Northwest Atlantic Fisheries Organization

Serial No. N812

NAFO SCR Doc. 84/VI/30

SCIENTIFIC COUNCIL MEETING - JUNE 1984

Dynamics of yellowtail flounder and American plaice in NAFO Divisions 3L, 3N and 3O

by

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Abstract

On the base of recent VPA and other data, for both yellowtail flounder (*Limanda ferruginea*) and American plaice (*Hippoglossoides platessoides*), effort-CPUE regressions, stock recruitment relationships, yield per recruit, total yield, and productivity rates, have been calculated. Yellowtail flounder is less dependent on variations of environment than American plaice. The latter shows two levels in the stock-recruitment relationship, in the total yield curve and in the productivity rate, which are related to ecological succession. For both species, population and fishing parameters, recruitment, biomass, fishing mortality and total yield, have been calculated, at several stages. $F_{0.1}$ calculated from the total yield curve has a greater value than when calculated from the yield per recruit curve. American plaice seems to be more sensitive to overfishing than yellowtail flounder, which appears to be resistent to collapse at the present partial recruitment-at-age values. The variations in year class strengh of these two flatfishes have been compared with those of Div. 3NO cod stock, for the period 1954-1979. From this comparative study, it appears that cod and yellowtail flounder are rather r-strategist, and that American plaice is more of a k-strategist. The prognoses for the incoming year classes of yellowtail flounder until 1986, and of American plaice until 1988, have been estimated.

Methods

The author has developed a method (Larrañeta, 1981) of using catch per unit effort in the ecological analysis of fisheries. When the points of a historical catch-per-unit effort against effort series fall consistently into two groups indicate ecological changes of the following types,

(i) If the regression lines are parallel or diverge to the right (high effort values), changes in: (a) the physical environment (temperature, pollutants, settling surfaces, etc); (b) niche (relative abundance of prey, competitors and predators); (c) genotype composition.

(ii) If regression lines converge to the right, changes in: (d) average fecundity; (e) larval food availability (normally changes in primary productivity)

If an effort-CPUE regression line is identified during a series of years, the parameters of a general production model for the period involved can be estimated, because

$$Y = af - bf^2$$

where, f is effort and a and b are the parameters of the regression line.

To study the stock-recruitment relationship, the equations of Ricker, $R=ASe^{-BS}$, and Beverton-Holt, $R=1/(\alpha+\beta/S)$, have been used. Parameters of these equations were estimated by the following regressions,

$$\ln R - \ln S = \ln A - BS \quad \text{and} \quad 1/R = \alpha + \beta/S$$

Goodness of fit of these curves was tested by the variance,

$$s^2 = \frac{\sum (R_{ob}/R_{cal})}{n - 1}$$

Brodie and Pitt (1983 a and b) have calculated yield-per-recruit curves using an empirical method. In this paper the Beverton-Holt equation (expression 4.4, Beverton and Holt, 1957) has been used to get a generalized curve which provides an estimate of the total yield in the same set of the computational operations.

Because $Y=(Y/R)R$, it is necessary to calculate recruitment as a function of the fishing mortality (F). The method to estimate recruitment and biomass as a function of fishing mortality is described in the Appendix.

Cohort analysis gives annual average biomass. The biomass at the beginning of year t will be,

$$B_t = (\overline{B}_{t-1} + \overline{B}_t)1/2$$

The biomass increment during year t will be,

$$\Delta B_t = B_{t+1} - B_t + C_t$$

where, C_t is the catch in year t. From the Schaefer equation,

$$\Delta B = aB(B_{oo} - B) = AB - aB^2$$

so that,

$$B_{oo} = A/a, \quad \text{and} \quad B_{max} = (A/a)1/2$$

where, B_{oo} is the biomass when $\Delta B=0$, and B_{max} when ΔB=a maximum.

The average catchability coefficient for a period will be,

$$\bar{q} = \sum Y_t / \sum f_t \bar{B}_t$$

Yellowtail flounder

Effort-CPUE relationship

Data from Brodie and Pitt (1983a) on total catch, effort and CPUE, during 1968-1982, are given in Table 1.

In Figure 1, the annual points of the effort-CPUE relationship are shown. No regression line has been calculated since no trend has been observed.

Stock-recruitment relationship

Data have been taken from cohort analysis carried out by Brodie and Pitt (1983a). Recruitment (R) is the number of fishes in the population at age four years (N_4), and parental stock (S) has been considered in two ways.

1) As spawning biomass, first maturation at age six years (B_{6+}).
2) As an index of number of eggs spawned (I_E), calculated from the number of fish at age, and from the Pitt (1971) expression for fecundity,

$$\log F = 2.10 + \log A + 4.31$$

where, A is age in years

Data on recruitment and parental stock are shown in Table 2, and parameters both for the Ricker and Beverton-Holt equations in Table 3. Because parameter β is negative in the Beverton-Holt equation it is concluded that this model is unsuitable for this population, in spite of a rather 'good' correlation coefficient. When using the Ricker equation, standard deviations of R_{ob}/R_{cal} were 0.146 if $S=I_E$ and 0.169 if $S=B_{6+}$.

The relationship between lnR-lnS and S($=B_{6+}$) is shown in Figure 2. Two regression lines are suggested, but they are not sufficiently distinct; or, perhaps, short period cycles occur.

In Figure 3 the stock-recruitment curve (Ricker equation), with 95% confidence limits, is shown. In Table 4 a set of recruitments derived from a parental stock scale is given.

Yield

A rather clear stock-recruitment relationship, such as that of the yellowtail flounder 3LNO stock, allows us to examine the difference between a yield-per-recruit curve and a total yield curve. To draw the yield-per-recruit curve, according to the Beverton and Holt yield equation, the following parameters were chosen:

W_{oo} = 1.1 kg ; deduced from Brodie and Pitt (1983a).

M = 0.3 ; according to Brodie and Pitt (1983a).

K = 0.28 ; according to Pitt (1974).

t_o = 0.63 yr; according to Pitt (1974).

t_c = 6.00 yr; deduced from Brodie and Pitt (1983a).

t_L = 11 yr ; according to Brodie and Pitt (1983a).

The values obtained by Brodie and Pitt, and those obtained in this study, are as follows:

	Brodie-Pitt	This paper
$F_{0.1}$	0.5176	0.6275
$Y/R(F_{0.1})$	0.1857 kg	0.3120 kg
F_{max}	2.6164	infinite
$Y/R(F_{0.1})$	0.2156 kg	0.3833 kg

Estimates of F_{max} are very sensitive to small parameter variations, but F_{max} of a yield-per-recruit curve does not have great descriptive value. The curve is better described by $F_{0.1}$, which was determined here by the point where the increment is a 10% of the yield when F is 0.01. Our yield-per-recruit estimates are higher than those of Brodie and Pitt, but when dealing with total yield, our estimates are closer to the data than those based on the Brodie and Pitt curve.

To estimate the steady-state recruitment (R') of reproduction curves, the following partial recruitments (Brodie and Pitt, 1983a) have been used,

r_4	0.01
r_5	0.13
r_6	0.46
r_{7+}	1.00

Fecundity indices at age, $I_H(i)$, have been calculated from Pitt's (1971) expression relating fecundity and age.

