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Back-calculating production from cohort analysis,
with discussion on surplus production for two redfish stocks.

by

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Abstract

A method is presented for back-calculating surplus and net production from cohort analysis. This method, which requires detailed information on the age-composition of the catch, as well as information on the mean weight-at-age, is used to assess trends in surplus production for two redfish stocks. Since these calculations refer to the transient state, the method does not require the assumption of 'an equilibrium state'. In fact, our results indicate that annual surplus production responds quickly to changes in the age-composition of the stocks and to changes in recruitment levels. For these two redfish stocks, the variations in stock biomass level and in the mean age of the stock are sufficient to explain most of the variability contained in surplus production without the need for either explicit density-dependent or climate-dependent term. The age composition of a stock appears as an important factor for controlling production. Results also indicate that, in certain years, up to 76% of redfish production is exogenous to the exploited stock. This indicates that the catch per unit of effort, which is often used as an index of stock level, provides only limited information on the annual production.

Résumé

Nous présentons une méthode pour rétro-calculer la production excédentaire et la production nette à partir de l'analyse de cohorte. Nous employons cette méthode qui se base sur les données de distribution des prises par groupe d'âge, ainsi que sur le poids moyen par groupe d'âge, pour évaluer les tendances dans la production excédentaire pour deux stocks de sébaste. Puisque ces calculs se basent sur un état de transition, la méthode n'a pas recours à l'hypothèse d'un état d'équilibre. En fait, nos résultats indiquent que la production excédentaire annuelle répond rapidement aux changements de la structure d'âge du stock, ainsi qu'aux changements enregistrés dans les niveaux de recrutement. Pour ces deux stocks de sébaste, les fluctuations du niveau de biomasse et de l'âge moyen du stock expliquent à elles-seules la plus grande partie de la variation observée dans la production excédentaire, sans faire appel à un facteur explicite pour tenir compte de la densité ou des paramètres climatiques. La structure d'âge d'un stock est donc un facteur important pour le contrôle de la production. Nos résultats indiquent également que, pour certaines années, jusqu'à 76% de la production chez le sébaste est exogène au stock exploité. Ceci indique que la prise par unité d'effort, qui est souvent utilisée comme un indice du niveau du stock, ne renferme que peu d'information sur la production annuelle.

Unlike the manager who is mainly concerned about the exploitation of the resource and the optimization of the long-term socio-economic benefits, a biologist is generally concerned about the basic mechanisms regulating fish production. What are the main components of production in an exploited fish population? Which age-groups are the main contributors to biological production? What are the basic mechanisms regulating recruitment and growth in a fish population? These questions, which are essential to our understanding of the responses of fish populations to exploitation, are only indirectly addressed by classical productivity and yield-per-recruit models (Schaefer, 1954 and 1957; Pella and Tomlinson, 1969; Fox, 1970; Beverton and Holt, 1957). Surplus yield models, for example, confound the effects of recruitment, growth and natural mortality. The parameters governing production models are generally estimated by relating catch per unit of effort and effort. For redfish stocks, the estimation of production through classical productivity models leads, too often, to suspicious results: for example, positive slopes are not uncommon when regressing catch per unit of effort against effort. Smoothing procedures, which are often necessary for approximating equilibrium conditions, are used for convenience only and do not lead to a clearer understanding of the factors controlling surplus production.

The purpose of this paper is to provide insight into processes governing biological production in redfish stocks. We develop hereafter a method for back-calculating production from cohort analysis. This method, which requires detailed information on the age-composition of the catch, as well as information on mean weight at age, is used to assess trends in surplus production for the redfish stocks off West Greenland and on the Scotian Shelf.

Notation

In order to distinguish between time-intervals and a reference point in time, the following notation is used for specifying subscripts: Greek letters are used to identify time-intervals while Roman letters are used to identify any reference point in time. For example, i and t will refer to a given age and a given time, respectively, while ι and τ will refer to the interval between age i and age $i+1$, and between time t and time $t+1$, respectively. The quantities t_0 and t_1 identify the beginning of the first and last year considered, while b and m refer to the age of the youngest and the oldest age-group as of January 1. Finally, β identifies the first age-group considered and μ , the last; the symbol τ_0 refers to the first year, while τ_1 identifies the last year.

Production from a single cohort.

As in Ricker (1975), we will assume that the biomass of a cohort is governed through time (t) by the relationship

$$B(t) = B_0 e^{(G-F-M)t} \quad , \quad (1)$$

where B_0 is the initial biomass of the cohort, G is the mean instantaneous rate of growth, F is the instantaneous rate of fishing mortality and M is the instantaneous rate of natural mortality. The parameters G , F and M are assumed to be constant over the year. The average biomass of the cohort during the year can be found from

$$\bar{B} = \int_0^1 B_0 e^{(G-F-M)t} dt \quad , \quad (2)$$

$$= B_0 \left((e^{G-F-M} - 1) / G-F-M \right) \quad . \quad (3)$$

The instantaneous net production at a given time t , $P^*(t)$, can be found from the instantaneous rate of change of population biomass, $B(t)$. That is

$$P^*(t) = \frac{dB(t)}{dt} = B_0 (G-F-M) e^{(G-F-M)t} \quad . \quad (4)$$

Over a unit period, say a year, the net production (or the overall change in biomass) is given by

$$P^*_{\text{over the year}} = \int_0^1 \frac{dB(t)}{dt} dt = \int_0^1 B_0 (G-F-M) e^{(G-F-M)t} dt, \quad (5)$$

$$= (G-F-M) B_0 \left((e^{G-F-M} - 1) / G-F-M \right) \quad . \quad (6)$$

By combining equations (3) and (6), we can express the net production as

$$P^*_{\text{over the year}} = (G-F-M) \bar{B} \quad , \quad (7)$$

$$= G\bar{B} - F\bar{B} - M\bar{B} \quad . \quad (8)$$

Equation (8) represents an important result since it serves to identify three components for net production: the increase of biomass through somatic growth, the loss of biomass through fishing and the loss of biomass through natural death. Ricker (1975) indicates that \overline{FB} represents the weight of the catch (or yield); similarly, \overline{MB} represents the weight of fish that die from natural causes. Total production, i.e., the total amount of tissue-weight gained by the cohort through growth over the year, is given by \overline{GB} : that is

$$P_{\text{over one year}} = \overline{GB} \quad (9)$$

This definition can be shown to be equivalent to the definition employed by Eggers et al. (1978):

$$P_{\text{over one year}} = \int_0^1 N(t) \frac{dW(t)}{dt} dt \quad (10)$$

where $W(t)$ is a time-dependent function describing somatic growth and $N(t)$ represents the number of fish in the population at time t . In our case, we can assume that

$$N(t) = N_0 e^{-(F+M)t} \quad (11)$$

and that

$$W(t) = W_0 e^{Gt} \quad (12)$$

consequently, we find

$$\begin{aligned} P_{\text{over the year}} &= N_0 W_0 \int_0^1 e^{-(F+M)t} G e^{Gt} dt \\ &= B_0 G \left((e^{G-F-M} - 1) / G-F-M \right) \\ &= \overline{GB} \end{aligned}$$

Finally, the excess of growth over natural mortality, say P^{**} can be expressed as

$$P^{**} \text{ over the year} = (G-M) \bar{B} \quad (13)$$

The quantity P^{**} represents the weight of fish which has to be removed from the cohort in order to leave the stock at its current level (assuming constant recruitment). It thus represents the portion of total production which is available for exploitation if the number of recruits entering the fishery is constant.

