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**Resource Assessment and Evaluation
of the Dynamics
of the Fishery Resources
in the Northeast Pacific
with Numerical Ecosystem Models**

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RESOURCE ASSESSMENT AND EVALUATION OF THE DYNAMICS
OF THE FISHERIES RESOURCES IN THE NE PACIFIC
WITH NUMERICAL ECOSYSTEM MODELS

By

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ABSTRACT

The development of offshore fisheries in the vast NE Pacific is relatively recent. Exploratory surveys in the late 1950's demonstrated the abundance of groundfish in this region. The resource surveys in the large area are expensive and without an inordinantly large field effort the accuracy of the results is low. Due both to the lack of conventional fisheries and biological data and the inherent shortcomings of single species models, those models are of questionable value for managing the multination, multispecies fisheries of the northeastern Pacific Ocean.

Two biomass-based, holistic, ecosystem models are being developed and are used at NWAFC for the evaluation of the abundance and dynamics of the fishery resources and for the study of the response of these resources to exploitation and to environmental changes (anomalies). The general background of these models is given below and a simplified version of one of them is given in skeleton form in the Appendix.

Equilibrium biomasses, as computed with the PROBUB model for the eastern Bering Sea and the western Gulf of Alaska, are given in this paper. These are computed (validated) with conventional trawling survey results, which have been converted with catchability and availability factors.

The nature of the dynamics of the biomasses in space and time is briefly described and the effects on the resource assessment is demonstrated with some results from the DYNUMES model.

1. CHARACTERISTICS OF THE NE PACIFIC FISHERY RESOURCES AND THEIR EXPLOITATION

The NE Pacific fishery area consists of three different regions--the eastern Bering Sea, Gulf of Alaska, and the North American coast from Vancouver Island to Point Conception. The Bering Sea is considerably different from the other two regions; it has a large continental shelf (twice the size of the North Sea) and has pronounced seasonal changes, including partial ice cover. The NE Pacific is, in general, a biologically rich area and contains great herds of marine mammals. The most abundant fish species undertake migration in the NE Pacific.

Although a limited coastal fisheries developed in the 19th century along the coasts of the NE Pacific, development of the modern large-scale offshore fishery started only in the 1960's by Japanese and Soviet fishing fleets. The maximum catch from the eastern Bering Sea was 2.2 million tons in 1975, consisting mainly of pollock and flatfish. The highest catch from the Gulf of Alaska was 380,000 tons in the late 1960's consisting primarily of Pacific ocean perch. About 200,000 tons of hake and rockfish were caught annually off the Washington and Oregon coasts by foreign fleets in the late 1960's.

Intensive investigations have been carried out on Pacific halibut, and its fishery has been regulated from the early 1930's. The five species of Pacific salmon have also been well investigated in the last half century, and their fishery is also regulated. The exploratory surveys of demersal fishery resources were carried out in the 1950's (Alverson, Pruter, and Ronholt 1964), wherewith the general abundance and distribution of these resources was ascertained but, with the exception of salmon and Pacific herring of the Canadian coast, the pelagic resources are as yet unexplored.

The most pressing present day fisheries research problem in the NE Pacific is the assessment of the state (magnitude) of the fish stocks and their fluctuations, and such information is required for fisheries management of the "200 mile fisheries conservation zone", including resource allocation to foreign countries. In addition, much additional basic information is needed for all species, such as spawning areas and time, growth rates, food composition and its variation, year class strengths, etc. The knowledge on the distribution and migrations of juveniles is also missing. In respect to specific knowledge on species-specific data and to knowledge on abundance and distribution of species, exploration and assessment in the NE Pacific is about fifty years behind that in the North Atlantic. Excluding the Canadian coast and some limited coastal areas in Alaska, the fisheries resource research is at present largely carried out by one laboratory with limited personnel and ship availability.

2. CONVENTIONAL MEANS OF RESOURCE ASSESSMENT IN THE NE PACIFIC, RESULTS AND LIMITATIONS

In recent years regular trawling surveys have been carried out in the eastern Bering Sea during the summer months and more occasionally in the Gulf of Alaska and along the west coast of North America. These expensive surveys provide only a general picture of the abundance and distribution of species vulnerable to capture with a bottom trawl. In general the accuracy of trawling survey results is at best \pm 50% (Grosslein 1976). For example, the 1975 trawling survey estimated the pollock biomass (exploitable) in the eastern Bering Sea to be 2,426 thousand tons. The corresponding mean value for the 1976 survey was only 679,000 tons (Bakkala and Smith 1978). Corresponding values for yellowfin sole were 1,039 and 2,095 thousand tons, and for Pacific cod 64 and 102 thousand tons; whereas the all nation commercial catch of cod from the same area was 57,000 tons. The reasons for the discrepancies are several; among the main causes are migrations

in and out of the area and the existence of considerable biomasses of semi-demersal fish over deep water, where they live a pelagic life and feed heavily on euphausiids.

Although various single species stock assessment models have been applied to evaluate the resources of various NE Pacific commercial species, the results of such applications are less reliable in the NE Pacific than in some other well explored and exploited areas, such as the North Atlantic. The reasons for this are several: for example, the Virtual Population Analysis (VPA) is not fully applicable, because: (a) the catch statistics and length-age frequency distribution data are haphazardly and incompletely collected, (b) most species undertake pronounced seasonal and "life cycle" migrations, (c) the "natural" mortality rate estimates are very unreliable, (d) most species are underexploited, and (e) there is a heavy consumption of fish by mammals (the mammals consume twice as much fish in the eastern Bering Sea as the total commercial catch).

Similarly, any other available single species model is not fully applicable to the stocks in the NE Pacific, because either initial stock size is not known, data for year class strength determination is deficient, natural mortality is variable and not known, and fisheries statistics are deficient. Furthermore, the main general shortcoming of single species approach is that each species is treated as an independent entity. However, there is an intensive interspecies interaction, mainly via predation--fish eat fish. The analysis of shortcoming of past resource assessment models (including a recent analysis of these problems by Dickie 1979) and the review of types, availability and reliability of basic data of NE Pacific fish and fisheries, suggested that a synthetic and holistic approach for resource evaluation must be taken in which use is made of all available data and knowledge.

3. OBJECTIVES AND PRINCIPLES OF ECOSYSTEM AND MULTISPECIES SIMULATION MODELS

It might be useful to differentiate between various types of models and simulations (models). Conventionally, a model has been considered to be an abstraction and simplification of a given condition and/or process, whereas a simulation is a numerical reproduction of a system of conditions and processes, based on available empirical data and knowledge and may contain many tested models.

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 empirical 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 represents 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.

In addition, the following requirements apply to ecosystem simulations which emphasize the "fisheries ecosystems".

—The simulation must be capable of solving the major part of the age-variable mortalities (especially predation, spawning stress, and fishing mortalities).

—There must be a unique solution to the system of basic equations in defined conditions (for determination of the "equilibrium biomasses").

—The system of equations should not be conditionally stable (except for unique solution in defined conditions).

4. BIOMASS BASED ECOSYSTEM SIMULATION MODELS IN NWAFC (PROBUB AND DYNUMES)

Most available population dynamics models are number based. This usually requires that each species must be divided into age groups to which initial numerical strength must be assigned and separate continuous bookkeeping for each age group must be carried out in the model. The distribution of numbers in juvenile stages is, however, usually unknown. Furthermore, there must be frequent conversion between numbers and weight (biomass), as growth rate is highly age dependent. In addition, predation is a highly predator-prey size dependent process.

Considering the practical (computational) complexities of number and biomass based models, it was decided to use a biomass based simulation model for marine ecosystem simulation. The Andersen-Ursin (1977) multispecies model is essentially a number based model and is applicable to areas where basic input data on species is readily available (e.g. the North Sea). It is not possible to describe the complex models here in detail, but to present only the essentials of the models with a "skeleton model". The full models have been documented by Laevastu and Favorite 1978a and 1978b.

