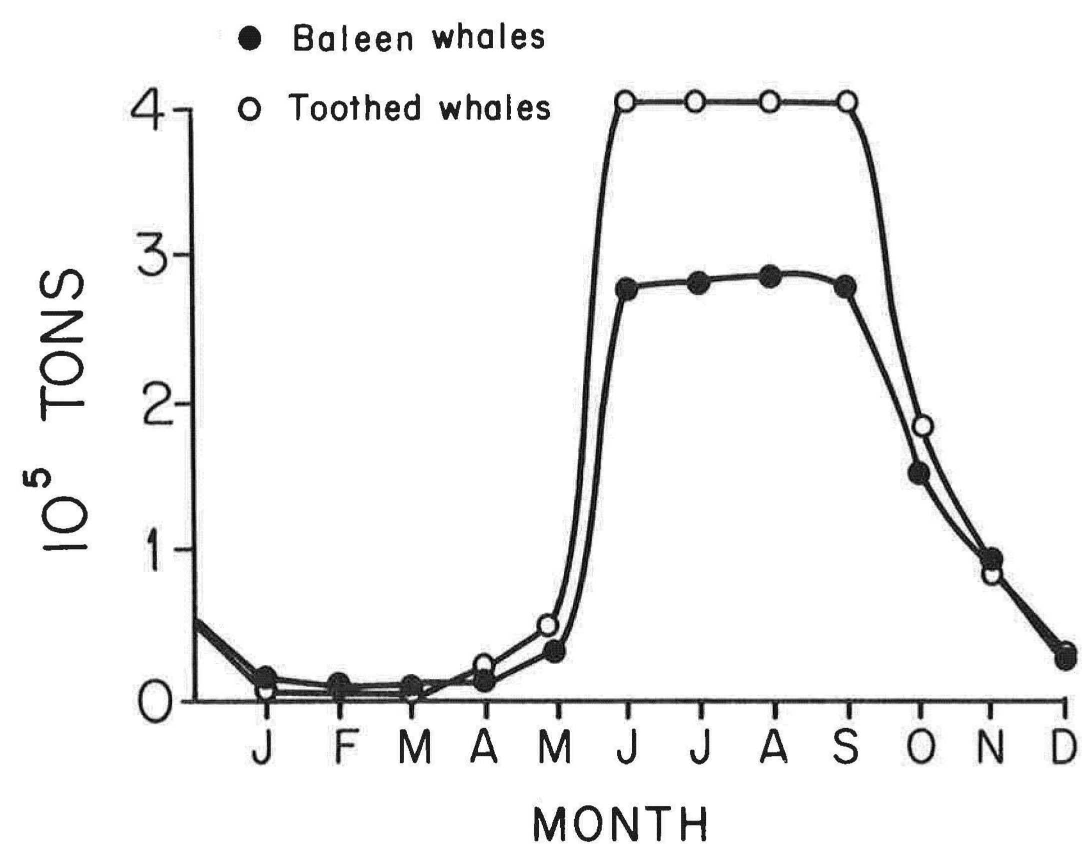

Figure 11. Estimated amounts of whales (including dolphins and porpoises) in the Bering Sea.

Table 6 .--Annual consumption by marine birds and mammals in the eastern Bering Sea (in 10^3 tons).

Species/group of species	Herring	Other pelagic	Salmon	Pollock	Other gadids	Flatfish	Total finfish	Zooplankton	Squids	Benthos	"Others" (Unspecified)
	Species/group of species consumed										
Marine birds	11.7	40.3	1.5	26.3	+	1.9	81.7	105.2	13.2	2.8	14.3
Fur seal	26.5	8.8	8.8	322.3	22.1	-	388.5	-	44.2	-	8.8
Sea lion	16.8	11.2	22.4	182.2	19.6	-	252.2	-	+	-	+
Bearded seal	25.0	25.0	8.3	83.5	41.7	41.7	225.2	-	66.8	509.2	33.4
Harbor seal	66.9	31.2	6.7	89.2	13.4	8.9	216.3	-	89.2	104.8	13.4
Ringed/ribbon seal	24.2	47.5	3.0	84.7	30.3	-	189.7	-	30.3	+	9.1
Walrus	+	+	1.6	6.6	+	4.9	13.1	-	+	311.4	3.3
Total pinnipeds	159.4	123.7	50.8	768.5	127.1	55.5	1,285.0	-	230.5	925.4	68.0
Baleen whales	20.7	27.7	-	13.8	6.9	-	69.1	1,189.3	124.5	-	+
Toothed whales	231.5	408.5	0.5	340.4	68.1	68.1	1,117.1	-	-	-	245.1
Total, whales, porpoises, dolphins	252.2	436.2	0.5	354.2	74.0	68.1	1,186.2	1,189.3	124.5	-	245.1
Total by birds and mammals	423.3	600.2	52.8	1,149.0	201.1	125.5	2,552.9	1,294.5	479.5	928.2	327.4

The general composition of food consumed by the pinnipeds permits grouping them into two categories: those species feeding mainly on benthos (e.g., walrus, bearded seals) and those who feed mainly on fish (e.g., fur seals). The latter are feeding mainly on larger fish and consume at least 1.3 million tons; a quantity comparable to that taken by man. Pollock is the main food for some species (Figures 14 and 15), and it is also the dominant fish species in the Bering Sea. However, there is considerable consumption of the most valuable fish in the area--salmon--during the summer months when salmon return to the rivers for spawning (Figure 16). The model computations show that 50,000 tons of salmon are consumed by pinnipeds (Table 6).

The estimated number of marine birds in the Bering Sea considered in our model is also conservative (compare Figure 17 with data in Sanger and Baird 1977). During the winter months the birds are feeding mainly in the ice free southern part of the area (Figure 18), whereas during the summer they penetrate further north, some species remaining nearer to the coast (e.g., murres, Figure 19), others feeding offshore all over the Bering Sea (e.g., shearwaters which breed in the southern hemisphere during the northern winter and feed in the Bering Sea during the summer).

Although the main food item for birds is euphausids, they consume at least 82,000 tons of fish, mainly small pelagic fish and 0 and 1 year classes of semipelagic species (Table 6). It should be noted that, besides the conservative number of birds, the food coefficient used for birds is also low (12% of body weight daily instead of the conventionally estimated 20%, Wiens and Scott 1975).

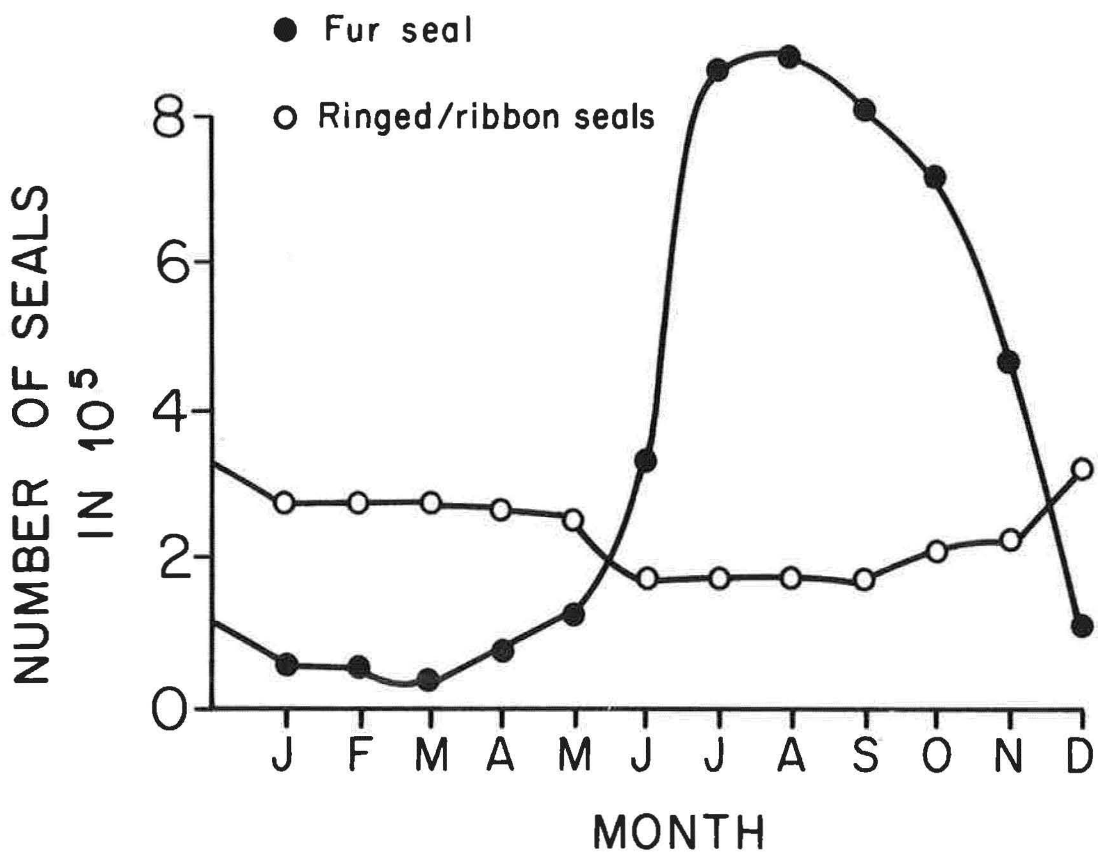

Figure 12. Estimated monthly numbers of fur seals and ringed/ribbon seals in the eastern Bering Sea.

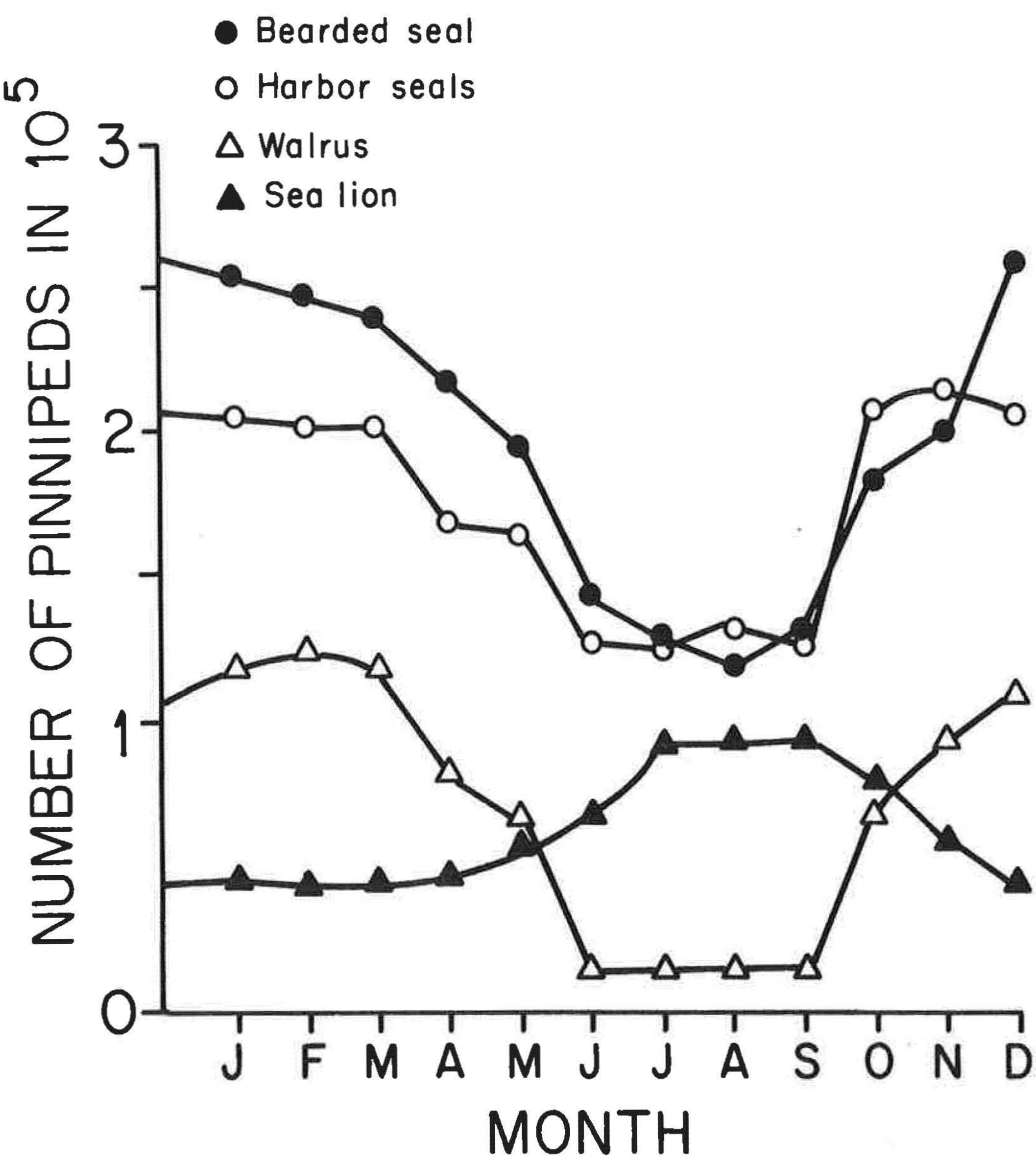

Figure 13. Estimated monthly numbers of bearded seals, harbor seals, walrus and sea lions in the eastern Bering Sea.

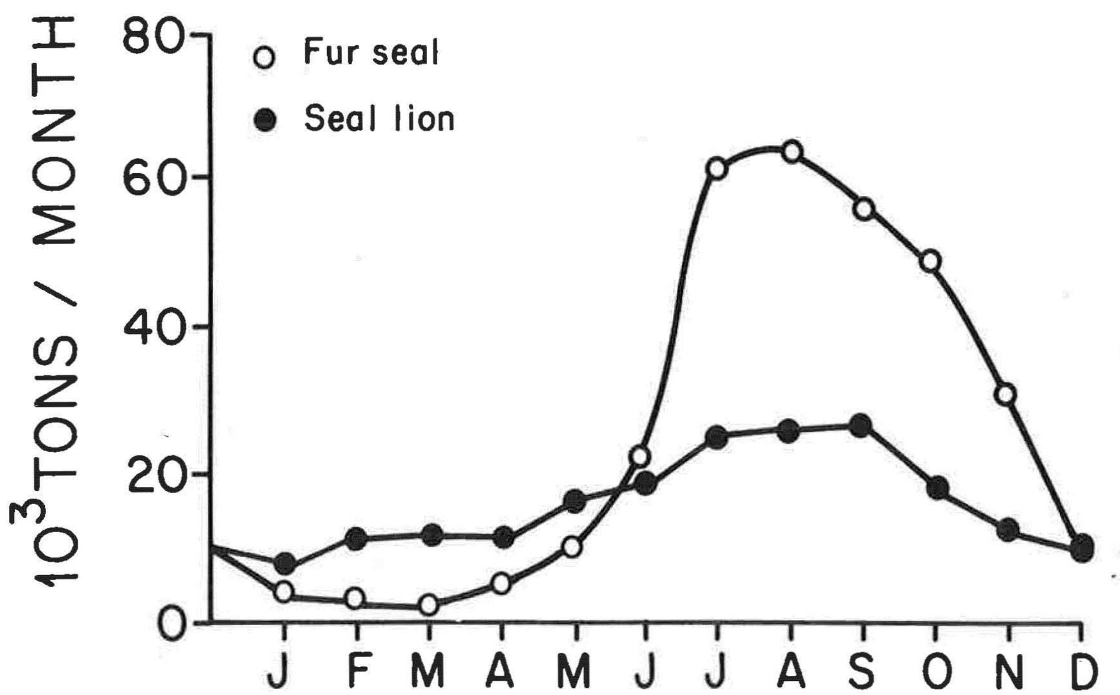

Figure 14. Consumption of pollock by fur seals and sea lions in the eastern Bering Sea.

