



# NOAA Technical Memorandum NMFS F/NWC-41

## A Single Species, Biomass Based, Time Dependent Model for Investigating the Effects of Fishing on the Dynamics of Fish Biomass

by  
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A SINGLE SPECIES, BIOMASS BASED, TIME DEPENDENT  
MODEL FOR INVESTIGATING THE EFFECTS OF FISHING  
ON THE DYNAMICS OF FISH BIOMASS

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## ABSTRACT

When fishing (fishing mortality) increases in a given population, spawning stress mortality (senescent mortality) decreases. Thus the change of a population (biomass) is not a linear function of recruitment minus catch and a constant "natural mortality". Furthermore, fishing removes the older slower growing fish. Consequently, the mean growth rate of the remaining biomass increases. These two fishing dependent changes (called "rejuvenation of population" by some earlier researchers) must be considered in biomass based fishery models because the removal of biomass by fishing is compensated by these changes to a considerable extent if recruitment remains constant. The magnitude of the "rejuvenation" effect varies from species to species, and depends on the growth rate of the species, age of full recruitment, and quantitative relation between prefishery juvenile and exploitable biomasses. The effects of fishing on "uncompensated" biomass dynamics, as well as biomass dynamics compensated for fishing (i.e., compensating for concomitant changes of growth rate and spawning stress mortality) are demonstrated with numerical examples for walleye pollock (Theragra chalcogramma) and yellowfin sole (Limanda aspera).

The predation mortality must be estimated in a single species dynamic computation. In this study the predation mortality is assumed to consist of a constant fraction simulating the predation by mammals and predation on shoals in general, and a biomass density dependent fraction of predation mortality.

Fishing yield can be computed with an exploitable biomass density dependent fishing mortality coefficient, as well as with a constant annual catch plus a biomass density dependent fishing mortality coefficient which simulates the incidental catch (or bycatch). The meaning of these types of computation of fishing and the effects of fishing in general are explored in this paper.



The results of the numerical studies show that different species tolerate different amounts of fishing. The effects of fishing are greatly compensated for by the concomitant decrease in spawning stress mortality and increase in the growth rate of the population. The growth rate of a stock biomass is a function of the distribution of biomass with age. This distribution is affected by fishing and by any disturbance in recruitment. When the recruitment to exploitable stock is changed with partial fishing on not fully recruited year classes, and the fraction of juveniles in the stock is affected by the change of larval recruitment in direct proportion to the spawning biomass removed by fishing, the compensation of the effects of fishing on the biomass are decreased, but not eliminated, and "overcompensation" can still occur in species where the fraction of exploitable stock is of the same size or smaller than the fraction of prefishery juveniles (e.g., yellowfin sole). Further, this study suggests that density dependent predation is not a linear function of prey density, and that recruitment to exploitable biomass is a function of both spawning biomass and cannibalistic predation on juveniles.





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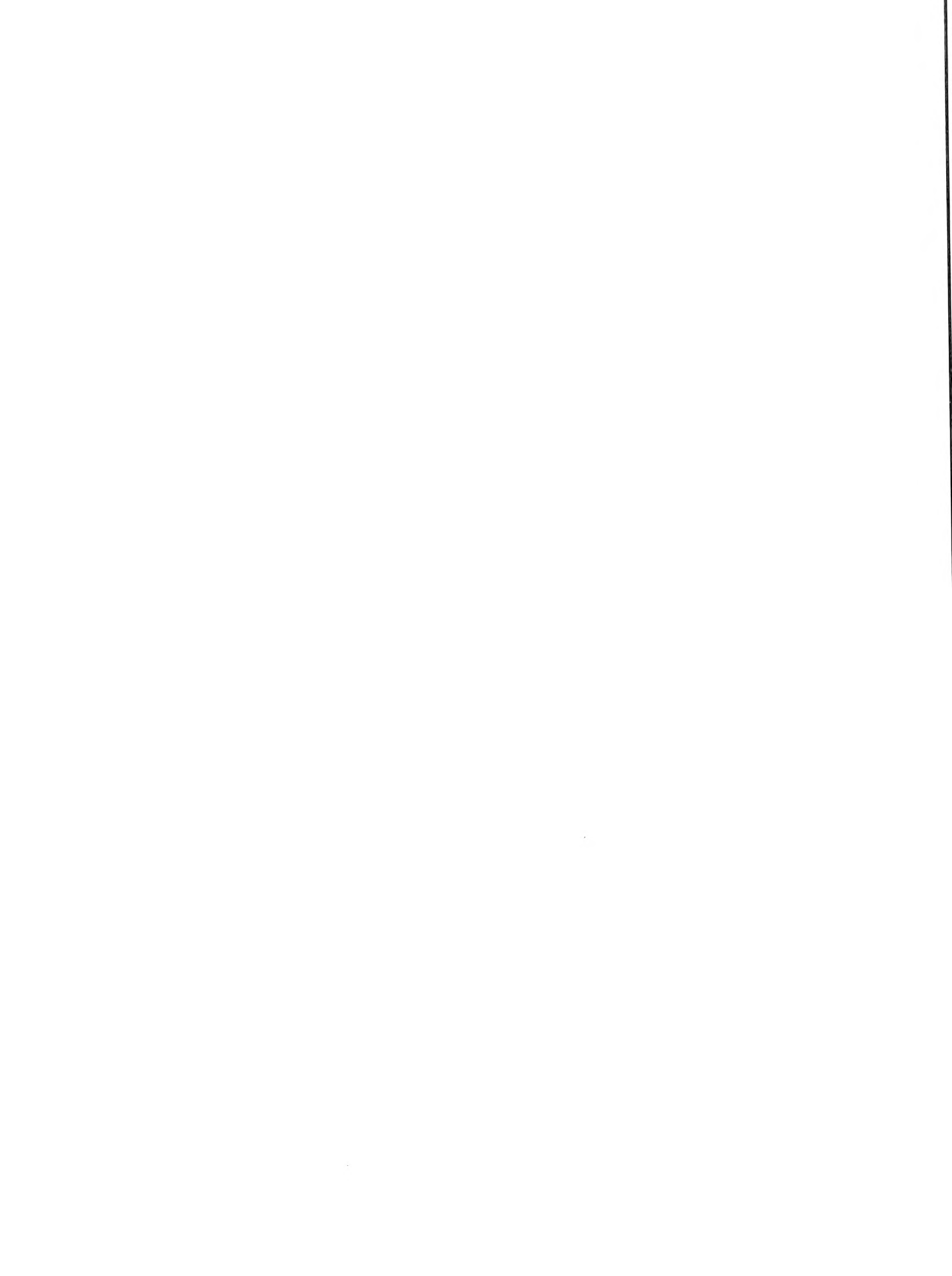


## 1. THE PURPOSE OF THIS STUDY

Fishing removes the older, larger specimens from a given stock. These older fish grow slower than the remaining younger fish, thus the mean growth rate of the stock could change with fishing. Furthermore, the old age (or senescent) mortality of the stock would decrease with the removal of older fish. The interactions between fishing and rejuvenation can be expected to be compensatory, and the results could affect management options. This numerical study attempts to clarify quantitatively the effects of fishing on a stock. The main objectives of the study were to:

- 1) Determine quantitatively the effects of rejuvenation on the dynamics of fish stocks.
- 2) Determine how different species respond to fishing.
- 3) Determine the nature of the interaction between fishing, rejuvenation, and recruitment.

This study pertains mainly to low to moderate levels of fishing, where most interactions can be linearized. At higher levels of fishing ( $F > 0.3$ ), when definite "recruitment overfishing" occurs, many changes in the stock parameters due to fishing are nonlinear. Another study is planned to examine "recruitment overfishing" and the events leading to the stock collapse.



## 2. EFFECTS OF FISHING ON THE BIOMASS PARAMETERS

Traditionally, annual fishing mortality has been computed in terms of the number of fish removed from the exploitable part of the population. It can be computed alternatively in terms of biomass removed from either the exploitable or total biomass. Time intervals other than a year (e.g., on monthly basis) may also be used. The relations between the different fishing mortality coefficients for two species are given by Laevastu (1983). In the present computations a monthly total biomass based fishing mortality and a fixed rate of (constant in weight) fishing were used.

Fishing removes older fish; thus, if recruitment remained constant, the exploitable portion of the biomass would decrease and the portion of prefishery juveniles would increase. This is called rejuvenation of population. Since the growth rate of the juvenile biomass is higher than that of the exploitable biomass (see e.g., Niggol 1982), the mean growth rate of the whole (total) biomass will increase as fishing intensity increases (Laevastu 1983).

Spawning stress mortality (also called senescent mortality) increases about 9 to 10% (number based) per year after 80% of the population has reached maturity (Beverton 1963, Cushing 1973, Laevastu and Larkins 1981). Fishing removes mature fish, some of which would have died as a result of spawning stress mortality. Consequently, this mortality decreases with increasing fishing, thus partially counteracting the effects of fishing on stock biomass.

Fishing would decrease the numbers of fish in the population and the size of the biomass is expected to decrease if recruitment remains constant. However, this decrease of stock biomass is not related in a linear manner with the decrease of spawning stress mortality, because the increase in population growth rate caused by the relative increase of faster growing juvenile biomass is expected to compensate for losses due to fishing.



The fishing of a highly cannibalistic species would remove older cannibalistic specimens, thus relieving cannibalistic predation pressure on the juveniles. This aspect of fishing has been studied numerically by Laevastu and Favorite (1976). Most fish species are cannibalistic to some degree. The effects of a fishery on cannibalism are briefly described in Section 3 on predation.

The impacts of various intensities of fishing were studied numerically, using the relations between the fishing effects and corresponding biomass parameter changes determined in another numerical model (Laevastu 1983). In the first numerical examples, recruitment to the exploitable stock was assumed to be constant. In the second set of computations, recruitment was made a function of fishing (see Section 7). In reality, recruitment is quite variable in space and time, and might mask most of the effects; thus, direct verification of the results in the field with empirical data would be very difficult.

### 3. SIMULATION OF PREDATION OF A SINGLE SPECIES POPULATION

Mortality due to being eaten by other, bigger fish (predation mortality), constitutes the greatest part of the traditionally used "natural mortality". Simulation of the dynamics of a single species population can be realistic only if the predation upon this population is also simulated in a realistic manner. A reasonably satisfactory simulation of predation is possible only in a holistic ecosystem simulation such as PROBUB or DYNUMES, where the predations are simulated in a detailed manner.

In the present single species model, an attempt was made to simulate predation on some known, but simplified, principles governing it as well as on the basis of knowledge gained from the above-mentioned holistic ecosystem models.





In some earlier fisheries population studies it has been assumed that natural (predation) mortality can be considered (and computed) as consisting of two parts: one part being independent of population density ("constant fraction"), and the other part changing in proportion to the change in stock size. We follow the same assumptions here. The "constant fraction" of predation mortality was about half of the total predation mortality when the biomass was at the equilibrium. The biomass density dependent part of predation mortality was made to change linearly with the size of the actual biomass. Thus, the effects of fishing on predation mortality (including the effects of cannibalism) are simulated indirectly via this density dependent predation.

Proportioning of constant and density dependent predation varies from species to species and is, in general, difficult to ascertain in a single species consideration, but can be computed in a holistic ecosystem simulation, such as DYNUMES. In the present study, an approximately half-half relation was selected and the total predation value was tuned at biomass equilibrium (which is the initial biomass input value).

#### 4. SIMULATION OF CONSTANT AND DENSITY DEPENDENT FISHING

The effects of fishing were simulated with three different approaches: 1) a constant catch, independent from biomass density, except it vanished entirely at low biomasses (i.e., when the biomass is about one fourth of the equilibrium biomass); 2) fishing consisting of a constant catch plus a biomass density dependent catch; and 3) a biomass density dependent catch only. The effects of these three different fishing mortalities at different levels were studied with the model.



Constant catch occurs in fisheries where there is a constant market and prices adjust to changes in demand and supply. If a fished biomass becomes lower, usually the catch per unit effort decreases (if the species is not a shoaling pelagic species and not caught exclusively during spawning), and the price usually increases, stimulating a higher effort of fishing. However, there is a lower limit for catch per unit effort (and/or an upper limit for price) and when these limits are reached, fishing might cease.

Fishing simulation with constant and density dependent portions presents most realistically what is happening in many fisheries; for example, there is a certain amount of stock (density) independent catch, as modern search methods are effective in locating fishable shoals even when stocks are at a low level of abundance, and also stock density dependent catch, either targeted or mostly bycatch. However, in some fisheries (e.g., trawl fishing for flatfishes) the catches are mostly stock biomass density dependent.

Fishing mortality operates on the exploitable biomass. In simulations of the effect of fishing, the fishing mortality coefficient must be adapted to either number based computations or biomass based computations. In the latter case, the fishing mortality coefficient is calculated relative to either exploitable or total biomass. The latter is used when no age (size) class separation is made in the model. The quantitative relations between these coefficients were described by Laevastu (1983). In this study the fishing mortality coefficient was calculated relative to the whole biomass.

## 5. FORMULAE AND INITIAL VALUES USED IN THIS STUDY

The monthly biomass ( $B_t$ ) was computed with Formula 1 from the previous month biomass ( $B_{t-1}$ ):

$$B_t = B_{t-1} e^{g-c-s-f} \quad (1)$$



The initial biomasses were arbitrarily selected and the constant portions of predation and fishing mortality were adjusted to be commensurate with this selected initial biomass (in the present example the input biomass was  $4200 \text{ kg/km}^2$  for both species, walleye pollock (henceforth called pollock) and yellowfin sole (called yellowfin)).

The effects of fishing on the growth coefficient were initially computed with values calculated theoretically (Laevastu 1983) assuming knife-edge recruitment and constant juvenile biomass:

$$g_v = g + pf_{tw} \quad (2)$$

where  $f_{tw}$  is the monthly fishing mortality coefficient operating on whole biomass and  $p$  was:

$$\text{Pollock, } p = 0.75$$

$$\text{Yellowfin, } p = 0.95$$

Other runs were made with partial fishing on year classes which were not fully recruited to the fishery, and with the fishing affecting juvenile biomass (i.e., fishing affecting juvenile recruitment) (see Section 6). Under these conditions coefficient  $p$  (from Laevastu 1983) was:

$$\text{Pollock, } p = 0.35$$

$$\text{Yellowfin, } p = 0.85$$

Predation mortality ( $C$ ) consists of a "constant" portion ( $C_k$ ) and of a biomass (density) dependent portion:

$$C = C_k + B_{t-1}^n \quad (3)$$

$C_k$  and  $n$  are identical in both species under study ( $95 \text{ kg/km}^2$  and  $0.02$ , respectively), as these parameters are dependent on input biomass. The biomass from the previous time step ( $B_{t-1}$ ) must be used because the biomass of the actual time step is not available before predation mortality is computed.



Finally, an instantaneous predation coefficient was computed:

$$c = \ln (1 - C/B_{t-1}) \quad (4)$$

Spawning stress mortality ( $s$ ) was prescribed from Laevastu (1983). In some runs it is made a function of fishing mortality for the quantitative study of the inverse relations between fishing and spawning stress mortality effects:

$$s = s - rf_{tw} \quad (5)$$

$$\text{Pollock, } r = 0.0175$$

$$\text{Yellowfin, } r = 0.01$$

In the first set of runs (see Section 5) where juvenile recruitment was not affected by fishing, the values for  $r$  were: pollock 0.6 and yellowfin 0.85.

In the second set of runs (see Section 6) where the juvenile recruitment was affected by fishing and some fishing occurred on not fully recruited year classes, the values for  $r$  were: pollock 0.4, yellowfin 0.65.

Fishing mortality ( $f_{tw}$ ) consists of "constant" catch ( $F_c$ ) and/or different stock density dependent fishing ( $F_d$ ) and/or a combination of both. The constant catch was converted to fishing mortality coefficient ( $f_c$ ):

$$F = F_c/B_{t-1}; f_c = \ln (1-F) \quad (6)$$

The biomass of previous time step ( $B_{t-1}$ ) is used for the same reason as in Formula 3 above.

$$f_d = f (F_d) \quad (7)$$

$$f_{tw} = f_c + f_d \quad (8)$$

$$\text{Pollock, } F_c = 32 \text{ kg/km}^2, f_d = 0, \text{ increment } 0.006, \text{ max. } 0.018$$

$$\text{Yellowfin } F_c = 32 \text{ kg/km}^2, f_d = 0, \text{ increment } 0.003, \text{ max. } 0.009$$





The percentage of biomass that is exploitable (E) was computed with the assumption that recruitment (and the biomass of prefishery juveniles (A)) remains constant:

$$E = A - hf_{tw} \quad (9)$$

Pollock, A = 70

Yellowfin, A = 45

In the first set of runs (juvenile recruitment not compensated), the values for h were: pollock 1200, yellowfin 2160. In the second set of runs juvenile recruitment was affected by fishing and the values for h were: pollock 700, yellowfin 1800. (Values derived from data in Laevastu 1983).

#### 6. EFFECTS OF FISHING ON THE DYNAMICS OF WALLEYE POLLOCK AND YELLOWFIN SOLE BIOMASSES WHEN KNIFE-EDGE RECRUITMENT TO FISHERY IS USED, AND FISHING DOES NOT AFFECT RECRUITMENT TO JUVENILES

Three different series of computer runs were made, each consisting of four numerical experiments (see Table 1). Each experiment contained two sets of different fishing. The first fishing set contained constant annual catch only (384 t/year, curve 1 on Figures 1 and 2), and constant catch plus three different density dependent fishing mortalities (curves 2 to 4 on Figures 1 and 2). Second set contained zero fishing and three different density dependent fishing mortalities without a constant annual catch. These different fishing mortalities operated on the whole biomass. The corresponding number based annual fishing mortality coefficients (F), operating on exploitable part of the stock would have been: 0.084, 0.198, and 0.38 for walleye pollock and 0.075, 0.16, and 0.30 for yellowfin sole.

In the first experiment growth rate and spawning stress mortality were assumed not to be affected by fishing. Fishing was made to affect spawning stress mortality only in the second experiment. In the third experiment fishing affected biomass



Table 1.--Set-up of numerical experiments and references to figures.

| Series no. | Experiment no. | Set no.               | Recruitment  | Spawning stress mortality   | Growth rate of population | Fishing mortality       | Figure no.            |
|------------|----------------|-----------------------|--|---|---------------------------|-------------------------|-----------------------|
| 1          | 1              | 1                     | Knife-edge, constant recruitment (pre-fishery juvenile biomass constant) | } Unaffected by fishing   | } Unaffected by fishing   | } Const. + density dep. | 1,2                   |
|            | 2              | } Affected by fishing |  |   |                           |                         | } Density dependent   |
|            | 3              |                       |  | } Unaffected by fishing   | } Const. + density dep.   | 5,6                     |                       |
|            | 4              | } Affected by fishing |  |   |                           | } Density dependent     | 7,8                   |
|            | 5              |                       |  | } Unaffected by fishing   | } Const. + density dep.   |                         | 9,10                  |
|            | 6              | } Affected by fishing |  |   |                           | } Density dependent     | 11,12                 |
|            | 7              |                       |  | } Unaffected by fishing   | } Const. + density dep.   |                         | 13,14                 |
|            | 8              | } Affected by fishing |  |   |                           | } Density dependent     | 15,16                 |
| 2          | 2              |                       | 4  | Recruits partially fished; recruitment function of spawning biomass                           | Affected by fishing       |                         | Unaffected by fishing |
|            | 3              | 6                     | } Unaffected by fishing  | } Unaffected by fishing   | } Density dependent       | 19,20                   |                       |
|            | 4              | 8                     |  |   |                           | } Affected by fishing   | } Density dependent   |
|            | 3              | 4                     | 8  | Same as series 2 except recruitment additionally affected by the size of sex products release | Affected by fishing       |                         |                       |



growth only, and in the fourth experiment fishing affected both spawning stress mortality and biomass growth rate.

