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## Estimating stock parameters from trawl cpue-at-age series using year-class curves

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### Abstract:

A year-class curve is a plot of log cpue (catch per unit effort) over age for a single year class of a species (in contrast to the better known catch curve, fitted to multiple year classes at one time). When linear, the intercept and slope estimate the log cpue at age 0 and the average rate of total mortality,  $Z$ , respectively. Here, we suggest methodological refinements within a linear least squares framework. Candidate models may include a selectivity term, fleet-specific parameters, and polynomials in *year* to allow for gradual variations of  $Z$ . An iterative weighting method allows for differing precisions among the different fleets, and a forward (one-step ahead) validation procedure tests predicted cpue against observed values. Choice of the best approximating model(s) is made by ranking the biological credibility of each candidate model, then by comparing graphic plots, precision of prediction, and the Akaike Information Criterion. Two example analyses are (i) a comparison of estimated and true results for five stock simulations carried out by the US National Research Council, and (ii) modelling three beam trawl surveys for plaice (*Pleuronectes platessa*) in the North Sea. Results were consistent with known, age-related, offshore migrations by plaice. Year-class curves are commended as a widely applicable, statistically based, visual, and robust method.

**Keywords:** analysis of relative residual variance, cpue, fish stock assessment, forward validation, iteratively weighted least squares, North Sea, plaice, year-class curve

## Introduction

A more or less linear decline in the logarithm of cpue indices over age is typically observed for many commercially important species of marine fish caught in trawls (Jensen, 1939; Silliman, 1943; Beverton and Holt, 1957, section 13), and has even been reported for the larval stages of Atlantic mackerel caught in plankton nets (Sette, 1943). We have also seen this for several species of European trawl-caught fish, at least for the older, fully selected ages. A noteworthy feature, also reported by Beverton and Holt (1957, p. 182), was that the slopes, which estimate a time-averaged value of  $Z$ , the coefficient of total mortality, showed little variation either across different year-classes or over a period of more than a decade (Cotter, 2001). It should be pointed out, since there is often confusion, that these 'year-class curves', as they are called here, are not the same as 'catch curves' (Ricker, 1975; Jensen, 1985). A year-class curve is fitted to the successive ages of one year-class but a catch curve is fitted to successive year-classes as observed at their respective ages in one catch, i.e. when no time-series is available. Year-class curves allow estimation of relative annual recruitments whereas catch curves only allow estimation of average recruitment.

Since  $Z$  is the sum of fishing and natural mortality ( $Z = F + M$ ), year-class curves, with  $Z$  described by a constant average value, stand in contrast to methods of fish stock assessment that estimate variations of  $F$ , and perhaps  $M$  as well, over  $A$  age classes and  $Y$  years. The models used for these methods replace the single parameter  $Z$  with up to  $(A + Y)$  or even  $(A * Y)$  parameters for  $F$ , and perhaps more again for  $M$  (Deriso *et al.*, 1985; Gavaris, 1988; Megrey, 1989; Shepherd and Nicholson, 1991; Shepherd, 1999; Grønnevik and Evensen, 2001). Cotter *et al.* (2004) argue that assessment models requiring estimation of large numbers of parameters can signal spurious changes in  $F$  or  $Z$  because of weaknesses in the data, the assumptions, or the model itself. It is concluded that, if there are major doubts about any of these aspects, a simpler modelling method is advisable, and that year-class curves have much to offer in that circumstance. Other uses for year-class curves could be as a visual screening method for cpue data preparatory to some more elaborate modelling method, or when only limited computing resources are available.

Year-class curves are easily estimated using ordinary least squares linear regression. The present paper proposes the following developments with the aim of improving estimation and prediction without loss of the computational and statistical benefits of the linear least squares method:

- use of an iterative weighting method for data sets from different sources (Cotter and Buckland, 2004);
- a set of nested, candidate models for the curves, and a general, albeit somewhat subjective, protocol for selecting the best;
- use of polynomials in *year* to permit  $Z$  to vary gradually over time with the minimum number of additional parameters;
- use of an analysis of relative residual variance (Cotter, 2001) to estimate the precision of different fleets, given the chosen model; and
- a forward (one step ahead) validation procedure for testing the predictive abilities of different models and for estimating prediction errors.

