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A surplus yield model which incorporates recruitment with applications to a stock of mackerel

by

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The "simple" mathematical models of fisheries studied by Schaefer (1954, 1957, 1968) and modified by Pella and Tomlinson (1969), Fox (1970) and Walter (1973) have a number of advantages over the detailed models of Beverton and Holt (1957) or Ricker (1958). They require only catch and effort data for their implementation and they are able to predict the future course of the fishery. Yet they are not as widely used as the latter. One reason is that the usual result of their application is a number giving the maximum sustainable yield under equilibrium conditions. However, since most exploited fisheries are not in a state of equilibrium (Edwards and Hennemuth, 1975), this number is of little practical value. This has been partially rectified by Walter (1976) who established techniques for regulating catch under nonequilibrium conditions.

There is another, perhaps more important, shortcoming of the simple models. That is their failure to respond to changes in year class strength which they treat as noise. Yet these changes are often considerably greater than the systematic changes incorporated into the model (see Walter and Hoagman (1975) for examples in which the year-class strength varies widely).

Accordingly, in this work, a modification of Schaefer's model is introduced. It separates instantaneous growth into two components, one of which corresponds to individual growth and mortality and the other to recruitment. The model will be structured so that both components may be assumed density-dependent. Recruitment will be assumed to occur instantaneously at the beginning of each year though not necessarily to be of one year-class. A number of different assumptions about recruitment will be made and the consequences explored. Both equilibrium and nonequilibrium strategies for exploitation are derived. The model is then applied to the mackerel stock of

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the Northwest Atlantic. The parameters are estimated by using the existing Schaefer model for this stock and modifying it by using age structure data. Historical catch data going back to 1876 is used to estimate the frequency of large year classes. The model is then used to predict the future size of the stock based on several different assumptions about fishing mortality and recruitment.

The Model

The form of the model will be

$$\frac{1}{P}\,\frac{dP}{dt} = b - aP + \sum_{i=-\infty}^{\infty} r_i\,\delta(t-i) - qf \tag{1}$$

where P is the biomass of the stock in question and f is the fishing effort. The symbol $\delta(t-i)$ stands for the unit impulse at time t=i which has the property that $\delta(t-i) = 0$ for $t \neq i$, but $\int_{-\infty}^{\infty}\delta(t-i)dt = 1$. It is the generalized derivative of the unit step function, the function which is zero for $t \leq i$ and 1 for $t > i$.

The left side of the equation is the instantaneous rate of change per unit mass of the biomass. The right side has an expression for the individual growth and natural mortality rate (b - aP), for the growth rate due to recruitment $(\Sigma r_i\delta(t-i))$, and for the fishing mortality (qf).

In the absence of fishing, the solution to the equation has the form

$$P(t) = \frac{b/a}{1-\{1-b/aP_0\}e^{-bt}} \tag{2}$$

in any given year when the biomass is P_0 at the beginning of the year after recruitment. The solution will be shown to have a jump due to recruitment at the beginning of the year,

$$P(i+) = P(i-)e^{r_i} \tag{3}$$

where P(i-) is the biomass in the ith year before recruitment and P(i+) after recruitment. The biomass will vary in time as shown in Figure 1; it tends toward the level b/a in the course of the year and jumps to a new level at the start of each year.

The relation (3) between r_i and the biomass of recruits each year may be derived by using the properties of the unit impulse. Indeed if we integrate over a period of time from just before the beginning of the kth year to just after the beginning we obtain the following equality:

$$\int_{k-\varepsilon}^{k+\varepsilon} \frac{1}{P}\,\frac{dP}{dt} = 2b\varepsilon - a\{\int_{k-\varepsilon}^{k+\varepsilon} P\}+r_k\ . \tag{4}$$

Since $\int_{k-\varepsilon}^{k+\varepsilon} \delta(t-i)dt = 0$ when $k \neq i$, the last expression reduces to the single constant. The integral on the left may be evaluated directly as

$$\ln P(k+\varepsilon) - \ln P(k-\varepsilon) = \ln \frac{P(k+\varepsilon)}{P(k-\varepsilon)} . \tag{5}$$

We now take the limit as ε approaches 0 to obtain

$$\ln \frac{P(k+0)}{P(k-0)} = r_k \tag{6}$$

By writing this in exponential form and replacing k by i, we obtain (3).

Let us denote by R_k the biomass of recruits in the kth year; we assume that all recruitment takes place at the beginning of the year and accounts for the difference between the two values of stock biomass in (6). That is,

$$P(k+0) - P(k-0) = R_k \tag{7}$$

from which we are able to derive the expression

$$r_k = \ln \left(\frac{R_k}{P(k-0)} + 1\right) \tag{8}$$

This enables us to calculate r_k since $R_k/P_{(k-0)}$ is the ratio of recruit to total biomass at the start of the kth year.

