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Quantitative Relations Between Fishing Mortality, Spawning Stress Mortality and Biomass Growth Rate (Computed with numerical model FISHMO)

by Taivo Laevastu

January 1983

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QUANTITATIVE RELATIONS BETWEEN
FISHING MORTALITY, SPAWNING STRESS MORTALITY
AND BIOMASS GROWTH RATE
(Computed with numerical model FISHMO)

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ABSTRACT

The effects of fishing on a given species biomass have been quantitatively evaluated. A constant recruitment is assumed in this study, but the evaluation can be computed on any known age distribution of exploitable biomass. Fishing mortality is assumed to be constant with age: (i.e., equal fraction of fish is removed from each fully recruited year class); however, spawning stress mortality (often called senescent mortality) increases with age.

When fishing (mortality) increases, the spawning stress mortality decreases relative to total and exploitable biomasses. Increased fishing also causes the increase of the fraction of prefishery juveniles in relation to exploitable biomass, assuming recruitment remains quasi-constant. As juveniles have higher individual growth rates than exploited year classes, the growth rate of the whole biomass increases when fishing increase's. The above relations are dependent on biomass distribution with age in a given population, and on the age of maturity; therefore, they vary from species to species. These changes are quantitatively shown for two species from the Bering Sea - walleye pollock, Theragra chalcogramma, and yellowfin sole, Limanda aspera.

The computations of spawning stress (or senescent) mortality and subsequent derivation of long term mean age composition of fully exploited portion of population is described in the Appendix.

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1. EFFECT OF FISHING ON THE POPULATION, ITS BIOMASS, AND ITS AGE STRUCTURE

Fishing removes a given fraction of older, larger fish from a population. If recruitment is not appreciably reduced by this removal, the rest of the population left in the sea would have a younger average age as a result of fishing. The younger fish have higher growth rates than older, exploitable fish (see Fig. 1). Thus, the average growth rate of the biomass of a given population would increase as a result of the "rejuvenation" of biomass by fishing.

The "natural mortality" in older fish increases with age. This increase of senescent mortality seems to be related to maturity; i.e., after maturation, mortality increases in each year about 10% above the mortality of the previous year (Beverton 1963 ; Laevastu and Larkins 1981). This mortality is called here spawning stress mortality. The term senescent mortality is also used for this age-specific mortality. When increased fishing removes older fish which would have died from spawning stress mortality later, the latter mortality is expected to decrease (in relation to total population) with increasing fishing.

The above described dynamical fishing dependent changes in a population can be quantitatively (numerically) computed given a few simplifying assumptions, which would not restrict the use of the results in more complex, real conditions.

In traditional fisheries population dynamics computations, the "natural mortality", which encompasses spawning stress mortality, is assumed to be constant with age. In most cases the magnitude (value) of this mortality is unknown and guessed at. In some cases, where age composition data of catches from a 'given stock are plentiful and the stock is reasonably fished, "natural mortality" and fishing mortality are computed as total mortality and partitioned. Fishing mortality has usually been made to increase with age, and in some species to decrease again in the few oldest year classes.

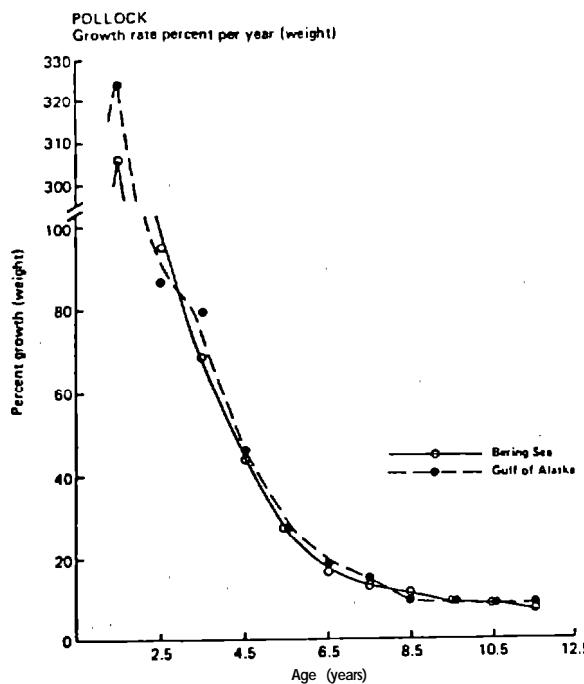


Figure 1. Annual growth rates (in weight of walleye pollock.)

