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Consideration of the Stable Age Distribution  
Assumption in 'Analytical' Yield Models

M. Sinclair, R. O'Boyle and T.D. Iles  
Marine Fish Division  
Department of Fisheries and Oceans  
Dartmouth, Nova Scotia  
B2Y 4A2

Abstract

The implications on the 'analytical' yield model of deviations from the stable age distribution are investigated for stocks of five species with a range of life history characteristics (cod, pollock, haddock, herring and mackerel). Recruitment variability for the stocks considered ranged from 21% for pollock to 104% for haddock. The growth rates at age for the five species were compared. The expected continuum in relative growth rates from cod to mackerel is clearly shown. With the population in a stable age distribution without fishing there is also a continuum from cod to mackerel in the manner in which age-specific production decreases through the life-span. It is thus to be expected that deviations from the stable age distributions for mackerel would have a much greater impact on population production than would a similar deviation for cod. Also species whose growth rates decrease more rapidly with age tend to have higher recruitment variability. To demonstrate the implications of deviations from the stable age distribution on the accuracy of model output, the MSY yields (that would have been generated given historical estimates of population numbers-at-age) are compared to estimates of annual population production. Cod and pollock production deviate relatively little from the 'analytical' model predictions. In contrast annual production for haddock, herring and mackerel deviate markedly from MSY yield as the age composition deviates in each direction from the stable age distribution. The analysis suggests that for some species the 'analytical' model may contribute to growth overfishing.

### Résumé

Nous avons examiné les implications des écarts que présente le modèle de rendement 'analytique' par rapport à une structure par âge stable dans des stocks de cinq espèces de poissons (morue, goberge, aiglefin, hareng et maquereau). La variabilité du recrutement dans les stocks étudiés est comprise entre 21 % pour la goberge et 104 % pour l'aiglefin. Les taux de croissance par âge des cinq espèces ont été comparés. Le continuum auquel on est en mesure de s'attendre dans les taux de croissance, de la morue au maquereau, apparaît clairement. Avec une population dont la structure par âge est stable en l'absence de pêche, il y a également continuum, de la morue au maquereau, dans la façon dont la production par âge diminue au cours de la vie. On devra donc s'attendre que les écarts par rapport à une structure d'âge stable chez le maquereau auront un impact beaucoup plus considérable sur la production de la population qu'un semblable écart chez la morue. En outre, les espèces dont la croissance diminue plus rapidement avec l'âge tendent à avoir un recrutement plus variable. Pour démontrer les implications des écarts par rapport à une structure par âge stable sur la précision des résultats du modèle, nous avons comparé les RMS (qui auraient été obtenus avec des estimations historiques des nombres par âge dans la population) avec les estimations de production annuelle de la population. Il y a relativement peu d'écart entre la production de morue et de goberge et celle prédite à l'aide du modèle 'analytique'. Par contraste, la production annuelle d'aiglefin, de hareng et de maquereau s'écarte notablement du RMS, étant donné que la structure par âge dévie dans chaque direction par rapport à une structure par âge stable. L'analyse laisse supposer que, dans le cas de certaines espèces, le modèle 'analytique' peut contribuer à une surexploitation de la croissance.

## Introduction

Essentially all models dealing with life history tactics assume that the members of the populations are in a stable age distribution (e.g. Fisher 1930, Cole 1954). Surprisingly the implications of relaxing this assumption have not been worked out (Stearns 1976). The exploited fish population 'analytical' yield model (Baranov 1918), and its derivations (Thompson and Bell 1934, and Beverton and Holt 1957), which allow estimation of sustainable yield as a function of fishing effort and gear selectivity-at-age, also assume a stable age distribution. Since the 'analytical' models are routinely used in fish stock assessments to provide management advice it is of some importance that the basic assumptions of the model are adequately met for natural populations. In addition, it is important that the biological limitations be evaluated since bioeconomic studies, both theoretical and applied, use such yield models as a starting point in the development of fisheries economic models (Clark 1976). It is the aim of this note then to critically evaluate the implications on the 'analytical' yield model of deviations from the stable age distribution.

