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## Biomass-Based Fisheries Ecosystem Simulations of the North Pacific

General overview of the DYNUMES and SKEBUB simulation models<br>June 1983

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# Biomass-Based Fisheries Ecosystem Simulations of the North Pacific - General Overview of the DYNUMES and SKEBUB Simulation Models 

By
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A biomass-based, multispecies, multidimensional Dynamic Numerical Marine Ecosystem model (DYNUMES) has been developed at the Northwest and Alaska Fisheries Center and applied to the eastern Bering Sea. The model has both temporal and spatial resolution, incorporates the effects of temperature on growth and survival, and provides for density-dependent growth, feeding, and predation. A Skeleton Bulk Biomass Ecosystem model (SKEBUB) has also been developed, and is an abbreviated version of the DYNUMES model without spatial resolution. The models serve several purposes, including diagnostic evaluation of marine resources and prognostic studies of exploitation.

Logic and general outline of the models are given. Emphasis is placed on DYNUMES and, in particular, the processes of density-dependent feeding and food item substitution. Selected outputs are provided, demonstrating model capability and conditions and processes of the marine ecosystem in the eastern Bering Sea.

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## 1. Introduction

Limitations in the application of deterministic single-species mathematical models to fisheries management problems, and in particular the computation of sustainable yields, has generated considerable interest in the concept of a multispecies approach to fisheries management (see Mercer 1982 for a review), and to the need for a more realistic view of the variability inherent in the processes of stock dynamics, particularly recruitment (Riffenburgh 1969; Lord 1973; Smith and Walters 1981; Getz and Swartzman 1981). At the same time, a variety of mathematical and simulation models have been developed to investigate the overall dynamics of the fisheries ecosystem, to provide a better understanding of system interactions, and to investigate the effect changes in model assumptions can have on resultant output (Lassiter and Hayne 1971; Kitchell et al. 1974; Anderson and Ursin 1977; Laevastu and Favorite 1977; Laevastu and Larkins 1981; Reed and Balchen 1982; Ploskey and Jenkins 1983). Although each varies considerably in technique and methodology, and independent of either their number-based or biomass-based formulations, most of these approaches have a common basis in the early works of Schaefer (1954) ; Beverton and Holt (1957); Ricker (1954, 1975), and the cohort analysis formulations of Gulland (1965) and Pope (1973).

Few of the various multispecies models currently in the literature, however, provide means for studying the temporal and spatial components of the ecosystem (i.e., migration and environmental and oceanographic variability). One exception is the biomass-based, multispecies, multidimensional Dynamic Numerical Marine Ecosystem model (DYNUMES) developed at the Northwest and Alaska Fisheries Center (Laevastu and Larkins 1981) and applied to the Bering Sea. A gridded model allowing detailed computations of species biomass at each grid point (576 in the Bering Sea, Fig. 1), DYNUMES simulates multispecies interactions


Figure 1.--DYNUMES Bering Sea $24 \times 24$ grid.
of predation, feeding, and growth for 27 fish species groups (Appendix Table 1) and 30 bird/mammal groups (Appendix Tables 2 and 3). It also simulates the effects of environmental and oceanographic variability, and incorporates a complex migration subroutine (both seasonal and temperature induced) that provides for spatial as well as time dependent resolution of fish biomass dynamics.

The purpose of this paper is to provide a general overview of the DYNUMES model and to set the stage for the two talks to follow on sensitivity analyses of the model and on the details of the spatial and temporal variations simulated via migration. Since DYNUMES is already well documented (Laevastu and Favorite 1977, 1978a, 1978b, 1978c; Laevastu and Larkins 1981; Laevastu and Larkins 1982), much of this presentation will be a review of the previously published material. Emphasis, however, will be placed on recent enhancements and modifications to the model, particularly those involving density-dependent growth, feeding, and predation. Where appropriate, reference will also be made to the Skeleton Bulk Biomass Ecosystem model (SKEBUB), an abbreviated version of DYNUMES without spatial resolution (Laevastu and Larkins 1982; Laevastu and Bax 1983; Bax 1983).