Steady-state Analysis

It is clear from the assumption and Figure 1 that there is no state of constant equilibrium under which growth exactly balances fishing mortality. However, it is possible to consider the long-term behavior of the fishery. That is, average annual behavior when the fishing effort is always the same f. We consider the behavior over a period of time from 0- to T- (just before recruitment). By integrating equation (1) over this period of time, we obtain

$$\ln \frac{P(T-)}{P(0-)} = T(b-a\overline{P}) + \sum_{i=0}^{T-1} r_i - Tqf, \tag{9}$$

where $\overline{P}$ denotes the mean population biomass. If we divide both sides of (9) by T and then take the limit as T approaches infinity, we obtain

$$0 = b + \overline{r} - a\overline{P} - qf \tag{10}$$

the steady-state equation. Here $\overline{r}$ denotes the mean recruitment rate. The average annual yield under this hypothesis is given by

$$Y = \frac{1}{T} \int_{0-}^{T-} g\ f\ P = q\ f\ \overline{P} = \frac{qf}{a}(b+\overline{r} - qf) \tag{11}$$

which is exactly the same expression as in Schaefer's model. Thus the analysis of the long-term equilibrium or steady-state would be the same for both models. Now, however, we are able to introduce a stock-recruitment relation and revise the optimum levels of f accordingly.

We first find the relation between $\overline{P}$ and the average biomass P- just prior to recruitment. This may be done by replacing $\overline{r}$ in equation (10) by $\ln(\frac{R}{P-} + 1)$ where $\frac{R}{P-}$ is the mean (geometric) ratio of recruit biomass to population biomass. Then (10) becomes

$$0 = b + \ln\left(\frac{R}{P-} + 1\right) - a\overline{P} - qf. \tag{12}$$

This equation may be used to calculate the yield under certain simple stock recruitment relations, those in which recruitment is proportional to spawning stock which in turn is proportional to stock biomass at some instant of time in the year. By adjusting the constants appropriately we may assume that the instant is just prior to recruitment, i.e.,

$$R = \alpha P- \tag{13}$$

The yield equation again has the same form as (11)

$$Y = \frac{qf}{a}\left(b + \ln(\alpha+1) - qf\right) \tag{14}$$

which again is analyzed as is Schaefer's yield equation.

It is when the recruitment is assumed to be a relationship other than proportional that complications arise. We now hypothesize that recruitment R is a function of P of the form

$$R = \alpha P G(P) \tag{15}$$

where G(P) is the density-dependent factor. Ricker (1975) assumes it to be of the form $G(P) = (1 + \beta P)^{-1}$ in some cases and $G(P) = e^{-\beta P}$ in others. In either case it is a monotonically decreasing function such that $G(0) = 1$ and $G'(0) = -\beta$.

The yield now becomes

$$Y = \frac{qf}{a}\left(b + \ln(\alpha G(P) + 1) - qf\right) \tag{16}$$

where P and f are not independent but must satisfy equation (12).

Here the P is the P- of equation (13), the stock just before recruitment. We may express Y in terms either of f or of P by eliminating the other between equations (12) and (16).

The equation (12) relating f and P is too complicated to solve directly since $\overline{P}$ must be expressed in terms of P and R. However, if we make some approximations, we can express equation (12) as an approximate linear equation and thus solve for P. We assume therefore that

$$P \approx \overline{P}, \tag{17}$$

$$\ell n(\alpha G(P) + 1) \approx \alpha G(P) \tag{18}$$

and

$$G(P) \quad 1 - \beta P \tag{19}$$

These are the standard linear approximations in (18) and (19) while (17) is valid when R/P is relatively small. Then equation (12) may be expressed as

$$\alpha + \beta - (a + \alpha\beta)P - qf \approx 0 \tag{20}$$

and the yield equation is

$$Y \approx \frac{qf}{a+\alpha\beta}(\alpha+b-qf) \tag{21}$$

Thus the effect of density dependence on recruitment will be to lower the long-term average yield. This can be seen by comparing the estimates obtained by (21) when $\beta = 0$ to $\beta > 0$.

If these approximations are not valid, in particular when recruits constitute most of the biomass each year, the comparison is not so simple and is shown in Figure 2. The maximum yield is lower in the more highly density-dependent case, but not necessarily the yield for a particular level of effort.

Transient Analysis

Few of the world's fisheries have in recent years been in a state of equilibrium or even close to it. Recently Walter (1976) presented a method for regulating a fishery under conditions of nonequilibrium. The approach was based on the Schaefer model and thus did not take into account year-class strength. Many of the same results apply equally well to the present model with the added provision that year-class strength may be taken into account to choose the best strategy.

The yield in year n may again be calculated by integrating qfP from n-1- to n-, and substituting equation (1) for P,

$$Y_n = \int_{n-1-}^{n-} qfP \, dt = \frac{qf}{a}\{b-qf+r_{n-1}-\ell n \frac{P(n-)}{P(n-1-)}\}. \tag{22}$$

The relation between P(n-) and P(n-1-) in turn may be obtained by using equations (2) and (3),

$$P(n-) = \frac{(b-qf)/a}{1-\{1-(b-qf)/aP(n-1-)e^{r_{n-1}}\}e^{-b+qf}}. \tag{23}$$

The effort must now be chosen in some way such that yield is optimized. If the fishery has been well regulated so that the biomass at the beginning of the year is close to the optimum level, a reasonable approach would be to choose f so that the biomass returns to the same level at the beginning of the subsequent year. Then the last term in (22) is 0 and the yield (which conserves biomass) is again a quadratic function of f (see Figure 3). The term r_{n-1} will determine which of the curves apply in a particular year.

