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MODELS OF GROWTH AND MATURITY FOR NORTH SEA COD

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Abstract

Although North Sea cod do not show the large changes in growth and maturity seen in other North Atlantic cod stocks, there are systematic changes which may affect routine assessments. Using weight at age data from annual ICES assessments and the International Bottom Trawl Survey (IBTS), a descriptive model which explains weight at age in terms of a conventional von Bertalanffy curve and a year class effect is developed. The fitted year class effects are correlated with stock biomass indicating a density dependent effect. IBTS maturity data are examined which show that the proportion of fish mature at age is a function both of weight and age. A life history model is constructed which can explain the qualitative changes in maturity in terms of an optimal age of maturity given expectations of growth and natural mortality. A descriptive model based on age and weight is used to reconstruct the historical series of maturity ogives where no direct observations are available. Using the derived maturities new spawning stock size estimates are calculated and compared with the conventional assessment. In general, taking into account the changes in growth and maturity for North Sea cod does not appear to substantially alter the estimates of sustainable exploitation rates for the stock.

Introduction

Growth and maturity are two fundamental biological characteristics used in stock assessment. They are essential for the calculation of basic quantities such as spawning stock biomass and equilibrium yield as well as biological reference points including F_{max} , $F_{0.1}$ and F_{med} . While growth and maturity tend to be characteristic for a species or stock, they nevertheless exhibit annual variation and in the case of some Atlantic cod (*Gadus morhua*) stocks this variation can be very large. For example in the case of Icelandic cod, between the years 1977-1997 the proportion mature at age six varied in the range 22%-85% while mean weight at the same age varied between 2900 - 4200 grammes (ICES 1997a). Clearly with such a large variation, the point estimates of the biological quantities used can have a profound effect on any stock assessment calculation and need to be taken into account (Helser and Brodziak, 1998).

It is likely that growth and maturity are related. Stearns and Crandall (1983) describe a life history model which can explain both age and size of maturity based on rate of growth and natural mortality. Given that growth will be affected by a variety of biotic and abiotic factors such as food availability and temperature, it is likely that maturity will also vary in response to these factors. Changes of this nature need to be adequately modelled in assessments if their effects are large.

Recently concern has been expressed about the state of the North sea cod stock (ICES 1996, Cook *et al* 1997) because in recent years the observed fishing mortality rate has exceeded F_{crash} , the fishing mortality rate calculated to be sufficient to cause the stock to collapse (Cook, 1998). The calculation of F_{crash} is dependent on estimates of growth and maturity which are usually assumed to be constant. If in fact these biological characteristics vary, then the estimate of F_{crash} will be affected. Thus there is a need to examine the sensitivity of F_{crash} to changes in growth and maturity.

The North Sea cod stock is assessed annually by International Council for the Exploration of the Sea (ICES) (*e.g.*, ICES 1997b). For all assessments a constant maturity ogive is used. In recent years an ICES co-ordinated survey, the International Bottom Trawl Survey (IBTS) has collected data on maturity for a number of common commercial species, including cod. These data provide an opportunity to examine the variability of maturity and investigate whether any

systematic changes are evident, and in particular, whether these are related to growth.

It is generally assumed that, although there are minor changes, the growth rate of the North Sea cod stock is relatively constant (Daan, 1978). Annual estimates of weight at age in the stock are routinely given in ICES assessment reports (eg ICES 1997b) and these do show some variability. This paper re-examines changes in weight at age to see if growth can be related to stock biomass and maturity and whether these changes are likely to be important in assessment calculations.