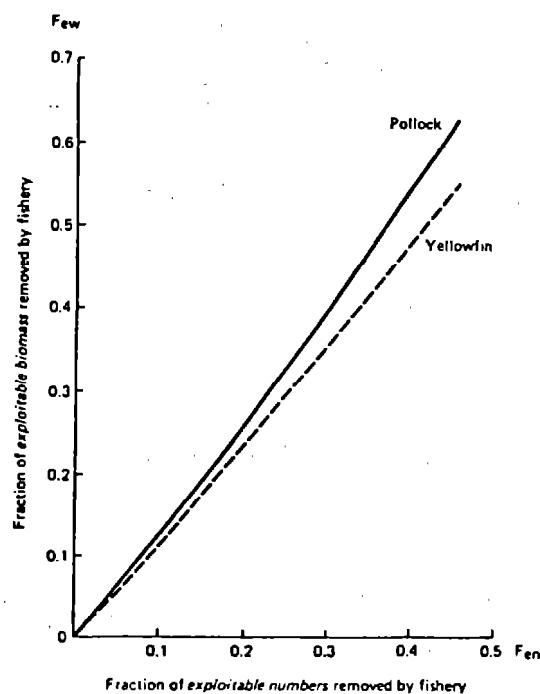


Figure 2. Relations between fraction of numbers and fraction of weight in exploitable biomasses of walleye pollock and yellowfin sole.

It can be argued that a relatively intense fishery on a given stock removes an equal fraction of fully recruited year classes (i.e., is nonselective in respect to size/age, and is directly proportional to the respective densities (strengths) of the year classes present). This consideration is not true in respect to year classes which are not fully recruited to fishery (re size selection by gear). The few oldest year classes in demersal and semidemersal species (such as Pacific cod, Gadus macrocephalus), might also be subject to lesser fishing pressure, due to greater depth distribution of these year classes.

In this study the fishing mortality (F) is assumed to remove the same fraction of numbers of fish from each age group of fully exploited population (termed here as F_{en}). Consequently, the fraction by weight removed by fishery (F_{ew}) is different than the fraction of numbers, depending on growth of the species. This is illustrated in Table 1 with different age groups of walleye pollock, Theragra chalcogramma, and yellowfin sole, Limanda aspera. This difference between the fraction of numbers and fraction of weight removed from exploitable population (F_{en} and F_{ew} , respectively) of walleye pollock and yellowfin sole is shown in Figure 2. The effect of fishing can also be referred to total biomass of the species (corresponding coefficient being F_{tw}). This relation in the two above-mentioned species is shown in Figure 3.

The three different fishing mortalities are compared on the abscissas of Figures 4 and 5. These two figures show the changing proportions of juveniles and exploitables under the varying levels of fishing pressure.

2. NUMERICAL COMPUTATIONS OF THE EFFECTS OF FISHING ON THE GROWTH RATE OF

BIOMASS AND ON THE SPAWNING STRESS MORTALITY

The mean growth rate (in terms of weight) of the biomass of any species can be computed if we know the distribution of biomass with age and have weight at age data at hand. The growth rate computations are carried out in a separate numerical

Table I.--Relative numbers and weights in kg of fish removed by fishing ($F=0.1$) from long-term mean populations of walleye pollock and yellowfin sole.

Age (yr)	Walleye pollock		Yellowfin sole	
	Numbers	Weights (kg)	Numbers	Weights (kg)
4	10.0	5.2	-	-
5	7.8	5.4	-	-
6	5.4	4.6	-	-
7	3.2	3.1	10.0	1.4
8	1.7	1.8	8.7	1.5
9	0.7	0.8	6.8	1.4
10	0.2	0.3	4.7	1.1
11	0.1	0.1	2.8	0.7
12	-	-	1.4	0.4
13	-	-	0.6	0.2
14	-	-	0.2	0.1
15	-	-	0.1	-

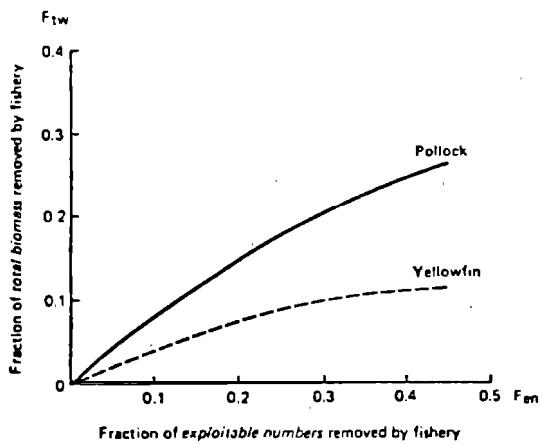


Figure 3. Relations between fraction of exploitable numbers removed by fishery and corresponding fraction of total biomass removed (walleye pollock and yellowfin sole),

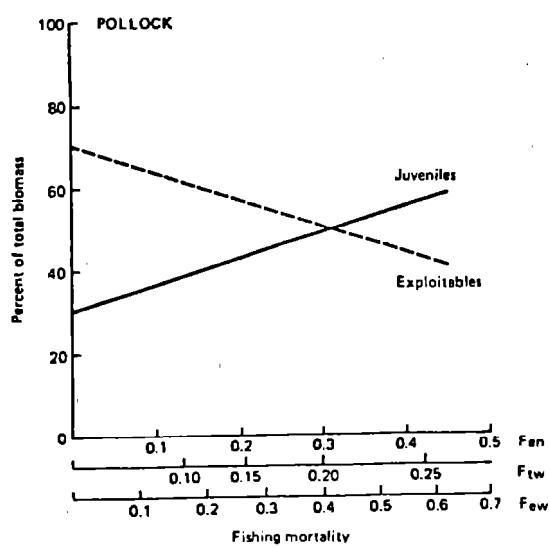


Figure 4. The percentages of juvenile and exploitable biomasses of walleye pollock with different fishing intensities.