The reader should note that the change in biomass over the year is equal to the net production, P^* over the year. In fact,

$$\begin{aligned} \Delta B \text{ over the year} &= B_1 - B_0 \\ &= B_0 e^{(G-F-M)t} - B_0 \\ &= B_0 (G-F-M) \frac{(e^{G-F-M} - 1)}{(G-F-M)} \\ &= (G-F-M) \bar{B} \end{aligned} \quad (14)$$

$$= P^* \text{ over the year} \quad (15)$$

Therefore, we can express total production over the year as (from equations (9) and (15))

$$P \text{ over the year} = \Delta B + F\bar{B} + M\bar{B} \quad (16)$$

where ΔB is the biomass change over the year, $F\bar{B}$ is the catch expressed in weight and $M\bar{B}$ is the loss of biomass through natural death.

Production from a stock over a period τ

From a stock management viewpoint, production can be described as being composed of two components: an exogenous component, recruitment, and an endogenous component, total amount of tissue weight gained by all cohorts through somatic growth. In other words, total production¹ from a given fish stock over a period τ can be expressed as

$$P'_{.,\tau} = B_{b,t} + P_{.,\tau} \quad , \quad (17)$$

where $B_{b,t}$ is the biomass of the youngest age-group entering the exploited population at the beginning of the period τ and $P_{.,\tau}$ is the total production over τ due to somatic growth. The quantity $B_{b,t}$ is thus a measure of the net contribution of pre-recruits to production over τ . The ratio $B_{b,t}/P'_{.,\tau}$ would also provide an indication of the relative contribution of recruitment to total production. The higher this ratio, the more dependent the fishery is upon new recruits. The rate of change of recruitment biomass can thus be used as an indicator of the stability of the fishery.

For a given year, a number of cohorts exist simultaneously in the exploited stock; each cohort contributes to total production through somatic growth. Thus, $P_{.,\tau}$ is really the summation of the increase of biomass due to growth over all age-groups:

$$P_{.,\tau} = \sum_i P_{i,\tau} \quad , \quad (18)$$

where $P_{i,\tau}$ is the total (gross) production for age-group i over the period τ . In practice, $P_{i,\tau}$ could be expected to respond to climatic variability, as well as to changes in the age-composition of the stock and to changes in stock level.

¹The term production is not taken here in the eco-physiological sense and does not refer to the total amount of energy needed for maintaining life, for somatic growth and for reproductive functions. Total production here refers to the annual increase of biomass due to somatic growth and to recruitment in the exploitable portion of a fish population.

For each age-group represented in the stock in a given year, the observed change in biomass over τ , say $\Delta B_{i,\tau}$ can be defined as the difference between the growth component of production and the biomass loss due to fishing and natural mortalities. From equation (16), we write

$$\Delta B_{i,\tau} = P_{i,\tau} - D_{i,\tau} - Y_{i,\tau} \quad , \quad (19)$$

where $Y_{i,\tau}$ refers to the loss of biomass for age group i over τ through fishing mortality, and where $D_{i,\tau}$ represents the loss of biomass for age group i over τ through natural mortality. The quantity $\Delta B_{i,\tau}$ can be either positive or negative, depending on the relative importance of the growth component with respect to the losses through fishing and natural deaths. If $\Delta B_{i,\tau}$, $D_{i,\tau}$ and $Y_{i,\tau}$ are known, the growth component of production over τ can be calculated for age group i by rearranging equation (19). That is,

$$P_{i,\tau} = \Delta B_{i,\tau} + D_{i,\tau} + Y_{i,\tau} \quad . \quad (20)$$

Consequently, total production over τ appears as

$$P'_{\cdot,\tau} = B_{b,t} + \sum_i \Delta B_{i,\tau} + \sum_i D_{i,\tau} + \sum_i Y_{i,\tau} \quad , \quad (21)$$

where the summations are taken over all age-groups. Annual net production can then be defined as the total production diminished by the losses of biomass due to fishing and natural death. That is

$$P'^*_{\cdot,\tau} = P'_{\cdot,\tau} - \sum_i D_{i,\tau} - \sum_i Y_{i,\tau} \quad , \quad (22)$$

$$= B_{b,t} + \sum_i \Delta B_{i,\tau} \quad . \quad (23)$$

From equation (23), annual net production appears as being composed of two components: an exogenous component, recruitment, and an endogenous component, the actual change in population biomass over τ . The manager has direct control on an annual basis over the endogenous component of net production through the management of the fishing effort. However, the exogenous component can only be weakly controlled through long-term management practices for 'optimum' recruitment.

Finally, the 'surplus production', i.e. the excess of recruitment and growth over natural deaths, is defined as

$$P'_{\cdot,\tau}^{**} = P'_{\cdot,\tau} - \sum_i D_{i,\tau} \quad (24)$$

The quantity $P'_{\cdot,\tau}^{**}$ represents the portion of total production which is available for exploitation if we want to keep the stock at its current level. In fact, we can rewrite equation (22) as

$$P'_{\cdot,\tau}^{**} = P'_{\cdot,\tau} - \sum_i Y_{i,\tau} \quad (25)$$

Equation (25) indicates that the sign of net production (and consequently the sign of the overall change in population biomass over τ) is governed by the quantity of fish removed.

Calculating Production from Cohort Analysis.

In order to evaluate quantitatively the total and the net production, we need for each period τ considered estimates of population biomass-at-age, as well as estimates of the losses due to fishing and to natural deaths.

Catch biomass yield. The loss of biomass due to fishing, $Y_{i,\tau}$, can be estimated from historical data on catch numbers-at-age ($C_{i,\tau} : i=b, \dots, \mu; \tau=\tau_0, \dots, \tau_1$) and from mean weight-at-age ($\bar{W}_{i+.5,t+.5} : i=b, \dots, m; t=t_0, \dots, t_1$). Weight data are taken as mid-year estimates, since they are assumed to be derived from research surveys which are carried on during the summer months. The catch biomass over τ can thus be approximated as

$$Y_{i,\tau} = \bar{W}_{i+.5,t+.5} C_{i,\tau} \quad (26)$$

Equation (26) assumes that the mid-year estimates of weight-at-age provide a good approximation of the average weight-at-age over τ , say $\bar{W}_{i,\tau}$.