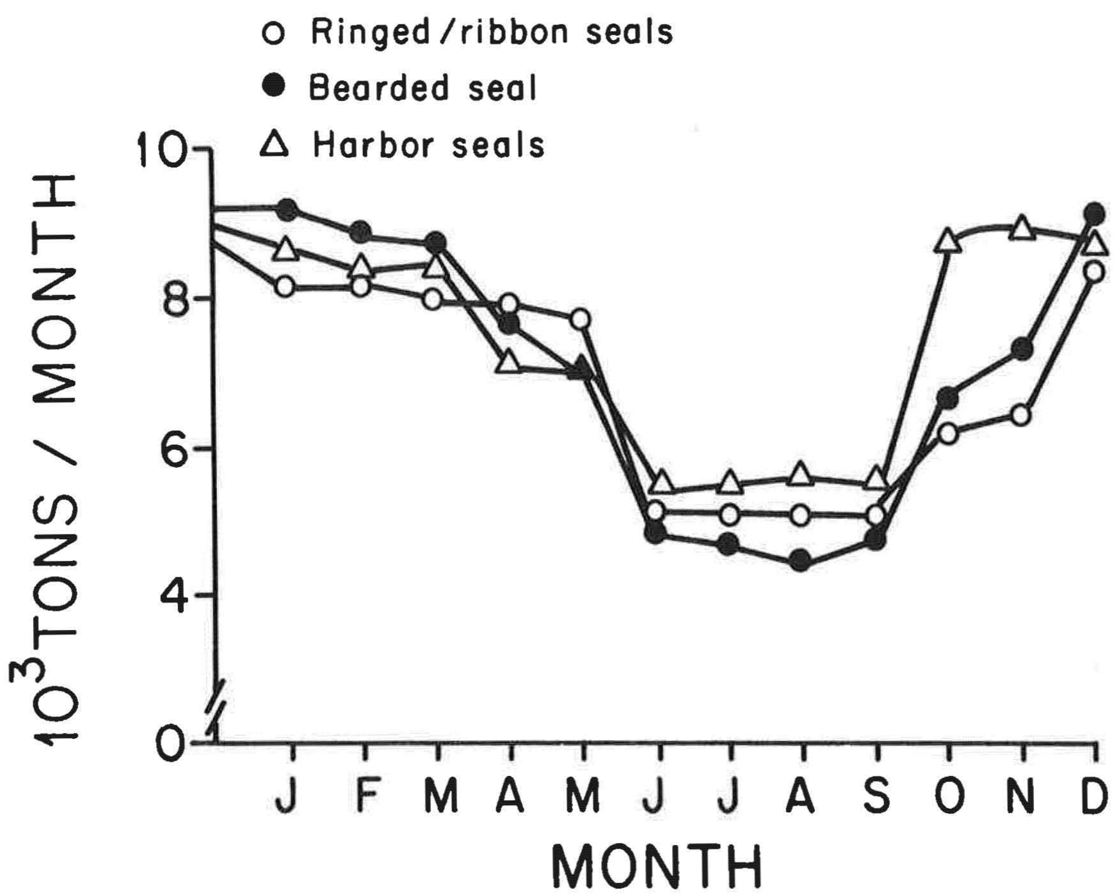

Figure 15. Consumption of pollock by bearded seals, harbor seals, and ringed/ribbon seals in the eastern Bering Sea.

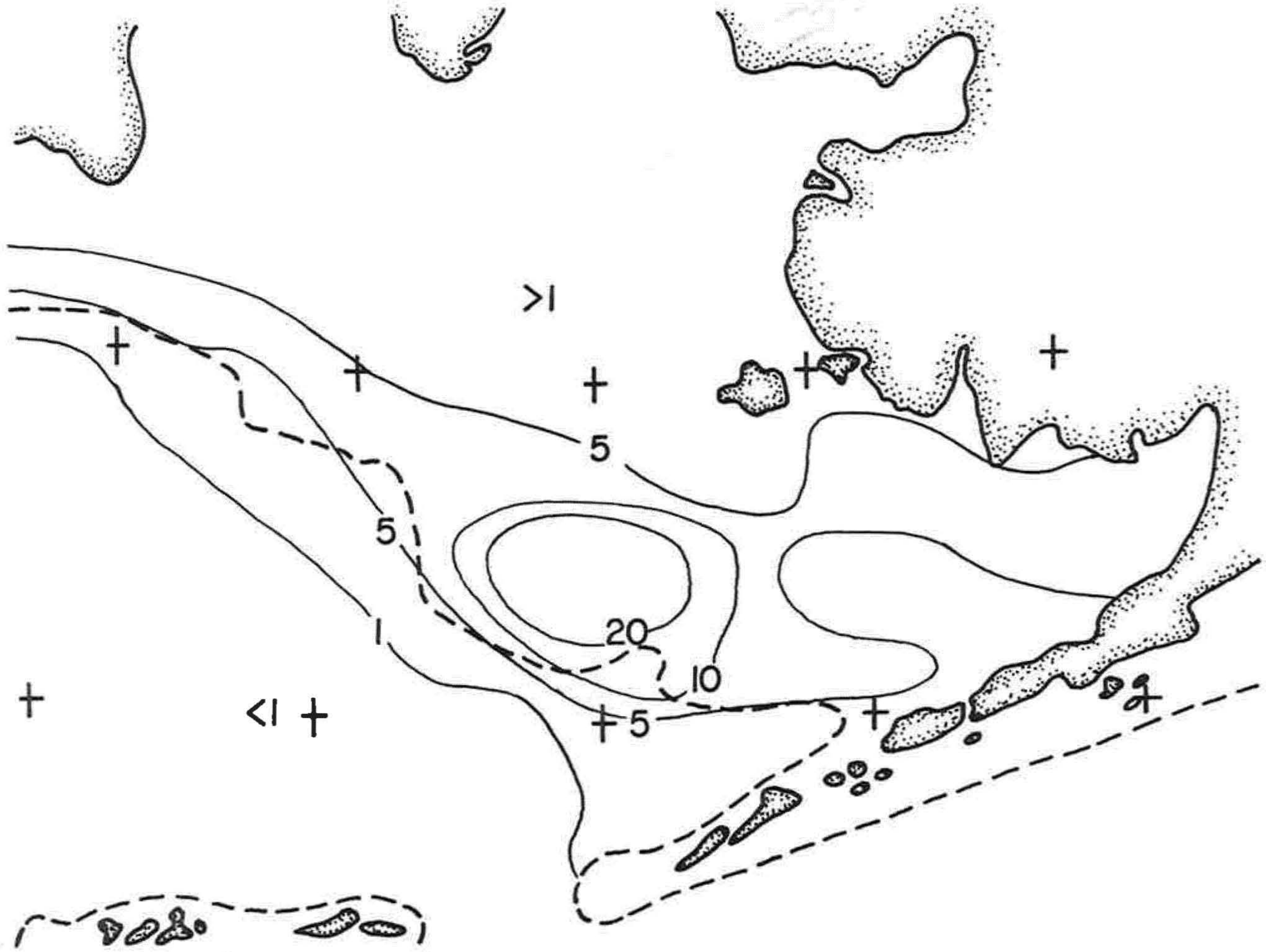

Figure 16. Consumption of salmon in August (tons/km^2).

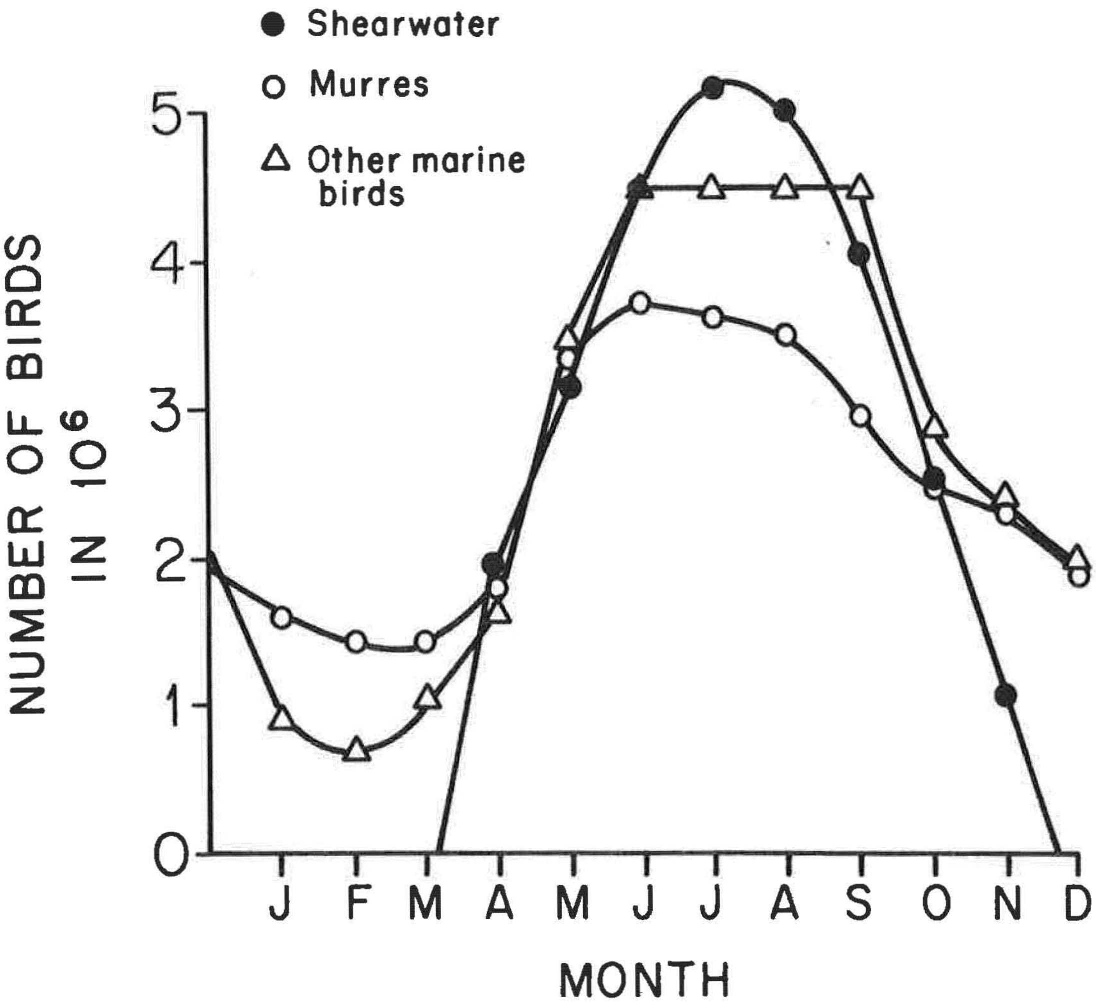

Figure 17. Estimated monthly numbers of adult marine birds in the eastern Bering Sea.

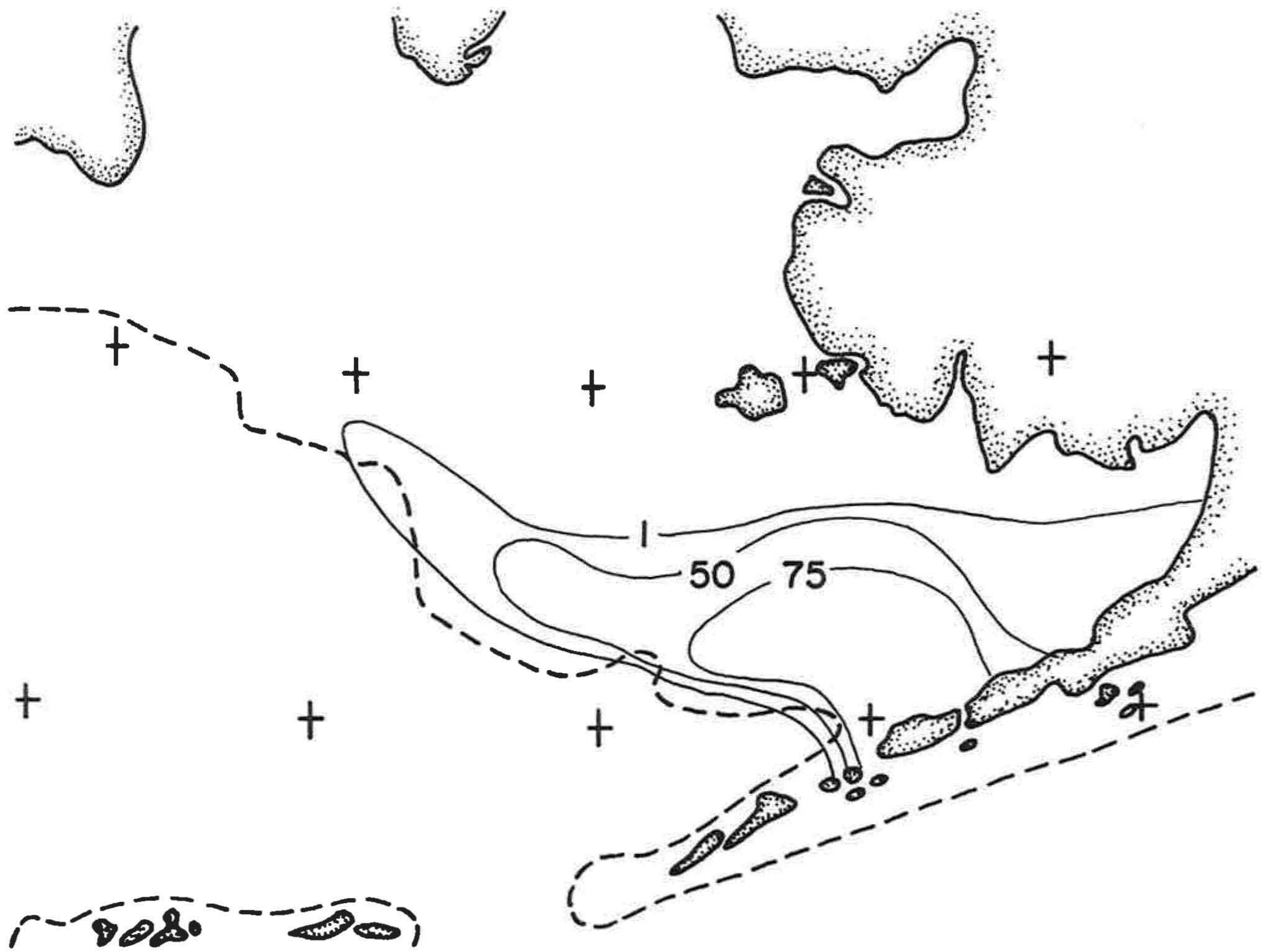

Figure 18. Distribution of murres in February (in thousands per $10^4 km^2$).