A schematic flow diagram of the computations in the skeleton model is given in Figure 1. This model and the equations used in it is briefly described in the Appendix. Some of the dynamic aspects of a marine ecosystem, which must be included in any dynamic simulation model, are shown on Figure 2.

The Dynamical Numerical Marine Ecosystem model (DYNUMES) is a gridded model (for grid see Fig. 3A), which allows detailed computation of dynamics. All computations are carried out at each grid intersection (grid point) at each time step (week or month). The Prognostic Bulk Biomass model (PROBUB) is a simplified version of DYNUMES, where computations are carried out in each defined area ("box") (see Fig. 3B).

Initial first guess biomass is used as the computation base in the first time step (Fig. 1). Before computing biomass growth, the prescribed mean growth coefficient is adjusted (recomputed) at each grid point (and in each box in the PROBUB model) according to factors affecting it. This adjustment is done in each time step. The predation mortality is taken as the sum of the consumption of the given species (or group of species) in the previous time step (in first time step a guess is used--e.g. 7% of the biomass present). All other mortalities

refer to actual time step. Using the computed growth and mortality rates, the actual biomass of each species is computed. In the DYNUMES model the migrations are computed thereafter, using prescribed u and v speed components. In the PROBUB model the migrations through the boundaries are adjusted empirically.

Before computing food uptake and actual composition of food, the availability of food items is checked at each grid point and adjustments are made, if necessary, to the composition of food. The consumption of each species during the time step is summed at the end of each time step.

A unique solution of a set of biomass and trophodynamic equations can be achieved if either the biomass of one major species is known (and kept constant during the iteration), or if part of the consumption (predation) is assumed to be known (e.g. consumption by mammals). In the iterative state of the PROBUB model the biomasses of the species must be adjusted at the end of each year (except of the species, the biomass of which is assumed to be known). The PROBUB model provides the initial input of biomasses to the DYNUMES model.

The biomass based model requires coefficients which are computed for biomass and for given time step length. A biomass growth coefficient is needed for the whole biomass. As this coefficient varies with age, a biomass distribution with age is required for its computation. The latter information is also used to estimate the portion of biomass which is vulnerable to predation (predator-prey size dependent predation). The computations of these biomass parameters are carried out in an auxiliary model (Laevastu and Favorite 1978c). An example of biomass distribution is given on Figure 4.

Recruitment changes in the biomass model are reflected in the changes of growth coefficient, as the latter is a function of biomass distribution with age. The recruitment can thus be controlled with a parameter which is a function of equilibrium biomass and the actual biomass (i.e. high biomass results in proportionally lower recruitment and vice versa).

5. EVALUATION OF RESOURCES IN THE BERING SEA AND IN THE GULF OF ALASKA WITH THE PROBUB MODEL.

Several applications of the bulk biomass model have been made in the NE Pacific for evaluation of the fishery resources (Laevastu and Favorite 1977, Laevastu, Larson, and Livingston 1978). The latest updated bulk biomass model - PROBUB - was used to determine the equilibrium biomasses in the eastern Bering Sea and in the western Gulf of Alaska. Example of the results from the eastern Bering Sea is given in Table 1.

The consumption of fish, benthos, and plankton by marine mammals was computed with prescribed monthly amounts of mammals present and with fixed food composition. Thus consumption by marine mammals provided the "forcing function" which allowed the determination of the unique solution - i.e. the equilibrium biomasses. The basic principle of the determination of the equilibrium biomasses which can be sustained in a given ecosystem is that the annual biomass growth must equal its removal by predation, other mortalities, and the fishery. It has been determined numerically and theoretically (considering the plausible errors in input data) that the error in the determination of equilibrium biomasses does not exceed $\pm 30\%$ of the computed mean value.

TABLE I.

Equilibrium Biomasses and Ecosystem Internal Consumption of some Species/Groups of Species in the Eastern Bering Sea (in 1,000 tons)

Species or Groups of Species	Total biomass, in 1,000 tons				% Exploitable Biomass	Total Exploitable Biomass	Consumption, in 1,000 tons				Annual Turnover Rate
	Area 1	Area 2	Area 3	Eastern Bering Sea			Area 1	Area 2	Area 3	Eastern Bering Sea	
Halibut, turbot	260.5	142.1	8.8	411.3	54	222.1	66.9	31.7	2.8	101.4	0.25
Flathead sole, arrowtooth flounder	945.1	236.4	17.0	698.4	54	377.1	147.7	69.6	7.0	224.3	0.32
Yellowfin sole, rock sole	661.8	444.7	24.0	1,130.5	45	508.7	174.1	87.6	9.2	270.9	0.24
Other flatfish	492.3	363.5	26.5	882.3	28	247.1	220.2	111.2	14.3	345.7	0.39
Cottids	2,478.1	1,450.0	189.5	4,117.6			1,347.2	664.7	115.8	2,127.7	0.52
Cods	593.9	391.5	50.6	1,036.0	72	745.9	301.2	168.6	31.5	501.3	0.48
Sablefish	71.3	37.7	18.0	127.0	40	50.8	18.6	10.2	1.4	30.2	0.24
Pollock	5,513.4	2,997.3	702.5	9,213.2	70	6,449.2	2,390.9	1,135.2	464.2	3,990.3	0.43
Rockfishes	1,009.9	477.3	139.0	1,626.3	30	487.9	445.2	210.9	65.8	721.9	0.44
Herring	1,219.1	578.5	171.4	1,968.9	30	590.7	832.9	399.1	125.6	1,357.6	0.69
Capelin, sand lance	2,165.8	1,047.8	292.3	3,505.8			1,550.7	749.5	219.2	2,519.4	0.72
Mackerel	701.3	330.4	131.9	1,163.6	45	523.6	387.9	183.0	78.3	649.2	0.56
Squid	523.3	248.4	498.3	1,270.1			621.5	307.5	668.1	1,597.1	1.26
Crab	522.2	309.9	14.3	846.4	40	338.6	180.0	93.1	5.9	279.0	0.33
Shrimp	427.3	479.9	24.3	931.5	65	605.5	350.0	187.8	14.2	552.0	0.59
Predatory benthos	466.6	378.0	41.7	886.3			198.0	138.4	20.8	357.2	0.40
Infauna	13,401.3	10,517.4	443.3	24,362.0			13,813.0	9,085.9	546.4	23,445.3	0.96
Epifauna	10,433.3	7,006.9	452.0	17,892.2			6,471.8	3,845.4	305.0	10,622.2	0.59

The equilibrium biomasses in the eastern Bering Sea (statistical and management areas 1, 2, and 3 - Fig. 3B), given in Table 1, are the "minimum sustainable equilibrium biomasses" obtained by using the highest plausible growth rates and the lowest plausible food requirements and are grouped into three different ecological groups: pelagic, semidemersal, and demersal (Fig. 5). The semidemersal species dominate all other ecological groups (12 million tons), mainly due to their more flexible feeding habits. The biomasses of pelagic and demersal species are about equal (ca 7.5 million tons each). The most abundant species is pollock (ca 9 million tons), followed by cottids and other smaller, noncommercial demersal species (4 million tons), and capelin, other smelts and sand lance (3.5 million tons). Pacific salmon, which occur seasonally in the eastern Bering Sea, are not included in Table 1 and Figure 5. The biomasses of the demersal species decrease more than one order of magnitude by moving from the continental shelf regime (Area 1) to the deep ocean, mainly due to disappearance of the benthic food resource. The semidemersal species live a pelagic life and consume pelagic food over the deep water.