## The Model and Its Application

The 'analytical' yield models consider the catch obtained from one year-class, or cohort, throughout its life. It follows that under steady state conditions (i.e. stable age distribution) the annual catch from the overall population under a given fishing strategy equals the catch that can be taken from a single cohort throughout its life under the same strategy. This has been called the "principle of equivalence". Thus annual yield at constant recruitment can be maximized by maximizing the following relationship for a single cohort,

$$Y = \int F.N_t.W_t,$$

in which  $Y$  is the annual yield,  $F$  is the instantaneous fishing mortality,  $N_t$  the abundance of the cohort at age  $t$  and  $W_t$  the fish weight at age  $t$ .

Beverton and Holt (1957) identified separately the age at recruitment to the population and the age of availability of the cohort to the fishing gear. In practical terms this allowed one to evaluate the effect of varying fishing gear selectivity, as well as fishing effort, on the sustainable yield. In the original formulation, as well as in most of the subsequent applications,  $N_t$  is a simple function involving constant recruitment, constant natural mortality at age and variable fishing mortality at age.  $W_t$  was described empirically (Thompson and Bell 1934) or by

using an appropriate growth equation (Beverton and Holt 1957). In the yield per recruit derivation (Beverton and Holt 1957); sustainable yield per recruit (again at constant recruitment and a stable age distribution) can be predicted as a function of various fishing strategies, involving

both the total fishing effort (i.e. fishing mortality,  $F$ ) and the manner in which it is distributed over ages. It is this latter derivation that is routinely used in fish stock assessments. The fishing mortality that predicts either maximum sustainable yield per recruit ( $F_{MSY}$ ), or an alternate sustainable yield for a different management strategy (such as  $F_{0.1}$  yield, Gulland 1968 and Gulland and Boerema 1973) for a given gear selectivity-at-age, is the model output of interest to management.

To generate biological advice on catch quotas for a fish stock on a yearly basis the fishing mortalities-at-age, which predict MSY yield or  $F_{0.1}$  yield, are applied against the present stock abundance-at-age estimates derived from cohort analysis (Pope 1972). The calculated removals-at-age times the weights-at-age provide an estimate of the catch quota in tonnes (the total allowable catch, or TAC) under the chosen management strategy (such as  $F_{0.1}$  yield or MSY). The key point here is that in the application of the 'analytical' model an optimal fishing mortality, defined under the assumption of a population producing with a stable age distribution, is applied against a population which may not be appropriately distributed. It is important to note that although the yield per recruit derivation of the 'analytical' model permitted its application under variable recruitment, it did not remove the constraint of the stable age distribution.

The other assumptions of the model are that the number of recruits, the coefficient of natural mortality and the rate of growth are all independent of population density. When the model is used to generate short-term advice (1-2 years), the latter assumption can be met by using the actual weights-at-age each year rather than theoretically derived weights. This approach is used in the following analysis. The other two assumptions, although major areas of concern, are not considered here.

#### Examples for Specific Fish Stocks

Two factors influence the degree of departure from the stable age distribution, recruitment variability coupled with the decrease in growth rate at age. Both factors vary considerably between species. The recruitment variability for several species fished off eastern Canadian waters which are managed using the 'analytical' model are shown in Table 1. The coefficients of variation range from 21% for pollock to 104% for haddock. The growth rates as well as the weights-at-age for five of these species are shown in Fig. 1. The weights-at-age were derived from either the Von Bertalanffy fitted growth curve or a linear regression of weight-at-age (pollock only). The mean weights-at-age used to fit the curves were calculated over the years indicated for the specific stocks in Table 1. The lowest  $R^2$  for the curve fitting was 98.8%, and the

Von Bertalanffy curve gave a better fit than a linear regression for each stock except pollock. The instantaneous growth rates ( $g$ ) (Ricker, 1975) were calculated from the predicted mean weights-at-age. The key point here is that certain species continue to grow relatively rapidly at older ages, particularly cod. At the other extreme mackerel growth rates decrease rapidly with age. The expected continuum in relative growth rates from cod to mackerel is clear.

