THE CONTROL OF PELAGIC FISHERY RESOURCES IN THE EASTERN BERING SEA
(A numerical ecosystem study of factors affecting fluctuations of pelagic fishery resources with emphasis on herring)

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T. Laevastu and F. Favorite

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(A numerical ecosystem study of factors affecting
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## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>1</td>
</tr>
<tr>
<td>1. Introduction</td>
<td>1</td>
</tr>
<tr>
<td>1.1 Purpose of the study</td>
<td>1</td>
</tr>
<tr>
<td>1.2 Methods</td>
<td>1</td>
</tr>
<tr>
<td>2. Abundance and distribution of pelagic fish in the eastern Bering Sea</td>
<td>5</td>
</tr>
<tr>
<td>2.1 Herring</td>
<td>7</td>
</tr>
<tr>
<td>2.1.1 Model studies</td>
<td>7</td>
</tr>
<tr>
<td>2.1.2 Present status</td>
<td>12</td>
</tr>
<tr>
<td>2.2 Other pelagic fish</td>
<td>13</td>
</tr>
<tr>
<td>3. Growth and consumption, including mortalities</td>
<td>15</td>
</tr>
<tr>
<td>3.1 Growth and factors affecting it</td>
<td>15</td>
</tr>
<tr>
<td>3.2 Fishing mortality and mortality from diseases and old age</td>
<td>18</td>
</tr>
<tr>
<td>3.3 Ecosystem internal consumption</td>
<td>19</td>
</tr>
<tr>
<td>3.3.1 Consumption by mammals and birds</td>
<td>22</td>
</tr>
<tr>
<td>3.3.2 Consumption by pollock and squids</td>
<td>25</td>
</tr>
<tr>
<td>4. Source and sink areas</td>
<td>31</td>
</tr>
<tr>
<td>5. Effects of environmental anomalies on pelagic resources</td>
<td>40</td>
</tr>
<tr>
<td>6. Effects of fishery</td>
<td>45</td>
</tr>
<tr>
<td>7. Long-term changes of abundance and distribution</td>
<td>47</td>
</tr>
</tbody>
</table>
8. Some additional factors determining biomass fluctuations of herring

8.1 Some stock-recruitment relations and threshold biomass...

8.2 "Herring equivalences"...

9. Summary

10. References
LIST OF FIGURES

Figure 1.--DYNUMES III grid on Mercator projection.

Figure 2.--Schematic outline of DYNUMES III.

Figure 3.--Distribution of herring in tons/km$^2$ in February (equilibrium biomass (EB), 2.75 million tons).

Figure 4.--Distribution of herring in tons/km$^2$ in August (EB, 2.75 million tons).

Figure 5.--Distribution of herring in tons/km$^2$ in December (EB, 2.75 million tons).

Figure 6.--Distribution of herring in tons/km$^2$ in February, fourth year, (biomass 0.94 million tons) (example of the distribution of a decreasing biomass).

Figure 7.--Monthly changes in equilibrium biomass of herring in the eastern Bering Sea over two years and monthly computed herring catches during the same period.

Figure 8.--Distribution of other pelagic fish in tons/km$^2$ in February (EB, 4.3 million tons).

Figure 9.--Distribution of other pelagic fish in tons/km$^2$ in August (EB, 4.3 million tons).

Figure 10.--Distribution of other pelagic fish in tons/km$^2$ in December (EB, 4.3 million tons).

Figure 11.--Weight and length of Pacific herring at different ages.

Figure 12.--Growth of biomass (weight) of Pacific herring at different ages, as percent per year.

Figure 13.--Average distribution of biomass and numbers of Pacific herring within different year classes (as percent of total biomass) (from Laevastu and Favorite 1977a).
Figure 14.--Distribution of "consumption" (grazing, mortality, and fishery) with age of Pacific herring (as percent of mean standing crop of each year class).

Figure 15.--Consumption of herring in tons/km$^2$ in February (EB, 2.75 million tons).

Figure 16.--Consumption of herring in tons/km$^2$ in August (EB, 2.75 million tons).

Figure 17.--Monthly consumption of herring in the eastern Bering Sea (total consumption, consumption by toothed whales and by pinnipeds).

Figure 18.--Monthly biomasses and consumptions of herring with normal mammal consumption and with half of normal mammal consumption in the eastern Bering Sea over two years.

Figure 19.--Herring sources and sinks in tons/km$^2$ in February; half of normal mammal consumption.

Figure 20.--Herring sources and sinks in tons/km$^2$ in August; half of normal mammal consumption.

Figure 21.--Herring distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.

Figure 22.--Other pelagic fish distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.

Figure 23.--Monthly biomasses and consumptions of herring with normal consumption and with half of normal consumption by squids in eastern Bering Sea over two years.
Figure 24.--Herring sources and sinks in tons/km$^2$ in February; half of normal consumption by squids.

Figure 25.--Herring sources and sinks in tons/km$^2$ in August; half of normal consumption by squids.

Figure 26.--Herring distribution in tons/km$^2$ in December, second year; half of normal consumption by squids.

Figure 27.--Other pelagic fish distribution in tons/km$^2$ in December, second year; half of normal consumption by squids.

Figure 28.--Herring sources and sinks in tons/km$^2$, January.

Figure 29.--Herring sources and sinks in tons/km$^2$, February.

Figure 30.--Herring sources and sinks in tons/km$^2$, March.

Figure 31.--Herring sources and sinks in tons/km$^2$, April.

Figure 32.--Herring sources and sinks in tons/km$^2$, May.

Figure 33.--Herring sources and sinks in tons/km$^2$, June.

Figure 34.--Herring sources and sinks in tons/km$^2$, July.

Figure 35.--Herring sources and sinks in tons/km$^2$, August.

Figure 36.--Herring sources and sinks in tons/km$^2$, September.

Figure 37.--Herring sources and sinks in tons/km$^2$, October.

Figure 38.--Herring sources and sinks in tons/km$^2$, November.

Figure 39.--Herring sources and sinks in tons/km$^2$, December.

Figure 40.--Other pelagic fish sources and sinks in tons/km$^2$, February.

Figure 41.--Other pelagic fish sources and sinks in tons/km$^2$, August.

Figure 42.--Monthly biomasses of herring with normal temperature and with a 1.5°C wintertime positive temperature anomaly in the eastern Bering Sea over two years.
Figure 43.--Herring sources and sinks in tons/km$^2$ in January (1.5°C positive anomaly).

Figure 44.--Herring sources and sinks in tons/km$^2$ in February (1.5°C positive anomaly).

Figure 45.--Herring sources and sinks in tons/km$^2$ in March (1.5°C positive anomaly).

Figure 46.--Distribution of herring in tons/km$^2$ in December, second year; wintertime 1.5°C positive anomaly.

Figure 47.--Other pelagic fish sources and sinks in tons/km$^2$ in February (1.5°C positive anomaly).

Figure 48.--Distribution of other pelagic fish in tons/km$^2$ in December, second year; wintertime 1.5°C positive anomaly.

Figure 49.--Monthly biomasses of herring with 47x10$^3$ and 75x10$^3$ tons annual catch in the eastern Bering Sea over two years.

Figure 50.--Herring distribution in tons/km$^2$ in December, (75x10$^3$ tons catch).

Figure 51.--Monthly herring biomasses in the eastern Bering Sea over five years (initial biomasses in million tons: A=2.75; B=1.59; C=0.94; D=0.45).

Figure 52.--Herring sources and sinks in tons/km$^2$ in February; fourth year; initial biomass 1.59 million tons.

Figure 53.--Distribution of herring in tons/km$^2$ in February, fourth year; initial biomass 1.59 million tons.

Figure 54.--Herring sources and sinks in tons/km$^2$ in February, fourth year; initial biomass 0.94 million tons.

Figure 55.--Percentage of mean zooplankton standing stock consumed in February.

Figure 56.--Percentage of mean zooplankton standing stock consumed in August.
LIST OF TABLES

Table 1.--Annual consumption of herring and other pelagic fish in the eastern Bering Sea (in 10^3 tons).

Table 2.--Estimated number of whales and porpoises in the eastern Bering Sea.

Table 3.--"Herring equivalences" in the eastern Bering Sea (factors and processes, each of which causes a 100x10^3 tons of herring biomass change per year (averaged over two year effects) in the eastern Bering Sea).
ABSTRACT

A Dynamic Numerical Marine Ecosystem model (DYNUMES III) which addresses interactions of major ecosystem components was used to study the dynamics of pelagic fish in the eastern Bering Sea, with emphasis on Pacific herring (Clupea harengus pallasi), and to determine quantitatively factors affecting relative abundances of stocks. The equilibrium biomass of herring in the eastern Bering Sea is 2.7 million tons; and the lower threshold value is 0.5 million tons (with density dependent grazing on herring) below which recovery would be very slow indeed. The equilibrium biomass of other pelagic fish is 4.3 million tons.

The herring biomass has long- and short-term fluctuations which are induced and affected by several factors, such as environmental anomalies and interspecies interactions. There is, for example, an inverse relationship between walleye pollock (Theragra chalcogramma) and herring biomasses due to older pollock grazing on herring. Although the present state of the herring biomass in the eastern Bering Sea cannot be determined with greater accuracy due to the lack of proper data, it can be assumed to have been at a low level a few years ago due to the high abundance of pollock and is expected to be on the increase in recent years due to the decrease in the abundance of older pollock. The biomass turnover rate for herring is 0.5 and for other pelagic fish 0.95.

Herring abundance in the eastern Bering Sea is primarily affected by marine mammals which annually may consume roughly ten times more than the commercial catch, sperm whales (Physeter macrocephalus) being the largest consumers. Herring abundance is also influenced by consumption by squids and other fish and, especially, by water temperature anomalies during winter and spring. Effects of the fluctuating offshore herring fishery has only
a moderate effect on the equilibrium biomass of herring; the hierarchy of the influences on the herring biomass is given in this report in terms of defined "herring equivalences."

Pelagic fish constitute an important ecosystem internal food resource for other marine ecological groups in the eastern Bering Sea. The ecosystem internal consumption (and its possible year-to-year fluctuations) far exceeds the effects of the fishery and its variations on the state of the biomass of pelagic fish. Adult squids are feeding mainly on pelagic fish and exercise considerable influence on the magnitude and fluctuations of the pelagic fish biomass. Unfortunately, the squid biomass itself can only be estimated with a Bulk Biomass model where emphasis is on the mean quantitative food composition of all ecosystem components.

The year class strength in most pelagic species is largely determined by the ecosystem internal consumption in larval and especially in postlarval stages (and during the first two years of the lifespan), rather than by the number of spawners. Model results show that an increasing population expands in its spatial distribution and a declining population shrinks towards the center of its main abundance, the fringe populations disappearing first.

The monthly source (growth exceeds consumption) and sink (consumption exceeds growth) areas for pelagic fish were found to be useful criteria in research and management problems. Temperature anomalies during the winter were found to affect considerably the sources and sinks of herring and other pelagic fish via physiological effects (food economy and growth). The growth rate of the biomass of a given species is a function of the distribution of its biomass with age and is affected especially by lower temperatures during the winter season. An 0.8°C temperature anomaly was found equivalent
to about 11.3 thousand tons change of annual catch. As the effect of a small temperature anomaly is relatively large in terms of possible increase of catch quotas, and as the anomaly would affect other commercial species as well, it seems to be imperative to monitor temperature anomalies during at least the winter and spring seasons in the eastern Bering Sea for optimum management of the fishery there.
1. INTRODUCTION

1.1 Purpose of the study

The main purpose of this study was to determine quantitatively those factors which control the biomasses of pelagic fish, especially Pacific herring (*Clupea harengus pallasi*), in the eastern Bering Sea and which affect fluctuations in their abundance. It was necessary to determine concurrently the equilibrium biomasses of these fish as well as the possible "threshold biomasses," and to consider long-term fluctuations. Obviously the study of the effects of variable year-to-year fishery catches constituted an initial central theme of the study, and it became apparent that an estimation of the effects of interspecies interactions was of particular importance in achieving the objectives of the study.

During the course of this study, it was discovered that the environmental anomalies could have profound effects on the pelagic resources in the higher latitudes, and the study was expanded to include the quantification of these effects. Further, the concept of defining of source-sink areas and their utility in evaluating the distribution and abundance of any given species was developed. It should be stated at the outset that walleye pollock (*Theragra chalcogramma*), the most abundant species in the area, is considered a semi-demersal fish.

1.2 Methods

This study was conducted with the Dynamic Numerical Marine Ecosystem model (DYNAMES III), which utilizes a wide variety of knowledge on interactions in the marine ecosystem as well as extensive empirical data from a great variety of sources. A more detailed description of the model is available in another report (Laevastu and Favorite 1977b)--therefore, only a general summary description of the model is presented.
The DYNUMES III model is four-dimensional (three space and one time dimension). The third space dimension, depth, is used in implicit manner in most cases, (e.g. bottom and/or surface temperature and/or a mean of these) depending on whether pelagic, demersal, or semi-demersal species are under consideration. The grid is an equal area grid (grid size 95.25 km) which is superimposed on a Mercator projection in Figure 1.

The computation of grazing and other interspecies and environment interactions requires that all predators are quantitatively included in the model, either as species or lumped into ecological groups. Thus, the DYNUMES III model is designed to include all essential biological elements in the eastern Bering Sea; most of the organisms being grouped into ecological groups (e.g. flatfish, gadids, etc.). However, species under special study can be presented separately and even by size and/or age groups. In the present study, Pacific herring is considered separately from a grouping of "other pelagic fish," which consists mainly of capelin (Mallotus villosus), other smelts, and Pacific sand lance (Ammodytes hexapterus).