However, we are not free to choose f as in the steady-state case since f must be chosen such that (23) is satisfied as well for P(n-) = P(n-1-). We may combine (22) and (23) most easily by integrating (2) directly over the nth year and replacing P_0 by P(n-1+), and b by q-qf.

$$Y_n = \frac{qf}{a} \ln P(n-1+)a\frac{(e^{b-qf}-1)}{b-qf} + 1. \qquad (24)$$

If we now approximate $\ln (1+x)$ by x and e^x by 1 + x we find that, approximately,

$$Y_n = qf\ P(n-1+). \qquad (25)$$

We may plot these values on the same plot as the graph as equilibrium yield and find the point of intersection of the two graphs (see Figure 4). The value of yield at that point is the yield attainable under the conditions of recruitment and initial population for that year. Of course greater and smaller values of yield are possible but would have the effect of decreasing or increasing the population.

In a well-regulated fishery the point of intersection will be close to the maximum if the recruitment is about average. However it is possible the recruitment is not average or the fishery is not well regulated. In either of these cases an alternate strategy must be devised.

The alternate strategy will be designed to approach the long-term optimum levels of yield and fishing mortality (or effort). That is, the population level should be adjusted up or down to approach, as closely as possible, the optimum P(n-), = $(b+\bar{r})/2a$. If the year-classes are of average strength, and the initial value of P while below the optimum is not so low as to endanger the stock, a good strategy would be to set the effort at the optimum and allow the fishery gradually to recover (as was described in Walter /1976/). The yield would then be approximately

$$Y = \frac{b+\bar{r}}{2} P(n-1-)e^{r_{n-1}} \qquad (26)$$

The same is true if the initial value of P is above the optimum. The yield for the optimum level of effort would again be given by (26).

If the recruitment for a particular year is above average, the yield given by (26) is too conservative. A larger yield is possible while still allowing the biomass to approach the optimum. The opposite of course is true for a smaller than average recruitment.

If the population is below the optimum at the beginning of a year and the recruitment is above average, it is possible to allow the fishery to recover somewhat while still taking an above-average yield. In this case the desired ratio of population biomass for two successive years must first be specified. The fishing effort to maximize the yield under this constraint may then be found. This is shown graphically in Figure 5.

A more typical problem would be to find the optimum level of effort in the presence of varying year-class strength. Indeed the yield for n successive years in which the initial and final biomass are the same may be found from equation (22). It is

$$Y = \sum_{i=1}^{n} y_i = \frac{qf}{a}\{(b-qf)n + \sum_{i=1}^{n} r_{i-1} - \sum_{i=1}^{n} \ell n\ (P(i-)-\ell n(P(i-1-))$$

$$= \frac{nqf}{a}\{b-qf+\bar{r}\} \tag{27}$$

which is the same as equation (11). Thus the optimum level of fishing is

$$f\ opt = \frac{b+\bar{r}}{2q} \tag{28}$$

The yield, however, will vary from year to year. It may be found by first calculating the biomass in year k in terms of the initial biomass and then substituting the value obtained into equation (24). The resulting formulas are excessively complicated but the calculations may easily be made in particular cases.

<u>A Stochastic Approach</u>

The number of recruits, rather than obeying any regular rule such as that in equation (15) seems usually to vary from year to year in a random fashion. Since survival to age of recruitment depends on many factors whose combined effect is multiplicative it is plausible that the biomass R have a log normal distribution. If the fishery is well-regulated by a scheme that keeps the population the same at the start of each year, then R/P has the same sort of distribution. If, moreover, the ratio R/P is small compared to 1, then the mean μ may be estimated by

$$\overline{R} = \frac{1}{n}\sum_{i=1}^{n} R_i = \frac{P}{n}\sum_{i=1}^{n}\frac{R_i}{P} \simeq \frac{P}{n}\sum_{i=1}^{n} \ell n\left(\frac{R_i}{P}+1\right)$$

$$= \frac{P}{n}\,\Sigma r_i = P\overline{r}. \tag{29}$$

Since in the well-regulated fishery we are hypothesizing $P = \frac{b+\overline{r}}{2a}$, we have as our estimator

$$\overline{R} \simeq \frac{(b+\overline{r})\overline{r}}{2a}\,. \tag{30}$$

There seems to be no simple formula for the variance apart from using the historical data.

We can now use these values of mean and variance to simulate the fishery by using random sequences of numbers for R_i (or r_i) drawn from a log normal population. The population in successive years is given by (23) and the yield by (24). Various schemes for effort may be postulated.