Two examples of using the year-class curve method are briefly presented. The first tests precision of estimation using simulated stocks (National Research Council, 1998) for which true results were available. The second uses cpue data for plaice (*Pleuronectes platessa*) from Dutch beam trawl surveys carried out by the Institute for Marine Resources and Ecosystem Studies (IMARES). It is intended to suggest how an analysis of year-class curves might be carried out, as well as to demonstrate one of the strengths of the year-class curve method, namely that alternative models can easily be tested and compared. Choosing the "best approximating model" is an important component of statistical modelling (Burnham and Anderson, 2002) but few, existing stock assessment methods allow much flexibility for that purpose. The analyses were carried out with a package written in the R programming language and referred to as YCC ('Year-class Curve'). It is freely available from the first

author, and is being built into the FLR software suite for fish stock assessments (<http://flr-project.org>).

## Theory

### Derivation of the year-class curve model

The following derivation aims to be pragmatic and simple, rather than conformable with the advancing mathematics of catch-age equations (Xiao, 2006). The usual model of mortality over time  $t$ , assuming no net migration to or from the stock, is

$$\frac{dN}{dt} = ZN$$

where  $Z$ , the instantaneous rate of total mortality, is here expected to have a negative value. [The absence of a minus sign before  $Z$  is unconventional in fisheries work but leads to Equation (2) having all terms positive, as is conventional for regression models.] Solving gives

$$N_t = N_0 \exp(Zt). \quad (1)$$

We now assume that catch per unit effort (cpue, denoted  $U$ ) is a constant proportion of  $N$ , i.e.  $U = qN$  for all ages included in the analysis, and that  $Z$  represents a constant, average value over time. Then, taking natural logarithms of Equation (1), restricting attention to one year-class,  $c$ , substituting  $age$  for  $t$ , and adding a random error term,  $e$ , gives the basic model for a year-class curve:

$$\log U_{a,c} = \log(U_{0,c}) + Zage + e_{a,c} \quad (2)$$

where  $U_{0,c}$  is the cpue index for age zero,  $a$  is the age-class, i.e. the age in years as an integer index, while  $age$  is age in years as a real number.  $e$  is assumed to be normally distributed around zero with residual variance  $\sigma_e^2$ .

### Allowing for non-linearity with age

Frequently, the observations appear to be better fitted by a curve over  $age$  than by the straight line represented by Equation (2). This could often, but not exclusively, be explained by the inclusion of young age groups that are not fully selected by the trawl. They can either be removed from the analysis, or a term can be added to Equation (2) to allow for the curvature, a convenient possibility being the term  $\log(age + 1)$ . It increases gradually from zero with  $age$  in a curve that seems to simulate trawl cpue data well when young fish are less well caught than old, while a negative coefficient simulates the opposite effect. For lack of a better name, it is here referred to as the *selectivity* term but there is no clear relationship with the well-known logistic selectivity function commonly used for trawls. That function is avoided here because its parameters cannot be estimated within a linear least squares framework. The regression coefficient for *selectivity* is denoted  $S$ . Equation (2) becomes

$$\log U_{a,c} = \log(U_{0,c}) + Z'age + S \log(age + 1) + e_{a,c} \quad (3)$$

Note that estimates of  $Z'$  and  $S$  will tend to be highly correlated because both relate to  $age$  and, for this reason,  $Z'$  estimated from fitting eq. (3) is likely to be a biased estimate of total fishing mortality,  $Z$ .  $Z$  can be estimated numerically as the slope of the fitted  $\log U_{a,c}$  for the

age at which full selectivity is thought to occur, often the oldest age for trawl fisheries. The estimation is over a small interval of age, i.e. as  $\Delta \ln U / \Delta \text{age}$ . The validity of the estimate depends on having an adequate range of ages in the data to find the age of full selectivity, and on the number of fish observed around that age.

### Alternative models for different fleets

The word 'fleet' is used here to refer either to a single vessel (such as a research vessel carrying out a survey) or to a fleet of many vessels (such as a commercial fishing fleet). Different fleets are likely to exhibit different cpue for a given stock density because of different fishing powers. This can be allowed for by adding a *fleet* factor,  $V_f$ , to Equation (3):

$$\log U_{a,c,f} = \log(U_{0,c}) + Z' \text{age} + S \log(\text{age} + 1) + V_f + e_{a,c,f} \quad (4)$$

where  $f = 1, \dots, N_F - 1$  and  $N_F$  is the number of fleets.  $V_f$  brings all fitted  $\log U_{a,c,f}$  to the level of one fleet treated as the standard (Cotter, 2001).