$I_H(6)$	0.0879621	$I_H(9)$	0.2060199
$I_H(7)$	0.1215363	$I_H(10)$	0.2570396
$I_H(8)$	0.1608756	$I_H(11)$	0.3139964

In Figure 4, recruitment and biomass curves, as functions of fishing mortality for ages 7+, are shown, and in Figure 5 both yield-per-recruit and total yield curves are shown. Finally, in Table 5 a series of population and fishing parameters is set out, first age of capture being 6 yr, as at present. All fishing parameters will vary with changes in t_c, except, of course, those refering to a virgin population.

Productivity

The productivity rate will be the ratio between increment in biomass and the average biomass ($\Delta B/\bar{B}$). The annual average biomass values ($\bar{B}_{4+}$) were taken from cohort analysis. The relationship between the average biomass and the annual productivity rate is shown in Figure 6. The parameters of the regression line are,

$$A = 0.51164$$

$$a = -2.947 \times 10^{-6}$$

$$r = -0.587 \ (0.02\text{-}P\text{-}0.05)$$

From parameters A and a, B_{oo} is 173,614 t, and B_{max} is 86,807 t.

Actually, B_{max} is similar to $B_{4+}(F_{max})$ in Table 4; the former is a parameter of the Schaefer general production equation, the latter a parameter of the Beverton-Holt analytical production equation. Both estimates, 86807 t and 84119 t, are very close, and because both equations are theoretically independent of each other, it may be concluded that these estimates of about 85000 t are rather consistent. Il must not be forgotten, however, that the production curves of both equations depend on the age at first capture (t_c), or on the partial recruitment pattern, and that therefore 85000 t is an estimate based on the actual t_c (6 yr).

Finally, the catchability coefficient has been estimated taking into account catch and effort data from Table 1. The average coefficient was $\bar{q}=7.3557\times10^{-6}$, or the mean of F during the period studied when an effort equivalent to one hour of trawling was applied. Multiplying this catchability coefficient by the effort data in Table 1, the estimate of the annual fishing mortality has ranged from 0.139 to 0.476. Comparing this range with the following estimates,

$F_{0.1}$(Y/R)	Brodie-Pitt	0.5176
$F_{0.1}$(Y/R)	Larrañeta	0.6275
$F_{0.1}$(Y)	Larrañeta	1.08

we get impression that this stock has been always underexploited.

American plaice

Effort-CPUE relationship

Data on catch, effort and CPUE (Table 6) have been taken from Brodie and Pitt (1983b). Points of the effort-CPUE relationship have been plotted on Figure 7. From our point of view, these points can be fitted very well with two regression lines, according to type (i). The upper line fits well the period 1963-71, and the lower one the period 1973-82; 1972 is a transitional year.

These regression lines have the following parameters,

1965-71, $U = 1.2456 - 6.0256f\ 10^{-6}$

1973-82, $U = 1.0699 - 6.6097f\ 10^{-6}$

and give the following general production expressions,

1965-71, $Y = 1.2456f - 6.0256f^2\ 10^{-6}$

1973-82, $Y = 1.0699f - 6.6097f^2\ 10^{-6}$

Curves generated by these expressions are shown in Figure 8. The corresponding fishing parameters are given in Table 7. A comparison of Tables 6 and 7 shows that the fishery was exploited during 1967-82 at a rate close to the MSY.

Stock-recruitment relationship

Data (Table 8) have been taken from the cohort analysis carried out by Brodie and Pitt (1983b). Recruitment is the number of fishes in the population at age six yr (N_6). From data on first maturity age (Pitt, 1975), age 11 yr has been selected as the average first maturity age during the period studied. So the parent stock was considered, i) as the biomass of fish eleven years old or more (B_{11+}), and ii) in terms of the egg-number index (I_E), calculated from the expression given by Pitt (1964) to relate age (A) and fecundity, $\log F = 1.3367 + 1.781 \log A$, and taken into account number of fishes at ages 11 and more.

Figure 7 suggested that there are two stages in the stock recruitment relationship. To examine this possibility, the variation of year class strength and their parent stock have been drawn (Fig. 9), and the regression between lnR-lnS and S (Fig. 10). In the 1960-65 year classes (Fig. 9) an increase of parent stock and a decrease in recruitment are observed; afterwards these tendencies reverse, reaching a recruitment peak in the 1970 year class. Taking 200×10^6 as an average recruitment level, recruitment to the 1967-73 year classes appears to have been high. On the other hand, in Figure 10 the points of the 1967-73 interval fall into a high line, and below this line are those of the 1960-66 and 1974-76 intervals

Therefore, as a hypothesis, it is supposed that there were two ecological states, one for the 1960-66 and 1974-76 year classes and the other for the 1967-73 year classes. Parameters for the Ricker and Beverton-Holt equations are given in Table 9. The goodness of fit of these curves is shown in Table 10. The Ricker equation seems to fit better than the Beverton-Holt one. On the other hand, curves using I_E and B_{11+} fit as well. Since B_{11+} is given directly by cohort analysis, it seems more practical to use this technique. The relationship between spawning biomass and recruitment for the two ecological states (solid lines) and for the total (1960-76) period (broken line) is shown in Figure 11. Recruitment values for a range of spawning biomass from 10,000 to 250,000 tons are given in Table 11. On the basis of these relationships, maximum recruitment occurs when B_{11+} is 85000 t in curves b and c, and 95000 t in curve a.

Yield

A yield-per-recruit curve for American plaice has also been calculated using the Beverton-Holt production equation. The following parameters were chosen:

W_{∞} = 2.5 kg ; deduced from Brodie and Pitt (1983b)

M = 0.2 ; according to Brodie and Pitt (1983b)

K = 0.065 ; deduced from Pitt (1975)

t_o = 0.45 yr; deduced from Pitt (1975)

t_c = 10.3 yr; deduced from Brodie and Pitt (1983b)

t_L = 20 yr ; according to Brodie and Pitt (1983b)

Comparison with the empirical yield-per-recruit curve obtained by Brodie and Pitt (1983b) shows the following values,

	Brodie-Pitt	This paper
$F_{0.1}$	0.2615	0.305
$Y/R(F_{0.1})$	0.1781	0.1892
F_{max}	3.1357	3.15
$Y/R(F_{max})$	0.2135	0.2170

These curves are very similar, so they may be taken as being equivalent.

If the hypothesis that there are two ecological states is acepted, two curves of recruitment in steady-state as a function of fishing mortality can be calculated. The partial recruitment values used have been taken from Brodie and Pitt (1983b), and are,

r_6	0.025	r_{10}	0.470
r_7	0.100	r_{11}	0.580
r_8	0.220	r_{12}	0.730
r_9	0.300	r_{13+}	1.000

The Ricker equation for the stock-recruitment curve has been used, and spawning stock biomass was taken as parent stock. Weight at age (Brodie and Pitt, 1983b) has been taken as fecundity index, with the following values,

$I_H(11)$	0.700	$I_H(16)$	1.803
$I_H(12)$	0.880	$I_H(17)$	2.022
$I_H(13)$	1.020	$I_H(18)$	2.233
$I_H(14)$	1.250	$I_H(19)$	2.401
$I_H(15)$	1.524	$I_H(20)$	2.428)

Recruitment (N_6) and biomass (B_{6+}) curves are shown in Figure 12, and yield-per-recruit and total yield curves in Figure 13. Population and fishing parameters in both ecological states are given in Table 12.