Models

(a) Weight at age

Weight at age, w , can commonly be modelled using a von Bertalanffy growth function. In the analysis performed here a generalized and re-parameterized version due to Schnute and Fournier (1980) is used *i.e.*:

$$w_i = w_1 + (w_A - w_1) \left(\frac{1 - k^{i-1}}{1 - k^{A-1}} \right)^c \quad i = 1, \dots, A$$

where I indexes age and k and c are parameters. In this formulation w_1 and w_A are model parameters corresponding to the weight at the youngest and oldest observed ages in the data. This function will predict constant weights at age whereas we seek a model which may explain variable weight at age. Jones (1983) noted that cohorts which are large when young tend to retain their higher than average weight throughout their lives. This might be modelled as a cohort specific effect, g . Thus the weight at age I in year j can be expressed as:

$$w_{i,j} = g_{j-i+A} \left[w_1 + (w_A - w_1) \left(\frac{1 - k^{i-1}}{1 - k^{A-1}} \right)^c \right] \quad i = 1, \dots, A; j = 1, \dots, Y$$

Given a set of observed weights at age, wN , the estimation of the model parameters can be achieved, assuming lognormal errors, by minimising the sum of squares:

$$\sum_{i=1}^M \sum_{j=1}^Y (\log(w'_{i,j}) - \log(w_{i,j}))^2$$

(b) Maturity at age

Typically, in the assessments of North Sea cod, maturity is assumed to be age dependent (ICES 1997b). The proportion of fish mature, p , increases with age and may be approximated by a logistic function of the type;

$$p_i = \left(\frac{e^{a_0 + a_1 i}}{1 + e^{a_0 + a_1 i}} \right)$$

where a_0 and a_1 are parameters. It is probably more realistic to assume that the time at which a fish matures is dependent both on age and size (Stearns and Crandall, 1983). Inspection of data on maturity for North Sea cod (see below) suggested that within an age class, the rate at which fish matured was size dependent. The dependence of maturity on size however, appears to be age specific. With a logit transformation of equation (4), a simple linear model which incorporates such affects may be written:

$$\log \left(\frac{p_{i,j}}{1 - p_{i,j}} \right) = a_0 + a_1 i + b_i w_{i,j} \quad i = 1, \dots, A; j = 1, \dots, Y$$

With appropriate data on the proportions of fish mature at age and weight at age, it is possible to estimate the parameters a and b by ordinary least squares, assuming normal errors.

(c) Life history model

In common with many other fish, cod grow throughout their lives. The larger an individual fish becomes, the less vulnerable it is to predation and it may carry a larger number of eggs. The rate of growth will depend on the relative investment of surplus energy into growth or reproduction. As more energy is invested in reproduction, growth rate will slow down. Early maturation will result in fish of a smaller size at age with concomitant smaller egg capacity and higher vulnerability to predation. However, early maturation means that there is a greater chance of spawning during the individual's life time. The optimum time of spawning is therefore a trade off between maximising size, to produce more eggs, against the risk of an early death while still immature. Models based on these ideas are well known (e.g., Emlen, 1973, Charlesworth, 1980, Stearns and Crandall, 1983, Ware, 1983, Myers and Doyle, 1983).

For exploratory purposes a model is developed here which examines maturation strategies which maximize the expected egg production over an individual life time. Using the formulation of Myers and Doyle (1983) surplus energy, $f(w_i)$, produced at age i is given by:

$$f(w_i) = \alpha w_i^\beta$$

If the proportion of energy which goes into reproduction is u_i , and v is the age of maturity then growth can be modelled as:

$$w_{i+1} = w_i + (1 - p_i u_i) f(w_i) \left| \begin{array}{l} p_i = 0; i < v \\ p_i = 1; i \geq v \end{array} \right.$$

Similarly the corresponding production of eggs will be proportional to $p_i u_i f(w_i)$ and will be a measure of fecundity at age. If the survival of fish to age i is n_i , then the total egg production of an individual will be proportional to:

$$\sum_{i=1}^{\infty} n_i p_i u_i f(w_i) \left| \begin{array}{l} p_i = 0; i < v \\ p_i = 1; i \geq v \end{array} \right.$$

In the absence of fishing, the survival rate will depend only on natural mortality, M and in particular;

$$n_i = \exp\left(-\sum_{j=1}^{i-1} M_j\right)$$

Estimates of natural mortality for cod in the North Sea are provided by ICES (1997b) and decline with age. On the assumption that natural mortality is primarily due to predation and is therefore likely to be size dependent, the change in natural mortality with size can be modelled as;

$$M_i = m_0 e^{-m_1 w_i} + m_2$$

The overall problem is now to find an age of maturity, v , which maximizes expression (8).