Very little is known about the benthos in the Bering Sea. The total equilibrium biomasses require about 50 g/m^2 standing stock of benthos. The existence of this standing stock is entirely possible if we compare the Bering Sea with the well-investigated Barents Sea.

Quantitative zooplankton data from the Bering Sea is also nearly absent. The Soviet works in the early 1960's were quantitatively deficient, giving only the minimum standing stocks of copepods and no quantitative data on abundant euphausiids. The total equilibrium biomasses consume about 50 g of zooplankton per square meter, thus annual production of zooplankton must be at least this amount. The exploitable biomasses in the Western Gulf of Alaska as computed with PROBUB model and as ascertained with trawling surveys is given in Table 2.

Table 2.--Comparison of exploitable biomasses (in 1,000 tons) as obtained by surveys and computed with PROBUB model. Western Gulf of Alaska.

<u>Species/group of species</u>	<u>1970's mean from surveys*</u>	<u>Minimum sustainable exploitable biomass from PROBUB model</u>
<u>Demersal</u>		
Greenland turbot, halibut	138	52
Flathead sole, arrowtooth flounder	77	50
Yellowfin and rock sole, Alaska plaice	78	90
Other flatfish	30	42
Elasmobranches, cottids	86	(493)
<u>Semi-demersal</u>		
Pollock	1,024	1,228
Cod	112	101
Sablefish	13	(20)
Rockfish	25	134
<u>Pelagic</u>		
Herring		129
Capelin, other smelt		(500)
<u>Varia</u>		
Atka mackerel, + macrurids		168
Squid		(600)
Crab	213	58
Shrimp		121

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* Survey results for 1970's from Ronholt et al, 1978. Converted with catchability coefficient.

The total exploitable finfish biomass (excluding capelin and cottids) over the continental shelf of the eastern Bering Sea is about 10 tons per km^2 (capelin and cottid total biomass is about 7.5 tons/ km^2). Of this biomass only about 1.6 tons/ km^2 is taken by the fishery. Marine mammals consume in addition more than 3 tons/ km^2 . Obviously many species are quite underexploited in the Bering Sea (flatfishes, capelin, Atka mackerel, etc.). Considering the relatively high consumption of fish by marine mammals and the relatively low commercial catch, it is very doubtful that the management of the fishery has any effect on the resources without simultaneous management of marine beast herds. Furthermore, components of the marine ecosystem have long-term fluctuations which are not necessarily caused by the fishery.

The long-term dynamics of the biomasses in the marine ecosystem can be and have been studied with the PROBUB model after determination of the equilibrium biomasses by introducing a cause of any change in any species in the ecosystem. The results of such studies have limited reliability beyond a few years because of the uncertainty in predicting the recruitment (spawning success). It should, however, be pointed out that the "natural", quasi-periodic fluctuations of biomasses in the marine ecosystem can have considerable magnitudes (e.g. the biomass can be a fraction of a few tenths to several times its long-term mean value). The periods can be from a few years to more than a few decades.

6. STUDY OF THE DYNAMICS OF MARINE ECOSYSTEM IN SPACE AND TIME AND ITS EFFECTS ON RESOURCE ASSESSMENT.

Two basically different causes for seasonal dynamics of biomasses can be recognized (i.e. changes in abundance and distributions in space and time). The first group of changes are caused by seasonally changing growth, predation (and other mortalities), and production and release of eggs and milt. The second cause of seasonal dynamics is seasonal migrations of species. The product (results) of

both major causes of seasonal dynamics must be viewed spatially. Unfortunately little consideration has been given to the spatial aspects of biomass (and ecosystem) dynamics in the past, mainly due to difficulties in its empirical study by non-synoptic resource surveys. However, the gridded ecosystem models with spatial resolution make these studies possible.

Examples of spatial and temporal aspects of biomass dynamics are shown in Figure 6 which depicts the biomass sources and sinks in February and August of juvenile pollock (<22 cm long) in the eastern Bering Sea (source refers to the condition where biomass growth in a given time interval, month, exceeds its losses by predation, fishery, and other mortalities; sink refers to opposite conditions, i.e. losses exceed growth).

The sources and sinks of all species change in space and time due to spatial and temporal changes of the processes associated with them. There is usually a sink at the periphery of the distribution of the biomass. This sink is usually compensated by outmigration from the center of main distribution (spreading). There is a quasi-continuous source of pollock off the continental slope over the deep water. During winter this source area is farther to the southwest where the temperature of the water is higher, allowing higher growth rates.

The distribution of the two different age groups of pollock in August is shown in Figure 7. A partial separation of juvenile and old pollock is brought about by cannibalistic predation of old pollock on its own juveniles and other factors. The highest concentration of biomass of older pollock is found off the continental slope, whereas the juveniles are found mainly on the continental shelf.

The effects of seasonal depth migrations of yellowfin sole on changes in its distribution are shown in Figure 8. The seasonal depth migrations of flatfish were investigated by Alverson (1964). On the basis of his work it was assumed that the yellowfin migrates from deep water into shallow water during May and June and back

into deep water in October and November. A migration speed of 3 km/day was assumed in the model. The distribution of yellowfin sole in August is given in Figure 9 as computed with the DYNUMES model.

The seasonal migrations have profound effects on other biota as well as on the evaluation of fishery resources with trawling surveys. For example, the flatfish is dependent on benthos as a food source. The migrations cause heavy grazing of benthos in some areas during some seasons, allowing "recovery period" during other seasons. A proper trawling survey evaluation must account for seasonal migration to avoid meaningless results.

Two dynamic effects of temperature anomalies are included in the DYNUMES model: the "forced" migration of most species out from areas with subzero bottom temperatures in the Bering Sea (including a slightly increased mortality), and the effect of temperature on growth (and food uptake).

An example of the resulting effect of temperature anomalies on the growth of herring biomass is given in Figure 10, showing the sources and sinks of biomass in an average February and in a February with 1.5°C positive temperature anomaly. The growth of biomass is considerably enhanced in the February with the positive temperature anomaly, especially in the southern, warmer part of the Bering Sea. It should be noted that the effects of cold anomalies on growth are less than the effects of warm anomalies, as the growth is nearly arrested at low temperatures.

7. VERIFICATION OF THE MODEL AND VALIDATION OF THE RESULTS

The verification of the ecosystem simulation models has been done by testing that the formulas used in the models reproduce known effects and behaviors for which they are designed. Furthermore, the verification has been done by simulating

events with the models which are known to produce given changes in the ecosystem. Thus the sensitivity study in large ecosystem models becomes a continuing study of the response of the ecosystem to changes in various rate and state parameters.

The validation of the ecosystem model is done by comparing the resulting state variables (e.g. the abundance and distribution of biomasses) with independently obtained empirical data (e.g. from fisheries surveys). The dynamic aspects of the Bering Sea ecosystem are, however, difficult to validate empirically, due to the absence of time series studies. Before validating the model results with available resource survey results, the latter must be properly converted using catchability coefficients. Examples of this validation are given in Tables 2 and 3 for the species which are more reliably reported quantitatively in the resource surveys. In general, the resource surveys are accurate only to about \pm 50% (Grossline 1976), whereas the error in the model computation results does not exceed \pm 30% of the reported value.

TABLE III

Comparison of exploitable biomasses of some species as obtained by surveys and as computed with PROBUB model. Eastern Bering Sea. (In 1,000 Tons.)