It is worthwhile observing that in Figure 12 the maximum biomass (B_{6+}max) may not necessarily occur when the stock is unexploited, but when fishing mortality is rather significant, e. g. 0.361, unless density-dependent factor compensate this apparent anomaly. Theoretical formulations of general production model have been based on the assumption that maximum biomass (B_{oo}) occurs when the stock is not exploited, and on the fact that fishing reduces the virgin biomass. For the same reason, and because CPUE is considered as a linear index of stock abundance, it is also assumed that F-B and F-CPUE curves have the same shape. But, properly, if there is a partial recruitment at some age, as normally occurs, then if the F-CPUE relationship is a linear regression the F-B relationship will be not be so, because when fishing mortality varies different proportions of the population will belong to the partial recruitment ages. Nevertheless, for a determinate pattern of partial recruitment at age, an empirical F-CPUE relationship will retain its practical use. The contradiction between Figure 12 and the general production model is due to the fact that the latter does not take into account the effects of fishing mortality on recruitment.

Productivity

Data used here were annual average biomass (B_{6+}), from Brodie and Pitt's (1983b) cohort analysis, and anual catches (Table 6). The relationship between productivity rate and annual average biomass is shown in Figure 14. This relationship is quite unexpected, since theory suggests that these two variables ought to be related by a negative regression, similar to that found for yellowtail flounder (Fig. 6). Here it is not possible to fit a regression line. On the contrary, there appears to be a cycle.

Biological production of a fishery resource depends on recruitment, growth and natural mortality. Evidently the most variable of these factors will be recruitment, which in this stock is computed at six years; thus, in Figure 14, a cycle of year classes emerges. If the 1973-78 interval indicates a high stock-recruitment relationship, it must be related to the ecological state of the population six years before; that is, to the period 1967-72, which is the period fitted by the higher line in Figure 10 relating lnR-lnS ans S.

From Figure 14, it seems as if this hypothetical cycle should have a period of 13-14 years. Because it is impossible to fit a regression line, it is also not possible to estimate a catchability coefficient.

Year class prognosis

Our initial intention has been to test the value of this approach as a prediction tool of year classes. Some results have been set in order to test in coming years the realism of this considerations and methods and to make a criticism on them.

Recruitment to the yellowtail flounder stock (N_4) during 1983-86 will depend on the spawning stocks of 1979-82 (Table 2), and thus of the American plaice (N_6) during 1983-88 on the spawning stocks of 1977-82(Table 8). For these prognoses the Ricker equation was used, and both egg-number index (I_E) and spawning biomass (B_{6+} and B_{11+}) were taken as parental stocks. The results for yellowtail flounder and American plaice are given in Tables 13 and 14, respectively.

According to these prognoses, the coming yellowtail flounder recruitment will show a downward trend owing to very high values of spawning biomass. $B_{6+}(R_{max})$ in Table 5 is 34816 t, and during the last few years parental stocks were above this level. On the other hand, American recruitment will be relatively constant until 1988, if no ecological change takes place. Spawning biomass during the last three years (Table 8) has in any case been greater than 84210 t (Table 8), i.e., greater than $B_{11+}(R_{max})$.

Ecological cycles

In Figure 15, variations of the 3NO cod stock recruitment, according to Bishop and Gavaris (1983), and those of yellowtail flounder and American plaice stocks are compared.

It can be seen that cod and yellowtail flounder year classes vary synchronously and with opposite sign to those of the American plaice. This observation was confirmed by calculating correlation coefficients (Table 15). It seems as though the population dynamics of both cod and yellowtail flounder in the area respond to stimuli of the same ecological pattern, and that the population dynamics of American plaice to a different one. Let us examine this possibility.

In the first place, the stock-recruitment curve of the yellowtail flounder (Fig. 4) is more skewed to the left than that of American plaice (Fig. 11). According to the literature, it is accepted that in flatfish recruitment is almost constant over a wide range of parental stock (Cushing and Harris, 1973). The most appropiate model would be that of Beverton and Holt. However, for the stock-recruitment curves of species studied in this paper a better fit is obtained with the Ricker equation, especially for yellowtail flounder. Since one of the determinants of Beverton-Holt curves is spatial limitation of the pre-recruitment habitat, it can be concluded that these species do not suffer significant space limitation.

Very skewed stock-recruitment curves will be characteristic of highly fecund species, those able to produce large generations at low levels of parental stock. Thus, L. ferruginea will be more of an r-strategist than H. platessoides. Cod is a species whose stock-recruitment curve is characteristically skewed to the left (Cushing and Harris, 1973; Larrañeta, 1983), like that of the yellowtail flounder.

According to Larrañeta and Vázquez (1982), the strongest year classes of the cod in the Arctic Ocean appear at the beginning of a polar motion period, when a new stage would be starting. It is surprising that cod, a large and long-lived fish, can be considered as an r-strategist. But in the region occupied by the cod, long-period trend are pronounced, especially in the neighbourhood of the polar desert. The longevity of the cod allows it to survive from one favourable period to another and its high fecundity allows it to behave as an 'opportunistic' species at the beginning of such periods.

American plaice shows a stock-recruitment relationship that better fitted by the Ricker equation than the Beverton-Holt equation, but it is not very different from the latter. Thus American plaice will be a more like k-strategist species than yellowtail flounder; this can be also deduced from the later age of maturity, as high as eleven years for female American plaice. The concept that American plaice is more of a k-strategist agrees with the observation in Figure 7 that the regression lines do not join at the right. This suggests (Larrañeta, 1981) that density-independent factors, such as ecological succession, may play an important role (type (i)). It also agrees with Figure 14, where the points could be interpreted as a sequential ecological cycle.

With respect to the yellowtail flounder the question is what part is played by the environment, and what part is played by the precise form of the stock-recruitment relationship, in determining variations in year class strength. In Figure 3, the stock-recruitment relationship seems to be clear; but Figure 1 is quite confused and suggests the existence of an important environmental signal. Pitt (1970) has related the apparent increase in abundance of yellowtail flounder on the Grand Bank from 1961 to 1968 with a general upward trend in bottom temperatures and a drastic reduction in the haddock population. We think that Figure 15 combines these two points of view. In fact, year class variation in yellowtail flounder is correlated with the variation of year-class stregth in cod. But the differences between good and bad year classes in cod are of greater amplitude. Thus, in the yellowtail flounder, environmental factors may be acting on the stock-recruitment pattern but in a smoother way than in cod.