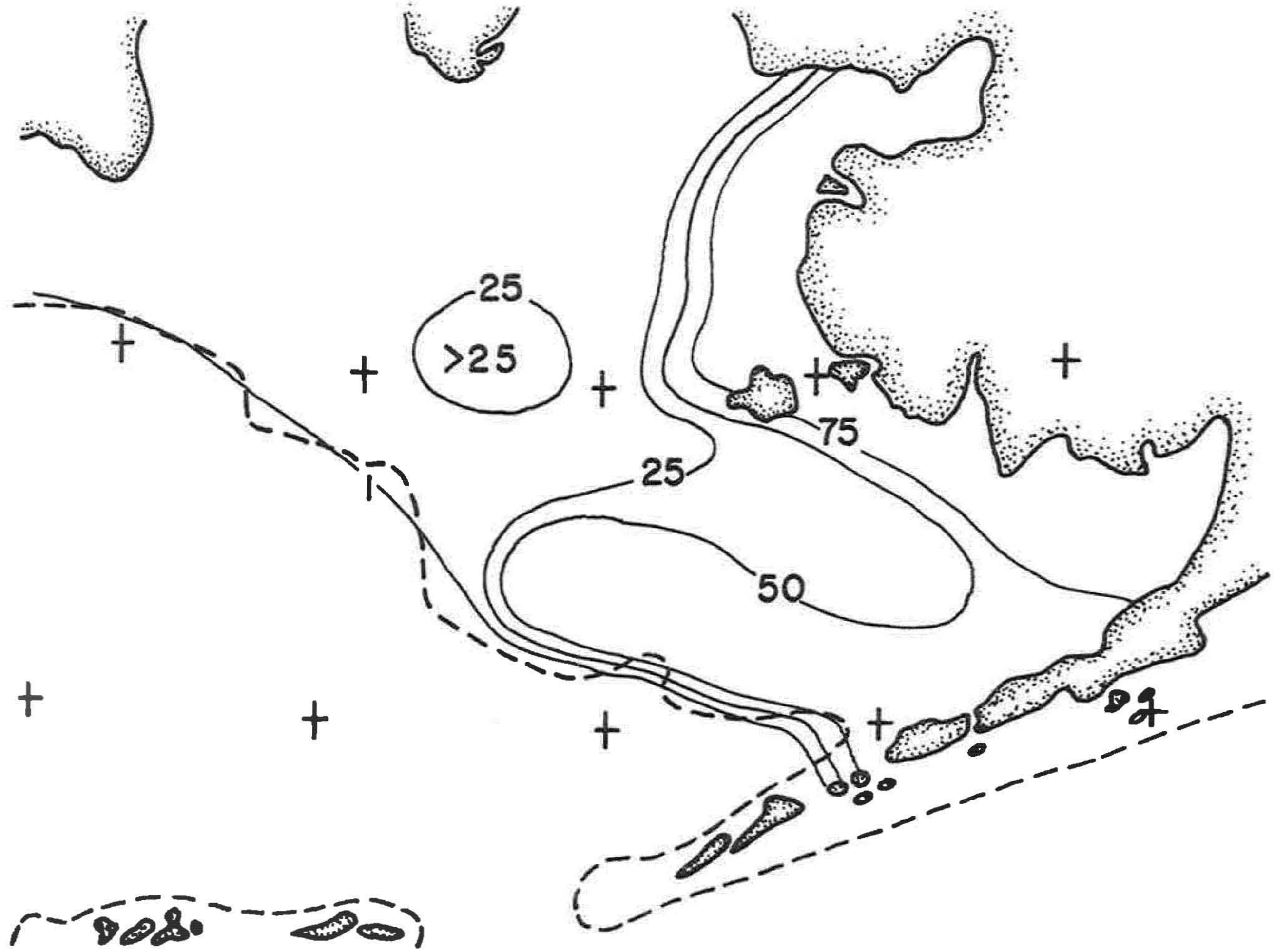

Figure 19. Distribution of murres in August (in thousands per $10^4 km^2$).

C. DISTRIBUTION, ABUNDANCE, AND DYNAMICS OF PELAGIC FISH

Pelagic fish (e.g., herring, capelin, other smelts) form an important food source (forage fish) for other fish species and mammals in the Bering Sea, as results of stomach analyses indicate. Only the herring has been subject to exploitation by man, primarily by Japanese and Soviet trawlers near the continental slope in the winter, and a subsistence fishery by native villagers near the coast during the summer. Research on pelagic species in the Bering Sea has been minimal, however, the recent surveys of coastal spawning of herring, capelin, and other smelts (Barton, Warner and Shafford 1977) show that the occurrence of spawning schools of these species is much more extensive that previously assumed.

The ecosystem model requires the presence of considerable quantities of pelagic fish in the eastern Bering Sea, dictated mainly by the food composition of predators. The herring has been considered separately and other smaller pelagic fish have been lumped into one ecological group--other pelagic fish. The model biomass requirements are 3.26 million tons for herring and 6.87 million tons for other pelagic fish (Table 7). The consumption of these species requires also that they be relatively widely distributed over the area (Figures 20 and 21). This requirement is in good agreement with a reasonable behavioral pattern of the principal species of pelagic fish, which must be dispersed during feeding during a large part of the year in order to be able to satisfy food requirements from the rather uniformly distributed zooplankton. The pelagic fish component is programmed to school near the continental slope, to move towards the coast during spring and early summer, and to disperse over the eastern Bering Sea during summer. The bulk of the pelagic fish biomass will move seaward towards the continental slope during autumn and early winter (Figure 22).

Table 7

Biomass, annual consumption, annual turnover rate, and relative monthly consumption of different species and/or ecological groups in the eastern Bering Sea.

Species/ecological group	Mean biomass (B) 10^3 tons	Annual consumption 10^3 tons	Annual turnover rate $T = \frac{C}{B}$	% of biomass consumed per month
Pollock	8,235	5,820	0.7	5.8
Herring	3,260	2,970	0.9	7.7
Other pelagic fish	6,870	6,595	1.0	8.7
Yellowfin sole	1,475	866	0.6	4.9
Other flatfish	2,030	1,630	0.8	6.7
Other gadids	2,840	2,680	0.9	8.1
Other demersal fish	2,550	2,790	1.1	9.0
Total finfish	27,260	23,350	0.86	
Squids	4,050	3,020	0.75	6.4
Benthos	25,600	19,730	0.77	6.3
Zooplankton		83,970		
Phytoplankton		(52,500)		

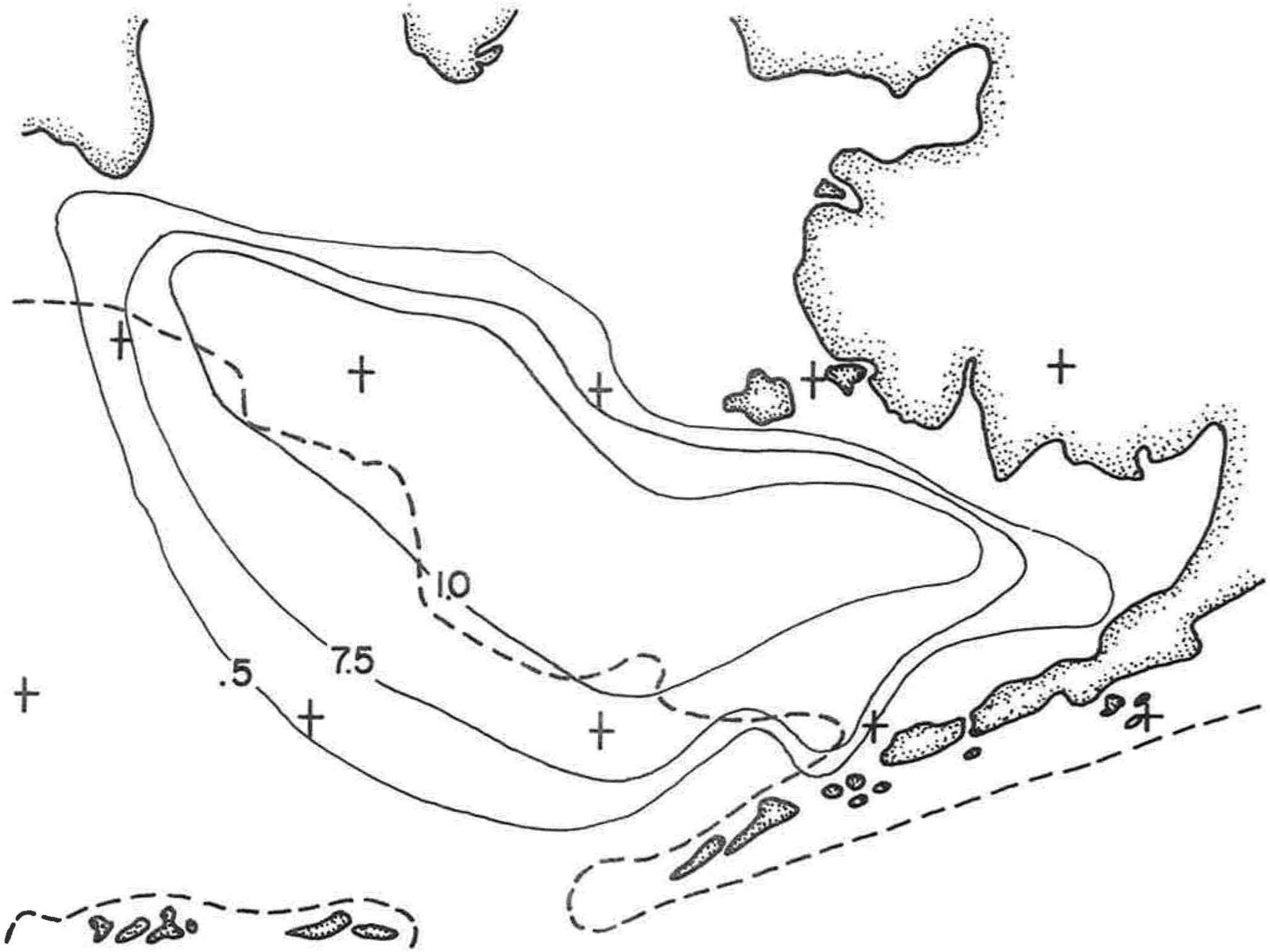

Figure 20. Consumption of herring in August in the eastern Bering Sea (tons/km^2).

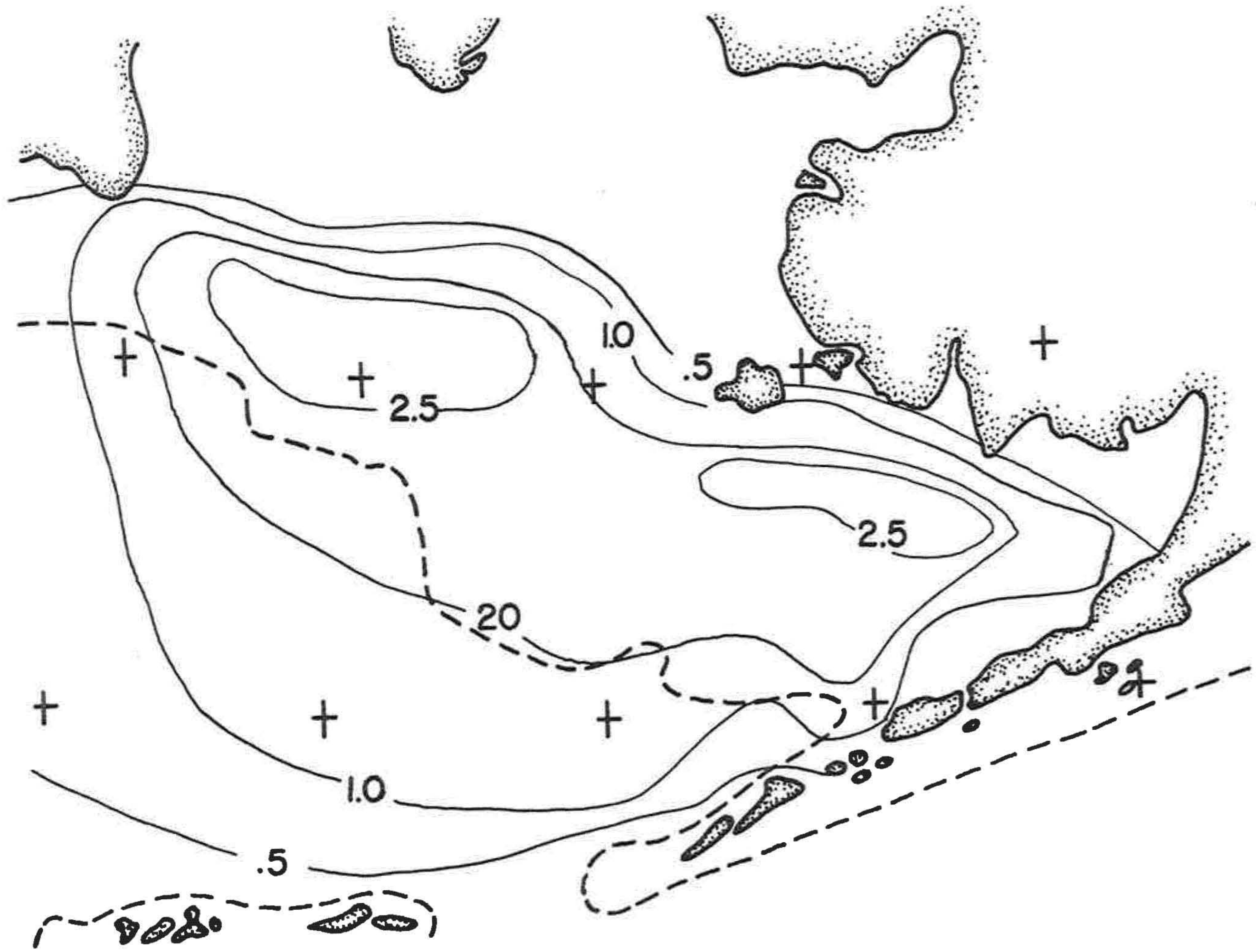

Figure 21. Consumption of other pelagic fish in August in the eastern Bering Sea (tons/km^2).