The results of the numerical experiments in the first series of computer runs are presented in Figures 1 to 16 as biomass change in eight years with the corresponding experimental conditions as described above. (The four experiments are presented on two figures each, corresponding to the two different, above-mentioned fishing set ups.)

Experiment 1 (Figures 1 to 4), no effect of fishing on spawning stress mortality or on growth rate ("uncompensated").

In case of constant catch (curve 1), pollock biomass decreases less (Figure 1) than the yellowfin biomass (Figure 2) with the same amount of catch. The larger percentage of the biomass that is exploitable and the higher growth rate for pollock are responsible for this difference. With constant catch plus density dependent fishing (curves 2 to 4), the pollock biomass decreases faster (Figure 1) than the yellowfin biomass (Figure 2) at approximately the same numerical fishing mortality coefficient ( $F$ ). However, the corresponding biomass based fishing mortality coefficient ( $f_{tw}$ ) is about twice as high for pollock as compared to yellowfin (due to specified input increments of  $f_d$ ). Therefore, a higher proportion of biomass would be removed in the case of pollock. The reason for this is that the fraction of exploitable biomass in a virgin pollock population is considerably higher (about 70%) than in yellowfin (about 45%). Some of the effects of above-mentioned differences in biomass parameters (growth rate and relative size of exploitable biomass) are more clearly shown in Figures 3 and 4, which show the dynamics of "uncompensated" and unfished biomasses (curve 1) and biomasses fished at different rates (curves 2 to 4).



Experiment 2 (Figures 5 to 8), spawning stress mortality compensated at different fishing intensities; growth is not compensated.

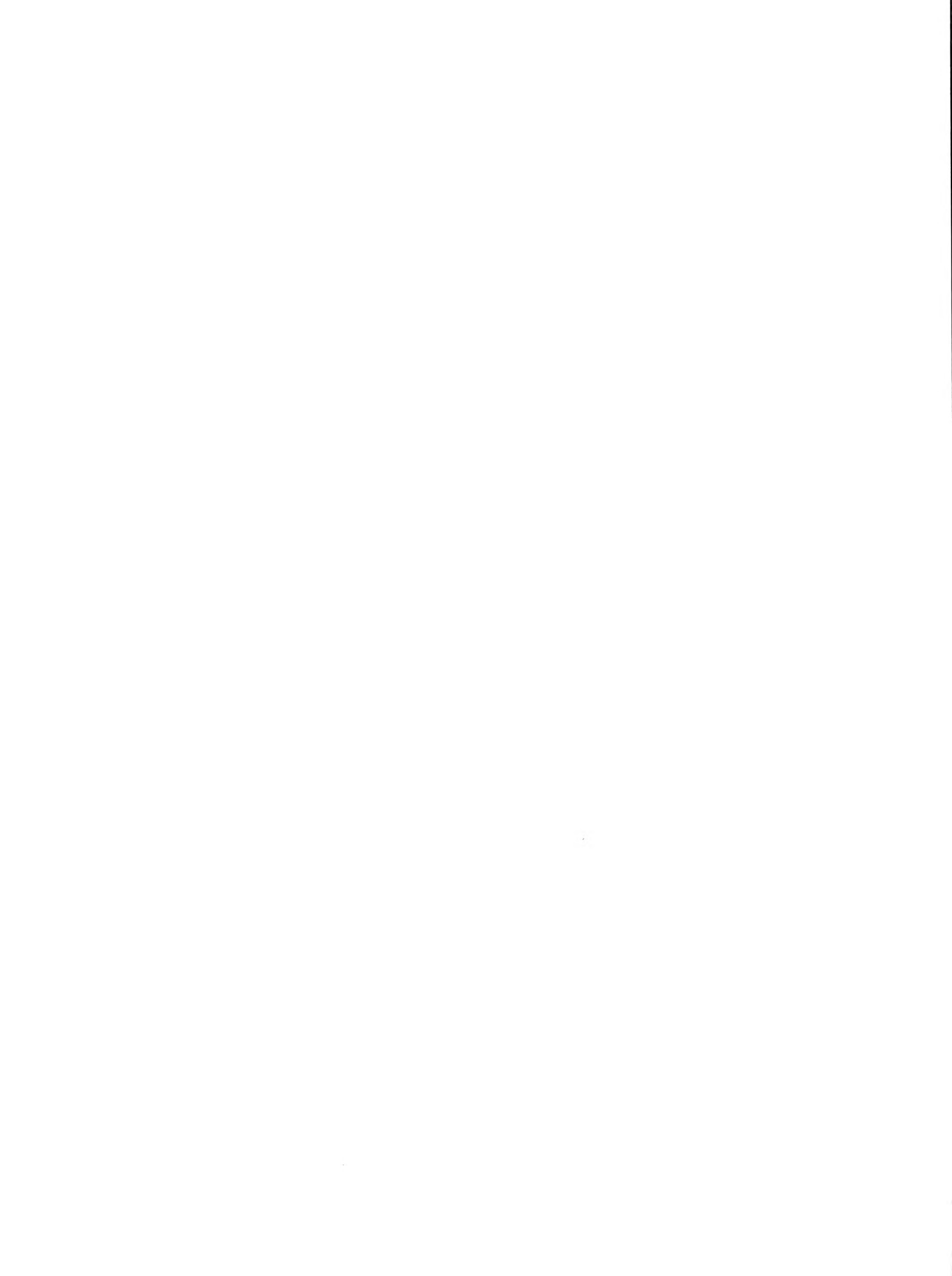
The lowering of spawning stress mortality with increased fishing causes considerable compensation in biomass losses (compare Figures 1 to 4 with Figures 5 to 8). There is less spread of resulting biomasses with time at high and low fishing levels than in the uncompensated experiment (Experiment 1). This is due to increased compensation at more intense levels of fishing (i.e., the spawning stress mortality decreases at a higher rate than the increase of fishing mortality). The biomass changes in Figures 7 and 8 are smaller than those in Figures 5 and 6. This is due to lower fishing mortality in Figures 7 and 8.

Experiment 3 (Figures 9 to 12), growth is compensated for effects of fishing; spawning stress mortality is not compensated.

The effects of fishing on growth produce quantitatively similar results on biomass dynamics to those caused by spawning stress changes (compare Figures 5 and 6 with 9 and 10), except in the case of density dependent fishing only (Figures 11 and 12) where the resulting biomasses are slightly higher. (At very high levels of fishing, (e.g.,  $F$  greater than 0.3) this increase of biomass might not occur.)

Experiment 4 (Figures 13 to 16), both biomass growth and spawning stress mortality are affected by fishing.

The biomass changes are heavily compensated - both biomasses increase with time and this increase is greater at the higher levels of fishing used in this experiment. The spreading of biomasses between low and high fishing is less in pollock than in yellowfin (Figures 13 and 14). (More biomass removed in pollock, thus higher compensation.) In case of density dependent fishing only (Figures 15 and 16), the increase of biomass is less than in Figures 13 and 14. This difference is due to less fishing and less compensation of biomass in Figures 15 and 16.





The most astonishing fact on the last four figures is that curve 4, presenting the highest level of fishing, shows the highest growth of biomass -- "the more you fish, the more there is to fish". This pronounced compensation is scarcely expected in reality, as the recruitment changes due to total spawning biomass changes (decrease) would counteract the compensation resulting from intense fishing.

#### 7. DYNAMICS OF WALLEYE POLLOCK AND YELLOWFIN SOLE BIOMASSES UNDER DIFFERENT FISHING INTENSITIES WHEN FISHING AFFECTS RECRUITMENT

The increase of stocks of fish as a result of compensating mechanisms caused by increased fishing to the extent computed in the previous section of this paper, seems somewhat unrealistic. However, some of the observed concomitant increases of stocks and landings might be due to the same mechanisms as applied in the previous computations, such as the increase of roundfish stocks and landings in the North Sea in the 1960's and 1970's, and the increases of many heavily exploited pelagic stocks a few years prior to the total collapse of these stocks due to excessive fishing (recruitment overfishing) on shoaling species.

The reasons for the "overcompensations" were considered to be mainly caused by two assumptions made in the computations of the changes of biomass parameters due to fishing (Laevastu 1983): 1) the knife-edge recruitment to exploitable stock, and 2) recruitment (and juvenile biomass) remains constant when fishing increases. These assumptions are probably unrealistic. Thus, new numerical computations of changes of biomass growth rate and spawning stress mortality at different levels of fishing were carried out, whereby year classes prior to full recruitment to fishery were subjected to partial fishing, and the recruitment from juveniles to exploitable biomass was made a function of fishing (Laevastu 1983). The new pertinent numerical coefficients are given in Section 5 of this paper.



Some of the results of the second series of computations with new, adjusted coefficients are shown in Figures 17 and 18. These two figures are directly comparable to Figures 15 and 16 and to Figures 3 and 4 (the latter presenting uncompensated biomass dynamics). Considerable decrease in the biomass of pollock occurred with the new coefficients when compared to previous computations with initial coefficients (Figure 17 compared to Figure 15), whereas the decrease of yellowfin biomass is smaller (Figure 18 compared to Figure 16). In the latter species, the biomass still increases with increasing fishing. The main reason for the differences in the dynamics of biomasses in the two species is that the fraction of prefishery juveniles in pollock is considerably smaller than in yellowfin. In this connection it is well known from empirical observations that stocks of different species respond differently to comparable (equal) fishing pressure.

The influence of fishing on the dynamics of a stock biomass is affected in about equal shares by the change of stock growth rate and by the change of total mortality via the change of relative contribution of spawning stress mortality. The growth rate change of the stock is affected via the change of biomass distribution with age, which also influences the recruitment to exploitable stock. The effects of the new (adjusted) growth rates of biomass on the biomass dynamics are shown in Figures 19 and 20. These figures are comparable to Figures 9 and 10, which were computed with the first set of coefficients of the effects of fishing. The corresponding effects of new (adjusted) spawning stress mortality coefficients are shown on Figures 21 and 22, which are comparable to Figures 7 and 8, computed with first set of coefficients of the effects of fishing without partial fishery on prefishery juveniles, and assuming constant recruitment.



The mature population (spawning biomass) releases about 9 percent of its biomass as "sex products" (eggs and milt) each year. Fishing changes the size of the spawning biomass, and consequently the total amount of "sex products" released changes also. The biomass decreases by the amount of "sex products" which are released. Furthermore, the larval recruitment is affected by the amount of eggs deposited and could also change the recruitment to exploitable part of the biomass in later years. These possible effects on biomass dynamics were tested in the third series of computer runs, assuming relatively conservative relations between the spawning biomass change due to fishing and recruitment of the juveniles:

$$D = (1 - (E_t/E_o)) * 0.09 \quad (10)$$

$$B_t = B_t - (B_t * D) \quad (11)$$

where D is a "change factor", being a function of the quotient between actual exploitable biomass as affected by fishing ( $E_t$ ) and exploitable biomass in an unfished population ( $E_o$ ).  $B_t$  is the actual biomass.

The above formulas (10 and 11) should not be considered as expressing explicitly any changes of recruitment per se, but only biomass change due to changes in sex product release.

The results of the computations with this "change factor" and with the adjusted (new) spawning stress mortality and growth coefficients are shown in Figures 23 and 24. These figures are directly comparable to Figures 17 and 18, showing that the effect of the adjustment on pollock biomass is small, whereas it is noticeably larger on yellowfin biomass. The reason for this species specific difference is that the fraction of exploitable biomass is considerably larger in pollock than in yellowfin, and consequently, fishing changes the quotient ( $E_t/E_o$ )



in pollock considerably less than in yellowfin. This difference might also be interpreted as another indication that in case of comparable stock sizes, pollock stock can be fished more heavily than yellowfin stock.

The results of the studies in this paper indicate that expected changes in biomasses due to fishing are counteracted to a considerable degree by concomitant changes in biomasses. The change of the growth rate of a stock is largely influenced by the change of biomass distribution with age. The latter is also affected by variations in predation on juveniles (including cannibalism), which in turn will affect the recruitment to exploitable stock. Numerical experiments suggest that the change in predation as a linear function of the biomass density in the environment has relatively little influence on biomass dynamics. However, predation does not change as a linear function if there is considerable selectivity of prey items.

The compensation mechanisms which counteract the effects of fishing on the stock will be affected by changes in predation of juveniles, which will also affect recruitment to the exploitable part of the stock in a more complex manner than presented in this single species model. Therefore, further study of the effects of fishing and changes in stock biomass caused by it, must be carried out in holistic ecosystem simulations, such as PROBUB and DYNUMES, which can also explain the mechanisms of interactions and nonlinearities in them in a more realistic manner than is possible with a single species approach.

## 8. CONCLUSIONS

1. Given low to moderate fishing ( $F$  maximum 0.4) the removal of the exploitable biomass by fishing is compensated for by the increase in the growth rate of the population and by the decrease of spawning stress mortality.

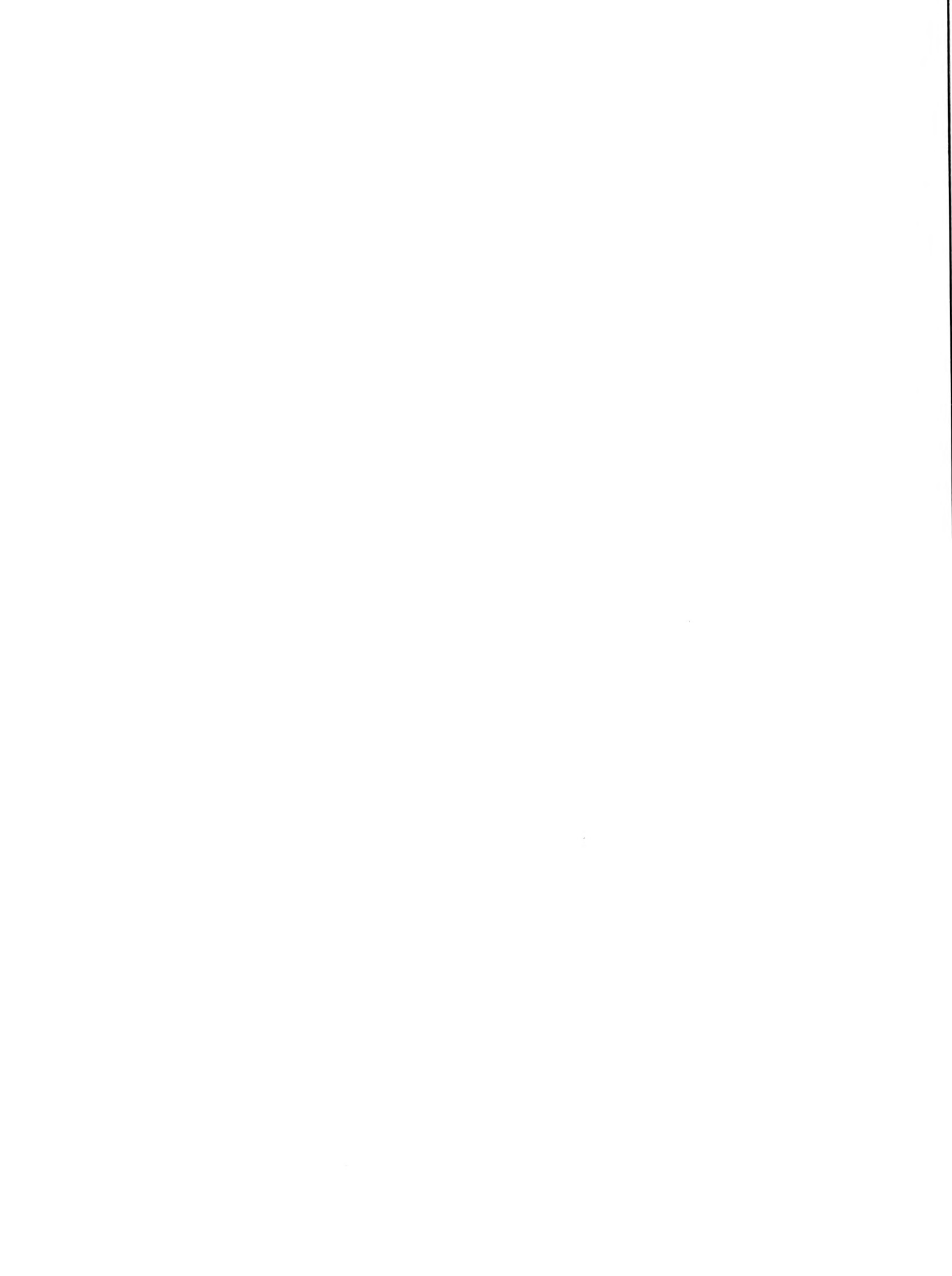




2. The effects of fishing and their compensation through the population growth rate and spawning stress mortality changes vary considerably from species to species, indicating among others that different species tolerate different amounts of fishing without decreasing the total biomass.

3. The numerical experiments demonstrate that some relation between spawning biomass and recruitment must exist at all levels of biomass, and that this relation neither decreases nor levels off at high spawning biomass.

4. Empirical results suggest that recruitment to exploitable stock must be a nonlinear function of prey density dependent predation on juveniles. These relations cannot be determined with a single species approach.