Population numbers and instantaneous rates of fishing mortality. The loss of biomass through natural mortality and the biomass change over τ can be evaluated from estimates of population numbers-at-age and from estimates of the instantaneous rates of fishing mortality. These estimates can be obtained by the method of cohort analysis (Pope, 1972). As input data, Pope's method requires 1) historical information on catch-at-age, $C_{i,\tau}$, 2) and estimate of the instantaneous rate of natural mortality (M) and, 3) an estimate of instantaneous fishing mortalities for the last year of historical catch ($F_{i,\tau_1} : i=b, \dots, \mu$) and for the last age-group in each year ($F_{\mu,\tau} : \tau=\tau_0, \dots, \tau_1$). Then the population numbers at age are calculated for $i=b, \dots, m-1$ and $t=t_0, \dots, t_1-1$ from the recursive equation

$$N_{i,t} = C_{i,\tau} e^{M/2} + N_{i+1,t+1} e^M \quad (27)$$

For each age-group in the final year (i.e., for $i=b, \dots, m$ and $t=t_1$), the population numbers are calculated as

$$N_{i,t_1} = C_{i,\tau_1} Z_{i,\tau_1} / F_{i,\tau_1} (1 - e^{-Z_{i,\tau_1}}) \quad (28)$$

$$\text{where } Z_{i,\tau_1} = F_{i,\tau_1} + M \quad (29)$$

Similarly, for the oldest age-group in each year (i.e. for $i=m$ and $t=t_0, \dots, t_1$), the population numbers-at-age are calculated as

$$N_{m,t} = C_{\mu,\tau} Z_{\mu,\tau} / F_{\mu,\tau} (1 - e^{-Z_{\mu,\tau}}) \quad (30)$$

$$\text{where } Z_{\mu,\tau} = F_{\mu,\tau} + M \quad (31)$$

Age-specific rates of fishing mortality are then calculated for each year (i.e., for $i=b, \dots, \mu-1$ and $\tau=\tau_0, \dots, \tau_1-1$) as

$$F_{i,\tau} = \ln (N_{i,t} / N_{i+1,t+1}) - M \quad (32)$$

Note that estimates of the instantaneous rates of fishing mortality are provided as input data for each age-group in the final year and for the oldest age-group in each year.

Adjusting weight-at-age data to the beginning of the year.
Weight-at-age data have to be adjusted to approximate mean weight at the beginning of the year in order to calculate both population biomass and recruitment at the beginning of a period τ . For $i=b+1, \dots, m$ and $t=t_0+1, \dots, t_1$, the $\bar{W}_{i,t}$ are approximated by

$$\bar{W}_{i,t} = e^{(\ln \bar{W}_{i-.5,t-.5} + \ln \bar{W}_{i+.5,t+.5}) / 2} \quad (33)$$

For $t=t_0$ and for $i=b$, the $\bar{W}_{i,t}$ are approximated by the relationship

$$\bar{W}_{i,t} = e^{(2 \ln \bar{W}_{i+.5,t+.5} - \ln \bar{W}_{i+1,t+1})} \quad (34)$$

Finally, for $t=t_1+1$ and $i=m+1$, the weights are approximated by rearranging equation (34) as

$$\bar{W}_{i+1, t+1} = e^{(2 \ln \bar{W}_{i+.5, t+.5} - \ln \bar{W}_{i, t})} \quad (35)$$

Population biomass. Recruitment biomass can be calculated from recruitment numbers, as defined in equation (27), and from the mean weight of recruits, which can be calculated from equation (34). That is,

$$B_{b, t} = \bar{W}_{b, t} N_{b, t} \quad (36)$$

Similarly, the observed change in biomass between t and $t+1$ (or say over a period τ) is calculated from the relationship

$$\Delta B_{t, \tau} = B_{i+1, t+1} - B_{i, t} \quad (37)$$

$$= N_{i, t} (\bar{W}_{i+1, t+1} e^{-(F_{t, \tau} + M)} - \bar{W}_{i, t}) \quad (38)$$

where the $N_{i, t}$ are the population numbers at the beginning of the year as calculated from Pope's formula, $F_{t, \tau}$ are the instantaneous rates of fishing mortality as determined from equation (32) and $\bar{W}_{i, t}$ are the mean weights as calculated from equations (33), (34) or (35).

Loss of biomass through natural deaths. Finally, the loss of biomass through natural mortality can be evaluated as

$$D_{t, \tau} = \frac{M}{F_{t, \tau} + M} \bar{W}_{i+.5, t+.5} N_{i, t} (1 - e^{-(F_{t, \tau} + M)}) \quad (39)$$

where the $N_{i, t}$ are evaluated from equations (27), (28) or (30), and the $F_{t, \tau}$, from equation (32).

As we indicated above, estimates of recruitment biomass, estimates of the change of biomass over the time interval considered and estimates of the losses of biomass due to fishing and natural deaths are necessary in order to evaluate annual production. In this section, we derived these estimates from population numbers-at-age and from estimates of the instantaneous rates of fishing mortality: both quantities have been obtained from Pope's method of cohort analysis. In addition to catch-at-age historical data, the calculation of production requires information on mean weight-at-age. Mean weight-at-age can be calculated from the mean length-at-age and from the length-weight relationships established either from annual research surveys or by sampling commercial catches (Pienaar and Ricker, 1968).

The basic assumptions underlying the calculation of production specify 1) that catch is taken uniformly during the year, 2) that the mean weights at age are mid-year estimates, and 3) that the instantaneous rate of natural mortality is a known constant which can be applied to all years and all age-groups represented in the catch matrix. For each cohort, it is also necessary to assume a value for the rate of fishing mortality in one age-group; these values (one for each cohort) serve as a starting point for the reconstruction of the cohorts.

Redfish at West Greenland

The exploitation of redfish (Sebastes marinus) at West Greenland (ICNAF Subarea 1) began in the mid 1950's by vessels from Iceland and the Federal Republic of Germany which have been dominating the fishery up till now. From a nominal catch of a few hundred tons in 1952, the catch increased to a maximum of 60352 tons in 1962 (Jensen, 1979). From 1962 to 1970, the nominal catch decreased to a level of 3000 tons, which level was maintained through 1970-75. In 1977, the nominal catch increased to 31000 tons, mainly due to an increase of the FRG fishery. Jensen (1979) estimated the amount of discarded redfish of commercial size in the trawl fisheries for cod. The amount of discarded redfish varied from 0-53% of the total nominal catch since 1950. The discard problem is less acute after 1973 (less than 2% of nominal catch).

The age-composition of the catch from 1962-78 and the mean weight per age-group are given by Schumacher (1979). However, the standard age-length key used by Schumacher introduces a systematic error in age-composition. This systematic bias is probably due to the difficulties associated with the aging of redfish and to insufficient data. It is therefore assumed that pooling adjacent age-groups to form larger groups would minimize the systematic errors introduced by the age-length key. Since only age-groups 17 and 18, and 20 and 21 were affected by a systematic error, the values of these age-groups were pooled, respectively, and replaced by their average. In addition, the age-composition presented by Schumacher does not consider the discards from the cod fishery. The amount of discarded adult redfish in the cod fisheries varies from 1% to 44% of the annual nominal catch of redfish (Jensen, 1979). The catch-at-age composition has thus been adjusted so as to include this by-catch of redfish.

