



**Northwest and  
Alaska  
Fisheries Center**

**National Marine  
Fisheries Service**

**U.S. DEPARTMENT OF COMMERCE**

## **NWAFRC PROCESSED REPORT 79-19**

**Interactions Between Biomass  
Distribution, Growth, Predation,  
and Spawning Stress Mortality  
of Marine Fish  
(and applications in management)**

**October 1979**

## **NOTICE**

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

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



INTERACTIONS BETWEEN BIOMASS DISTRIBUTION, GROWTH, PREDATION,  
AND SPAWNING STRESS MORTALITY OF MARINE FISH  
(and applications in management)

By

Erich Granfeldt

Resource Ecology Task  
Resource Ecology and Fisheries Management Division  
Northwest and Alaska Fisheries Center  
Seattle, WA 98112

October 1979

U.S. Department of Commerce  
National Oceanic and Atmospheric Administration  
National Marine Fisheries Service  
Northwest and Alaska Fisheries Center  
2725 Montlake Boulevard East  
Seattle, Washington 98112

INTERACTIONS BETWEEN BIOMASS DISTRIBUTION, GROWTH, PREDATION,  
AND SPAWNING STRESS MORTALITY OF MARINE FISH  
(and applications in management)

by

Erich Granfeldt

Northwest and Alaska Fisheries Center  
Seattle, WA 98112

Annotation: An examination of biomass dynamics of some exploited populations of marine fish using empirical data, with special emphasis on the importance of growth rate and predation. Determination of spawning stress mortality and the application of biomass dynamics and spawning stress mortalities in fisheries management.

Abstract.

1. Introduction.
2. Numerical methods and data.
3. Peculiarities in growth of species and population biomass.
4. Distribution of biomass with age within a population.
5. Change of total mortality with age, and spawning stress mortality.
6. Use of biomass distribution, age variable mortality, and growth in fisheries management.
7. Summary.
8. References.

## ABSTRACT

Growth rate of a species is a function of food intake, state of maturity, and of temperature of the environment (via physiological effects). The growth rate of a population is, in addition, dependent on the distribution of the biomass by age within the population. The change of the biomass of a population cohort with time and the age of biomass maximum are primarily functions of growth and total mortality rates and their changes with the age of the cohort.

The total mortality rate of the exploited part of the population can be computed from long-term mean (composite) numerical year class strength data. This study demonstrates that there is a considerable increase of mortality after a certain age, which is called here spawning stress mortality. The rate of increase of this mortality is similar in all species studied here. The total mortality of a cohort is at a minimum before the population has reached about 80% maturity, i.e., at the age (and size) where the predation mortality has become low due to the increased size of the species and before spawning stress mortality has commenced.

The total mortality of prefishery juveniles can be computed, assuming a turnover rate for the population, derived from large-scale ecosystem models. As the predation mortality is a function of predator-prey size dependent feeding in the ecosystem, the predation mortality rate decreases rapidly with the size of the species and is thus also a function of growth rate.

The interactions between growth rate, predation, and spawning stress mortality determine the source and sink areas and periods of a cohort biomass. There can be two biomass maxima in a slow growing cohort. The maximum yield per cohort occurs 1 to 5 years after full recruitment to the fishery.

## 1. INTRODUCTION

Cushing (1973) noted that the age structure of a marine fish population has rarely been described in full. Cushing also pointed out that the trend of natural mortality with age should be known and that a death rate that is constant in age is unlikely because the population cannot be terminated in age. Furthermore, Cushing (1973) showed that the age distribution of biomass must reach a maximum at a given critical age when biomass growth and mortality rates are equal.

In an earlier report (Alverson and Carney 1975) a theory of growth and decay of a cohort was developed in general terms, using von Bertalanffy equation parameters and various constant natural mortalities. This report presents results of detailed studies of biomass distribution with age of a number of fish populations from the Bering Sea and Gulf of Alaska, using empirical data on growth (as the von Bertalanffy equation has severe limitations in presenting the growth at younger ages) and an empirically computed total mortality which changes with the age of the cohort.

The changes in growth rates of most species with latitudes (and general locations) as well as with time in a given region are well known. It can be expected that these growth rate changes will affect the distribution of cohort biomass within a population, which was studied and reported here.

Natural mortality of a cohort is expected to change with age (and with growth rates), especially if predation is a predator-prey size dependent process (as has been abundantly demonstrated lately, e.g. Daan 1973) and if there exists a considerable spawning stress mortality (Andersen and Ursin 1977) or an age dependent senescent mortality (Beverton 1963, Cushing 1973). These changes in mortality rates with age would affect the biomass

distribution with age within a population. The change of mortality with age was studied on a number of species from the Bering Sea and Gulf of Alaska and is reported herein. Furthermore, the implications of the above-mentioned changes of the biomass distribution of a cohort on the fisheries management are also explored.

### 3. NUMERICAL METHODS AND DATA

The method for computation of various biomass parameters with age in a marine fish population has been described by Granfeldt (1979). This method allows the extrapolation of juvenile (prefishery) biomasses using biomass turnover rate as one of the criterions. Furthermore, the method permits the computation of age-dependent total mortality.

Empirical data on weight at age are needed for computation of growth rates. These data are usually available, separated by sexes. For the present study the data for both sexes were combined. Some difficulties are usually encountered in obtaining accurate weight data for the youngest ages (1 and 2 year olds). As the condition factor does not change materially in marine fishes (except during sex product development), the length at age data can be converted to weight at age, using a previously established conversion graph ("key"). The von Bertalanffy equation, although useful in some earlier population dynamics work, is not useful in the present study because of its inherent inaccuracy in younger and older ages and because it smoothes out some small, but biologically significant changes in growth rate. The weights at age of five species from the Bering Sea are shown on Figure 1. Figure 2 shows the weight at age of rock sole, Lepidopsetta bilineata, in the Bering Sea

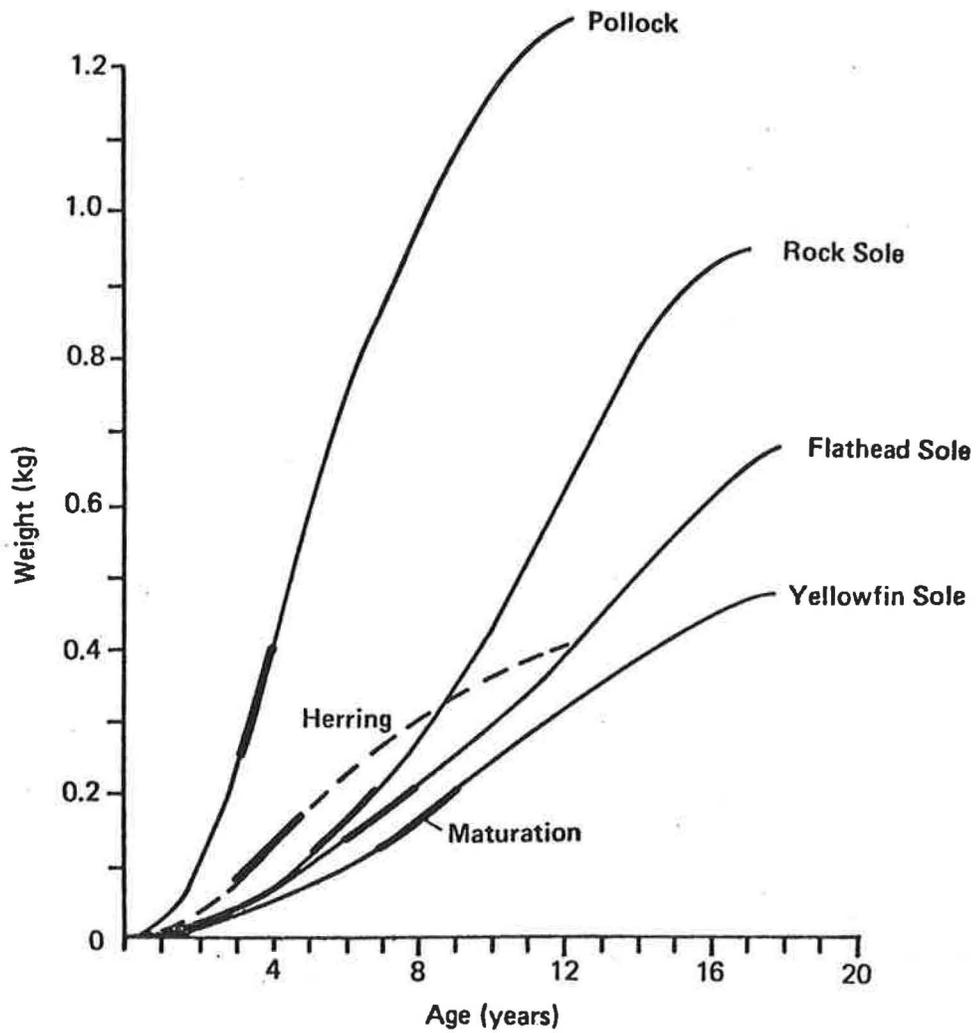


Figure 1.--Weight at age of five species from the eastern Bering Sea.