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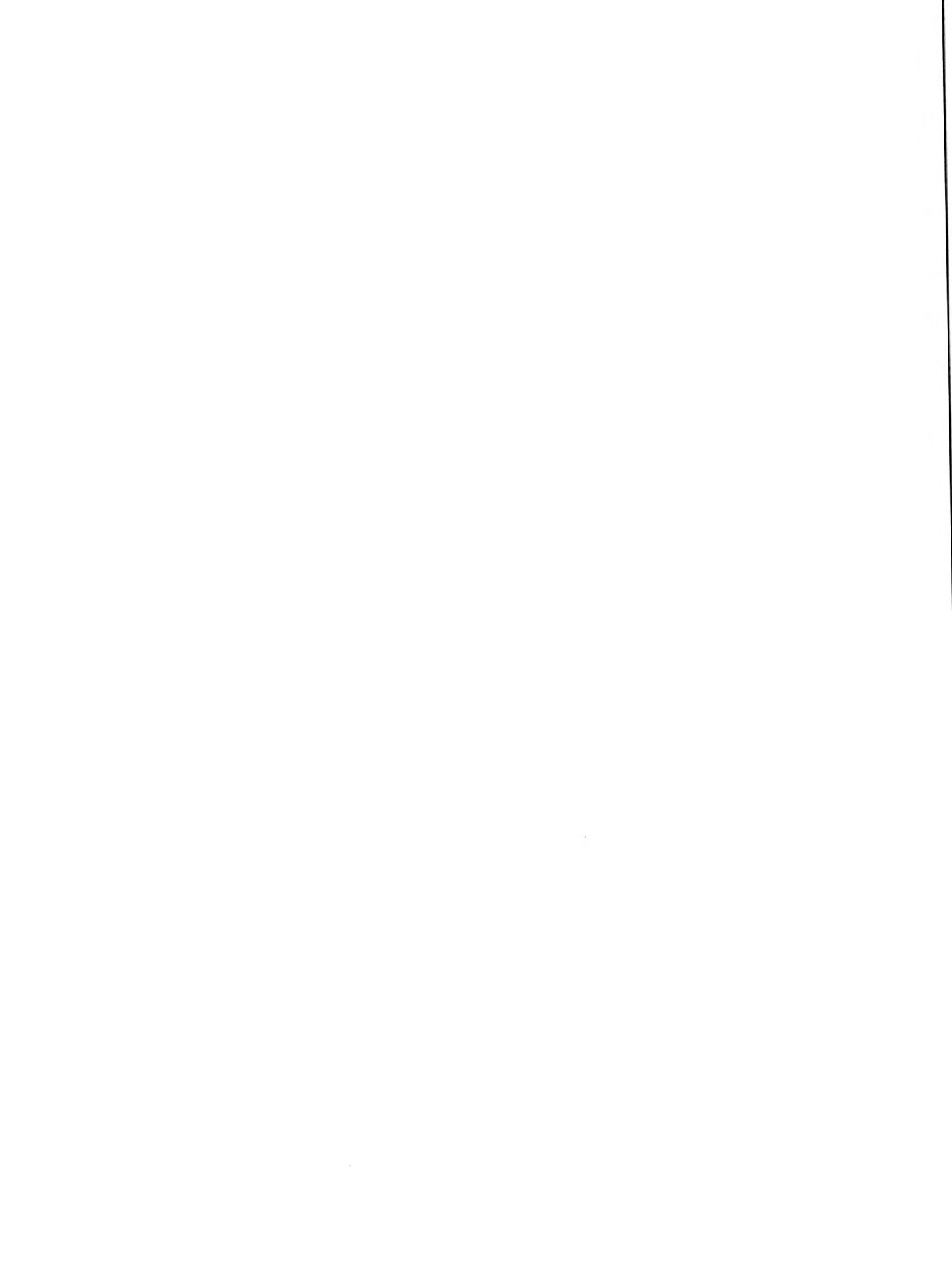
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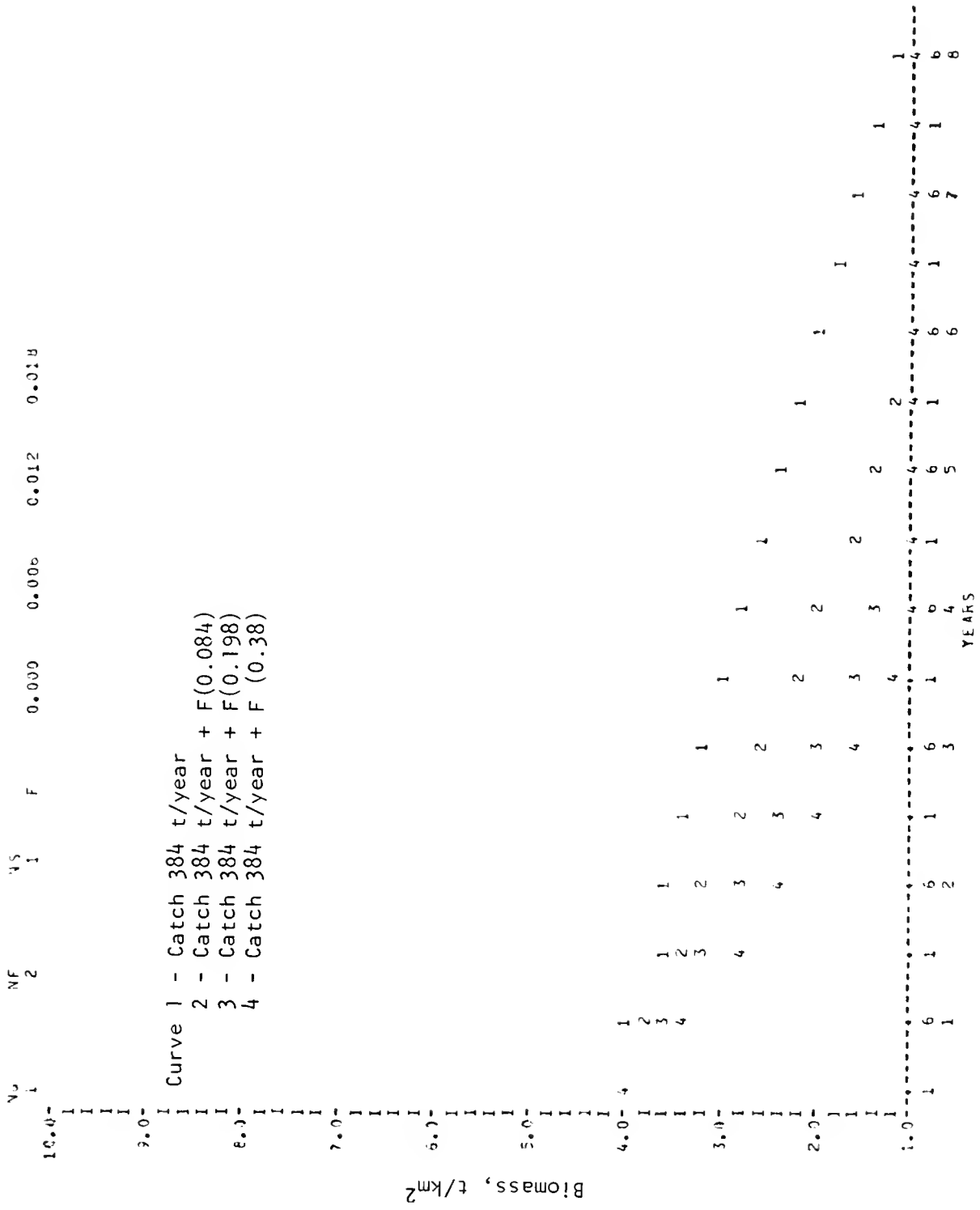
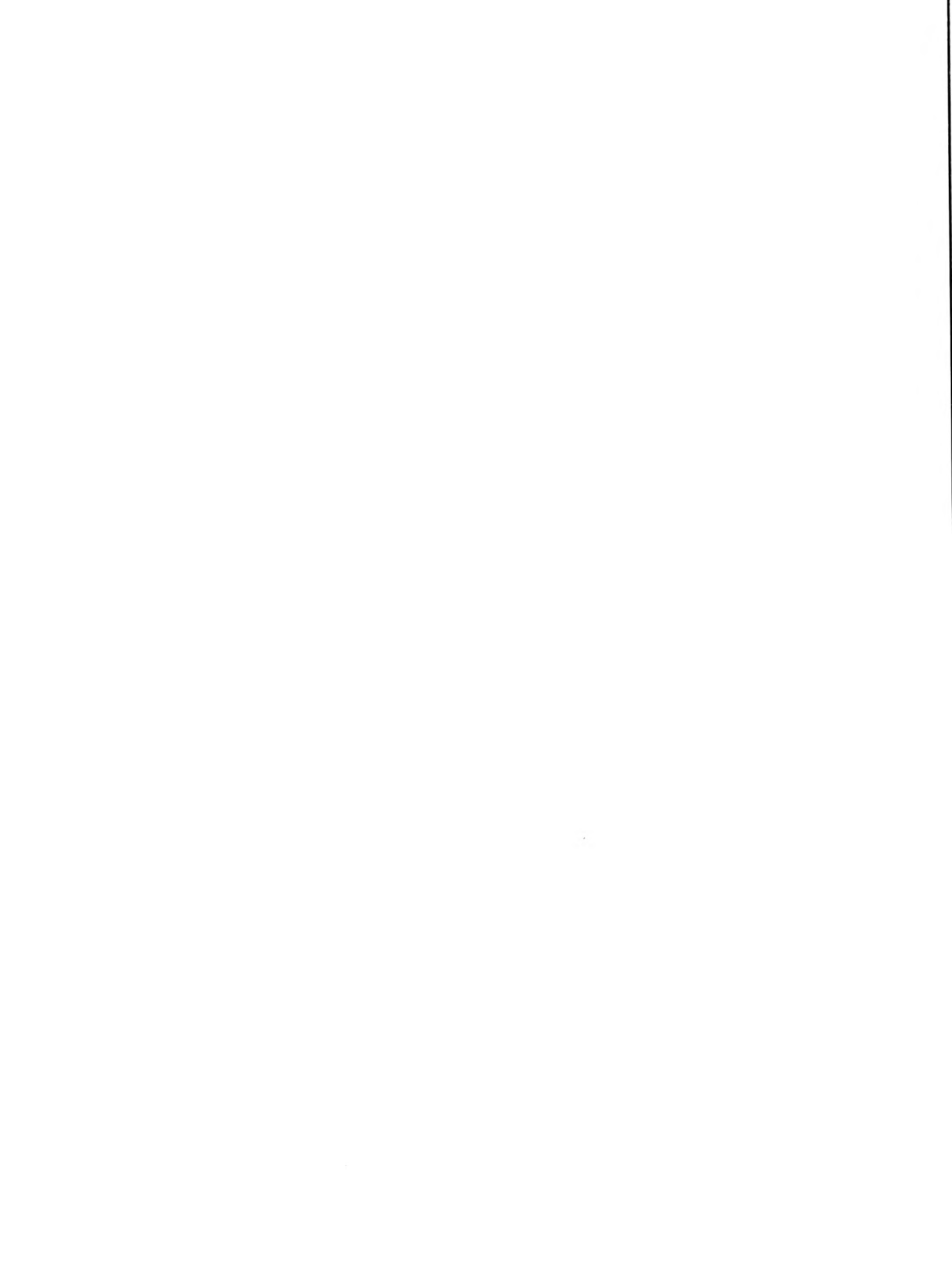


Figure 1.--Change of biomass of pollock with time with different fishing intensities which include a constant catch. Growth rate and spawning stress mortality are unaffected by fishing.



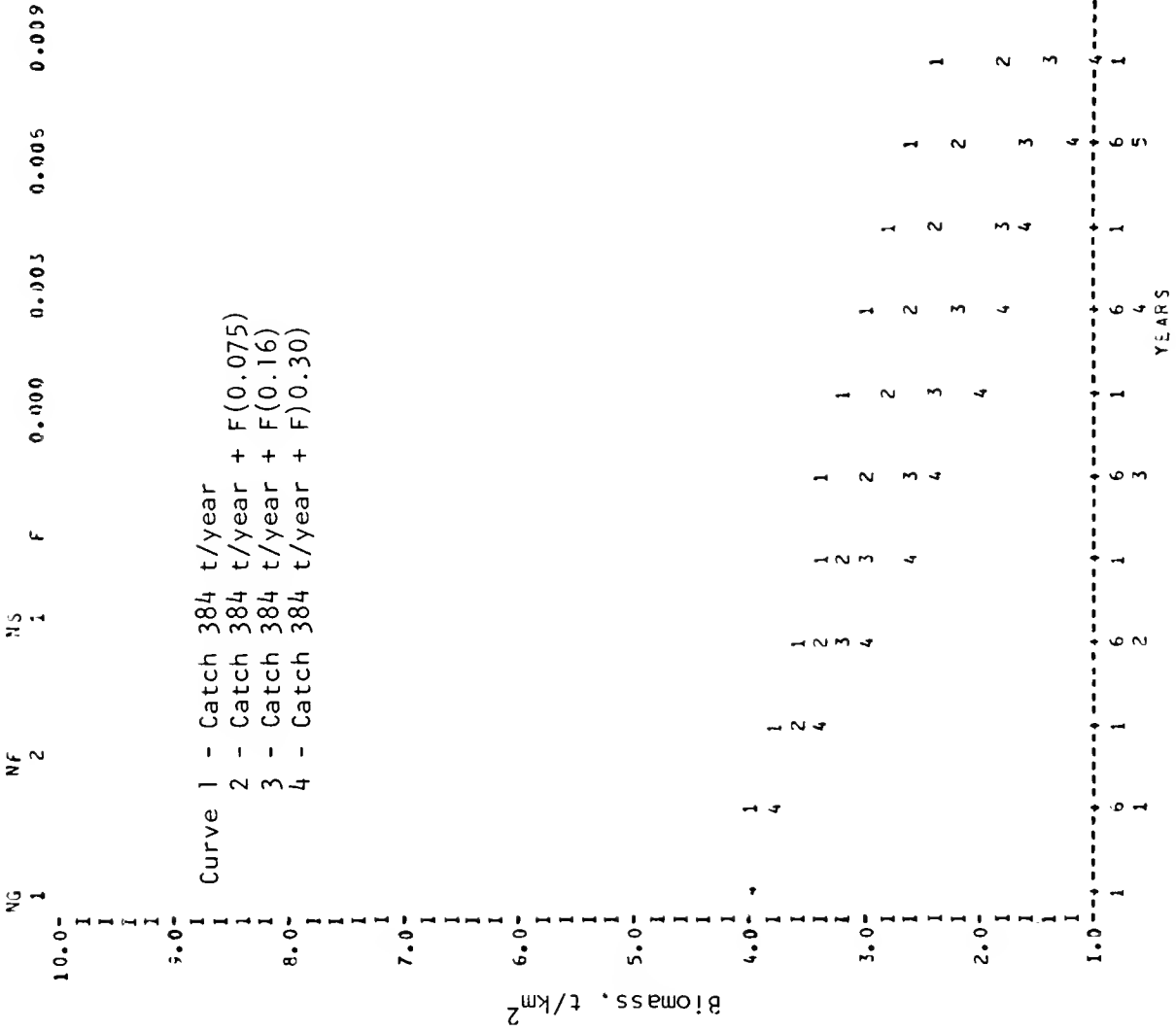
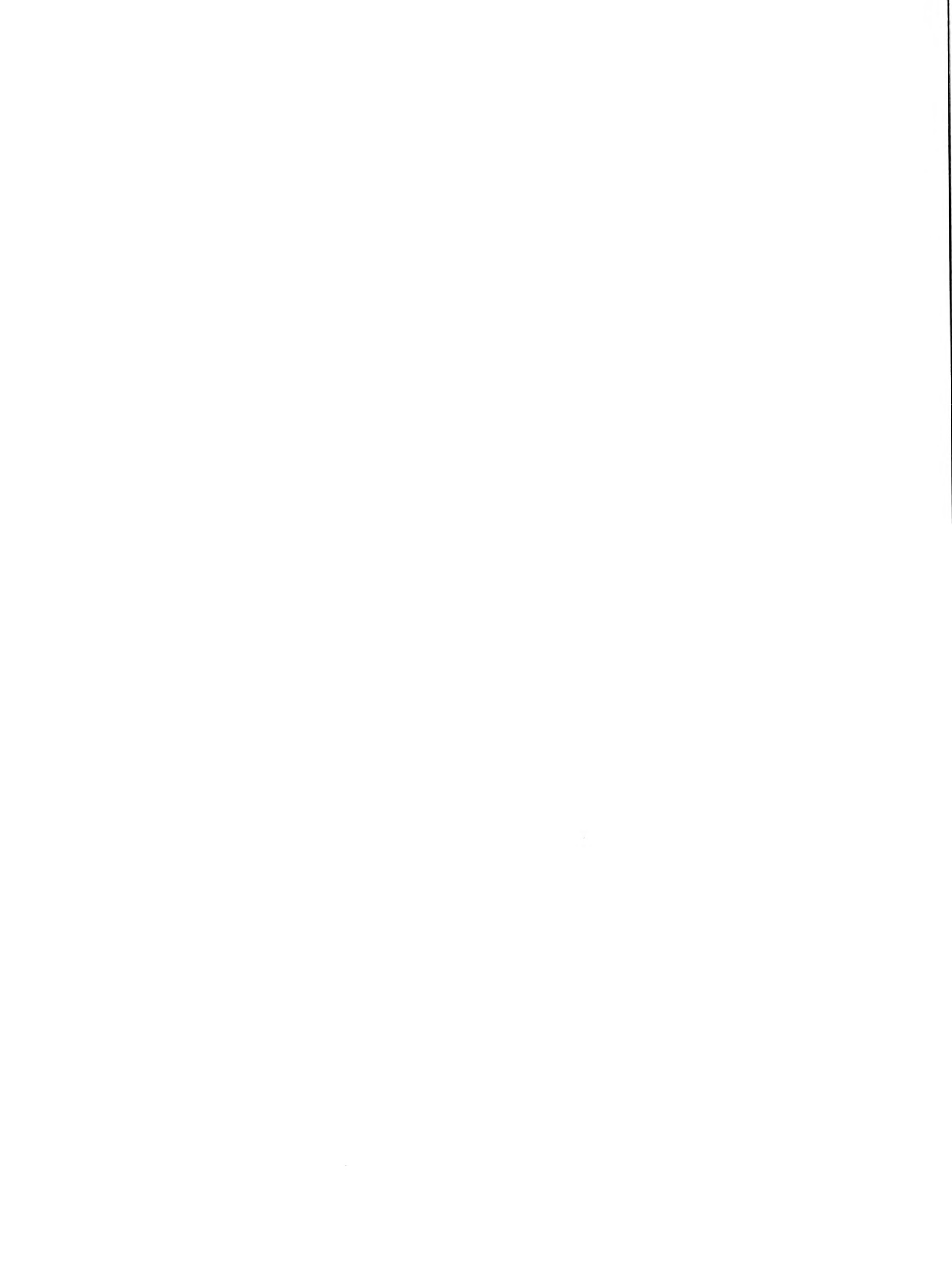


Figure 2.--Change of biomass of yellowfin sole with time with different fishing intensities which include a constant catch. Growth rate and spawning stress mortality are unaffected by fishing.





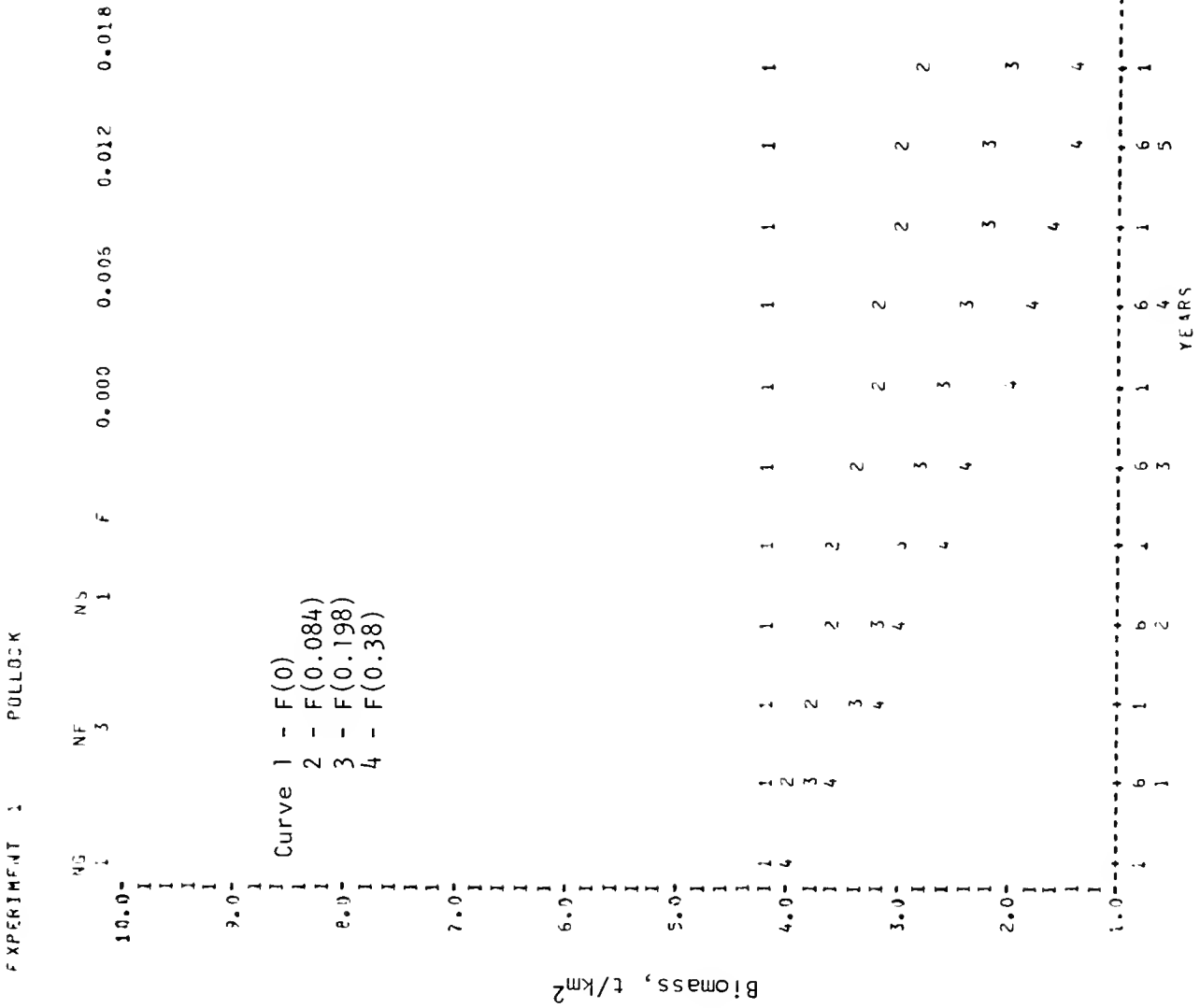


Figure 3.---Change of biomass of pollock with time with different biomass density dependent fishing coefficients. Growth rate and spawning stress mortalities are unaffected by fishing.