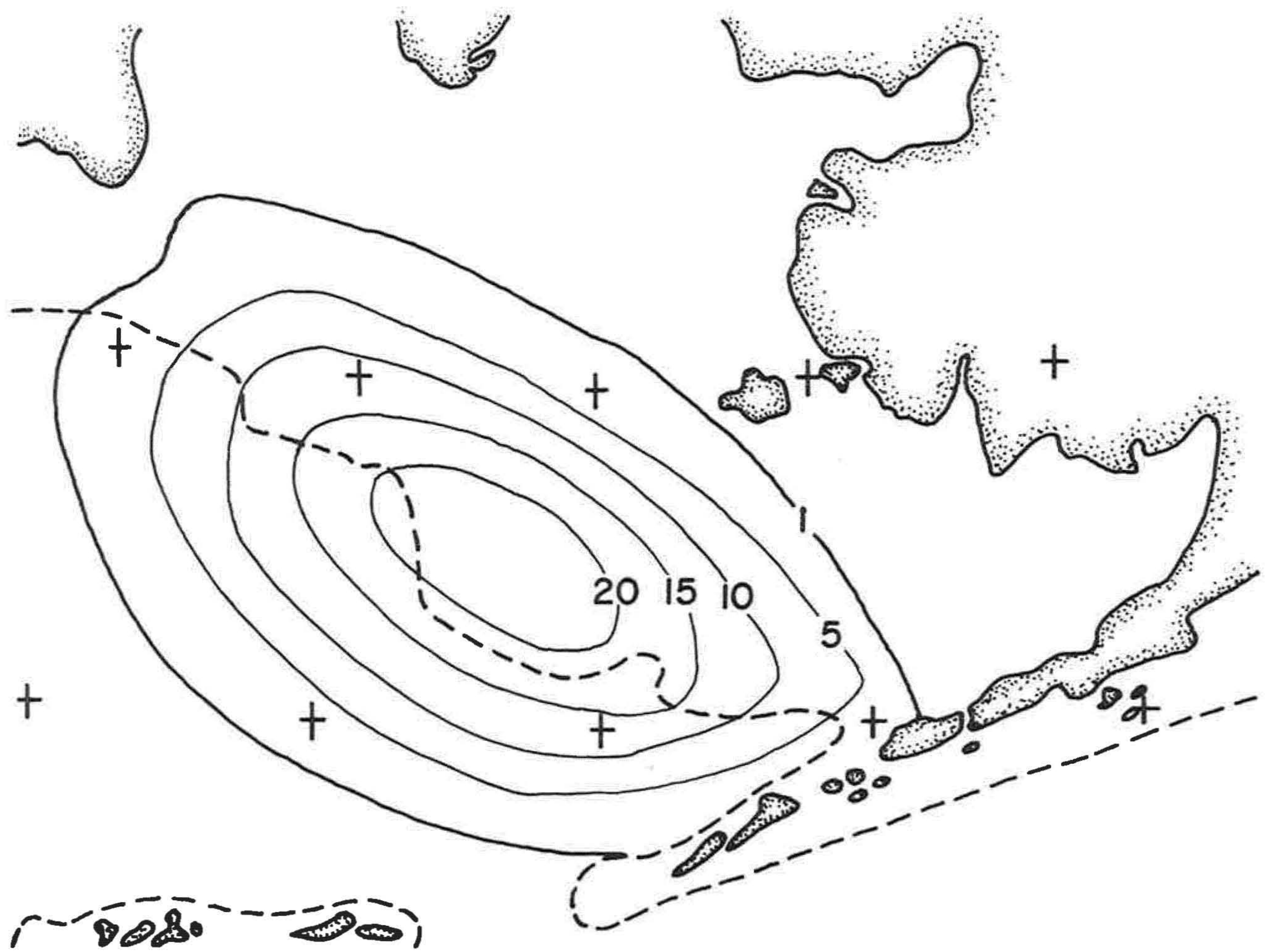

Figure 22. Distribution of herring in November (tons/km^2).

Some aspects of the herring and pollock populations interactions were studied with an earlier model (Laevastu and Favorite 1976c), and more detailed studies on the total ecosystem interactions and environmental effects on the pelagic fish populations will be conducted using DYNUMES III. The present model computes only the consumption of salmon, but a separate salmon migration model is being programmed at NWAFC.

D. DISTRIBUTION, ABUNDANCE, AND DYNAMICS OF SEMIDEMERSAL FISH

Semidemersal fish (generally gadids) are computed in four separate groups: pollock, in three size (age) groups, and other gadids. Pollock dynamics have been a subject of a special study, described in another report (Laevastu and Favorite 1976c). The ecological group referred to as other gadids consists of Pacific cod (mainly in the central and southern part of the area), polar or Arctic cod, and Saffron cod (in the northern part of the area), and longfin cod and black cod or sablefish on the continental slope and over deep water. Detailed distributions, migrations, and spawning areas of several of these species are not yet well known, therefore, the distribution of this group is relatively approximate (Figure 23) and no seasonal migrations were prescribed. The model requires a 2.84 million tons biomass of other gadids in the eastern Bering Sea. The initial distribution is modified by model computations particularly in the Pribilof Island area (Figure 24) because of increased consumption by pinnipeds during the summer months (Figure 25).

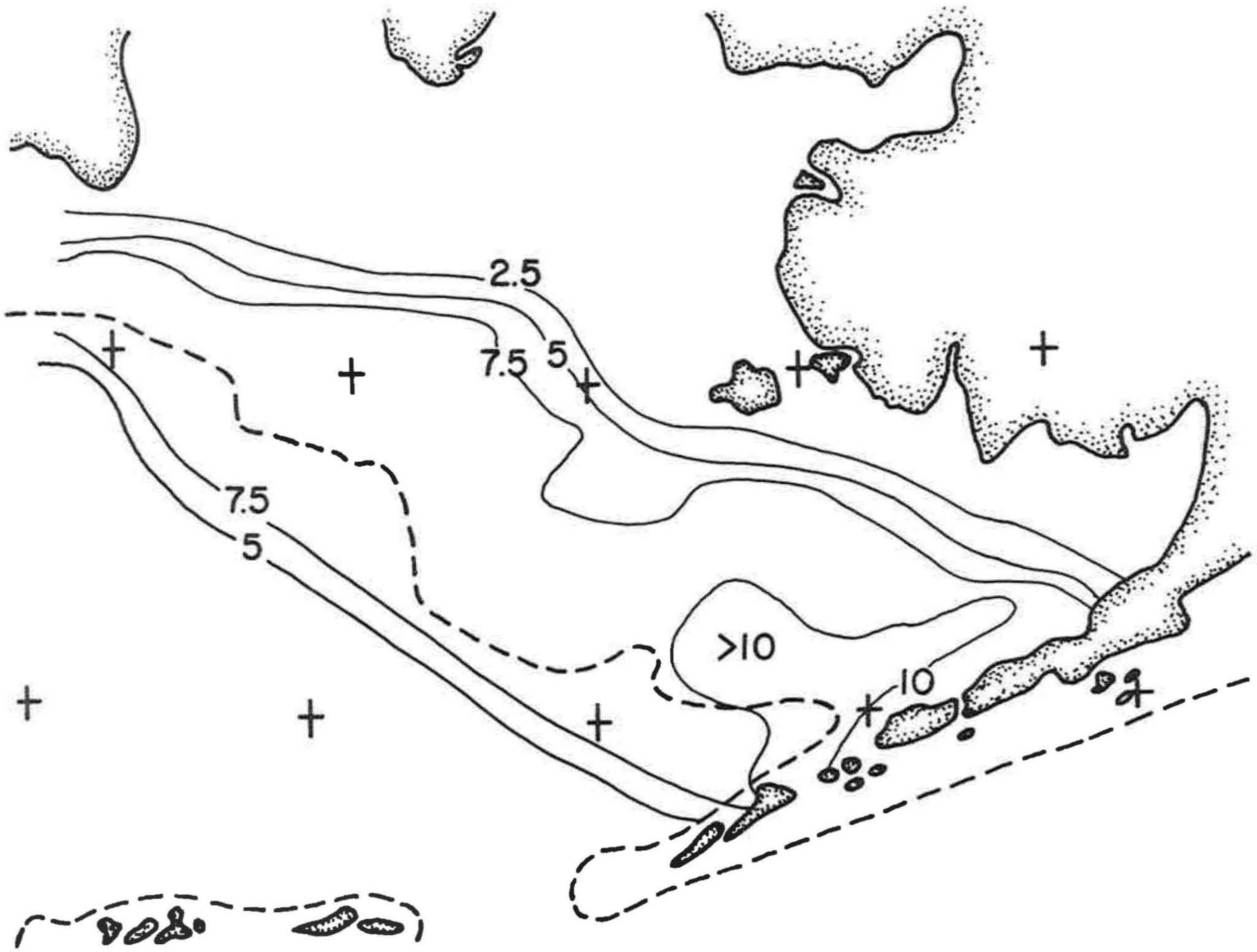

Figure 23. Distribution of other gadids in February (tons/km^2).

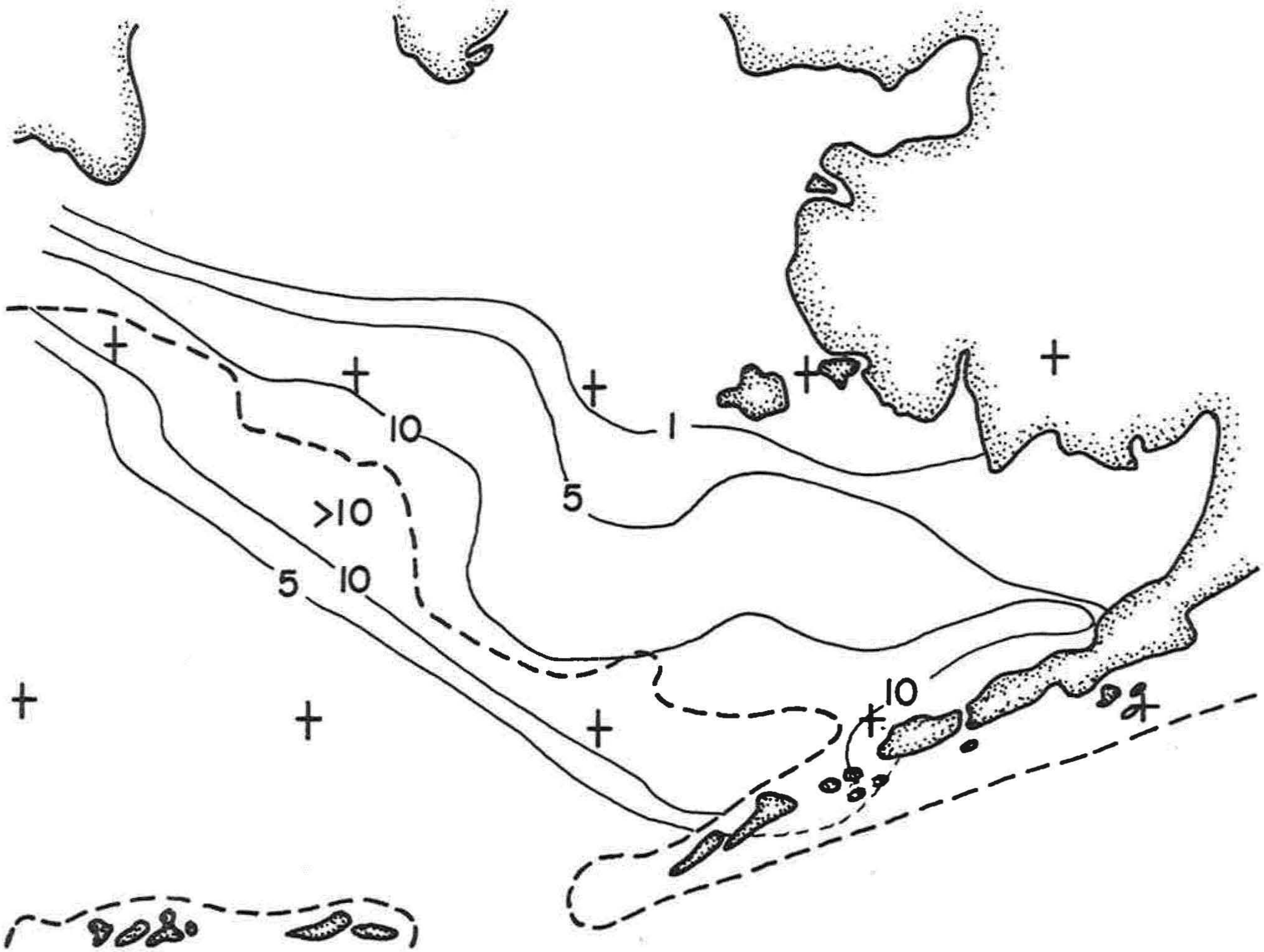

Figure 24. Distribution of other gadids in August (tons/km^2).

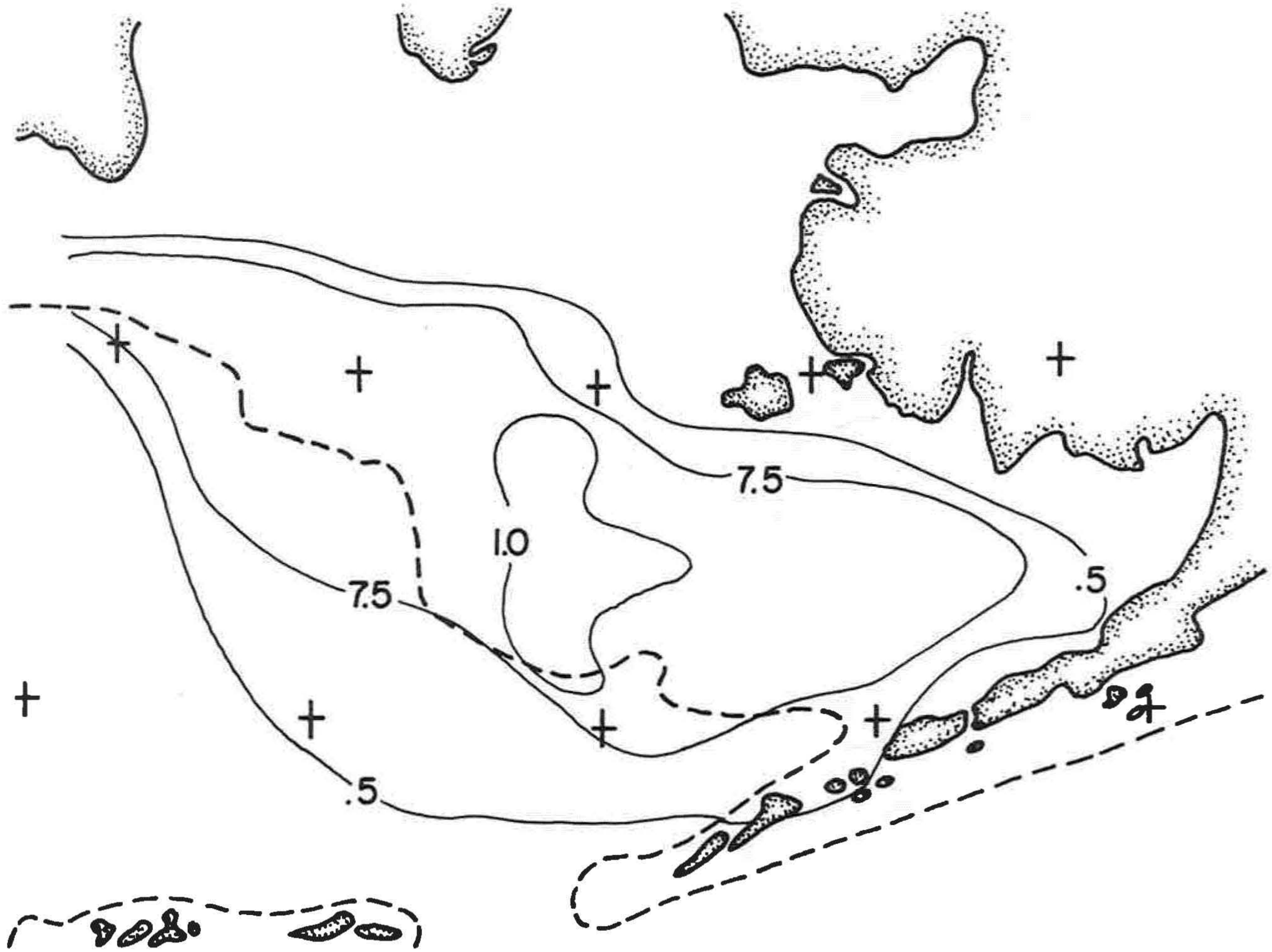

Figure 25. Consumption of other gadids in August (tons/km^2).