The initial (e.g. January) distribution of a given species is prescribed, using all available sources of data. The size of the initial equilibrium biomass of any given species (or ecological group) is determined with another model developed at the Northwest and Alaska Fisheries Center, a Bulk Biomass Model (BBM) (Laevastu and Favorite 1976a). The biomass is moved in weekly time steps as known migration patterns dictate and biomass increases and decreases are accounted for. It is generally known that metabolic rate decreases with temperature (re. Krogh's metabolic curve). Therefore, in the study of the effects of temperature anomalies on the growth of pelagic fish the growth coefficients were changed (decreased linearly) when monthly temperature was below 4°C, with cessation of growth below 0°C. Below zero temperatures also
Figure 1.--DYNUMES III grid on Mercator projection.
accelerate migrations in the model out of the cold areas and mortality is also slightly increased in these cold areas. The mortality coefficient in the model refers to mortality from old age and diseases, and is relatively small (0.3 to 2% per month, depending on individual species and their life span). The larval stages (younger than 6 months) are not considered within the species groups but are included in zooplankton where they are grazed (consumed) at the same rate as zooplankton. The recruitment is assumed to be proportional to biomass and does not enter directly into essential computations. Therefore, the year class variations in this model are determined by grazing in zero, one, and, in some species, the second year of life, if mean biomass does not increase or decrease from one year to another.

Grazing (synonymous to consumption in this report) is computed in monthly time steps at each grid point for all groups of species. Minimum food requirement coefficients for maintenance and growth are prescribed, but they are modified at low temperatures and at grid points and time steps when food availability is limited. Average composition of food is prescribed for each species or species group and used as food selection (preference) criteria (the composition of food in the DYNUMES model can vary at each grid point and time step) depending on the availability of food items in a given location and month. If computations indicate that a given food item is not present in the required abundance, a partial or full substitution is automatically made according to preference criteria. If there is a lack of food, starvation is assumed to occur, altering not only the growth coefficient but, if severe, also the mortality coefficient. The fishing intensity coefficients are prescribed in space and time (according to known fisheries areas and seasons) and tuned to present and/or past catch statistics.
The abundance and distribution of mammals is prescribed in monthly time steps. Conservative abundance numbers, as well as conservative food requirements, were used in the model runs presented here (for example, recent reports give 1.2 million northern fur seals (Eumetopias jubatus) in the Bering Sea—our model used only a maximum of 0.85 million; food uptake of these seals is reported to be between 5 and 8% body weight daily—our model uses 5%).

A schematic outline of DYNUMES III model is given in Figure 2. Although most of the components of the marine ecosystem are included in the model, this report deals mainly with Pacific herring and with the ecological group termed "other pelagic fish," which comprises mainly capelin and sand lance.

2. ABUNDANCE AND DISTRIBUTION OF PELAGIC FISH IN THE EASTERN BERING SEA

The equilibrium (or minimum sustainable) biomass (EB) of a given species or group of species is defined as the biomass in a complete ecosystem in a defined area which does not decrease nor increase on an annual basis; thus, the annual growth is in equilibrium with removal. Equilibrium biomasses (EB) were determined with the Bulk Biomass Model (BBM) and adjusted (fine tuned) in DYNUMES III. This equilibrium biomass is dependent upon quantative consumption by all species in the ecosystem, distributions of predators and prey, and growth factors. It is postulated by Beyer (1976) that there might be a lower threshold value for any given biomass, below which the biomass does not recover or recovers very slowly. The DYNUMES model permits the study of the threshold biomass, which seems to exist in most species, even with density dependent grazing. It should also be noted that the biomass of individual species is affected by a pronounced deviation of year class strengths from a mean or normal year class. The effects of the year class
Removal from system

- MAMMALS, BIRDS

- FISH I
  - Growth (environm., food affected)
  - Consumption (food requirements aff.)
  - Mortality (environ., food, age aff.)
  - Migrations (environ., food, age aff.)

- FISH II, etc.

- BENTHOS ("fish food" benthos)
  - Growth, consumption
  - Mortality

- ZOOPLANKTON (simulated standing crop)
  - Consumption

- PHYTOPLANKTON
  - Consumption

Removal from system, nutrient regeneration

- Quantitative distribution in space and time
- By ecological groups, species, and/or year classes
- Affected by distribution, environment, and interspecies interaction
- Variable in space and time, environment, and biomass distribution dependent

- Affected by metabolic processes

Figure 2.--Schematic outline of DYNUMES III.
variations on the herring biomass will be studied using an extended DYNUMES model having added stock-recruitment subroutines. Results will be included in a subsequent report.

Thus, the initial model inputs related to distributions and interactions of species have been prescribed from available data and knowledge. Subsequent iterations from initial distributions indicate that there is considerable adjustment within the first-year computations.

2.1 Herring

The distribution of herring in the eastern Bering Sea has been studied rather superficially in the past. The offshore distribution of herring is best described by Shaboneev (1965). Additional scattered data are available in numerous reports for Japanese fisheries investigations. The distribution of coastal spawning has recently been surveyed annually by the Alaska Department of Fish and Game. All this available information was used to digitize January distribution of herring and its seasonal migrations.

2.1.1 Model studies

Examples of some monthly quantitative distributions of herring as determined by using initial inputs and DYNUMES III are given in Figures 3 to 5. The main concentrations of herring overwinter are found in and northward of the Pribilof Islands area and along the continental slope southwest of this area (simulated distribution in Figure 3). Some undoubtedly remain under the ice; the Norton Sound stock is assumed to overwinter in the deeper areas of this Sound and in brackish water. It is known from empirical studies that about one-third of the biomass starts spawning migrations toward the Alaskan coast in late winter—where spawning occurs from the end of April along the northern
Figure 3. -- Distribution of herring in tons/km² in February (equilibrium biomass (EB), 2.75 million tons).

Figure 4. -- Distribution of herring in tons/km² in August (EB, 2.75 million tons).
coast of the Alaskan Peninsula during colder years and in May along the west Alaska coast during normal years (I.M. Warner, Alaska Dept. of Fish and Game, Kodiak, pers. comm.). Spawning in Norton Sound occurs in June and further northward, in July. After spawning, the herring is assumed to disperse for feeding over the continental shelf (Figure 4). The migrations to overwintering grounds start at the end of October (Shaboneev, 1965), and the winter distribution pattern is established by December (Figure 5).

Environmental anomalies and interspecies interactions change the distribution patterns somewhat, and these factors are discussed later in the report. Earlier numerical studies (Laevastu and Favorite 1976b), as well as this study shows that an increasing population expands its area of distribution and a decreasing population shrinks towards the center of its main abundance (compare Figures 3 and 6).

The model estimates of equilibrium biomass of herring in the eastern Bering Sea is 2.75 million tons; the magnitude of annual fluctuation of this biomass is about 0.3 million tons (Figure 7). There are two fishing periods on herring (Figure 7) during the winter months on the overwintering herring (EB model input about $8 \times 10^3$ tons per month) and during the spring and early summer on spawning herring (less than $2 \times 10^3$ tons per month).

Shaboneev (1965) found the biomass of wintering herring north and northwest of the Pribiloffs to be 2.16 million tons, which compares favorably with our model results. For comparison, the biomass of the herring in the North Sea has been estimated by Andersen and Ursin (1977) to be 1.8 million tons at the end of 1959.
Figure 5.--Distribution of herring in tons/km$^2$ in December (EB, 2.75 million tons).

Figure 6.--Distribution of herring in tons/km$^2$ in February, fourth year, (biomass C.94 million tons) (example of the distribution of a decreasing biomass).
Figure 7.---Monthly changes in equilibrium biomass of herring in the eastern Bering Sea over two years and monthly computed herring catches during the same period.

Figure 8.---Distribution of other pelagic fish in tons/km² in February (EB, 4.3 million tons).
The DYNAMES model shows that the threshold biomass of herring in the eastern Bering Sea is 0.5 million tons, with density dependent feeding of all ecosystem components (see further Chapter 7). If the biomass would fall below this value, the recovery would be questionable and/or slow even with some successive good year classes.

2.1.2 Present status

The exact state of the existing herring biomass in the eastern Bering Sea cannot be estimated with any great accuracy due to the limited field investigations and scarcity of data between the end of the 1960's and the present. The herring catches in the western Bering Sea declined rapidly in the late 1960's and a bilateral Japanese-USSR agreement closed the fishery in 1970 (Wespestad 1977). The Japanese and USSR catch of herring in the central eastern Bering Sea declined in the early 1970's. Although some of this decline is undoubtedly due to declining herring biomass, three other factors have contributed to it: first, the largest catches in the late 1960's were made from an essentially virgin (previously little fished) population, which had also two strong year classes; second, the main fishery in the eastern Bering Sea switched to the very abundant pollock; and, third, there is an inverse relation between pollock and herring biomasses (Laevastu and Favorite 1976b). It is hoped that when the 1975 and subsequent surveys of spawning herring by the Alaska Department of Fish and Game (P. Jackson, Alaska Department of Fish and Game, Kodiak, pers. comm.) have been quantified, considerably more information on the present state of herring stocks in the eastern Bering Sea will be forthcoming.
2.2 Other pelagic fish

Little is known about other pelagic fish (pollock and sablefish (*Anoplopoma fimbria*), etc. are considered "semi-demersal" fish) in the eastern Bering Sea as none of the species has been subject to exploitation or investigations in the past. However, it is known from stomach analyses of mammals and fish that capelin and sand lance constitute an important food source (forage fish) in the Bering Sea ecosystem. Furthermore, large capelin schools have been observed to spawn all along the Alaskan coast in shallow water about the same time as the herring spawning but with a preference for a sandy substrate.

The equilibrium biomass of the eastern Bering Sea ecosystem requires, according to DYNUMES III, a biomass of 4.3 million tons of other pelagic fish. Furthermore, the equilibrium ecosystem dictates also to a large degree the distribution of these fish. The distributions during February, August, and December (Figures 8 to 10) indicate an interesting feature, the bipartition of the center of abundance in all months—one near the continental slope and another off Bristol Bay. Whether these distributions indicate the main distribution centers of the two major species, capelin (near the slope) and sand lance (over the south central shelf), cannot be determined at this stage.

It should also be noted that, although the biomasses of different species and ecological groups vary from year to year due to several influencing factors, the total biomass of pelagic and semidemersal species (e.g. pollock) changes little. Similar wide fluctuations of an individual species, but quasi-constancy of the biomass of all species including those from slightly different ecological groups, have been observed also in the North Sea (Andersen and Ursin 1977).
Figure 9.--Distribution of other pelagic fish in tons/km$^2$
in August (EB, 4.3 million tons).

Figure 10.--Distribution of other pelagic fish in tons/km$^2$
in December (EB, 4.3 million tons).
3. GROWTH AND CONSUMPTION, INCLUDING MORTALITIES

3.1 Growth and factors affecting it

The growth parameter is one of the important parameters in marine ecosystem dynamics. In this chapter a few characteristics of the herring biomass (growth, consumption, and mortalities) are summarized; similar considerations are valid for other pelagic fish and other components of the marine ecosystem.

The average age-weight curve (Figure 11) for eastern Bering Sea herring and growth rates (Figure 12) were computed using available data in the literature (e.g. Rumyantsev and Darda 1970; Takahashi and Konda 1974). Because growth rates decrease with age, it is necessary to know the distribution of the biomass of a given species, or group of species, over its life span. Individual growth coefficients are prescribed for each year class and the mean distribution of herring biomass with age is given in Figure 13 (Laevastu and Favorite 1977a). The basic DYNUMES III model computations use a growth coefficient which is very close to the growth rate in percent per month (used in the model: herring 7.8% and other pelagic fish 9.0%).

The growth of most species in higher latitudes is seasonal and can be assumed to be affected by temperature (e.g. Krogh's metabolic curve). This slowing of growth during the cold season is also depicted in the scales and otoliths of most high latitude pelagic species. Thus, the growth coefficient in our model is reduced linearly when temperature of the environment at a given location and time drops below 4°C, with cessation of growth occurring at 0°C. Additional empirical data are required in this subject. Growth is also affected by the availability of food, and this effect is also included in DYNUMES III (see Chapter 1.2).
Figure 11. Weight and length of Pacific herring at different ages.

Figure 12. Growth of biomass (weight) of Pacific herring at different ages, as percent per year.
Figure 13. Distribution of biomass and numbers of Pacific herring within different year classes (% of total).

Figure 14. Distribution of "consumption" (grazing, mortality, and fishery) with age of Pacific herring, as percent of mean standing crop of each year class.
3.2 Fishing mortality and mortality from old age and diseases

Fishing mortality is prescribed in the model at monthly intervals as fishing effort and is variable in space and time (winter and spring fishery near the continental slope and the Pribilof Islands, summer fishery near the coast). The computed catches are also a function of the availability of the biomass at the prescribed fishing locations. The equilibrium biomass (EB) model computations yield a value of $47 \times 10^3$ tons of herring annually, which is close to the 1972-73 catch of $42.2 \times 10^3$ tons (Wespestad 1977). Further effects of the changing fishing effort on the herring biomass are described in Chapter 6.

Mortality from old age is affected by the life span of the species and the fishery (i.e. the fishery removing part of the older fish which otherwise would have died from old age). Considering these factors, rough estimates of the mortality coefficients were made (herring 0.3% per month, other pelagic fish 0.5% per month). These are small and any anticipated error in these estimates would necessitate only minor adjustments of the growth coefficients. No quantitative information is available on disease mortality and consequently this mortality is assumed to be included in the above mortality coefficient.

The mortality coefficient in the model is increased in unfavorable conditions, such as low temperatures and low availability of food (starvation). It should also be increased during and after spawning (spawning mortality), as done in the Andersen and Ursin model. This will be done in future versions of DYNUMES, when "stock-recruitment" subroutines are added.
3.3 Ecosystem internal consumption

The ecosystem internal consumption comprises the largest part of the biomass removal. Although it is conventionally included as "natural mortality" in population dynamics considerations, in the DYNUMES model the ecosystem internal consumption is computed directly in considerable detail. Values depend on the availability of all prey or forage, as well as all predators, at any given location and time period (i.e. grid point and time step). Food type preferred and consumed is a function of both predator and prey size (Ursin 1972). The smaller (younger) fish, which grow faster (in weight) than older fish, are also consumed at a higher rate. This might lead to an assumption that due to high consumption rate at young ages, the year class strength in most species may be largely controlled by consumption (grazing) at these young stages rather than by spawning success. Additional studies in this subject will be conducted in the future.

Fish eating mammals consume mainly medium and large size fish and thus compete directly with man (fishery) (see Figure 14). Ecosystem internal consumption determines largely the biomass turnover rate (i.e. annual consumption divided by annual monthly mean biomass) and, in the eastern Bering Sea, these turnover rates for equilibrium biomasses are: herring 0.50 and other pelagic fish 0.95. Variability in monthly consumption of herring is reflected in February and August values (Figs. 15 and 16), and summarized in Figure 17, in which high consumption by mammals during summer is readily apparent.
Figure 15.--Consumption of herring in tons/km$^2$ in February (EB, 2.75 million tons).