EXPERIMENT 1 YELLOWFIN

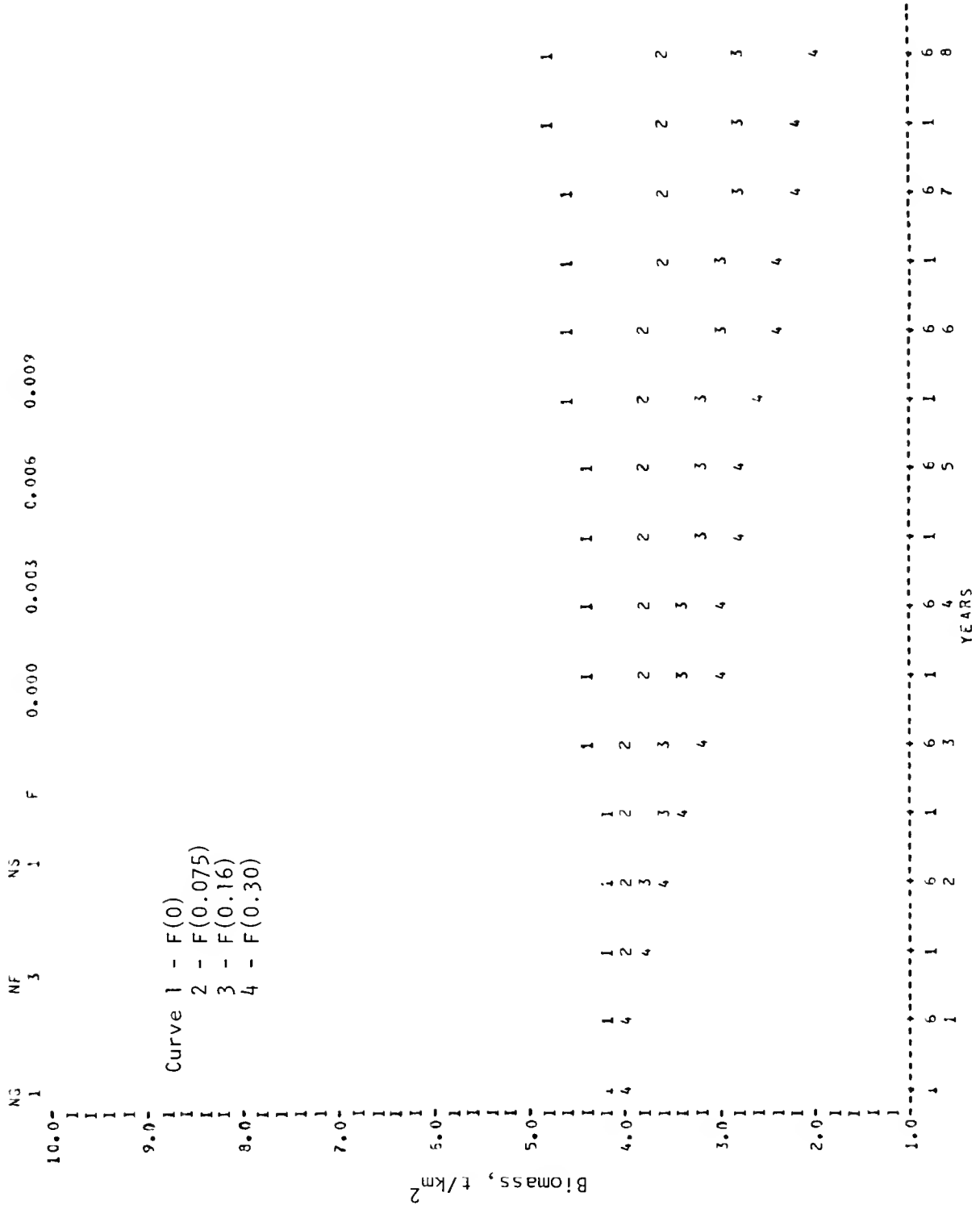


Figure 4.--Change of biomass of yellowfin sole with time with different biomass density dependent fishing coefficients. Growth rate and spawning stress mortalities are unaffected by fishing.



EXPERIMENT 2 POLLOCK

10.0--  
9.0--  
8.0--  
7.0--  
6.0--  
5.0--  
4.0--  
3.0--  
2.0--  
1.0--

- Curve 1 - Catch 384 t/year
- 2 - Catch 384 t/year + F(0.084)
- 3 - Catch 384 t/year + F(0.198)
- 4 - Catch 384 t/year + F(0.38)

NS 2  
NF 2  
F 0.0000 0.0006 0.0012 0.0018

Biomass, t/km<sup>2</sup>

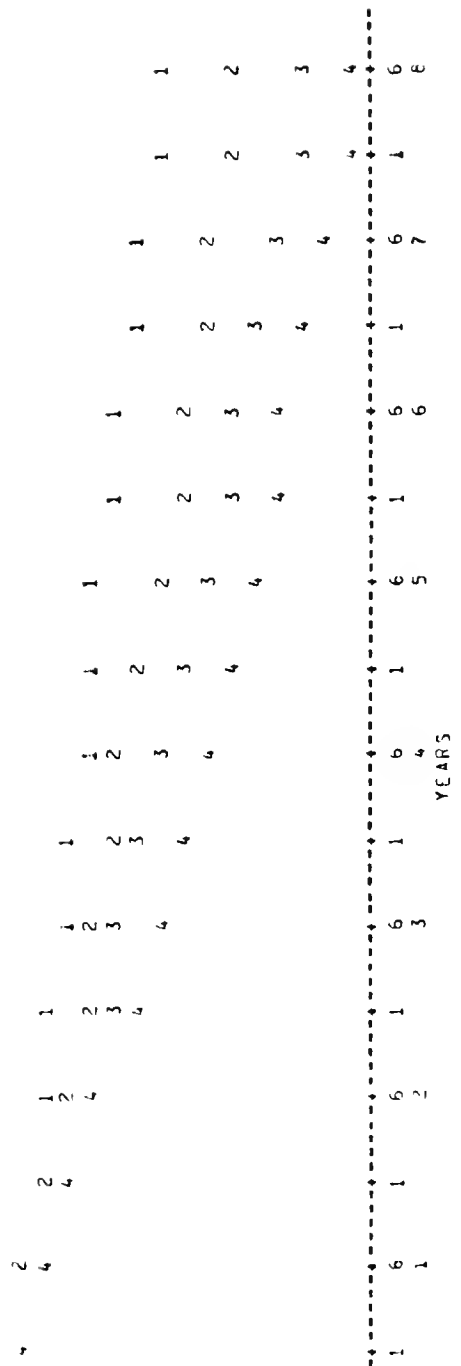


Figure 5.--Change of biomass of pollock as in Figure 1 except spawning stress mortality is affected by fishing.



EXPERIMENT 2 YELLOWFIN

NG 1 MF 2 NS 2 F 0.000 0.003 0.006 0.009

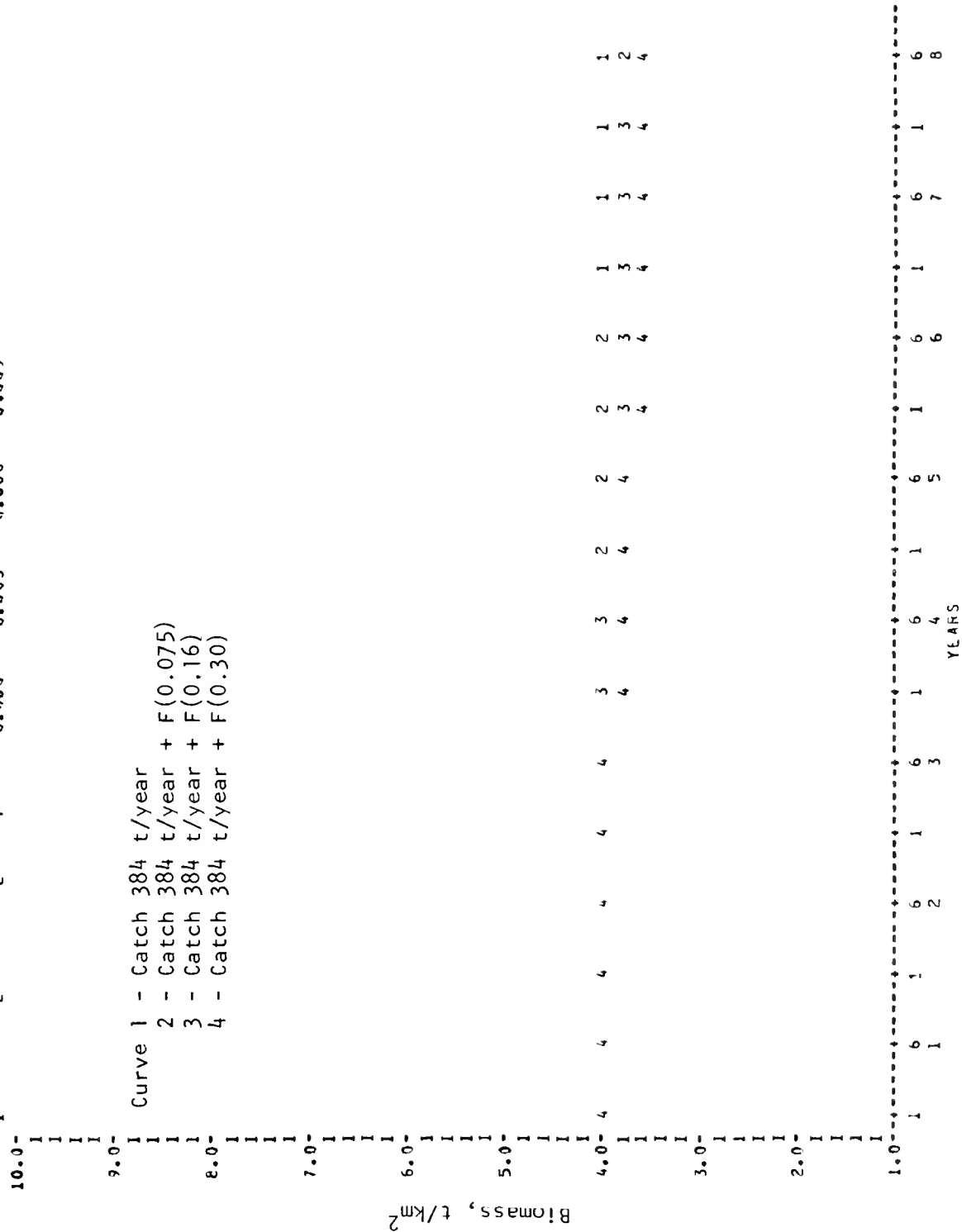


Figure 6.--Change of biomass of yellowfin sole as in Figure 2 except spawning stress mortality is affected by fishing.





EXPERIMENT 2 POLLOCK

NS 1 MF 3 NS 2 F 7 0.000 0.005 0.012 0.018

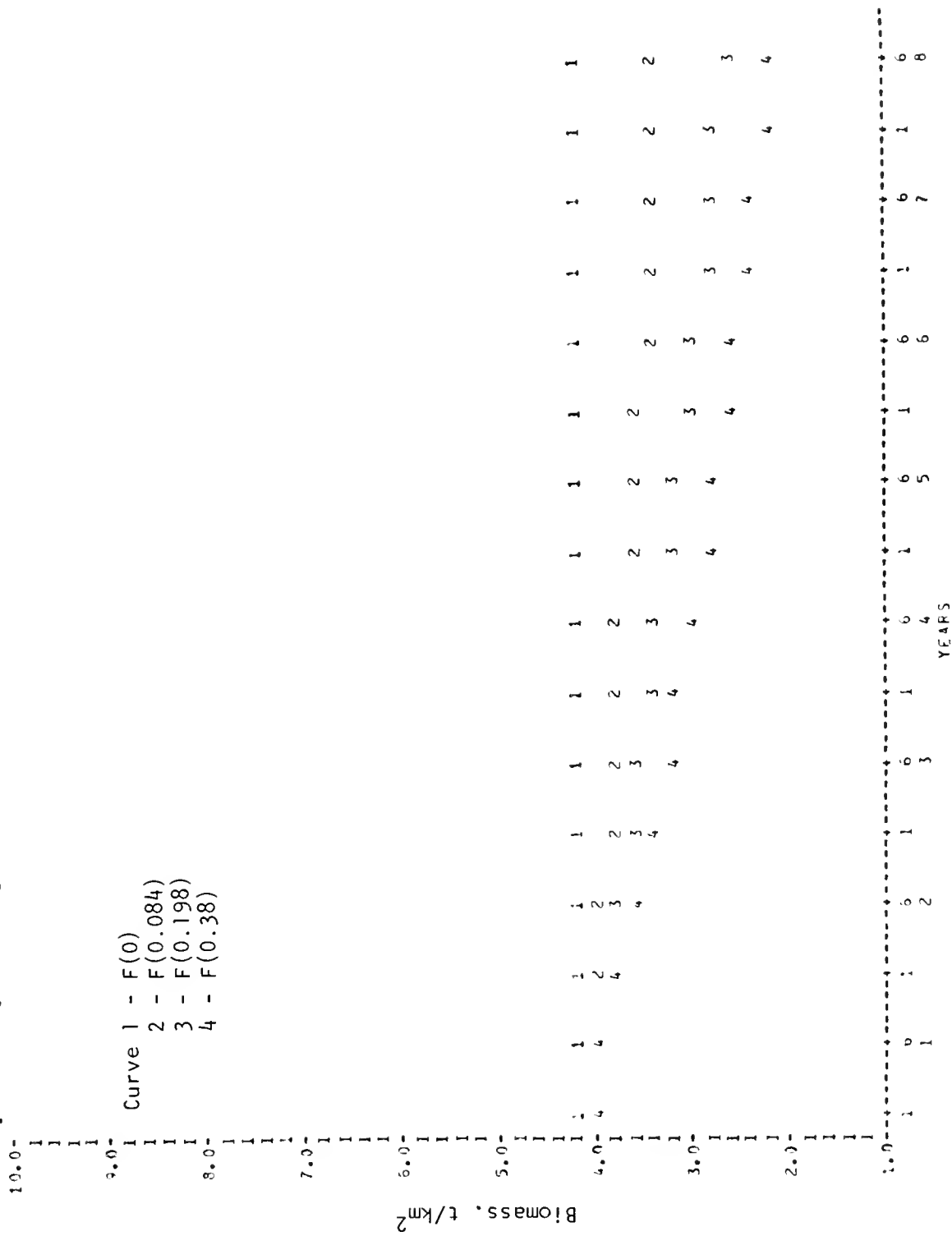
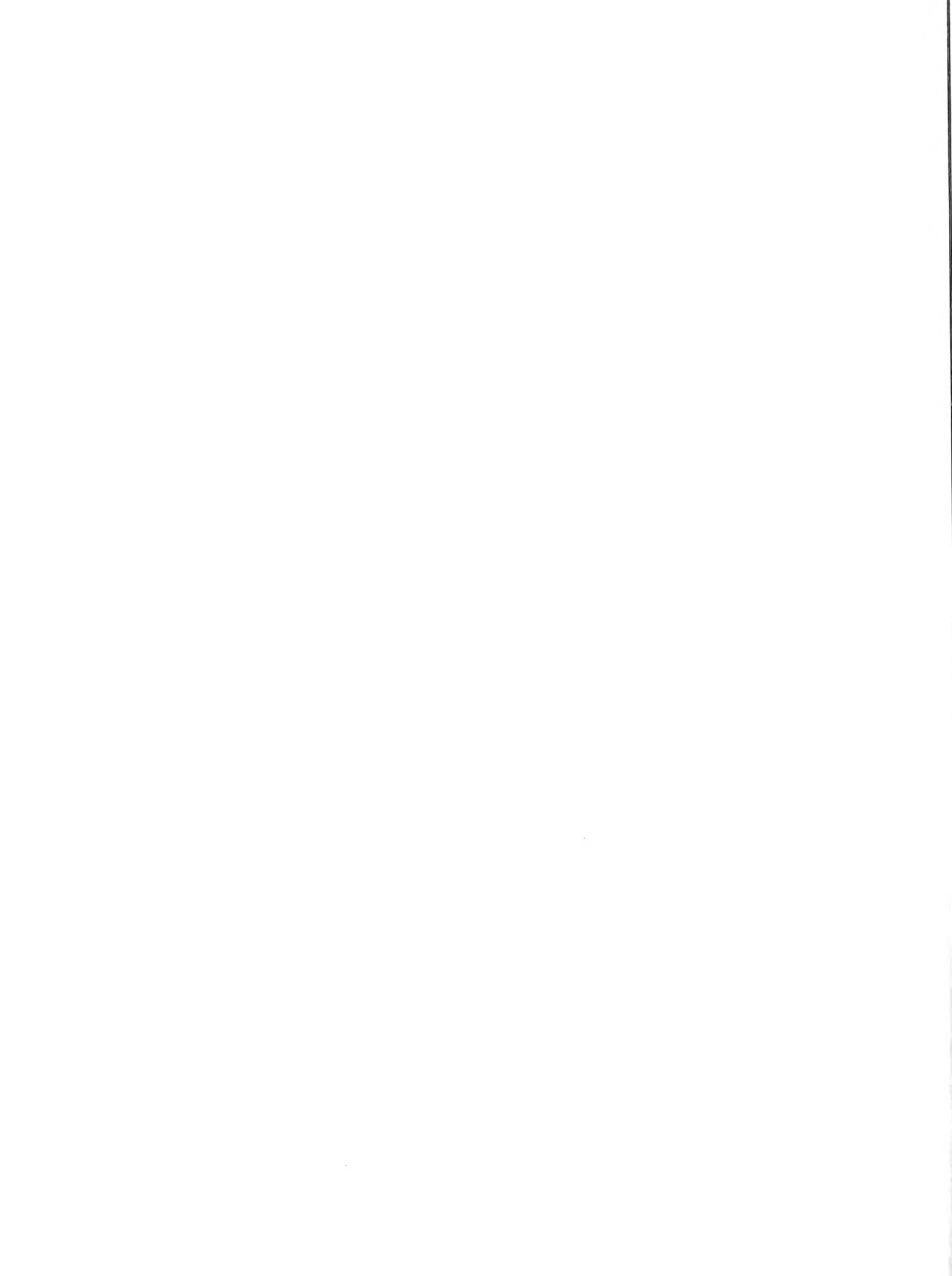


Figure 7.--Changes of biomass of pollock as in Figure 3 except spawning stress mortality is affected by fishing.