A value of M equal to 0.1 is used for the cohort analysis, this value being based on estimates found for redfish in literature (Sandeman, 1973). Several cohort analyses were produced with different starting F 's, by replacing the initial fishing mortality for the oldest age-groups by the

weighted average F found in the previous run. When consecutive runs produced almost identical weighted average F 's for the 1962-75 period, a linear regression of F against effort was calculated ($r = 0.93$) and was used to produce estimates of starting F 's from 1962-78. We expressed our results in relative terms (percent of annual production or percent of average biomass level) since these relative expressions are less 'sensitive' to the values of the starting F 's used.

Table 1 indicates that recruitment biomass, which is exogenous to the exploited stock, represents in a given year 34% to 76% of the total production (average: 56%). Recruitment biomass, in this case, refers to the total weight of redfish entering age-group 12. Therefore, the net contribution of a cohort entering the fishery at age 12 represents 34% to 76% of the annual production. These high values have serious implications on the use of catch per unit of effort for the estimation of redfish production in Subarea 1. They indicate that catch per unit of effort, which is often used as an index of stock level, bears only limited information on the annual production of this redfish stock. Moreover, ages 12-15 are only partially recruited to the fishery. When considering that these ages account for 28-66% of the growth component of production (Table 2), the catch per unit of effort appears as a poor indicator of annual production. It is also important to note that there are substantial changes in the distribution of the components of production over the period considered. While the annual production is mainly dependent on growth of 14+ in the early sixties, it becomes mostly dependent upon recruitment and growth of 12-14 age-groups in the late seventies (tables 1 and 2).

The production/biomass ratio varies from 15% to 40% for the 1962-1978 period (Table 3). The trends of this ratio are directly linked to recruitment trends since the growth/biomass ratio is constant for the whole period. In addition, Table 3 indicates that the 'surplus production'/biomass ratio is approximately equal to the recruitment/biomass ratio. In other words, surplus production for this stock within each year is approximately equal to recruitment biomass. If we let $P'_{t,t}^{**} = B_{b,t}$ in equation (24), we see that the biomass gain through somatic growth of age-groups 12-30 is approximately equal to the biomass loss through natural mortality. Consequently, the harvesting strategy for maintaining constant stock size consists in taking a yield equivalent to recruitment biomass. The estimation of 'surplus production' is therefore translated into a 'recruitment-estimation problem'.

Surplus production and the nominal catch varied considerably during the 1962-1978 period (Figure 1). In the early sixties, the annual yield exceeded considerably surplus production for a gradual decrease of the stock biomass. From 1962 to 1968, surplus production was mainly kept constant through constant recruitment which is estimated at 12000 mt, on the average, for that period. From 1968 through 1976, annual surplus production exceeded annual removals. In fact, the 1974-1976 increase of recruitment may be seen as a direct result of the gradual decrease of fishing effort in the mid-sixties, i.e. a 10-12 years lag as expected. The relative increase of the endogenous component of production in the late seventies is thus an indication of stock biomass increase for the youngest age-groups (12-15). The conclusion of a stock size increase is supported by improved catch rates in the directed fishery for that period. Catch rates are not expected to improve as quickly as shown in the

'surplus production' versus 'time' plot because of the time lag necessary for newly recruited fish to be fully recruited to the fishery (probably around age 17-19). Even though surplus production in the late seventies is much higher than in the early sixties, the 15+ population biomass is still, in 1978, only 80% of its 1962 biomass level. The reader will note that for the 1970-78 period, the relative biomass levels are very sensitive to our starting F-values. Nevertheless, an increase of the starting F's for 1978 would provide a lower rate of recovery for the 15+ biomass. This supports our conclusion that catch rates are not expected to improve as quickly as shown in the surplus production time trends. In summary, redfish at West Greenland is experiencing a new situation since the early seventies. The fishery is increasingly dependent on the biomass and growth of newly recruited fish and the annual surplus production is increasing.

Because of the rapid growth of young fish, the age-composition of the stock can be expected to play a certain role in the determination of surplus production per unit biomass. But from Table 3, surplus production per unit biomass is also seen to respond to the variations in recruitment biomass. For redfish in Subarea 1, annual recruitment biomass is seen to explain more than 82% of the variance of surplus production per unit biomass. But the mean age of individuals in the stock, say \bar{X}_t , explains more than 71% of the remaining variance. Consequently, the regression

$$P'_{.,\tau} / \bar{B}_{.,\tau} = 0.747 - 0.041 \bar{X}_t + 1.326 \times 10^{-6} B_{b,t} \quad (40)$$

explains more than 94% of the overall variance ($r = 0.97$). Equation (40) can be translated into a transient model for annual surplus production. That is,

$$P'_{.,\tau} = 0.747 \bar{B}_{.,\tau} - 0.041 \bar{X}_t \bar{B}_{.,\tau} + 1.326 \times 10^{-6} B_{b,t} \bar{B}_{.,\tau} , \quad (41)$$

where surplus production is expressed as a function of the average biomass over τ , of the mean age of individuals in the stock and of annual recruitment biomass. For a given average biomass level, annual surplus production can be augmented either by an increased recruitment biomass or by decreasing the mean age of the stock. Most of the annual variability of surplus production can thus be explained without the need for the explicit formulation of a density-dependent term. In equation (41), density-dependence can however operate through the recruitment term. Since \bar{X}_t and $B_{b,t}$ are correlated ($r = 0.71$), it has not been possible to infer the relative importance of recruitment and mean age of the stock for controlling surplus production.

Redfish on the Scotian Shelf.

The historical catch of redfish on the Scotian shelf (ICNAF Division 4VWX) shows two periods of high exploitation in the fishery since the early forties (Mayer and Miller, 1976). While the nominal catch before 1944 remained around 2,000-4,000 mt, it reached a peak value of 68,000 mt, on the average, for the 1948-1951 period and decreased sharply thereafter to reach a value of 10,000 mt in 1955. Between 1956 and 1970, the nominal catch varied between 17,000-40,000 mt. In 1971 and 1972, the nominal catch of redfish on the Scotian Shelf peaked again to reach 62,000 mt and 50,000 mt, respectively. It then declined sharply to 18,000 mt, in 1976. The 1977 and 1978 nominal catch reached 16,363 mt and 15,494 mt, respectively.

Biological sampling of commercial catch was carried out from 1965 through 1978 and served to estimate catch composition during that period. Only one age-length key, derived from the 1975 Canadian research data, is available from which to estimate the catch-at-age composition during this period (Mohn, 1978). Clay (1979) raises some questions regarding the accuracy of the length-frequencies derived from the commercial catch sampling. In fact, since the gear mesh-sizes used by vessels landing redfish are not recorded, it becomes very difficult to assess, with certainty, the length-frequencies. Mohn (1978) calculates the length frequency-distribution by assuming that the port samples are from the directed catches. Clay (1979) suggests that port samples could come from the incidental catches. Since the two fleets use different mesh sizes (90mm and 120mm, respectively) and since the selection ogives for these gear are quite different, the length-frequency distribution calculated from port sampling may be irrelevant to the overall catch composition. Keeping these potential sources of error in mind, our analysis will be based on Clay's adjusted catch-composition. Finally, the calculation of production over the 1965-78 period is based on the 1975 mean weight-at-age, which is also derived from the Canadian research data. From Clay's relative catch-composition and from these mean weight-at-age, the catch-composition has been reconstructed so as to recover the historical landings.