## 2. General Overview of DYNUMES

DYNUMES is a multispecies, multidimensional gridded model with detailed biomass computations at each grid point ( $24 \times 24$ ) and at each time step (currently one month). Overlaying this grid is a land-sea and subregion table that provides information on model-specific bird/mammal regions, land areas, and areas outside the Bering Sea; a depth table that gives the bottom depth for each grid point; and 24 temperature tables that provide mean monthly temperatures for each grid point for both surface and bottom layers (Figs. 2a and 2b).


Figure 2a.--Mean Bering Sea surface temperature for May (from Ingraham 1983).


Figure 2b.--Mean Bering Sea bottom temperature for May (from Ingraham 1983).

The first step in the DYNUMES simulation is the computation of bird/mammal consumption at each grid point. Input biomass data for birds/mammals are provided for each grid point as 12 monthly tables arranged by bird/mammal group and by region. There are currently 23 mammal and 7 bird ecological groups, using average food composition as the criterion for grouping. These data are provided explicitly rather than computed in the model, since the gains in accuracy afforded by such computation would be less than that caused by errors in the current estimates of mammal abundance. Accordingly, each bird/mammal group has associated with it a set of empirically determined parameters, including: population abundance and distribution by month and by sub-region, mean body weight, daily food requirement as a fraction of body weight, and food composition (percentage contribution of each prey species to the predators' diet). Since descriptions of both the input data and equations for computing bird/mammal consumption are documented elsewhere, they will not be repeated here (Laevastu et al. 1980a, 1980b; Livingston 1980; Laevastu and Larkins 1981).

The next step in the simulation is the computation of seasonal and temperatureinduced migrations for each fish species. This topic is considered in detail in Swan (1983) and the reader is referred there for discussion. Following migration, the processes of density-dependent growth and predation are simulated in a subroutine called FEDGRO. Biomass computations for feeding and growth are done at each grid point and each time step for all species, excluding plankton and zooplankton. (Plankton and zooplankton computations are simulated in a separate subroutine using simple empirical formulations and are documented in Laevastu and Larkins 1981).

Input biomass data (Appendix Table 4) and species-specific parameters for the fish species groups in the DYNUMES simulation are obtained from a variety of
sources and are documented in Laevastu et al. 1980; Laevastu and Larkins 1981; and Niggol 1982. The feeding and growth computations are the dominating force of the model and contain all of the inter-species fish interactions. They will be discussed in detail below. To avoid duplication, however, the extensive theoretical discussions presented in Laevastu and Larkins (1981) will not be repeated here. Emphasis will be placed instead on describing specific formulations and, in particular, those enhancements incorporated over the past year.

## 3. Growth and Feeding Formulations

## Growth

Species-specific mean growth rates ( $\mathrm{g}_{0}$ ) are adjusted at each time step and grid point to reflect spatial and temporal changes in growth resulting from a variety of biotic and abiotic factors (Laevastu and Larkins 1981). These factors include seasonal variations, temperature effects, and starvation. In the current version of DYNUMES, monthly mean growth rates are adjusted for seasonal variation via an harmonic function:

$$
\begin{equation*}
g_{t}=g_{0}+A_{g} \cos \left(\alpha t-k_{g}\right) \tag{1}
\end{equation*}
$$

where $g_{t}$ is the adjusted monthly growth rate for month $t, A_{g}$ is the half annual magnitude of change of the growth rate, $\alpha$ is the phase speed ( $30^{\circ}$ to reflect the monthly time step), $t$ is time (months), and $k_{g}$ is the phase lag (used for prescribing the time at which $g_{t}$ is at a maximum).

The monthly growth rate ( $g_{t}$ ) obtained from equation ( 1 ) is adjusted to simulate the effects of starvation on growth. Starvation ( $S_{i}$ ) is computed as the difference between consumption $\left(C_{i}\right)$ and the required food ration ( $R_{i}$ ), with its effect on growth computed as:

$$
\begin{equation*}
g_{t}=g_{t}-\left[\frac{S_{i}}{R_{i}}\left(g_{t}\right)\right] \tag{2}
\end{equation*}
$$

This is a slight modification of the formula given in Laevastu and Larkins (1981). Before discussing equation (2) in detail, a brief comment is necessary regarding temperature effects on growth.