EXPERIMENT 2 YELLOWFIN

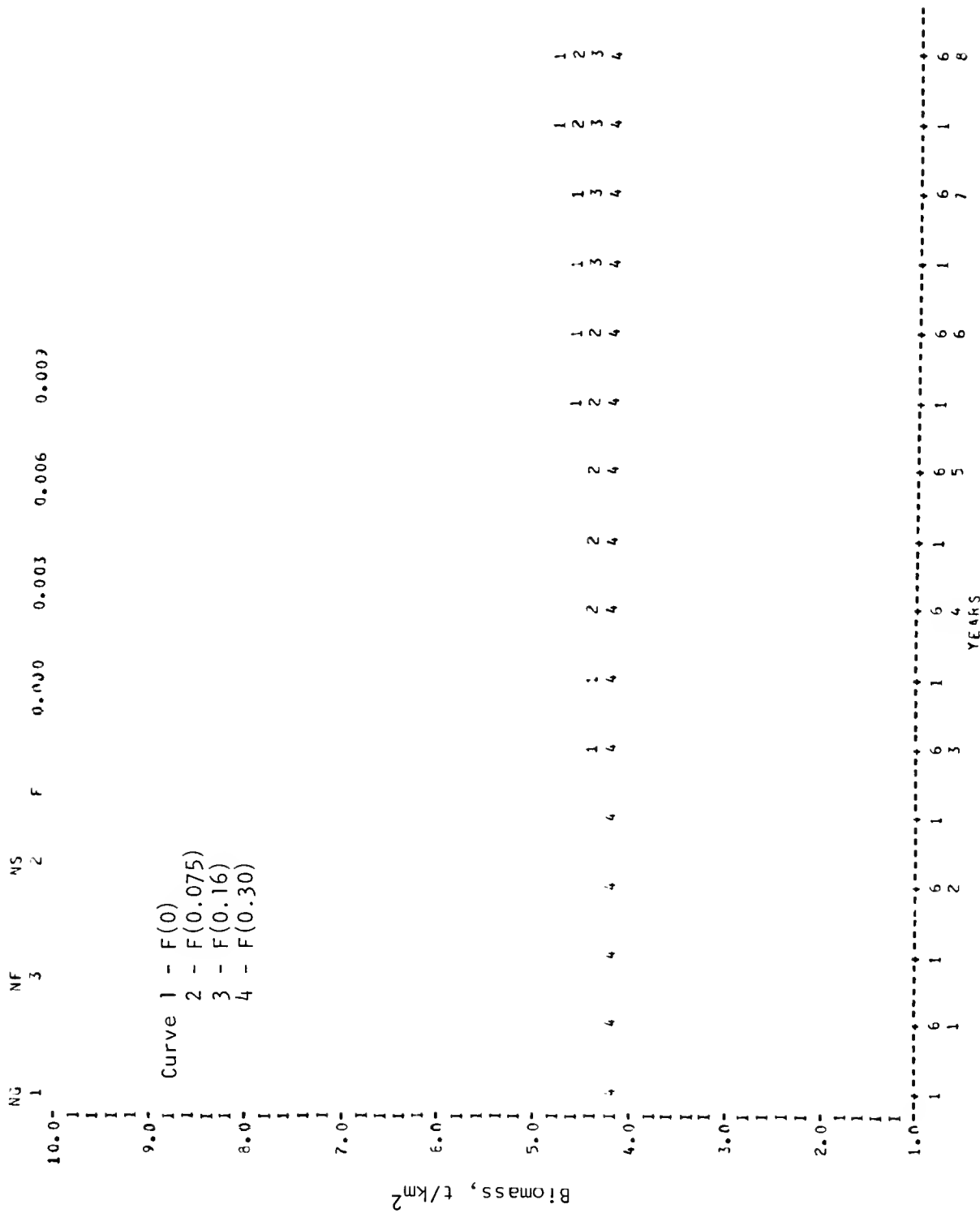


Figure 8.--Changes of biomass of yellowfin sole as in Figure 4 except spawning stress mortality is affected by fishing.



VF 2 VS 1 F 0.000 0.006 0.012 0.018

Curve 1 - Catch 384 t/year  
 2 - Catch 384 t/year + F(0.084)  
 3 - Catch 384 t/year + F(0.198)  
 4 - Catch 384 t/year + F(0.38)

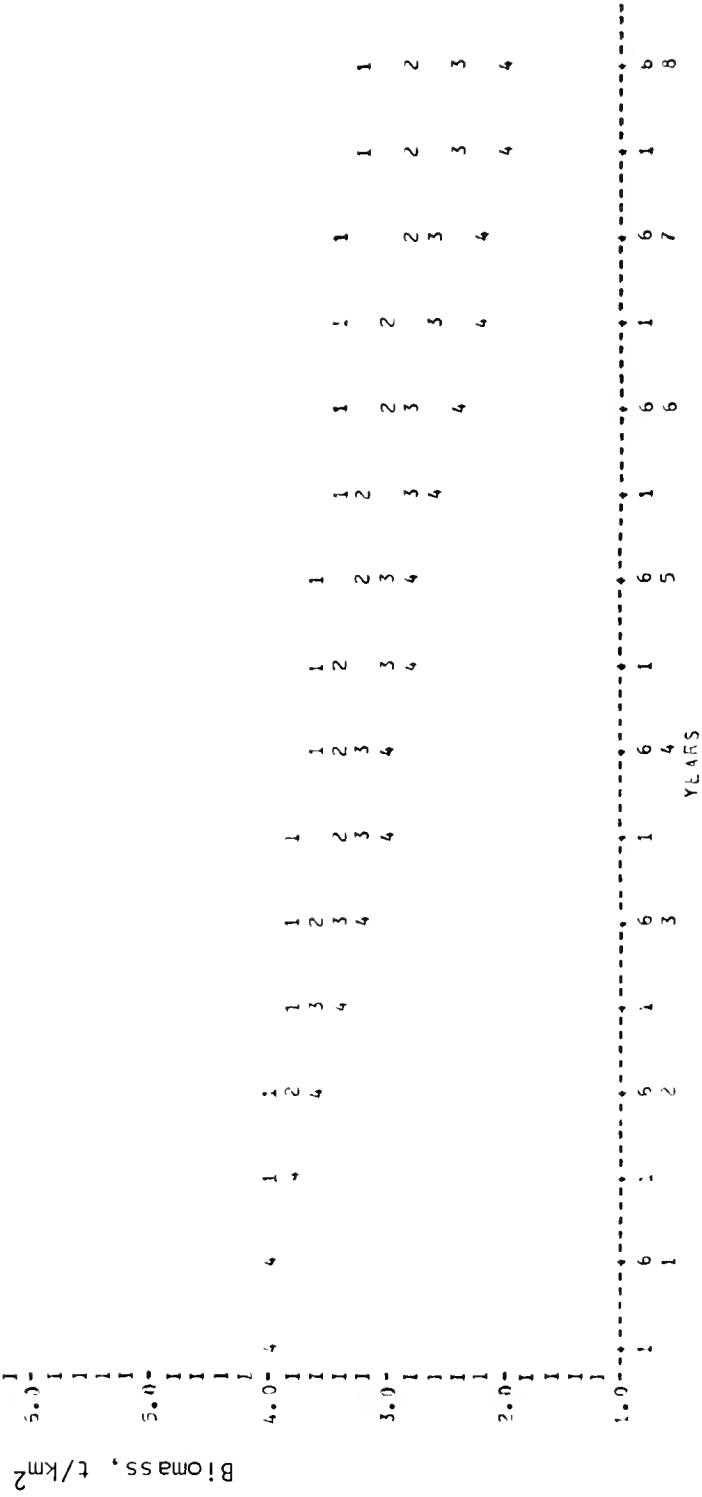
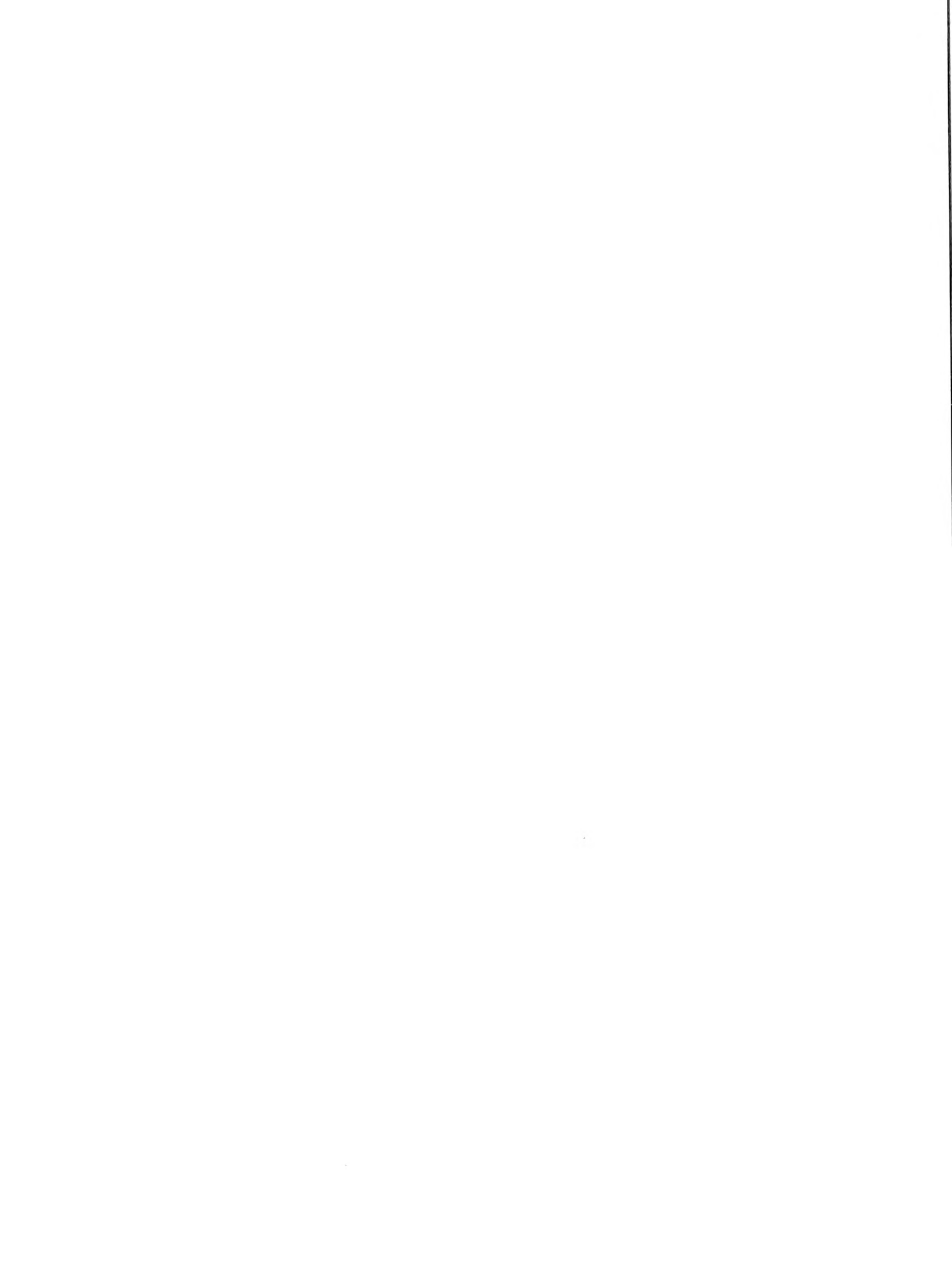


Figure 9.--Changes of biomass of pollock as in Figure 1 except growth rate of biomass is affected by fishing.



EXPERIMENT 3 YELLOWFIN

NG 2 NF 2 N<sub>2</sub> 1 F 0.000 0.003 0.006 0.009

Curve 1 - Catch 384 t/year  
 2 - Catch 384 t/year + F(0.075)  
 3 - Catch w8r t/year + F(0.16)  
 4 - Catch 384 t/year + F(0.30)  
 (Note: one or a few numbers of curves indicate that curves coincide with each other)

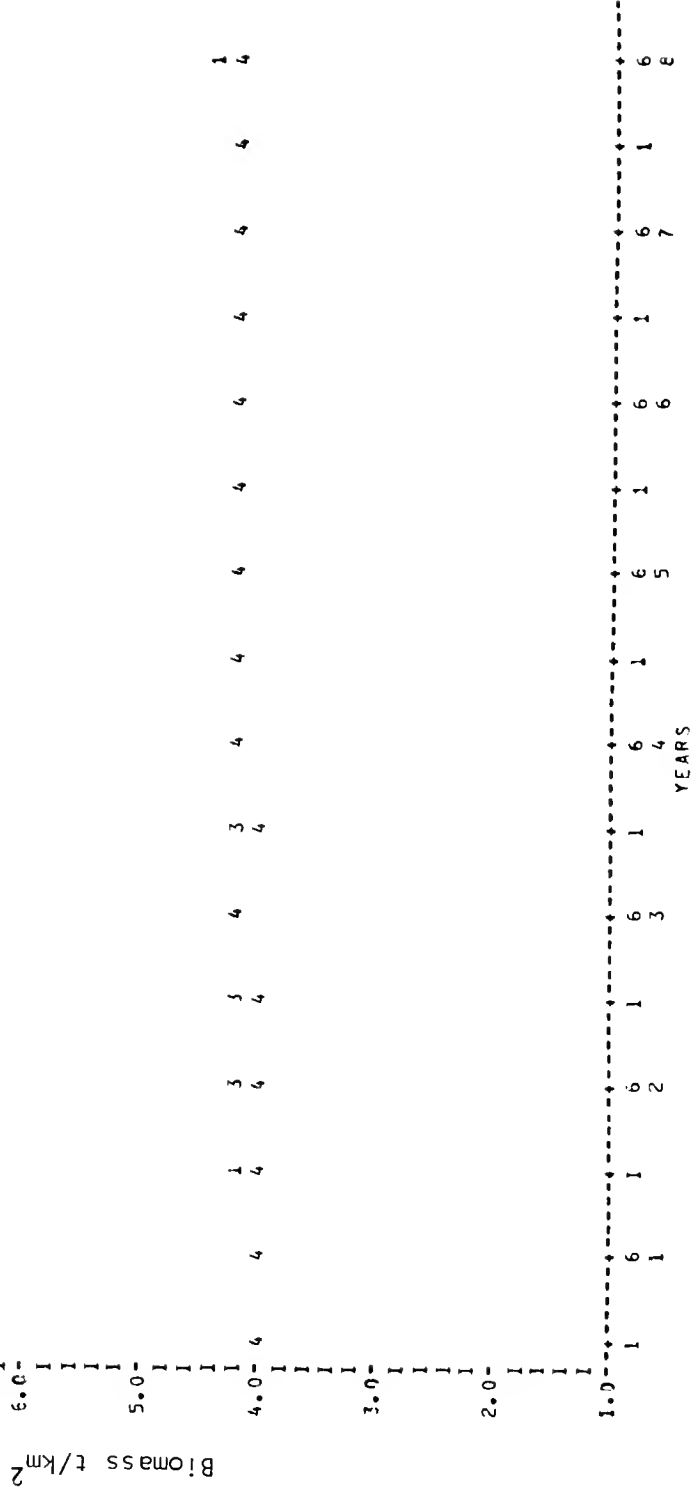


Figure 10.---Changes of biomass of yellowfin sole as in Figure 2 except growth rate of biomass is affected by fishing.