Figure 16.--Consumption of herring in tons/km$^2$ in August (EB, 2.75 million tons).
Figure 17.—Monthly consumption of herring in the eastern Bering Sea (total consumption, consumption by toothed whales and by pinnipeds).

Figure 18.—Monthly biomasses and consumptions of herring with normal mammal consumption and with half of normal consumption in the eastern Bering Sea over two years.
3.3.1 Consumption by mammals and birds

A summary of the consumption of herring and other pelagic fish in the eastern Bering Sea (Table 1) reveals a startling result, the consumption of herring by mammals is ten times higher than the commercial catch. The main consumers of pelagic fish (and squids) in the eastern Bering Sea are "toothed whales" (mainly sperm whales (*Physeter macrocephalus*)), followed by pinnipeds. These results are based on conservative estimates of mammals in the eastern Bering Sea used in the model runs (Table 2). This suggests that successful management of fishery resources in the eastern Bering Sea requires concurrent management of the mammal herds.

In order to study the quantitative effects of grazing by mammals on herring, the model was run with a 50% reduction in mammal consumption (Figure 18). Interpolations of the results indicate that a reduction of mammals by 22% would result in an increase in the herring biomass of 100,000 tons.

The effects of decreased mammal consumption on the dynamics of pelagic fish can be studied by comparing the quantitative monthly source and sink areas (see Chapter 4). The effects of changing mammal consumption during winter are relatively small (compare Figures 19 and 29), but these differences are considerable during summer (compare Figures 20 and 35). The effects of reduced mammal consumption are also noticeable when comparing pelagic fish distributions in December, second year computations (Figures 21 and 22 compared with Figures 5 and 10, respectively).

The consumption of herring and other pelagic fish by birds, less than 30% of the 1972-73 herring catch, is rather insignificant (Table 1).
Table 1.--Annual consumption of herring and other pelagic fish in the eastern Bering Sea (in $10^3$ tons).

<table>
<thead>
<tr>
<th>Consumers</th>
<th>Herring</th>
<th>Other pelagic fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammals &amp; birds (total)</td>
<td>423</td>
<td>607</td>
</tr>
<tr>
<td>Pinnipeds (total)</td>
<td>158</td>
<td>130</td>
</tr>
<tr>
<td>Fur seals</td>
<td>26</td>
<td>9</td>
</tr>
<tr>
<td>Sea lions</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>Bearded seals</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Harbor seals</td>
<td>65</td>
<td>30</td>
</tr>
<tr>
<td>Ringed/ribbon seals</td>
<td>24</td>
<td>55</td>
</tr>
<tr>
<td>Toothed whales</td>
<td>232</td>
<td>409</td>
</tr>
<tr>
<td>Baleen whales</td>
<td>21</td>
<td>28</td>
</tr>
<tr>
<td>Birds</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>Fish</td>
<td>739</td>
<td>3,521</td>
</tr>
<tr>
<td>Total consumption</td>
<td>1,362</td>
<td>4,128</td>
</tr>
<tr>
<td>Catch (1973)</td>
<td>42.2</td>
<td>?</td>
</tr>
<tr>
<td>Mean turnover rate</td>
<td>0.50</td>
<td>0.95</td>
</tr>
<tr>
<td>Percent of catch from mammal consumption</td>
<td>10</td>
<td>?</td>
</tr>
</tbody>
</table>
Table 2.—Estimated number of whales and porpoises in the eastern Bering Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average weight (tons)</th>
<th>Estimated number</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Summer</td>
<td>Winter</td>
</tr>
<tr>
<td><strong>Baleen whales</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin</td>
<td>50</td>
<td>5,000</td>
<td>-</td>
</tr>
<tr>
<td>Gray</td>
<td>40</td>
<td>5,000</td>
<td>-</td>
</tr>
<tr>
<td>Mink</td>
<td>9</td>
<td>2,000</td>
<td>-</td>
</tr>
<tr>
<td>Bowhead</td>
<td>10</td>
<td>2,000</td>
<td>2,000</td>
</tr>
<tr>
<td><strong>Toothed whales</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sperm</td>
<td>40</td>
<td>20,000</td>
<td>-</td>
</tr>
<tr>
<td>Humpback</td>
<td>10</td>
<td>300</td>
<td>-</td>
</tr>
<tr>
<td>Giant bottlenose</td>
<td>10</td>
<td>2,000</td>
<td>-</td>
</tr>
<tr>
<td>Killer</td>
<td>12</td>
<td>800</td>
<td>800</td>
</tr>
<tr>
<td>Beluga</td>
<td>3</td>
<td>2,000</td>
<td>2,000</td>
</tr>
<tr>
<td>Porpoises</td>
<td>0.1</td>
<td>5,000</td>
<td>5,000</td>
</tr>
</tbody>
</table>
3.3.2 Consumption by pollock and squids

Older pollock (e.g. >30 cm in length) consume herring as food. Because pollock is presently the most abundant species in the eastern Bering Sea, a special numerical simulation study was made with a simplified DYNAMES model to investigate quantitatively the pollock-herring biomass relations (Laevastu and Favorite 1976b). The results of this study indicated an inverse relation between pollock and herring biomasses. Furthermore, it was found that the pollock biomass has a long-term fluctuation (~12 years), caused mainly by cannibalism interactions, that also affects the herring biomass fluctuations.

Adult squids feed mainly on pelagic fish (Akimushkin 1963). Although the actual magnitude of squid resources in the Bering Sea is at present unknown, the EB biomass of squids has been computed via food composition considerations, and a numerical study was made with the DYNAMES model to investigate quantitatively the effects of a reduced squid biomass (reduction 50% from "equilibrium biomass" of squids) on pelagic fish biomasses. Interpolation of data (Figure 23) indicates that a 100,000 ton increase in the herring biomass could be achieved by reducing the "equilibrium biomass" of squids by 26%. The effects of reduced squid biomass on sources and sinks of herring are effective throughout the year (compare Figures 24 and 25 with Figures 29 and 35). Furthermore, the effects of reduced consumption by squids on the distribution of pelagic fish is quite noticeable after two years of simulation (compare Figures 26 and 27 with Figures 5 and 10, respectively).
Figure 19.—Herring sources and sinks in tons/km² in February; half of normal mammal consumption.

Figure 20.—Herring sources and sinks in tons/km² in August; half of normal mammal consumption.
Figure 21.--Herring distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.

Figure 22.--Other pelagic fish distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.
Figure 23.--Monthly biomasses and consumptions of herring with normal consumption and with half of normal consumption by squids in eastern Bering Sea over two years.

Figure 24.--Herring sources and sinks in tons/km² in February; half of normal consumption by squids.
Figure 25.--Herring sources and sinks in tons/km$^2$ in August; half of normal consumption by squids.

Figure 26.--Herring distribution in tons/km$^2$ in August; half of normal consumption by squids.
Figure 27.--Other pelagic fish distribution in tons/km\(^2\) in December, second year; half of normal consumption by squids.

Figure 28.--Herring sources and sinks in tons/km\(^2\), January.
4. **SOURCE AND SINK AREAS**

In the DYNUMES model, a given biomass increases at a given location and time if its growth exceeds losses (consumption and mortality but excluding migrations) and decreases if losses exceed growth. These biomass increases/decreases are computed and displayed in three-dimensional (two space and one time dimensions) outputs which indicated that these biomass changes follow some relatively orderly spatial and temporal patterns. Source (growth exceeds losses) and sink (losses exceed growth) areas have been mapped in monthly quantitative terms (increase/decrease in tons/km$^2$/month), but before examining source and sink areas, it is of value to make a few statements pertinent to the computation of these charts. The model does not use isometric growth but initial growth rates which were determined for each species from empirical data. The growth rates are affected by age composition of the species, food availability, and water temperature. As the time step is relatively short, second-order terms in growth and mortality are neglected because other possible errors—such as the neglect of mortality from diseases and spawning mortality—exceed these relatively small second-order terms.

The spatial and temporal source-sink mappings provide useful information on many scientific as well as practical fisheries management considerations. Monthly source and sink maps for herring in the eastern Bering Sea are presented (Figs. 28-39). During the winter months (January to March, Figs. 28-30) losses exceed increases; however, small source (increase) areas are found during this season in the southern part of the area near the continental slope and over the deep water seaward of the slope.
The sources and sinks depend also on the levels of biomass present at any location and time. There is always a sink at the periphery of a distribution (see further notes on the behavior of increasing/declining biomasses in Chapter 7).

Examples of sources and sinks of other pelagic fish in February and August are shown (Figs. 40 and 41). Comparing these Figures with Figures 8 and 9, which present the distributions of other pelagic fish in the corresponding months, it is apparent that the greatest sink (lowest source) areas of other pelagic fish are located between the two centers of greatest abundance of these fish. In fact, this bipartitioned distribution in the model runs was caused by consumption requirements.
Figure 29.--Herring sources and sinks in tons/km$^2$, February.

Figure 30.--Herring sources and sinks in tons/km$^2$, March.
Figure 31.—Herring sources and sinks in tons/km$^2$, April.

Figure 32.—Herring sources and sinks in tons/km$^2$, May.
Figure 33.—Herring sources and sinks in tons/km², June.

Figure 34.—Herring sources and sinks in tons/km², July.
Figure 35.--Herring sources and sinks in tons/km$^2$, August.

Figure 36.--Herring sources and sinks in tons/km$^2$, September.
Figure 37.---Herring sources and sinks in tons/km², October.

Figure 38.---Herring sources and sinks in tons/km², November.
Figure 39.--Herring sources and sinks in tons/km², December.

Figure 40.--Other pelagic fish sources and sinks in tons/km², February.
Figure 41.—Other pelagic fish sources and sinks in tons/km$^2$, August.

Figure 42.—Monthly biomasses of herring with normal temperature and with a 1.5°C wintertime positive temperature anomaly in the eastern Bering Sea over two years.
5. EFFECTS OF ENVIRONMENTAL ANOMALIES ON PELAGIC RESOURCES

The DYNUMES model permits evaluation of the effect of water temperature on the growth and feeding. Thus the effects of temperature anomalies in the eastern Bering Sea on the changes of biomass of pelagic fish were investigated, using the effect of lower temperatures on growth as described in Chapter 3.1. In one of the model runs, a $+1.5^\circ C$ temperature anomaly in the surface layers was prescribed. The monthly biomass changes of equilibrium biomass of herring in normal temperature conditions and with a wintertime anomaly reduces normal growth suppression by prevailing low temperatures during the winter. Interpolation of the directly computed biomass change shows that an $0.8^\circ C$ temperature anomaly will cause a 100,000 ton annual biomass difference from EB as averaged over two years.

The sources and sinks of the herring biomass during a winter with $+1.5^\circ C$ positive temperature anomaly are shown on Figures 43 to 45 which depict rather pronounced changes from normal conditions (see Figures 28 to 30). The resulting distribution of herring in December after two winters with the positive anomaly is shown on Figure 46. Comparison with normal conditions (see Figure 5) indicates a considerable increase of biomass, especially in the northern part of its main distribution.

The sources and sinks of other pelagic fish for February during a $+1.5^\circ C$ positive anomaly (Fig. 47) when compared with normal conditions (Fig. 40), indicate a considerable increase in the source levels off the continental slope and a decrease in the sink levels on the continental shelf NNW of the Pribilof Islands. The distribution of other pelagic fish for December, after two years of computation with $+1.5^\circ C$ positive anomaly is given in Figure 48. Comparison with normal EB distribution in the same month (see Figure 10) indicates an increase in the biomass of both centers of abundance.
Figure 43.--Herring sources and sinks in tons/km$^2$ in January (1.5°C positive anomaly).

Figure 44.--Herring sources and sinks in tons/km$^2$ in February (1.5°C positive anomaly).
Figure 45.--Herring sources and sinks in tons/km² in March (1.5°C positive anomaly).

Figure 46.--Distribution of herring in tons/km² in December, second year; wintertime 1.5°C positive anomaly.
Figure 47.--Other pelagic fish sources and sinks in tons/km$^2$ in February ($1.5^\circ$C positive anomaly).

Figure 48.--Distribution of other pelagic fish in tons/km$^2$ in December, second year; wintertime $1.5^\circ$C positive anomaly.
The magnitude of the effect of the temperature anomaly on the biomass changes (via physiological processes) turned out to be considerably larger and more significant than expected before computations. These effects might explain a great part of the relatively large fluctuations of fish stocks observed in other high latitude areas.

Although the model also contains temperature effects on feeding (food uptake), slightly increased natural mortalities in subzero temperatures, and an accelerated migration of most fish species out of areas colder than about -0.2°C, it does not include some specific effects on ripening and on spawning area dislocations. Shavoneev (1965) observed that herring ripened earlier in warm years. Furthermore, the herring spawned in many locations along the north coast of the Alaska Peninsula in spring 1976 which was anomalously cold. No spawning along the Alaska Peninsula was observed in spring 1977 which was preceded by a warm winter (P. Jackson, Alaska Department of Fish and Game, Kodiak, pers. comm.). This observation might indicate that Bering Sea herring do not have a pronounced "homing instinct" as observed in the herring in the Gulf of Alaska. Furthermore, the northward shift of spawning (and distribution) of Bering Sea herring during warm years seems to be analogous to some degree to the long-term northward shift of Hokkaido herring during warm years (Nagasaki 1973).
6. EFFECTS OF FISHERY

The effects of fishery in the DYNAMES model can be simulated by changing the fishing effort (intensity) coefficient either as to location, time, or magnitude or a combination of these changes. A few computer runs were made with changed magnitude of fishing effort coefficient to study the resulting effects of increased/decreased catches on the biomass. Results of two runs with different fishing effort are presented in Figure 49. Interpolation of the results shows that 11,300 tons of annual change in the fishery (at EB) would result in 100,000 tons of annual herring biomass change as averaged over two years.

As the annual migration cycle remains unchanged in the model, the increased winter fishery near the continental slope northwest of the Pribilof Islands causes a lowering of herring biomass in this area, as comparison of Figures 50 and 5 indicate.