The semidemersal fish are the dominant group in the eastern Bering Sea. This is largely due to their ability to utilize both benthic and pelagic food, and the extensive cannibalism in the larger and older groups. Because of their flexible and voracious feeding habits, the semdemersal species grow fast in their juvenile years, with the exception of polar and saffron cods which live in cold environments where metabolic rates are suppressed.

The biomass of pollock, the most abundant species in the eastern Bering Sea (8.24 million tons), is computed in the model with time and space variable fishing intensity coefficients. The fishery is largely concentrated near the continental slope (e.g., see Figure 26).

E. DISTRIBUTION, ABUNDANCE, AND DYNAMICS OF DEMERSAL FISH

The demersal species are divided into three groups: yellowfin sole, which is the dominant flatfish species in the area (initial biomass ca 1.48 million tons, Table 7); other flatfishes (13 other species of family Pleuronectidae, such as arrowtooth flounder, Alaska plaice, and rock sole, and one species of family Bothidae, the lefteye flounder--initial biomass ca 2.03 million tons); and, other demersal fish (initial biomass 2.55 million tons), a group which consists mainly of sculpins and eelpouts. Rockfishes and rattails have also been included into this group as a minor constituent.

There are four basic characteristics common to demersal species and/or groups of species: 1) they spend most of their lives on or in close proximity of the bottom, having thus essentially a two-dimensional living space, and are mostly affected by the cold, subzero temperatures which occur over large areas of the continental shelf in the Bering Sea during winter and spring;

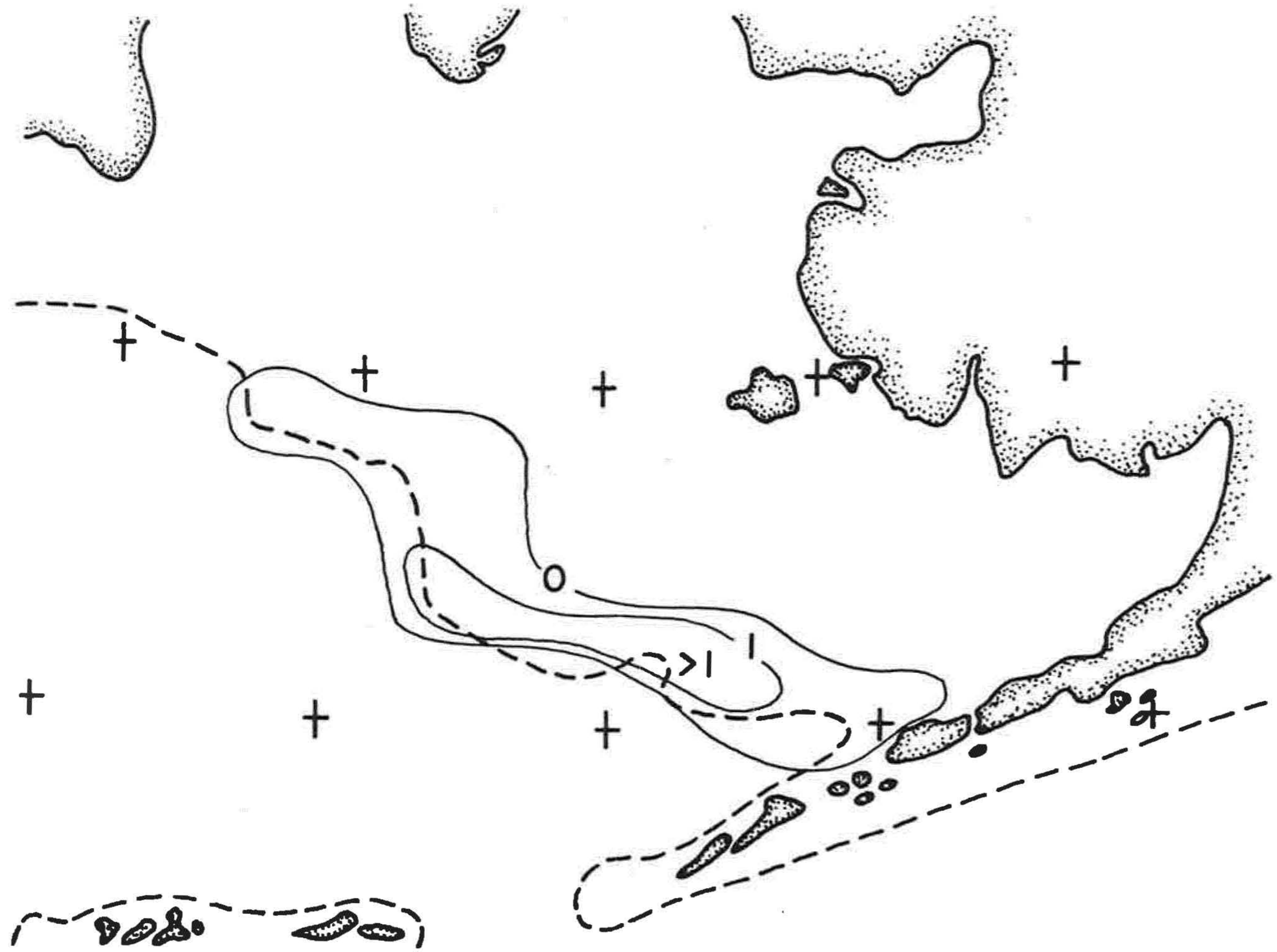

Figure 26. Pollock catches in February (tons/km^2).

2) their food consists mainly of benthos, although some species undertake short feeding migrations into the water mass; 3) seasonal migrations to considerable depth occur in most species; 4) most species are slow growing, thus being available a longer period for ecosystem internal consumption than faster growing species.

The yellowfin sole concentrations are found near the continental slope during the winter (Figure 27) and they migrate towards shallower water during the summer (Figure 28), when the cold bottom waters have warmed. Other flatfishes cover the central and southern part of the continental shelf (Figure 29); their seasonal migrations are not well known as yet and have been suppressed in the model (Figure 30). No seasonal migrations have been prescribed to the group, other demersal fish, either (Figure 31); however, this group is more abundant in the areas where other flatfish abundances are somewhat lower (compare Figures 30 and 31), and is a major ecosystem internal food source (Figure 32).

F. CONSUMPTION OF PLANKTON

In an earlier study with the model Laevastu, Dunn, and Favorite (1976) concluded that the past quantitative studies of zooplankton are deficient in reporting the standing stocks of zooplankton, especially euphausids. Furthermore, the same study indicated that the areas of high zooplankton consumption change seasonally due to seasonal migrations of the consumers (predation). In addition the abovementioned study suggested that starvation might be rather widespread in the sea. The latter aspect will be studied in greater detail with DYNUMES III.

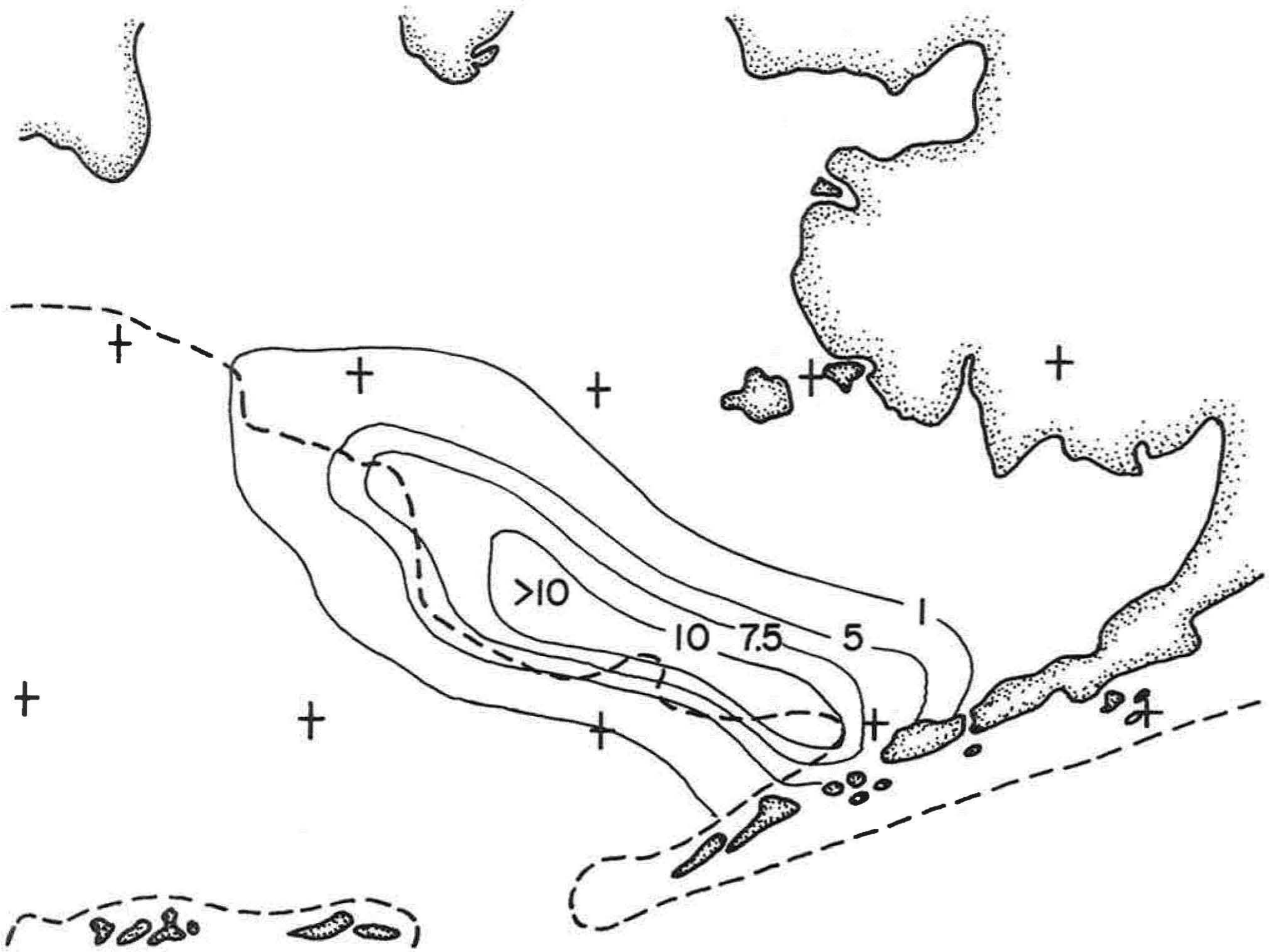

Figure 27. Distribution of yellowfin sole in February ($tons/km^2$).

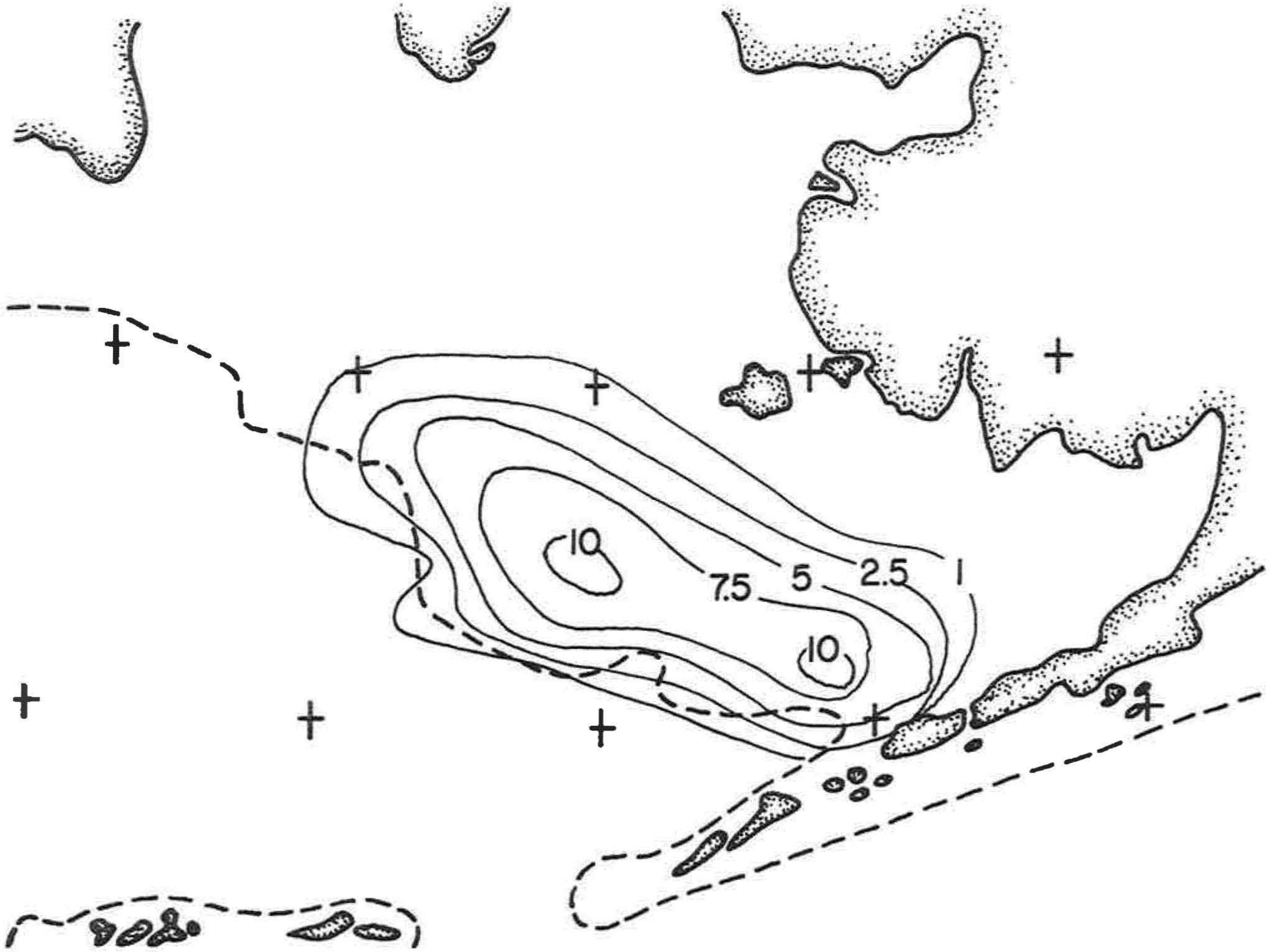

Figure 28. Distribution of yellowfin sole in August (tons/km^2).