NS NF FS F 0.000 0.006 0.012 0.018

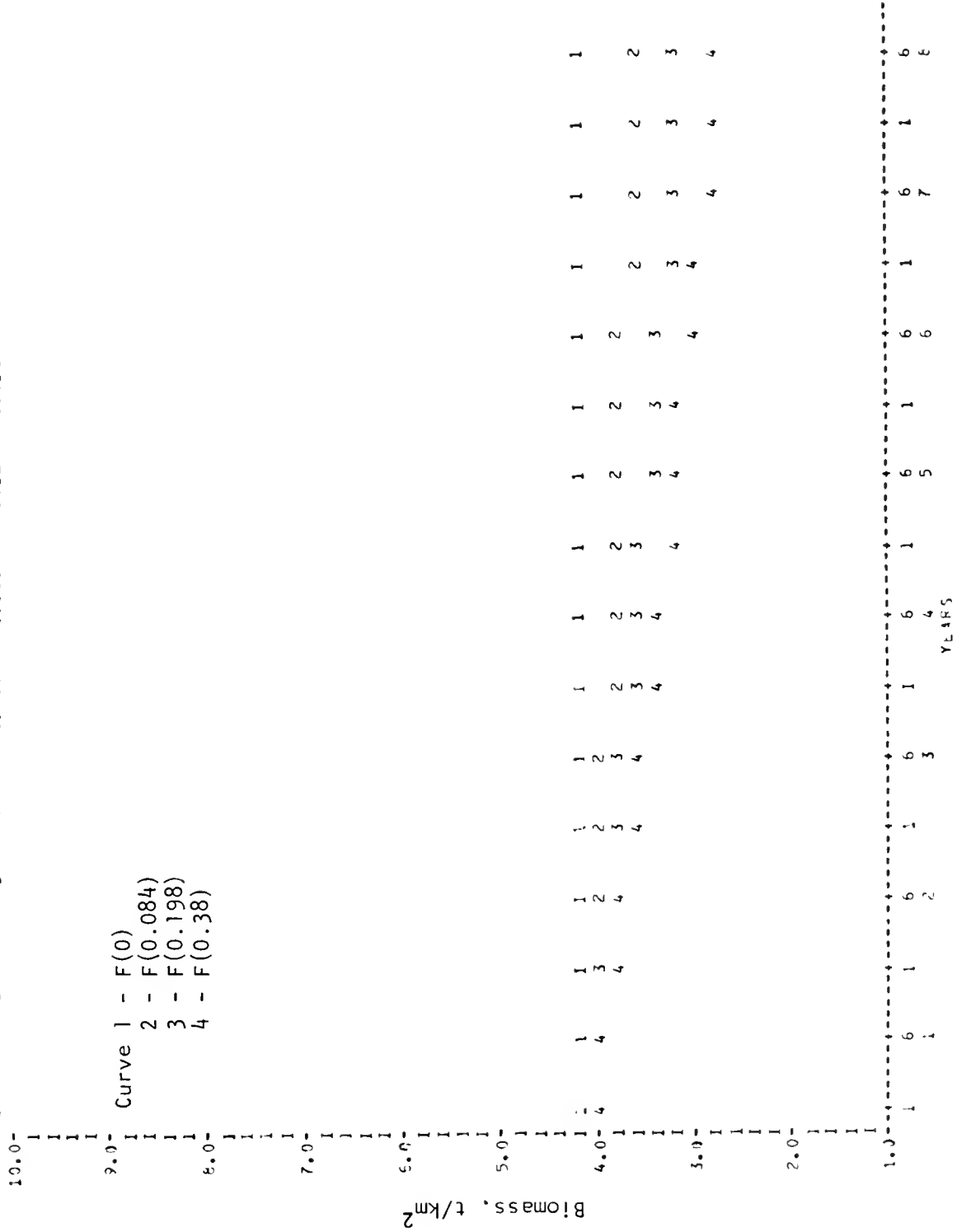
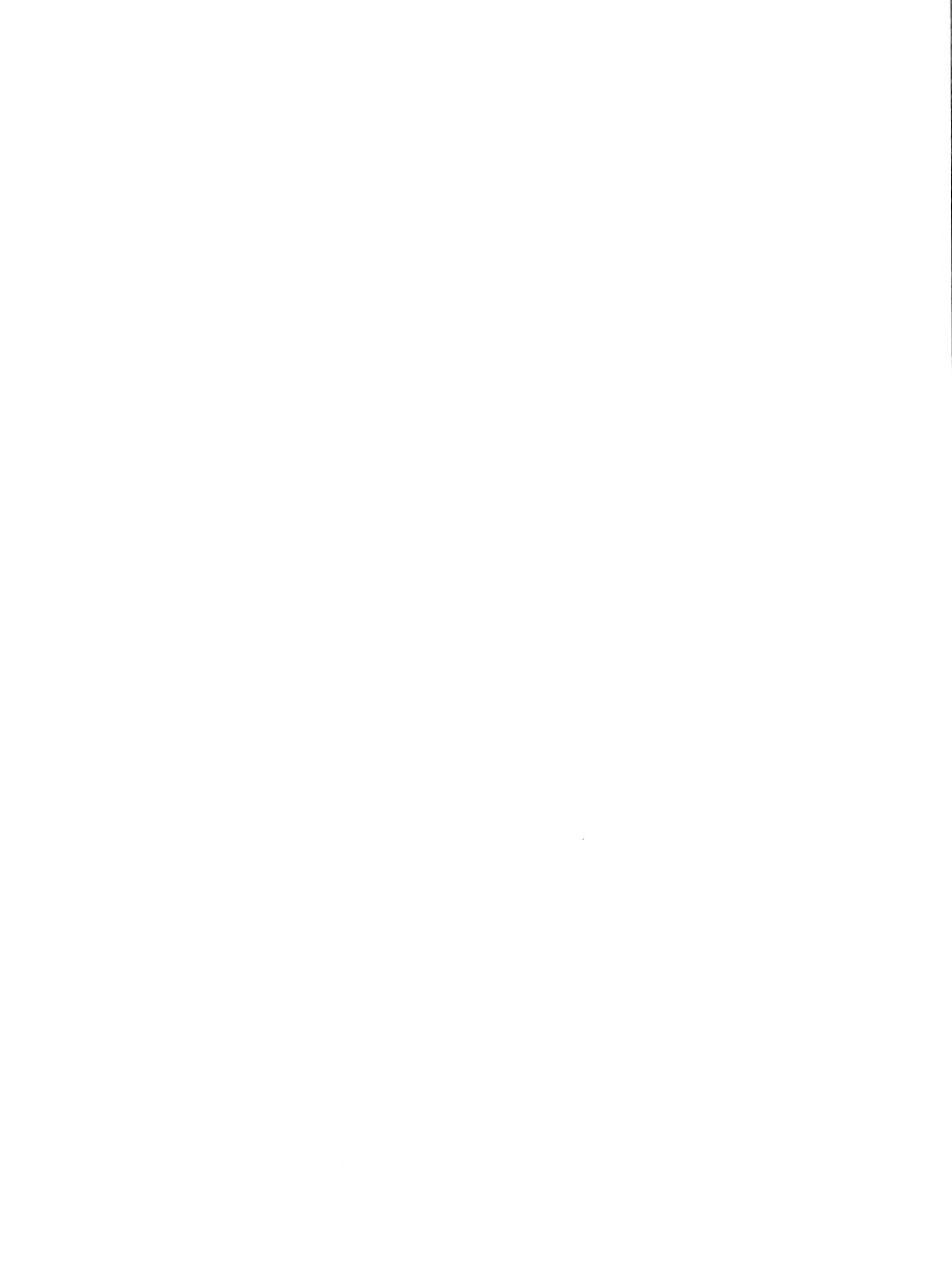


Figure 11.--Changes of biomass of pollock as in Figure 3 except spawning stress mortality is affected by fishing.



EXPERIMENT 3 YELLOWFIN

NG 2 NF 3 NS 1 F 0.000 0.003 0.006 0.009

Curve 1 - F(0)  
 2 - F(0.075)  
 3 - F(0.16)  
 4 - F(0.30)

(Note: one or few numbers on curves indicate coincidence of curves.)

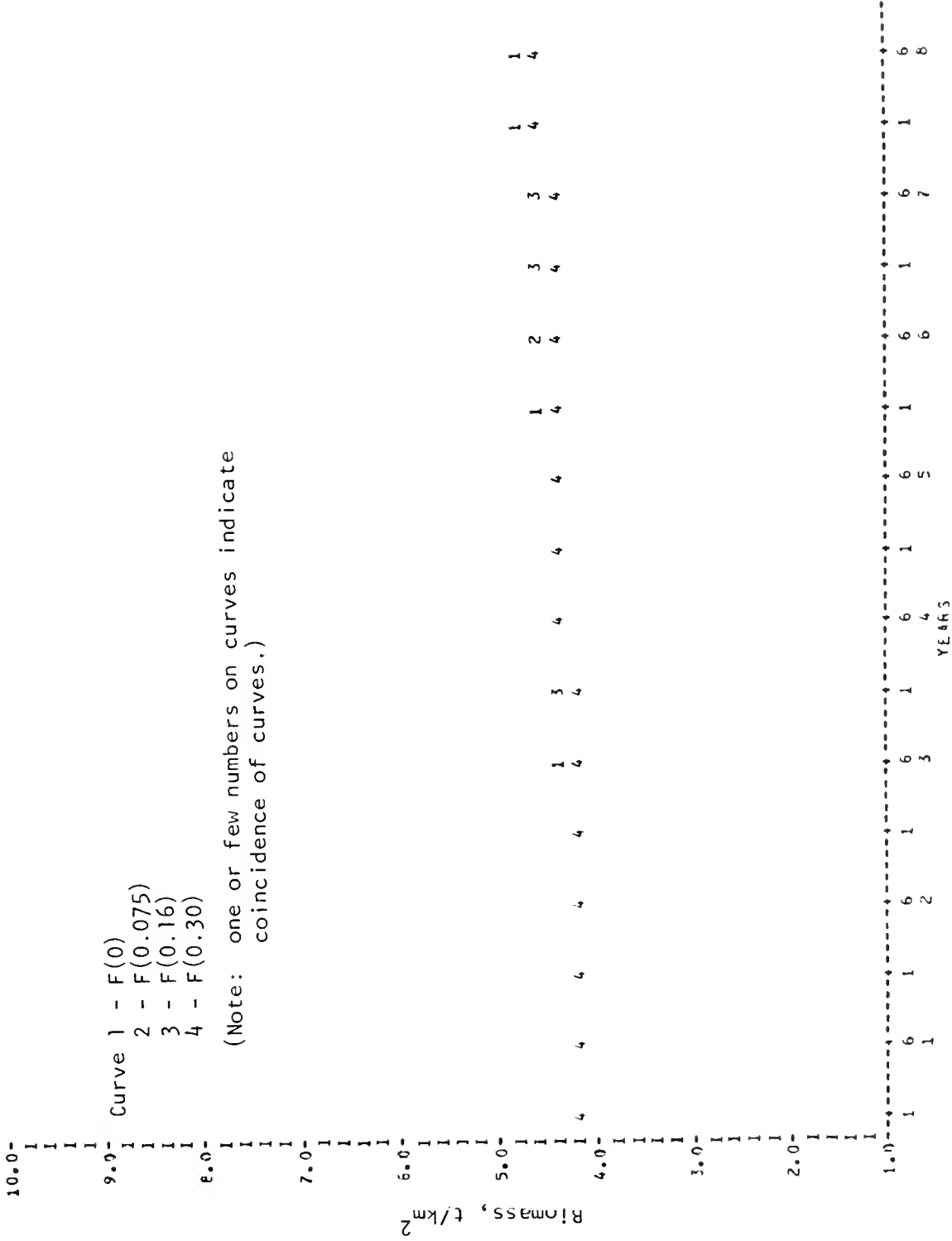


Figure 12.--Changes of biomass of yellowfin sole as in Figure 4 except spawning stress mortality is affected by fishing.



EXPERIMENT 4 POLLOCK

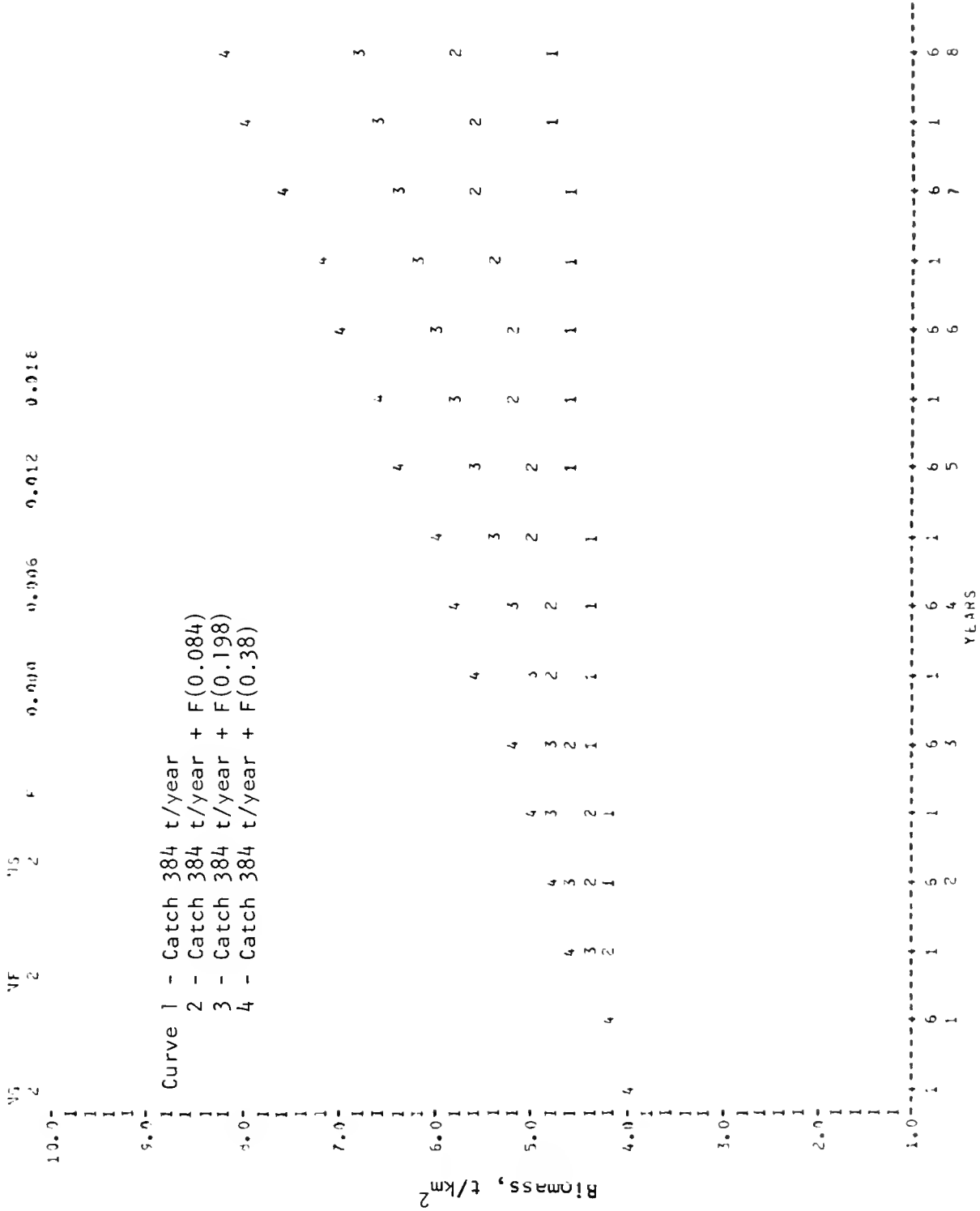


Figure 13.--Changes of biomass of pollock as in Figure 1 except both spawning stress mortality and growth rate are affected by fishing.









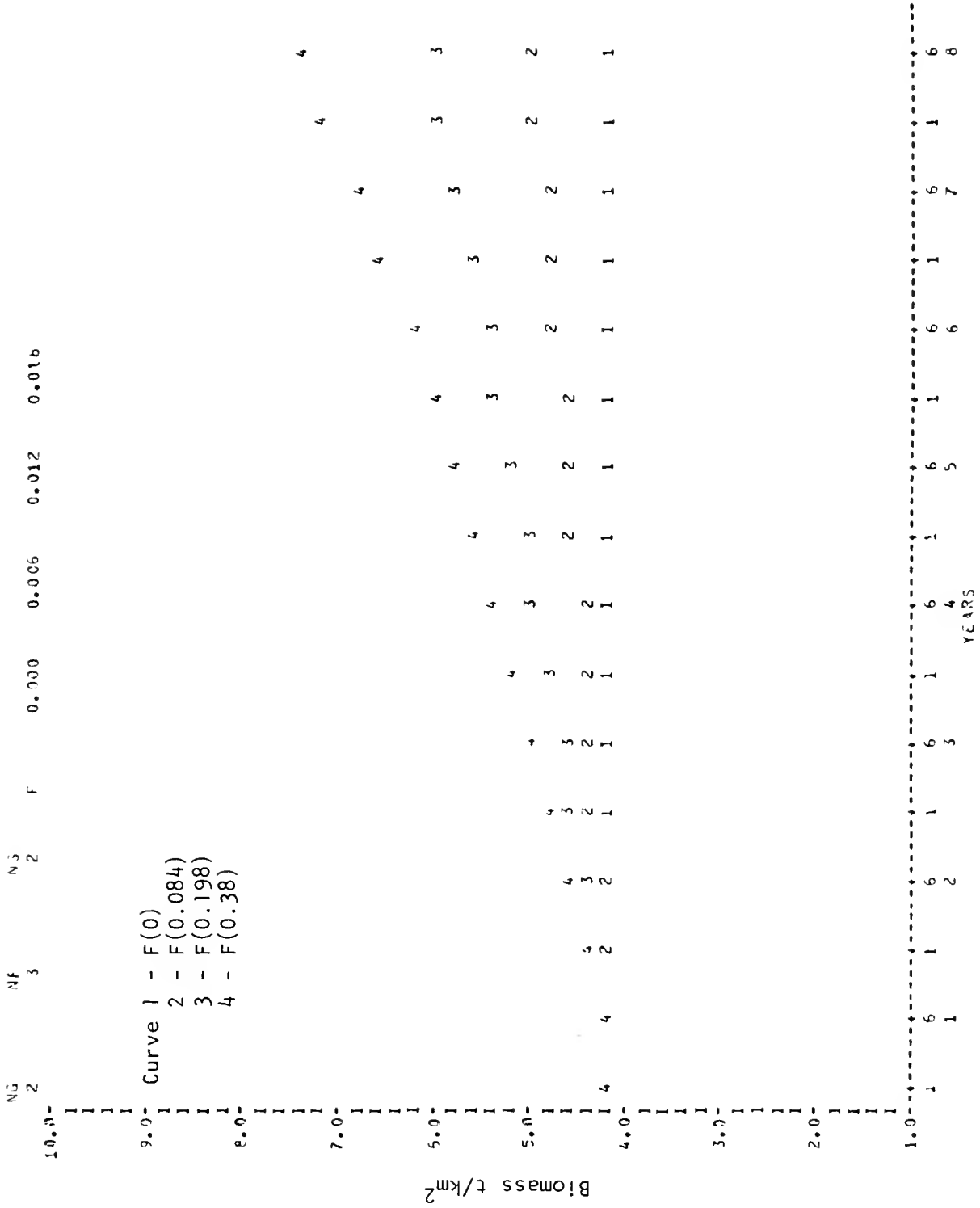


Figure 15.--Changes of biomass of pollock as in Figure 3 except both spawning stress mortality and growth rate are affected by fishing.



EXPERIMENT 4 YELLOWFIN

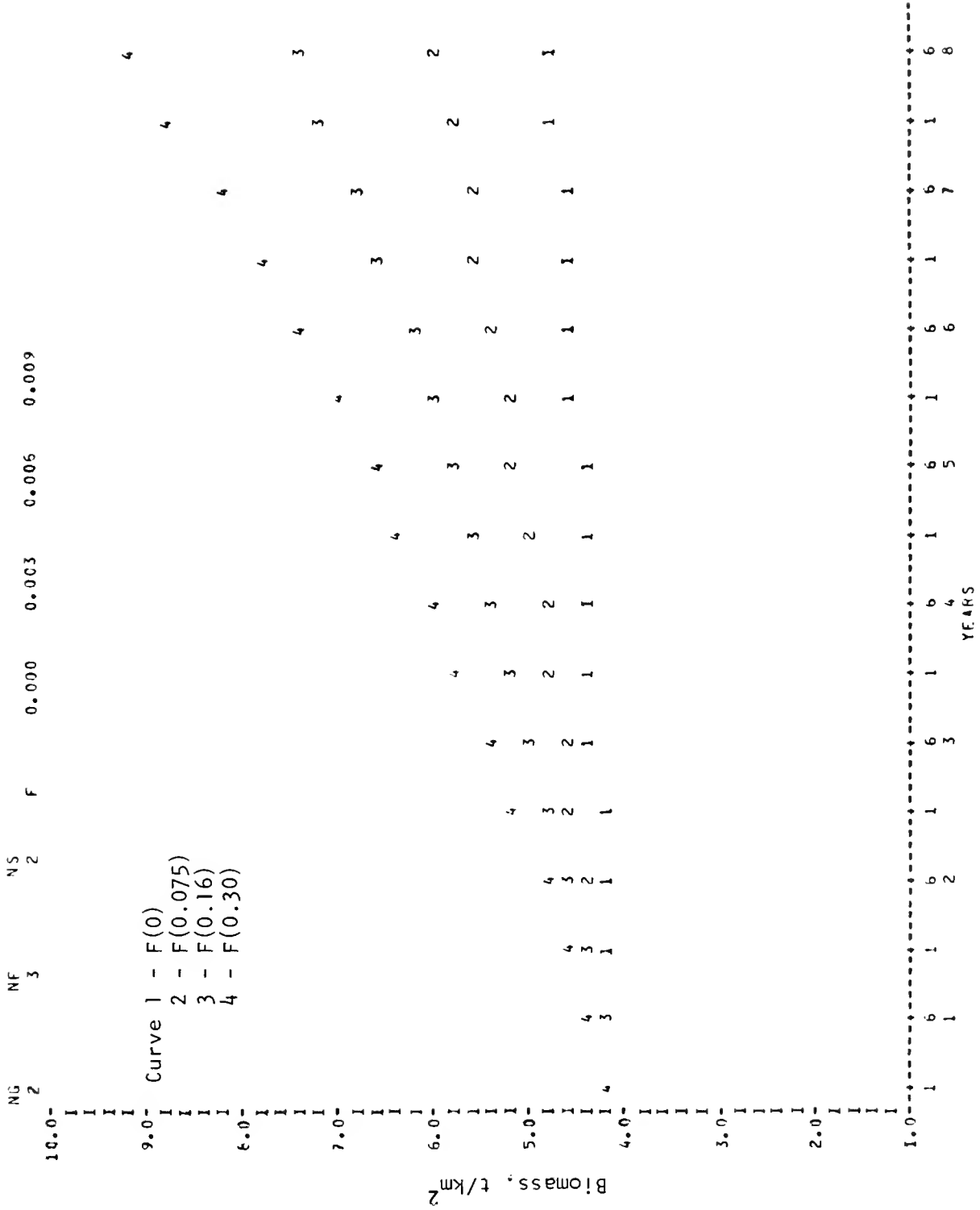


Figure 16. --Changes of biomass of yellowfin sole as in Figure 4 except both spawning stress mortality and growth rate are affected by fishing.