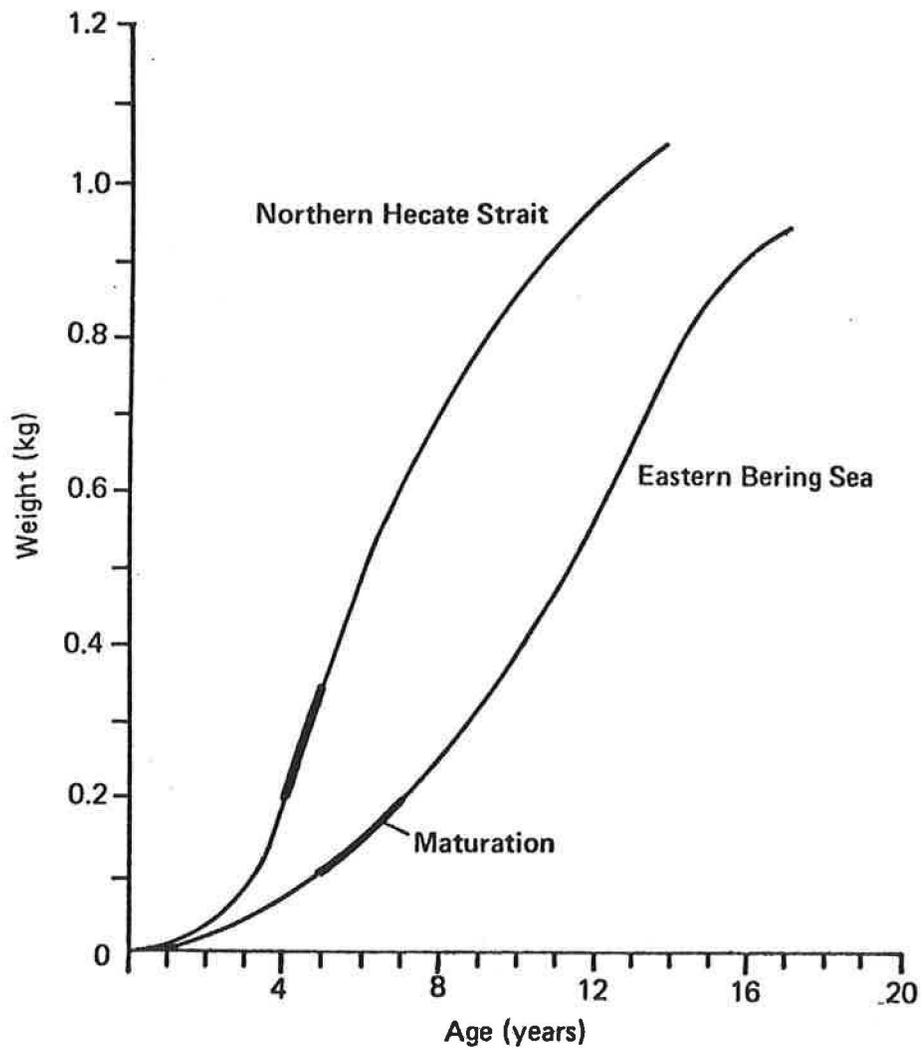


Figure 2.--Weight at age of rock sole from the eastern Bering Sea and northern Hecate Strait, British Columbia.

and in northern Hecate Strait off British Columbia, demonstrating the pronounced differences in growth in one given species in different regions with different temperature conditions.

The second set of basic data for this study is the long-term mean age frequency distribution of fully recruited year classes. To eliminate the effects of strong and weak year classes, it was established that the basic data series for this purpose should cover at least 10 years and that the sampling in individual years should cover several seasons and different area/depth zones. Furthermore, the minimum number of fish measured in any given year was about 2,000 and the average was more than twice this number.

Year classes which were not fully recruited to fishery were excluded from the summary. Despite this exclusion some adjustment was usually necessary in the first year selected as fully recruited year class. This adjustment did not exceed about 12% of the given year class strength, limiting the possible total error in this compilation to a maximum of about 2%.

The percent composition of fully recruited population of four species are given in Figure 3; the percent composition of exploitable population of rock sole in the Bering Sea and in northern Hecate Strait are given in Figure 4. The data originate from the Northwest and Alaska Fisheries Center's surveys in the eastern Bering Sea and cover the period from 1963 to 1976. The data for yellowfin sole, Limanda aspera, were taken from Maeda (1977) and data for rock sole in northern Hecate Strait, British Columbia, from Forrester and Thompson (1969).

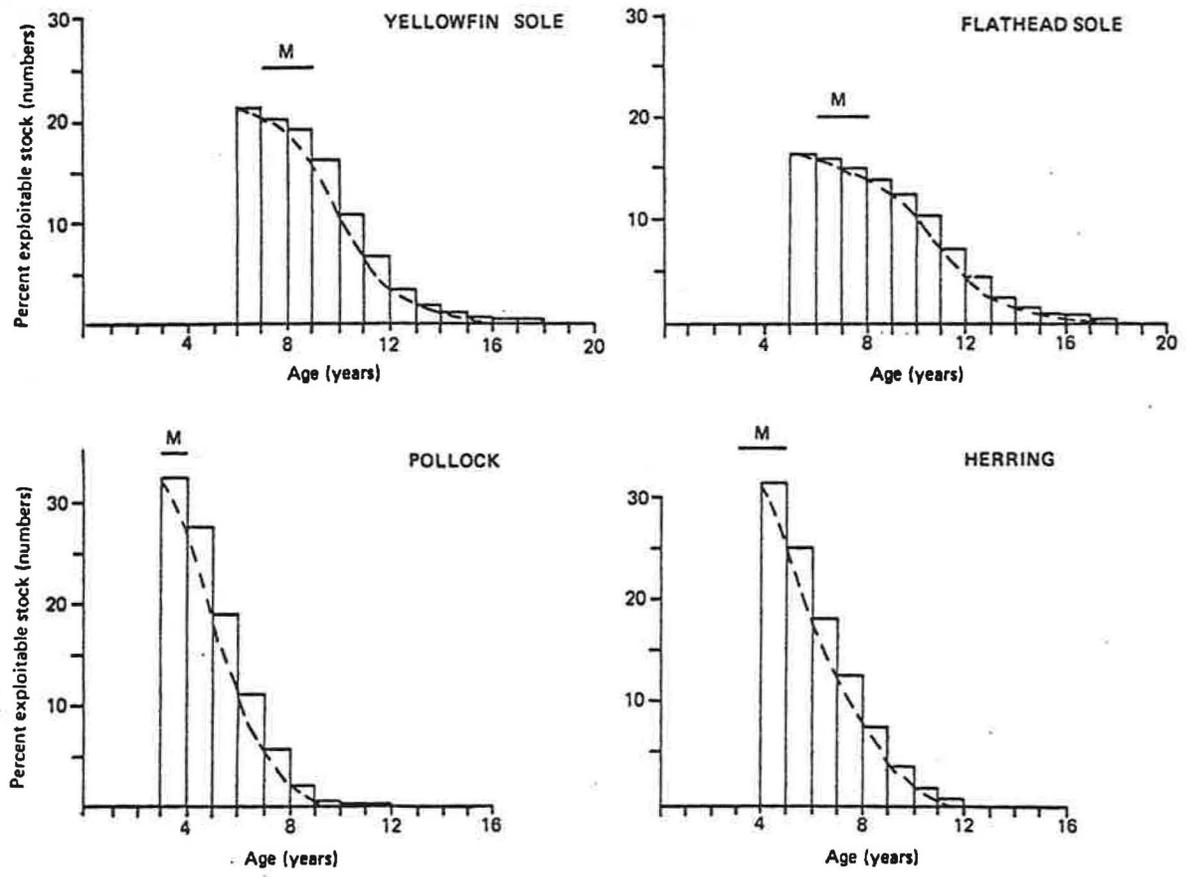


Figure 3.--Long-term mean age frequency distribution of fully recruited year classes (in % of numbers) of four species from the eastern Bering Sea. (M - maturation period).

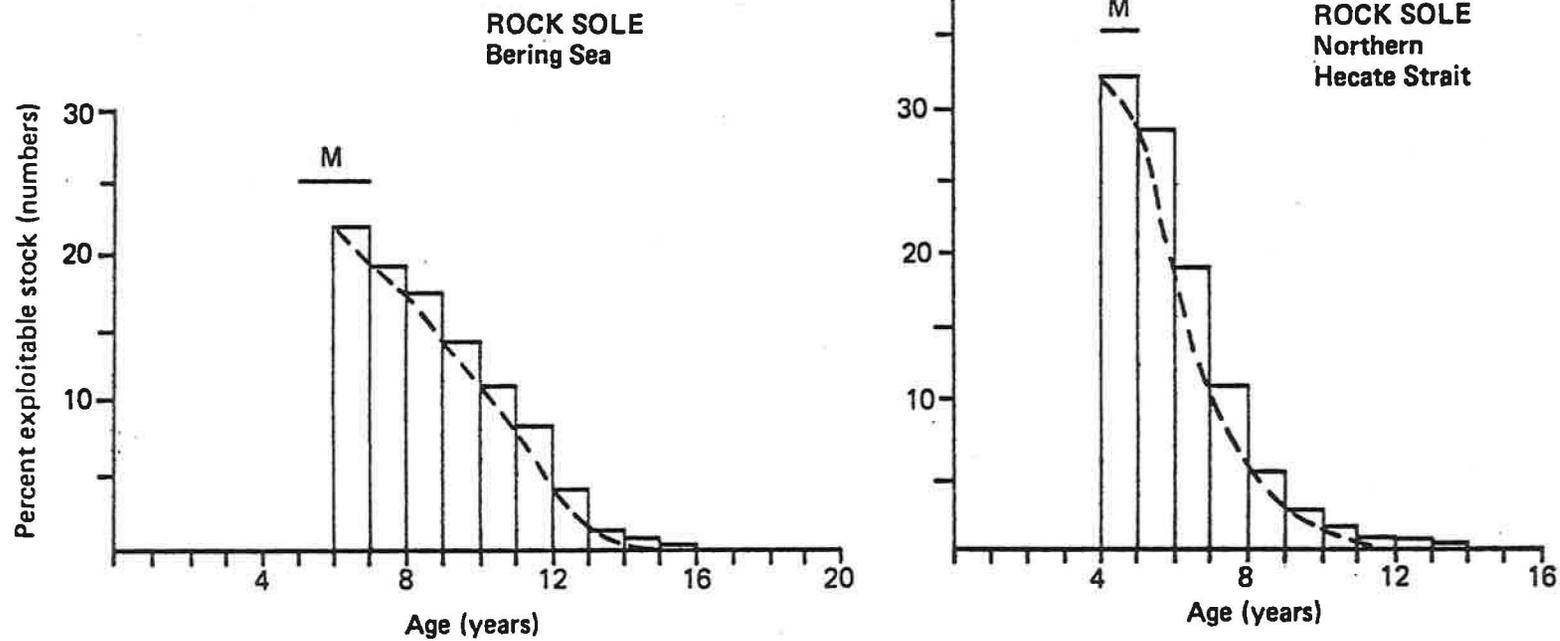


Figure 4.--Long-term mean age frequency distribution of fully recruited year classes (in % of numbers) of rock sole from the eastern Bering Sea and northern Hecate Strait (M - maturation period).