computer programme BIODIS (see Laevastu and Larkins 1981; Laevastu 1979). The mean biomass growth rate changes when the distribution of biomass with age is changed by fishing. This change can be numerically computed in a numerical programme FISHMO (Laevastu 1982). The dependence of growth rate (g) on fishing mortality was computed assuming knife-edge constant recruitment, using long-term mean age composition of exploitable biomass (although the computations can be made on any known age composition) and assuming that the spawning stress mortality increases 9% per year after maturation; fishing mortality is assumed to be constant in fully exploited year classes (see further Appendix).

The relations between the fishing mortalities in numbers of exploitable population (F_{en}) and in terms of weight of total biomass (F_{tw}) and monthly growth rates are given in Figures 6 and 7 for walleye pollock and yellowfin sole. These figures show that the growth rate changes are species specific and must be evaluated as such.

The quantitative relations between fishing mortality (expressed in three different terms as described above, F_{en} , F_{ew} , and F_{tw}), and corresponding changes in spawning stress mortality with reference to exploitable biomass, are shown in Figures 8 and 9 for walleye pollock and yellowfin sole, respectively. As fishing mortality increases, spawning stress mortality decreases. This change is different in different species in terms of biomass and is largely dependent on the growth rate of the species, but depends also on the age of maturity (see further Appendix).

In numerical biomass based ecosystem models, both fishing mortality and spawning stress mortality are expressed on the basis of total biomass of the species. The relations between the mortalities expressed on this basis are shown in Figure 10. This figure also demonstrates that these relations vary from species to species and consequently they must be determined for individual species and populations.

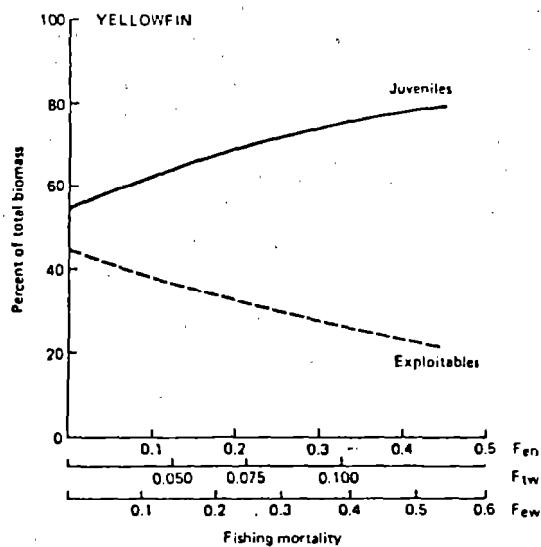


Figure 5. The percentages of juvenile and exploitable Biomasses of yellowfin sole with different fishing intensities,

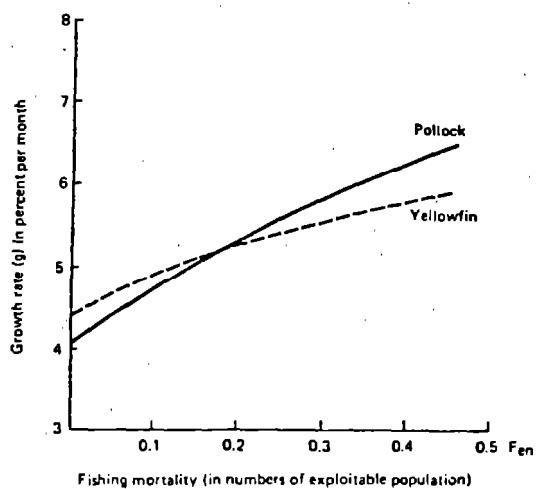


Figure 6. Relation between monthly growth rate and fishing mortality (in terms of numbers of exploitable population) in walleye pollock and yellowfin sole.

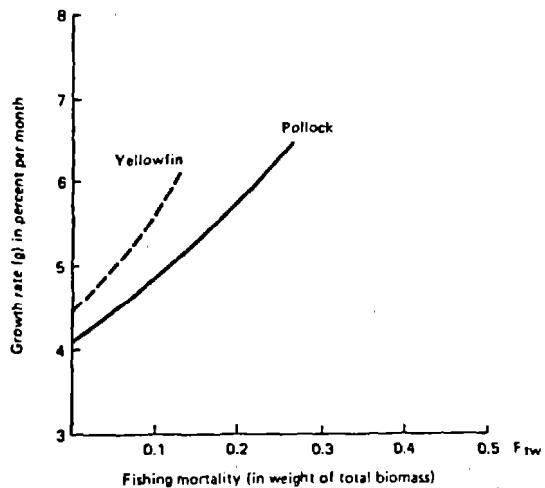


Figure 7. Relation between monthly growth rate and fishing mortality (in terms of weight of total biomass) in walleye pollock and yellowfin sole.