Equation (4) implies that  $Z'$  and  $S$  are common to all fleets. This may be appropriate if all fleets fish the same subset of the stock with gears having similar selectivity functions with age. On the other hand, nesting of one or more of these parameters within *fleet* may be more appropriate. This is denoted by subscripting with  $f$ . So, if each fleet fishes the same subset of the stock but with a different selectivity function we would estimate  $N_F$  parameters  $S_f$ , or if, say, catches of some fleets are affected by age-dependent migrations into, or out of the survey area we would estimate  $N_F$  parameters  $Z'_f$ . The model with all terms nested within fleets, including the log cpue index at age 0, is referred to as the 'global' model:

$$\ln U_{a,c,f} = \ln(U_{0,c,f}) + Z'_f \cdot \text{age} + S_f \cdot \ln(\text{age} + 1) + V_f + e_{a,c,f} \quad (5)$$

It is equivalent to fitting Equation (3) separately to each fleet except that only one common residual variance is estimated.

### Allowing for changing slopes over time

$Z$  may vary over time because of changing fishing practices, rates of natural mortality, or migrations. The  $Z$  or  $Z'$  slope of a set of year-class curves can be made linearly variable over time by adding an  $\text{age} \cdot \text{year}$  variable to one of the models above. Curvature can be added with the polynomial terms  $\text{age} \cdot \text{year}^2$  and  $\text{age} \cdot \text{year}^3$ . This is more parsimonious with parameters than using  $Z_{a,y}$  for each year and age class, leaving more degrees of freedom for estimating precision. Polynomials also have the advantage that they are easily estimated within a linear least squares framework. Random walks or autocorrelated processes might be used instead but would require a more elaborate estimation procedure.

Polynomials can result in huge numbers (e.g.  $\text{year}^3$ ) in the predictor matrix that can cause serious rounding errors during least squares matrix inversion. To reduce the problem, the *year* variables should be transformed to  $y_i = \text{year}_i - \text{mean}(\text{year})$  where  $i$  indexes rows in the predictor matrix. Next, the polynomials should be orthogonalised so as to reduce changes in  $Z'$  from values previously estimated without the polynomial term. This is achieved with  $y'_i = (y_i - \text{mean}(y_i))$ ,  $y_i'^2 = (y_i^2 - \text{mean}(y_i^2))$ ,  $\bar{y}$  etc.. (This transform may not be important for the odd powers since the mean is then expected to be zero for balanced data.) The transformed variables are orthogonal because, if the same ages are present in every year,  $\sum y'_i(0 + 1 + \dots + A) = 0$ , as required, and the same for the other powers of  $y'_i$ . Thus, instead of  $Z \text{ age}$  in models (2) to (5) above, we can use  $Z_0 \text{ age} + Z_1 \text{ age } y' + Z_2 \text{ age } y'^2 + Z_3 \text{ age } y'^3$  or a subset of these terms.

## Weighting different fleets

Different series of cpue data are likely to estimate stock parameters and year-class curves with different precision depending on the season and area covered by the fleet, on the precision of age-reading and other practical aspects, and on how well the chosen model fits the data. Weighting of different data sets to reflect their precision with respect to the chosen model is therefore desirable. Cotter and Buckland (2004) suggest that the weighting estimated for each fleet's data set should be balanced with the reciprocal of the estimated residual variance specific to that fleet computed after the model is fitted, i.e.  $\hat{w}_f \propto \hat{\sigma}_f^{-2}$ .

They describe how the method can be implemented using iteratively weighted least squares (IWLS) taking into account the d.o.f. contributed by each fleet to the estimates of each parameter. Usually, 2 or 3 iterations produce stable values. Additionally, using the fleet specific residual variances, the relative precision of the different fleets can be compared using  $F$  tests (Cotter, 2001). Note that biased cpue series will produce biased weights (Quinn and Deriso, 1999, p. 353). Fleets that appear exceptionally precise should be scrutinised to see whether biased sampling may be the cause, e.g. due to clustering of observations in restricted times or places (Cotter and Buckland, 2004).