In the PROBUB (Prognostic Bulk Biomass model, Laevastu and Larkins 1981) and SKEBUB (Bax 1983) simulations, explicit formulations are given for representing temperature effects on growth. Both of these models, however, lack spatial resolution. DYNUMES reflects the effects of temperature on biomass distribution by means of a detailed migration subprogram that considers seasonal, spawning, and temperature-induced migrations. In conjunction with the explicit formulae given above for adjusting growth for seasonal variations and starvation effects, this temperature-induced migration of biomass presents a more holistic simulation of the ecosystem. This has particular importance for the computation of consumption ( $\mathrm{C}_{\mathrm{i}}$ ) and possible starvation ( $\mathrm{S}_{\mathrm{i}}$ ), since consumption as detailed below is an explicit function of prey availability at each time step and grid point in the simulation. If full substitution of food which is absent or in short supply at a given location and time is not possible, partial starvation is considered to occur. Thus temperature effects on growth are linked dynamically through means of temperature-induced migrations, prey availability, and the resulting effects of starvation (if any) on growth.

## Food Ration

Required food ration ( $R_{i}$ ) is computed for each time step and at each grid point and is the sum of the food requirement for maintenance and the food requirement for growth given unlimited food availability. Its general form is given by Laevastu and Larkins, 1981, as:

$$
\begin{equation*}
R_{i}=b \bar{B}+a G \tag{3}
\end{equation*}
$$

where $R_{i}$ is the total food requirement of each species per unit time (and at each grid point), b is food requirement coefficient for maintenance in terms of percent body weight daily (BWD), $\bar{B}$ is mean biomass, a is food requirement coefficient for growth (including sex products development) and $G$ is the estimated growth in biomass. More explicitly,

$$
\begin{equation*}
R_{i}=\left(\frac{\left[B_{i} e^{g-M-F}-f_{i} B_{i}\right]+B_{i}}{2}\right) r_{i} t_{d}+\left[\left(\frac{\left[B_{i} e^{g-M-F}-f_{i} B_{i}\right]+B_{i}}{2}\right) e^{g}-\bar{B}\right] r_{g, i} \tag{4}
\end{equation*}
$$

with a full list of symbols and definitions given in Table 1.
In terms of equation (3), $r_{i}{ }^{t}{ }_{d}$ corresponds to $b$, and refers to the fraction of body weight of food required daily for maintenance ( $r_{i}$ ) and the length of the time step in days ( $t_{d}$; i.e., 30 days). Since $r_{i}$ is a seasonally varying parameter, its value is adjusted at each time step by the harmonic function:

$$
\begin{equation*}
r_{i}=r_{0}+.35\left(r_{0}\right)[\cos (\alpha t-k g)] \tag{5}
\end{equation*}
$$

where $r_{0}$ is the species-specific food coefficient for maintenance expressed as percent of body weight daily and is estimated from the current literature and the best available emperical data. The cosine terms are the same as in equation (1). (For a fuller discussion please see Laevastu and Larkins 1981.)
$\bar{B}$, or mean biomass from equation (3), is expressed in equation (4) as:

$$
\begin{equation*}
\frac{\left[B_{i} e^{g-M-F}-f_{i} B_{i}\right]+B_{i}}{2} \tag{6}
\end{equation*}
$$

where $B_{i}$ is biomass, $g$ is the growth rate ( $g_{t}$ ) computed in equation (2), $M$ is the mortality coefficient for senescent, spawning stress, and disease mortalities, $F$ is the coefficient for fishing mortality, and $f_{i}$ is the expected fraction of biomass of species $i$ consumed by its predators.