Data and Methods

Basic weight at age data are taken from ICES 1997b (Table 1). This report contains estimates of weight at age in the stock which are essentially estimates of mean weight in the catch based on market sampling. The mean weights of fish

at the youngest ages are therefore likely to suffer from positive bias. However, most of the analysis in this paper involves mature fish, *i.e.* age groups largely unaffected by such bias. The weight model was fitted to data for the years 1974-1995 and the year class effect estimated. This was then correlated with estimates of total stock biomass given in ICES (1997b).

Data on maturity are routinely collected as part of the ICES co-ordinated International Bottom Trawl Survey (IBTS) of the North Sea in the first quarter of the year. Estimates of the proportion of fish mature at age for both sexes combined (Table 2) were obtained from Poulding (1997). These estimates were obtained from data supplied by the ICES Secretariat from the IBTS database. Equation (5) was fitted to the maturity data in Table 2 with the weight data in Table 1 as an explanatory variable. This provided a relationship linking maturity to weight at age in the stock. Using this relationship estimates of maturity were made for the years in which no measurements of maturity were available. The predicted maturities for all years were then used to reconstruct estimates of the historical time series of spawning stock biomass. The revised SSB values were then used to calculate F_{crash} and F_{med} which were compared to the values based on conventional data. In the analysis, F_{crash} was calculated using the methodology described in Cook (1998).

In order to explore the behaviour of the life history model, parameter estimates of the surplus energy function were taken from Myers and Doyle (1983). Estimates of the parameters in equation (10) were obtained by an ordinary least squares regression of natural mortality at age (given in ICES 1997b) on mean weight at age. In the regression the value of m_2 was fixed at 0.2. The value of u_1 was arbitrarily taken as 0.7. The value was chosen because it gave the closest correspondence between predicted and observed mean weights at age when the age of maturity is four, close to the observed value. The parameter estimates are given in Table 3.

Given the parameter estimates in Table 3, equation (8) can be maximized with respect to v , the age of maturity. This will give a unique age of maturity of an individual fish or a group of identical fish. In order to simulate the population effects on the proportion of fish mature at any age, the nominal parameter values were randomized to simulate different growth strategies and different expectations of survival. This was done by assigning a variance to each parameter and drawing a random value from a normal distribution with the nominal value as the mean. Two hundred individual strategies were set up in this way and the optimal age of maturity determined. Subsamples of 20 were then taken from these to obtain mean weights at age and the corresponding proportion mature at age. Subsampling in this way is analogous the way sampling is done to obtain real estimates of maturity ogives.

Results

The year class effects and growth parameters estimated for the weight at age data are given in Table 4. Inspection of the year class effects shows that they change gradually from year to year suggesting they may be autocorrelated. However, the standard deviations of the parameter estimates is such as to suggest the year class effects do not differ significantly from each other. Thus one may not conclude that there is a unique size effect for each cohort. Figure 1 shows the year class effects plotted against total stock size. Here stock biomass is measured in the year the year class was age 1. There is a strong indication of a negative relationship with a significant linear correlation coefficient ($r=0.51$; $0.05 > p > 0.01$). This provides some evidence that growth may be density dependent.

Figure 2 shows the maturity data plotted against mean weight at age. The typical pattern of increasing maturity with age can be seen. In addition it appears from inspection that within an age group maturity increases with size. It does not appear that maturity can be explained by size or age alone. The results of fitting the maturity model to the data are given in Table 5 and Figure 2. With the exception of the two oldest ages, the slopes associated with both age and size are significant. The age specific effects of size appear to decrease with age. However, only some of these slopes are significantly different.