The fishing effort coefficient acts as a density dependent parameter; consequently, a given constant total catch has different effects at different biomass magnitudes. Thus, management decisions for regulation of the fishery by total allowable catch would require best available and reliable knowledge of the level of biomass of the species under consideration. Various biomass levels for this purpose can be simulated with the DYNAMES model which can be used in a relative and comparative manner in the estimation of the various effects of fishery. The latter can also be simulated as a spatial and temporal variable according to realistic fishing possibilities and their limits.
Figure 49.--Monthly biomasses of herring with $47 \times 10^3$ and $75 \times 10^3$ tons annual catch in the eastern Bering Sea over two years.

Figure 50.--Herring distribution in tons/km$^2$ in December, ($75 \times 10^3$ tons catch).
7. LONG-TERM CHANGES OF ABUNDANCE AND DISTRIBUTION

Long-term changes in most individual members of the ecosystem are dependent on changes in abundance and/or distribution of any one of the components of this system, biological and/or environmental. A complete, prognostic ecosystem model, such as DYNAMES, is a prerequisite for realistic long-term fluctuation studies. There are numerous possible causes for the long-term changes and the need for long computer runs make these studies costly.

Some of the major causes of long-term changes are:

a) Increase/decrease of consumption of a given species, caused by changes of abundance and/or distribution of the predator(s), and changes of abundance and distribution of prey (density dependent feeding).

b) Effects of environmental anomalies (changes of growth rates and availability of food).

c) Effects of the fishery.

d) Spawning and larval survival fluctuations (dependent mainly on grazing and environmental factors).

In an earlier work (Laevastu and Favorite 1976b), the effects of long-term changes in pollock biomass, caused by cannibalistic interactions, on the biomass of herring were studied and an inverse correlation between pollock and herring biomasses was found. It was postulated that the high pollock biomass in the early 70's in the eastern Bering Sea might have contributed materially to the lowering of herring biomass in the area. Such cyclic changes can occur within other species as well. The effects of grazing by squids and marine mammals on herring have been described, as have been the effects of the environment and the fishery.
All long-term changes are time dependent processes and their magnitudes also depend greatly on the state of biomass in relation to the equilibrium biomass at the time of the action of the forcing (i.e. initial influence of the causing event and/or condition). Four 5-year model runs with various initial biomasses of herring were made with density dependent feeding on herring and a constant fishing effort (i.e. annual catch being proportional to biomass present). If the biomass (Fig. 51) is below EB (curve A) level, such as curves B and C, it recovers slowly towards EB (see remarks at the end of the curves) even with direct density dependent feeding—the recovery would be somewhat faster with more selective feeding. If the biomass is, however, below a "threshold value" (curve D) it continues to decline (see Chapter 8). The magnitudes of annual fluctuations within the biomass decrease with decreasing biomass.

Long-term changes can be initiated with individual alterations in most components of the ecosystem by such factors as cannibalistic interactions, successive low year classes, and other causative factors listed above. The magnitudes and periods of long-term cycles are affected by the speed of recovery, which in turn is affected by the same causative factors with opposite signs.

The magnitudes of sources and sinks, and to a lesser extent their areal distributions, change also with the changing magnitude of biomasses (compare Figures 52 and 54 with Figure 29). It has been generally observed for many species and areas that the distribution patterns of increasing and declining populations behave differently. Our model results clearly indicate that declining populations (biomass) shrink toward the center of their main abundance (compare Figures 53 and 6 with Figures 5 and 3, respectively) and that the fringe populations disappear first. Increasing biomasses, however, expand in their areal distributions.
Figure 51.—Monthly herring biomasses in the eastern Bering Sea over five years (initial biomasses in million tons: A=2.75; B=1.59; C=0.94; D=0.45).

Figure 52.—Herring sources and sinks in tons/km² in February, fourth year; initial biomass 1.59 million tons.
Figure 53.—Distribution of herring in tons/km\(^2\) in February, fourth year; initial biomass 1.59 million tons.

Figure 54.—Herring sources and sinks in tons/km\(^2\) in February, fourth year; initial biomass 0.94 million tons.
8. SOME ADDITIONAL FACTORS AFFECTING BIOMASS FLUCTUATION OF HERRING

One of the serious problems in past population dynamics considerations has been the inability to distinguish quantitatively between the components of "natural mortality" (grazing (consumption), starvation, diseases, etc.) and the man-made mortality (fishing). A complete ecosystem model, such as DYNUMES, has made the separate, detailed evaluation of the dominating component--grazing--possible. As a result, many of the earlier used terms become nebulous, such as recruitment overfishing (assuming that the fishery affects the recruitment of juveniles to adult stock), and growth overfishing (assuming that the fishing exceeds growth, causing stock decline).

Our results with the DYNUMES model clearly demonstrate that the ecosystem internal consumption can far exceed any fishery effects on biomass fluctuations in the eastern Bering Sea and that growth overfishing consequently loses its definition (and at best becomes a space-time dependent minor factor in source-sink considerations). The problems of (juvenile) recruitments are briefly discussed below and will be subject to special study with an extended DYNUMES model in the future.

8.1 Some stock recruitment relations and threshold biomass

There is a general lack of quantitative knowledge on the early life dynamics of all species; therefore, recruitment is made proportional to biomass levels in the DYNUMES model. This assumption is supported by other earlier conclusions that mean recruitment levels are almost constant (Beyer 1976; Andersen and Ursin 1977). Still, stronger than normal year classes occur in most species which are important in the fishery and its management. Thus, it is of interest to examine briefly the causes of year class variations,
such as the size of spawning stock dependence, survival of eggs and early larval starvation as affected by temperature (via growth rate, food availability, and hatching time), transport to unfavorable areas and depths and, above all, the postlarval grazing.

The number of spawners seems not to be of great importance in determining year class strength in most pelagic fishes if the biomass has not fallen close to the threshold value (for definition see below). Strong year classes can rise from a relatively small number of spawners, because optimum best survival of larvae is usually related to an intermediate number of spawners. When Pacific herring and capelin spawning is intense on limited spawning grounds in shallow water, several layers of eggs are deposited and hatching success is low. Additional egg mortalities are caused by intensive wave action (storms), exposure to air (low tides and wind effects), and by heavy predation by birds.

Generally the Pacific herring biomass in the eastern Bering Sea is assumed to consist of western, eastern, and Norton Sound stocks. There is, however, no firm basis for this division, nor further division into different races with specific spawning grounds (Prokhorov 1968). If separate wintering and spawning areas exist, these can be altered by environmental anomalies (Shaboneev 1965; P. Jackson, ADFG, personal communication). During cold spring conditions, herring spawn in abundance on southern spawning grounds, whereas during warm spring conditions the northern spawning grounds are crowded. After hatching, the availability of proper plankton as food is surely one of the factors affecting larval survival. This plankton availability is enhanced by environmental factors, such as temperature and radiation anomalies, and
piling up of warmer and plankton-rich water near the coast. Early transport of larvae to offshore areas might be detrimental to proper food availability (deep mixing, spring plankton blooms starting earlier near the coast, etc.).

Grazing might take over the control of larval biomasses already in rather early stages. The larval stages can be considered as part of zooplankton standing stock. Thus the larvae can be expected to be grazed at the same rate as zooplankton, the grazing rate of which can be high in some areas and seasons (see Figures 55 and 56). However, if the abundant occurrence of larvae does not coincide with areas of high zooplankton consumption, the larval survival is enhanced.

After larvae become nektonic, grazing in an active selective feeding mode takes over. This feeding is largely size dependent and is considerable during larval and early juvenile stages (see Figure 14). Considering the above, it appears that the year class strength is not determined by the size of the spawning stock but by the survival in late larval and postlarval stages.

It can be postulated that there might be some threshold size of a biomass of a given species below which the population cannot regenerate to its previous size, because it is suppressed by other species that have utilized their opportunity to take over the ecological niche. This succession can be caused by overgrazing (i.e. sinks exceed sources), competition for food, too low a density of spawners on spawning grounds (egg fertilization problems and/or heavy grazing on eggs), and difficulties in school formation (which is an integral part of spawning migrations, and spawning). Only the first possible cause, mentioned above, can be investigated with the present DYNAMES model,
Figure 55.--Percentage of mean zooplankton standing stock consumed in February.

Figure 56.--Percentage of mean zooplankton standing stock consumed in August.
for which runs were made to determine the possible threshold biomass for herring. A density dependent feeding was used in this run (i.e. herring consumption by predators is dependent on the quotient: present biomass/EB (equilibrium biomass)). The results showed that the threshold biomass of the herring in the eastern Bering Sea is 0.5 million tons (see Figure 51, curve D).

8.2 "Herring equivalences"

It is of importance to quantify and rank the various factors affecting the biomass fluctuations of any commercially important species. It is also of paramount importance to determine the degree to which fisheries management can affect the resource abundance.

In the earlier chapters, several factors affecting the pelagic fish biomasses were singled out and special computer runs were made with two years' real time simulation to determine quantitatively their effects. The results are summarized in Table 3. It should be noted that these equivalences would be different if the biomass were below EB. Furthermore, there are numerous other factors in the ecosystem that will cause magnification of these equivalences; thus they should be used only for comparative purposes.

One of the striking features in these equivalences is the large effect of surface temperature anomalies where the effect of only $0.8^\circ C$ temperature anomaly during the winter is equivalent to the effect of $11.3 \times 10^3$ tons of herring catch. Therefore, wise, flexible fisheries management in the eastern Bering Sea would require the monitoring of the wintertime (surface) temperature anomalies and their accounting in management decisions. Satellite imagery of ice cover is extremely useful in this regard.
Table 3.--"Herring equivalences" in the eastern Bering Sea. (Factors and processes each of which cause a $100 \times 10^3$ tons of herring biomass change per year (averaged over two year effects) in the eastern Bering Sea.)

<table>
<thead>
<tr>
<th>Factors and processes</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Decrease of consumption of herring by mammals (i.e. decimating mammal herds)</td>
<td>22%</td>
</tr>
<tr>
<td>2) Increase/decrease of consumption of herring by squids (i.e. lower biomass of squids)</td>
<td>26%</td>
</tr>
<tr>
<td>3) Increase/decrease of fishery on herring (per year)</td>
<td>$1.3 \times 10^3$ tons</td>
</tr>
<tr>
<td>4) Surface temperature anomaly during winter months</td>
<td>0.8°C</td>
</tr>
<tr>
<td>5) Increase/decrease of older/larger pollock (&gt;45 cm length) biomass</td>
<td>$390 \times 10^3$ tons</td>
</tr>
</tbody>
</table>
Secondly, one can notice that the direct fishery effects on herring are relatively small as compared to the effects of grazing by mammals. Thus it is questionable to try to manage fisheries in the eastern Bering Sea if marine mammals are not managed simultaneously by the same management body.

It should also be borne in mind that the effects of changes of many other ecological factors propagate through this system in various ways, usually favorable to one but unfavorable to another component. Equivalences, such as presented in Table 3 can be computed for additional effects/factors and for other species as well, if proper manpower and funds were made available.
9. SUMMARY

The factors and processes controlling the abundance of pelagic fish in the eastern Bering Sea were studied quantitatively with the DYNUMES III model. This model permits a relative assessment of the total ecosystem and allows, among others, a detailed quantitative computation of ecosystem internal consumption, which has been the greatest unknown quantity in conventional natural mortality coefficients.

1) The "equilibrium biomass" (EB) of the herring in the eastern Bering Sea is 2.7 million tons, which compares favorably with Shaboneev's (1965) evaluation of 2.2 million tons.

2) A threshold value for herring biomass has been found (0.5 million tons), below which the recovery could be very slow indeed.

3) There are long-term fluctuations in abundances of most species. Due to interspecies interactions these long-term fluctuations propagate through the whole ecosystem. Pollock have a long-term fluctuation caused by cannibalistic interactions and the herring biomass fluctuates inversely with pollock biomass.

4) There are no data available to determine the exact state of the biomass of herring at present. Because of the great abundance of older pollock a few years ago, it could be assumed that the herring biomass was low, but is recovering at the present due to the decrease of the older pollock biomass by the intensive fishery on this species.

5) The equilibrium biomass of other pelagic species in the eastern Bering Sea is 4.3 million tons.

6) The ecosystem internal consumption and its year-to-year changes far exceed the fishery effects on the biomass changes.
7) Annual consumption of herring by marine mammals is at present more than 10 times higher than the annual herring catch. The main herring consumers by mammals are toothed whales (including the sperm whale), followed by pinnipeds. For meaningful fishery management it is, therefore, imperative to manage mammal herds concurrently with fisheries management, preferably by the same management body.

8) The annual turnover rate of herring is 0.5 and of other pelagic fish, 0.95. The magnitude of the annual biomass fluctuation in herring decreases with decreasing biomass.

9) The monthly source (growth exceeds removal) and sink (removal exceeds growth) areas of pelagic fish have been mapped. These source-sink maps are useful in devising research and management criteria.

10) There is, in general, a sink of biomass at the periphery of distribution which decreases from center toward periphery. Declining populations shrink towards the centers of main abundance and many fringe populations disappear first. Increasing populations expand their areal extent.

11) Growth rate of the biomass of any species depends on the distribution of biomass with age, due to rapidly decreasing growth rates with age. The average distribution of herring biomass with age is presented.

12) Growth rate is also dependent on temperature and is affected by cold winter temperatures at high latitudes. The effect of temperature anomaly during the winter was surprisingly high. An 0.8°C temperature anomaly during the winter months had equivalent effect of 11.3x10³ tons of annual herring catch increase/decrease. Consequently, it is of great importance to monitor the temperature anomalies in the eastern Bering Sea in order to achieve optimum fisheries management.
13) The study of the effects of changing annual catches on the EB showed that 11,300 tons annual catch change is equivalent to 100,000 tons annual biomass change at EB.

14) The early larval stages of pelagic fish are grazed at the same rate as zooplankton, the grazing rate of the latter being relatively high in some areas and season. Year class strength in general seems to be largely determined by ecosystem internal grazing in postlarval and early juvenile stages, rather than by the number of spawners.