Table 1.--List of symbols and abbreviations

| a | Food requirement coefficient for growth |
| :---: | :---: |
| A | Constant used in equation (1)--specifies maximum level of upward and downward adjustment of food item substitution |
| $\mathrm{A}_{\mathrm{g}}$ | Half annual magnitude of change of the growth rate |
| b | Food requirement coefficient for maintenance in percent body weight daily (BWD) |
| B | Constant used in equation (11)--specifies rate of change of food item substitution |
| $B_{i}$ | Species biomass |
| $\bar{B}$ | Mean biomass |
| BWD | Body weight daily |
| $c_{i}$ | Total consumption by species (i) |
| $C_{i j}$ | Consumption of species ( $j$ ) by species (i) |
| $C 口_{\text {¢ }}$ | Ratio of available food to required food of prey (j) |
| ${ }^{\text {fi}}$ | Expected fraction of biomass of species (i) consumed |
| F | Coefficient for fishing mortality |
| $\mathrm{FCN}_{i j}$ | Adjusted percentage food composition table |
| g | Equals $g_{t}$ as computed in equation (2) |
| $\mathrm{g}_{0}$ | Species specific mean growth rate |
| ${ }^{\text {g }}$ t | Adjusted monthly growth rate for month $t$ as computed in equation (1) |
| G | Estimated growth in biomass |
| $\mathrm{k}_{\mathrm{g}}$ | Phase lag--prescribes time when $g_{t}$ is maximum |
| M | Mortality coefficient for senescent, spawning, and disease |
| $P_{i j}$ | Input percentage food composition table |
| $r_{\text {g, }}$ | Food requirement for growth--species specific constant |
| $r_{i}$ | Fraction of body weight of food required for daily maintenance (seasonally varying parameter) |

Table 1 (cont'd)
$r_{0} \quad$ Species specific food coefficient for maintenance expressed as percent body weight daily
$\mathrm{R}_{\mathrm{i}} \quad$ Total food requirement for species (i)
$S_{i} \quad$ Starvation of species (i) (the difference between consumption and required food ration)
t Time step (month)
$\mathrm{t}_{\mathrm{d}} \quad$ Length of time step in days (1.e., 30 days)

In order to estimate the expected fraction of biomass lost due to consumption in the current time step ( $\mathrm{f}_{\mathrm{i}, \mathrm{t}}$ ), the fraction of species biomass consumed the previous time step $\left(f_{i, t-1}\right)$ is used as a first approximation, and along with the current months biomass ( $\mathrm{B}_{\mathrm{i}, \mathrm{t}}$ ), is used in estimating the current months consumption. In this way, the fraction consumed at each grid point reflects the expected consumption of existing biomass at each grid point following migration at the beginning of the time step.

In equation (4), the food requirement for growth (parameter a in equation is given as $r_{g, i}$, and is a species-specific constant (see Laevastu and Larkins 1981 for details). Growth of biomass per unit time (G in equation (3)), is given as:

$$
\begin{equation*}
\left[\frac{\left(\left[B_{i} e^{g-M-F}-f_{i} B_{i}\right]+B_{i}\right)}{2} e^{g}\right]-\bar{B} \tag{7}
\end{equation*}
$$

or by substitution of $\bar{B}$ above (equation (6)),

$$
\begin{equation*}
\mathrm{G}=\overline{\mathrm{B}} \mathrm{e}^{\mathrm{g}}-\cdot \overline{\mathrm{B}} \tag{8}
\end{equation*}
$$

Thus growth (per unit time) is computed as the difference between expected mean biomass and its growth over the time step.

These formulations for food requirement for maintenance and food requirement for growth are slight modifications of those given in Laevastu and Larkins (1981) and the reader is referred there for a fuller discussion of this topic.

## Consumption

The consumption of species $j$ by species $i\left(C_{i j}\right)$ is given by:

$$
\begin{equation*}
C_{i j}=R_{i} P_{i j} \tag{9}
\end{equation*}
$$

where $P_{i j}$ (the input food composition table) is the fraction of species $j$ (prey) in the diet of species $i$ (predator), and $R_{i}$ is computed as detailed previously.

Total consumption by species $i$ (predator) is then computed by:

$$
\begin{equation*}
C_{i}=\sum_{j} C_{i j} \tag{10}
\end{equation*}
$$

or substituting equation (9) in equation (10),

$$
c_{i}=R_{i} \sum_{j}^{E P}
$$

Since the sum of the $P_{i j}$ 's would equal 1 in the presence of unlimited food supply, $C_{i}$ would, of course, equal $R_{i}$ and starvation would be zero. The individual fractions $P_{i j}$ can vary in space and time, however, depending on the availability of the prey species $j$ (density-dependent feeding). Thus the basic food composition $\left(P_{i j}\right)$ of each predator species ( $i$ ) must be adjusted at each time step and location. This adjustment will yield the quantitative parameters of partial starvation.