The results on the simulation experiment using the life history model are shown in Figure 3. The realization shown illustrates some of the features seen in the real data in Figure 2. It can be seen that the proportion of fish mature is both size and age dependent with a tendency for maturity to increase rapidly with size given age. The simulations do not provide strong evidence of decreasing size dependent slopes with age, however.

Figure 4 shows the spawning stock biomass recalculated using the predicted maturity ogive based on the fitted model and observed stock weights. For comparison the spawning biomasses using the conventional maturity ogive are shown. Although there are variations in weight leading to a variable ogive over time, the effect of the fitted ogive is mainly to re-scale the SSBs to higher value. This arises mainly because the ogive from the IBTS data generally shows higher proportions mature at younger ages than the conventional ogive and results in SSBs which are about 10 - 15% larger.

Table 6 shows the calculated values of F_{crash} and F_{med} based on the new analysis. These values show almost no change compared with the standard calculation.

Discussion

Weights at age for North Sea cod do not show a large amount of variability. The coefficient of variation ranges between 5% - 10% depending on age. In recent years there has been an increase in weight at age and this is seen as an increase in the year class effect for the more recent cohorts (Table 4). The increase is associated with a decline in the total stock and spawning stock biomasses. It is quite likely that this link is causal through competition resulting in density dependent growth.

There is good reason on the basis of recent maturity data to believe that the age of maturity is affected by growth rate. Furthermore, maturity appears to be related both to age and size. When the maturity model was fitted to the observed data the slopes associated with age and weight were significantly different from zero. There is some evidence that the rate of change of maturity with size is age dependent. At younger ages fish mature more rapidly with size than at older ages.

The observed changes in maturity with age and size are explicable in terms of a model which maximizes egg production over an individual life time. The optimum age of maturity in the model is a trade off between the need to delay maturity grow fast and produce more eggs against the need to mature early and spawn before dying young. While one might expect egg maximization to result from natural selection, it is not a sufficient condition for an evolutionarily stable strategy (ESS) (Maynard Smith, 1972). This requires the maximisation of the population intrinsic rate of increase. Evaluating such a strategy would require more information on the conversion of surplus energy into eggs and has not been attempted here.

Revised estimates of spawning stock biomass based on the new maturity data alter the scale of the SSB values without making any substantial change to the trajectory over time. In general the revised estimates are about 10% larger than those based on a constant maturity ogive. Since estimates of recruitment are unaffected by the analysis this means that the observed cod recruitment has been produced by larger SSBs than was previously thought. However, although such a change revises the estimate of the slope of the stock-recruitment function at the origin it makes little or no difference to biological reference points such as F_{crash} and F_{med} . This is because although the steepness of the slope changes, it is compensated for in the calculation of the F values by a decrease in the average age of first maturity. Overall, therefore, for North Sea cod, including the effect of density dependent growth and adopting more realistic maturity data do not make a significant difference to the calculation of certain critical reference points.

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Table 1. North Sea Cod Stock Weights (Kg).