Species/Group of Species	Mean 1975, 1976 Surveys (converted) from Bakkala and Smith, 1978	Equilibrium exploitable biomass from PROBUB model	Catch 1975
Greenland turbot, halibut	176	222	65
Flathead sole, arrowtooth flounder	206	377	26
Yellowfin and rock sole, Alaska plaice	2,716	509	74
Pollock	3,698	6,449	1,285
Cod	233	746	57

Some special qualitative validation of the simulation models can be provided by occasional species fisheries surveys. The following serves as an example. In the early stage of the Bering Sea ecosystem modeling, it became obvious that there must be a considerable amount of pollock (and some other fish species) over the deep water in the Bering Sea. However, pollock were never caught over deep water and the model results were severely criticized until a recent Japanese survey showed considerable amounts of older (larger) pollock over deep water. Furthermore, the deep water areas turned out to be source areas of biomass for many pelagic and semipelagic species at least part of the year. The abundant euphausiids in this area provide ample food source. However, no extensive schooling occurs over deep water, making the fishery less profitable there than over the continental shelf.

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APPENDIX

SKELETON BULK BIOMASS MODEL

The skeleton bulk biomass model, SKEBUB, derived from Laevastu-Favorite (1978a) Bulk Biomass Model (BBM) is the simplest multispecies ecosystem model. It is a biomass based model (in contrast to conventional number based models).

The equations presented here can be applied to any fish species. The formulations and treatment of plankton and mammal (apex predator) are excluded. The biomass and trophodynamic equations can also be applied, with some modifications, to single cohort of any species. The numerical behavior of the individual formulas is well known and thus not described here.

The biomass growth and mortality is computed in discrete time steps. The biomass growth rate is computed from empirical data of annual growth rates and distribution of biomass with age. The latter is computed with an auxiliary model (Laevastu and Favorite 1978b).

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

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

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

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

As relatively short time step is used in the computation, the second order terms, such as nonlinearities in growth and mortality during the time step, can be neglected.

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

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

If there was no starvation in previous time step ($s_{i,t-1} = 0$), the rate of growth ($g_i(t)$) will take the prescribed value g_i^0 , but if the species was not able to get all the food required for maximum growth rate ($R_{i,t-1}$), the prescribed growth rate will be reduced by the ratio of the amount of food which the species was not able to get during the previous time step ($s_{i,t-1}$) over the total amount of food required by the biomass to grow under unlimited conditions ($R_{i,t-1}$).

Both values are available from previous time step and the possible error caused by this necessary backstepping choice is again minimized by the use of short time step in the computations.

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

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

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

All rates of change are presented as instantaneous coefficients and are therefore additive. Fishing mortality ($\phi_{i(t)}$) and natural mortality from old age and diseases, including also spawning stress mortality (μ_i) are prescribed, but the predation mortality coefficient ($\beta_{i,t-1}$) is computed trophodynamically in previous time step from the ratio of consumption of the species over its biomass ($\beta_{i,t-1} = \ln(1 - (C_{i,t-1}/B_{i,t-1}))$).

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

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

where r_i is the prescribed daily ration (in fraction of body weight daily) and τ is the length of time step in days. If the growth rate (g_i^0) is made a harmonic function over the year, r_i must also be made a harmonic function ($r_i = \rho_i + \delta_i * \cos(\alpha_i t - \kappa_i)$).

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

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

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

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

and the starvation would be 0. However, some food might be in limited supply and only part of the biomass of a prey is usually accessible as suitable food (re size dependent feeding). The vulnerability of one species (prey) to another species (predator) is prescribed by average composition of the food of predator. Therefore the fraction of each species which is allowed to be consumed in each time step is prescribed in the model (p_j), considering mainly the size composition of the

biomasses of individual species. Furthermore, substitution of low-availability food items with high-availability items must be used. However, conditions can arise where full substitution is unrealistic and partial starvation will occur. There are various ways of computing the actual consumption with above described limitations.

The recruitment is usually depicted in number based models as a discontinuity relating it to discrete spawning period. In our biomass based model we have treated it as a continuous process. This treatment is acceptable if we think in terms of size groups rather than age groups and consider variations in growth of individuals belonging otherwise into the same age group, and assume a longer spawning period.

Considering a continuous recruitment to all size groups and assuming that there are no exceptionally strong or weak year class of postlarval juveniles, the recruitment would be proportional to the biomass present. The variations in postlarval recruitment would be depicted in biomass based model by the variations of growth coefficient in the species biomass.

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

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

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

If the biomasses of all species in the ecosystem do not change over a year (i.e. previous January biomass is the same as actual January biomass), then we can say that the biomasses are in equilibrium. This implies that the growth of the biomass equals its removal by mortalities (specially by predation). If we want to achieve this equilibrium, we can change either growth rate, mortality rate, or biomass level itself. The growth rate is determined by empirical data and the other factors, such as temperature, are assumed in equilibrium case to be the same from one year to another (although seasonal changes can occur). Fishing and other mortality rates are also assumed to remain the same from one year to another. The predation mortality (consumption) (together with other mortalities which remain unchanged) must then balance the growth rate. This balancing can be achieved if the biomass levels of the predators are adjusted so that the biomasses remain constant from one January to another January. This adjustment can be done by finding a unique solution to the biomass equations of all species (or groups of species) in the ecosystem. This unique solution exists when one of the biomasses and consumption by it is predetermined (assumed to be known and fixed). In this case an iterative solution can be applied to adjust the biomasses of other species once after each year's computation:

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

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

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

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

SYMBOLS FOR CONSTANTS, CALCULATED PARAMETERS, AND STATE VECTORS

Constants

α_i -phase speed, time step dependent (e.g. 30 degrees per month, radians)

γ_i -annual average instantaneous growth rate

ϕ_i -instantaneous fishing mortality coefficient

δ_i -half amplitude of annual change of food requirement (fraction of body weight daily)

σ_i -half amplitude of annual change of growth rate

ρ_i -annual average food requirement (fraction of body weight daily)

κ_i -phase lag (in radians)

μ_i -instantaneous rate of mortality (other than predation mortality)

$\pi_{i,j}$ - fraction composition of prey j in the food of predator i

p_j -fraction of biomass j allowed to be taken in one time step (month)

r_i -prescribed rate of food requirement (fraction of body weight daily)

g_i^o - prescribed instantaneous growth rate

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

Dynamically calculated parameters

$g_{i,(t)}$ -calculated instantaneous growth rate

$Z_{i(t)}$ -calculated total instantaneous total mortality rate

B_i^E -equilibrium biomass

State vectors

$B_{i,t}$ -biomass of species i at time t

$C_{i(t)}$ -consumption of species i (predation) during time step t

$R_{i(t)}$ -food requirements

$S_{i(t)}$ -starvation (the amount of food missing from the full food requirement $R_{i(t)}$)