## Feeding Algorithm

In order to reflect differences in feeding with depth, two input food composition tables are provided in DYNUMES; one for shallow ( 5000 m ) and one for deep ( $>500 \mathrm{~m}$ ) water.

The basic theory underlying the food composition tables and their temporal and spatial adjustment, is given in Laevastu and Larkins (1981). The actual computation procedure has changed, however, since that earlier formulation. The current procedure is more computer efficient, optimizes core requirements, and allows for the simultaneous adjustment of the $P_{i j}$ table and the consumption $\left(C_{i}\right)$ and starvation $\left(S_{i}\right)$ values for all fish species. It was one of several methods studied in a comparative analysis of techniques for the simulation of density-dependent feeding and food item substitution and was first tested in the SKEBUB simulation model (Bax 1983). After testing in SKEBUB, the procedure was then adapted to reflect the 3-dimensional spatial resolution of DYNUMES.

Before discussing the details of the current algorithm used in simulating density-dependent feeding and food item substitution, some comments are appropriate regarding one of the alternative approaches tested, linear programming (LP). The LP method seemed particularly relevant to our task since the feeding problem is essentially determining how limited resources (prey) are likely to be shared among various possible users (predators), bearing in mind the constraints (e.g., density-dependent availability of prey) and pressures (e.g., ration requirements) under which the predators operate--a classic example of an allocation program (Shepard $\varepsilon$ Garrod 1982). Unfortunately, the LP solution proved to be more costly, time consuming, and demanding of computer core than the algorithm finally chosen.

The optimal solution for total food consumed from the LP technique differed from the current algorithm's solution only when starvation was present, and then by less than five percent (two or three iterations of the current algorithm removes this difference). The redistribution of percentage food composition in a predator's diet, however, was very extreme using the LP technique. These results agreed with those of other researchers (Shepard \& Garrod 1982, Flain \& Story 1982) who found that LP solutions "inherently lead to solutions which are extreme, sparse, and ruthless" (Shepard $\varepsilon$ Garrod 1982, P. 231). This means that LP solutions always "lie hard up against whatever constraints are placed on the system", utilize only a small fraction of alternative types of predation patterns, and make large and unacceptable changes in the basic pattern of predator food composition. By making wholesale changes in the basic food composition table ( $P_{i j}$ ), the LP technique provided results that were inconsistent with our present
knowledge of predator-prey feeding interactions. Additional constraints were incorporated into the LP model to correct this problem, but the increased computer time and core requiirements made this approach unfeasible. These results and those of the authors cited above are instructive and should be noted when considering LP solutions in other models.

The basic approach developed for solving the feeding problem has been documented in Bax (1983) in discussion of the SKEBUB model. Accordingly, it will only be briefly reviewed here. Specific details of, and modifications to, the procedure for use in the DYNUMES model (in particular, the resolution of the spatial dynamics of migration) are contained in program documentation of the subroutine (Gallagher 1983). The procedure is as follows:

After computing the food requirement for maintenance and growth of each predator species, the biomass of each prey species required for consumption by each predator is determined via the input food composition table ( $\mathrm{P}_{\mathrm{ij}}$ ). This is done for each species and at each grid point, with the total consumption requirement for all predators for each type of prey computed and compared with the amount of each prey biomass designated available. The input food composition table ( $\mathrm{P}_{\mathrm{ij}}$ ) is then adjusted to increase the correspondence between the actual availability of prey items and the predator diet requirements, using a function of the ratio of available food to required food for each prey biomass ( $C C_{j}$ )

$$
\begin{equation*}
\left.F C N_{i j}=P_{i j}\left[\left(1+A e^{-B}\right) /\left(1+A e^{-B(C C}{ }_{j}\right)\right)\right] \tag{11}
\end{equation*}
$$