The time of maturation of the species became an essential consideration in the analyses of the senescent spawning stress mortality. The data on this subject are rather deficient and mostly limited to occasional notes in the literature. Thus the maturation times marked on most of the figures with a bar and M are in some species somewhat uncertain as discussed later. The definition of maturation of a population is complicated by the maturation process itself. The maturation marks on the figures indicate the period (years) when the population is about 40% to 80% mature (end of the bar). The maturation is a function of growth (size); thus if a species grows faster in a given location, it matures earlier (see rock sole on Figure 2). Furthermore, it has become apparent in many stocks that if the growth rate of a species in a given region increases, the maturation would occur earlier. Further complications in determining the maturation state of a population are caused by differing growth rates and maturation times of males and females.

### 3. PECULIARITIES IN GROWTH OF SPECIES AND POPULATION BIOMASS

The weight at age data for the species studied are shown in Figures 1 and 2. As the growth rate of species also varies with time in a given region, apparently as a function of its density (and food availability as well as temperature anomalies), an attempt was made to establish a long-term mean weight-age data set.

The growth rate is a necessary parameter in a variety of population dynamics and ecosystem computations. Its change with age reveals some typical episodes during the lifetime of the species (Figures 5 and 6).

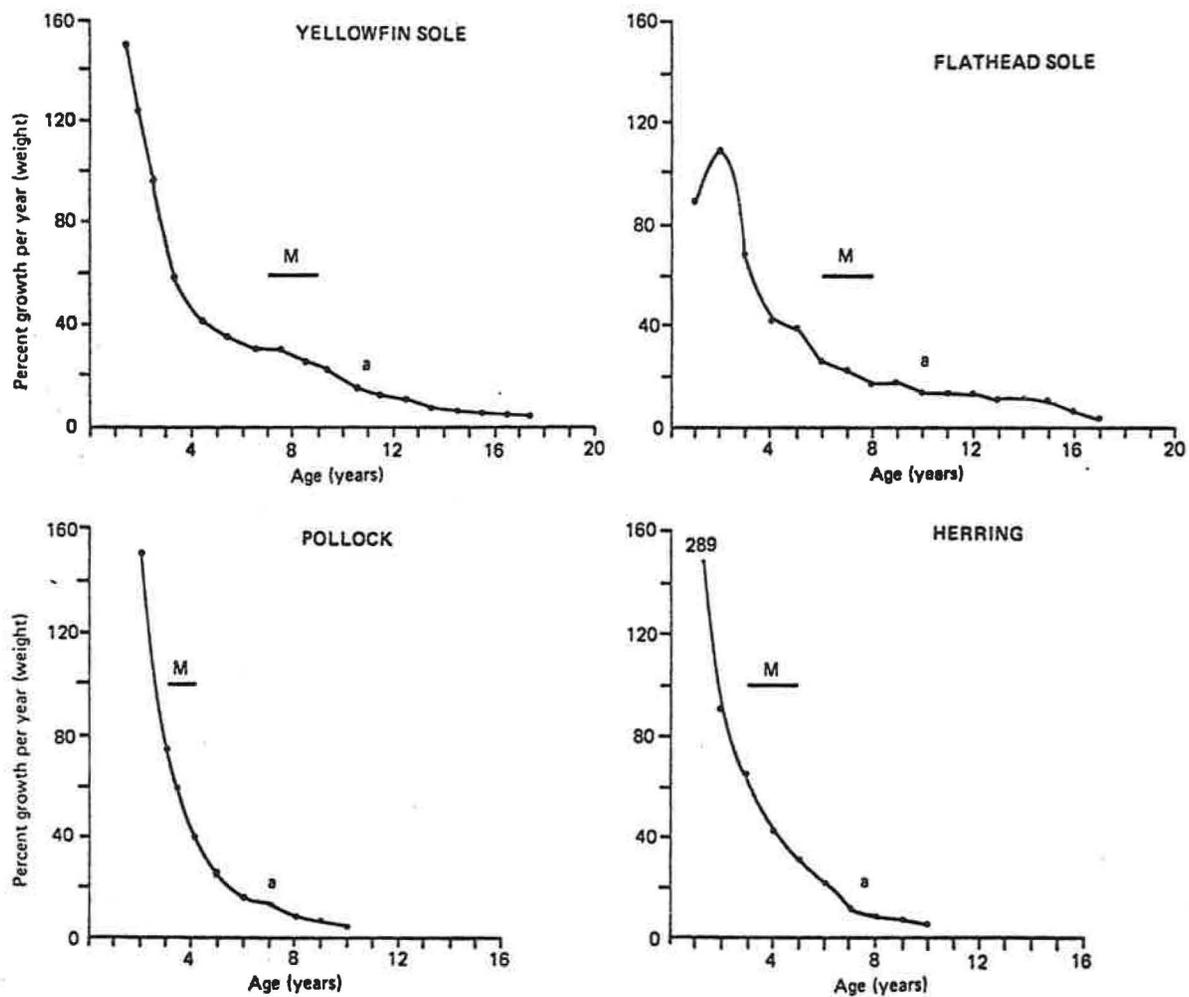


Figure 5.--Annual growth rates (in % of weight per year) of four species in the eastern Bering Sea.

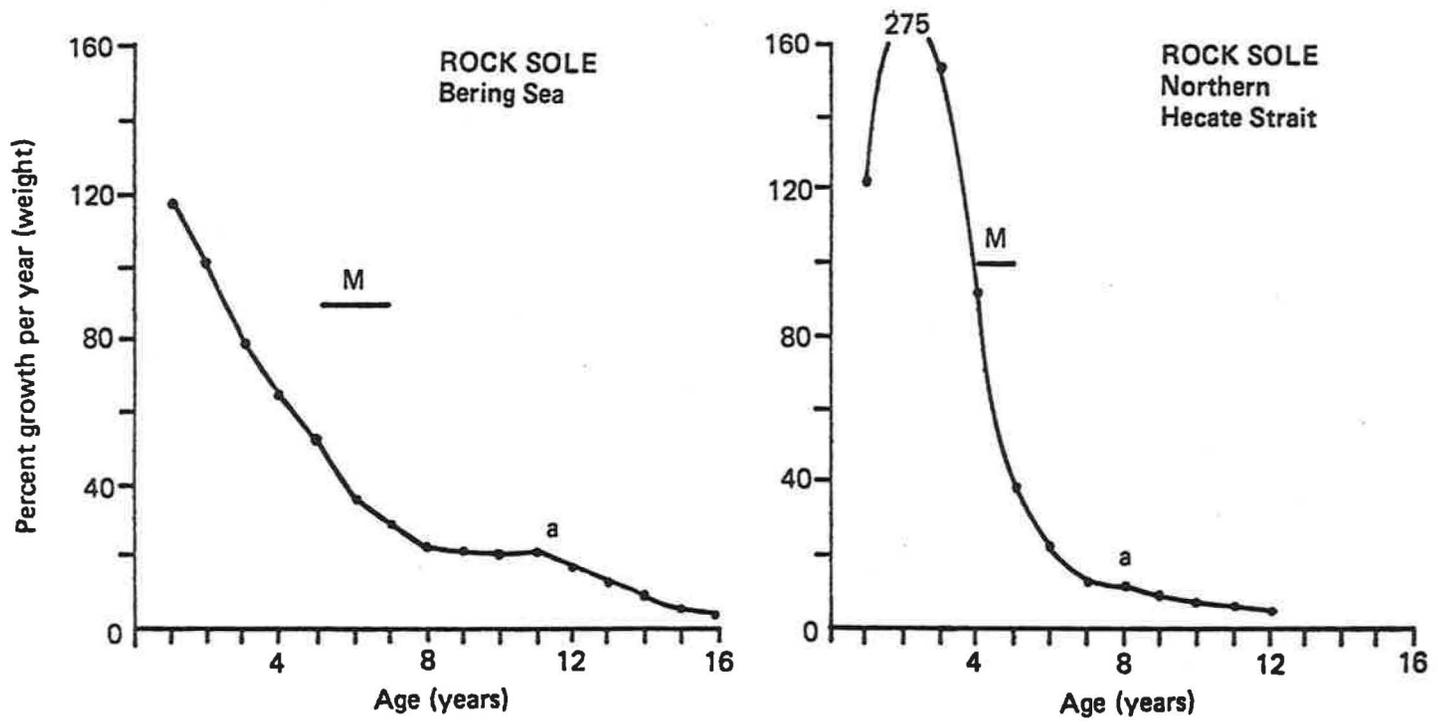


Figure 6.--Annual growth rates (in % of weight per year) of rock sole in the eastern Bering Sea and northern Hecate Strait.

The growth rate of a fast growing species in the first and second year can be several hundred percent of the mean biomass of the year class. By the fourth year the growth rate has decreased in most species to about 40% per year. About 1 year after maturation the annual growth rate decreases to 20% and below. The inflection in growth curves has been pointed out earlier by Paloheimo and Dickie (1965). About 3 years after maturation there is another characteristic sharp drop in growth rate (marked with "a" on Figures 5 and 6), the significance of which is not fully clear. The lower growth rates after sexual maturity are most probably caused by physiological causes, such as energy requirements for sex product development and difficulties in obtaining adequate amount of food.

The growth rate of a population is different from the growth of the species. It can be computed after the biomass distribution with age in the population has been determined (see next chapter). A summary of biomass growth coefficients for rock sole from the eastern Bering Sea and from northern Hecate Strait are given in Table 1 as monthly compound percent of growth (analog to compound interest rate). The biomass growth coefficients are also dependent on the turnover rate of the whole biomass of the population. (Two turnover rates were used for data in Table 1: 0.60 and 0.75). The most pronounced difference in the growth rates of rock sole in two locations is in the juvenile population, which grows much faster in more southern latitudes (northern Hecate Strait) than in the Bering Sea. The theoretically computed growth rate of this part of the population which has died (been eaten) during the year ("deceased" population) is normally higher than the mean for the whole population, because the greatest removal of the population biomass occurs in juveniles through predation mortality, where the growth rates are higher.