$Y_{i(t)}$ -yield

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

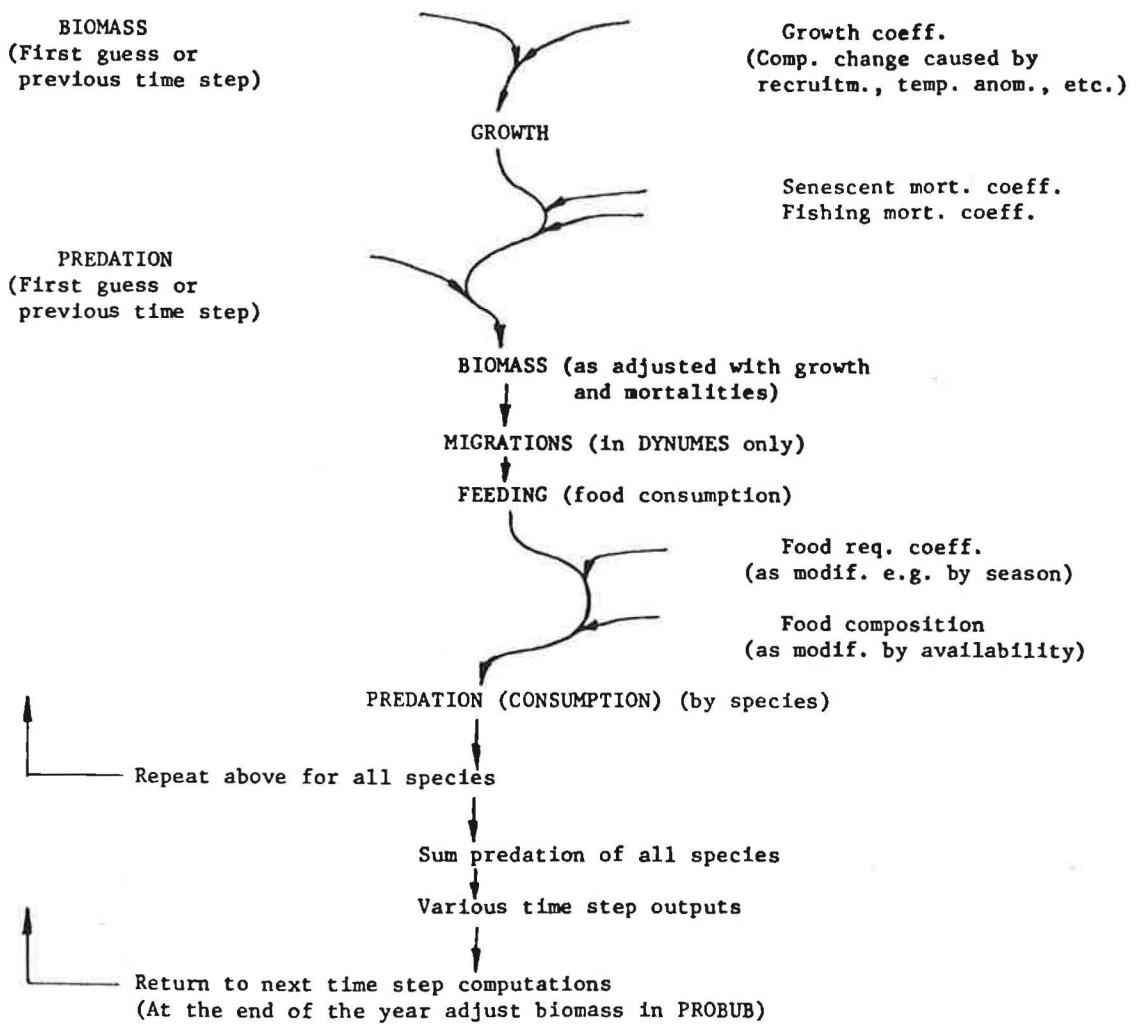
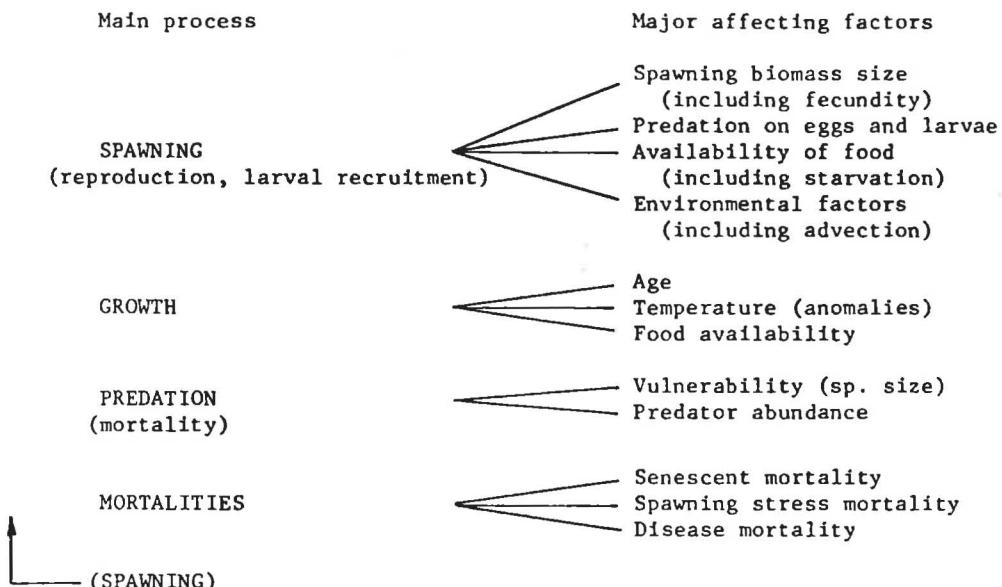


Fig. 1.--Schematic flow diagram for computations.

A. Biomass abundance affecting processes



B. Biomass distribution affecting processes

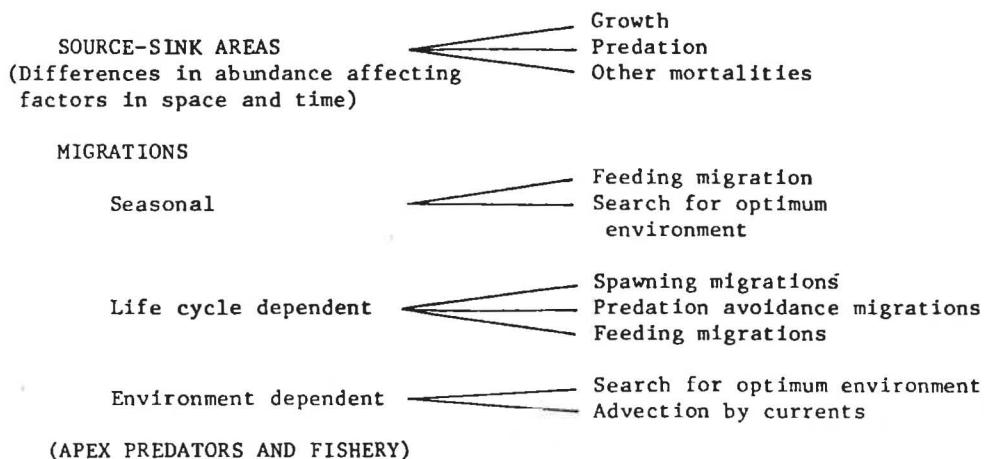


Fig. 2.--Major dynamic processes in the marine ecosystem.