Another approach would be to use (30) to calculate the probability that the population will fall into a certain range or that the yield be at least a certain value.

Fitting parameters

While the Schaefer approach requires only catch and effort data, the model described here requires additional information about recruitment. The coefficient b'(intrinsic growth rate) in Schaefer's model must be split into two terms, b the individual growth, and $\overline{r}$ the average recruitment rate. This may be done in a number of different ways. If the (average) proportion of new recruits to the already recruited biomass is known, it may be used as an estimate of R/P and $\overline{r}$ may be taken as $\ell n\ (\frac{R}{P} + 1)$. This may then be subtracted from b' to obtain b.

An example - Mackerel in ICNAF Subarea 5 and Stat. Area 6.

The Schaefer model for this stock was calculated by Walter (1976), based on the data of Anderson (1975) to be

$$\frac{1}{P}\frac{dP}{dt} = 0.5\left(1 - \frac{P}{2.5 \times 10^6}\right) - 1 \times 10^{-6}\ f. \tag{31}$$

The average instantaneous recruitment rate may be calculated from knowledge of the year-class strength which in turn may be based on age composition of the catch. The age composition estimates were found in 1975 ICNAF assessment report on Mackerel, pg. 45, Table 2. The number of recruits was taken to be the number of one-year-olds, which was multiplied by the average weight as corrected by Anderson. The resulting recruitment proportions and rates are given in Table 1.

In order to use this model to predict the future course of the fishery, some sort of estimation of the expected year-class strength must be made. From the analysis of the years 1968 to 1975 given in Table 1, the recruitment rate seems to vary less than the year-class strengths. In fact, the rate r_i was stable about $r = 0.1$ except for the one year 1968 in which it was $r = 0.6$.

We shall try to predict this population under various assumptions on recruitment. One is that the recruitment rate be constant at the average rate $r = 0.2$ from 1976 to 1980, another that it be proportional to the spawning population, and finally that an occasional large year-class enters the fishery.

The big problem, of course, is the last case. How often do large year-classes enter the fishery? While an exact estimate is difficult, we can make an educated guess by considering the historical catch data. It goes back to 1804 for the USA and 1876 for the Canadian catch. We shall use the latter since it seems to contain fewer wild variations (see Table 2).

We shall adopt the following procedure in order to estimate the frequency of large year-classes. It consists (roughly) of noting how often the catch jumps up beyond that consistent with the model. In order to do this we first filter out the years where an increase is followed immediately by a decrease. In such cases the increase was assumed not to have been caused by a larger year-class.

In order to approach this quantitatively, we assume that the biomass and fishing effort are such that the combined mortality is close to the optimum. We also assume then that the catch is proportional to the abundance except for those isolated years mentioned above.

If we assume that P and f are both optimum and the stock satisfies the model we have constructed then

$$P = \frac{b+\bar{r}}{2a} \text{ and } f = \frac{b+\bar{r}}{2q}.$$

If we denote by P_i the biomass just prior to recruitment, and R_i the biomass of recruits, then, the growth rate during the ith year is

$$b - aP - qf = b - \frac{b+\bar{r}}{2} - \frac{b+\bar{r}}{2} = -\bar{r}$$

and hence

$$P_{i+1} = (P_i + R_i)e^{-\bar{r}}.$$

The annual recruitment rate r_i is given by

$$r_i = \ell n\left(\frac{R_i}{P_i} + 1\right)$$

$$= \ell n\left(\frac{R_i + P_i}{P_i}\right)$$

$$= \ell n\left(e^{\bar{r}}\frac{P_{i+1}}{P_i}\right) = \bar{r} + \ell n\,\frac{P_{i+1}}{P_i}$$

We now assume that $\frac{P_{i+1}}{P_i}$ is proportional to $\frac{Y_{i+1}}{Y_i}$ and use this to calculate r_i. However, since r_i cannot be negative we delete those years when it is and replace them by the average of the preceding and following years. This corresponds to those years for which $\frac{Y_{i+1}}{Y_i} < e^{-0.2} = .819$. We then consider the remaining years for evidence of large year-classes. We classify a year-class as large if the recruitment rate is more than two times the average, (in 1968 it was three times the average.) i.e. when $r_i > 0.4$. This corresponds to $\frac{Y_{i+1}}{Y_i} > 1.22$. This occurred 12 times in the 100-year history or approximately once every eight years.

Thus in the period from 1976 to 1980, we would expect at most one large year-class. The largest yield would result if it occurred at the beginning of the period. Accordingly, we assume that it occurs in 1976 and corresponds to a recruitment rate of 0.6 while the other years are such that the average is 0.2.

We now consider five cases and project to 1980 using various assumptions about fishing effort and recruitment rate.

<u>Case 1</u>: <u>No fishing, recruitment rate</u> r = 0.2 <u>for each year</u>. We use equation (23) to find the biomass each year prior to recruitment. It is:

$$P(i+1-) = \frac{0.3/0.2\cdot 10^{-6}}{1-\{1-0.3/0.2\cdot 10^{-6}P(i-)e^{0.2}\}e^{-0.3}}$$

The recruitment biomass $R_i = P_{i-}(e^{0.2}-1) = 0.22\ P_{i-}$. The prognosis for years 1976-1980 is given in Table 3.