15) Some "herring equivalences" are given which show that grazing by marine mammals, interspecies interactions (e.g. consumption by squids), and wintertime water temperature anomalies have greater effects on herring biomass fluctuations than a modest fishery.
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THE CONTROL OF PELAGIC FISHERY RESOURCES
IN THE EASTERN BERING SEA
(A numerical ecosystem study of factors affecting fluctuations of pelagic fishery resources with emphasis on herring)

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T. Laevastu and F. Favorite

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T. Laevastu* and F. Favorite*
# CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>1</td>
</tr>
<tr>
<td>1. Introduction</td>
<td>1</td>
</tr>
<tr>
<td>1.1 Purpose of the study</td>
<td>1</td>
</tr>
<tr>
<td>1.2 Methods</td>
<td>1</td>
</tr>
<tr>
<td>2. Abundance and distribution of pelagic fish in the eastern Bering Sea</td>
<td>5</td>
</tr>
<tr>
<td>2.1 Herring</td>
<td>7</td>
</tr>
<tr>
<td>2.1.1 Model studies</td>
<td>7</td>
</tr>
<tr>
<td>2.1.2 Present status</td>
<td>12</td>
</tr>
<tr>
<td>2.2 Other pelagic fish</td>
<td>13</td>
</tr>
<tr>
<td>3. Growth and consumption, including mortalities</td>
<td>15</td>
</tr>
<tr>
<td>3.1 Growth and factors affecting it</td>
<td>15</td>
</tr>
<tr>
<td>3.2 Fishing mortality and mortality from diseases and old age</td>
<td>18</td>
</tr>
<tr>
<td>3.3 Ecosystem internal consumption</td>
<td>19</td>
</tr>
<tr>
<td>3.3.1 Consumption by mammals and birds</td>
<td>22</td>
</tr>
<tr>
<td>3.3.2 Consumption by pollock and squids</td>
<td>25</td>
</tr>
<tr>
<td>4. Source and sink areas</td>
<td>31</td>
</tr>
<tr>
<td>5. Effects of environmental anomalies on pelagic resources</td>
<td>40</td>
</tr>
<tr>
<td>6. Effects of fishery</td>
<td>45</td>
</tr>
<tr>
<td>7. Long-term changes of abundance and distribution</td>
<td>47</td>
</tr>
</tbody>
</table>
8. Some additional factors determining biomass fluctuations of herring

8.1 Some stock-recruitment relations and threshold biomass... 51
8.2 "Herring equivalences".............................................. 55

9. Summary........................................................................ 58

10. References..................................................................... 61
LIST OF FIGURES

Figure 1.--DYNUMES III grid on Mercator projection.

Figure 2.--Schematic outline of DYNUMES III.

Figure 3.--Distribution of herring in tons/km\(^2\) in February (equilibrium biomass (EB), 2.75 million tons).

Figure 4.--Distribution of herring in tons/km\(^2\) in August (EB, 2.75 million tons).

Figure 5.--Distribution of herring in tons/km\(^2\) in December (EB, 2.75 million tons).

Figure 6.--Distribution of herring in tons/km\(^2\) in February, fourth year, (biomass 0.94 million tons) (example of the distribution of a decreasing biomass).

Figure 7.--Monthly changes in equilibrium biomass of herring in the eastern Bering Sea over two years and monthly computed herring catches during the same period.

Figure 8.--Distribution of other pelagic fish in tons/km\(^2\) in February (EB, 4.3 million tons).

Figure 9.--Distribution of other pelagic fish in tons/km\(^2\) in August (EB, 4.3 million tons).

Figure 10.--Distribution of other pelagic fish in tons/km\(^2\) in December (EB, 4.3 million tons).

Figure 11.--Weight and length of Pacific herring at different ages.

Figure 12.--Growth of biomass (weight) of Pacific herring at different ages, as percent per year.

Figure 13.--Average distribution of biomass and numbers of Pacific herring within different year classes (as percent of total biomass) (from Laevastu and Favorite 1977a).
Figure 14.--Distribution of "consumption" (grazing, mortality, and fishery) with age of Pacific herring (as percent of mean standing crop of each year class).

Figure 15.--Consumption of herring in tons/km² in February (EB, 2.75 million tons).

Figure 16.--Consumption of herring in tons/km² in August (EB, 2.75 million tons).

Figure 17.--Monthly consumption of herring in the eastern Bering Sea (total consumption, consumption by toothed whales and by pinnipeds).

Figure 18.--Monthly biomasses and consumptions of herring with normal mammal consumption and with half of normal mammal consumption in the eastern Bering Sea over two years.

Figure 19.--Herring sources and sinks in tons/km² in February; half of normal mammal consumption.

Figure 20.--Herring sources and sinks in tons/km² in August; half of normal mammal consumption.

Figure 21.--Herring distribution in tons/km² in December, second year; half of normal mammal consumption.

Figure 22.--Other pelagic fish distribution in tons/km² in December, second year; half of normal mammal consumption.

Figure 23.--Monthly biomasses and consumptions of herring with normal consumption and with half of normal consumption by squids in eastern Bering Sea over two years.
Figure 24.--Herring sources and sinks in tons/km\(^2\) in February; half of normal consumption by squids.

Figure 25.--Herring sources and sinks in tons/km\(^2\) in August; half of normal consumption by squids.

Figure 26.--Herring distribution in tons/km\(^2\) in December, second year; half of normal consumption by squids.

Figure 27.--Other pelagic fish distribution in tons/km\(^2\) in December, second year; half of normal consumption by squids.

Figure 28.--Herring sources and sinks in tons/km\(^2\), January.

Figure 29.--Herring sources and sinks in tons/km\(^2\), February.

Figure 30.--Herring sources and sinks in tons/km\(^2\), March.

Figure 31.--Herring sources and sinks in tons/km\(^2\), April.

Figure 32.--Herring sources and sinks in tons/km\(^2\), May.

Figure 33.--Herring sources and sinks in tons/km\(^2\), June.

Figure 34.--Herring sources and sinks in tons/km\(^2\), July.

Figure 35.--Herring sources and sinks in tons/km\(^2\), August.

Figure 36.--Herring sources and sinks in tons/km\(^2\), September.

Figure 37.--Herring sources and sinks in tons/km\(^2\), October.

Figure 38.--Herring sources and sinks in tons/km\(^2\), November.

Figure 39.--Herring sources and sinks in tons/km\(^2\), December.

Figure 40.--Other pelagic fish sources and sinks in tons/km\(^2\), February.

Figure 41.--Other pelagic fish sources and sinks in tons/km\(^2\), August.

Figure 42.--Monthly biomasses of herring with normal temperature and with a 1.5°C wintertime positive temperature anomaly in the eastern Bering Sea over two years.
Figure 43.--Herring sources and sinks in tons/km² in January (1.5°C positive anomaly).

Figure 44.--Herring sources and sinks in tons/km² in February (1.5°C positive anomaly).

Figure 45.--Herring sources and sinks in tons/km² in March (1.5°C positive anomaly).

Figure 46.--Distribution of herring in tons/km² in December, second year; wintertime 1.5°C positive anomaly.

Figure 47.--Other pelagic fish sources and sinks in tons/km² in February (1.5°C positive anomaly).

Figure 48.--Distribution of other pelagic fish in tons/km² in December, second year; wintertime 1.5°C positive anomaly.

Figure 49.--Monthly biomasses of herring with 47×10³ and 75×10³ tons annual catch in the eastern Bering Sea over two years.

Figure 50.--Herring distribution in tons/km² in December, (75×10³ tons catch).

Figure 51.--Monthly herring biomasses in the eastern Bering Sea over five years (initial biomasses in million tons: A=2.75; B=1.59; C=0.94; D=0.45).

Figure 52.--Herring sources and sinks in tons/km² in February; fourth year; initial biomass 1.59 million tons.

Figure 53.--Distribution of herring in tons/km² in February, fourth year; initial biomass 1.59 million tons.

Figure 54.--Herring sources and sinks in tons/km² in February, fourth year; initial biomass 0.94 million tons.

Figure 55.--Percentage of mean zooplankton standing stock consumed in February.

Figure 56.--Percentage of mean zooplankton standing stock consumed in August.
LIST OF TABLES

Table 1.--Annual consumption of herring and other pelagic fish in the eastern Bering Sea (in $10^3$ tons).

Table 2.--Estimated number of whales and porpoises in the eastern Bering Sea.

Table 3.--"Herring equivalences" in the eastern Bering Sea (factors and processes, each of which causes a $100x10^3$ tons of herring biomass change per year (averaged over two year effects) in the eastern Bering Sea).
ABSTRACT

A Dynamic Numerical Marine Ecosystem model (DYNUMES III) which addresses interactions of major ecosystem components was used to study the dynamics of pelagic fish in the eastern Bering Sea, with emphasis on Pacific herring (Clupea harengus pallasi), and to determine quantitatively factors affecting relative abundances of stocks. The equilibrium biomass of herring in the eastern Bering Sea is 2.7 million tons; and the lower threshold value is 0.5 million tons (with density dependent grazing on herring) below which recovery would be very slow indeed. The equilibrium biomass of other pelagic fish is 4.3 million tons.

The herring biomass has long- and short-term fluctuations which are induced and affected by several factors, such as environmental anomalies and interspecies interactions. There is, for example, an inverse relationship between walleye pollock (Theragra chalcogramma) and herring biomasses due to older pollock grazing on herring. Although the present state of the herring biomass in the eastern Bering Sea cannot be determined with greater accuracy due to the lack of proper data, it can be assumed to have been at a low level a few years ago due to the high abundance of pollock and is expected to be on the increase in recent years due to the decrease in the abundance of older pollock. The biomass turnover rate for herring is 0.5 and for other pelagic fish 0.95.

Herring abundance in the eastern Bering Sea is primarily affected by marine mammals which annually may consume roughly ten times more than the commercial catch, sperm whales (Physeter macrocephalus) being the largest consumers. Herring abundance is also influenced by consumption by squids and other fish and, especially, by water temperature anomalies during winter and spring. Effects of the fluctuating offshore herring fishery has only
a moderate effect on the equilibrium biomass of herring; the hierarchy of the influences on the herring biomass is given in this report in terms of defined "herring equivalences."

Pelagic fish constitute an important ecosystem internal food resource for other marine ecological groups in the eastern Bering Sea. The ecosystem internal consumption (and its possible year-to-year fluctuations) far exceeds the effects of the fishery and its variations on the state of the biomass of pelagic fish. Adult squids are feeding mainly on pelagic fish and exercise considerable influence on the magnitude and fluctuations of the pelagic fish biomass. Unfortunately, the squid biomass itself can only be estimated with a Bulk Biomass model where emphasis is on the mean quantitative food composition of all ecosystem components.

The year class strength in most pelagic species is largely determined by the ecosystem internal consumption in larval and especially in postlarval stages (and during the first two years of the lifespan), rather than by the number of spawners. Model results show that an increasing population expands in its spatial distribution and a declining population shrinks towards the center of its main abundance, the fringe populations disappearing first.

The monthly source (growth exceeds consumption) and sink (consumption exceeds growth) areas for pelagic fish were found to be useful criteria in research and management problems. Temperature anomalies during the winter were found to affect considerably the sources and sinks of herring and other pelagic fish via physiological effects (food economy and growth). The growth rate of the biomass of a given species is a function of the distribution of its biomass with age and is affected especially by lower temperatures during the winter season. An 0.8°C temperature anomaly was found equivalent
to about 11.3 thousand tons change of annual catch. As the effect of a small temperature anomaly is relatively large in terms of possible increase of catch quotas, and as the anomaly would affect other commercial species as well, it seems to be imperative to monitor temperature anomalies during at least the winter and spring seasons in the eastern Bering Sea for optimum management of the fishery there.
1. INTRODUCTION

1.1 Purpose of the study

The main purpose of this study was to determine quantitatively those factors which control the biomasses of pelagic fish, especially Pacific herring (*Clupea harengus pallasi*), in the eastern Bering Sea and which affect fluctuations in their abundance. It was necessary to determine concurrently the equilibrium biomasses of these fish as well as the possible "threshold biomasses," and to consider long-term fluctuations. Obviously the study of the effects of variable year-to-year fishery catches constituted an initial central theme of the study, and it became apparent that an estimation of the effects of interspecies interactions was of particular importance in achieving the objectives of the study.

During the course of this study, it was discovered that the environmental anomalies could have profound effects on the pelagic resources in the higher latitudes, and the study was expanded to include the quantification of these effects. Further, the concept of defining of source-sink areas and their utility in evaluating the distribution and abundance of any given species was developed. It should be stated at the outset that walleye pollock (*Theragra chalcogramma*), the most abundant species in the area, is considered a semi-demersal fish.

1.2 Methods

This study was conducted with the Dynamic Numerical Marine Ecosystem model (DYNAMES III), which utilizes a wide variety of knowledge on interactions in the marine ecosystem as well as extensive empirical data from a great variety of sources. A more detailed description of the model is available in another report (Laevastu and Favorite 1977b)—therefore, only a general summary description of the model is presented.
The DYNAMES III model is four-dimensional (three space and one time dimension). The third space dimension, depth, is used in implicit manner in most cases, (e.g. bottom and/or surface temperature and/or a mean of these) depending on whether pelagic, demersal, or semi-demersal species are under consideration. The gird is an equal area grid (grid size 95.25 km) which is superimposed on a Mercator projection in Figure 1.

The computation of grazing and other interspecies and environment interactions requires that all predators are quantitatively included in the model, either as species or lumped into ecological groups. Thus, the DYNAMES III model is designed to include all essential biological elements in the eastern Bering Sea; most of the organisms being grouped into ecological groups (e.g. flatfish, gadids, etc.). However, species under special study can be presented separately and even by size and/or age groups. In the present study, Pacific herring is considered separately from a grouping of "other pelagic fish," which consists mainly of capelin (Mallotus villosus), other smelts, and Pacific sand lance (Ammodytes hexapterus).