## Finding the best model: AIC and forward validation

The possible models for year-class curves have widely different numbers of parameters, and too few or too many in a model can both lead to biased estimation. Burnham and Anderson (2002) make a good case for using the Akaike information criterion (AIC) to select the best approximating model or models, rather than a sequence of  $F$  and  $t$  tests for the statistical significance of parameters. A summary of their approach is:

1. Create a list of candidate models based on "thoughtful, science-based, *a priori*" reasoning. One of these models should be the global model that includes all feasible and important parameters so far as is consistent with the principle of parsimony. Biologically infeasible models should be excluded from the list.
2. Fit all the candidate models and estimate the AIC using exactly the same set of data for all cases. The small sample AIC, denoted  $AIC_c$ , should be used when the number,  $n$ , of independent observations is less than approximately 40 times the number,  $K$ , of estimated parameters,  $\hat{\theta}$ :

$$AIC_c = -2\log(\text{Likelihood}(\hat{\theta})) + 2K(n/(n - K - 1))$$

3. Compute the AIC differences for each model relative to the best (minimum AIC), i.e.  $\Delta_i = AIC_i - AIC_{\min}$ , and use these to compute the odds against each of the models relative to the best, i.e.  $1/\exp(-0.5\Delta_i)$ .
4. Select the best model if it is clearly more likely than any other, or alternatively, select the set of  $R$  best supported models and use the methods of multi-model inference (MMI) based on Akaike weights.

When modelling fish stocks, the *a priori* reasoning referred to concerns the biology and fishery for the species. For example: are there good reasons to expect that selectivity, apparent mortality over time taking into account possible migrations, and apparent recruitments by year-class will be similar or different among different fleets? Equation (4) above, with or without nested parameters and polynomials in  $year$ , is intended to provide candidate models for cpue data, with Equation (5) being the global model. However, it may be possible to eliminate some of these models on prior scientific grounds and, if so, this should be done. A clearly best model may not appear at step (4) which, as Burnham and Anderson (2002) point out, is perfectly reasonable because of the complexity of biological systems.

Here, we partially adopt Burnham and Anderson's approach to model selection and estimation, and we have not attempted MMI. One reservation is that a model that fits all available data well is not necessarily good for predicting next year's stock, the primary task of a stock assessment. A second is that the AIC statistic for year-class curves may be invalidated because of dependence among observations of cpue across different ages within a year and within a fleet. Estimation of random  $year$  effects would remove some within-year

dependence, e.g. due to weather or cruise-leader effects, but it appears to be a complicated task for the range of nested models suggested here, and may not improve predictive abilities of fitted models (since a random effect is not predictable). For these reasons, we did not attempt it.

The method of *forward validation* was developed to supplement the AIC method because of these reservations. Starting from an early year and proceeding forwards in the time-series, it finds the differences between the predicted log cpue and the observed log cpue for one year after the time domain of the data used to fit the model. The preferred model is the one whose mean difference is closest to zero, and for which the mean square of the differences is lowest. This is merely a simulation of a fish stock assessment working group making predictions each year for the coming year, then checking them when the outcome is known, and, for this reason, we are proposing forward-validation in preference to the more widely used cross-validation.

Forward validation starts with selection of a starting year,  $v$ , near the beginning of the data series and for which there are sufficient observations to estimate all parameters of the selected model. All available data up to and including year  $v$  are fitted, and predictions formed for year  $v+1$ . For linear models, the fitted model may be used directly for prediction, but for polynomial models, extrapolation beyond  $v$  may produce erratic results. A Taylor series prediction method based on differential coefficients estimated close to, but behind the  $v$ 'th observation is then preferable. This is described in an Annex. The predicted log cpue are compared with observed log cpue for each fleet and each age in year  $v+1$  to form prediction errors,  $\delta_{v+1} \log U$ . Next, the same model is fitted in the same way to  $v+1$  observations, and predictions and errors prepared for year  $v+2$ , and so on, until the penultimate data year is reached and prediction errors are formed with the final data year. Note that successive prediction errors from forward validation are not independent. An outlier at the beginning of a series could cause serial correlation of prediction errors for that fleet for several years afterwards.

A weighted estimator of the mean square prediction error for next year's log cpue for age-class  $a$  and fleet  $f$  is

$$\text{MSPE}_{a,f} = \sum n_i (\delta_{i+1} \log U_{a,f})^2 / \sum n_i \quad (6)$$

where  $n_i$  is the number of years of observations fitted for the  $i$ 'th forward validation step. This estimator assumes a linear relationship between the number of years of observations and the reliability of the model fitted to them, whilst also giving more weight to recent observations. The MSPE would often be greater than the residual variance,  $\sigma_e^2$ . Similarly, a mean prediction bias factor can be estimated from

$$\text{MPB}_{a,f} = \exp(\sum n_i (\delta_{i+1} \log U_{a,f}) / \sum n_i) \quad (7)$$

This estimator is anti-logged and so has value 1 when prediction is perfect.