<u>Case 2</u>: <u>Moderate fishing</u> F = 0.25, <u>recruitment rate</u> r = 0.2 <u>each year</u>.

An F = 0.25 corresponds to f = 250,000 std. days. The équation (23) is now

$$P_{(i+1-)} = \frac{.05/0.2\cdot 10^{-6}}{1-\{1-.05/0.2\cdot 10^{-6}P(i-)e^{0.2}\}e^{-0.05}}$$

and the future course is given by Table 4.

Case 3. Moderate Fishing F = 0.25, recruitment rate heavy first year followed by lower rate to make average 0.2. Results are given in Table 7.
Thus the prognosis even in the most optimistic case is not too favorable. The recovery under moderate fishing will still be considerably less than the optimum which is 1250 x 10^3 MT.

Case 4. Heavy Fishing with F = 1.0 as f = 10^6 std. days. r = .2 all years. The results are given in Table 6. Thus under heavy fishing, the yield would be very large initially but the stock would be reduced to less than 10% of the 1975 level.

Case 5. Moderate Fishing F = 0.25 recruitment proportional to population biomass two years previous. From the 1968 to 1975 data we find that the proportion is approximately 5%. Similar calculations lead to projections in Table 5.

Year	R_i	P_{i-}	Y_i
1976	115	270	93
1977	30	374	97
1978	20	392	99
1979	20	400	101
1980	20	410	103

That is, the biomass will stabilize at a level considerably below the optimum.

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Table 1. Estimates of biomass after recruitment P(i+), recruitment R_i, and growth rate due to recruitment r_i for the years 1968-1977 for the mackerel stock of ICNAF Subarea 5 and Statistical Area 6 (Data from Anderson).

Year i	P(i+)(10^6 Kg.)	R_i (10^6 Kg.)	r_i
1968	1974	912	.62
1969	2529	374	.16
1970	1986	254	.14
1971	1816	119	.08
1972	1556	135	.09
1973	1177	76	.07
1974	786	103	.14
1975	574	80	.15
1976	386	115	.35

Table 2. Historical landings data (MT) for Atlantic mackerel, 1876-1975.

CANADA			
Year	Catch	Year	Catch
1876	14,226	1926	5,239
1877	22,479	1927	7,203
1878	25,134	1928	20,368
1879	25,999	1929	6,929
1880	31,902	1930	8,095
1881	14,702	1931	8,902
1882	15,555	1932	8,094
1883	17,523	1933	11,944
1884	24,737	1934	8,656
1885	20,285	1935	7,280
1886	20,789	1936	10,326
1887	16,418	1937	10,848
1888	8,597	1938	12,953
1889	8,647	1939	23,617
1890	13,354	1940	16,209
1891	18,397	1941	15,927
1892	12,774	1942	13,748
1893	10,222	1943	16,822
1894	7,860	1944	15,546
1895	5,776	1945	18,238
1896	6,240	1946	13,389
1897	3,784	1947	11,913
1898	4,604	1948	11,737
1899	4,708	1949	15,206
1900	11,435	1950	12,352
1901	10,503	1951	11,223
1902	5,931	1952	9,975
1903	11,355	1953	8,373
1904	5,006	1954	11,572
1905	6,829	1955	11,277
1906	9,311	1956	9,586
1907	7,003	1957	8,801
1908	10,318	1958	7,300
1909	7,448	1959	4,287
1910	3,166	1960	5,958
1911	4,088	1961	5,603
1912	4,898	1962	6,729
1913	9,773	1963	7,801
1914	6,519	1964	10,844
1915	8,209	1965	11,274
1916	7,079	1966	11,000
1917	7,578	1967	11,000
1918	8,826	1968	11,000
1919	10,427	1969	18,000
1920	6,457	1970	15,000
1921	6,602	1971	13,000
1922	11,395	1972	14,000
1923	6,430	1973	19,000
1924	9,779	1974	15,000
1925	8,512	1975	13,663

Table 3. Projected biomass with F = 0, r = 0.2 for each year.

Year	r	$P_{i-}(10^3MT)$	$R_i(10^3MT)$	$Y(10^3MT)$
1976	.35*	270*	115*	0
1977	.2	480	105	0
1978	.2	690	150	0
1979	.2	950	210	0
1980	.2	1230	270	0

*actual

Table 4. Projected biomass with F = 0.25, r = 0.2 for each year.

Year	r	P_{i-}	R_i	Y
1976	.35*	270*	115*	90
1977	0.2	375	80	120
1978	0.2	440	95	140
1979	0.2	505	110	150
1980	0.2	574	130	160

*actual

Table 5. Projected biomass with one large year-class and others average and F = 0.25.

Year	r	P_i	R_i	Y
1976	.035	270	115	90
1977	.6	375	310	170
1978	.1	360	40	100
1979	.1	345	35	95
1980	.1	325	35	90

Table 6. Projected biomass under assumption F = 1.0, r = 0.2 for all years.