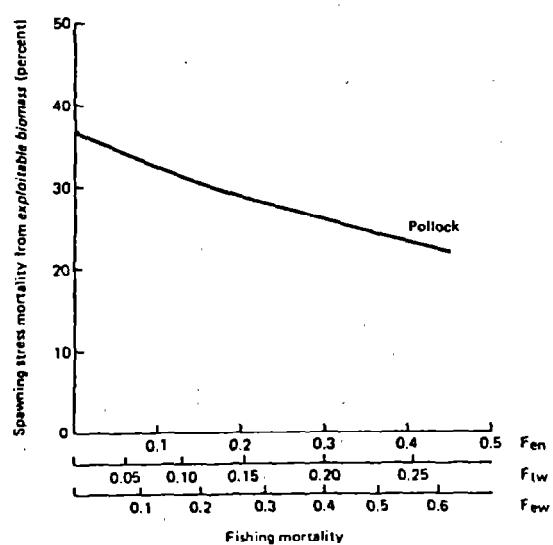


Figure 8. Relation between fishing mortality (expressed as F_{en} , F_{tw} , and F_{ew}) and spawning stress mortality (in % of exploitable biomass) in walleye pollock,

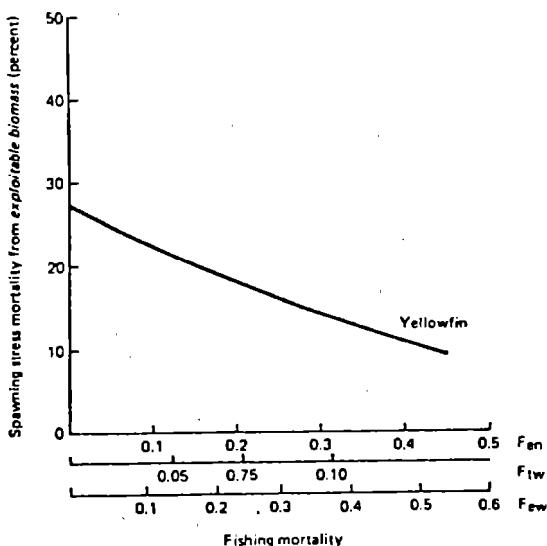


Figure 9. Relation between fishing mortality (expressed as F_{en} , F_{tw} , and F_{ew}) and spawning stress mortality (in % of exploitable biomass) in yellowfin sole.

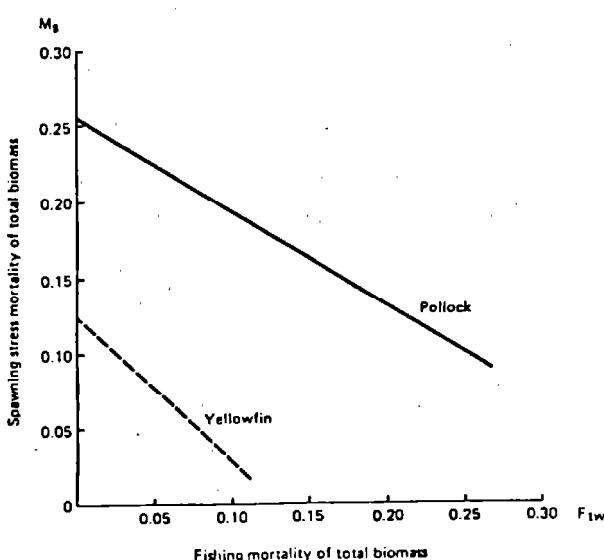


Figure 10. Relation between fishing mortality (expressed on the basis of total biomass - F_{tw}) and spawning stress mortality of total biomass (M_s) in walleye pollock and yellowfin sole.

3. SOME POSSIBLE EFFECTS OF FISHING ON RECRUITMENT, AND CONSEQUENT CHANGES IN GROWTH RATE AND IN BIOMASS AGE STRUCTURE

The numerical results of growth rate and spawning stress mortality changes due to fishing (as described in previous sections) were applied in a single species, biomass based Schaefer type model to investigate the biomass dynamics with time (Laevastu and Marasco 1983). These studies showed that the changes of growth rate and spawning stress mortality "overcompensated" the removal of biomass of fishing; i.e., the biomass increased with increased fishing. Two possible causes for this "overcompensation" might arise from simplifications in the model, described in a previous chapter: a) the knife-edge recruitment to exploitable biomass is not fully realistic, as one- or two-year classes younger than the first fully recruited year class are partially subjected to fishing which will affect the age structure and consequently the growth rate and spawning stress mortality rate; and b) when the biomass of spawners decreases due to fishing, the larval and juvenile recruitment could decrease. Consequently the juvenile biomass would decrease, which would have two effects: the growth rate increase due to fishing would be less than with constant juvenile biomass, and the recruitment to exploitable biomass would be decreased .