The following ecological cycle can be proposed for the period studied. Starting in the 1960's a favourable period began, which allowed production of very large cod year classes. As the ecosystem matured, the cod year classes became smaller and smaller. Yellowtail flounder year classes showed a similar evolution but in a smoother way. Maturation of the ecosystem favoured the development of some strong American plaice year classes. But, finally, the 'favourable' period ended, and the year classes of the three species were reduced to low levels.

According to Pitt (1975), the age at 50% maturity of American plaice in 1969-72 was significantly lower than in the earlier period in Div. 3L and 3N. Beacham (1983) has shown that median length and age at sexual maturity of Atlantic cod on the Scorian Shelf decline about 50% in most stocks between 1959 and 1979. Beacham thinks that these changes may be due to the commercial fishery removing larger, older immature fish, or to a general decline in stock biomass between 1960 and 1975 due to heavy exploitation, or to both processes. Long-lived species which are heavily fished frequently suffer a decline in median age at sexual maturity. This indicates that fishing should produce genetic selection by favouring r-strategist genotypes, because precocity is a sing of it. According to previous papers, a change in the genetic composition produces a change in parameter A (the density-independent one) of the Ricker equation (Larrañeta 1979 and 1981). Thus, fishing should select genotypes which generated more domed shape stock-recruitment curves. That is to say, fishing selects populations more resistent to overfishing and collapse.

Conclusions

1.- Yellowtail flounder, Div. 3LNO, shows a rather dome-shaped stock-recruitment curve.

2.- From the total yield curve, it appears that MSY for yellowtail flounder is about 40000 t, F_{MSY}=1.9 and $F_{0.1}$=1.1. F_{ext} would be 5.9, which would appear to be a strong defence against collapse.

3.- The yellowtail flounder stock shows maximal production, for t_c=6 yr, when B_{4+} is about 85000 t.

4.- American plaice, Div. 3LNO, seems to exhibit two stock recruitment curves, in response to changes in the environmental state.

5.- Fishing parameters for American plaice have been calculated from these two stock-recruitment curves (Table 12). This stock is vulnerable to collapse.

6.- The productivity rate of the American plaice stock shows a cycle with a period of 13-14 years, in agreement with the hypothesis of two ecological states.

7.- Different values of $F_{0.1}$ and F_{max} are obtained, depending on whether they are calculated from the yield-per-recruit curve or from the total yield curve; the last must be regarded as the best criterion to determine optimel fishing rates.

8.- Present parental stocks of both species are equal to or greater than the $B(R_{max})$ level.

9.- When dealing with stock-recruitment curves, it appears that CPUE is not necessarily linearly related with the stock density, and that maximum biomass may occur at a significant fishing mortality.

10.- A comparison of these stocks with that of Div. 3NO cod, suggests that cod and yellowtail flounder are r-strategists, and American plaice a k-strategist. Cod and yellowtail flounder would have their strongest year classes at the beginning of a 'favourable' period, and American plaice would have it some time later.

Acknowledgement

I wish to acknowledge the help of I. Elias who has participated in a great part of this work. I am indebted with Dr. A. Vázquez who prepared the computer programmes. Particular thanks go to Mr. T. Wyatt for the revision of the draft. My gratitude also to M. T. Fernández for her careful drawing of the figures and to A. Pastor Feria for his valuable help.

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APPENDIX

Recruitment and biomass as a function of fishing mortality

From given values of recruitment (R_1), natural mortality (M), fishing mortality (F) and partial recruitment (r_j), the abundance at ages 1, 2, 3, ... will be,

$$N_1=R_1; \quad N_2=R_1e^{-(Fr_1+M)}; \quad N_3=R_1e^{-(Fr_1+Fr_2+2M)}; \quad ...$$

If $I_H(i)$ is the fecundity index at age $\underline{i}$, the fecundity index derived from R_1 is,

$$I_E(1) = \sum_{i=1}^{n} R_1 e^{-\left[F\sum_{j=1}^{i-1} r_j+(i-1)M\right]} I_H(i)$$

Using parameters A and B of the Ricker stock-recruitment equation, the next recruitment (R_2) can be calculated with S equal to $I_E(1)$. The fecundity index $I_E(2)$, generated by R_2, is obtained from,

$$I_E(1)/R_1 = I_E(2)/R_2$$

A third recruitment (R_3) is calculated from $I_E(2)$ again using parameters A and B. With R_1, R_2 and R_3 it is possible to calculate parameters A_r and B_r of a reproduction curve (parental and filial stock census at the same age). Thus,

$$R_2 = A_rR_1e^{-B_rR_1}$$

and

$$R_3 = A_rR_2e^{-B_rR_2}$$

Using the expression,

$$\ln(R_n/R_{n-1}) = a - B_rR_{n-1}$$

$\underline{a}$ and B_r can be estimated. Then recruitment (R') to a steady state population will be,

$$R' = a/B_r$$

Biomass is estimated using the same expression as for $I_E(k)$, but replacing $I_H(i)$ by the average weight at age (w_i). For biomass B_{i+}, n=1 will be age-group $\underline{i}$, and recruitment will be R'.

Table 1. Yellowtail flounder. Total catch (t), total effort (h) and catch-per-unit effort. Data from Brodie and Pitt (1983a).

Year	Catch	Effort	CPUE
1968	13 340	18 921	0.705
1969	15 708	25 750	0.610
1970	26 426	44 191	0.598
1971	37 342	62 236	0.600
1972	39 259	64 677	0.607
1973	32 815	50 876	0.645
1974	24 318	57 762	0.421
1975	22 894	56 950	0.402
1976	8 057	24 268	0.332
1977	11 638	27 513	0.423
1978	15 466	31 181	0.496
1979	18 351	35 495	0.517
1980	12 377	19 939	0.640
1981	14 580	23 745	0.614
1982	11 631	22 154	0.525

Table 2. Yellowtail flounder. Spawning stock (6+) as egg number (EN) by 10^{-10} and biomass (t), and recruitment ($N_4 x 10^{-3}$).

Year	EN	Biomass	Recruitment
1964	-	-	156 799
1965	-	-	147 013
1966	-	-	119 893
1967	-	-	110 608
1968	7375	25 926	121 788
1969	11237	40 372	113 159
1970	14686	50 199	75 826
1971	15610	48 747	71 914
1972	12794	33 846	82 921
1973	9006	24 050	102 114
1974	7165	21 035	131 122
1975	6827	18 164	125 633
1976	5071	19 200	122 718
1977	6549	18 901	80 055
1978	7388	22 586	93 617
1979	8500	21 567	-
1980	9992	41 608	-
1981	13431	41 419	-
1982	15679	49 396	-

Table 3. Yellowtail flounder. Parameters of the stock-recruitment curve. Correlation coefficient of regression line.