Year	r	P_i	R_i	Y
1976	.35	270	115	270
1977	.2	180	40	160
1978	.2	105	23	90
1979	.2	60	14	50
1980	.2	35	7	30

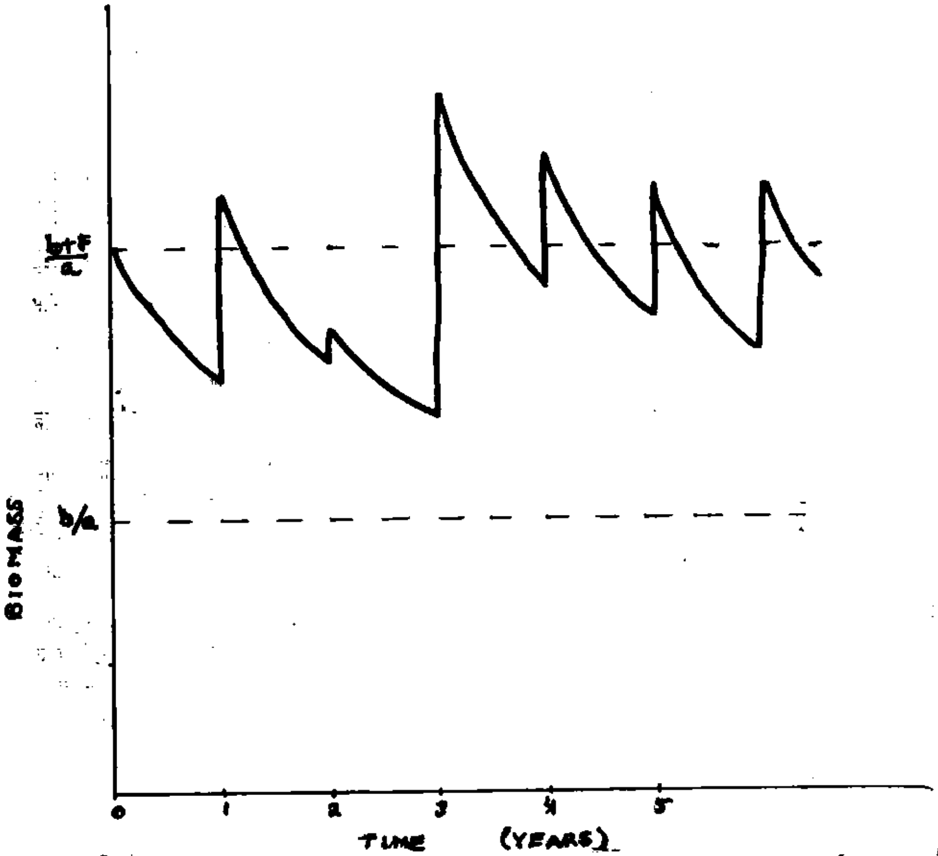

Fig. 1. Changes in biomass over time for a fishery satisfying the model $\frac{1}{P}\frac{dP}{dt} = b - aP + \Sigma r_i \delta(t-i)$. The jumps at the start of the year correspond to recruitment, the line P = b/a represents equilibrium in the absence of recruitment and could be negative, $\bar{r}$ represents average recruitment rate, and the line $P = \frac{b+\bar{r}}{a}$ gives the equilibrium value.

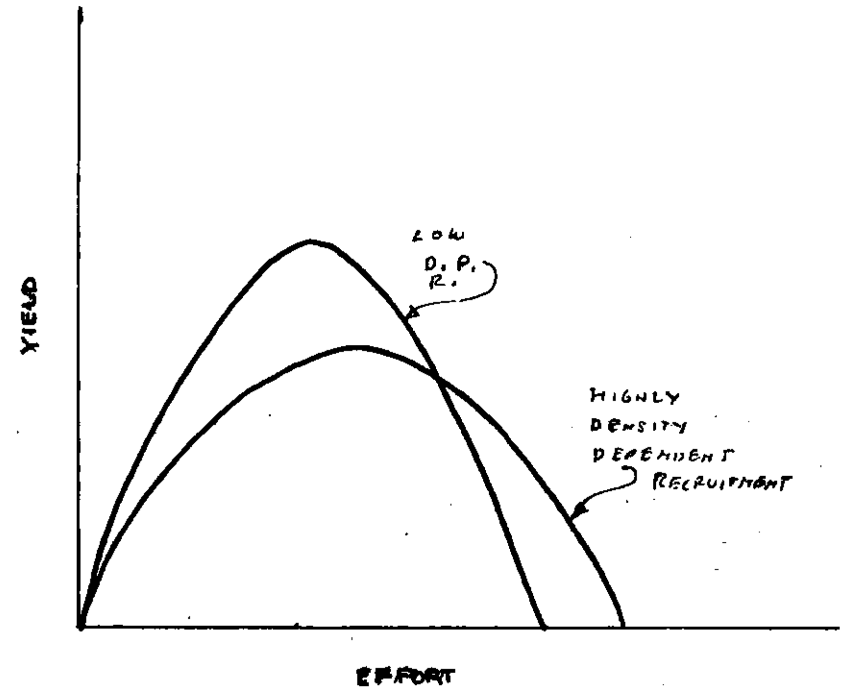

Fig. 2. Comparison of a long-term average equilibrium yield curve for low and high density dependence of recruits.