A complication with forward validation arises when  $Z$  is allowed to vary over time. Here, we are using low degree polynomials in *year* for this purpose. It can be expected that, when the index,  $i$ , is small, the polynomial terms will fit short period fluctuations of  $Z$  over time but, when  $i$  approaches the penultimate data year, the same polynomial terms will fit longer period trends in  $Z$  leaving the short period fluctuations to appear as noise. For this reason it is suggested that MSPE for polynomial functions should be estimated using only the last half of the data series, depending on the length of the series available and the amount of short period noise that is thought to exist in the data.

A further choice to be made is whether to estimate prediction errors separately or jointly for each age and/or fleet. Initial screening of candidate models is much simpler if interest is

restricted to one measure for each fleet. For this purpose, the average MSPE per age class can be calculated:

$$\sum_{a=1}^{A_f} \text{MSPE}_{a,f} / A_f \quad (8)$$

where  $A_f$  is the number of age classes in fleet  $f$  for which prediction errors are available. Another approach that might be more suitable for skewed prediction errors would be to examine quantiles of the prediction errors for each fleet pooled across all ages. Later evaluation of the short-list of preferred models could involve examination of MSPE and MPB for age-classes individually, particularly those of most importance for predicting the future size of the stock.

## Examples

### *NRC simulated stocks*

The Committee on Fish Stock Assessment Methods of the US National Research Council (NRC) published details of catch-at-age simulations of five stocks that were used as part of a review of various assessment methods (National Research Council, 1998). Summaries of the principal varying features of the NRC data sets are given in table 1. Here we used the 30-year series of simulated survey abundance indices of numbers-at-ages 2 – 14, and weight-at-age matrices. Candidate models were fitted with the YCC package to each set of data and compared, then the preferred model was used to estimate numbers-at-age and recruitment annually without knowledge (at the time) of the true values underlying the simulations. Since both biomass and recruitment were estimated on a 'per unit effort' basis by YCC whilst the NRC values were absolute, it was necessary to standardise both the NRC true values and the YCC estimates to units of standard deviations from their respective mean values in order to compare the two time-series on the same scales. (Note that this also standardised the variances of the series.)

Details of the preferred models, their estimated MPB factor, and, very briefly, the reasons for preferring them over other candidate models plus any reservations about them are given in table 2. Some of the comments relate to voluminous, unreported diagnostic results. True, and estimated trajectories of biomass and recruitment obtained with the preferred model for each data set are shown in Figure 1a, b respectively. For biomass, the trajectories of the simulated survey observations are also shown in Figure 1a since they formed the input to YCC and their variance around the truth could have caused some of the imprecision of the YCC estimates. Inspection of Figure 1a and b indicates that biomass and recruitment were estimated with reasonable precision for most of the five simulations, especially considering that only the survey data were used. Set 3 gave most difficulties, as expected due to the step change in survey catchability after year 15 (Table 1). It was handled by splitting the survey into two 'fleets'. Forward validation was extended back to 25 years (instead of to 10 years for the other sets) so that the MSPE/Age class included results for the first survey. Catchability of the survey over years 16 to 30 was estimated to be 2.4 times that during years 1 to 15. The true value was 2.0. Figure 1a shows a large overshoot of estimated biomass in year 15 apparently due to over-estimation of 6 to 9 year-olds in that year which in turn was linked with over-estimation of recruits in years 6 to 9 (Figure 1b). Bearing in mind the irregularities in set 3, the analysis with YCC was considered acceptable.

### *Plaice in the North Sea*

This example uses survey cpue ("tuning") data for North Sea plaice taken from an ICES stock assessment report (ICES, 2005). It illustrates how an analysis of year-class curves might be applied in a stock assessment, suggests uses for some of the outputs offered by YCC, and gives results consistent with known migrations of plaice. Data were for three beam trawl surveys carried out by IMARES for the stock assessments of plaice and sole. The short names for the surveys and details of the data they provided are:

- 'BTS Isis', for fish aged 1 to 9 years, for years 1985 to 2003;
- 'BTS Tridens' for fish aged 2 to 9 years for years 1996 to 2003; and

- ‘SNS’ for fish aged 1 to 3 years, for years 1982 to 2002.