where $F C N_{i j}$ is the adjusted percentage food composition, and $A$ and $B$ are constants.
This equation is a modification of the logistic equation (Bax 1983), and forces the inflection point to be at $x=y=1$. In this way no adjustment is made in the food composition table (i.e., $F C N_{i j}=P_{i j}$ ) when the food requirement for a
prey type is equal to the amount available for consumption ( $C C_{j}=1$ ). The maximum upward adjustment of the percentage food requirement of any prey item is equal to:

$$
\begin{equation*}
\operatorname{MaxUp}=1+A e^{-B} \tag{12}
\end{equation*}
$$

and the maximum downward adjustment:

$$
\begin{equation*}
\text { MaxDown }=\operatorname{MaxUp} /(1+A) \tag{13}
\end{equation*}
$$

The rate of change is specified by $B$, with a value of 1.5 found to be reasonable in practice. The maximum upward adjustment is currently set at MaxUp=1.5, with A computed from equation (12). Where $A$ is set explicitly, an increase in $A$ results in an increase in the maximum upward and downward adjustments to the percentage diet composition. A fuller discussion of this subject is given in Bax (1983).

After computing the values of food requirement $\left(R_{i}\right)$, actual consumption ( $C_{i}$ ) and starvation $\left(\mathrm{S}_{\mathrm{i}}\right)$, the final step in the simulation is the adjustment of fish biomasses given the adjusted rates of growth and consumption and the designated natural and fishing mortalities. This process is carried out at each grid point and time step in the simulation.

## 4. Automatic $1 / 0$

The DYNUMES model has had several software packages written for it in the past year to facilitate its use. Model runs can be made via an easy to use inputer program that allows the user to prescribe the length of the simulation run (in years) and to choose from a range of output options (Table 2), which can be selected for printing, plotting, or both. The plotting options (a separate software package, Swan 1983) include coastline and bathymetry (Fig. 3), contour plots (Fig.s. 6a and 6b), and cross-sectional plots (Fig. 4), among others. Printed output is provided in a variety of tabular forms and the Bering Sea

Table 2.--List of output options available for DYNUMES*

1. Consumption by birds and mammals
2. Velocities for normal migration
3. Change in biomass due to normal migration
4. Velocities for temperature-induced migrations
5. Change in biomass due to temperature-induced migrations
6. Food requirement
7. Growth in percent initial months biomass
8. Starvation in percent food missing
9. Percent consumption of specific prey items
10. Fishery
11. Consumption by all predators
12. Month-end biomass
13. Change in biomass from previous month
14. Percent of standing stock consumed
15. Total month-end biomass (/1000 tons)
16. Consumption by all predators (/1000 tons)
17. Total biomass change due to normal migration
18. Total fishery

* Sedections 1 through 14 are available by species, month, and grid point. Selections 15 through 18 are available by species and month and are summed over the grid.


Figure 3.--DYNUMES grid showing coastline bathymetry and $50 \mathrm{~m}(\ldots .$.$) and$ $500 \mathrm{~m}(----)$ isobaths.

```
*=LAND VALUE (INTERPOLATED)
UNITS DIVIDED BY 100.
```




Figure 4.--Example of DYNUMES output showing cross-sectional plot with grid insert.
coastline and bathymetry may be superimposed to assist in the interpretation of results (Figs. 5a and 5b). Output can be selected by month, year, and species, and either for each grid point or as the total sum over the grid.

A second software package has been developed to allow easy access to the input data base used in making model runs. The program creates a user defined copy of the input data file that can include changes to any of the input data or species specific parameters. This user-defined file can then be used in place of the 'basic data file" for making model runs. This option allows for the immediate update of data to reflect currently available information and provides the facility for easily adjusting model parameters to study the effects of system perturbations on model output.