Cohort analyses were used in an iterative manner until the relationship between F weighted by population numbers and effort became nearly linear ($r = 0.97$). As for redfish in ICNAF Subarea 1, we assumed a constant instantaneous rate for natural mortality ($M = 0.1$).

For redfish on the Scotian Shelf, recruitment biomass to age 3 represents between 2% to 14% of annual production (Table 1). However, recruitment and growth of age-groups 3-12 contribute between 40% to 82% of annual production which values agree with those observed for redfish at West Greenland (34-76%). For redfish on the Scotian Shelf, age-groups 3-12 constitute a sizeable portion of the catch; catch per unit of effort could thus have some bearing on information on annual surplus production. While representing 11-15% of annual production in the late sixties, recruitment biomass is seen to reach a minimum of 2-3% in 1974-75; this minimum represents a three-year lag after the peak removals of 62,000 mt and 50,000 mt in 1971-72. Population structure also has a significant effect on the distribution of production due to somatic growth over ages. While the age-composition of the sixties permitted ages 3-10 to be the major contributors to annual production, growth for these age-groups represents less than 30% of annual production in the late seventies.

The production/biomass ratio varies between 10% to 18% during the 1965-78 period (Table 3). Unlike redfish at West Greenland, the production/biomass trends for this stock follow a similar pattern to the growth/biomass ratio. This is to be expected since growth of 3+ represents 88-98% of annual

production (Table 1). The variations in annual production are therefore linked to population biomass changes and to changes in the mean age of the stock. It is also important to note that the surplus production/biomass ratio is, in this case, approximately equal to the growth/biomass ratio, minus 10%, where 10% represents the assumed death/biomass ratio (from an assumed instantaneous rate of natural mortality equal to 0.1). Consequently, surplus production should correlate well with population biomass and good correlations with annual mean catch per unit of effort could be expected.

The temporal trends of surplus production and fishing loss from 1965 through 1978 are summarized in Figure 2. From 1965 to 1970, surplus production exceeded fishing loss for a slow biomass growth. However, removals through fishing appear to have exceeded surplus production in the seventies. This pattern is also present when we analyse the unadjusted catch data of Mohn (1978). The downward trend of surplus production in the seventies can be related to a gradual decrease in recruitment, as well as to an important increase in the mean age of the stock during that period (Table 1). The mean age of the stock in the late seventies is around 13; at this age, the gain of biomass through somatic growth (G) is approximately equal to the loss of biomass through natural mortality (M). Consequently, surplus production of the late seventies is relatively low in comparison with the 1965 - 1973 levels. The higher removal rate of the early seventies then led to a slow biomass decrease in the mid and late seventies (Table 5). This conclusion is supported by the catch rates of the Canadian side otter trawlers (150-499 tons). If we exclude the 1966 catch rate which appears unreasonably high, the 1972-78 catch rates decreased by 14% when compared with those of 1965-71. A similar comparison for population biomass suggests a 10% decrease between the first and second halves of the biomass time series. The 4% difference is within reasonable limits since catch rates are also a function of the age-composition of the stock, which changed considerably over the 1965-78 period.

The preceding analysis indicates that somatic growth is the main component of annual production for redfish on the Scotian Shelf. Consequently, surplus production per unit biomass is expected to be a function of the age composition of the stock. In fact, we find that mean age and surplus production are highly correlated ($r = -0.96$). The correlation is negative since production per unit biomass is expected to decrease as mean age increases. The linear regression of surplus production per unit biomass against mean age, which explains more than 92% of the overall variance, appears as

$$P'_{.,\tau} / \bar{B}_{.,\tau} = 0.293 - 0.015 \bar{X}_{\tau} \quad (r = 0.96) \quad (42)$$

From (42), we derive the following transient model for annual surplus production

$$P'_{.,\tau} = 0.293 \bar{B}_{.,\tau} - 0.015 \bar{X}_{\tau} \bar{B}_{.,\tau} \quad (43)$$

where surplus production is expressed as a function of the average biomass over τ and of the mean age of individuals in the stock. As in the preceding case, most of the variation of annual surplus production can be explained without reference to a density dependent mechanism. In fact, age composition of the stock appears as an important factor for controlling production. As the mean age of the stock increases, production per unit biomass decreases. Consequently, as fishing effort goes up and as the increased exploitation rate reduces the mean age of the stock, production per unit biomass is

expected to increase since older individuals require more food to produce a unit of new body weight (Brett, 1970). Older fish also require more food to maintain a unit of body weight because of annual synthesis of eggs and sperm. The effect of changes in age-composition has been stated by Ricker (1975) as one of the three mechanisms for controlling surplus production. For redfish on the Scotian Shelf, age-composition appears as the main control. Under current stock levels, density-dependent recruitment per unit biomass and density-dependent growth are assumed to have a minimum impact on surplus production.

Underlying assumptions and data requirements.

The preceding analysis is based on the back-calculation of surplus production from cohort analysis. Since these calculations refer to the transient state, the method does not require the assumption of 'an equilibrium state'. In fact, our results indicate that annual surplus production respond quickly to changes in the age composition of the stock and to changes in recruitment levels. The transient state may thus be the only reality for many stocks under exploitation. Perturbations are currently introduced through changes in fishing pressure, variations of natural mortality (predation, diseases, etc.), variations of recruitment and of growth due to climatic variability.

Since the back-calculation of surplus production is based upon catch-at-age data, the sampling schemes have to be representative of the commercial catch. Stratified sampling should be carried when different gear or different fleet components are involved. More than one age-length key and mean weight-at-age vector are necessary to estimate long term trends in somatic growth and recruitment. For many stocks, somatic growth is known to change over decades but our knowledge of growth through research surveys and commercial sampling is often incomplete. The assessment of growth parameters should be based upon sampling schemes which are relevant to the stock, and not only to a local sub-population.

The back-calculation of the components of production assumes a constant rate of natural mortality. For many stocks under exploitation, estimates of natural mortality are the most difficult to obtain. In most cases, cohort analyses are based on an arbitrary value for natural mortality, which value is assumed to be representative of the average instantaneous rate of natural mortality(s). In practice, the effect of temporal variability of M on the back-calculation of production could be assessed by assuming that M is a stochastic variable with known characteristics (mean variance and probability distribution).

Short-term and long-term projections.

For the provision of management advice, the back-calculation of production has to be accompanied by short-term and long-term projections. Short-term projections for the transient state could be obtained by forward-calculating production from catch projections (Rivard and Doubleday, 1979). This method allows the projection of the transition states following changes of fishing effort.