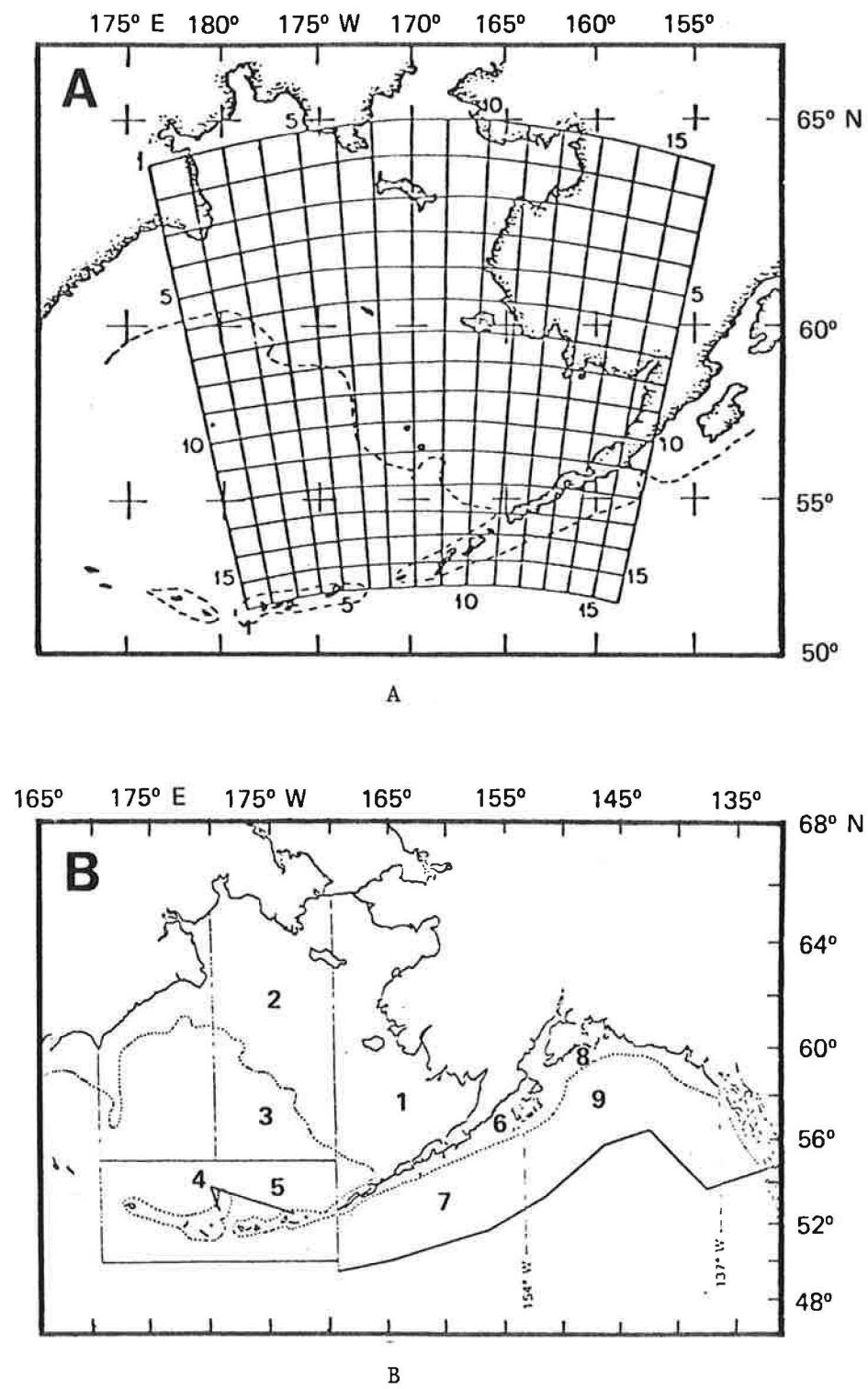


Fig. 3.--Computation grid of DYNUMES for the eastern Bering Sea (A) and the fisheries management and statistical areas (B).

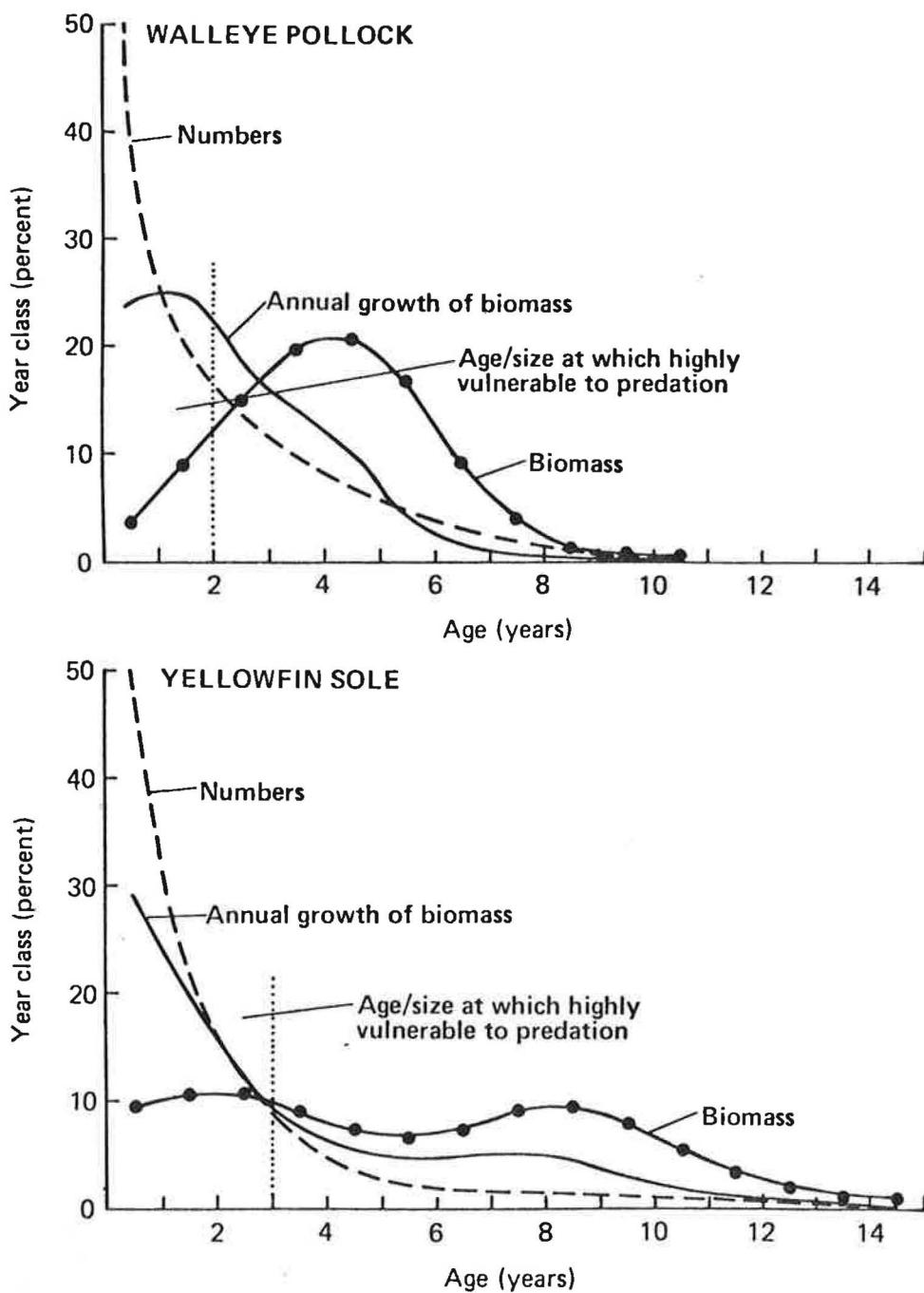


Fig. 4.--Mean biomass and its annual production distribution with age in pollock and yellowfin sole. The portion of biomass highly vulnerable is indicated.