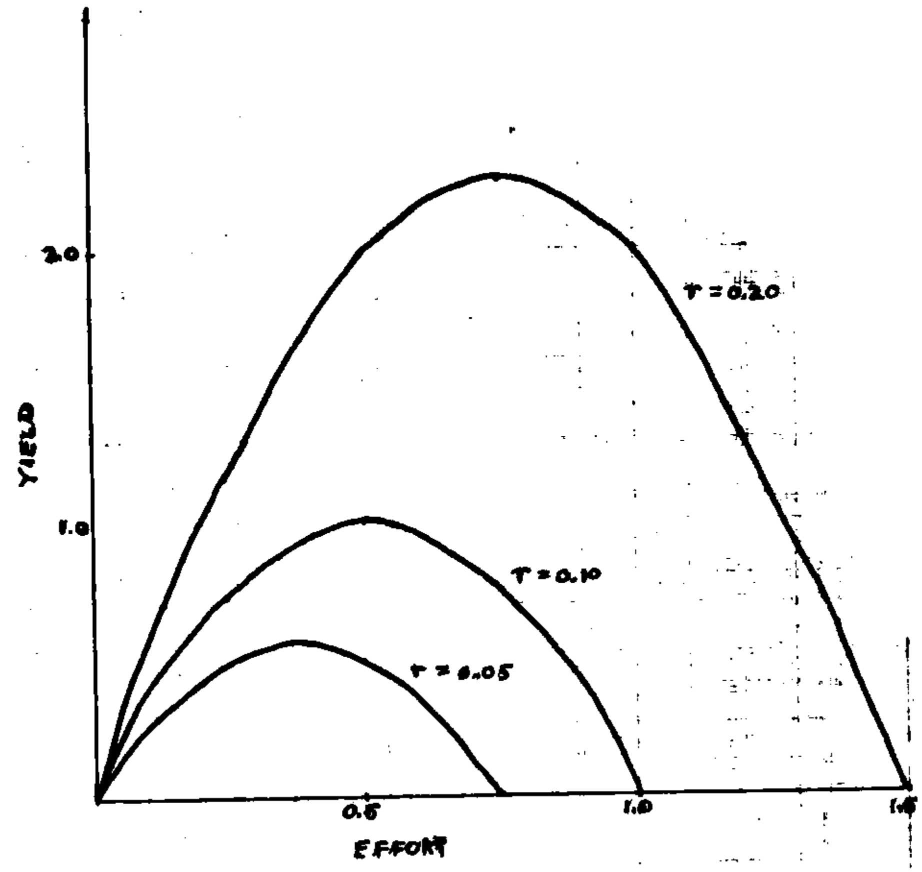

Fig. 3. Conservation of biomass annual yield for a fishery satisfying equation 1 with b = 0.1, a = 0.01, F = 0.1, standardized f, recruitment rates r = 0.1, r = 0.2 and r = 0.05. The yield is given by Y = 20f(0.1+r-2f) and represents the catch that keeps the biomass constant in the face of varying recruitment.

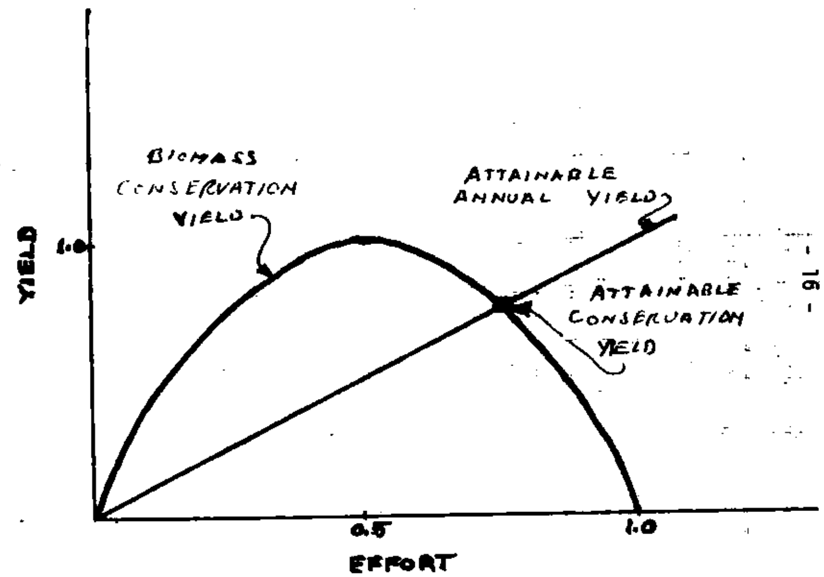

Fig. 4. Plot of conservation yield and annual yield as a function of effort. The parameters are b = 0.1, q = 0.2, a = 0.01, and r = 0.1. The annual yield corresponds to an initial level P(0t) after recruitment of 5. The point of intersection establishes the attainable conservation yield.