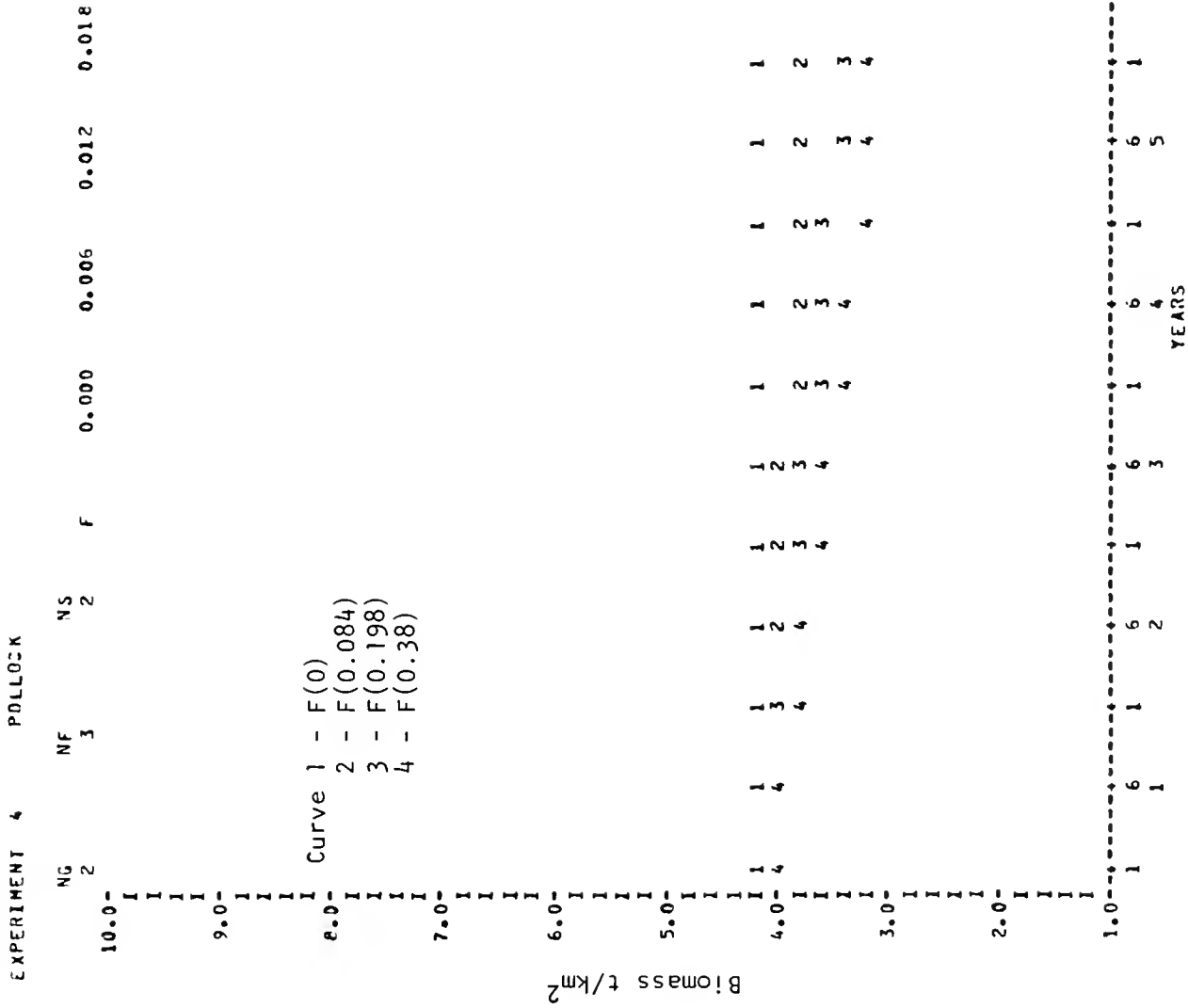
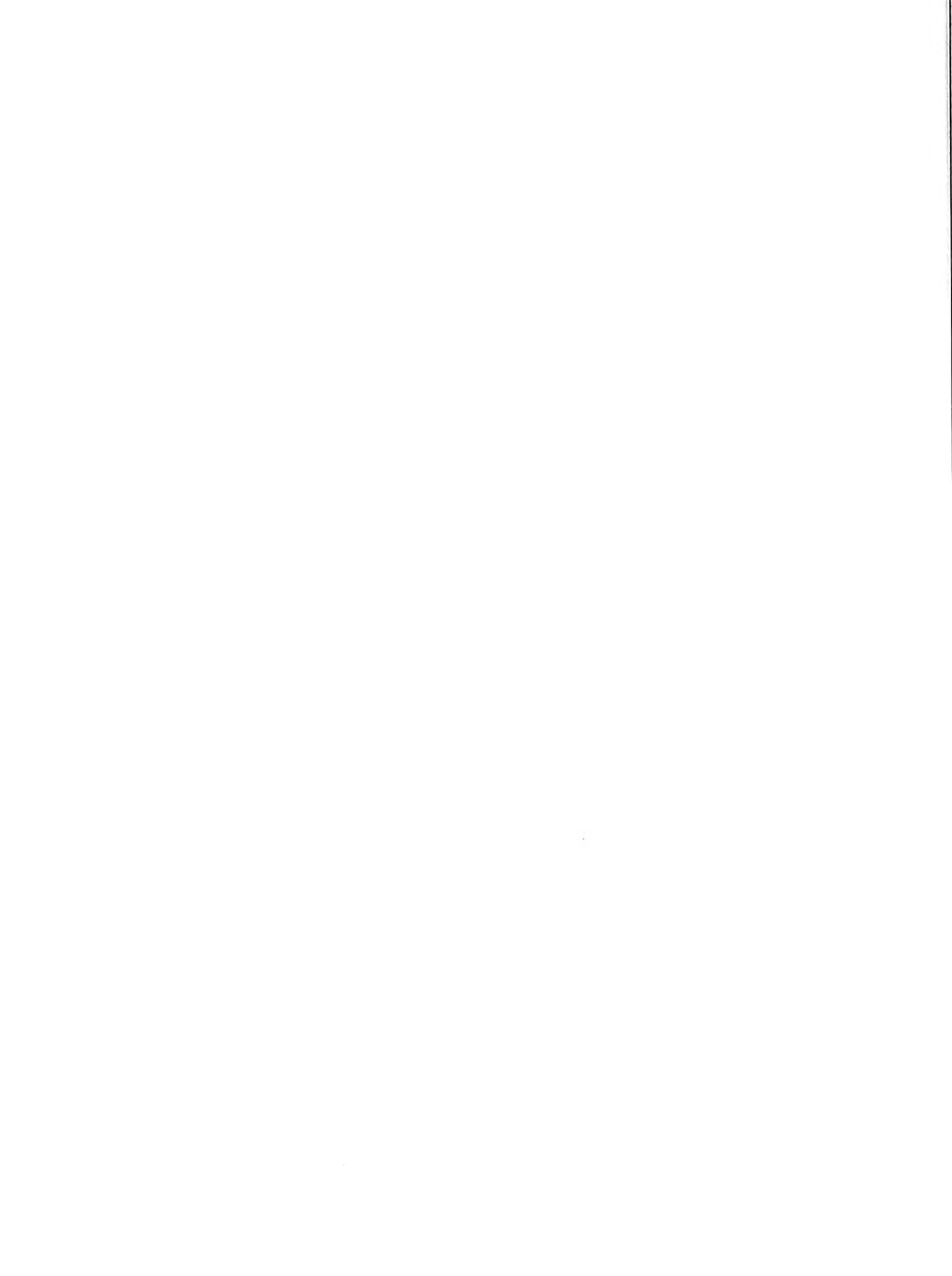


Figure 17.--Changes of biomass of pollock with time with different biomass density dependent fishing coefficients. Spawning stress mortality and growth rate changes to fishing are applied. These changes were computed in assuming a partial fishery on year classes prior to full recruitment, and juvenile biomass (and recruitment) is function of fishing.



EXPERIMENT 4 YELLOWFIN

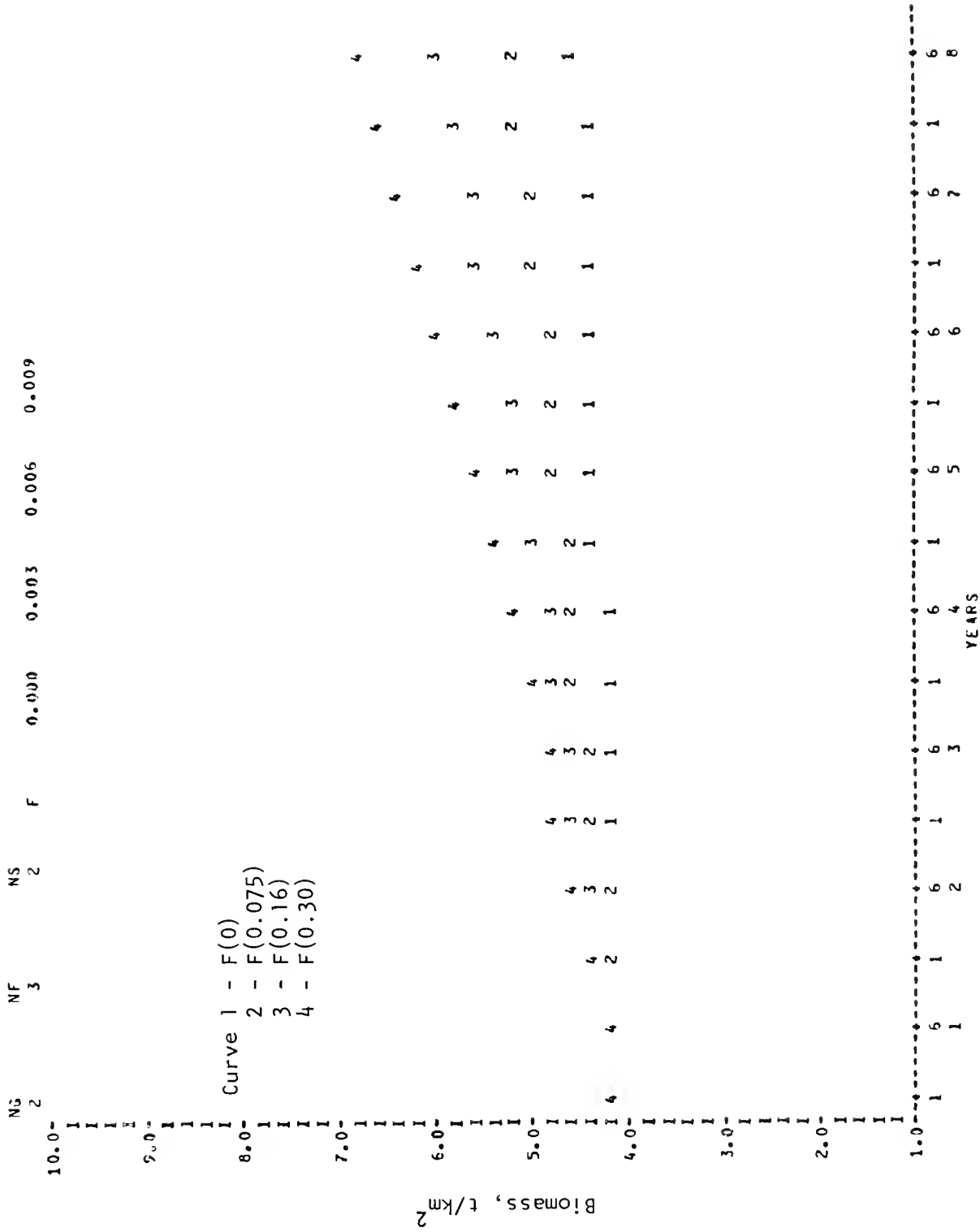


Figure 18.--Changes of biomass of yellowfin sole with time with different biomass density dependent fishing coefficients. Spawning stress mortality and growth rate changes to fishing are applied. These changes were computed in assuming a partial fishery on year classes prior to full recruitment, and juvenile biomass (and recruitment) is function of fishing.





NG 2 NF 3 MS 1 F 0.000 0.006 0.012 0.018

Curve 1 - F(0)  
 2 - F(0.084)  
 3 - F(0.198)  
 4 - F(0.38)

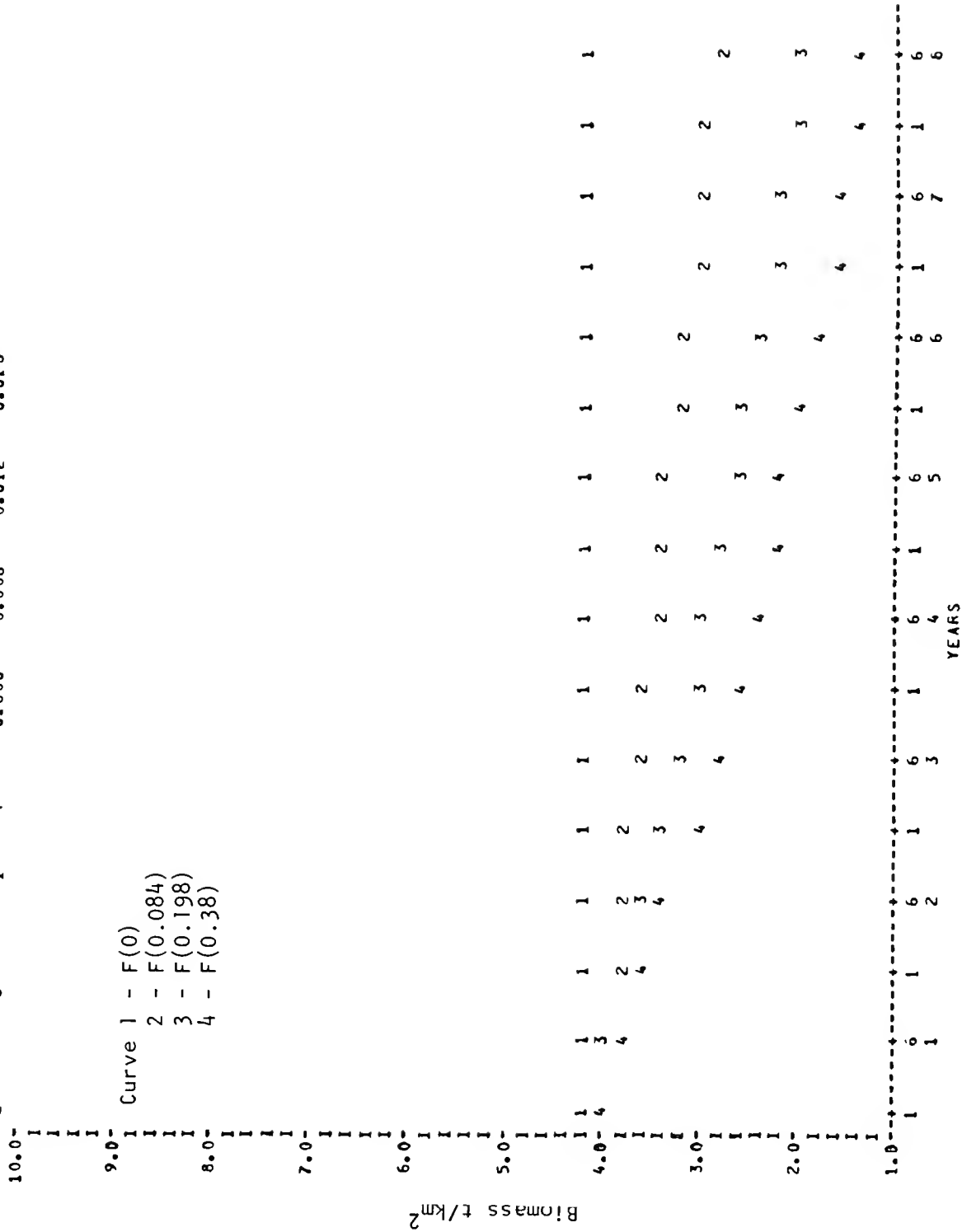


Figure 19. --Changes of biomass of pollock with time when growth rate of biomass is affected by fishing. Juvenile biomass is also a function of fishing.



EXPERIMENT 3 YELLOWFIN

NG 2      NF 3      NS 1      F      0.000      0.003      0.006      0.009

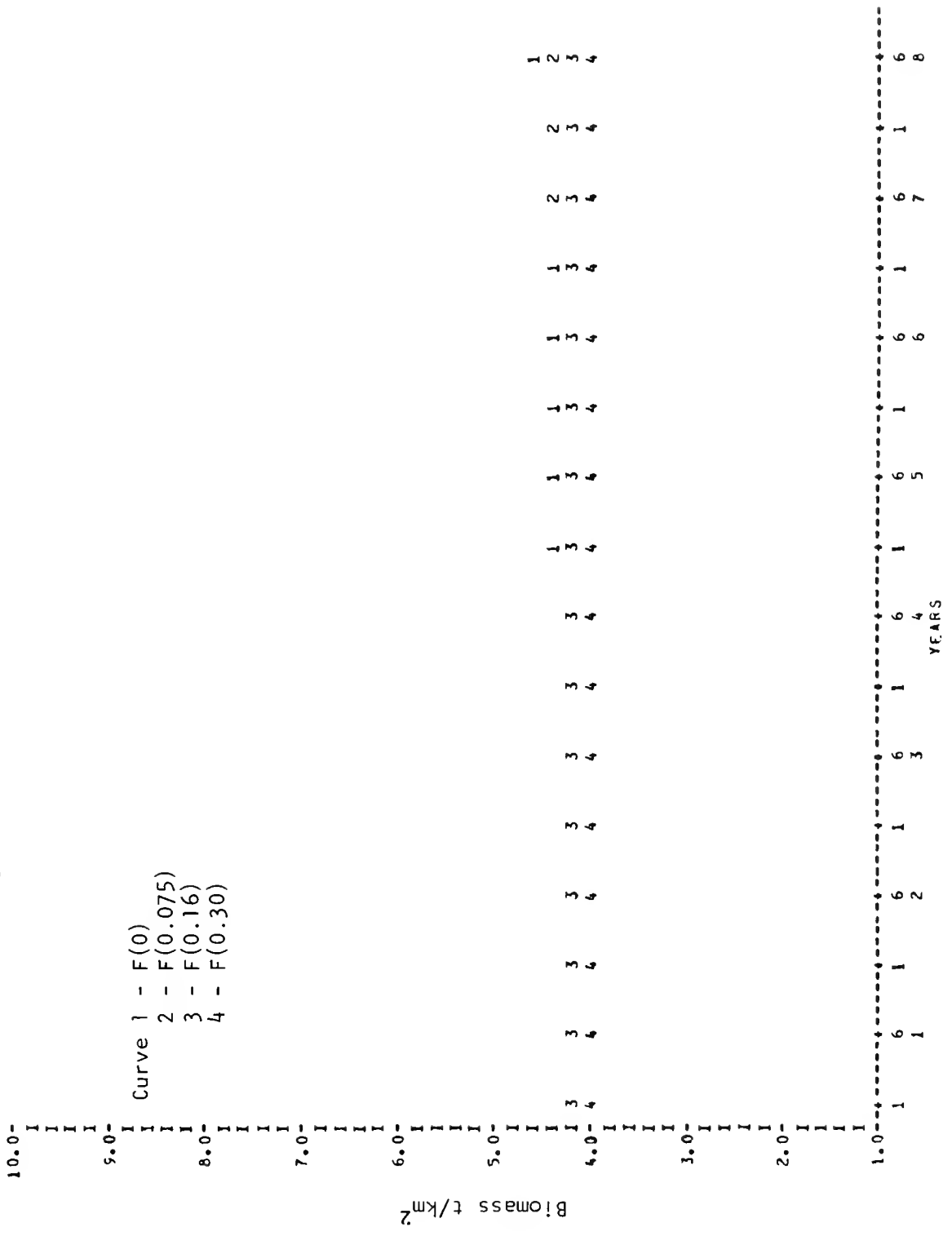


Figure 20.--Changes of biomass of yellowfin sole with time when growth rate of biomass is affected by fishing. Juvenile biomass is also a function of fishing.