With the population in the stable age distribution without fishing there is also a continuum from cod to mackerel in the manner in which age-specific production decreases through the life-span (Figure 2). Cross-age biomass ( $\bar{B}$ ) is the average of consecutive biomasses at age (weight-at-age times numbers-at-age in the stable age distribution). The stable age distributions were estimated assuming constant recruitment and natural mortality-at-age using the data sources indicated in Table 1. Production at various portions of the life-span was normalized by the value at the 50% point of the age span considered in order to facilitate between species comparisons of the life history growth strategies. It is evident that deviations from the stable age distributions for mackerel would have a much greater impact on population production than would a similar deviation for cod. Thus it is to be expected that the assumption of adherence to the stable age distribution for the analytical yield models can be expected to vary between species. Cod and pollock would be expected to be little influenced by deviations; haddock, herring and mackerel progressively more influenced. It is of interest that haddock grows like a herring over the age span considered.

It is unfortunate in terms of the model, but perhaps related in evolutionary terms, that the species whose growth rates decrease more rapidly with age also have a higher recruitment variability. Examples of the deviation of the age distribution for each species from the stable age distribution at  $F_{MSY}$  (generated using the mean weights-at-age and more recent gear selectivity-at-age distributions for the specific fisheries, sources in Table 1) are shown in Figure 3. In the lower half of the figure extreme deviations towards older ages in the population are shown, whereas examples of extreme deviations towards younger age classes are shown in the upper half. Haddock and herring show more dramatic departures from stable age distribution. The effects on population production are compounded when growth rates at age (Figure 2) are also considered.

To demonstrate the implications of these deviations from the stable age distribution on the accuracy of model output, the MSY yield that would have been generated given the estimated population numbers-at-age and the observed weights-at-age are compared to an estimate of annual population production (Figure 4). Population production is estimated by  $\sum (W_t - W_{t+1}) \cdot N_{t+1}$ , where  $W_t$  and  $W_{t+1}$  are the observed mean weights-at-age (from the fished population) and  $N_{t+1}$  is the cohort analysis estimate of numbers-at-age  $t+1$  (January 1). The MSY yields are averaged over consecutive years in order to provide an equal number of observations as derived for production. It is stressed that it is realized that the respective fish stocks were not managed by MSY or  $F_{0.1}$  yield over these time periods but that the historical fluctua-

tions in population structure provide a realistic empirical data base for which the importance of deviations from the stable age distribution can be explored.

It is the between species differences in the relative distributions of MSY yield and annual population production that are of interest. Cod and pollock production deviate relatively little from the 'analytical' model predictions as the age composition deviates in each direction from the stable age distribution. In contrast annual production for haddock, herring and mackerel deviate markedly from MSY yield. For example as the exceptional 1962 haddock year-class progresses through the life-span, the population production deviates progressively from MSY yield advice that would have been generated using the 'analytical' model. A similar distribution is observed for the herring example. As the age composition was skewed towards older ages in the early 70's and during 1976 and 1977 population production was much lower than is predicted using the 'analytical' model which assumes that the population biomass is distributed through the life-span in the stable age distribution. The situation is worse for mackerel. Even slight deviations from the stable age distribution markedly affect the accuracy of the model output. These results suggest that the 'analytical' model would consistently overestimate the production capacity of the stock. The biologically more conservative  $F_{0.1}$  yield, a frequently adopted management strategy, is also often higher than the short term production capacity of several of the populations.

The continuum (for the five species considered here) in the distribution of  $g\bar{B}$  through the life-span (Figure 2) is roughly paralleled by their degree of deviation from the MSY yield predictions (Figure 4). The between species recruitment variability modifies the continuum somewhat. Pollock with the lowest year-class strength variability does somewhat better than cod, whereas haddock with the highest variability fares worse than herring. An intermediate recruitment variability for mackerel, however, does not change its relative position.

The conclusion of this analysis is that the assumption of the stable age distribution in the 'analytical' yield model is a rigorous one, but that there is a range in sensitivity according to the growth strategy and recruitment variability of the fished species. It may be no accident that haddock, herring and mackerel are frequently examples of stocks that have been overfished under management regimes using the 'analytical' model to generate TAC's. Cushing (1975) has stated that the 'analytical' model has resolved the growth overfishing problem. This analysis suggests rather that for some species or stocks the 'analytical' model may contribute to growth overfishing.