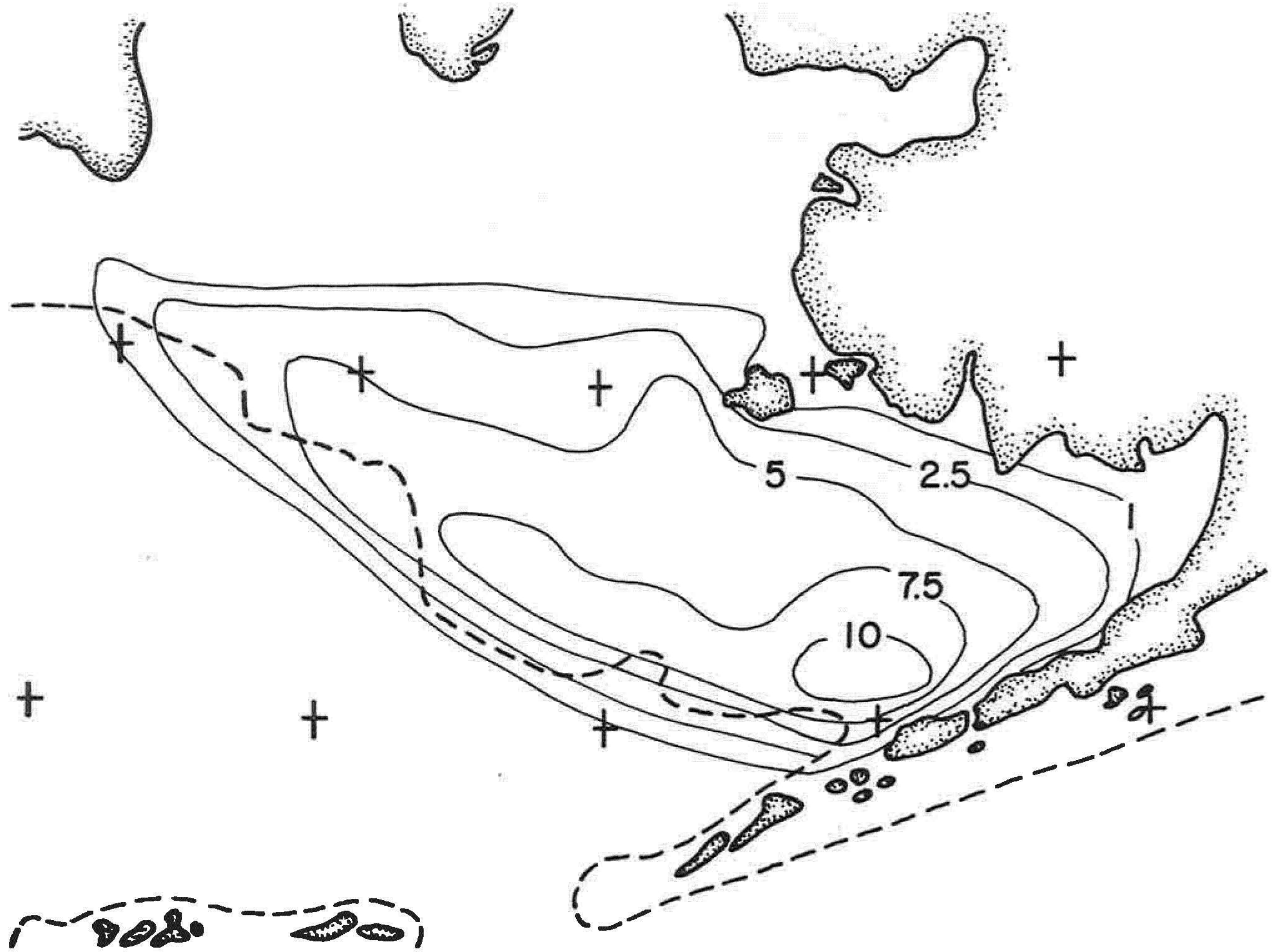

Figure 29. Distribution of other flatfish in February (tons/km^2).

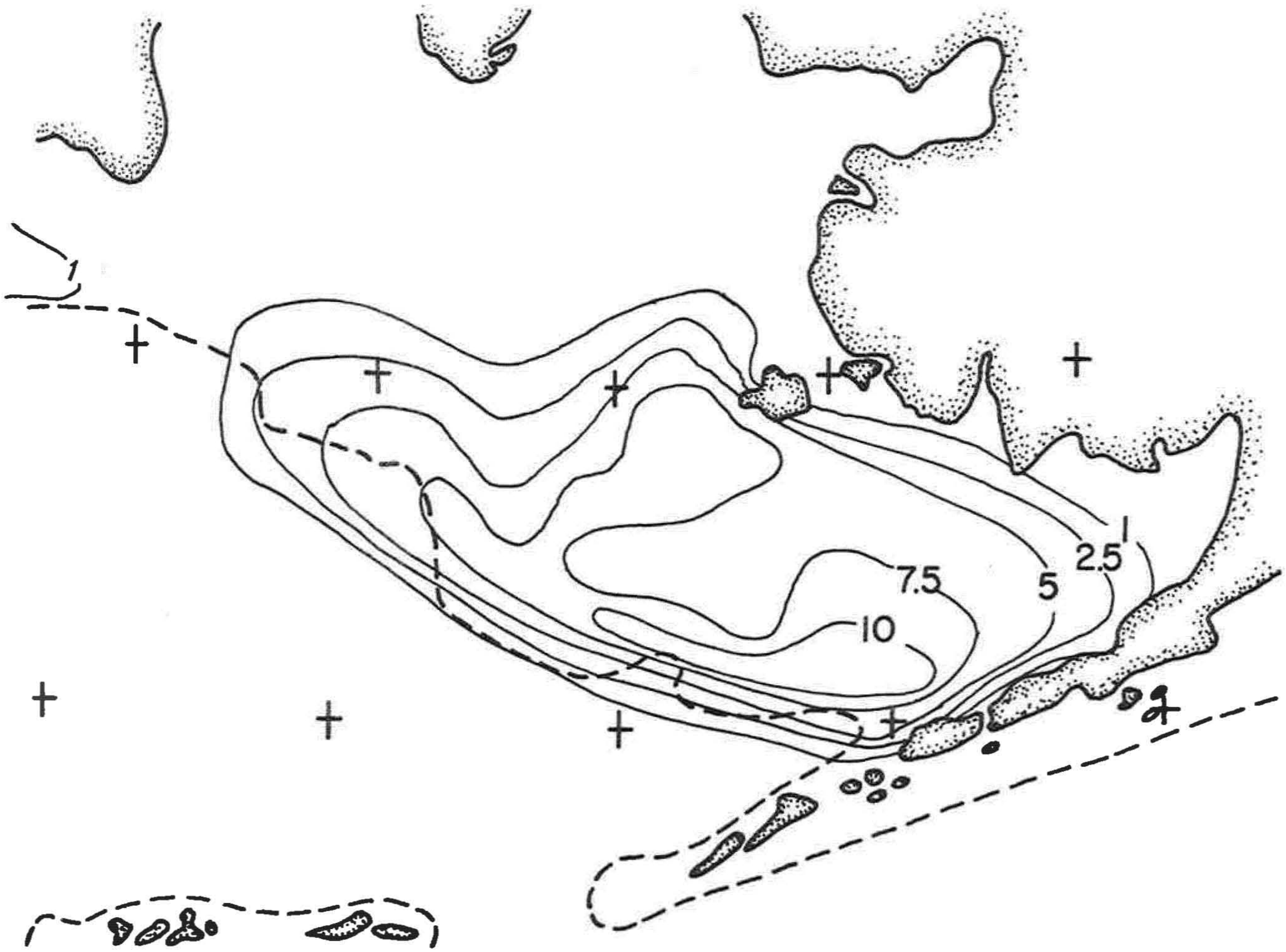

Figure 30. Distribution of other flatfish in November ($tons/km^2$).

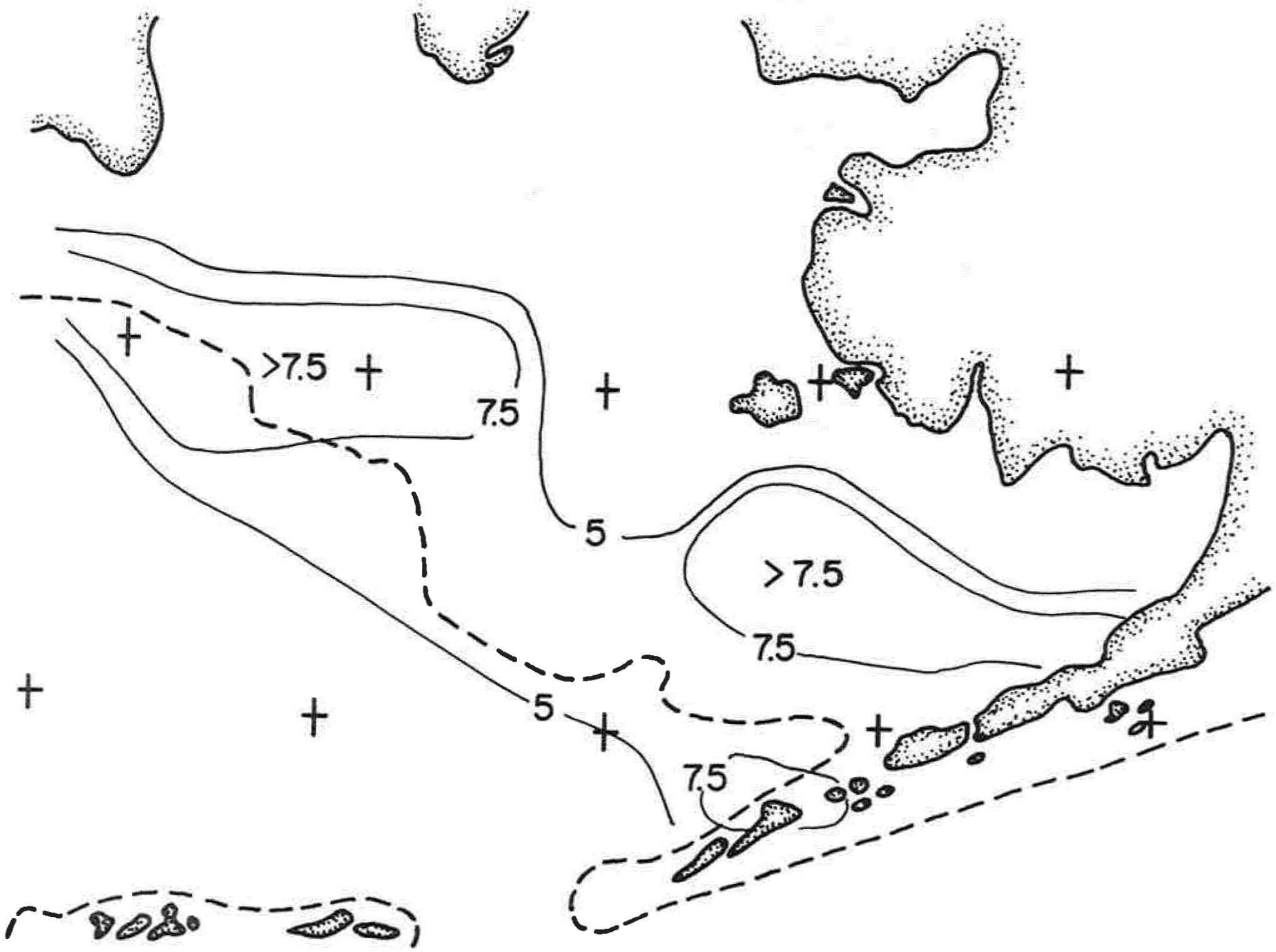

Figure 31. Distribution of other demersal fish in May (tons/km^2).

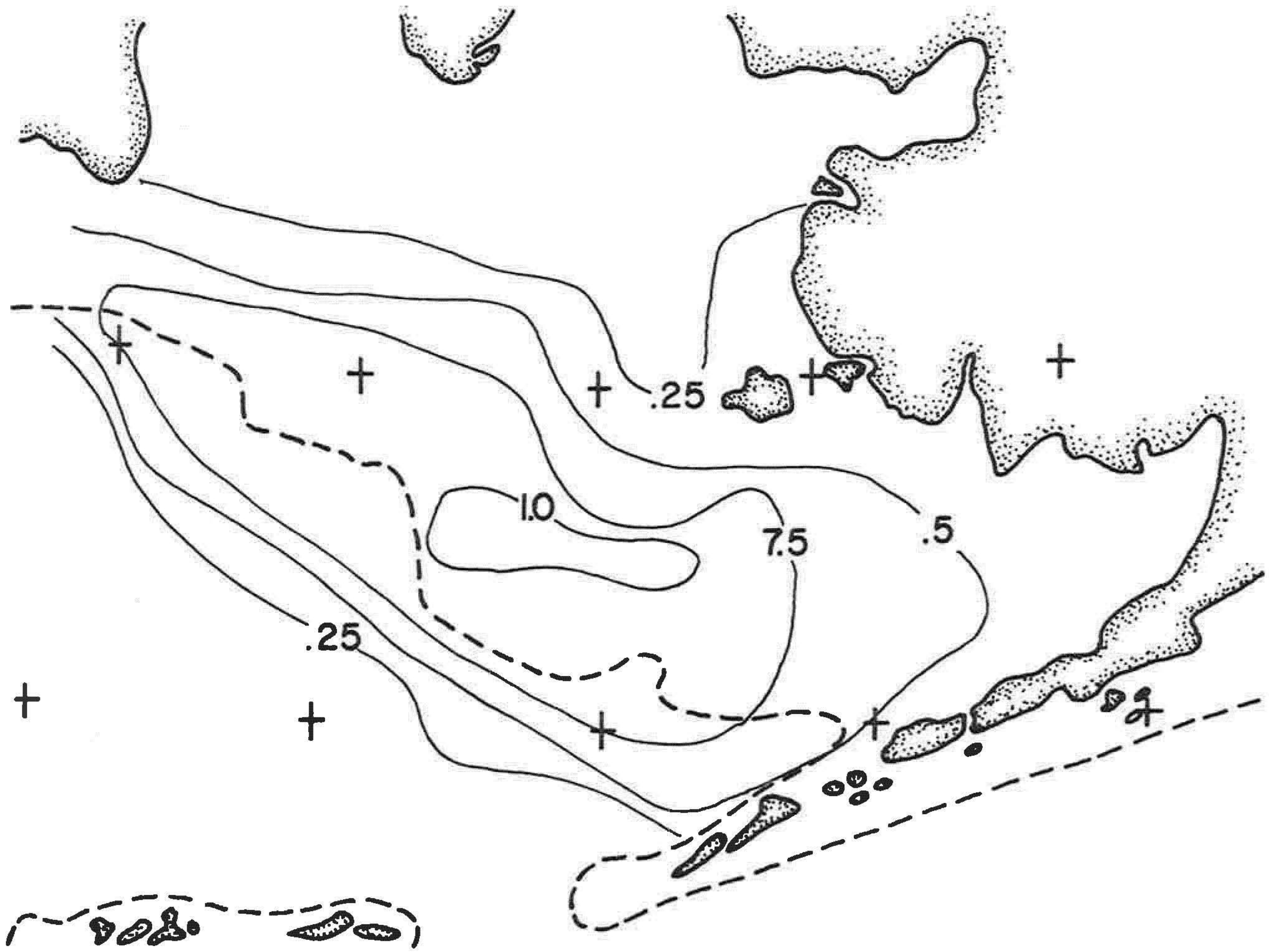

Figure 32. Consumption of other demersal fish in August (tons/km^2).