The initial (e.g. January) distribution of a given species is prescribed, using all available sources of data. The size of the initial equilibrium biomass of any given species (or ecological group) is determined with another model developed at the Northwest and Alaska Fisheries Center, a Bulk Biomass Model (BBM) (Laevastu and Favorite 1976a). The biomass is moved in weekly time steps as known migration patterns dictate and biomass increases and decreases are accounted for. It is generally known that metabolic rate decreases with temperature (re. Krogh's metabolic curve). Therefore, in the study of the effects of temperature anomalies on the growth of pelagic fish the growth coefficients were changed (decreased linearly) when monthly temperature was below 4°C, with cessation of growth below 0°C. Below zero temperatures also
Figure 1.--DYNUMES III grid on Mercator projection.
accelerate migrations in the model out of the cold areas and mortality is also slightly increased in these cold areas. The mortality coefficient in the model refers to mortality from old age and diseases, and is relatively small (0.3 to 2% per month, depending on individual species and their life span). The larval stages (younger than 6 months) are not considered within the species groups but are included in zooplankton where they are grazed (consumed) at the same rate as zooplankton. The recruitment is assumed to be proportional to biomass and does not enter directly into essential computations. Therefore, the year class variations in this model are determined by grazing in zero, one, and, in some species, the second year of life, if mean biomass does not increase or decrease from one year to another.

Grazing (synonomous to consumption in this report) is computed in monthly time steps at each grid point for all groups of species. Minimum food requirement coefficients for maintenance and growth are prescribed, but they are modified at low temperatures and at grid points and time steps when food availability is limited. Average composition of food is prescribed for each species or species group and used as food selection (preference) criteria (the composition of food in the DYNUMES model can vary at each grid point and time step) depending on the availability of food items in a given location and month. If computations indicate that a given food item is not present in the required abundance, a partial or full substitution is automatically made according to preference criteria. If there is a lack of food, starvation is assumed to occur, altering not only the growth coefficient but, if severe, also the mortality coefficient. The fishing intensity coefficients are prescribed in space and time (according to known fisheries areas and seasons) and tuned to present and/or past catch statistics.
The abundance and distribution of mammals is prescribed in monthly time steps. Conservative abundance numbers, as well as conservative food requirements, were used in the model runs presented here (for example, recent reports give 1.2 million northern fur seals (Eumetopias jubatus) in the Bering Sea--our model used only a maximum of 0.85 million; food uptake of these seals is reported to be between 5 and 8% body weight daily--our model uses 5%).

A schematic outline of DYNUMES III model is given in Figure 2. Although most of the components of the marine ecosystem are included in the model, this report deals mainly with Pacific herring and with the ecological group termed "other pelagic fish," which comprises mainly capelin and sand lance.

2. ABUNDANCE AND DISTRIBUTION OF PELAGIC FISH IN THE EASTERN BERING SEA

The equilibrium (or minimum sustainable) biomass (EB) of a given species or group of species is defined as the biomass in a complete ecosystem in a defined area which does not decrease nor increase on an annual basis; thus, the annual growth is in equilibrium with removal. Equilibrium biomasses (EB) were determined with the Bulk Biomass Model (BBM) and adjusted (fine tuned) in DYNUMES III. This equilibrium biomass is dependent upon quantative consumption by all species in the ecosystem, distributions of predators and prey, and growth factors. It is postulated by Beyer (1976) that there might be a lower threshold value for any given biomass, below which the biomass does not recover or recovers very slowly. The DYNUMES model permits the study of the threshold biomass, which seems to exist in most species, even with density dependent grazing. It should also be noted that the biomass of individual species is affected by a pronounced deviation of year class strengths from a mean or normal year class. The effects of the year class
Removal from system

○ MAMMALS, BIRDS

○ * FISH I

× Growth
 (environm., food affected)

△ Consumption
 (food requirements aff.)

△ Mortality
 (envir., food, age aff.)

× Migrations
 (envir., food, age aff.)

Spawning

○ * FISH II, etc.

○ BENTHOS ("fish food" benthos)
 Growth, consumption
 Mortality

○ ZOOPLANKTON
 (simulated standing crop)
 Consumption

○ PHYTOPLANKTON
 Consumption

Removal from system, nutrient regeneration

△ ○ * MAN (fishery)

Quickly identifying the types of ecological processes involved:

- Quantitative distribution in space and time
- By ecological groups, species, and/or year classes
- Affected by distribution, environment, and interspecies interaction
- Variable in space and time, environment, and biomass distribution dependent
- Affected by metabolic processes

Figure 2.--Schematic outline of DYNUMES III.
variations on the herring biomass will be studied using an extended DYNUMES model having added stock-recruitment subroutines. Results will be included in a subsequent report.

Thus, the initial model inputs related to distributions and interactions of species have been prescribed from available data and knowledge. Subsequent iterations from initial distributions indicate that there is considerable adjustment within the first-year computations.

2.1 Herring

The distribution of herring in the eastern Bering Sea has been studied rather superficially in the past. The offshore distribution of herring is best described by Shaboneev (1965). Additional scattered data are available in numerous reports for Japanese fisheries investigations. The distribution of coastal spawning has recently been surveyed annually by the Alaska Department of Fish and Game. All this available information was used to digitize January distribution of herring and its seasonal migrations.

2.1.1 Model studies

Examples of some monthly quantitative distributions of herring as determined by using initial inputs and DYNUMES III are given in Figures 3 to 5. The main concentrations of herring overwinter are found in and northward of the Pribilof Islands area and along the continental slope southwest of this area (simulated distribution in Figure 3). Some undoubtedly remain under the ice; the Norton Sound stock is assumed to overwinter in the deeper areas of this Sound and in brackish water. It is known from empirical studies that about one-third of the biomass starts spawning migrations toward the Alaskan coast in late winter—where spawning occurs from the end of April along the northern
Figure 3.---Distribution of herring in tons/km$^2$ in February (equilibrium biomass (EB), 2.75 million tons).

Figure 4.---Distribution of herring in tons/km$^2$ in August (EB, 2.75 million tons).
coast of the Alaskan Peninsula during colder years and in May along the west Alaska coast during normal years (I.M. Warner, Alaska Dept. of Fish and Game, Kodiak, pers. comm.). Spawning in Norton Sound occurs in June and further northward, in July. After spawning, the herring is assumed to disperse for feeding over the continental shelf (Figure 4). The migrations to overwintering grounds start at the end of October (Shaboneev, 1965), and the winter distribution pattern is established by December (Figure 5). Environmental anomalies and interspecies interactions change the distribution patterns somewhat, and these factors are discussed later in the report. Earlier numerical studies (Laevastu and Favorite 1976b), as well as this study shows that an increasing population expands its area of distribution and a decreasing population shrinks towards the center of its main abundance (compare Figures 3 and 6).

The model estimates of equilibrium biomass of herring in the eastern Bering Sea is 2.75 million tons; the magnitude of annual fluctuation of this biomass is about 0.3 million tons (Figure 7). There are two fishing periods on herring (Figure 7) during the winter months on the overwintering herring (EB model input about $8 \times 10^3$ tons per month) and during the spring and early summer on spawning herring (less than $2 \times 10^3$ tons per month). Shaboneev (1965) found the biomass of wintering herring north and northwest of the Pribiloffs to be 2.16 million tons, which compares favorably with our model results. For comparison, the biomass of the herring in the North Sea has been estimated by Andersen and Ursin (1977) to be 1.8 million tons at the end of 1959.
Figure 5.--Distribution of herring in tons/km$^2$ in December (EB, 2.75 million tons).

Figure 6.--Distribution of herring in tons/km$^2$ in February, fourth year, (biomass C.94 million tons) (example of the distribution of a decreasing biomass).
Figure 7.---Monthly changes in equilibrium biomass of herring in the eastern Bering Sea over two years and monthly computed herring catches during the same period.

Figure 8.---Distribution of other pelagic fish in tons/km$^2$ in February (EB, 4.3 million tons).
The DYNUMES model shows that the threshold biomass of herring in the eastern Bering Sea is 0.5 million tons, with density dependent feeding of all ecosystem components (see further Chapter 7). If the biomass would fall below this value, the recovery would be questionable and/or slow even with some successive good year classes.

2.1.2 Present status

The exact state of the existing herring biomass in the eastern Bering Sea cannot be estimated with any great accuracy due to the limited field investigations and scarcity of data between the end of the 1960's and the present. The herring catches in the western Bering Sea declined rapidly in the late 1960's and a bilateral Japanese-USSR agreement closed the fishery in 1970 (Wespestad 1977). The Japanese and USSR catch of herring in the central eastern Bering Sea declined in the early 1970's. Although some of this decline is undoubtedly due to declining herring biomass, three other factors have contributed to it: first, the largest catches in the late 1960's were made from an essentially virgin (previously little fished) population, which had also two strong year classes; second, the main fishery in the eastern Bering Sea switched to the very abundant pollock; and, third, there is an inverse relation between pollock and herring biomasses (Laevastu and Favorite 1976b). It is hoped that when the 1975 and subsequent surveys of spawning herring by the Alaska Department of Fish and Game (P. Jackson, Alaska Department of Fish and Game, Kodiak, pers. comm.) have been quantified, considerably more information on the present state of herring stocks in the eastern Bering Sea will be forthcoming.
2.2 Other pelagic fish

Little is known about other pelagic fish (pollock and sablefish (*Anoplopoma fimbria*), etc. are considered "semi-demersal"fish) in the eastern Bering Sea as none of the species has been subject to exploitation or investigations in the past. However, it is known from stomach analyses of mammals and fish that capelin and sand lance constitute an important food source (forage fish) in the Bering Sea ecosystem. Furthermore, large capelin schools have been observed to spawn all along the Alaskan coast in shallow water about the same time as the herring spawning but with a preference for a sandy substrate.

The equilibrium biomass of the eastern Bering Sea ecosystem requires, according to DYNAMES III, a biomass of 4.3 million tons of other pelagic fish. Furthermore, the equilibrium ecosystem dictates also to a large degree the distribution of these fish. The distributions during February, August, and December (Figures 8 to 10) indicate an interesting feature, the bipartition of the center of abundance in all months—one near the continental slope and another off Bristol Bay. Whether these distributions indicate the main distribution centers of the two major species, capelin (near the slope) and sand lance (over the south central shelf), cannot be determined at this stage.

It should also be noted that, although the biomasses of different species and ecological groups vary from year to year due to several influencing factors, the total biomass of pelagic and semidemersal species (e.g. pollock) changes little. Similar wide fluctuations of an individual species, but quasi-constancy of the biomass of all species including those from slightly different ecological groups, have been observed also in the North Sea (Andersen and Ursin 1977).
Figure 9.—Distribution of other pelagic fish in tons/km$^2$
in August (EB, 4.3 million tons).

Figure 10.—Distribution of other pelagic fish in tons/km$^2$
in December (EB, 4.3 million tons).
3. GROWTH AND CONSUMPTION, INCLUDING MORTALITIES

3.1 Growth and factors affecting it

The growth parameter is one of the important parameters in marine ecosystem dynamics. In this chapter a few characteristics of the herring biomass (growth, consumption, and mortalities) are summarized; similar considerations are valid for other pelagic fish and other components of the marine ecosystem.

The average age-weight curve (Figure 11) for eastern Bering Sea herring and growth rates (Figure 12) were computed using available data in the literature (e.g. Rumyantsev and Darda 1970; Takahashi and Konda 1974). Because growth rates decrease with age, it is necessary to know the distribution of the biomass of a given species, or group of species, over its life span. Individual growth coefficients are prescribed for each year class and the mean distribution of herring biomass with age is given in Figure 13 (Laevastu and Favorite 1977a). The basic DYNUMES III model computations use a growth coefficient which is very close to the growth rate in percent per month (used in the model: herring 7.8% and other pelagic fish 9.0%).

The growth of most species in higher latitudes is seasonal and can be assumed to be affected by temperature (e.g. Krogh's metabolic curve). This slowing of growth during the cold season is also depicted in the scales and otoliths of most high latitude pelagic species. Thus, the growth coefficient in our model is reduced linearly when temperature of the environment at a given location and time drops below 4°C, with cessation of growth occurring at 0°C. Additional empirical data are required in this subject. Growth is also affected by the availability of food, and this effect is also included in DYNUMES III (see Chapter 1.2).
Figure 11. Weight and length of Pacific herring at different ages.

Figure 12. Growth of biomass (weight) of Pacific herring at different ages, as percent per year.
Figure 13. Distribution of biomass and numbers of Pacific herring within different year classes (% of total).

Figure 14. Distribution of "consumption" (grazing, mortality, and fishery) with age of Pacific herring, as percent of mean standing crop of each year class.
3.2 **Fishing mortality and mortality from old age and diseases**

Fishing mortality is prescribed in the model at monthly intervals as fishing effort and is variable in space and time (winter and spring fishery near the continental slope and the Pribilof Islands, summer fishery near the coast). The computed catches are also a function of the availability of the biomass at the prescribed fishing locations. The equilibrium biomass (EB) model computations yield a value of $47 \times 10^3$ tons of herring annually, which is close to the 1972-73 catch of $42.2 \times 10^3$ tons (Wespestad 1977). Further effects of the changing fishing effort on the herring biomass are described in Chapter 6.

Mortality from old age is affected by the life span of the species and the fishery (i.e. the fishery removing part of the older fish which otherwise would have died from old age). Considering these factors, rough estimates of the mortality coefficients were made (herring 0.3% per month, other pelagic fish 0.5% per month). These are small and any anticipated error in these estimates would necessitate only minor adjustments of the growth coefficients. No quantitative information is available on disease mortality and consequently this mortality is assumed to be included in the above mortality coefficient.

The mortality coefficient in the model is increased in unfavorable conditions, such as low temperatures and low availability of food (starvation). It should also be increased during and after spawning (spawning mortality), as done in the Andersen and Ursin model. This will be done in future versions of DYNUMES, when "stock-recruitment" subroutines are added.
3.3 **Ecosystem internal consumption**

The ecosystem internal consumption comprises the largest part of the biomass removal. Although it is conventionally included as "natural mortality" in population dynamics considerations, in the DYNAMES model the ecosystem internal consumption is computed directly in considerable detail. Values depend on the availability of all prey or forage, as well as all predators, at any given location and time period (i.e. grid point and time step). Food type preferred and consumed is a function of both predator and prey size (Ursin 1972). The smaller (younger) fish, which grow faster (in weight) than older fish, are also consumed at a higher rate. This might lead to an assumption that due to high consumption rate at young ages, the year class strength in most species may be largely controlled by consumption (grazing) at these young stages rather than by spawning success. Additional studies in this subject will be conducted in the future.