Table 1.--Distribution of growth, biomass, and numbers between juvenile and exploitable population of rock sole from the Bering Sea and from northern Hecate Strait.

Subject		Bering Sea		Hecate Strait	
		<u>turnover rate</u>	<u>turnover rate</u>	<u>turnover rate</u>	<u>turnover rate</u>
		.60	.75	.60	.75
Monthly growth coefficient (%)	Whole population	3.25	3.64	3.20	3.75
	Juvenile population	5.22	5.34	8.69	8.64
	Exploitable population	1.73	1.74	2.21	2.27
	* "Deceased" population	4.19	4.62	.07	5.44
Biomass (%)	Juvenile population	43.6	52.8	15.3	23.3
	Exploitable population	56.4	47.2	84.7	76.7
Numbers (%)	Juvenile population	92.2	94.8	77.1	86.7
	Exploitable population	7.8	5.2	22.9	13.3
Total Mortality					
Biomass (%)	Juvenile population	66.8	75.3	32.9	49.8
	Exploitable population	33.2	24.7	67.1	50.2
Numbers (%)	Juvenile population	97.8	98.5	92.2	96.1
	Exploitable population	2.2	1.5	7.8	3.9

\* Computed growth rate of the part of the population which has died during the year (mostly from being eaten).

#### 4. DISTRIBUTION OF BIOMASS WITH AGE WITHIN A POPULATION

The long-term mean distribution of numbers in a fully exploited population was obtained from data, and the distribution of numbers of prefishery juvenile year classes was computed with an iterative procedure as described by Granfeldt (1979). The distribution of juvenile numbers (and biomass) is also dependent on turnover rate of the biomass of the population. To demonstrate (and evaluate) the effect of turnover rate on the computed parameters, the results of computations with two turnover rates (0.60 and 0.75) are shown on the figures in this paper.

The relative distributions of the numbers in year classes of slow-growing species (yellowfin sole) and another faster-growing species (walleye pollock, Theragra chalcogramma) are shown on Figure 7. By the fourth year the percentage of total numbers per year class has decreased in both species below 10% of the total numbers. The faster growing species (pollock) has somewhat higher percentage of numbers of fish in year classes 4 to 7 than the slower growing yellowfin sole. This difference is mainly caused by the faster growth of pollock, whereby the juveniles grow faster to the size where the number (and amount) of predators is smaller (re size dependent feeding/predation), thus decreasing the predation in numbers.

The distribution of biomass of four species from the Bering Sea is given on Figure 8 and the biomass distribution of rock sole from two different locations (with different growth rates) is given on Figure 9. In slow growing species (yellowfin sole; flathead sole, Hippoglossoides elassodon; rock sole from the Bering Sea; Pacific herring, Clupea harengus pallasii) there is one

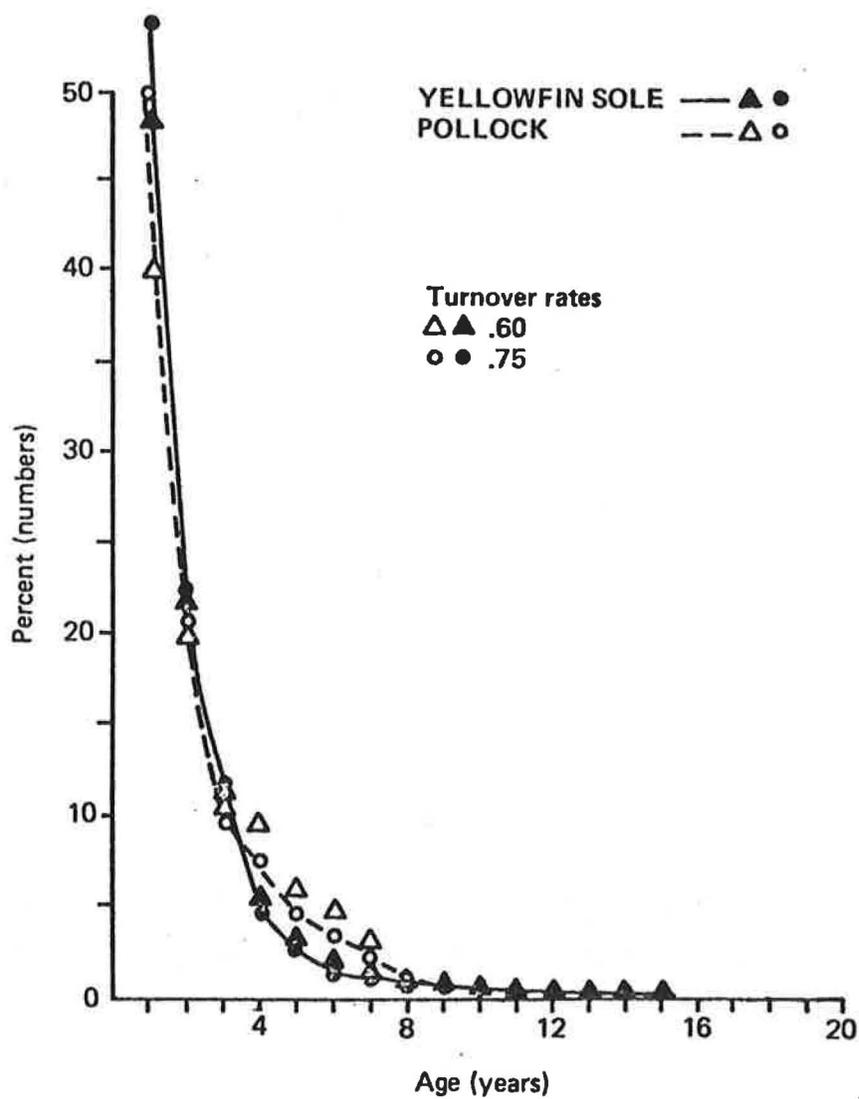


Figure 7.--Relative distribution of numbers of fish in different year classes (in % of total numbers) for yellowfin sole and pollock from the eastern Bering Sea.

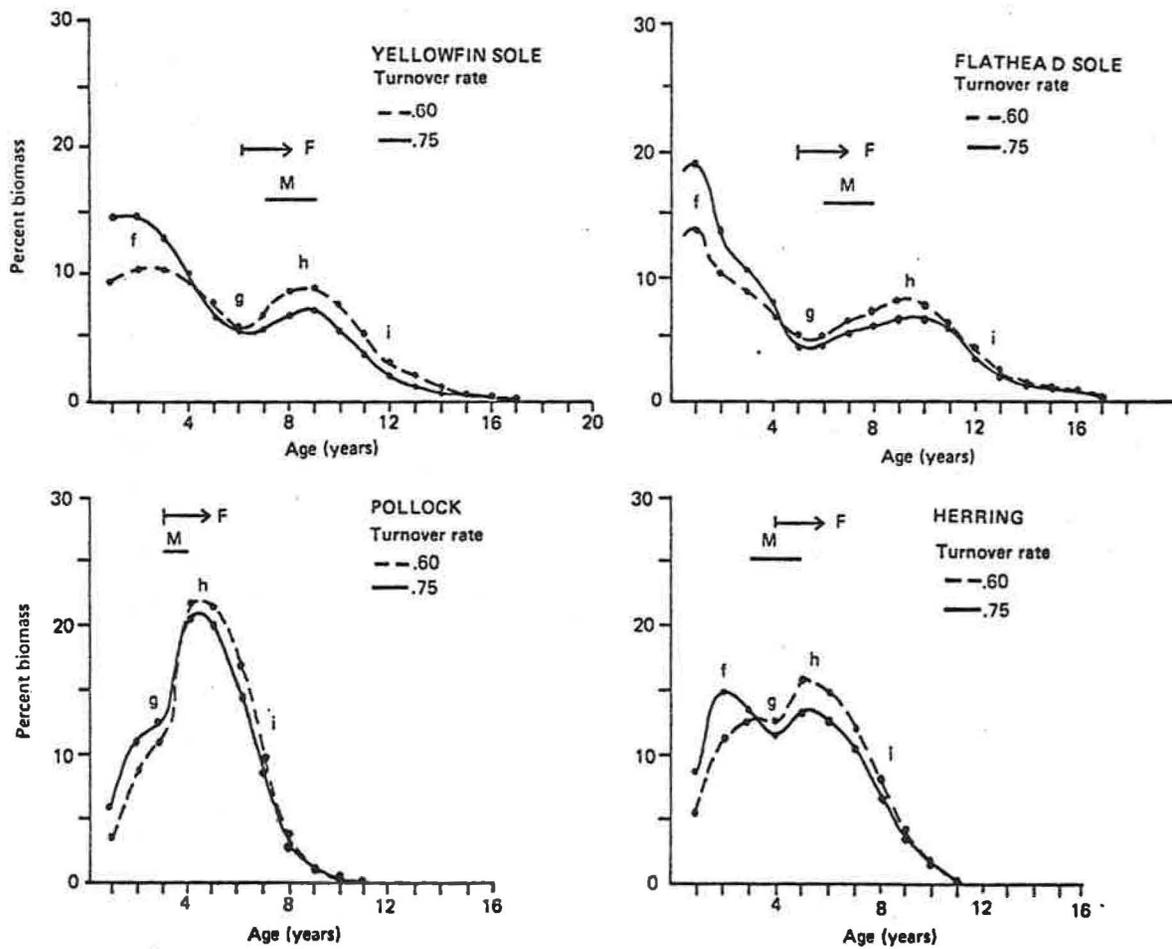


Figure 8.--Distribution of biomass with age (at two different turnover rates) of four species from the eastern Bering Sea.