Year	Age									
	1	2	3	4	5	6	7	8	9	10
1974	0.594	1.039	2.217	4.156	6.174	8.333	9.889	10.790	12.175	12.425
1975	0.619	0.899	2.348	4.226	6.404	8.691	10.107	10.910	12.339	12.976
1976	0.568	1.029	2.470	4.577	6.494	8.620	10.132	11.341	12.888	14.140
1977	0.542	0.948	2.160	4.607	6.713	8.828	10.071	11.052	11.824	13.134
1978	0.572	0.937	2.001	4.146	6.531	8.667	9.686	10.950	12.427	12.778
1979	0.550	0.936	2.411	4.423	6.580	8.475	10.637	11.253	13.057	14.148
1980	0.550	1.003	1.948	4.401	6.109	9.120	9.550	11.824	12.782	14.081
1981	0.723	0.837	2.189	4.615	7.045	8.884	9.934	11.457	13.338	14.897
1982	0.589	0.962	1.858	4.130	6.784	8.903	10.399	12.517	13.469	12.890
1983	0.632	0.919	1.835	3.880	6.491	8.423	9.848	11.878	12.797	12.562
1984	0.594	1.007	2.156	3.972	6.190	8.362	10.317	11.454	13.505	13.408
1985	0.589	0.932	2.135	4.161	6.310	8.404	10.372	12.077	13.033	13.209
1986	0.576	0.886	1.836	3.538	6.188	8.071	9.895	11.473	12.710	13.566
1987	0.626	0.963	1.931	3.614	5.983	8.241	9.888	11.510	12.149	15.542
1988	0.574	0.867	1.939	3.175	5.859	7.844	9.738	11.873	13.489	14.353
1989	0.669	1.057	1.819	3.549	5.250	7.818	9.498	11.062	12.774	14.066
1990	0.737	0.976	2.174	3.795	5.903	7.867	10.245	10.782	12.661	15.089
1991	0.668	1.078	2.040	3.987	6.071	7.986	9.530	11.010	13.574	13.250
1992	0.699	1.143	2.543	4.223	6.239	8.465	10.079	10.095	11.832	13.790
1993	0.696	1.063	2.472	4.545	6.523	8.065	9.632	10.394	12.320	13.393
1994	0.673	1.074	2.201	4.469	7.144	8.422	9.482	10.527	12.230	14.214
1995	0.718	1.021	2.204	4.289	7.215	8.966	10.278	11.757	13.234	11.986

Table 2. Cod maturity data from North Sea International Bottom Trawl Survey.

Year	Age					
	1	2	3	4	5	6
1980	0.01	0.10	0.08	0.56	1.00	0.88
1981	0.01	0.04	0.16	0.52	0.85	0.87
1982	0.00	0.03	0.17	0.64	0.93	1.00
1983	0.00	0.03	0.20	0.50	0.96	0.99
1983	0.00	0.06	0.25	0.42	0.81	0.98
1985	0.00	0.04	0.10	0.45	0.56	0.91
1986	0.00	0.09	0.18	0.35	0.63	0.90
1987	0.00	0.02	0.15	0.60	0.76	0.98
1988	0.00	0.05	0.27	0.53	0.90	0.95
1989	0.00	0.13	0.24	0.59	0.77	0.97
1990	0.01	0.19	0.54	0.73	0.93	0.99
1991	0.00	0.09	0.39	0.50	0.89	0.98
1992	0.00	0.21	0.52	0.85	0.85	1.00
1993	0.00	0.07	0.42	0.70	0.88	0.96
1994	0.00	0.14	0.43	0.77	0.98	1.00
1995	0.01	0.05	0.30	0.82	1.00	0.97

Table 3. Parameters used in life history model and CVs used to generate simulated population.

Parameter	Value	CV
m_0	7.86	0.10
m_1	3.60	0.10
m_2	0.20	0.10
w_1	0.70	0.30
α	40.00	0.01
β	0.51	0.01
U	0.70	0.00

Table 4. Parameters estimated when fitting the growth model to stock weight data.

Year	Year-class effect	s.d.
67	0.0785	0.0739
68	0.0774	0.0697
69	0.0758	0.0676
70	0.1097	0.0663
71	0.1213	0.0655
72	0.1323	0.0649
73	0.1635	0.0645
74	0.1253	0.0641
75	0.1412	0.0638
76	0.1164	0.0638
77	0.1332	0.0638
78	0.1336	0.0638
79	0.1150	0.0638
80	0.0740	0.0638
81	0.1189	0.0638
82	0.0922	0.0638
83	0.0888	0.0638
84	0.0525	0.0638
85	0.0224	0.0638
86	0.0440	0.0638
87	0.0656	0.0638
88	0.1081	0.0643
89	0.1395	0.0648
90	0.2481	0.0654
91	0.2435	0.0662
92	0.1921	0.0672
93	0.2038	0.0686
94	0.2009	0.0708
95	0.2640	0.0751
w1	0.5514	0.0870
wA	12.4250	0.0346
k	0.7517	0.7493
c	2.8465	0.0074

Table 5. Parameters estimated when fitting the maturity model.