The simulation of zooplankton standing crop was the same as in DYNUMES I. The simulated quantities are thus in agreement with the highest reported mean zooplankton standing stock (see references in Laevastu, Dunn, and Favorite 1976), but are lower than required by the ecosystem model. An example of a simulated monthly mean standing stock of zooplankton is given in Figure 33. The minimum consumption of zooplankton is computed within the model in each time step and grid point, by summing the zooplankton (mainly euphausids and copepods) consumption by each species and/or ecological group. Assuming that the simulated zooplankton standing stock (g/m^3) is distributed evenly in the upper 50 meters, one can compute the percentage of zooplankton mean standing stock consumed in each month (examples in Figures 34 and 35). These figures show that more than 75% of the mean standing stock of zooplankton is consumed over large areas in May (Figure 34), substantiating the earlier conclusion that the reported amounts of zooplankton standing stock are too low. These figures also show that the areas of high consumption move seasonally, the consequences of which were described in the abovementioned earlier study. The zooplankton standing stocks (and production) in the northern part of the Bering Sea and in the southwestern part of the Bering Sea over deep water are not fully utilized by the ecosystem in these areas.

Phytoplankton consumption was computed only for the benthos (as detritus), and small pelagic fish, however, preliminary additional computations show that only less than a quarter of the phytoplankton production is utilized by the ecosystem, the rest going to a regeneration cycle. Phytoplankton production is apparently not a limiting factor of total biomass in the ecosystem in the eastern Bering Sea. Further detailed studies on this subject will be carried out with DYNUMES III.

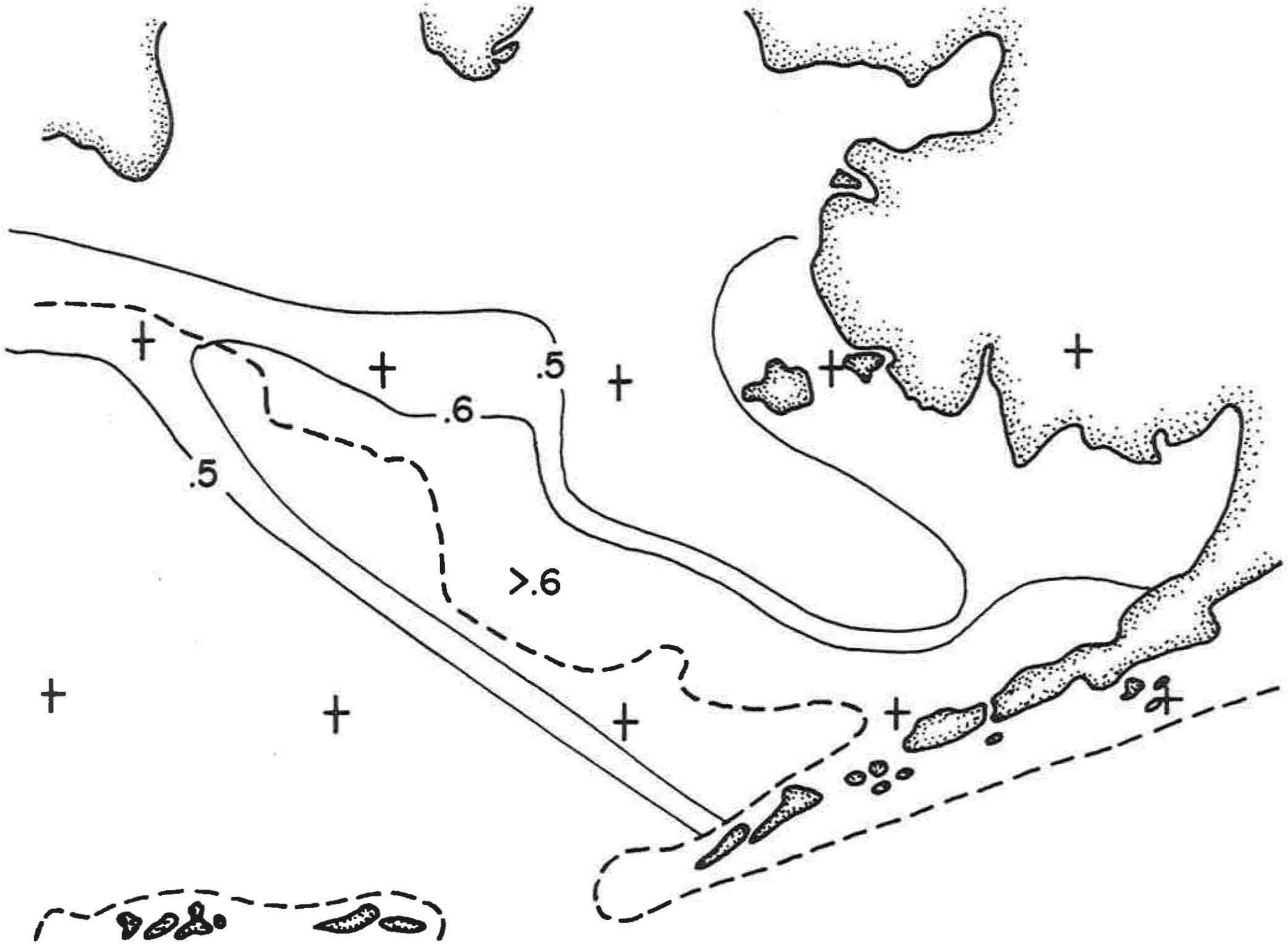

Figure 33. Simulated distribution of zooplankton in May (g/m^3).

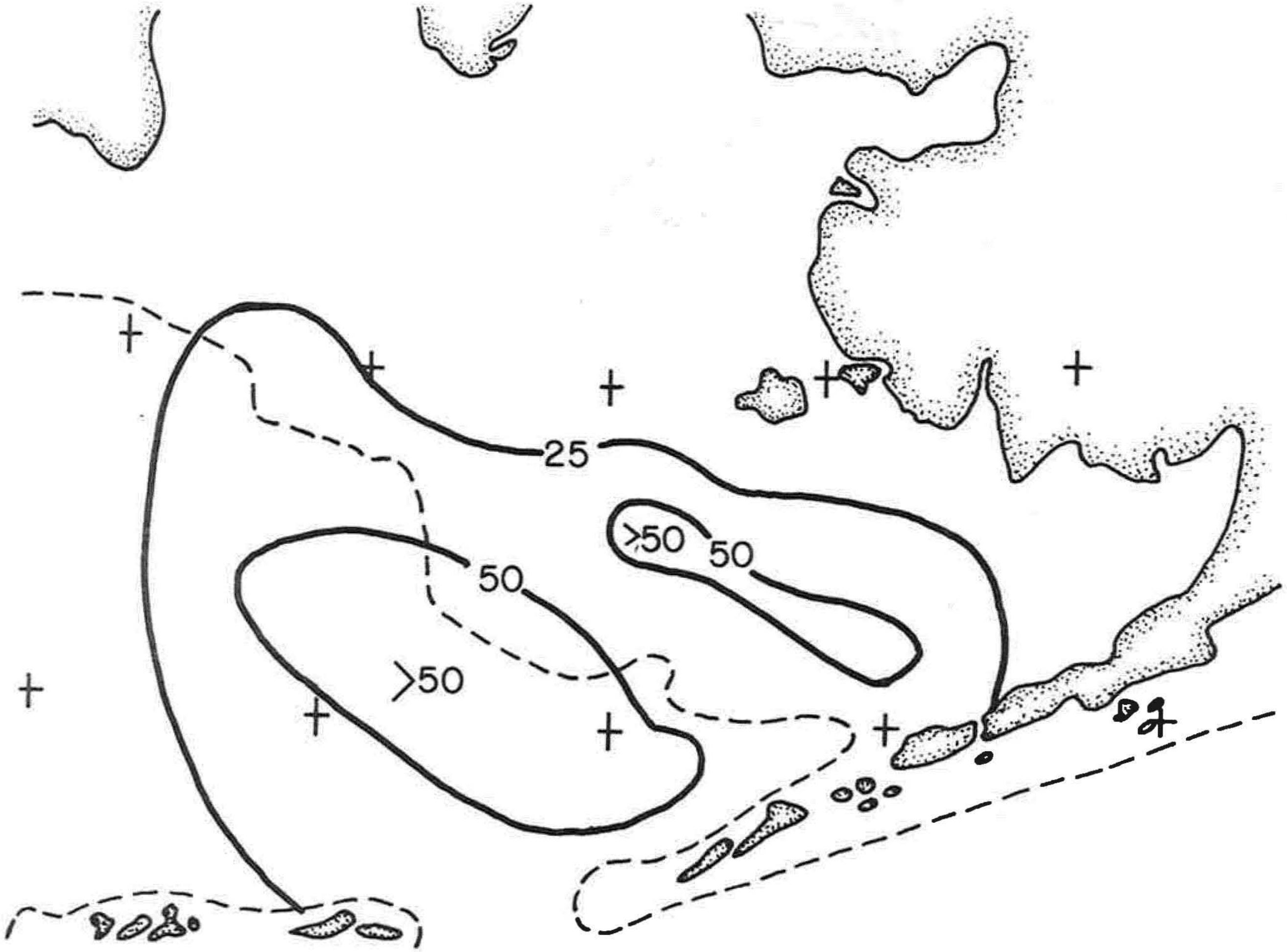

Figure 34.--Percent of mean zooplankton standing stock consumed in May.

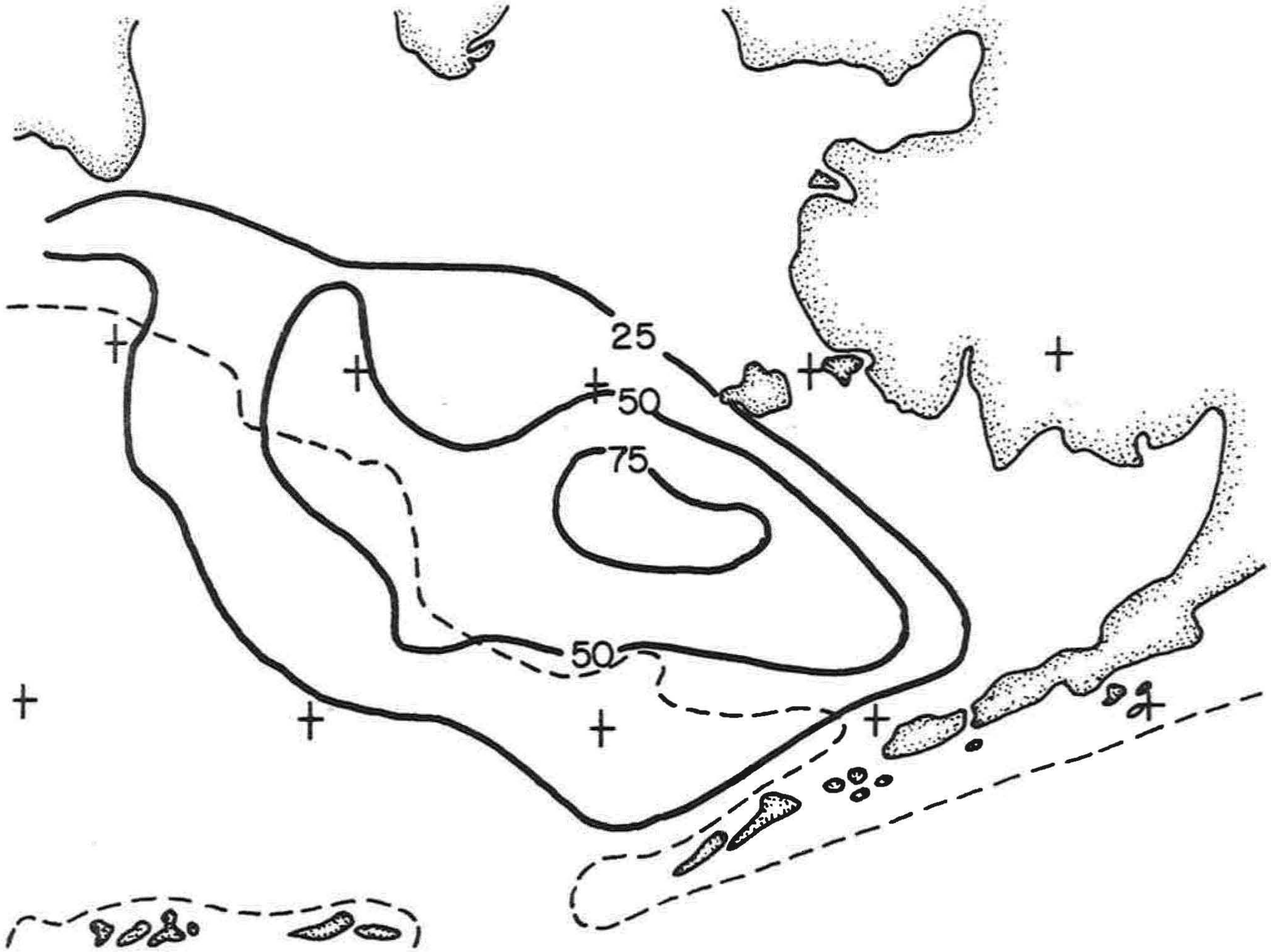

Figure 35.--Percent of mean zooplankton standing stock consumed in August.

G. GENERAL BIOMASS DYNAMICS IN THE EASTERN BERING SEA

The mean standing stocks, annual consumption and annual turnover rates of species and/or groups of species of fish, benthos, and plankton in the eastern Bering Sea are given in Table 7. As pointed out earlier, the inputs into the model are adjusted so that the numbers given in this table should be considered as minimum values (i.e., minimum in the defined ecosystem sustainable biomasses). The mean annual turnover rate of the finfish is slightly less than one (0.89). This means that the mean biomass of the finfish reproduces itself approximately once a year.

Although most of the initial input distributions are prescribed as relatively smooth fields, many of these fields show patchy distributions after a period of computations (six months to two years) (example on Figure 36). This patchiness is mainly brought about by ecosystem internal consumption in species where little or no migrations occur and also causes partial separation of distribution of species. Both patchiness and partial separation of species occur in the sea as normal conditions.

The 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. Detailed quantitative effects of these changes as well as the effects of environment will be investigated with DYNUMES III.