Long-term projections require the consideration of additional assumptions. In the past, MSY has been used as a reference point to establish long term management goals. For redfish on the Scotian Shelf, for example, maximum sustainable yields (MSY) of 43,500 and 32,300 mt have been estimated by using a Schaefer model with 8-year and 12-year effort average, respectively (Mayo and Miller, 1978). As a means to provide long-term projections, we calculate (Figure 3) the yield corresponding to an average recruitment level of 11,700 mt,

which value corresponds to the average recruitment biomass calculated for the 1965-78 period. If this average recruitment level could be maintained annually, surplus production could reach a maximum of 30,500 mt, which value would be achieved with a weighted-F of 0.14 (it is interesting to note that the nominal catch, when averaged between 1942-78, is 30,400 mt). The value of 30,500 mt represents the maximum equilibrium yield that could be obtained given the realization of an average recruitment of 11,700 mt. But this long term projection assumes that our knowledge of the growth parameter provides a good indication of the average growth for the coming years (decades). When long term projections are put in these terms, we clearly see that the definition of long term goals (MSY or others) requires the assumption of environmental homeostasis. While random deviations of average environmental conditions are allowed, they are not expected to be accompanied by climatic shifts or trends. If it is found desirable to maintain the stock around a certain average equilibrium level, it should be kept in mind that the management strategy will have to be adjusted in accordance with the random fluctuations of the equilibrium levels due to environmental variability.

Discussion.

The back-calculation of production from cohort analysis requires the availability of an extensive data-base for the fish stock considered. For redfish at West Greenland and on the Scotian Shelf, only one age-length key is available and information of mean weight at age is available for one year only. In both cases, sampling of commercial catch was either incomplete or totally absent in certain years. For redfish on the Scotian Shelf, the uncertainty as to the origin of the port samples creates some difficulties for the analysis; it should be noted however that similar results were obtained when the unadjusted catch composition was submitted to a similar analysis.

Heally, annual data on mean weight at age should be available in order to consider temporal growth variations. For redfish at West Greenland, the catch biomass reconstructed with a constant weight vector lies within 9-13% of the nominal catch and a systematic bias could not be detected (Schumacher, 1979). We thus assume that growth variation is minimal for this redfish stock and that the weight vector used is a good indicator of the average mean weight at age over the period.

The age-composition of the two redfish stocks which have been submitted to our analysis shows important changes over time. Obviously, these stocks do not exhibit a stable age-composition and the fishery has not been operating under 'equilibrium conditions'. Annual production can be expected to respond to climatic factors, as well as to changes in stock level and age-composition of the stock. In these redfish stocks, stock biomass level and mean age of the stock - the variations in which have been taken as an indicator for the variations in age-composition - were sufficient to explain most of the variability contained in surplus production, without the need for either an explicit density-dependent or climate-dependent term.

Up to 76% of redfish production at West Greenland is exogenous to the stock: any correlation found between catch rates and surplus production in that case would thus be fortuitous and any productivity model based upon such a relationship would produce spurious predictions. The alternative situation, i.e. when the endogenous component or growth represents a significant portion of annual production, does not ensure the realization of a well-defined linear relationship between catch rates and surplus production. Weak correlations could still be found because of the presence of temporal changes or trends in

the defined unit effort, or because of important shifts in the age composition of the stock.

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Year	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
<u>A. West Greenland</u>																	
-recruitment to age 12	34	36	39	46	59	57	61	58	58	59	56	55	59	61	64	71	76
-growth of 12+	66	64	61	54	41	43	49	42	42	41	44	45	41	39	36	29	24
<u>B. Scotian Shelf</u>																	
-recruitment to age 3	--	--	--	12	11	13	14	12	9	7	6	4	3	2	3	4	9
-growth of 3-11	--	--	--	70	70	67	64	65	67	64	61	58	54	48	42	36	31
-growth of 12+	--	--	--	18	19	20	22	23	24	29	33	38	43	50	55	60	60

TABLE 1. Recruitment biomass and growth, expressed in percent of total annual production, for redfish at West Greenland and on the Scotian Shelf.

Age	Years																
	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
12	5.0	5.4	6.0	8.2	14.3	12.8	15.1	13.5	13.4	13.9	12.2	12.1	13.8	15.2	17.4	23.8	30.0
13	6.7	6.1	6.5	6.9	8.7	15.0	12.6	14.2	12.7	12.2	12.6	10.9	10.6	12.1	13.1	14.3	18.0
14	7.9	7.9	6.9	7.0	7.0	9.0	14.7	11.9	13.4	11.5	11.0	11.3	9.6	9.3	10.4	10.5	10.7
15	11.6	8.9	8.5	6.8	6.6	6.9	8.4	13.7	11.1	12.1	10.4	9.8	9.8	8.3	7.8	8.1	7.7
16	8.9	13.2	9.1	8.0	6.1	6.2	6.2	7.7	12.7	9.9	10.8	9.2	8.5	8.4	6.8	5.8	5.8
17	8.7	9.4	14.4	8.5	7.1	5.4	5.4	5.5	7.0	11.4	8.9	9.6	8.0	7.2	6.9	5.1	4.1
18	8.7	8.9	9.3	14.7	7.6	6.3	4.3	4.7	4.9	6.2	10.2	7.9	8.4	6.7	5.8	5.2	3.6
19	8.3	8.5	8.3	8.3	14.1	6.5	5.1	3.6	4.1	4.3	5.5	9.1	6.8	7.0	5.3	4.3	3.7
20	8.0	7.8	7.7	7.2	7.0	13.2	5.0	4.1	2.9	3.4	3.7	4.9	7.9	5.7	5.6	3.9	2.9
21	7.1	7.3	7.0	6.8	6.1	5.7	11.8	4.1	3.3	2.2	2.9	3.2	4.2	6.6	4.5	4.2	2.7
22	6.8	5.7	6.0	5.7	5.2	4.5	4.0	10.3	3.0	2.5	1.7	2.4	2.7	3.3	5.3	3.3	2.9
23	5.0	4.9	3.9	4.7	3.9	3.6	2.8	2.7	8.7	1.9	1.9	1.4	2.0	2.1	2.5	4.1	2.3
24	3.3	2.7	3.1	2.6	2.3	2.2	2.0	1.5	1.3	7.1	1.3	1.5	1.1	1.6	1.5	1.8	2.9
25	1.9	1.4	1.3	2.0	1.2	0.8	1.2	1.0	0.6	0.5	5.9	0.9	1.2	0.9	1.2	1.1	1.3
26	1.1	0.8	0.9	0.9	0.9	0.5	0.3	0.6	0.5	0.3	0.2	5.1	0.7	1.0	0.7	0.6	0.8
27	0.6	0.5	0.5	0.8	0.7	0.3	0.3	0.1	0.3	0.3	0.2	0.1	4.5	0.6	0.9	0.4	0.3
28	0.3	0.2	0.4	0.4	0.4	0.5	0.2	0.2	0.1	0.3	0.2	0.1	0.0	3.9	0.5	0.2	0.2
29	0.2	0.0	0.1	0.5	0.3	0.2	0.5	0.1	0.1	0.1	0.3	0.1	0.0	0.0	3.8	0.1	0.0
30	0.2	0.2	0.0	0.1	0.5	0.3	0.2	0.5	0.1	0.1	0.1	0.3	0.1	0.0	0.0	3.1	0.0

Table 2. Distribution of the growth (endogenous) component of production over ages for redfish at West Greenland. Each entry is calculated as $(P_{i,t}/P_{.,t}) \times 100$.