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Table 1. Recruitment variability

	Years	C.V.%	Relative Confidence in VPA
Cod 4T <sup>1</sup>	1950-1977	40	Good
Haddock 4X <sup>2</sup>	1962-1978	104	Good
Herring 4WX <sup>3</sup>	1968-1979	86	Medium-Good
Mackerel 3-6 <sup>4</sup>	1968-1977	77	Poor
Pollock 4VWX-5 <sup>5</sup>	1973-1978	21	Poor

<sup>1</sup> Gray (1979) and Lett (1978)

<sup>2</sup> O'Boyle (1980)

<sup>3</sup> Sinclair and Iles (1980)

<sup>4</sup> Maguire (1980)

<sup>5</sup> Cleary (1980)



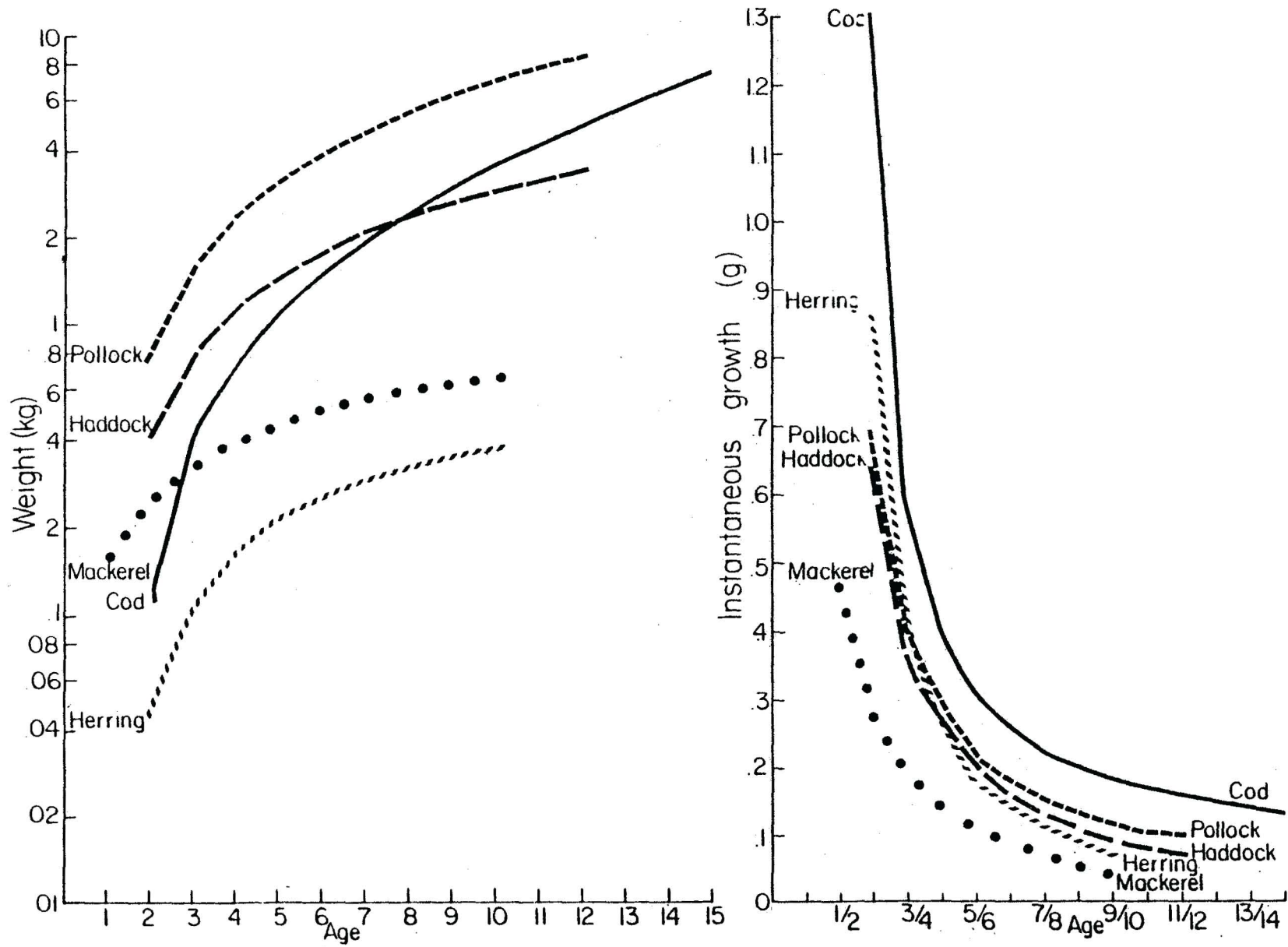


Fig. 1. Weights-at-age and growth rates-at-age for the five stocks considered.

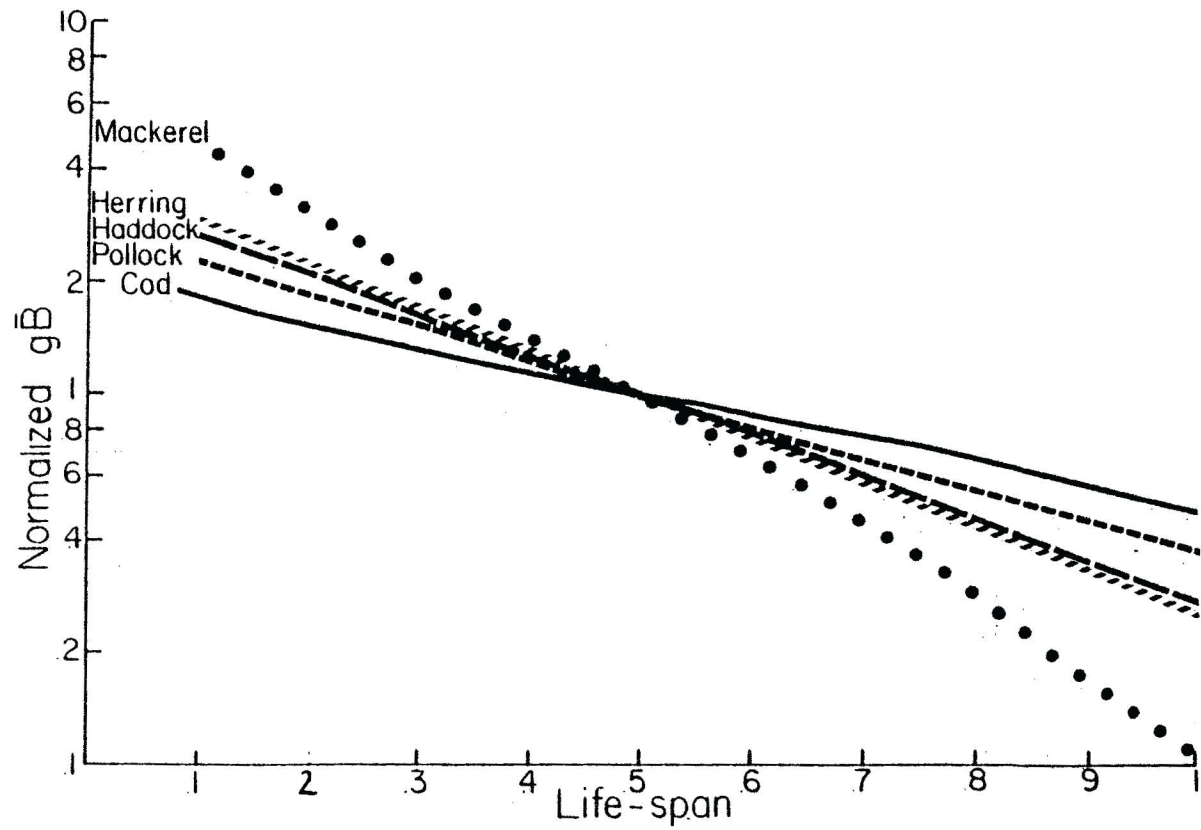


Fig. 2. Normalized production in relation to life span for the five stocks considered.