	$S = I_E$	$S = B_{6+}$
Ricker eq.		
A	44.4114	12.8381
B	1.46×10^{-4}	4.294×10^{-5}
r	-0.959	-0.949
Beverton-Holt eq.		
A	1.45×10^{-5}	1.42×10^{-5}
B	-3.55×10^{-2}	-0.1008
r	-0.637	-0.573

Table 4. Yellowtail flounder. Recruitments ($N_4 \times 10^{-3}$), from Ricker equation; parent stock in EN ($\times 10^{-12}$) and biomass (B_{6+})($t \times 10^{-3}$)

EN	R	Biomass	R
5	20 642	5	51 787
20	66 330	10	83 561
35	93 248	15	101 123
50	107 011	20	108 778
65	111 754	25	109 699
80	110 491	30	106 203
95	105 403	35	99 963
110	98 042	40	92 168
125	89 499	45	83 654
140	80 524	50	74 983
155	71 617	55	66 549
170	63 099	60	58 571
185	55 162	65	51 192
200	47 905	70	44 477
215	41 370	75	38 446
230	35 552	80	33 085
245	30 422	85	28 361
260	25 935	90	24 225
275	22 035	95	20 631

Table 5. Yellowtail flounder. Population parameters, being t_c= 6 yr.

R(virgin)	... 62,598,000	F_{max}(Y)	... 1.87
B_{4+}(virgin)	... 105,341 t	R(F_{max})	... 111,450,000
B_{6+}(virgin)	... 75,735 t	B_{4+}(F_{max})	... 84,119 t
B_{4+}max	... virgin	B_{6+}(F_{max})	... 31,876 t
F_{ext}(R=0)	... 5.914	Y(F_{max})	... 40,633 t
$F_{0.1}$(Y)	... 1.08	R_{max}	... 111,904,391
R($F_{0.1}$)	... 108,585,000	B_{4+}(R_{max})	... 87,331 t
B_{4+}($F_{0.1}$)	... 94,463 t	B_{6+}(R_{max})	... 34,816 t
B_{6+}($F_{0.1}$)	... 43,372 t	F(R_{max})	... 1.637
Y($F_{0.1}$)	... 37,623 t	Y(R_{max})	... 40,427 t

Table 6. American plaice. Total catch (t), total effort (h) and catch-per-unit effort. Data from Brodie and Pitt (1983b).

Year	Catch	Effort	CPUE
1965	51 304	56 836	0.905
1966	53 273	60 813	0.876
1067	62 875	76 864	0.818
1968	59 164	94 060	0.629
1969	67 322	122 850	0.548
1970	60 379	117 013	0.516
1971	60 724	126 772	0.479
1972	50 708	105 422	0.481
1973	40 986	79 276	0.517
1974	37 727	86 929	0.434
1975	36 479	87 689	0.416
1976	43 735	101 709	0.430
1977	40 306	99 275	0.406
1978	43 588	94 756	0.460
1979	43 420	87 717	0.495
1980	46 835	78 451	0.597
1981	47 897	84 030	0.570
1982	44 703	79 542	0.562

Table 7. American plaice. Fishing parameters from the effort(f) and CPUE relationship.

	1965-71	1973-82
f_{MSY}, h.	103 350	80 900
MSY, t.	64 372	43 296
2/3 f_{MSY}, h.	68 900	53 933
Y(2/3 f_{MSY}), t.	57 217	38 477
CPUE(f_{MSY}), t.	0.623	0.535
CPUE(2/3 f_{MSY}), t.	0.830	0.713

Table 8. American plaice. Spawning stock (11+) as egg number (EN) by 10^{-10} and biomass (t), and recruitment ($N_6 x 10^{-3}$).

Year	EN	Biomass	Recruitment
1954	-	-	177 500
1955	-	-	206 613
1956	-	-	200 181
1957	-	-	186 373
1958	-	-	184 119
1959	-	-	183 930
1960	6680	123 002	193 320
1961	6623	123 437	171 843
1962	6851	127 650	157 020
1963	7239	135 947	122 383
1964	7376	140 707	120 957
1965	7427	144 590	116 195
1966	7644	163 135	152 962
1967	7769	161 241	203 439
1968	6920	141 917	258 434
1969	6150	122 730	269 084
1970	5432	96 212	334 262
1971	4725	82 727	289 648
1972	3984	63 180	222 749
1973	3044	54 060	229 788
1974	2394	52 035	173 950
1975	2257	47 542	165 626
1976	2263	41 927	106 931
1977	2497	50 108	-
1978	3300	58 998	-
1979	4264	79 420	-
1980	5803	95 728	-
1981	7530	98 154	-
1982	7473	118 665	-

Table 9. American plaice. Parameters of the stock-recruitment curves. Correlation coefficient of regression line.

		1960-66 1974-76	1967-73	1960-76
Ricker eq.				
$S = I_E$				
	A	111.385	146.912	134.249
	B	2.398×10^{-4}	2.020×10^{-4}	2.377×10^{-4}
	r	-0.950	-0.926	-0.853
$S = B_{11+}$				
	A	5.4212	7.9402	6.7450
	B	1.1874×10^{-5}	1.0638×10^{-5}	1.1956×10^{-5}
	r	-0.947	-0.965	-0.857
Beverton-Holt eq.				
$S = I_E$				
	A	7.038×10^{-6}	3.742×10^{-6}	5.392×10^{-6}
	B	-2.160×10^{-5}	1.128×10^{-3}	1.745×10^{-3}
	r	0.002	0.119	0.002
$S = B_{11+}$				
	A	6.8071×10^{-6}	3.7957×10^{-6}	5.4619×10^{-6}
	B	1.737×10^{-2}	1.555×10^{-2}	2.587×10^{-2}
	r	0.082	0.109	0.079

Table 10. American plaice. Standard deviations of R_{ob}/R_{cal}.

	1960-66 1974-76	1967-73	1960-76
Ricker eq.			
$S = I_E$	0.190	0.141	0.306
$S = B_{11+}$	0.178	0.120	0.312
Beverton-Holt eq.			
$S = I_E$	0.207	0.174	0.376
$S = B_{11+}$	0.207	0.175	0.378

Table 11. American plaice. Recruitments ($N_6 x10^{-3}$), from Ricker equation; parent stock as biomass(B_{11+})($tx10^{-3}$).

Biomass	a 1967-73	b 1960-76	c 1960-66 1974-76
10 000	71 389	59 849	48 142
20 000	128 369	106 210	85 505
30 000	173 122	141 361	113 897
40 000	207 535	167 242	134 860
50 000	233 238	185 494	149 701
60 000	251 641	197 509	159 528
70 000	263 954	204 461	165 279
80 000	271 219	207 338	167 741
90 000	274 329	205 969	167 581
100 000	274 049	204 051	165 354
110 000	271 033	199 163	161 525
120 000	265 834	192 785	156 480
130 000	258 924	185 315	150 540
140 000	250 701	177 080	143 969
150 000	241 501	168 349	136 982
160 000	231 605	159 336	129 755
170 000	221 246	150 217	122 430
180 000	210 620	141 130	115 118
190 000	199 885	132 183	107 908
200 000	189 172	123 460	100 870
210 000	178 585	115 025	94 055
220 000	168 209	106 923	87 502
230 000	158 108	99 186	81 237
240 000	148 333	91 836	75 279
250 000	138 920	84 882	69 636

Table 12. American plaice. Population parameters. t_c = 10.3 yr.