Fish eating mammals consume mainly medium and large size fish and thus compete directly with man (fishery) (see Figure 14). Ecosystem internal consumption determines largely the biomass turnover rate (i.e. annual consumption divided by annual monthly mean biomass) and, in the eastern Bering Sea, these turnover rates for equilibrium biomasses are: herring 0.50 and other pelagic fish 0.95. Variability in monthly consumption of herring is reflected in February and August values (Figs. 15 and 16), and summarized in Figure 17, in which high consumption by mammals during summer is readily apparent.
Figure 15.--Consumption of herring in tons/km$^2$ in February (EB, 2.75 million tons).

Figure 16.--Consumption of herring in tons/km$^2$ in August (EB, 2.75 million tons).
Figure 17.--Monthly consumption of herring in the eastern Bering Sea (total consumption, consumption by toothed whales and by pinnipeds).

Figure 18.--Monthly biomasses and consumptions of herring with normal mammal consumption and with half of normal consumption in the eastern Bering Sea over two years.
3.3.1 Consumption by mammals and birds

A summary of the consumption of herring and other pelagic fish in the eastern Bering Sea (Table 1) reveals a startling result, the consumption of herring by mammals is ten times higher than the commercial catch. The main consumers of pelagic fish (and squids) in the eastern Bering Sea are "toothed whales" (mainly sperm whales (Physeter macrocephalus)), followed by pinnipeds. These results are based on conservative estimates of mammals in the eastern Bering Sea used in the model runs (Table 2). This suggests that successful management of fishery resources in the eastern Bering Sea requires concurrent management of the mammal herds.

In order to study the quantitative effects of grazing by mammals on herring, the model was run with a 50% reduction in mammal consumption (Figure 18). Interpolations of the results indicate that a reduction of mammals by 22% would result in an increase in the herring biomass of 100,000 tons.

The effects of decreased mammal consumption on the dynamics of pelagic fish can be studied by comparing the quantitative monthly source and sink areas (see Chapter 4). The effects of changing mammal consumption during winter are relatively small (compare Figures 19 and 29), but these differences are considerable during summer (compare Figures 20 and 35). The effects of reduced mammal consumption are also noticeable when comparing pelagic fish distributions in December, second year computations (Figures 21 and 22 compared with Figures 5 and 10, respectively).

The consumption of herring and other pelagic fish by birds, less than 30% of the 1972-73 herring catch, is rather insignificant (Table 1).
Table 1.--Annual consumption of herring and other pelagic fish in the eastern Bering Sea (in $10^3$ tons).

<table>
<thead>
<tr>
<th>Consumers</th>
<th>Herring</th>
<th>Other pelagic fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammals &amp; birds (total)</td>
<td>423</td>
<td>607</td>
</tr>
<tr>
<td>Pinnipeds (total)</td>
<td>158</td>
<td>130</td>
</tr>
<tr>
<td>Fur seals</td>
<td>26</td>
<td>9</td>
</tr>
<tr>
<td>Sea lions</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>Bearded seals</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Harbor seals</td>
<td>65</td>
<td>30</td>
</tr>
<tr>
<td>Ringed/ribbon seals</td>
<td>24</td>
<td>55</td>
</tr>
<tr>
<td>Toothed whales</td>
<td>232</td>
<td>409</td>
</tr>
<tr>
<td>Baleen whales</td>
<td>21</td>
<td>28</td>
</tr>
<tr>
<td>Birds</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>Fish</td>
<td>739</td>
<td>3,521</td>
</tr>
<tr>
<td>Total consumption</td>
<td>1,362</td>
<td>4,128</td>
</tr>
<tr>
<td>Catch (1973)</td>
<td>42.2</td>
<td>?</td>
</tr>
<tr>
<td>Mean turnover rate</td>
<td>0.50</td>
<td>0.95</td>
</tr>
<tr>
<td>Percent of catch from mammal consumption</td>
<td>10</td>
<td>?</td>
</tr>
</tbody>
</table>
Table 2.—Estimated number of whales and porpoises in the eastern Bering Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average weight (tons)</th>
<th>Estimated number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Summer</td>
</tr>
<tr>
<td>Baleen whales</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin</td>
<td>50</td>
<td>5,000</td>
</tr>
<tr>
<td>Gray</td>
<td>40</td>
<td>5,000</td>
</tr>
<tr>
<td>Mink</td>
<td>9</td>
<td>2,000</td>
</tr>
<tr>
<td>Bowhead</td>
<td>10</td>
<td>2,000</td>
</tr>
<tr>
<td>Toothed whales</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sperm</td>
<td>40</td>
<td>20,000</td>
</tr>
<tr>
<td>Humpback</td>
<td>10</td>
<td>300</td>
</tr>
<tr>
<td>Giant bottlenose</td>
<td>10</td>
<td>2,000</td>
</tr>
<tr>
<td>Killer</td>
<td>12</td>
<td>800</td>
</tr>
<tr>
<td>Beluga</td>
<td>3</td>
<td>2,000</td>
</tr>
<tr>
<td>Porpoises</td>
<td>0.1</td>
<td>5,000</td>
</tr>
</tbody>
</table>
3.3.2 Consumption by pollock and squids

Older pollock (e.g. >30 cm in length) consume herring as food. Because pollock is presently the most abundant species in the eastern Bering Sea, a special numerical simulation study was made with a simplified DYNAMES model to investigate quantitatively the pollock-herring biomass relations (Laevastu and Favorite 1976b). The results of this study indicated an inverse relation between pollock and herring biomasses. Furthermore, it was found that the pollock biomass has a long-term fluctuation (~12 years), caused mainly by cannibalism interactions, that also affects the herring biomass fluctuations.

Adult squids feed mainly on pelagic fish (Akimushkin 1963). Although the actual magnitude of squid resources in the Bering Sea is at present unknown, the EB biomass of squids has been computed via food composition considerations, and a numerical study was made with the DYNAMES model to investigate quantitatively the effects of a reduced squid biomass (reduction 50% from "equilibrium biomass" of squids) on pelagic fish biomasses. Interpolation of data (Figure 23) indicates that a 100,000 ton increase in the herring biomass could be achieved by reducing the "equilibrium biomass" of squids by 26%. The effects of reduced squid biomass on sources and sinks of herring are effective throughout the year (compare Figures 24 and 25 with Figures 29 and 35). Furthermore, the effects of reduced consumption by squids on the distribution of pelagic fish is quite noticeable after two years of simulation (compare Figures 26 and 27 with Figures 5 and 10, respectively).
Figure 19.—Herring sources and sinks in tons/km² in February; half of normal mammal consumption.

Figure 20.—Herring sources and sinks in tons/km² in August; half of normal mammal consumption.
Figure 21.—Herring distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.

Figure 22.—Other pelagic fish distribution in tons/km$^2$ in December, second year; half of normal mammal consumption.
Figure 23.—Monthly biomasses and consumptions of herring with normal consumption and with half of normal consumption by squids in eastern Bering Sea over two years.

Figure 24.—Herring sources and sinks in tons/km² in February; half of normal consumption by squids.
Figure 25. -- Herring sources and sinks in tons/km$^2$ in August; half of normal consumption by squids.

Figure 26. -- Herring distribution in tons/km$^2$ in August; half of normal consumption by squids.
Figure 27.--Other pelagic fish distribution in tons/km² in December, second year; half of normal consumption by squids.

Figure 28.--Herring sources and sinks in tons/km², January.
4. SOURCE AND SINK AREAS

In the DYNUMES model, a given biomass increases at a given location and time if its growth exceeds losses (consumption and mortality but excluding migrations) and decreases if losses exceed growth. These biomass increases/decreases are computed and displayed in three-dimensional (two space and one time dimensions) outputs which indicated that these biomass changes follow some relatively orderly spatial and temporal patterns. Source (growth exceeds losses) and sink (losses exceed growth) areas have been mapped in monthly quantitative terms (increase/decrease in tons/km²/month), but before examining source and sink areas, it is of value to make a few statements pertinent to the computation of these charts. The model does not use isometric growth but initial growth rates which were determined for each species from empirical data. The growth rates are affected by age composition of the species, food availability, and water temperature. As the time step is relatively short, second-order terms in growth and mortality are neglected because other possible errors—such as the neglect of mortality from diseases and spawning mortality—exceed these relatively small second-order terms.

The spatial and temporal source-sink mappings provide useful information on many scientific as well as practical fisheries management considerations. Monthly source and sink maps for herring in the eastern Bering Sea are presented (Figs. 28-39). During the winter months (January to March, Figs. 28-30) losses exceed increases; however, small source (increase) areas are found during this season in the southern part of the area near the continental slope and over the deep water seaward of the slope.
The sources and sinks depend also on the levels of biomass present at any location and time. There is always a sink at the periphery of a distribution (see further notes on the behavior of increasing/declining biomasses in Chapter 7).

Examples of sources and sinks of other pelagic fish in February and August are shown (Figs. 40 and 41). Comparing these Figures with Figures 8 and 9, which present the distributions of other pelagic fish in the corresponding months, it is apparent that the greatest sink (lowest source) areas of other pelagic fish are located between the two centers of greatest abundance of these fish. In fact, this bipartitioned distribution in the model runs was caused by consumption requirements.
Figure 29.--Herring sources and sinks in tons/km², February.

Figure 30.--Herring sources and sinks in tons/km², March.
Figure 31.--Herring sources and sinks in tons/km$^2$, April.

Figure 32.--Herring sources and sinks in tons/km$^2$, May.
Figure 33.—Herring sources and sinks in tons/km$^2$, June.

Figure 34.—Herring sources and sinks in tons/km$^2$, July.
Figure 35.—Herring sources and sinks in tons/km², August.

Figure 36.—Herring sources and sinks in tons/km², September.
Figure 37.--Herring sources and sinks in tons/km$^2$, October.

Figure 38.--Herring sources and sinks in tons/km$^2$, November.
Figure 39.--Herring sources and sinks in tons/km$^2$, December.

Figure 40.--Other pelagic fish sources and sinks in tons/km$^2$, February.
Figure 41.--Other pelagic fish sources and sinks in tons/km$^2$, August.

Figure 42.--Monthly biomasses of herring with normal temperature and with a 1.5°C wintertime positive temperature anomaly in the eastern Bering Sea over two years.
5. EFFECTS OF ENVIRONMENTAL ANOMALIES ON PELAGIC RESOURCES

The DYNUMES model permits evaluation of the effect of water temperature on the growth and feeding. Thus the effects of temperature anomalies in the eastern Bering Sea on the changes of biomass of pelagic fish were investigated, using the effect of lower temperatures on growth as described in Chapter 3.1. In one of the model runs, a +1.5°C temperature anomaly in the surface layers was prescribed. The monthly biomass changes of equilibrium biomass of herring in normal temperature conditions and with a wintertime anomaly reduces normal growth suppression by prevailing low temperatures during the winter. Interpolation of the directly computed biomass change shows that an 0.8°C temperature anomaly will cause a 100,000 ton annual biomass difference from EB as averaged over two years.

The sources and sinks of the herring biomass during a winter with +1.5°C positive temperature anomaly are shown on Figures 43 to 45 which depict rather pronounced changes from normal conditions (see Figures 28 to 30). The resulting distribution of herring in December after two winters with the positive anomaly is shown on Figure 46. Comparison with normal conditions (see Figure 5) indicates a considerable increase of biomass, especially in the northern part of its main distribution.

The sources and sinks of other pelagic fish for February during a +1.5°C positive anomaly (Fig. 47) when compared with normal conditions (Fig. 40), indicate a considerable increase in the source levels off the continental slope and a decrease in the sink levels on the continental shelf NNW of the Pribilof Islands. The distribution of other pelagic fish for December, after two years of computation with +1.5°C positive anomaly is given in Figure 48. Comparison with normal EB distribution in the same month (see Figure 10) indicates an increase in the biomass of both centers of abundance.
Figure 43.—Herring sources and sinks in tons/km$^2$ in January (1.5°C positive anomaly).

Figure 44.—Herring sources and sinks in tons/km$^2$ in February (1.5°C positive anomaly).
Figure 45.—Herring sources and sinks in tons/km$^2$ in March ($1.5^\circ$C positive anomaly).

Figure 46.—Distribution of herring in tons/km$^2$ in December, second year; wintertime $1.5^\circ$C positive anomaly.
Figure 47.--Other pelagic fish sources and sinks in tons/km\(^2\) in February (1.5\(^\circ\) C positive anomaly).

Figure 48.--Distribution of other pelagic fish in tons/km\(^2\) in December, second year; wintertime 1.5\(^\circ\)C positive anomaly.
The magnitude of the effect of the temperature anomaly on the biomass changes (via physiological processes) turned out to be considerably larger and more significant than expected before computations. These effects might explain a great part of the relatively large fluctuations of fish stocks observed in other high latitude areas.

Although the model also contains temperature effects on feeding (food uptake), slightly increased natural mortalities in subzero temperatures, and an accelerated migration of most fish species out of areas colder than about $-0.2^\circ C$, it does not include some specific effects on ripening and on spawning area dislocations. Shavoneev (1965) observed that herring ripened earlier in warm years. Furthermore, the herring spawned in many locations along the north coast of the Alaska Peninsula in spring 1976 which was anomalously cold. No spawning along the Alaska Peninsula was observed in spring 1977 which was preceded by a warm winter (P. Jackson, Alaska Department of Fish and Game, Kodiak, pers. comm.). This observation might indicate that Bering Sea herring do not have a pronounced "homing instinct" as observed in the herring in the Gulf of Alaska. Furthermore, the northward shift of spawning (and distribution) of Bering Sea herring during warm years seems to be analogous to some degree to the long-term northward shift of Hokkaido herring during warm years (Nagasaki 1973).
6. EFFECTS OF FISHERY

The effects of fishery in the DYNAMIES model can be simulated by changing the fishing effort (intensity) coefficient either as to location, time, or magnitude or a combination of these changes. A few computer runs were made with changed magnitude of fishing effort coefficient to study the resulting effects of increased/decreased catches on the biomass. Results of two runs with different fishing effort are presented in Figure 49. Interpolation of the results shows that 11,300 tons of annual change in the fishery (at EB) would result in 100,000 tons of annual herring biomass change as averaged over two years.

As the annual migration cycle remains unchanged in the model, the increased winter fishery near the continental slope northwest of the Pribilof Islands causes a lowering of herring biomass in this area, as comparison of Figures 50 and 5 indicate.