These enhancements to the model should assist in making DYNUMES a more usable tool for fishery managers in the future.
5. Comments and Conclusions

DYNUMES simulates multispecies interactions of predation, feeding, and growth, and provides for spatial as well as time-dependent resolution of fish biomass dynamics. Figures 6a and 6b show the summer (September) and winter (February) biomass distributions for pollock, and illustrate the considerable shifts of maximum biomass concentrations over time. The effect of these changes in biomass distribution on feeding can be seen in Figs. 7 and 8 which give the proportional change in percentage food composition of each prey item in the pollock diet for selected months and grid points. These adjustments in percentage food composition reflect shifts in both prey availability and total predator food requirement for the given time step and grid point, and demonstrate DYNUMES' unique ability to simulate the temporal and spatial changes in predator-prey dynamics.
 seasonal migrations during October (from Swan 1983).
 Figure 5b. --Monthly biomass change (in tens of $\mathrm{kg} / \mathrm{km}^{2}$ ) of pollock due to


Figure 6a.--Summer (September) biomass distribution (in tens of $\mathrm{kg} / \mathrm{km}^{2}$ ) for pollock (from Swan 1983).


Figure 6b.--Winter (February) biomass distribution (in tens of $\mathrm{kg} / \mathrm{km}^{2}$ ) for pollock (from Swan 1983).


Figure 7.--Proportional change in percentage food composition from input food composition for pollock for February. Diet prey species are given in Appendix Table l., and grid point locations are shown in Fig. 3. (. refers to the deep ( $>500 \mathrm{~m}$ ) input food composition table.)


Figure 8.--Proportional change in percentage food composition from input food composition for pollock for September. Diet prey species are given in Appendix Table 1., and grid point locations are shown in Fig. 3. (\% refers to the deep ( $>500 \mathrm{~m}$ ) input food composition table.)

By comparing these results to current empirical data, holistic ecosystem models such as DYNUMES can be useful tools in testing our understanding and hypotheses of ecosystem processes. To the degree that these hypotheses can be assumed or demonstrated to be valid, models such as DYNUMES can also be useful in evaluating the effects of system perturbations (i.e., by changing either input data or model parameters of growth, mortality, and fishing) on the abundance and dynamics of fishery resources. (For specific results of the DYNUMES simulation please see Laevastu and Larkins 1981.)

Current work on DYNUMES and its ancillary models PROBUB and SKEBUB, is considerable and varied. It includes the continued updating of data bases and the detailed sensitivity analyses of model dynamics; the extension of migration subroutines for simulating the effects of food scarcity on biomass distribution; a study of methods for the inclusion of age/size structure into the DYNUMES and SKEBUB models; the application of the models to areas other than the Bering Sea (i.e., DYNUMES and SKEBUB to the Gulf of Alaska; SKEBUB to Georges Bank); a study of methods for better simulating the effects of environmental variability on fish biomass dynamics; a study of the effects of potential oil spilis on fishery resources in Bristol Bay; and the inclusion of economic formulations to address the economic and social considerations of management.

Simulation modelling as reflected in the DYNUMES model is an ongoing process that requires both a continued awareness of current research results and an open and ongoing dialogue with scientists and colleagues in a variety of disciplines. Often the results provide us with more questions that answers. But that is the nature of ecosystem study, independent of method. As Dr. Laevastu often reminds us, the dynamic processes of the fishery ecosystem is a subject that our grandchildren will continue to study in the years ahead.

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APPENDIX TABLES

Table l.--Species and ecological groups, including numerical relations within some groups in the Bering Sea (from Laevastu and Larkins 1981).

1-4 Species under special study (by age groups)

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Demersal (L-"largemouth", S-"smallmouth")
    5 - Greenland halibut (turbot), Pacific halibut (L) (3.5:1 in Bering Sea)
    6 - Flathead sole, arrowtooth flounder (L) (4:1 in Bering Sea; 1:2 in
        Gulf of Alaska)
    7 - Yellowfin sole (until Vancouver Island), rock sole, Alaska plaice (S)
        (9:1.5:1 in Bering Sea; 2:8:0.5 in Gulf of Alaska)
    8 - Other flatfishes (S) longhead dab, Dover sole, rex sole (last two in
        Gulf of Alaska
    9 - Cottids and others (e.g., elasmobranchs and other noncommercial
        demersal fish)
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Semi-demersal
10 - Pacific cod, saffron cod (saffron cod, polar cod in northern part of
Bering Sea)
11 - Sablefish (or black cod, single species)
12 - Pollock (single species)
13 - Pacific ocean perch (and other Sebastes and Sebastolobus spp.)
Pelagic
14 - Herring (Pacific herring, single species)
15 - Capelin, other smelts, sand lance, and other noncommercial pelagic fish
16 - Atka mackerel and other greenlings, macrourids
17 - Salmon (5 species, temporary presence)
18 - Squids (mainly gonatids)