		1960-66 1974-76	1967-73
R(virgin)	....	93,033,000	119,577,000
B_{6+}(virgin)	....	342,905 t	440,742 t
B_{11+}(virgin)	....	211,647 t	272,036 t
F_{ext}(R=0)	....	0.9455	1.1788
$F_{0.1}$(Y)	....	0.4285	0.569
R($F_{0.1}$)	....	167,760,000	273,245,000
B_{6+}($F_{0.1}$)	....	303,702 t	444,335 t
B_{11+}($F_{0.1}$)	....	88,389 t	103,614 t
Y($F_{0.1}$)	....	33,901 t	57,032 t
F_{max}(Y)	....	0.486	0.641
R(F_{max})	....	167,223,000	274,225,000
B_{6+}(F_{max})	....	298,892 t	433,121 t
B_{11+}(F_{max})	....	86,813 t	96,056 t
Y(F_{max})	....	34,353 t	57,762 t
R_{max}	....	167,959,241	274,585,104
B_{6+}(R_{max})	....	298,891 t	433,121 t
B_{11+}(R_{max})	....	84,210 t	75,840 t
F(R_{max})	....	0.4484	0.6168
Y(R_{max})	....	34,158 t	57,681 t
B_{6+}max	....	virgin	464,113 t
F(B_{6+}max)	....	0.0	0.361
R(B_{6+}max)	....	virgin	240,389,000
B_{11+}(B_{6+}max)	....	virgin	151,447 t
Y(B_{6+}max)	....	0.0	47,191 t

Table 13. Yellowtail flounder. Prognosis of recruitments (N_4), from Ricker equation; spawning stocks, $S=I_E$ and $S=B_{6+}$

Year	I_E	B_{6+}
1983	109,132,000	109,672,000
1984	103,177,000	89,484,000
1985	83,943,000	89,804,000
1986	70,576,000	76,037,000
$s_{(R_{ob}/R_{cal})}$	0.146	0.169

Table 14. American plaice. Prognosis of recruitment ($N_{6+}x10^{-3}$) from Ricker equation; spawning stocks, $S=I_E$ and $S=B_{11+}$. From curves a, b and c.

Year	a	b	c
		I_E	
1983	152,826	221,523	185,165
1984	166,597	248,925	202,190
1985	170,834	264,730	207,752
1986	160,743	264,013	196,114
1987	137,854	241,692	168,799
1988	138,693	242,641	169,807
$s_{(R_{ob}/R_{cal})}$	0.190	0.141	0.306
		B_{11+}	
1983	149,832	233,272	185,655
1984	158,742	250,090	196,552
1985	167,676	270,919	207,267
1986	166,526	274,539	205,570
1987	165,898	274,325	204,754
1988	157,212	266,636	193,707
$s_{(R_{ob}/R_{cal})}$	0.178	0.120	0.312

Table 15. Correlation coefficients between 3NO cod, yellowtail flounder and American plaice recruitments, for the same year classes.

	r	P
Cod - American plaice	-0.535	0.01-0.02
Cod - yellowtail flounder	0.744	0.001-0.01
Am. plaice - yellowtail f.	-0.802	<0.001

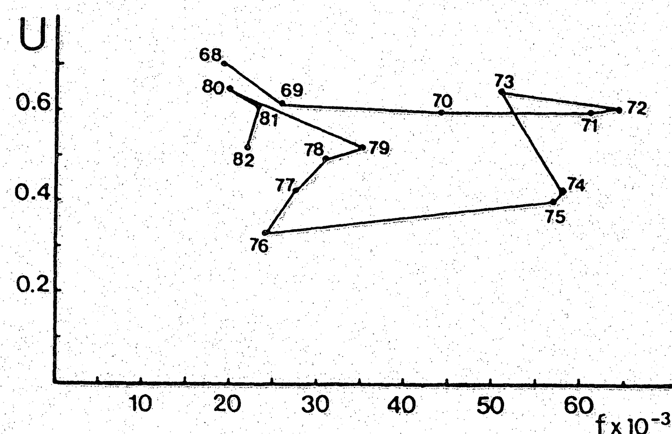

Figure 1. Yellowtail flounder. Effort-CPUE relationship.

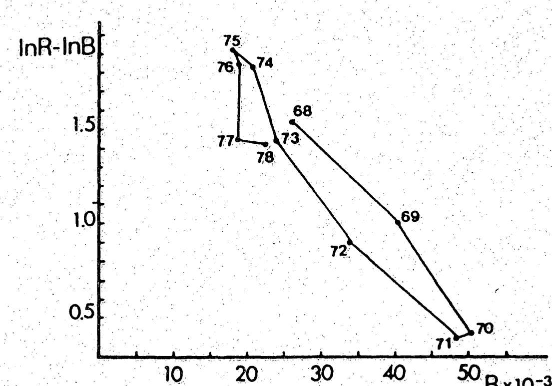

Figure 2. Yellowtail flounder. R, recruitment. B, spawning biomass.

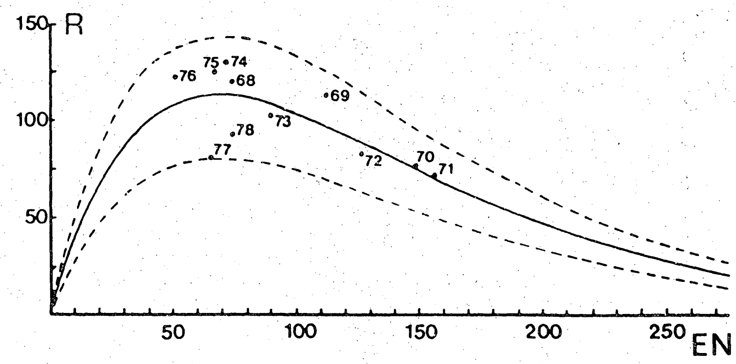

Figure 3. Yellowtail flounder. Stock-recruitment curve, from Ricker equation, with 95% confidence limits.

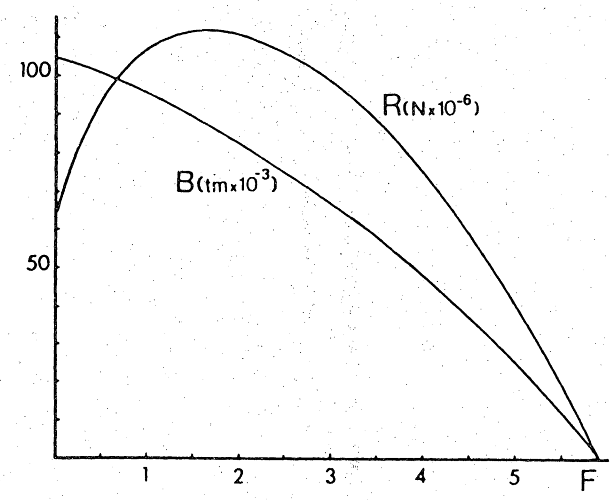

Figure 4. Yellowtail flounder. Recruitment (N_4) and biomass (B_{4+}) as functions of fishing mortality.