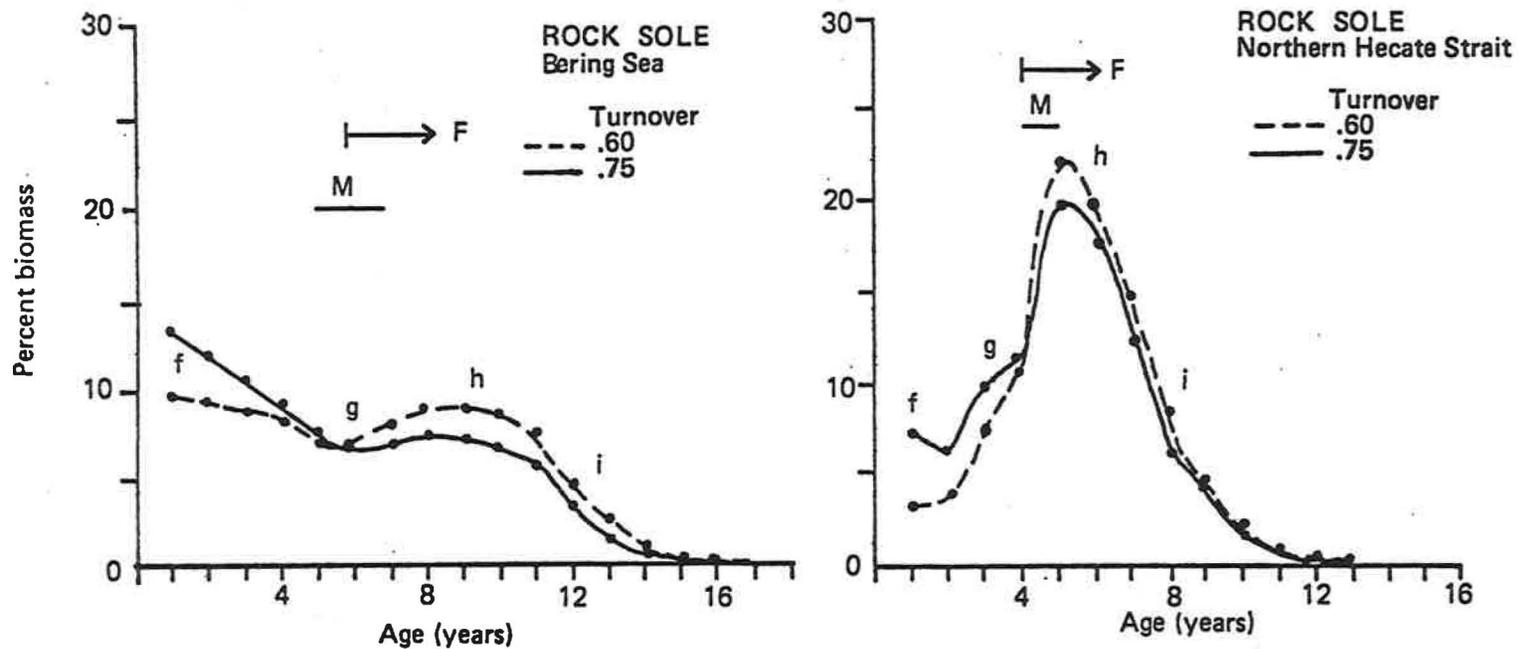


Figure 9.--Distribution of biomass with age (at two different turnover rates) of rock sole from the eastern Bering Sea and northern Hecate Strait.

biomass maximum in the first or second year (marked with "f" on the figures) and another maximum later, when the fish is already sexually mature and being fished (marked with "h" on the figure). These two maxima are separated with a minimum (g) which occurs just before or during the maturation of the population. In fast growing species (pollock, rock sole from northern Hecate Strait) there is only one biomass maximum, which occurs in the year after the maturation of the population. The population matures also during shorter period (within 1 year) in faster growing species. The "minimum" biomass period might also be recognized in a change of biomass increase rate in faster growing species (marked with "g" on the figures). The incline of the biomass (i) after its maximum is in most species rather rapid and might be related to increase in spawning stress mortality (see next chapter). The effect of different turnover rates on relative biomass distribution within the population is also shown on Figures 8 and 9. Figure 9 demonstrates the effect of growth rate on the biomass distribution within the population by presenting the same species (rock sole) from two different locations with different growth rates. The bar with F indicates when the year class has been fully recruited to the fishery.

The nonlinear relations between the growth rate (and/or weight) and numbers is demonstrated on Figure 10, with long-term mean age composition of catches in numbers and in weight. This figure also shows that the maximum yield per cohort is a function of growth rate. These effects are explored further in Chapter 6 in respect of fisheries management.

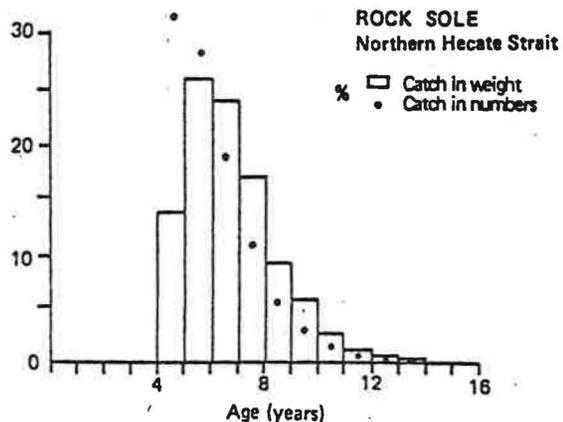
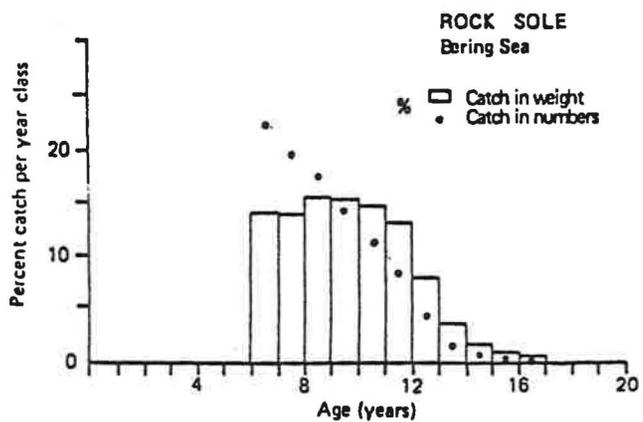
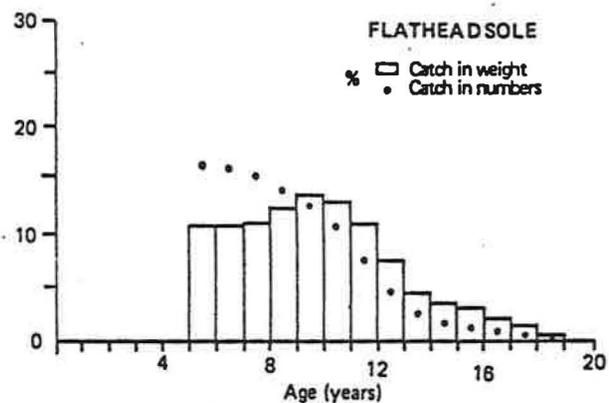
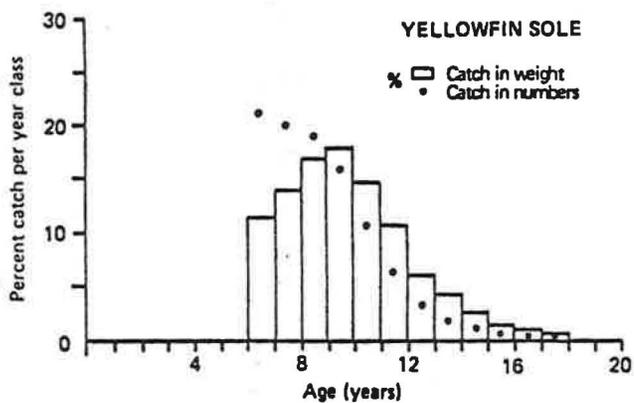


Figure 10.--Distribution of catch with age (in weight and numbers) of yellowfin sole, flathead sole, and rock sole from the eastern Bering Sea and rock sole from northern Hecate Strait.

The number and biomass distribution within a population between the prefishery juveniles and exploitable population and the effects of growth rates and turnover rates on this distribution, are shown on Table 1. The comparison of the biomass and number distribution of rock sole from the Bering Sea with corresponding numbers of rock sole from northern Hecate Strait shows the profound effect of growth rate on this distribution.

#### 5. CHANGE OF TOTAL MORTALITY WITH AGE, AND SPAWNING STRESS MORTALITY

The numerical mortality rates for individual year classes of the exploited part of the population can be computed directly using the long-term mean numerical age composition of fully exploited part of the population (Figures 3 and 4). These total mortalities are plotted on Figures 11 and 12 as percent of mortality (in numbers) from previous, fully exploited year class. The beginning of the year in which the species is fully recruited to the fishery is marked with a vertical bar (F) and the maturation period, with a horizontal bar (M).

Before and during the maturation period the numerical mortality remains in general below 15% and lower in other species than herring. As herring, and partly pollock, are important forage fish for marine mammals, their mortalities during maturation are somewhat higher than in other fish (15 to 20%). The "prematurity mortality" in exploitable part of the population consists mainly of long-term mean fishing mortality plus a very small mortality from diseases and grazing (predation) mortality by mammals (the latter only in pelagic and semipelagic species--herring and pollock). In most species the total mortality during this period is essentially fishing