The fishing of year classes which are not fully recruited was simulated by assuming that 42% of the year class prior to the full recruitment was subject to fishing. The fully recruited year class was reduced by the amount of fishing mortality in the previous year class. Any other scheme, based on actually observed distribution of year classes, as well as observed year class strengths, could also be introduced in the model. However, a well defined general case serves better for investigation and demonstration of the changes in biomass parameters caused by fishing.

The definitions of the model conditions and the consequent computations of the parameters described above included assumptions which were based on simple and known conditions. However, hypotheses must be established for simulation of the effects of fishing on recruitment and on change of juvenile biomass. The hypotheses in this model must be limited by the model restraint -- i.e., what can be computed with the parameters available in the model. One of the factors affecting the recruitment to exploitable stock is the variation of predation on juveniles. This process is quantitatively simulated in large ecosystem models such as DYNUMES. In the present model it was assumed that the juvenile biomass decreases in direct relation to the quotient of total biomass (as affected by fishing) divided by unfished total biomass (B_t/B_e). This computation utilizes an iterative procedure.

The results of the computations with fishing affecting not fully recruited year class and with juvenile biomass adjustments to depict recruitment changes are given in Tables 2 and 3, Columns B. The corresponding values with the "unadjusted" model are given in Columns A for comparison.

The percent adults is higher in the adjusted model because of the decrease of juvenile biomasses. Spawning stress mortalities, which refer to total biomass, are also correspondingly higher. The growth rates have decreased in "adjusted" model. The growth rate decrease is different in the two species -- the growth rate decreased considerably more in the pollock because the juvenile biomass in the pollock is smaller than in the yellowfin.

The computed changes in the biomass parameters and rates of processes in the biomasses caused by different fishing intensities in two different fish species demonstrate the necessity of using species-specific data in any fisheries population dynamics computations.

To investigate further the dynamics of the biomass due to fishing, the fishing dependent parameters and rates must be used in an ecosystem model such as DYNUMES or in a single species model, such as described by Laevastu and Marasco (1983) .

Table 2. Monthly growth rates, percentages of adults, and spawning stress mortalities in pollock at different fishing intensities; A with knife'-edge recruitment and constant juvenile biomass, and B with fishing on not fully recruited year class and with juvenile biomass adjusted to depict some changes in recruitment.

F	g (monthly)		Percent adults		Spawning stress mortality	
	A	B	A	B	A	B
0	4.1	4.1	70.0	70.0	25.4	24.5
0.1	4.7	4.4	63.1	67.5	20.3	20.8
0.2	5.3	4.8	56.4	64.6	16.2	17.6
0.3	5.8	5.1	50.1	61.3	12.9	14.8
0.4	6.3	5.4	44.5	57.7	10.3	12.4

A - Knife-edge recruitment to fishery; juvenile biomass constant ("constant recruitment")

B - 42% of year class prior to full recruitment subjected to fishery; juvenile biomass decreased by B_t/B_e (see text),

F - Fishing mortality (on the bases of numbers of fish)

g - Growth rate of biomass (in percent per month).

Spawning stress (or senescent) mortality given in percent of total biomass

Table 3. Month 1 y growth rates, percentages of adults and spawning stress mortalities in yellowfin at different fishing intensities; A with knife-edge recruitment and constant juvenile biomass, and B with fishing on not fully recruited year class and with juvenile biomass adjusted to depict some changes in recruitment.

F	g (monthly)		Percent adults		Spawning stress mortality	
	A	B	A	B	A	B
0	4.4	4.4	45.0	45.0	12.3	11.8
0.1	4.9	4.7	37.3	40.0	8.4	8.4
0.2	5.3	5.0	31.0	35.1	5.6	5.9
0.3	5.5	5.3	26.0	30.5	3.7	4.0
0.4	5.8	5.5	22.0	26.4	2.4	2.7

A - Knife-edge recruitment to fishery; juvenile biomass constant ("constant recruitment")

B - 42% of year class prior to full recruitment subjected to fishery; juvenile biomass decreased by B_t/B_e (see text)

F - Fishing mortality (on the bases of numbers of fish)

g - Growth rate of biomass (in percent per. month)

Spawning stress (or senescent) mortality given in percent of total biomass

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APPENDIX

COMPUTATION OF SPAWNING STRESS (OR SENESCENT) MORTALITY, AND SUBSEQUENT DERIVATION OF LONG-TERM MEAN AGE COMPOSITION OF FULLY EXPLOITED PORTION OF POPULATION

Some comments by the reviewers of this paper indicated that the concepts of spawning stress mortality and long-term mean age structure of the exploitable portion of the fish population are not fully understood by all. Furthermore, different practices of the application of mortalities are in existence. Most commonly, the "natural mortality" is assumed to be constant whereas fishing mortality is assumed to be age specific. In this paper, the reverse is assumed. These above-mentioned concepts are clarified in this appendix.