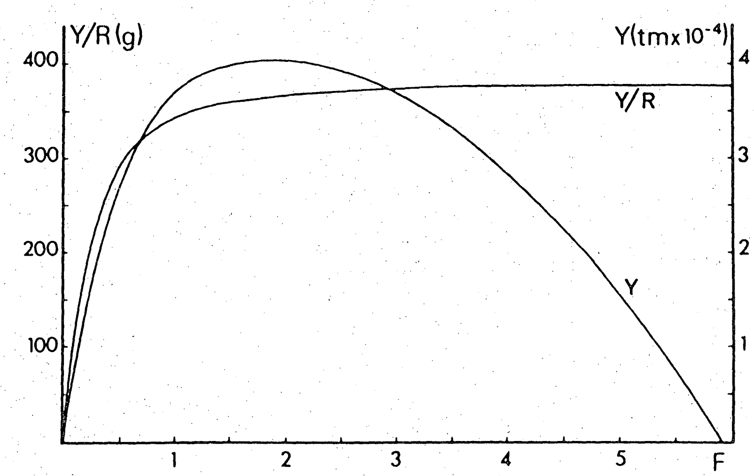

Figure 5. Yellowtail flounder. Yield-per-recruit and total yield, as functions of fishing mortality.

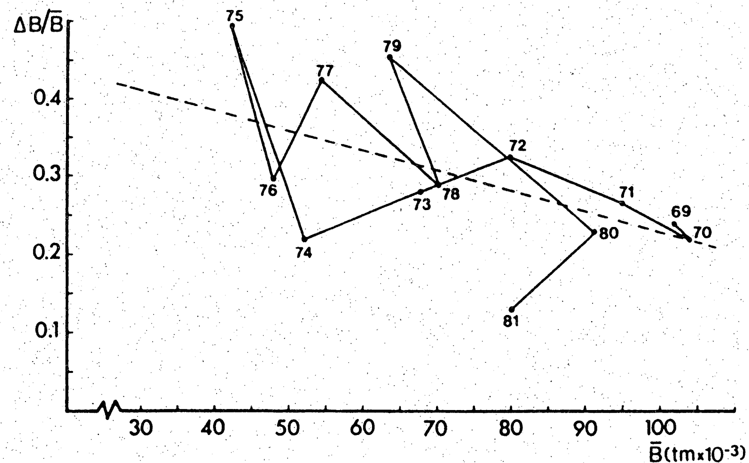

Figure 6. Yellowtail flounder. Regression between productivity rate and average biomass.

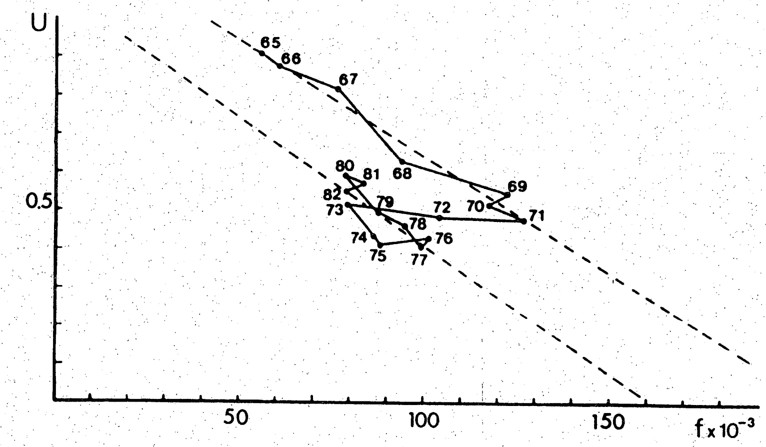

Figure 7. American plaice. Effort-CPUE relationship.

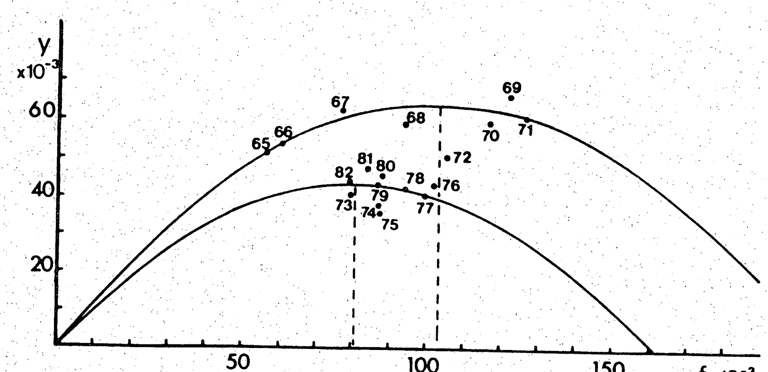

Figure 8. American plaice. General production curves.

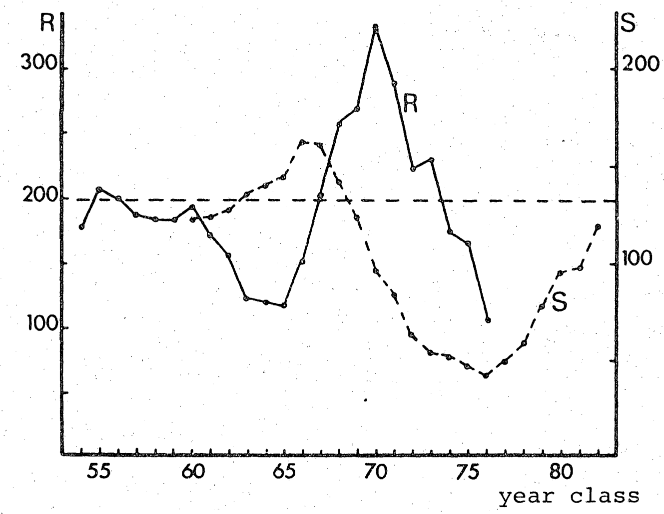

Figure 9. American plaice. Variations of recruitment ($N_6 x10^{-6}$) and parent stock (B_{11+}; $tx10^{-3}$)

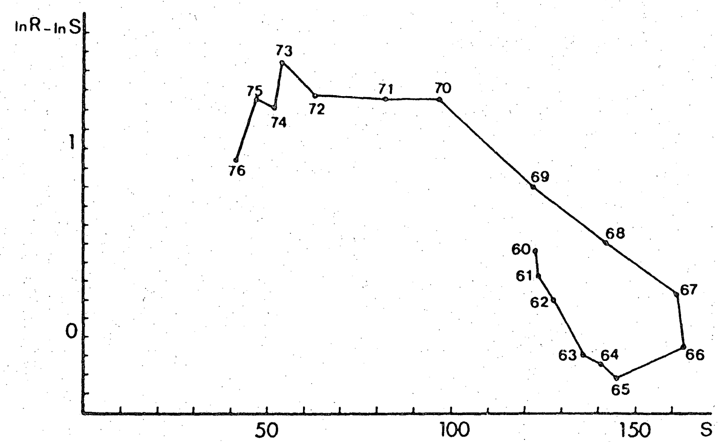

Figure 10. American plaice. R, recruitment. S, spawning biomass.