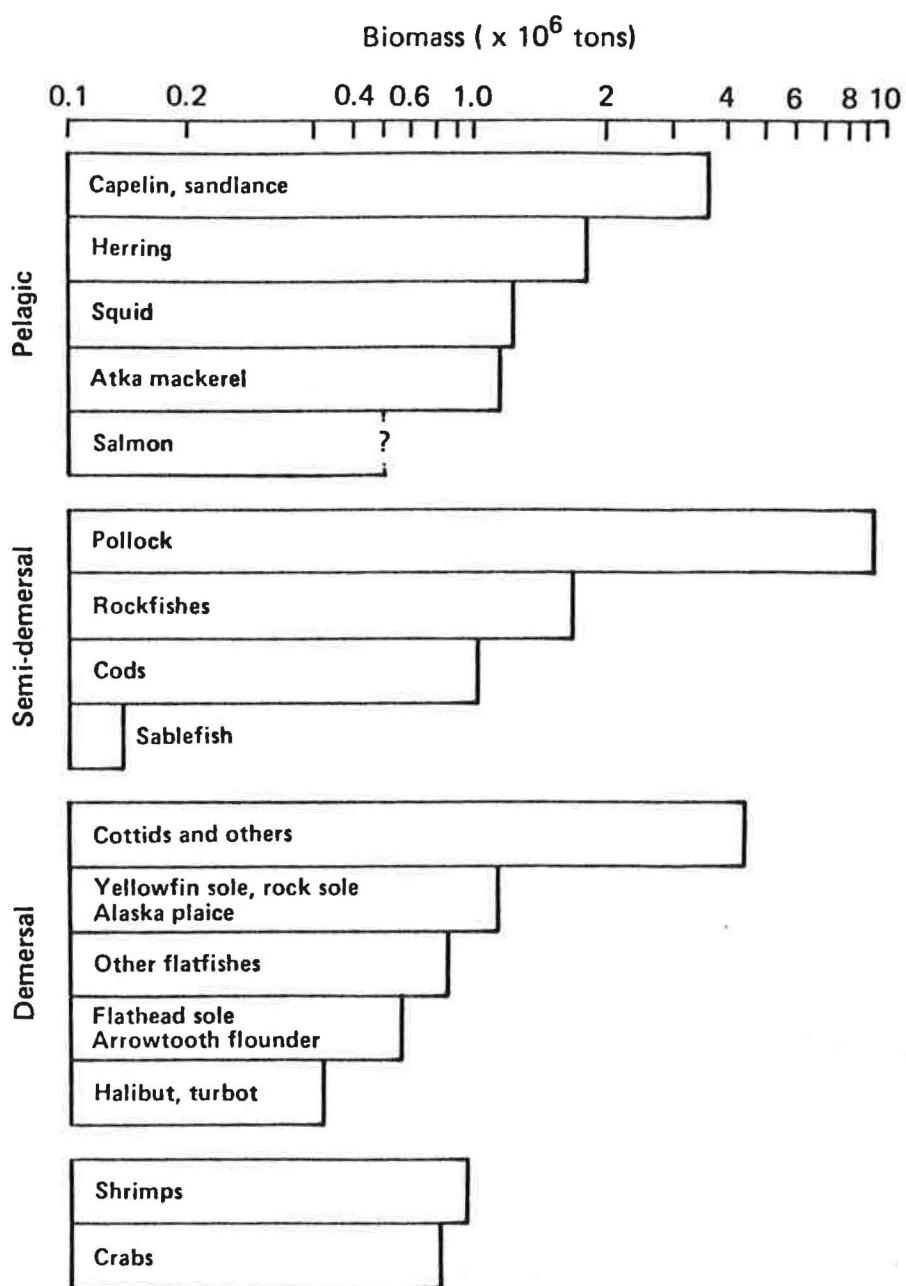


Fig. 5.--Equilibrium biomasses of three different regimes
in the eastern Bering Sea.

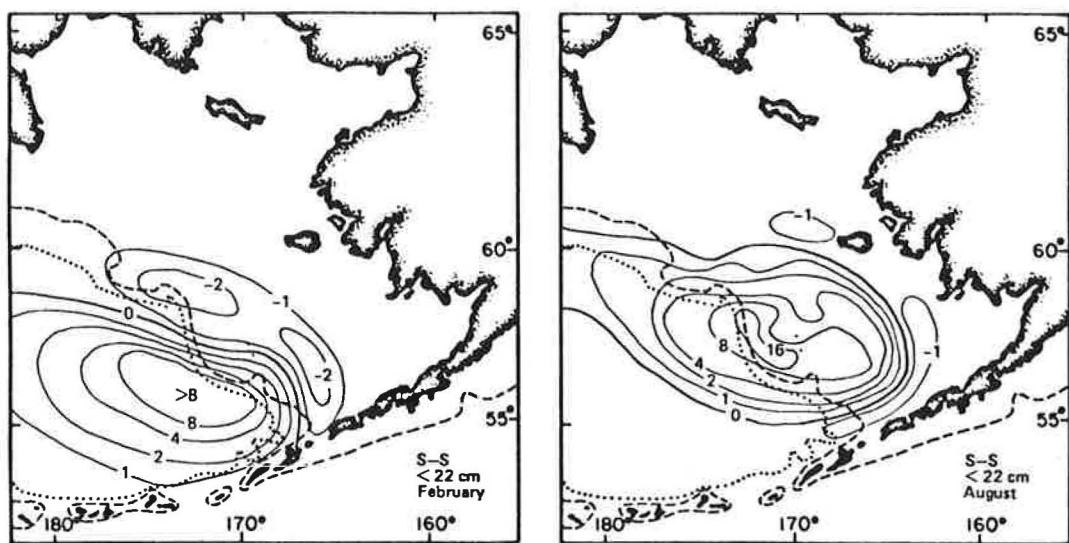


Fig. 6.--Sources and sinks of juvenile pollock (<22 cm long) in February and in August in the eastern Bering Sea (in 100 kg/km^2).

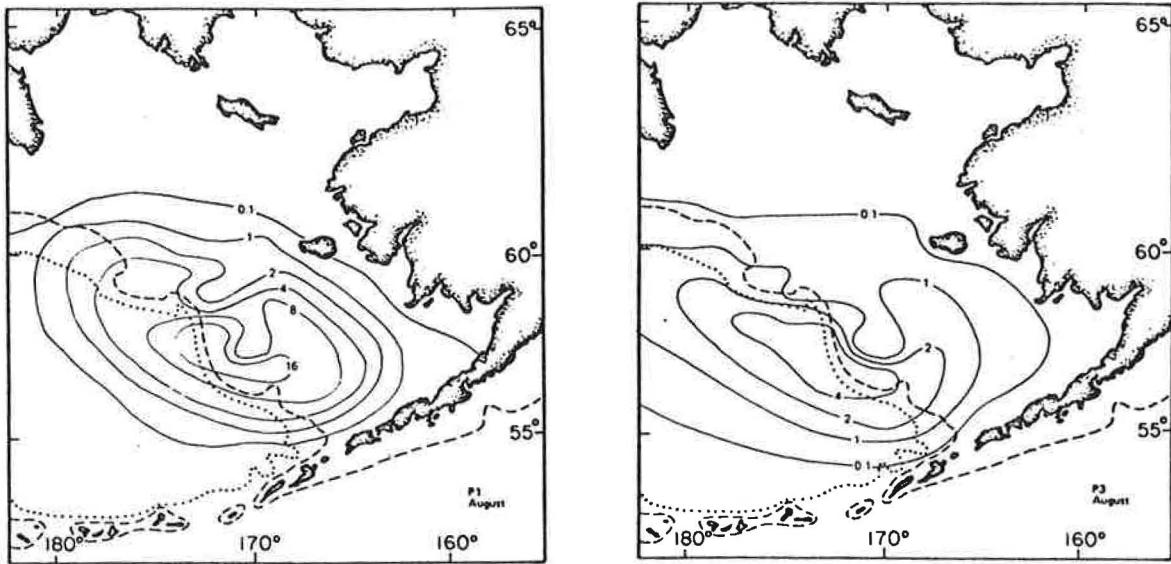


Fig. 7.--Distribution of juvenile pollock (<22 cm long) and old pollock (>45 cm long) in August in the eastern Bering Sea (tons/km^2).