In most modern fisheries (trawling, purse seining, etc.) the fishing on fully recruited year classes can be considered as taking an equal fraction from each year class (i.e., it is not age (size) specific). Obviously, the lower size limits depend on mesh size used, and thus affect year classes which are not fully recruited to the fishery. There are obviously cases where the fishery is somewhat size selective, such as a fishery on spawning concentrations only, and on fish species where there is a pronounced segregation of age (size) groups with depth. In some species (e.g., cod) old, large individuals are assumed to inhabit deeper depths, and thus might be subject to the fishery in a lesser degree than younger fish. This condition has never been quantified. Furthermore, the amount of biomass (and numbers) in these old year classes is low and the error introduced by assuming age-constant fishing mortality will be small. However, in some species which are predominantly caught with size-selective gear (gill nets, long lines), the fishing mortality is age specific.

The spawning stress mortality can be determined from the long-term age composition of a stock. To obtain a long-term age composition, the observed year class strengths during at least 10 years (greater number of years for species which have great variations in year class strength) are summarized and normalized. Furthermore, we need data on the age (size) of maturation (i.e., at which age 50 and 80% of the stock is sexually mature).

The features which appear in long-term mean age composition of the population are schematically shown in Figure 11. First we should eliminate partially recruited year classes. The first year class selected as fully recruited can be at times ambiguous, and minor adjustments might be needed. In these species where the maturation (to ca 80% of the population as determined from corresponding empirical data) occurs after the full recruitment to fishery, two different slopes (which are not fully straight lines) of the decrease of the numbers can be estimated. Before maturation, total mortality is mainly due to fishing (the natural mortality from disease and other causes being apparently very small). After maturation, total mortality increases each year. As this mortality increases after maturation, it is called spawning stress mortality by the present author, although some other authors (e.g., Beverton 1963) have called it senescent mortality. Thus, if it is assumed that the fraction of each age class removed by fishing is a constant for each year once the stock is fully recruited, then any increase in mortality can be attributed to spawning stress, or senescent mortality. Once high age classes are reached, the mortality (measured as percentage change in numbers) will appear to decrease. This is due to the "tail end" which is a consequence of some strong year classes which have existed during the period used in summation of the data. As in this region the summation is bounded by zero (no negative year classes possible); the normalized mean in this age region produces the "tail end" which is not fully compatible with previous year class data.

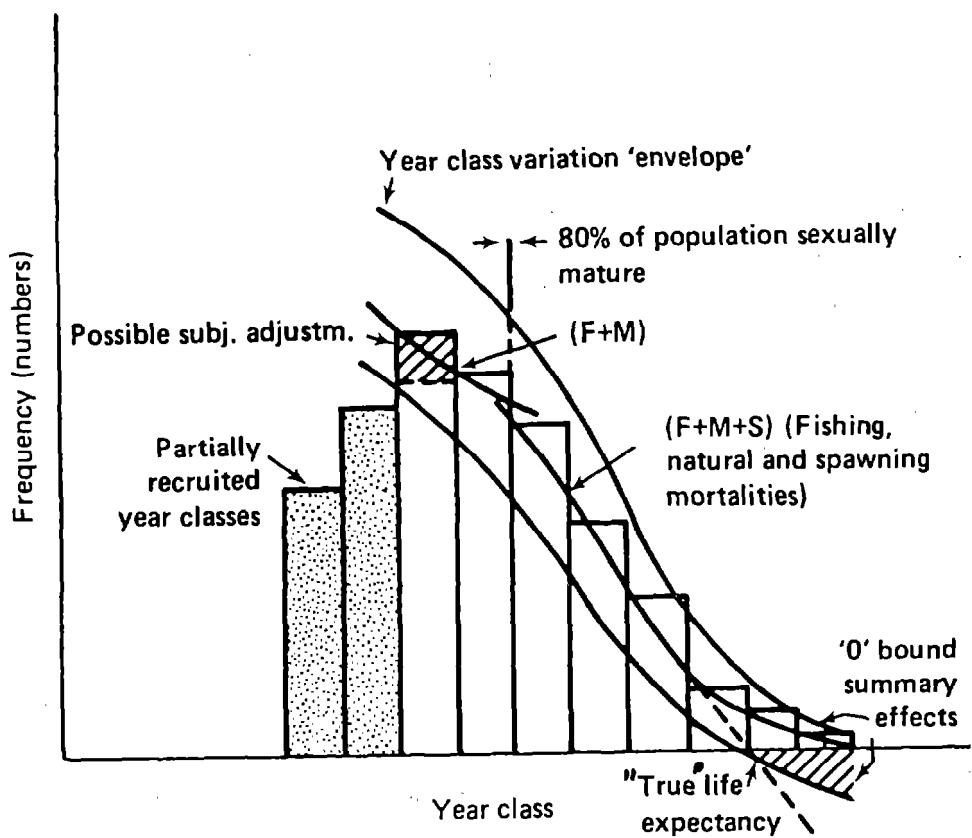


Figure 11. Schematic presentation of the derivation of long-term mean age frequency distribution.