Year	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
<u>A. West Greenland</u>																	
-recruitment																	
to age 12	5	5	6	8	14	13	15	13	13	14	12	12	14	15	18	24	30
-growth of																	
12+	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
-surplus																	
production	5	5	6	8	14	13	15	13	13	14	12	12	14	15	18	24	30
<u>B. Scotian Shelf</u>																	
-recruitment																	
to age 3	-	-	-	2	2	2	3	2	1	1	1	1	0	0	0	0	1
-growth of																	
3+	-	--	-	15	16	16	16	16	15	14	13	12	12	11	10	10	11
-surplus																	
production	-	-	-	7	8	8	8	8	7	5	4	3	2	1	0	0	2

TABLE 3. Recruitment biomass, growth and surplus production, expressed in percent of the average stock biomass over the year. Results have been rounded off to the nearest percent.

Year	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Average population biomass ¹ of 15 ⁺	100	77	60	49	40	34	31	35	37	42	48	54	62	67	71	74	77
Mean age in exploited population	17.1	16.9	16.9	16.7	16.3	15.8	15.4	15.3	15.3	15.3	15.4	15.6	15.6	15.5	15.3	14.8	14.2
Mean age of catch	19.7	18.9	18.6	18.2	20.3	19.2	19.2	21.3	21.2	22.0	21.2	17.5	17.9	18.3	17.6	17.4	17.6

¹ Expressed as % of the 1962 population biomass of 15⁺

Table 4. Some characteristics of the redfish stock at West Greenland, as calculated from cohort analysis.

Year	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Biomass of 3 ⁺	93	96	100	106	112	116	115	110	106	101	95	89	83	77
Catch rates	92	148	108	114	102	101	109	101	94	81	81	78	103	87

Table 5. Temporal trends of 3⁺ population biomass for redfish on Scotian Shelf and catch rates for Canadian side otter trawler. Both population biomass and catch rates are expressed as percent of their respective mean.

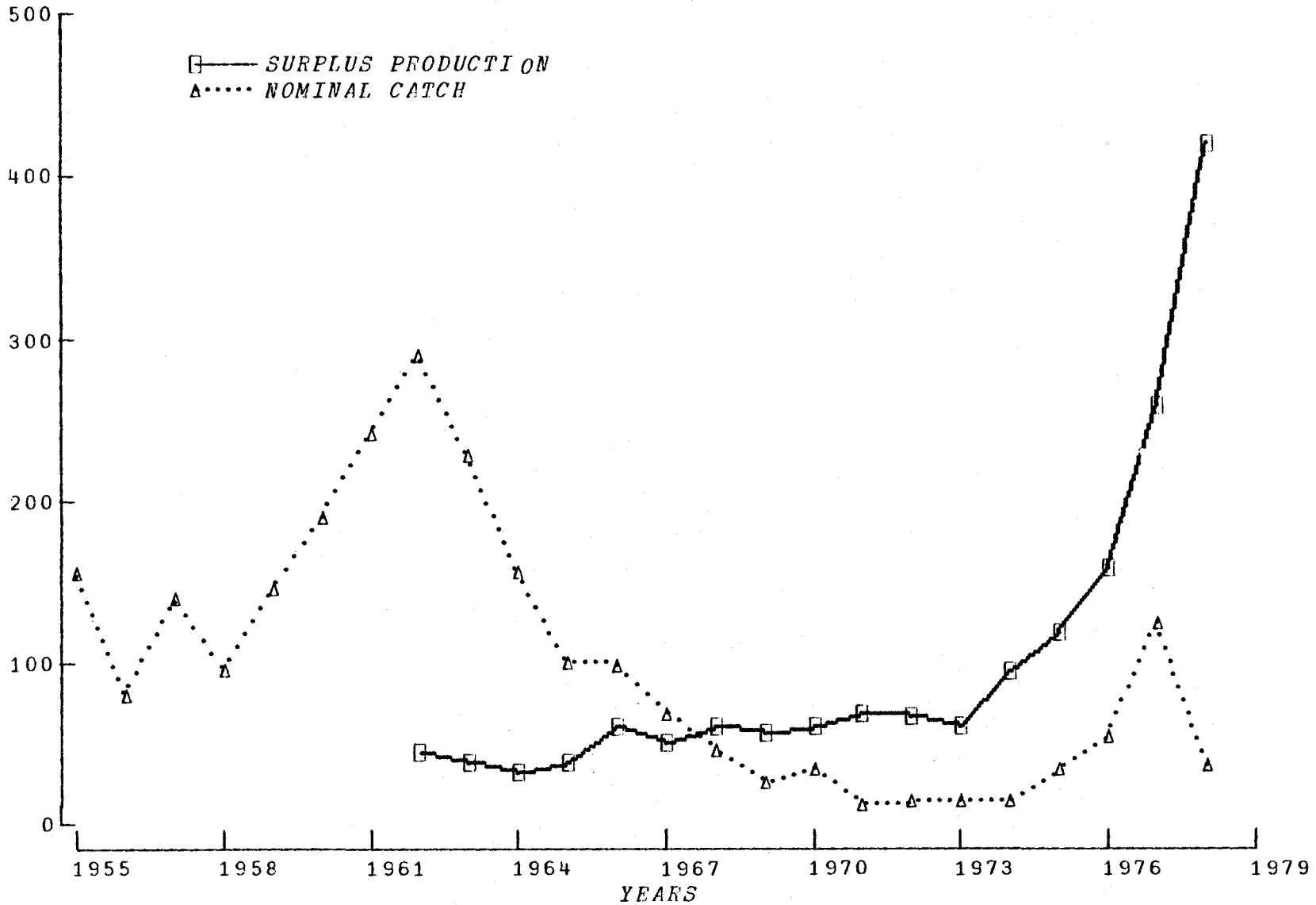


Figure 1. Temporal changes of surplus production and nominal catch (including estimated discards) for redfish at West Greenland. Surplus production has been back-calculated from cohort analysis for 1962 through 1978. Both time series are expressed in percent of their respective mean.