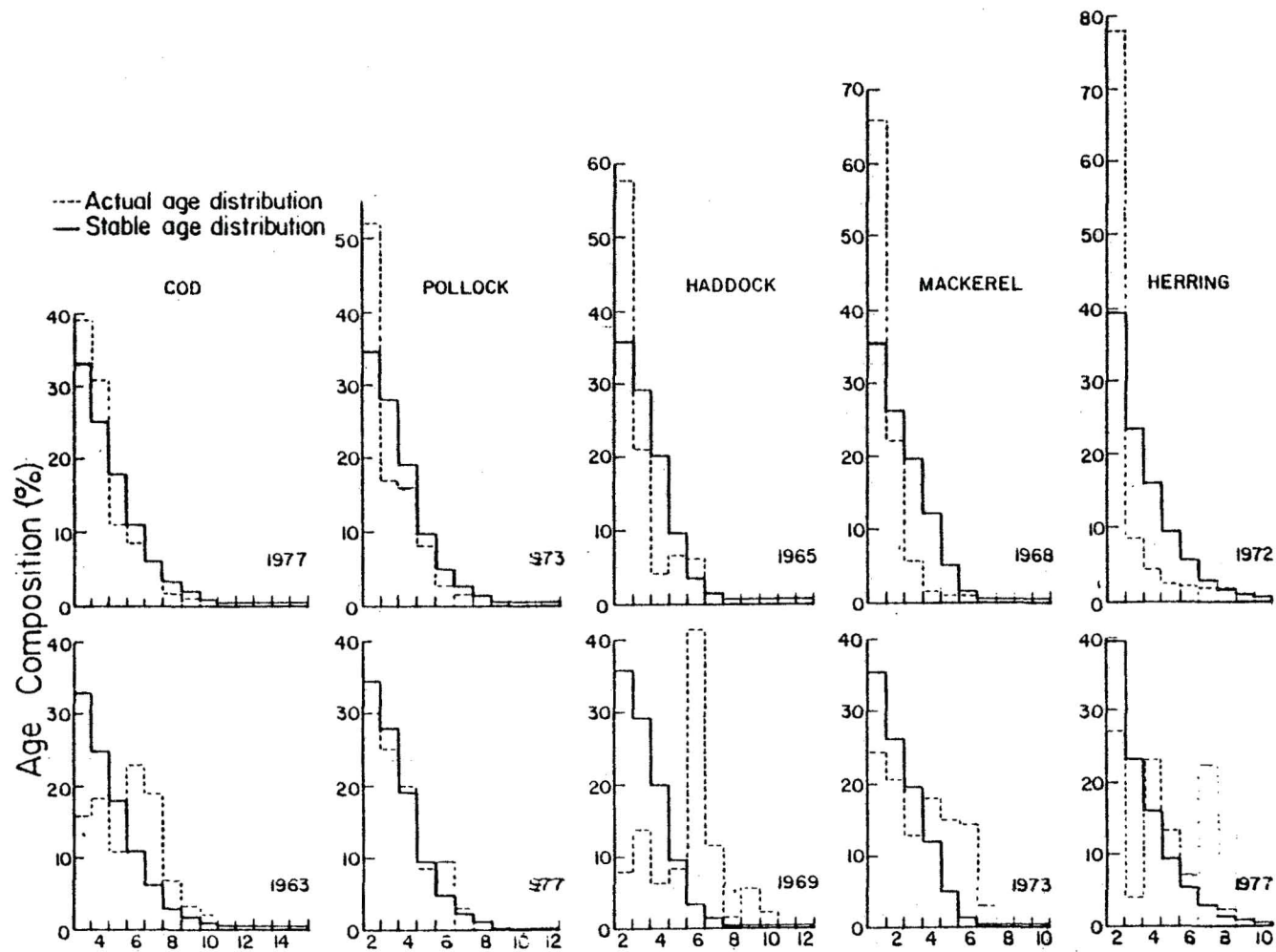


Fig. 3. Comparison of examples of actual population age distributions to the stable age distribution for the five stocks considered.