Parameter	Value	s.d.
a0	-11.1806	2.6888
a1	2.2174	0.7482
b1	6.3252	2.9627
b2	4.1995	1.4265
b3	1.6579	0.4899
b4	0.6820	0.2732
b5	0.3203	0.2514
b6	0.1337	0.2667

Table 6. Estimates of two biological reference points, F_{crash} and F_{med} , using conventional and revised data.

	Conventional estimate	Revised estimate
F_{crash}	0.89	0.88
F_{med}	0.82	0.82

Figure 1. The log year class effects estimated after fitting the growth model to cod stock weight data plotted against total stock biomass in the year the cohort was age 1. The linear correlation coefficient, r , is 0.51 ($p < 0.05$).

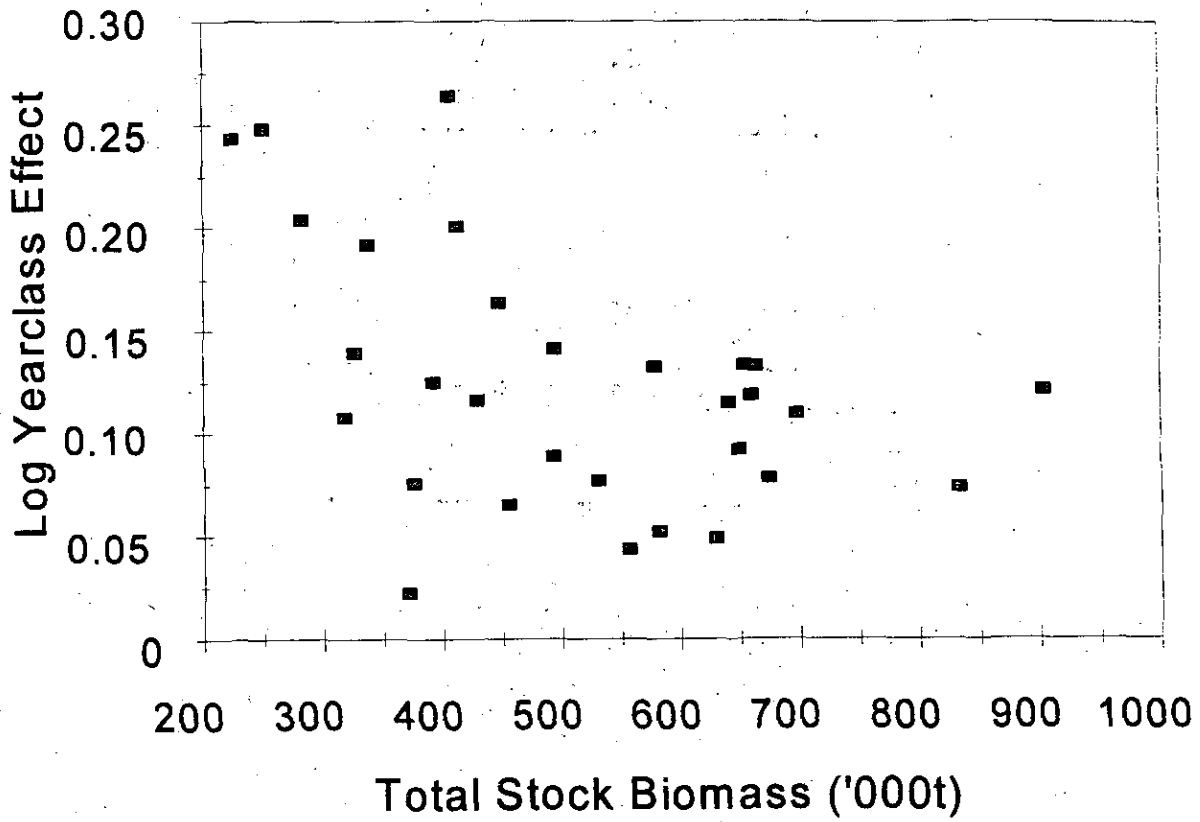


Figure 2. Proportion mature at age plotted against mean weight at age. The numeric labels indicate the ages. The lines show the fitted proportions mature, estimated from the model.

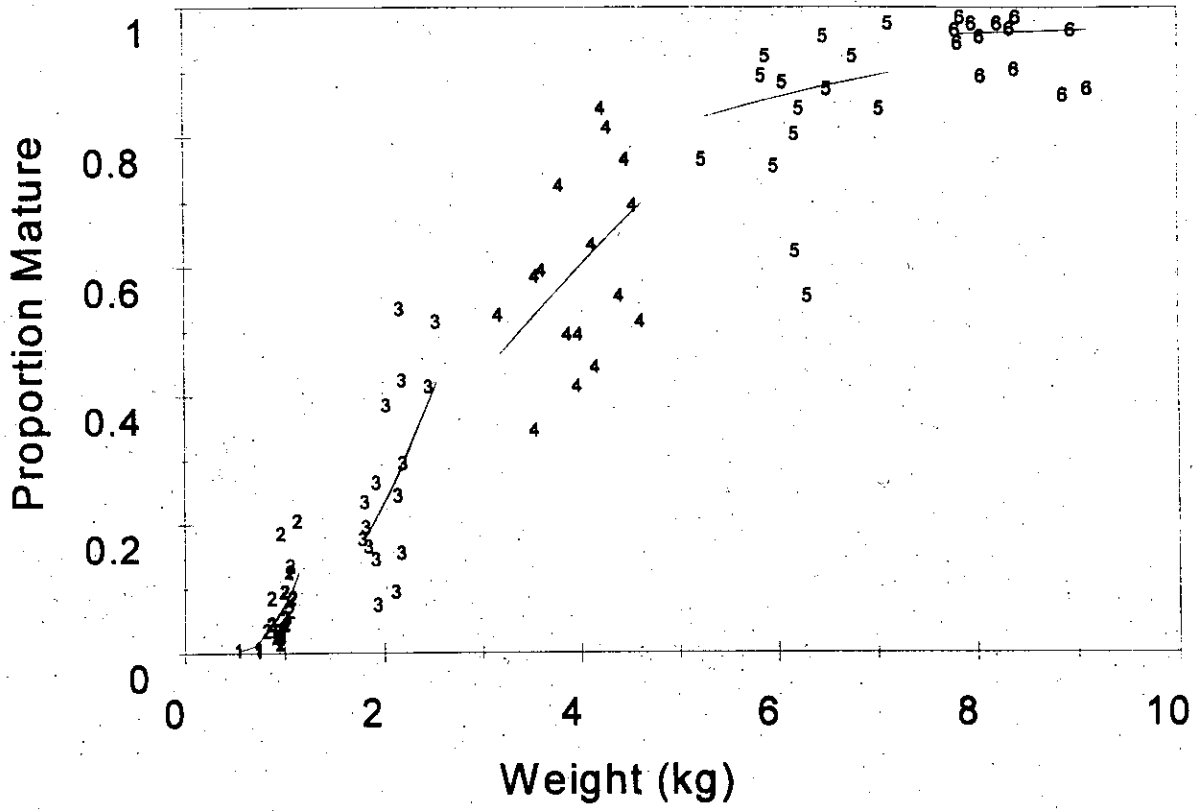


Figure 3. Results of a simulation experiment using the life history model predicting optimal age of maturity. The proportions of fish mature at age/weight are the results from a population with variable growth rates and expectations of natural mortality. Numeric labels indicate age.