The long-term mean year class strengths (normalized to 100%) of yellowfin sole, flathead sole, pollock, and herring from the Bering Sea are shown in Figure 12 (data from Niggol 1982). These data allow the computation of the rate of change of mortality with reference to previous year class strength, which is graphically given in Figure 13. From the age where the stock is known to have reached 80% maturity, a dashed line is drawn, representing 10% increase of mortality per year. This trend line coincides in all four species relatively well with the trend of increased mortality during the first five years after the maturation. The difference in the position of the 10% increase trend line from the actual values for yellowfin sole is apparently caused by incomplete data on maturation. If the maturation occurs one year earlier (age 8), a good correlation is obtained. The scattering of the data at older ages is due to the previously mentioned "tail end" in long-term mean age composition, caused by some strong year classes which have occurred during the period of the data used in the summation.

The mean rate of increase of the spawning stress mortality in the four species in Figure 13 is slightly less than 10% per year during the first five years after maturation. On the other hand, Beverton (1963) found an increase of senescent mortality slightly over 9% per year, using a different approach. In the present study a 9% per year increase of spawning stress mortality was used. (This lower value also compensates for the values which are caused by the "tail end".)

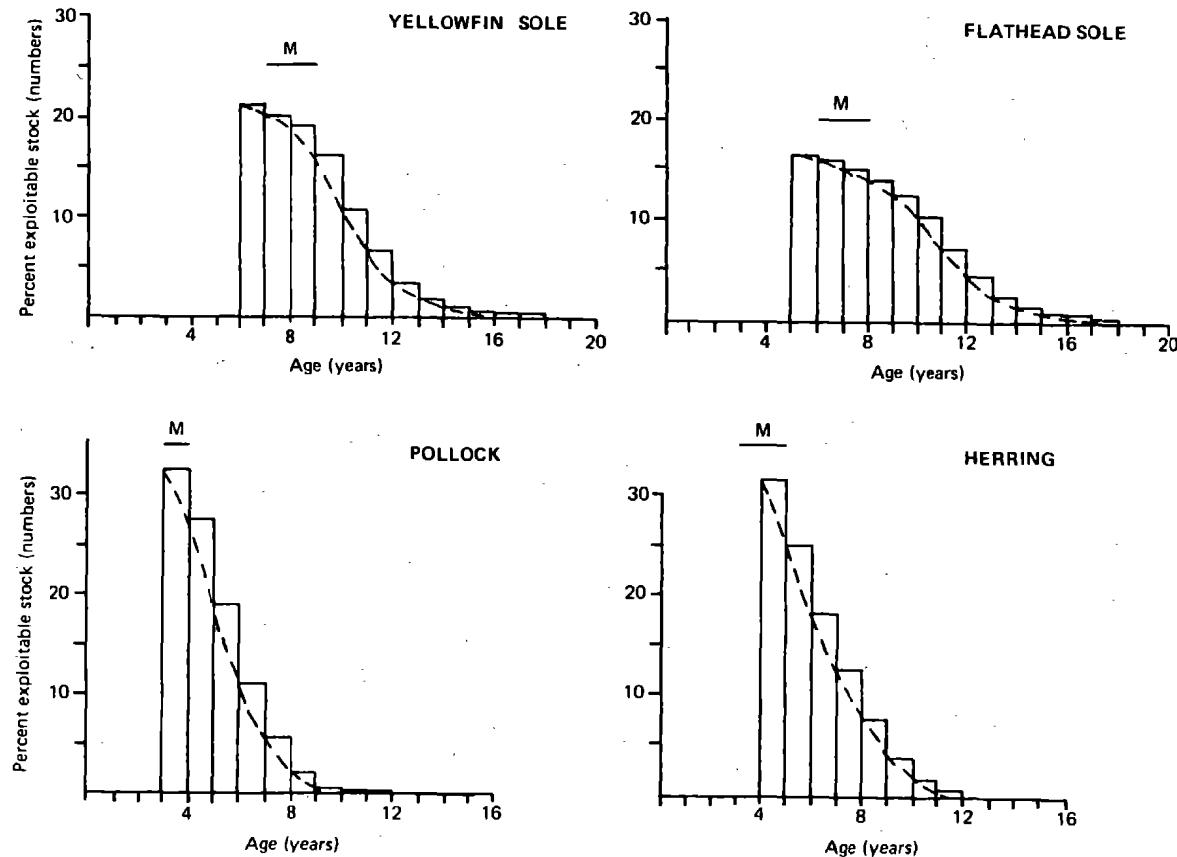


Figure 12. Long term mean (normalized) year class strengths of yellowfin sole, flathead sole, pollock, and herring from the Bering Sea.
(Data from Niggol 1982).