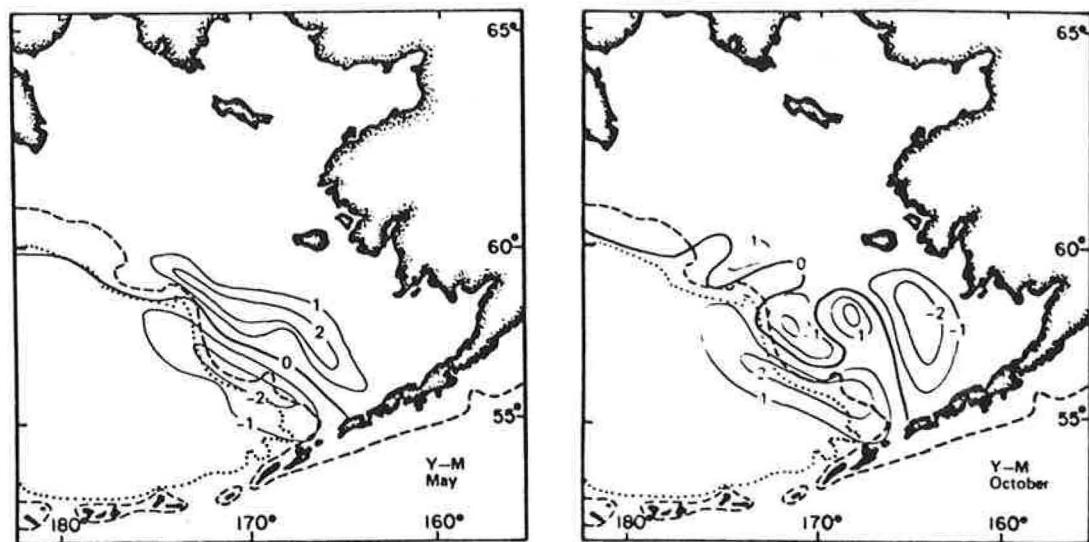


Fig. 8.--Changes of yellowfin sole biomass distribution due to migrations in May and in October (tons/km^2).

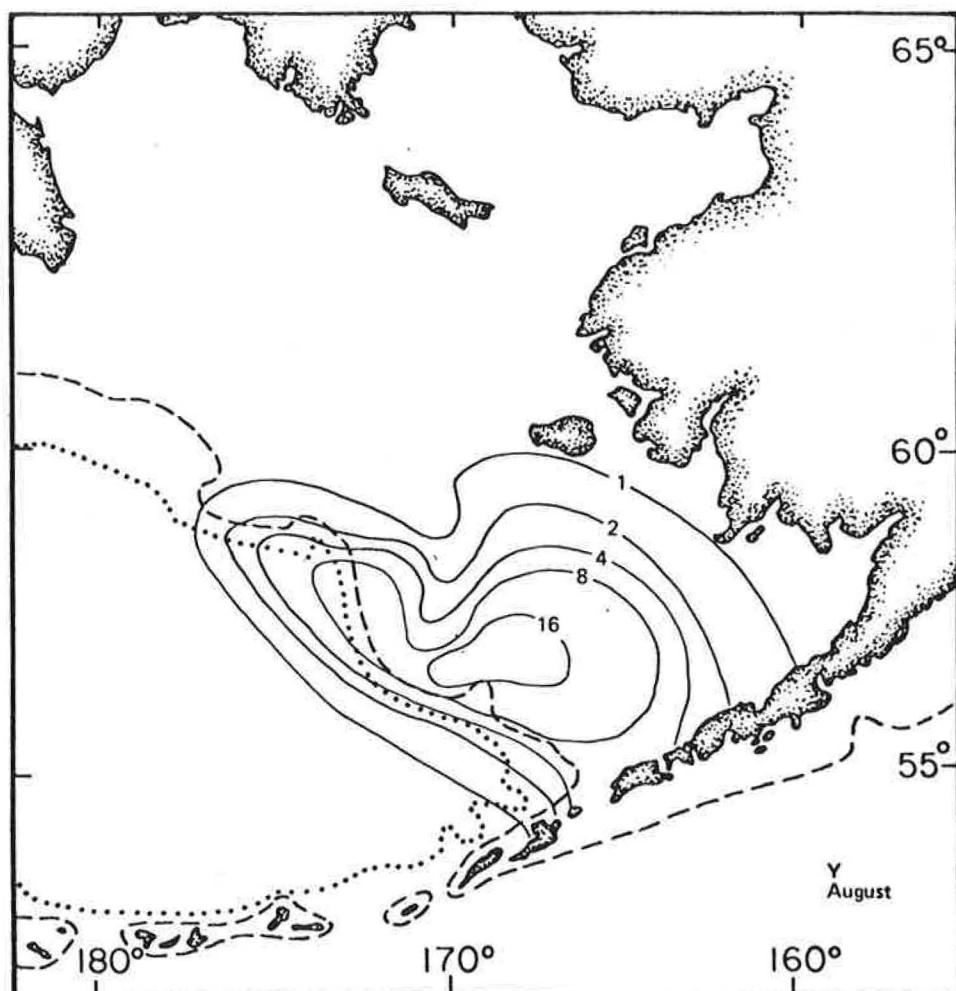


Fig. 9.--Distribution of yellowfin sole in August in the
eastern Bering Sea (tons/km²).

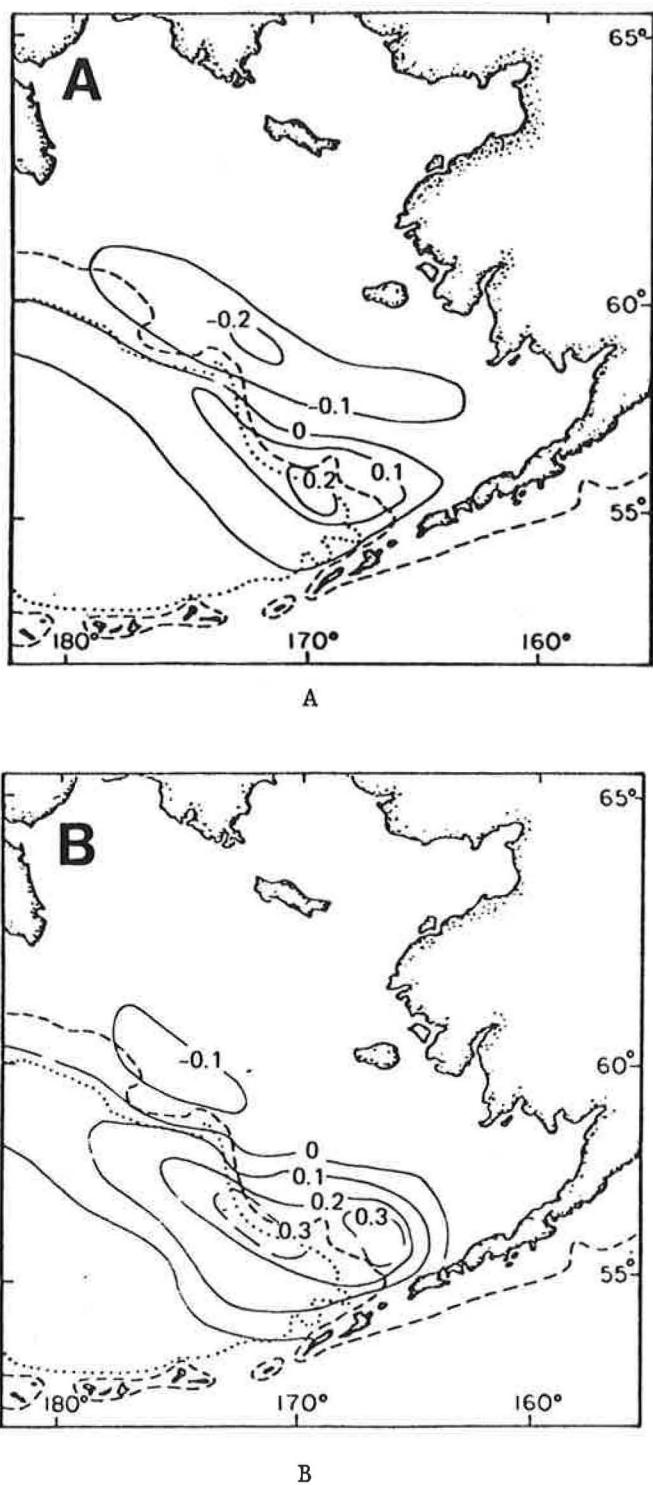


Fig. 10.--Effect of temperature anomaly on the source and sink of herring in February in the eastern Bering Sea (A—"normal" February, B—February with a $+1.5^{\circ}\text{C}$ temperature anomaly).