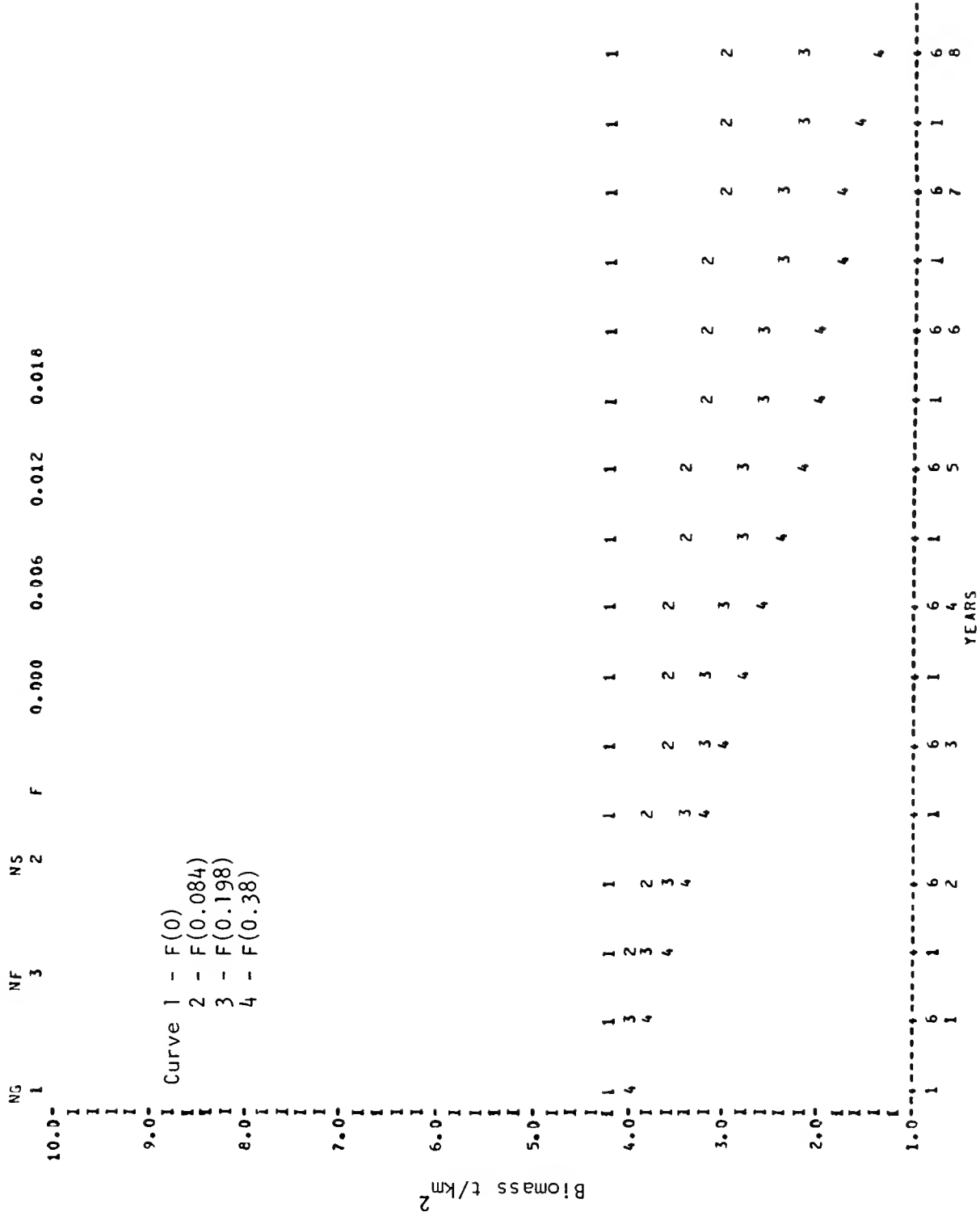


Figure 21.--Changes of biomass of pollock with time when spawning stress mortality is affected by fishing. Juvenile biomass is also function of fishing.



EXPERIMENT 2 YELLOWFIN

NG 1 NF 3 NS 2 F 0.000 0.003 0.006 0.009

Curve 1 - F(0)  
 2 - F(0.075)  
 3 - F(0.16)  
 4 - F(0.30)

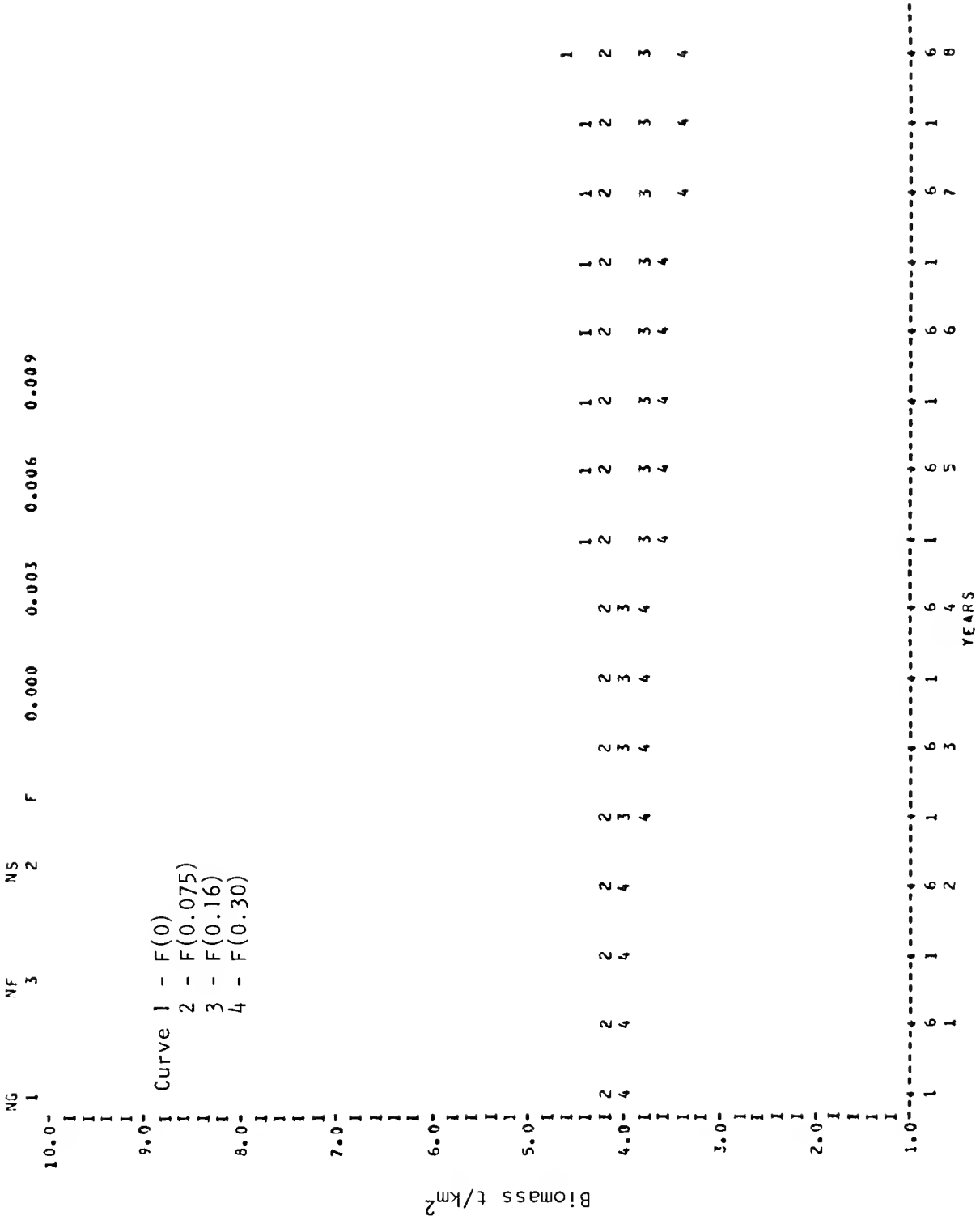


Figure 22.--Changes of biomass of yellowfin sole with time when spawning stress mortality is affected by fishing. Juvenile biomass is also a function of fishing.





EXPERIMENT 4 POLLOCK

NG 2      NF 3      NS 2      F      0.000      0.006      0.012      0.018

10.0-  
1  
1  
1  
1  
1  
9.0-  
1  
1  
1  
1  
1  
8.0-  
1  
1  
1  
1  
1  
7.0-  
1  
1  
1  
1  
1  
6.0-  
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1  
5.0-  
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4.0-  
1  
1  
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1  
1  
3.0-  
1  
1  
1  
1  
1  
2.0-  
1  
1  
1  
1  
1  
1.0-

Curve 1 - F(0)  
2 - F(0.084)  
3 - F(0.198)  
4 - F(0.38)

Biomass t/km<sup>2</sup>

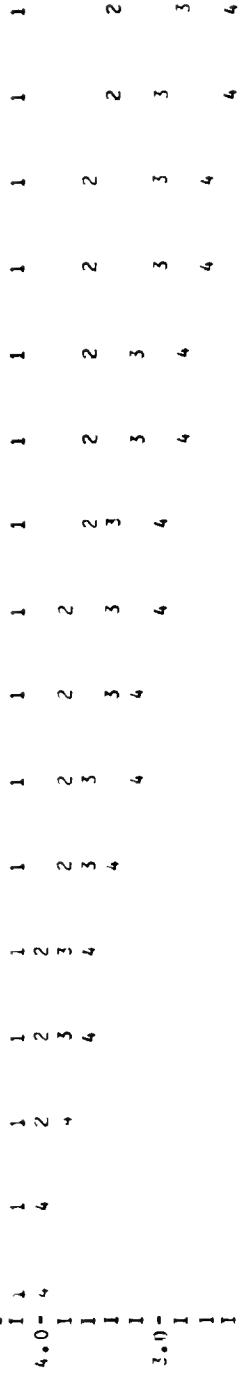
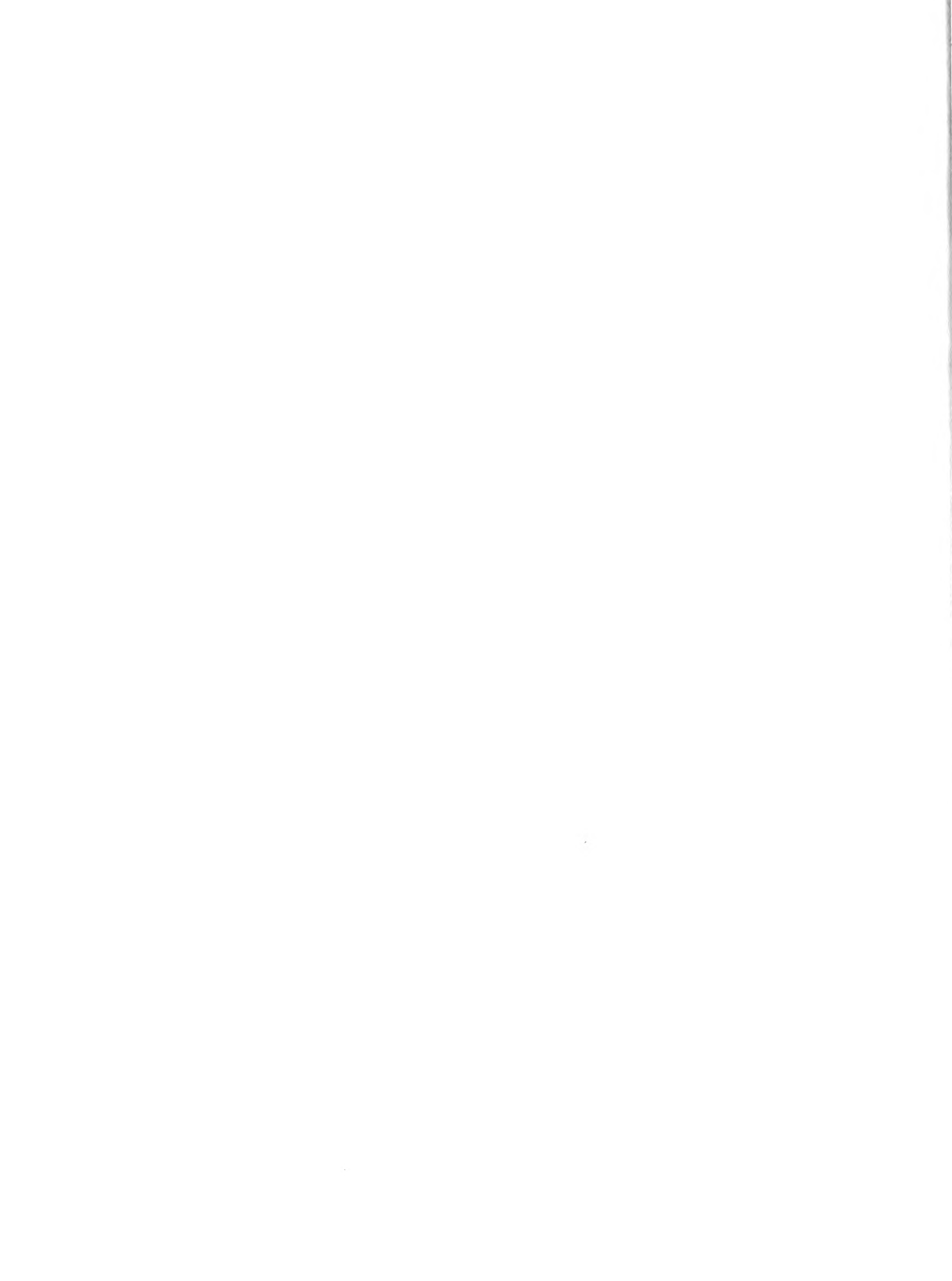


Figure 23.--Changes of biomass of pollock with time as in Figure 17 (with new set of biomass coefficients which are affected by fishing). In addition, spawning biomass size is affecting recruitment (see text).



EXPERIMENT 4 YELLOWFIN

NG 2 NF 3 NS 2 F 0.000 C.006 0.009

Curve 1 - F(0)  
 2 - F(0.075)  
 3 - F(0.16)  
 4 - F(0.30)

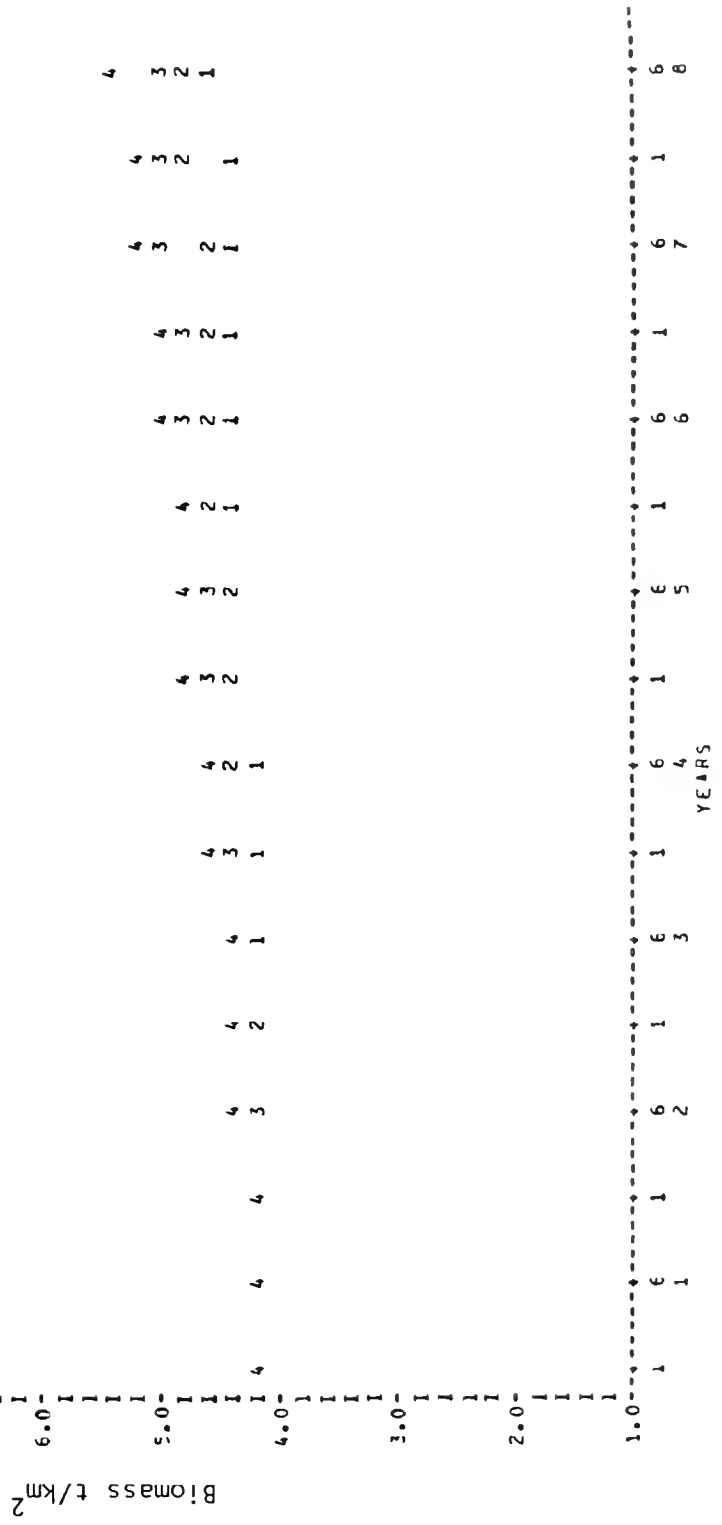


Figure 24.--Changes of biomass of yellowfin sole with time as in Figure 21 (with new set of biomass coefficients which are affected by fishing). In addition, spawning biomass size is affecting recruitment (see text).