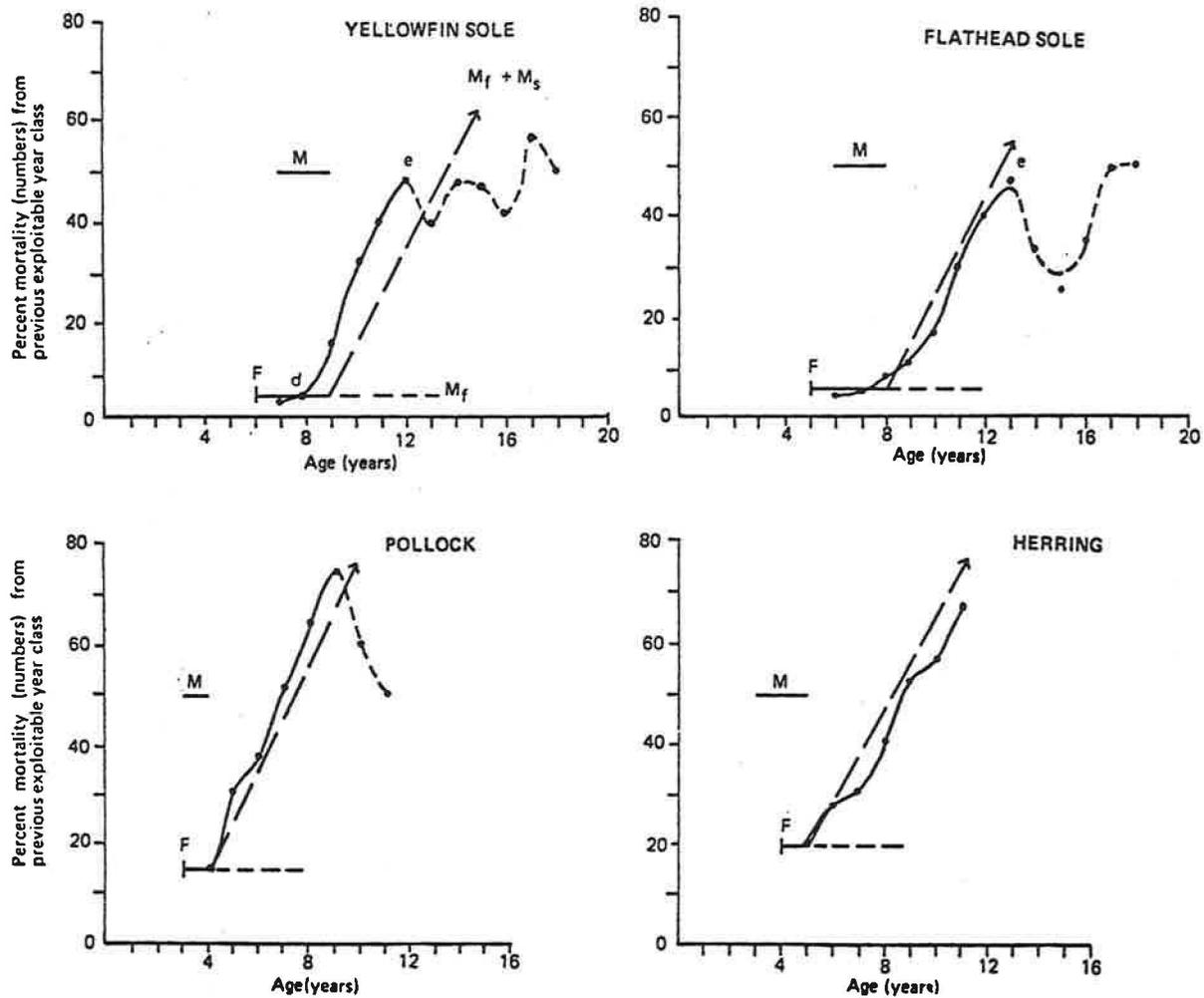


Figure 11.--Percent mortality (in numbers) from previous fully recruited year class, for four species from the eastern Bering Sea (explanations see text).

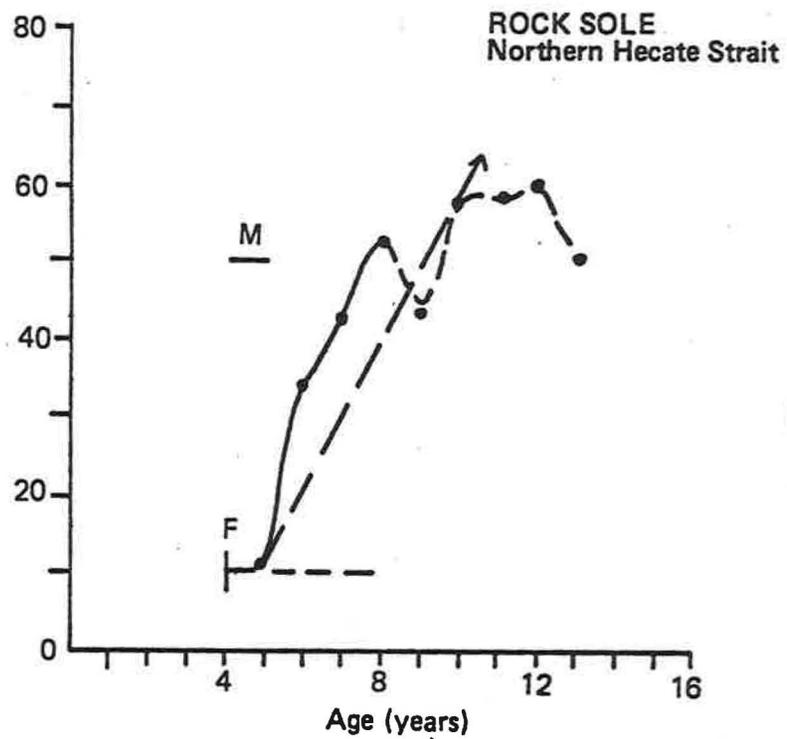
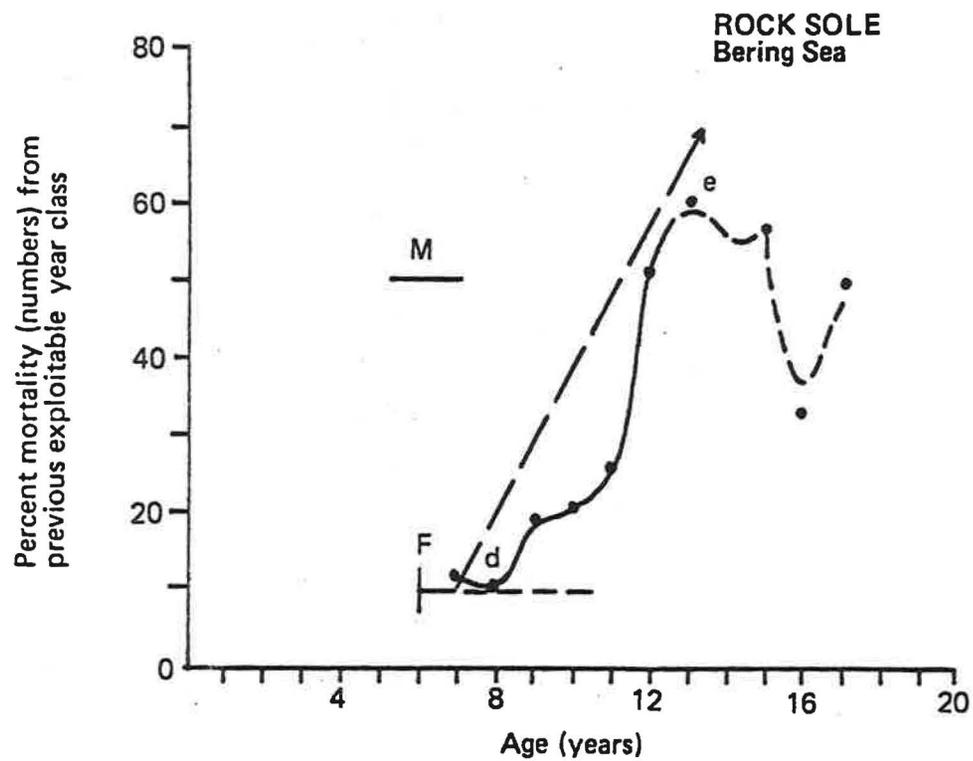


Figure 12.--Percent mortality (in numbers) from previous fully recruited year class for rock sole from the eastern Bering Sea and northern Hecate Strait (explanations see text).

mortality, as the small additional mortality from diseases and predation can be ignored (Dementjeva 1964). If no additional mortality component will arise in a subsequent year, this long-term mean fishing mortality should remain constant in each year class. (Observe that the numerical mortality in Figures 11 and 12 is computed relative to previous year class numbers and would thus remain constant if mortality rate would not change with age). A horizontal line of graphically estimated fishing mortality ( $M_f$ ) has been drawn on Figures 11 and 12. It could also be noted that there is a possible maximum error of 12% in estimating the relative year class strength of the first fully recruited year class (see Chapter 2) which would affect only the first value of mortality on Figures 11 and 12. The prematurity (mainly fishery) mortality has been roughly estimated at 6% per year in yellowfin and flathead sole, 10% in rock sole, 15% in pollock, and 19% in herring; some predation mortality by mammals is included in the latter two species.

After the cohort has reached about 80% maturity, the mortality shows an increase of about 10% per year for the next 4 to 5 years, whereafter the mortality undergoes irregular fluctuations. These irregular fluctuations (and corresponding mortality values) are somewhat uncertain, due to smallness of the sample (too few individuals alive) and might be caused also by a positive bias of year class strength in the formation of mean, induced by stronger year classes in area of the summation where variation is bounded by zero. A sloping dashed line has been drawn on Figures 11 and 12 (designated  $M_f + M_g$ ), starting from the estimated fishing mortality level in the year when the cohort reaches about 80% maturity. This line has a slope of 10% increase

of mortality per year on each figure and coincides well with the average slope of empirical mortality data during the first 4 to 5 years. However, there are some small displacements either toward younger or older years. The reasons for these displacements (and possibilities to achieve better agreements between the 10% trend line in mortality increase and corresponding empirical data) are most likely in the uncertainties in the preliminary data on the maturation of population as discussed in Chapter 2. A 1-year earlier full maturation of yellowfin sole and 1-year later maturation of flathead and rock sole from the Bering Sea would produce closer fits between the trend lines and empirical data. Furthermore, year-to-year variations in growth rates and correspondingly earlier or later maturation can occur in most marine species (Dementjeva 1964).

The increase of apparent mortality with age might be partly due to decreased vulnerability of larger fish to the gear and partly due to different distribution (e.g. bigger fish in deeper water). Although the above mentioned factors might contribute to the increased mortality with age, it is unlikely that they are the only factors especially considering that the mortality increase starts at and after the maturation and is nearly the same in all species studied, despite the fact that their biological characteristics and modes of life are quite different.

Beverton (1963) and Cushing (1973) have also noted this increase of mortality with age and have attributed this to increased senescent mortality. Cushing (1973) found the senescent mortality increase in North Sea plaice to be 8.9% per year, using a quite different approach from the approach in this study.