## Crustaceans

19 - Crabs (King and Tanner crabs and noncommercial species)
20 - Shrimp (several commercial and noncommercial species)

## Benthos

21 - Predatory benthos (starfishes and other mobile predatory benthos)
22 - Infauna (annelids and other burrowing forms)
23 - Epifauna (bivalves, benthic crustaceans)
Plankton

24 - Phytoplankton
25 - Copepods
26 - Euphausiids (including sagittas)
27 - Ich thyop lankton (temporary)

Table 2.--Marine mammal groups used in DYNUMESI.


Porpoises and Dolphins
$11\left\{\begin{array}{l}\text { Pacific white-sided dolphin } \\ \text { Dall's porpoise }\end{array}\right.$
12 Harbour porpoise
$\left\{\begin{array}{l}\text { Northern right whale dolphin } \\ \text { Risso's dolphin } \\ \text { Common dolphin } \\ \text { Bottlenose dolphin } \\ \text { Pilot whale }\end{array}\right.$
14

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    Sea otter
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1/ Table compiled from Laevastu and Larkins, 1981.
2/ The groups "sperm whales" and "toothed whales" signify groups by feeding habits.
3/ Humpback whale, although a baleen whale, has been included in the "toothed whale" group because of its rather extensive fish diet.

Table 3.--Marine bird groups used in DYNUMES (from Livingston, 1980).

| Group | Group members |
| :--- | :--- |
| Gulls | Glaucous gull, glaucous winged gull, black-legged <br> kittiwake, red-legged kittiwake, arctic and <br> aleutian terns. |
| Petrels | Fork-tailed and Leach's storm petrels. |
| Other alcids | Ancient murrelet, Cassin's auklet, rhinoceros <br> auklet, tufted puffin, horned puffin, parakeet <br> auklet, crested auklet, least auklet, whiskered <br> auklet, pigeon guillemot. |
| Murres | Common and thick-billed murres. |
| Northern fulmar | Double-crested, pelagic, red-faced cormorants. |
| Cormorants | Sooty and short-tailed shearwaters, |

Table 4.--Maximum equilibrium biomasses of species and ecological groups in the eastern Bering Sea (in 1,000 tonnes). Estimated minimum equilibrium biomasses and mean exploitable biomasses are given for comparison (from Laevastu and Larkins, 1981).

| Species/ecological group designation | Maximum equillibrium biomass | ```Estimated minimum equilibrium biomass``` | Mean exploitable biomass |
| :---: | :---: | :---: | :---: |
| Halibut | 585 | 400 | 220 |
| Flathead sole | 875 | 650 | 380 |
| Yellowfin sole | 1,660 | 1,100 | 510 |
| Other flatfish | 1,160 | 850 | 245 |
| Cottids | 4,438 | 4,000 | - |
| Cod | 1,468 | 1,000 | 745 |
| Sablefish | 183 | 120 | 51 |
| Pollock | 15,165 | 8,000 | 6,450 |
| Rockfish | 1,825 | 1,000 | 485 |
| Herring | 2,327 | 1,500 |  |
| Capelin | 5,149 | 3,500 | $(1,000)=$ |
| Mackerel | 1,438 | 1,100 | 520 |
| Sa Imon | (73) | (50) |  |
| Squid | 2,310 | 1,200 | (500) $\frac{21}{21}$ |
| Crab | 1,225 | 800 | (300) $\frac{21}{2 /}$ |
| Shrimp | 1,792 | 900 | (600) ${ }^{-1}$ |
| Predatory benthos | 818 | 700 | - |
| Infauna | 24,219 | 20,000 | - |
| Epifauna | 20,9471/ | 15,000 | - |
| Zooplankton | 58,430- | 35,000 | - |

1/ $500 \mathrm{mg} / \mathrm{m}^{3} ; 100 \mathrm{~m}$ depth.
2/ Includes species which are not exploited at present.