The fishing effort coefficient acts as a density dependent parameter; consequently, a given constant total catch has different effects at different biomass magnitudes. Thus, management decisions for regulation of the fishery by total allowable catch would require best available and reliable knowledge of the level of biomass of the species under consideration. Various biomass levels for this purpose can be simulated with the DYNAMIES model which can be used in a relative and comparative manner in the estimation of the various effects of fishery. The latter can also be simulated as a spatial and temporal variable according to realistic fishing possibilities and their limits.
Figure 49.--Monthly biomasses of herring with $47 \times 10^3$ and $75 \times 10^3$ tons annual catch in the eastern Bering Sea over two years.

Figure 50.--Herring distribution in tons/km$^2$ in December, (75x10$^3$ tons catch).
7. LONG-TERM CHANGES OF ABUNDANCE AND DISTRIBUTION

Long-term changes in most individual members of the ecosystem are dependent on changes in abundance and/or distribution of any one of the components of this system, biological and/or environmental. A complete, prognostic ecosystem model, such as DYNAMES, is a prerequisite for realistic long-term fluctuation studies. There are numerous possible causes for the long-term changes and the need for long computer runs make these studies costly.

Some of the major causes of long-term changes are:

a) Increase/decrease of consumption of a given species, caused by changes of abundance and/or distribution of the predator(s), and changes of abundance and distribution of prey (density dependent feeding).

b) Effects of environmental anomalies (changes of growth rates and availability of food).

c) Effects of the fishery.

d) Spawning and larval survival fluctuations (dependent mainly on grazing and environmental factors).

In an earlier work (Laevastu and Favorite 1976b), the effects of long-term changes in pollock biomass, caused by cannibalistic interactions, on the biomass of herring were studied and an inverse correlation between pollock and herring biomasses was found. It was postulated that the high pollock biomass in the early 70's in the eastern Bering Sea might have contributed materially to the lowering of herring biomass in the area. Such cyclic changes can occur within other species as well. The effects of grazing by squids and marine mammals on herring have been described, as have been the effects of the environment and the fishery.
All long-term changes are time dependent processes and their magnitudes also depend greatly on the state of biomass in relation to the equilibrium biomass at the time of the action of the forcing (i.e. initial influence of the causing event and/or condition). Four 5-year model runs with various initial biomasses of herring were made with density dependent feeding on herring and a constant fishing effort (i.e. annual catch being proportional to biomass present). If the biomass (Fig. 51) is below EB (curve A) level, such as curves B and C, it recovers slowly towards EB (see remarks at the end of the curves) even with direct density dependent feeding--the recovery would be somewhat faster with more selective feeding. If the biomass is, however, below a "threshold value" (curve D) it continues to decline (see Chapter 8). The magnitudes of annual fluctuations within the biomass decrease with decreasing biomass.

Long-term changes can be initiated with individual alterations in most components of the ecosystem by such factors as cannibalistic interactions, successive low year classes, and other causative factors listed above. The magnitudes and periods of long-term cycles are affected by the speed of recovery, which in turn is affected by the same causative factors with opposite signs.

The magnitudes of sources and sinks, and to a lesser extent their areal distributions, change also with the changing magnitude of biomasses (compare Figures 52 and 54 with Figure 29). It has been generally observed for many species and areas that the distribution patterns of increasing and declining populations behave differently. Our model results clearly indicate that declining populations (biomass) shrink toward the center of their main abundance (compare Figures 53 and 6 with Figures 5 and 3, respectively) and that the fringe populations disappear first. Increasing biomasses, however, expand in their areal distributions.
Figure 51.--Monthly herring biomasses in the eastern Bering Sea over five years (initial biomasses in million tons: A=2.75; B=1.59; C=0.94; D=0.45).

Figure 52.--Herring sources and sinks in tons/km² in February, fourth year; initial biomass 1.59 million tons.
Figure 53.—Distribution of herring in tons/km² in February, fourth year; initial biomass 1.59 million tons.

Figure 54.—Herring sources and sinks in tons/km² in February, fourth year; initial biomass 0.94 million tons.
8. SOME ADDITIONAL FACTORS AFFECTING BIOMASS FLUCTUATION OF HERRING

One of the serious problems in past population dynamics considerations has been the inability to distinguish quantitatively between the components of "natural mortality" (grazing (consumption), starvation, diseases, etc.) and the man-made mortality (fishing). A complete ecosystem model, such as DYNUMES, has made the separate, detailed evaluation of the dominating component--grazing--possible. As a result, many of the earlier used terms become nebulous, such as recruitment overfishing (assuming that the fishery affects the recruitment of juveniles to adult stock), and growth overfishing (assuming that the fishing exceeds growth, causing stock decline).

Our results with the DYNUMES model clearly demonstrate that the ecosystem internal consumption can far exceed any fishery effects on biomass fluctuations in the eastern Bering Sea and that growth overfishing consequently loses its definition (and at best becomes a space-time dependent minor factor in source-sink considerations). The problems of (juvenile) recruitments are briefly discussed below and will be subject to special study with an extended DYNUMES model in the future.

8.1 Some stock recruitment relations and threshold biomass

There is a general lack of quantitative knowledge on the early life dynamics of all species; therefore, recruitment is made proportional to biomass levels in the DYNUMES model. This assumption is supported by other earlier conclusions that mean recruitment levels are almost constant (Beyer 1976; Andersen and Ursin 1977). Still, stronger than normal year classes occur in most species which are important in the fishery and its management. Thus, it is of interest to examine briefly the causes of year class variations,
such as the size of spawning stock dependence, survival of eggs and early larval starvation as affected by temperature (via growth rate, food availability, and hatching time), transport to unfavorable areas and depths and, above all, the postlarval grazing.

The number of spawners seems not to be of great importance in determining year class strength in most pelagic fishes if the biomass has not fallen close to the threshold value (for definition see below). Strong year classes can rise from a relatively small number of spawners, because optimum best survival of larvae is usually related to an intermediate number of spawners. When Pacific herring and capelin spawning is intense on limited spawning grounds in shallow water, several layers of eggs are deposited and hatching success is low. Additional egg mortalities are caused by intensive wave action (storms), exposure to air (low tides and wind effects), and by heavy predation by birds.

Generally the Pacific herring biomass in the eastern Bering Sea is assumed to consist of western, eastern, and Norton Sound stocks. There is, however, no firm basis for this division, nor further division into different races with specific spawning grounds (Prokhorov 1968). If separate wintering and spawning areas exist, these can be altered by environmental anomalies (Shaboneev 1965; P. Jackson, ADFG, personal communication). During cold spring conditions, herring spawn in abundance on southern spawning grounds, whereas during warm spring conditions the northern spawning grounds are crowded. After hatching, the availability of proper plankton as food is surely one of the factors affecting larval survival. This plankton availability is enhanced by environmental factors, such as temperature and radiation anomalies, and
piling up of warmer and plankton-rich water near the coast. Early transport of larvae to offshore areas might be detrimental to proper food availability (deep mixing, spring plankton blooms starting earlier near the coast, etc.).

Grazing might take over the control of larval biomasses already in rather early stages. The larval stages can be considered as part of zooplankton standing stock. Thus the larvae can be expected to be grazed at the same rate as zooplankton, the grazing rate of which can be high in some areas and seasons (see Figures 55 and 56). However, if the abundant occurrence of larvae does not coincide with areas of high zooplankton consumption, the larval survival is enhanced.

After larvae become nektonic, grazing in an active selective feeding mode takes over. This feeding is largely size dependent and is considerable during larval and early juvenile stages (see Figure 14). Considering the above, it appears that the year class strength is not determined by the size of the spawning stock but by the survival in late larval and postlarval stages.

It can be postulated that there might be some threshold size of a biomass of a given species below which the population cannot regenerate to its previous size, because it is suppressed by other species that have utilized their opportunity to take over the ecological niche. This succession can be caused by overgrazing (i.e. sinks exceed sources), competition for food, too low a density of spawners on spawning grounds (egg fertilization problems and/or heavy grazing on eggs), and difficulties in school formation (which is an integral part of spawning migrations, and spawning). Only the first possible cause, mentioned above, can be investigated with the present DYNUMES model,
Figure 55.—Percentage of mean zooplankton standing stock consumed in February.

Figure 56.—Percentage of mean zooplankton standing stock consumed in August.
for which runs were made to determine the possible threshold biomass for herring. A density dependent feeding was used in this run (i.e. herring consumption by predators is dependent on the quotient: present biomass/EB (equilibrium biomass)). The results showed that the threshold biomass of the herring in the eastern Bering Sea is 0.5 million tons (see Figure 51, curve D).

8.2 "Herring equivalences"

It is of importance to quantify and rank the various factors affecting the biomass fluctuations of any commercially important species. It is also of paramount importance to determine the degree to which fisheries management can affect the resource abundance.

In the earlier chapters, several factors affecting the pelagic fish biomasses were singled out and special computer runs were made with two years' real time simulation to determine quantitatively their effects. The results are summarized in Table 3. It should be noted that these equivalences would be different if the biomass were below EB. Furthermore, there are numerous other factors in the ecosystem that will cause magnification of these equivalences; thus they should be used only for comparative purposes.

One of the striking features in these equivalences is the large effect of surface temperature anomalies where the effect of only 0.8°C temperature anomaly during the winter is equivalent to the effect of 1.3x10³ tons of herring catch. Therefore, wise, flexible fisheries management in the eastern Bering Sea would require the monitoring of the wintertime (surface) temperature anomalies and their accounting in management decisions. Satellite imagery of ice cover is extremely useful in this regard.
Table 3.--"Herring equivalences" in the eastern Bering Sea. (Factors and processes each of which cause a $100 \times 10^3$ tons of herring biomass change per year (averaged over two year effects) in the eastern Bering Sea.)

<table>
<thead>
<tr>
<th>Factors and processes</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Decrease of consumption of herring by mammals (i.e. decimating mammal herds).</td>
<td>22%</td>
</tr>
<tr>
<td>2) Increase/decrease of consumption of herring by squids (i.e. lower biomass of squids).</td>
<td>26%</td>
</tr>
<tr>
<td>3) Increase/decrease of fishery on herring (per year)</td>
<td>$11.3 \times 10^3$ tons</td>
</tr>
<tr>
<td>4) Surface temperature anomaly during winter months</td>
<td>$0.8^0C$</td>
</tr>
<tr>
<td>5) Increase/decrease of older/larger pollock (&gt;45 cm length) biomass</td>
<td>$390 \times 10^3$ tons</td>
</tr>
</tbody>
</table>
Secondly, one can notice that the direct fishery effects on herring are relatively small as compared to the effects of grazing by mammals. Thus it is questionable to try to manage fisheries in the eastern Bering Sea if marine mammals are not managed simultaneously by the same management body.

It should also be borne in mind that the effects of changes of many other ecological factors propagate through this system in various ways, usually favorable to one but unfavorable to another component. Equivalences, such as presented in Table 3 can be computed for additional effects/factors and for other species as well, if proper manpower and funds were made available.
9. SUMMARY

The factors and processes controlling the abundance of pelagic fish in the eastern Bering Sea were studied quantitatively with the DYNAMES III model. This model permits a relative assessment of the total ecosystem and allows, among others, a detailed quantitative computation of ecosystem internal consumption, which has been the greatest unknown quantity in conventional natural mortality coefficients.

1) The "equilibrium biomass" (EB) of the herring in the eastern Bering Sea is 2.7 million tons, which compares favorably with Shaboneev's (1965) evaluation of 2.2 million tons.

2) A threshold value for herring biomass has been found (0.5 million tons), below which the recovery could be very slow indeed.

3) There are long-term fluctuations in abundances of most species. Due to interspecies interactions these long-term fluctuations propagate through the whole ecosystem. Pollock have a long-term fluctuation caused by cannibalistic interactions and the herring biomass fluctuates inversely with pollock biomass.

4) There are no data available to determine the exact state of the biomass of herring at present. Because of the great abundance of older pollock a few years ago, it could be assumed that the herring biomass was low, but is recovering at the present due to the decrease of the older pollock biomass by the intensive fishery on this species.

5) The equilibrium biomass of other pelagic species in the eastern Bering Sea is 4.3 million tons.

6) The ecosystem internal consumption and its year-to-year changes far exceed the fishery effects on the biomass changes.
7) Annual consumption of herring by marine mammals is at present more than 10 times higher than the annual herring catch. The main herring consumers by mammals are toothed whales (including the sperm whale), followed by pinnipeds. For meaningful fishery management it is, therefore, imperative to manage mammal herds concurrently with fisheries management, preferably by the same management body.

8) The annual turnover rate of herring is 0.5 and of other pelagic fish, 0.95. The magnitude of the annual biomass fluctuation in herring decreases with decreasing biomass.

9) The monthly source (growth exceeds removal) and sink (removal exceeds growth) areas of pelagic fish have been mapped. These source-sink maps are useful in devising research and management criteria.

10) There is, in general, a sink of biomass at the periphery of distribution which decreases from center toward periphery. Declining populations shrink towards the centers of main abundance and many fringe populations disappear first. Increasing populations expand their areal extent.

11) Growth rate of the biomass of any species depends on the distribution of biomass with age, due to rapidly decreasing growth rates with age. The average distribution of herring biomass with age is presented.

12) Growth rate is also dependent on temperature and is affected by cold winter temperatures at high latitudes. The effect of temperature anomaly during the winter was surprisingly high. An 0.8°C temperature anomaly during the winter months had equivalent effect of $1.13 \times 10^3$ tons of annual herring catch increase/decrease. Consequently, it is of great importance to monitor the temperature anomalies in the eastern Bering Sea in order to achieve optimum fisheries management.
13) The study of the effects of changing annual catches on the EB showed that 11,300 tons annual catch change is equivalent to 100,000 tons annual biomass change at EB.

14) The early larval stages of pelagic fish are grazed at the same rate as zooplankton, the grazing rate of the latter being relatively high in some areas and season. Year class strength in general seems to be largely determined by ecosystem internal grazing in postlarval and early juvenile stages, rather than by the number of spawners.

15) Some "herring equivalences" are given which show that grazing by marine mammals, interspecies interactions (e.g. consumption by squids), and wintertime water temperature anomalies have greater effects on herring biomass fluctuations than a modest fishery.
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