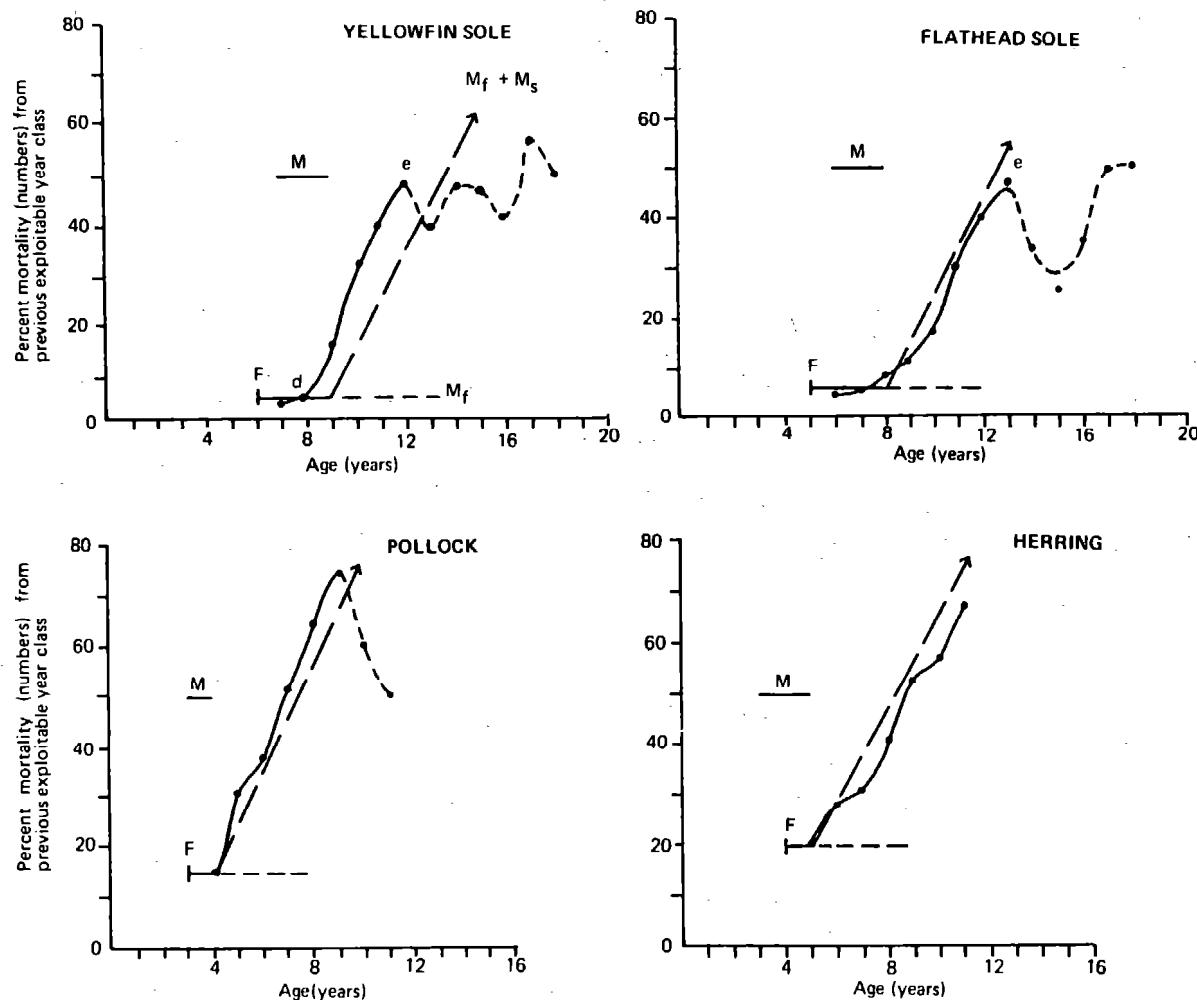


Figure 13. Percent of mortality (in numbers) from previous year class for four species (yellowfin sole, flathead sole, pollock, and herring) from the Bering Sea. Dashed line presents 10% of annual increase in mortality from the age when 80% of the population is sexually mature. M - presents 50% (start of the line) and 80% (end of the line) maturity of the population. F - fishing mortality.

If the spawning stress mortality rate were the same for all species, we could construct the mean year class strength directly if the fishing mortality were known. Furthermore, using age composition data for a given year, we could compute back to what any year class strength was when the year class was first considered fully exploited, and what it would be in future years.

However, spawning stress mortality rate cannot be considered universally applicable. It is considerably higher in salmonids (including capelin) and also in some pelagic fish (e.g., anchovy). It might also vary in the same species with latitudes, as temperature affects the growth rate and maturation is a function of size in many species.