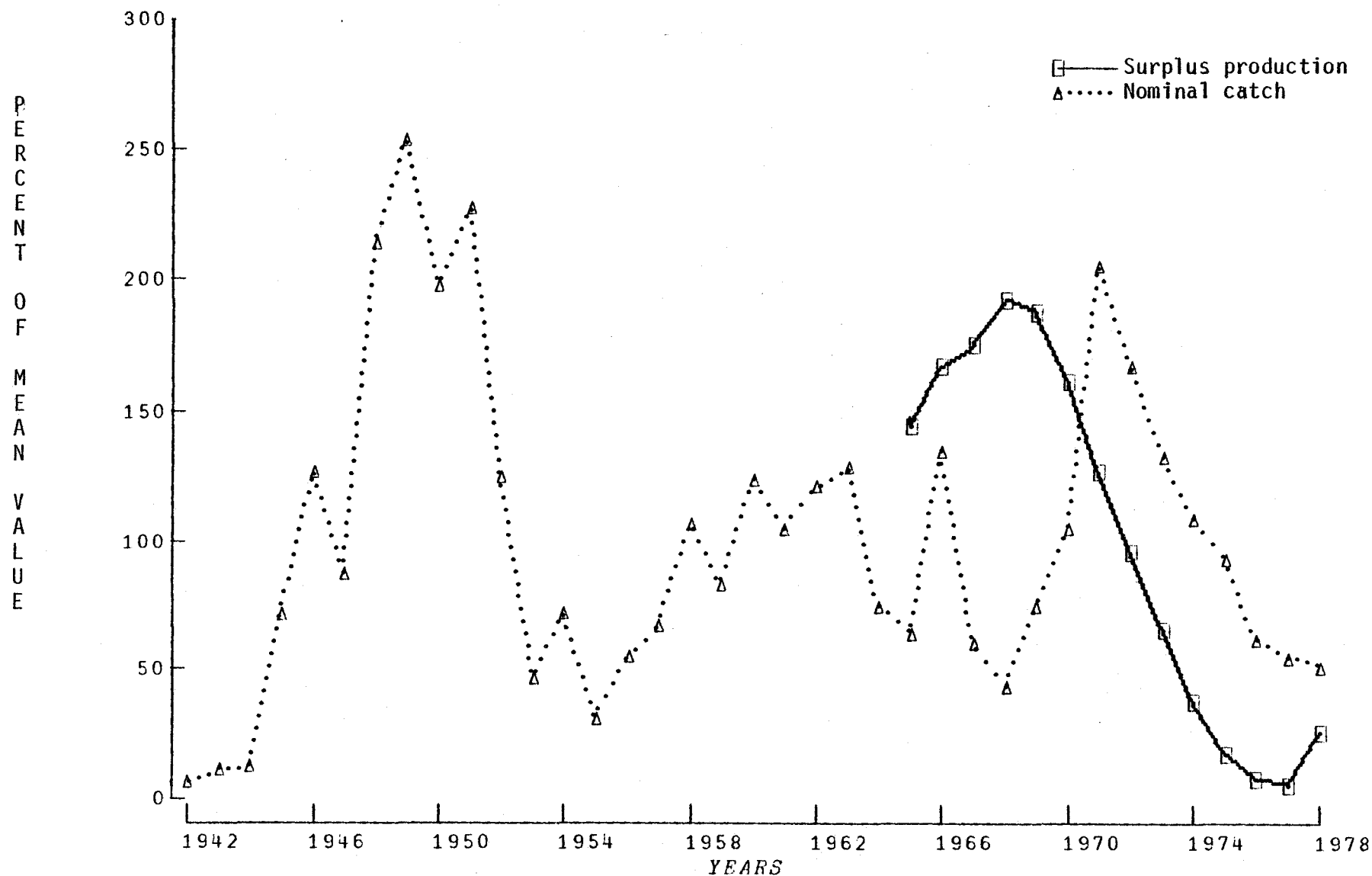


Figure 2. Temporal changes of surplus production and nominal catch for redfish on the Scotian Shelf. Surplus production has been back-calculated from cohort analysis for 1965 through 1978. Both time series have been expressed in percent of their respective mean.

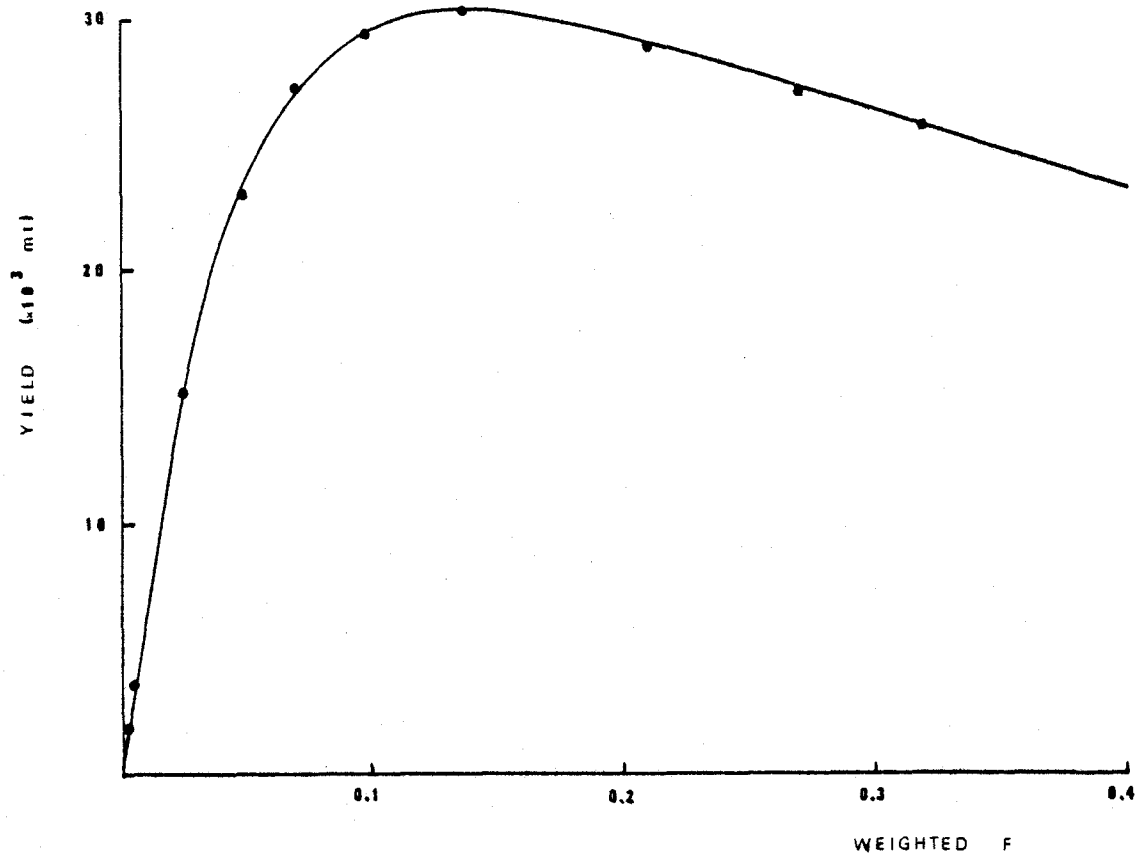


Figure 3. Equilibrium yield for an average recruitment level of 11,700 mt, which value corresponds to the average recruitment biomass calculated from cohort analysis for the 1965-78 period.