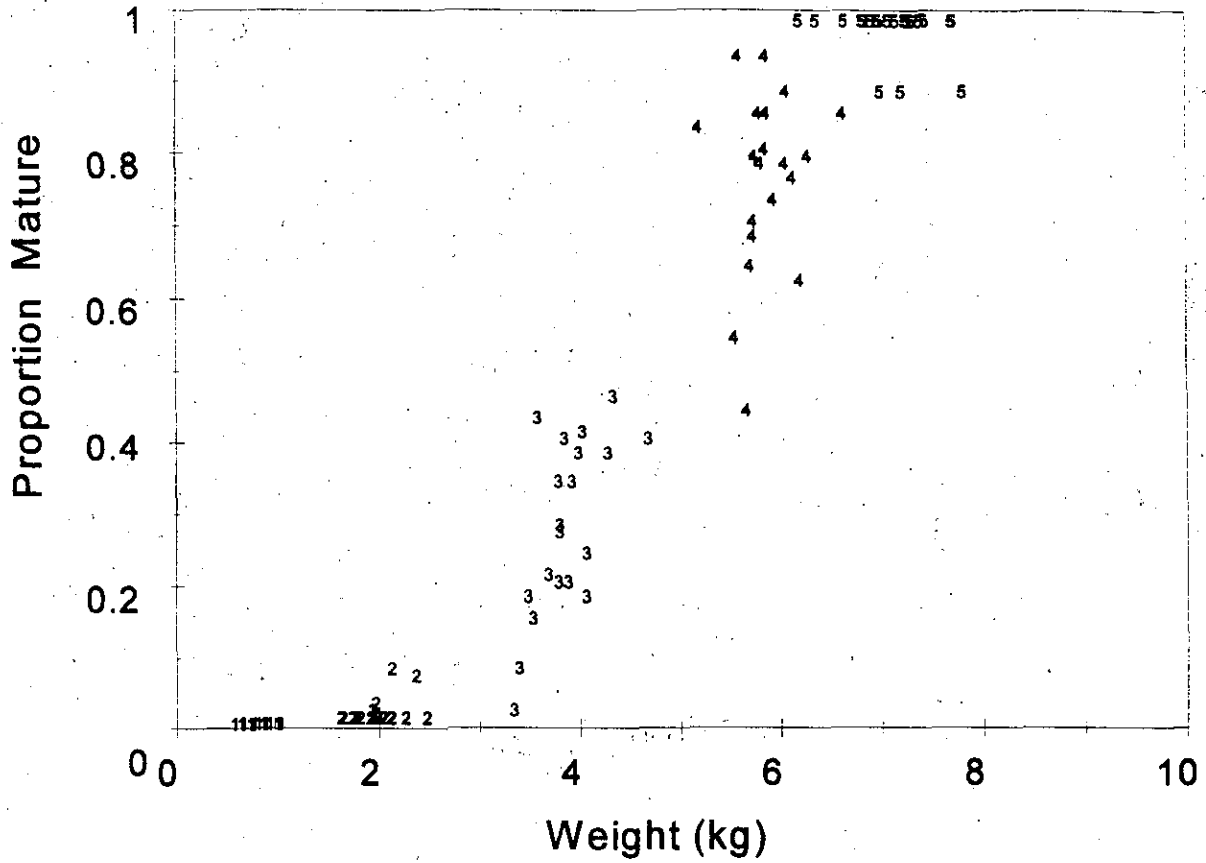


Figure 4. Spawning stock biomass estimated (a) using the maturity model to reconstruct historical ogives, and (b) using the conventional fixed maturity ogive in ICES (1997b).