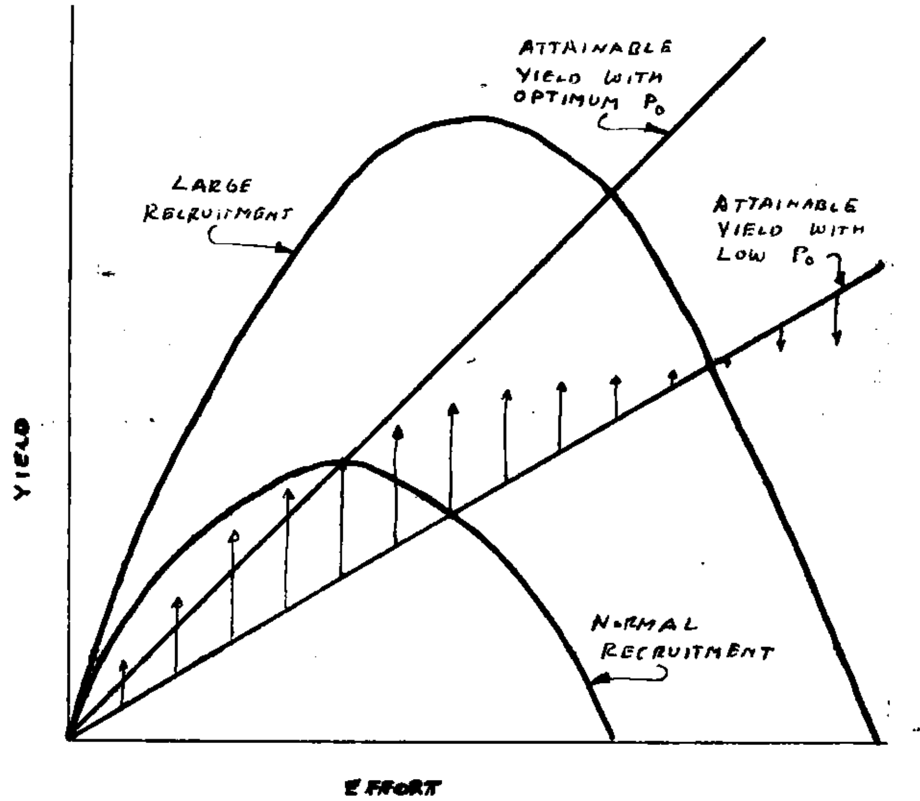

Fig. 5. Graphical representation of yield vs. effort when the initial biomass P_0 is below the optimum and recruitment r is above average. The arrows indicate the growth or decline in the biomass in the course of the year. A line through the origin and the head of an arrow is the yield for the next year.

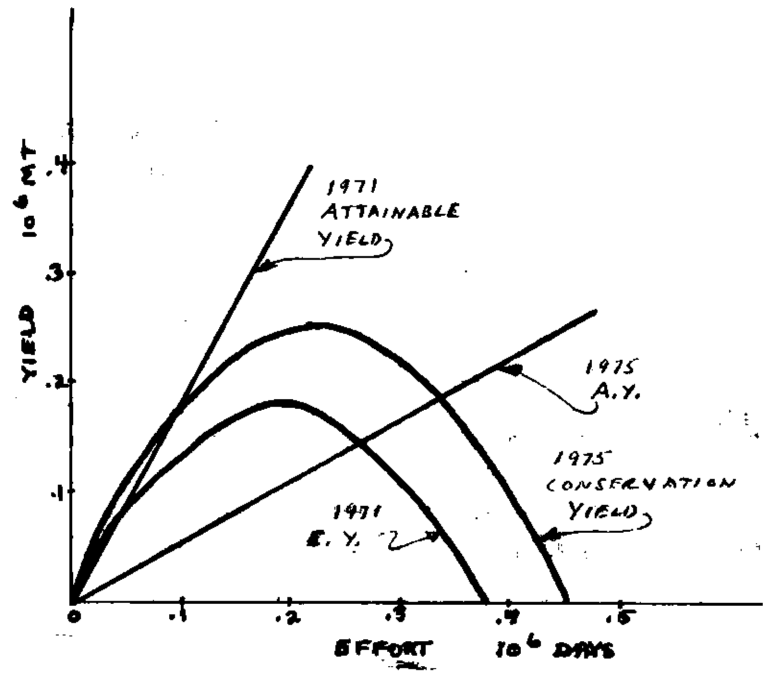

Fig. 6. Conservation yield curves and possible annual yield curves for the years 1971 and 1975 for a Northeast Atlantic mackerel stock. Equation is $\frac{1}{P}\frac{dP}{dt} = 0.3 - 0.2\cdot10^{-6}P + \Sigma r_i\delta(t-i) - 10^6 f$.