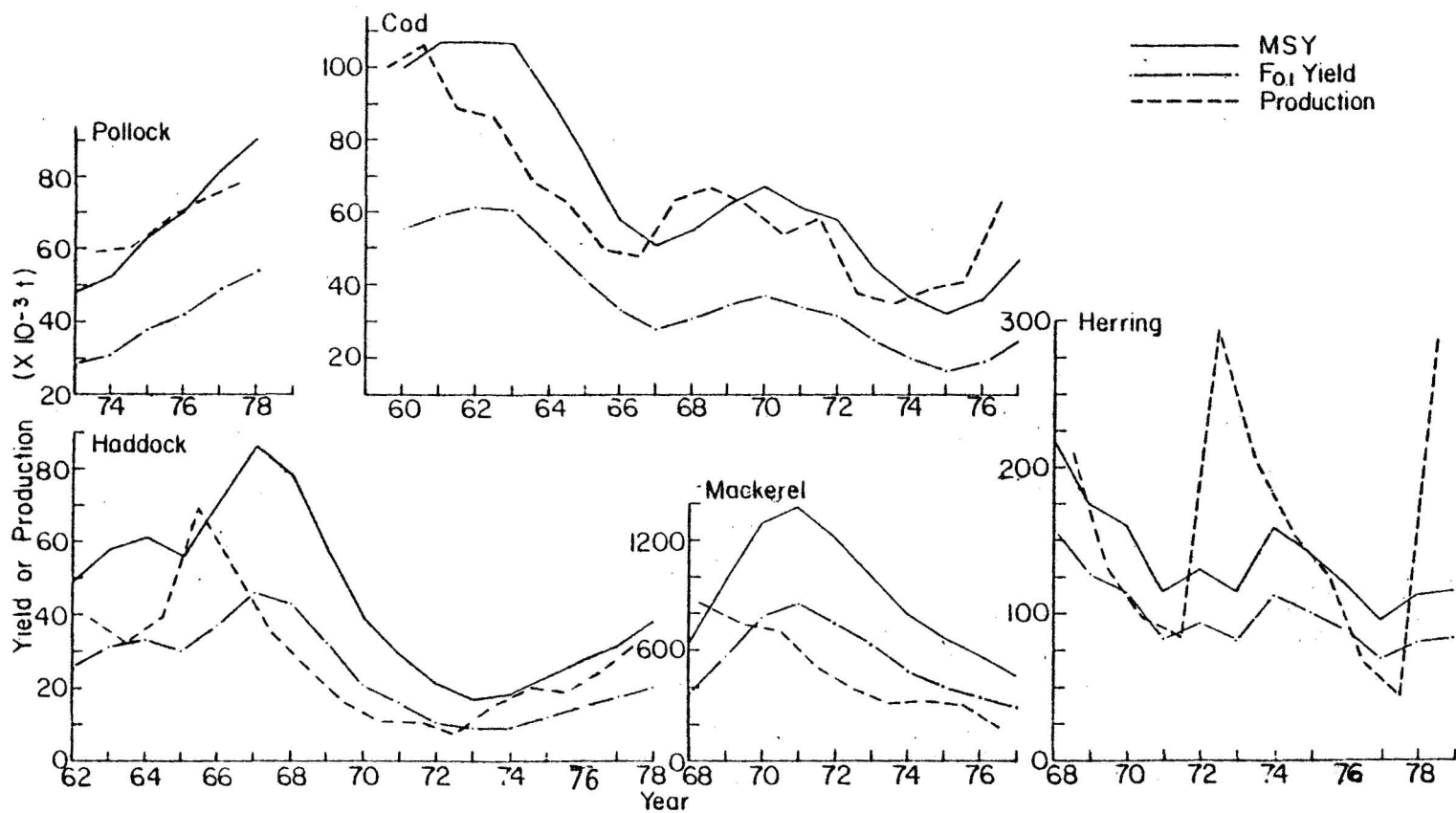


Fig. 4. Comparison of MSY and  $F_{0.1}$  yield estimates to annual production calculated using historical population-at-age estimates.