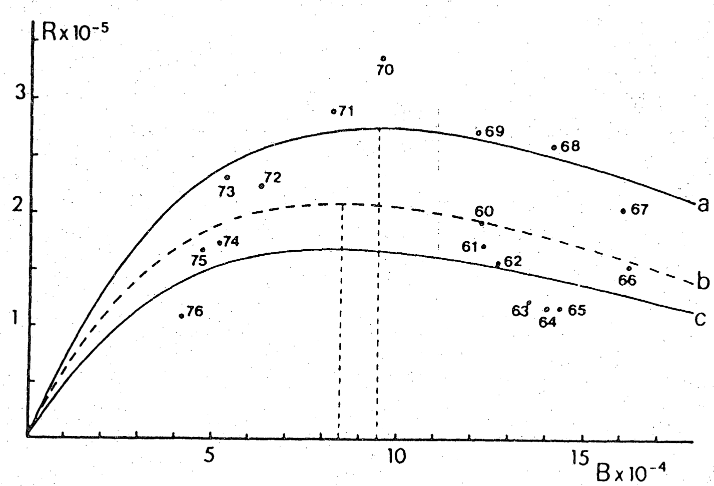

Figure 11. American plaice. Stock-recruitment curves, from Ricker equation. a, for 1967-73; b, for 1960-76; c, for 1960-66 and 1974-76.

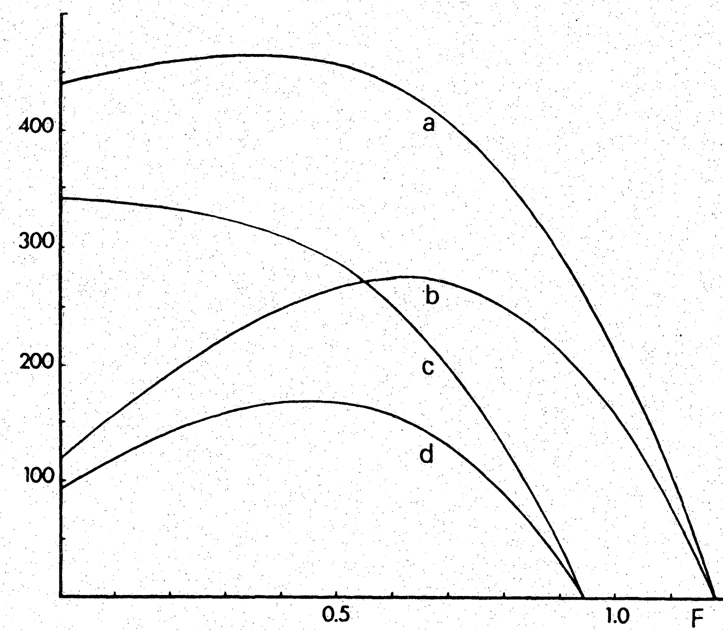

Figure 12. American plaice. Curves of: a, B_{6+} for 1966-73; b, N_6 for 1966-1973; c, B_{6+} for 1960-66 and 1974-76; d, N_6 for 1960-66 and 1974-1976.

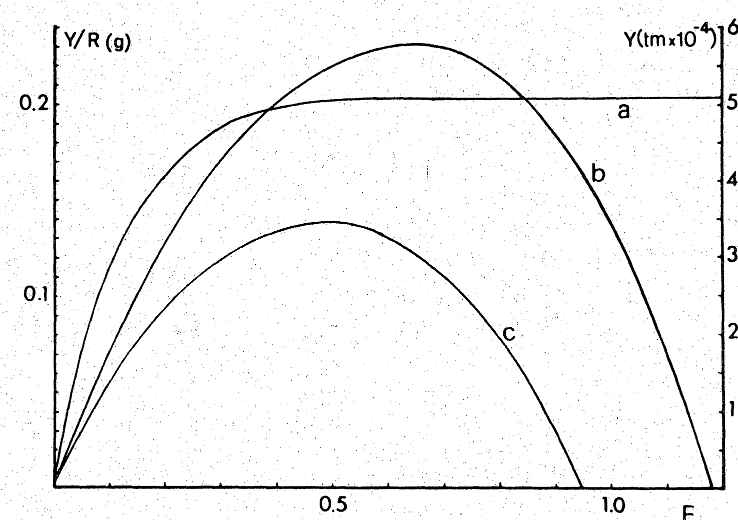

Figure 13. American plaice. Yield-per-recruit curve, and total yield curves: b for 1967-73; c for 1960-66 and 1974-76.

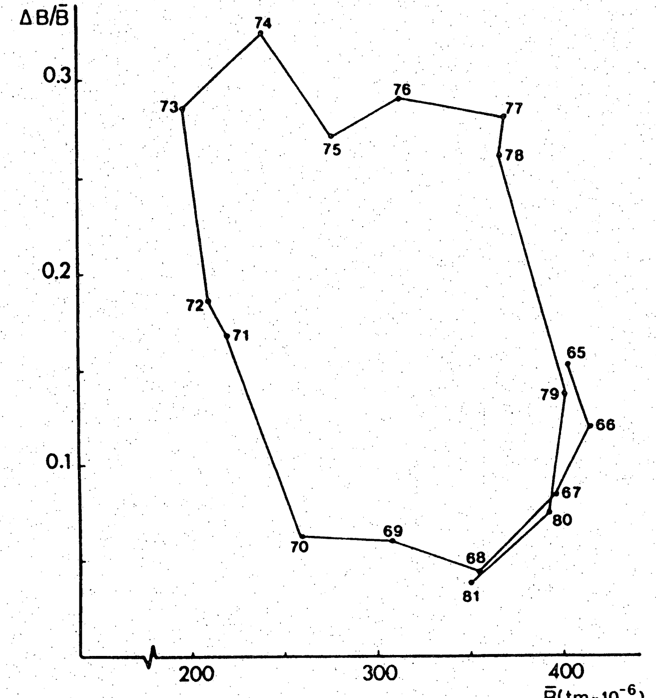

Figure 14. American plaice. Relationship between productivity rate and average biomass.

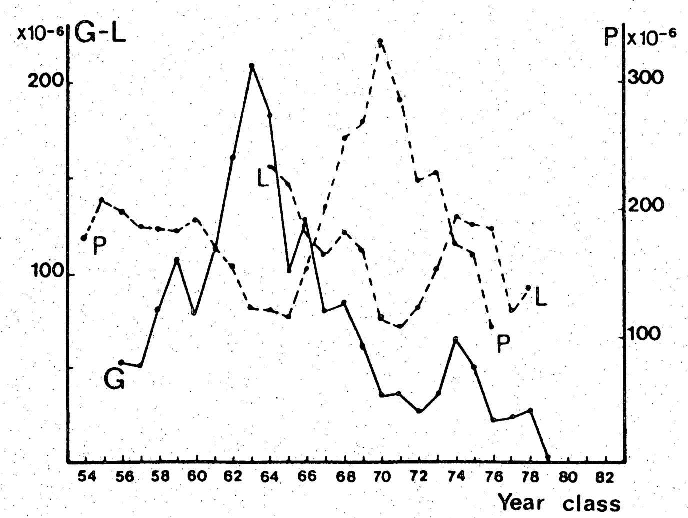

Figure 15. Year class variation of cod (G), yellowtail flounder (L) and American plaice (P).