As the mortality starts to increase after the maturation, the present author believes that the main cause of this mortality increase is spawning stress. The spawning stress mortality is well known and pronounced in anadromous and catadromous fish. In marine fish it has been quantitatively considered first by Andersen and Ursin (1977). The present data indicate that the total mortality of any species in exploited year class where predation mortality can be ignored can be computed with a relatively universal formula, which is in essence Gompertz's Law (Beverton 1963):

$$M_t = M_f + n_s M_s \quad (1)$$

where  $M_t$  is total mortality of the year class (in % of numbers from previous exploitable year class);  $M_f$  is the basic fishing mortality (5 to 20% in our examples),  $n_s$  is the number of years after the cohort has reached 80% maturity and  $M_s$  is a constant spawning stress mortality (10% per year). If the spawning stress mortality follows a linear increase with time, and if fishing mortality rate can be estimated from other data, the above approach can be used to compute mean total mortality for exploitable part of a population if the age composition of this population has been ascertained.

$$M_{tm} = \sum N_n (M_f + n_s M_s) \quad (2)$$

where  $M_{tm}$  is the total mean mortality of the exploitable part of the population expressed either as percent or converted to instantaneous mortality coefficient and expressed as pertaining to numbers or to biomass, depending on whether the decimal fraction  $N_n$  of a year class is given on the bases of numbers or biomass. The remainder of Formula 2 in parenthesis is the same as Formula 1, where  $M_s$  is expressed as the "universal average spawning mortality increase rate" (10% per year class or 0.096 as instantaneous rate per year).

One of the consequences of the spawning stress mortality was mentioned by Dementjeva (1964), although she did not recognize the spawning stress mortality per se: "The earlier a fish reaches maturity, the shorter is its span of life." Dementjeva furthermore suggested that the increase of growth and earlier maturation leads to rejuvenation of stocks, i.e., to an increase of the biomass in younger year classes and corresponding decrease in the abundance of the older specimens of the fished stock (see the effect of growth and maturity changes on biomass distribution in rock sole in Figure 11). Intensity of fishing also plays a role in this process.

Figures 13 and 14 present the computed total mortality of the population biomass with age, expressed as percent of mortality of the corresponding annual mean biomass of the year class.

There are a number of characteristic features in this total mortality distribution with age which are found in all species presented on these figures. First, there is high mortality of biomass of young year classes of all species. This juvenile mortality declines rapidly with age--the more rapid the decline, the faster the growth of the species. The high mortality in larvae and juveniles is mainly due to predation. When the fish reaches the size category where the number of predators who are able to catch and/or swallow the given bigger size of fish is small, the mortality reaches the lowest value (marked with "k" on the figures). During this low predation mortality period, the main mortality is fishing mortality in commercially caught species.

As soon as the cohort reaches full maturity, the spawning stress mortality sets in ( $\ell$ ) as discussed above. Obviously the numerical values of the spawning

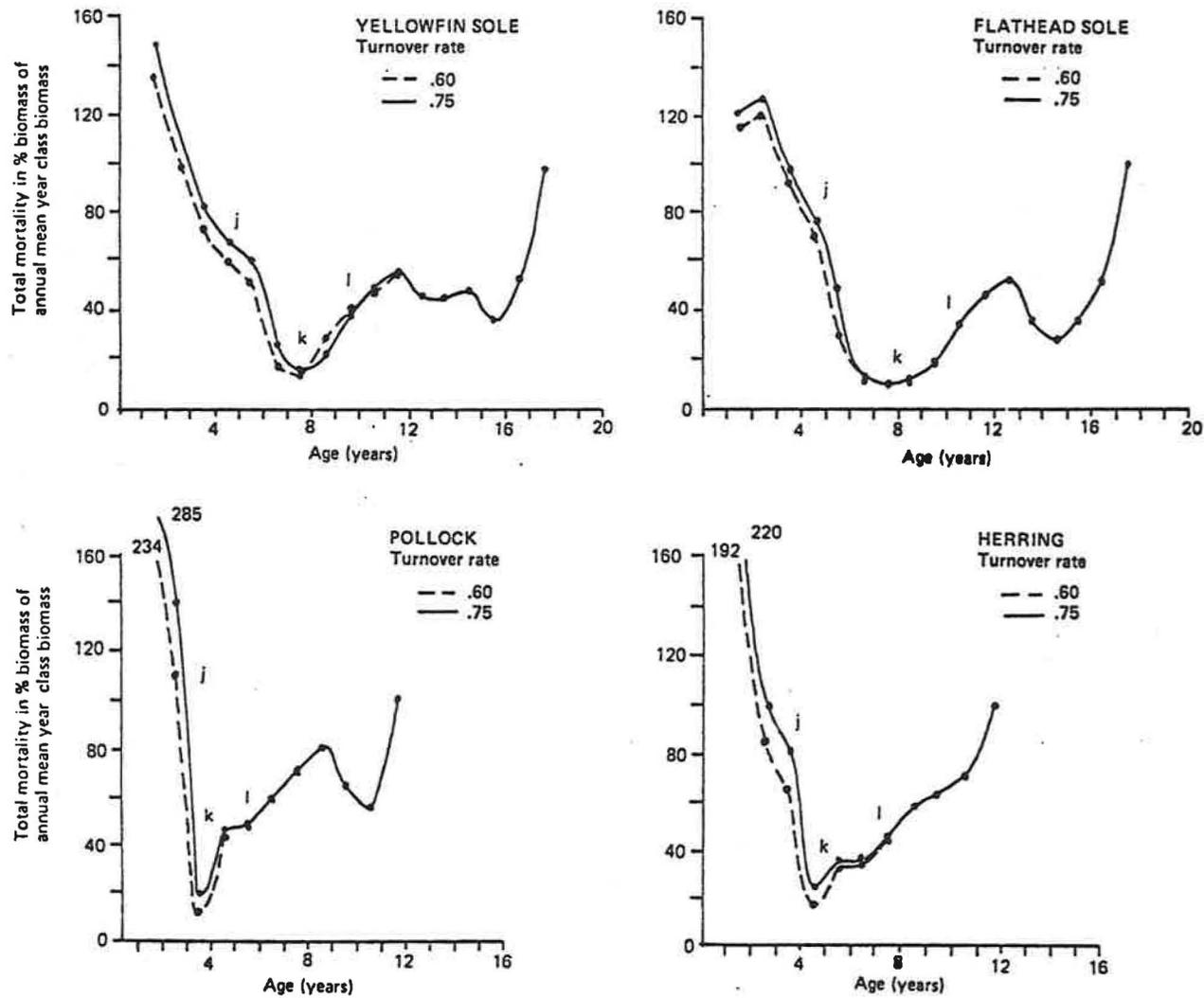


Figure 13.--Distribution of total mortality with age (in percent of biomass of the annual mean biomass of given year class) for four species from the eastern Bering Sea.

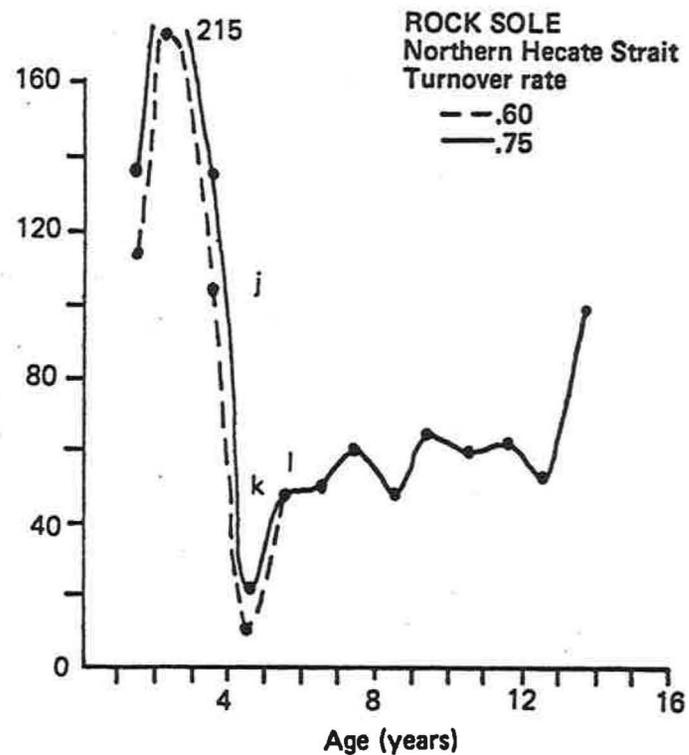
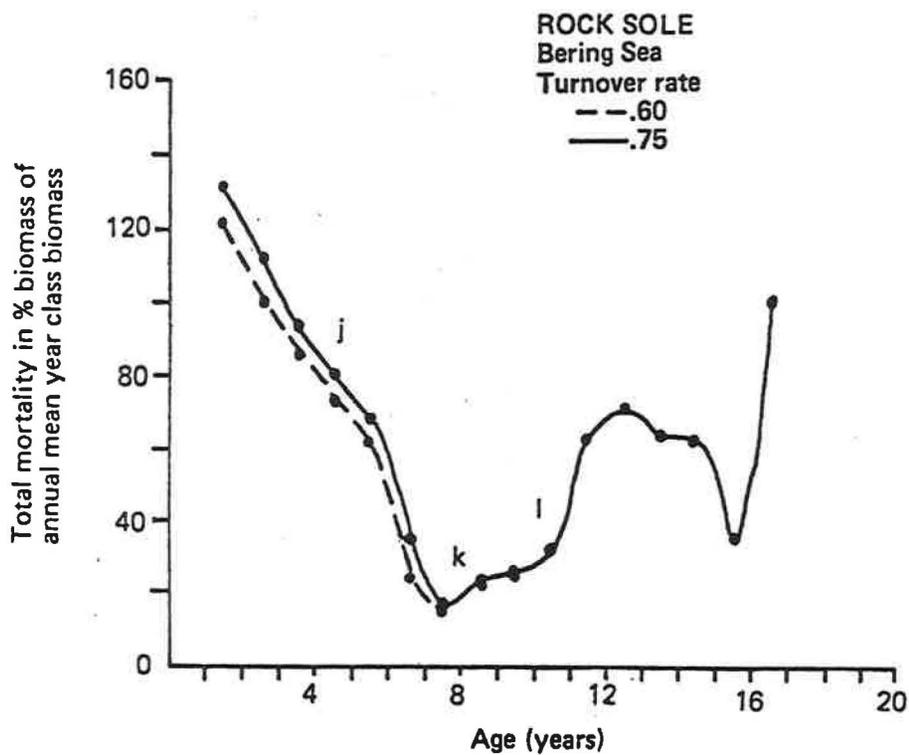


Figure 14.--Distribution of total mortality with age (in percent of biomass of the annual mean biomass of given year class) for rock sole from the eastern Bering Sea and northern Hecate Strait.

stress mortality increases are different in terms of biomass (Figures 13 and 14) than in terms of numbers (Figures 11 and 12).