Due to the multiple interactions in the ecosystem, the abundance and distribution of most species show quasi-cyclic variations. The long-term cyclic changes of pollock and herring populations was described in an earlier report (Laevastu and Favorite 1976c). An additional indication of these long-term fluctuations is shown on Figure 37. Further studies of these long-term fluctuations and possible effects of man on these fluctuations will be conducted with DYNUMES III.

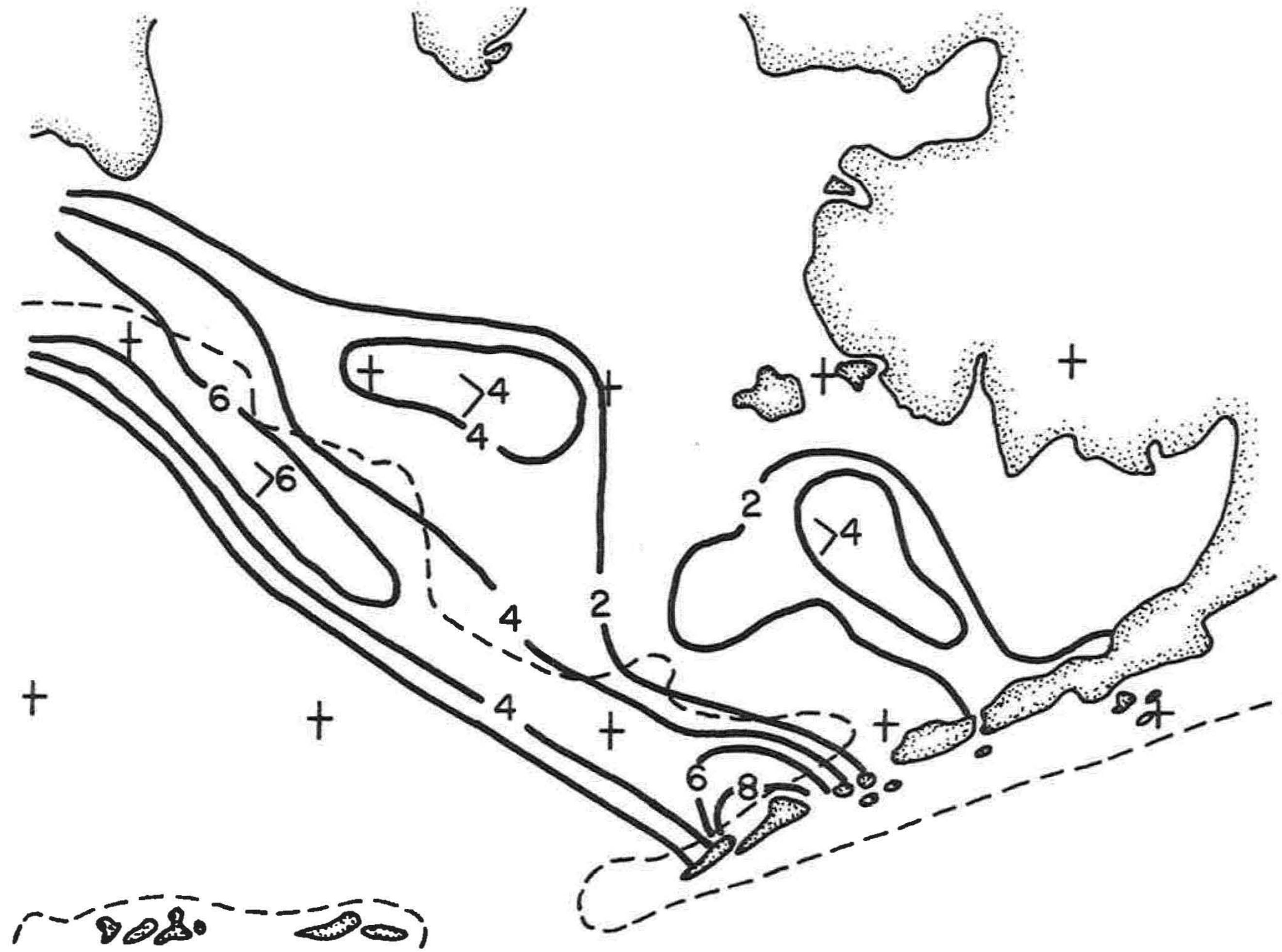

Figure 36.--Distribution of gadids (excluding pollock) in the eastern Bering Sea (in January, third year of computation) in tons per km^2.

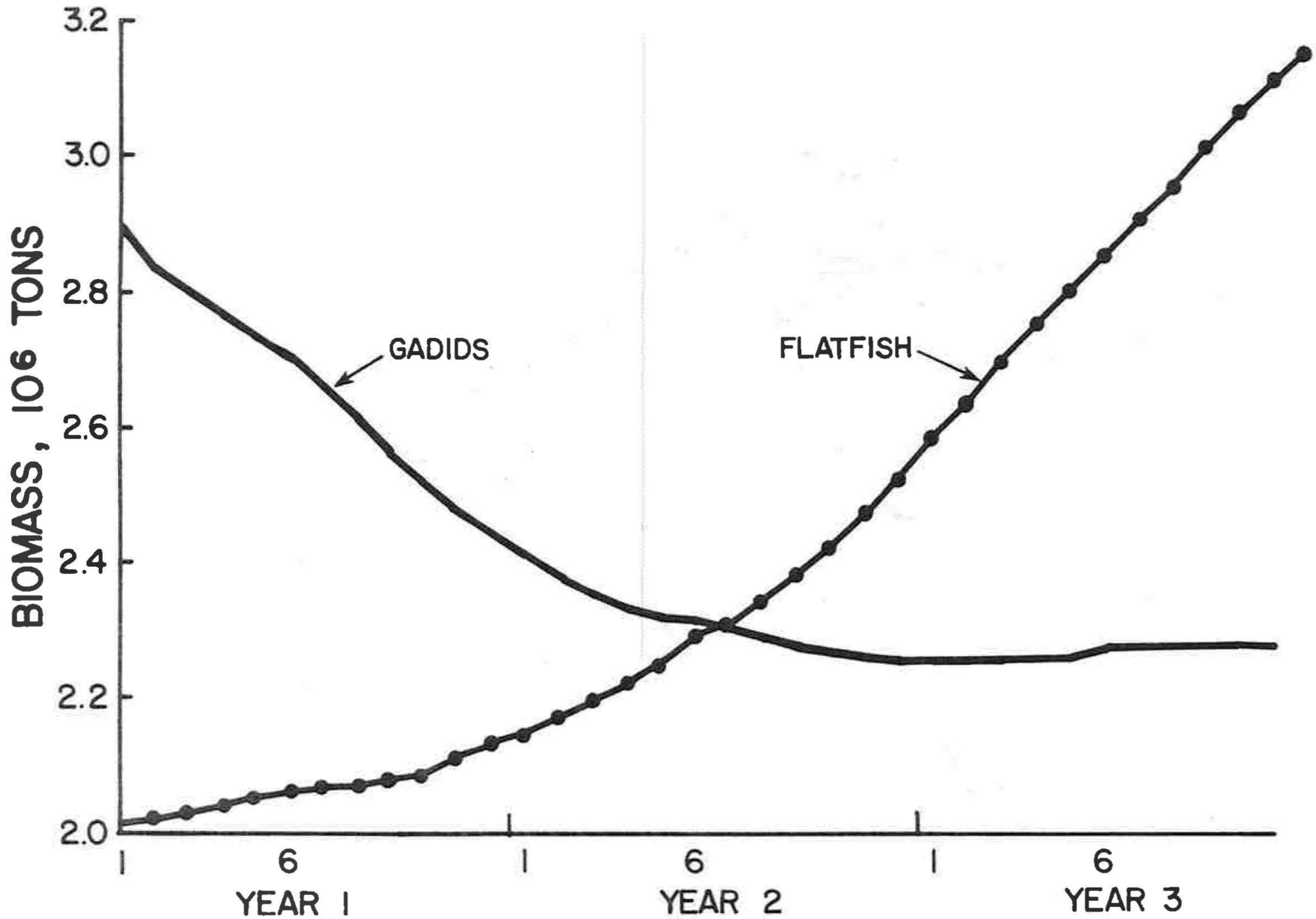

Figure 37.--Examples of changes in biomass of gadids (exluding pollock) and flatfish (excluding yellowfin sole) in the eastern Bering Sea over a three year period, as computed with DYNUMES II with specific inputs.

IV. POSSIBLE EFFECTS OF OIL EXPLORATION AND FISHERY ON MARINE ECOSYSTEM

The possible effects of oil exploration on the marine ecosystem will be studied with the more complete ecosystem model DYNUMES III. Only a few general conclusions on these effects are pointed out below, which have become apparent during the use of the present model.

1) As the marine ecosystem is relatively unstable and as rather extensive fluctuations in abundance and distribution of nearly all species occur in all time scales, it will be extremely difficult, if not impossible, to distinguish between the natural changes in the ecosystem from those caused by oil explorations.

2) All small scale (1 <ca 50 km and t <ca 1 week) disturbances are relatively rapidly smoothed out by the mobility of the ecosystem in offshore areas and there seems to be no effective process which will permit the propogation of small-scale effects within the marine ecosystem.

3) Some exceptions to 2 above are found only along the coastline and in shallow water where one space dimension disappears and where a physical convergence (and convergence line--the beach) exists in the nature. Here the effects are, however, local in nature, although they may be bothersome to limited sectors of local human populations.

4) As the ecosystem internal consumption and consequent turnover rate of the biomass is high (considerably higher than heretofore assumed), and as relatively widespread starvation is expected to occur in the marine ecosystem, it is very difficult to postulate that any essential quantitatively determinable damage can be caused to the marine ecosystem even by relatively extensive temporary accidental damage to part of the ecosystem.

5) The consumption of finfish and other marine resources by mammals is higher than the removal of these resources by man in the intensively fished eastern Bering Sea. Therefore, any attempts to manage marine resources through controlling the fishery by man without managing (controlling) the marine mammal populations, might not achieve the desired effect. It does not seem feasible that any mortalities resulting from oil explorations can reach a noticeable fraction of the removal of resources by mammals and man.

V. SUMMARY

1) The four-dimensional ecosystem model (DYNUMES II) can be used for diagnostic studies on the distribution of the species, for prognostic studies on the effects of environmental anomalies and changing intensity on the marine resources, and for quantitative determination of the possible effects of offshore oil developments on the marine ecosystem in the eastern Bering Sea.

2) The model includes also as inputs the end consumers (mammals, birds, man) whose consumption of other ecological groups is computed in trophodynamic computations within the model.

3) The monthly distribution and abundance of each species (and/or group of species) is computed, using in time and space variable growth coefficients (as influenced by environment and availability of food), fishery and grazing (consumption). Trophodynamic computations within the model give details of the amounts of various food items consumed by different species. The formulas used in the model are given in the text.

4) The ecosystem model requires the knowledge of the biomass distribution with age of the species. A method to compute this distribution is outlined in the paper and examples of Pacific herring biomass distribution is given. The model is found to be sensitive to the growth coefficient. The knowledge of biomass allows the selection of the correct growth coefficient, which is dependent on the mean age of the species biomass.

5) The model shows that the distribution of less migratory species is relatively patchy (as known from the fishery), which is, according to the model results, mainly brought about by grazing. Furthermore, different species/groups of species have rather unique, and in space and time distinct, bulk distribution centers, where only one, or very few, species are predominant. This condition is also known from other higher latitude fisheries.

6) Grazing, which is included in the natural mortality coefficient in conventional, single-species population dynamics approaches, but which is computed separately in the DYNUMES II model, is one of the most important factors in determining the marine ecosystem dynamics (and abundance and distribution of species). Realistic and detailed computation of grazing requires a complete four-dimensional ecosystem model such as the present DYNUMES approach.

7) A number of processes and conditions require additional field studies, before they can be well simulated within ecosystem models, such as the possible distribution and abundance of species under the ice, mortalities caused by subzero temperatures, and principal spawning areas and times of several, more abundant, species.

8) Baleen whales consume a minimum 1.2 million tons of euphausids during the summer in the Bering Sea.

9) Toothed whales consume the same amount of finfish, 1.2 million tons, which is more than half of the total commercial catch.

10) Marine birds consume a minimum of 82 thousand tons of small pelagic fish and fish larvae.

11) Pinnipeds consume about 50 thousand tons of salmon.

12) The model requires that the eastern Bering Sea contain 33 million tons of herring and 6.9 million tons of other pelagic fish (e.g., capelin, Atka mackerel, etc.). Quantitative research on pelagic species in the Bering Sea has been limited in the past and should be accelerated.

13) The model requires also about 8.2 million tons of pollock and more than 2.8 million tons of other gadids in the Bering Sea. Due to their flexible feeding habits and relatively fast growth (i.e., shorter time available for ecosystem internal consumption), the semidemersal species are most abundant species in the area.

14) The biomass of yellowfin sole is about 1.5 million tons, other flatfish about 2 million tons, and other demersal fish (sculpins, eelspouts) about 2.6 million tons. Their distribution is affected by subzero bottom temperatures.

15) Although the availability and production of zooplankton is a limiting factor in fish production in the eastern Bering Sea, the phytoplankton production is not limiting zooplankton or fish production in the area. Only less than one-fourth of the phytoplankton production is consumed directly by the ecosystem.

16) The mean annual turnover rate of the finfish in the eastern Bering Sea is slightly less than one (0.89).

17) Most species seem to have long-term quasi-cyclic variations in abundance.

18) Due to instabilities in the marine ecosystem (e.g., fluctuations of abundance and distributions in all time scales), it is extremely difficult, if not impossible, to distinguish between those changes in the ecosystem that might be caused by oil explorations and those related to the natural fluctuation.

19) All small scale (1 <ca 50 km and t <ca 1 week) disturbances are relatively rapidly smoothed out by the dynamics of the ecosystem in offshore areas and there seems to be no effective process which will permit the propogation of small-scale effects within the marine ecosystem.

20) Some exception to (19) above are found only along the coastline and in shallow water, where one space dimension disappears and where a physical convergence (and convergence line--the beach) exists in nature. Here the effects are, however, local in nature, although they may be bothersome to limited sectors of local human populations.

21) As the ecosystem internal consumption and consequent turnover rate of the biomass is high (considerably higher than heretofore assumed), and as relatively widespread starvation can be expected to occur, it appears that with the existing or expected biological data base that it may be very difficult to quantitatively determine any damage to the marine ecosystem caused even by a relatively extensive but temporary accidental oil spill, with the possible exception of accidents during fish or crustacean spawning activities which may be highly localized.

22) The consumption of finfish and other marine resources by mammals is higher than the removal of these resources by man in the intensively fished eastern Bering Sea. Therefore, any management attempts of marine resources through controlling the fishery by man without managing (controlling) the marine mammal populations, might not achieve the desired effect. It does not seem feasible that any oil exploration effects could reach a noticeable fraction of the removal of resources by the beasts and the man.

23) It is expected that DYNUMES III, a model already well along in development and verification, will considerably advance the accuracy and effectiveness of the present model, DYNUMES II.

VI. ACKNOWLEDGMENTS

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