The summary of total mortality in juvenile and in exploitable populations is given for rock sole from two different regions (with different growth rates) in Table 1. The most pronounced difference in respect to growth rate is in the biomass mortality.

#### 6. USE OF BIOMASS DISTRIBUTION, AGE VARIABLE MORTALITY, AND GROWTH IN FISHERIES MANAGEMENT.

A long-term (minimum 10 years) mean numerical year class strength of the exploitable part of the population can serve as the basis for computation of the mean fishing mortality during the same time period if the predation by marine mammals on the given species is low. Knowing the landings from the same stock and region during the same time period, mean stock size of the exploitable part of the population over the same time span can thus be computed, giving another method for stock assessment.

In case the younger year classes of the exploited part of the population are not fully sexually mature, the total mortality closely equals fishing mortality. However, as the population matures, a considerable spawning stress mortality sets in. The spawning stress mortality seems to be relatively constant in all species (increase 10% per year--i.e. per spawning), and the "effective life length" of a population after the maturation is limited to about 5 years. Thus we can compute the fishing and spawning stress mortalities as time (and age) dependent variables on any age frequency distribution of a species and use the results for management purposes. The application of

age dependent mortality, as computed with Formula 1, would improve considerably the reliability and accuracy of cohort (virtual population) analyses, leading to better standing stock estimates.

The time of maturation of a population varies with its growth rate. There are year-to-year variations in the growth rates which affect maturation, as the maturation is a function of fish size rather than age. The growth rate change also affects the predation mortality of juveniles--the faster the growth rate, the faster the fish "passes through" the dangerous size range where predation is high (re. predator-prey size dependent feeding in the marine ecosystem). The magnitude of the predation mortality and its fluctuations largely determine the recruitment to fishery (and consequently the stock size). Thus the study of predation on prefishery juveniles and its spatial and year-to-year variations is of great value to fisheries management and should receive more attention than in the past.

Total mortality in an exploitable population can be computed, using Formula 1, if fishing mortality coefficient and actual age frequency distribution are at hand. Considering requirements of minimum spawning stock size, a decision about future fishery could be made, provided recruitment to exploitable population can be estimated (e.g. from special recruitment surveys).

When the fish grows faster (e.g., due to positive temperature anomalies, higher food abundance in given years and areas, and/or other causes), it reaches maturity earlier and consequently its span of life shortens, whereas its spawning stress mortality rate in older year classes remains unchanged, but shifts 1 year towards younger year classes, which causes overall higher

spawning stress mortality in the exploited part of the population (consider Formula 1 with increased  $n$ ). This leads to a rejuvenation of the stock, i.e., increase of biomass of younger year classes and decrease in the abundance of older year classes. Thus the fishery (fishing intensity) can be increased on whole stock and can be shifted toward younger year classes.

The maximum yield per cohort is dependent on growth rate, as pointed out by Alverson and Carney (1975). The maximum yield occurs usually 1 to 5 years after full recruitment to fishery and can be determined only if relative numerical year class strength is converted to weight (Figure 10). Furthermore, Alverson and Carney (1975) found a good relation between the time of biomass maximum and maximum age. The time of biomass maximum is in turn a function of growth rate, which leads to the same conclusion as above, that the fishing intensity can vary with growth rate.

## 8. SUMMARY

1. Long term mean numerical year class strength of exploited part of the population has been constructed for five species from the Bering Sea and one from British Columbia waters. These year class strengths have been used to deduce long term mean fishing mortalities and spawning stress mortalities.

2. In the immature part of a fully recruited flatfish population, the total mortality consists mainly of fishing mortality, which is 6 to 10% for the flatfishes studied. However, immature herring and pollock are consumed extensively by marine mammals in the Bering Sea and therefore the total mortality of fully recruited immature year classes in these species is 15 and 19%, respectively.

3. After the population matures (about 80% maturity), the mortality increases about 10% per year. This is assumed to be spawning stress mortality and is about the same in the six species studied. Thus an age dependent mortality coefficient can be computed for an exploitable population (Formula 2), which is connected to age (size) of maturity.

4. An iterative method is developed and described to compute numbers and biomass distribution for a juvenile (prefishery) population, using turnover rates of biomass as criterion.

5. The biomass distribution with age and growth rates of individual species are used to determine growth rates of total, juvenile, and exploited populations.

6. Predation is the prevailing cause of mortality in juveniles. The predation mortality decreases rapidly with the increase in size of the fish and is thus a function of growth rate. Consequently the fluctuations in growth rates and predation of juveniles will largely determine the fluctuations of the recruitment to the fishery.

7. There is a minimum mortality in the year classes preceding maturation, when spawning stress mortality is absent and predation mortality is very low due to (increased) size of the fish.

8. Maturation time is related to the size (thus to growth rate) rather than to age of the species. The determination of the maturation of the population is of great utility in determining the total mortality and life span of the population. The year-to-year variations of growth rates thus also affect the maturity state of the population.

9. The earlier the fish reaches maturity the shorter is its life span. This can lead to rejuvenation of the populations by increasing the abundance of younger year classes and decreasing the abundance of older ones.

10. In slow growing species there are two maxima of biomass, the first in 1- and/or 2-year-old fish and the second maximum occurs after sexual maturation of the population. A biomass minimum precedes the sexual maturation in slow growing populations. In fast growing species only one biomass maximum occurs shortly after maturation of the population.

11. The time of biomass maximum is a function of the growth rate of the species and therefore there is a good correlation between the growth rate, time of biomass maximum, and maximum age of the population.

12. The time of maximum yield per cohort is dependent on growth rate of the species and occurs 1 to 5 years after full recruitment age to the fisheries.

#### ACKNOWLEDGMENTS

The author wishes to express his thanks to Dr. D. L. Alverson, former Director of Northwest and Alaska Fisheries Center for suggesting this study and for his stimulating discussions and advice during the completion of this work.

## 9. REFERENCES

Alverson, D.L., and M.J. Carney. 1975.

A graphic review of the growth and decay of population cohorts. *J. Cons.* 36(2):133-143.

Andersen, K.P., and E. Ursin. 1977.

A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Medd. Dan. Fisk.-Havunders. N.S.* 7:319-435.

Beverton, R.J.H. 1963.

Maturation, growth, and mortality of clupeid and engraulid stocks in relation to fishery. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 154:44-67.

Cushing, D.H. 1973.

Recruitment and parent stock in fisheries. Univ. Wash., Div. Mar. Resour., Wash. Sea Grant Program, WSG 73-1, 197 p.

Daan, N. 1973.

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

Dementjeva, T.F. 1964.

Correlations between indices of relative abundance of young fish, recruitment size and maturity rate as a basis for annual prediction. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 155:183-187.

Forrester, C.R., and J.A. Thomson. 1969.

Population studies on the rock sole (Lepidopsetta bilineata) of Northern Hecate Strait, British Columbia. *Fish. Res. Board Can., Tech. Rep.* 108, 104 p.

Granfeldt, E. 1979

Numerical method for estimation of fish biomass parameters. NW and Alaska Fisheries Center, Proc. Rpt.

Maeda, T. 1977.

Relationship between annual fluctuation of year classes of yellowfin sole in the eastern Bering Sea. In Fisheries biological production in the subarctic Pacific Region, p. 259-268. Res. Inst. North Pac. Fish., Hokkaido Univ., Spec. Vol.

Paloheimo, J.E. and L.M. Dickie. 1965.

Food and growth of fishes. J. Fish. Res Board Can., 22(2):521-542.

## LIST OF FIGURES

- Figure 1.--Weight at age of five species from the eastern Bering Sea.
- Figure 2.--Weight at age of rock sole from the eastern Bering Sea and northern Hecate Strait, British Columbia.
- Figure 3.--Long-term mean age frequency distribution of fully recruited year classes (in % of numbers) of four species from the eastern Bering Sea. (M - maturation period.)
- Figure 4.--Long-term mean age frequency distribution of fully recruited year classes (in % of numbers) of rock sole from the eastern Bering Sea and northern Hecate Strait. (M - maturation period.)
- Figure 5.--Annual growth rates (in % of weight per year) of four species in the eastern Bering Sea.
- Figure 6.--Annual growth rates (in % of weight per year) of rock sole in the eastern Bering Sea and northern Hecate Strait.
- Figure 7.--Relative distribution of numbers of fish in different year classes (in % of total numbers) for yellowfin sole and pollock from the eastern Bering Sea.
- Figure 8.--Distribution of biomass with age (at two different turnover rates) of four species from the eastern Bering Sea.
- Figure 9.--Distribution of biomass with age (at two different turnover rates) of rock sole from the eastern Bering Sea and northern Hecate Strait.
- Figure 10.--Distribution of catch by age (in weight and numbers) of yellowfin sole, flathead sole, and rock sole from the eastern Bering Sea and rock sole from northern Hecate Strait.
- Figure 11.--Percent mortality (in numbers) from previous fully recruited year class for four species from the eastern Bering Sea (explanations see text).

Figure 12.--Percent mortality (in numbers) from previous fully recruited year class for rock sole from the eastern Bering Sea and northern Hecate Strait (explanations see text).

Figure 13.--Distribution of total mortality with age (in percent of biomass of the annual mean biomass of given year class) for four species from the eastern Bering Sea.

Figure 14.--Distribution of total mortality with age (in percent of biomass of the annual mean biomass of given year class) for rock sole from the eastern Bering Sea and northern Hecate Strait.