BTS Isis covered the south eastern North Sea with twin 8-m beam trawls with 8 tickler chains. BTS Tridens was an expansion into the central and northern part of the North Sea. The same gear was used but with the addition of a flip-up rope to cope with rough ground. SNS covered transects within coastal waters of the south eastern North Sea using twin 6-m beam trawls and aiming at younger age-groups than the two BTS surveys. Figure 2 shows the coverage of the three surveys. More information about them is available in two project reports (Beare *et al.*, 2002; Piet, 2004). A total of 291 observations of cpue at all ages was analysed. Forward validation was started 10 years behind the final data year using the Taylor series method. Note that only 6 or 7 forward predictions were available for BTSTridens, and only 2 age-classes for SNS, suggesting that MSPE for those surveys was estimated poorly relative to those for BTS Isis.

Table 3 shows the short-list of 6 candidate models considered, notes on the assumed biological meaning of each model, and in each case, comments on its scientific implications, plus a three-level subjective ranking of its overall credibility prior to any statistical analysis. Models including polynomials in *year* were omitted at this stage because the biological credibility of various terms is little affected by whether or not *Z* is allowed to vary gradually over time.

After fitting the different models in Table 3, models #4 and #10 were preferred. Table 4 shows selected diagnostic results, plus reasons for preferring them over other candidate models, together with any reservations. Models #4 and #10 showed the lowest  $AIC_c$ , good MSPE/age-class, and similar levels of MPB factor/age-class. These models were therefore re-fitted with the addition of polynomial terms in *year* to see whether better fits or predictive abilities could be found. For model #4,  $AIC_c$  was improved by polynomial terms but MSPE/age-class was either unchanged or became worse, and the unsteady behaviour of residuals on *age* observed with the linear models was not improved. Giving priority to MSPE/age-class and the principle of parsimony, the preferred model was the linear model, #4. For model #10, 1<sup>st</sup> and 2<sup>nd</sup> degree polynomials neither improved  $AIC_c$  nor predictive abilities. The 3<sup>rd</sup> degree polynomial did improve  $AIC_c$  but not MSPE/age-class, or the unsteady behaviour of residuals. For the same reasons as for model #4, the preferred model was the linear model, #10.

Model #10 might be preferred to model #4 at this stage because of its higher prior credibility (Table 3), its lower  $AIC_c$ , and its comparable MSPE/age-class for each of the three fleets (Table 4). Taking model #10 as  $AIC_{min}$ ,  $\Delta_4 = 555.699 - 554.848$ , and the odds against model #4 are  $1/\exp(-0.426) = 1.53$  to 1, making model #10 only slightly preferable to model #4.

The values of *Z* estimated numerically from models #4 and #10 at the maximum observed ages for each survey are compared in Table 5. BTS Tridens showed the shallowest slopes (least negative values). This is consistent with BTS Tridens covering the largest area of sea consisting of mainly offshore stations since estimated *Z* is, in that case, likely to be less affected by age-dependent migrations of plaice out of the survey area. SNS showed the steepest *Z* (most negative values) even though the maximum observed age was only 3. Model #4 estimated  $Z = -1.84 \text{ year}^{-1}$  which is substantially different from the estimates for the other fleets. This would imply very high losses of older fish from the SNS transects to offshore waters. Model #10 estimated *Z* for SNS as  $-1.34 \text{ year}^{-1}$  which is also quite distinct from the values for the other two fleets. Since SNS was designed as a survey of young fish, detection of offshore migrations is not surprising and lends support for use of the YCC method. Beverton and Holt (1957, p. 182-3) found average *Z* for North Sea plaice aged 5 to 10 years old between 1929 and 1938 to be 0.83, a low value which they attributed to immigration to the fishing area off Lowestoft, and to discarding. Concerning estimates of log cpue indices for plaice aged 0, models #4 and #10 gave series with different elevations but identical patterns (not illustrated), implying that the choice of model was unimportant for estimation of relative recruitment to year-classes in this case.



Figure 3 shows grey scale representations of the correlations of log residuals across ages obtained with model #10 for each survey. The patterns for models #4 and #1, not illustrated, were nearly identical, implying that the observed correlation structure was a property of the data rather than a consequence of the model. Patterns were different for each survey. Correlations were positive and high for SNS whilst BTS Isis showed more independence, i.e. more medium grey in Figure 3, and BTS Tridens was intermediate. High correlations imply that parameters estimated by a survey should have larger standard errors than those obtained by least squares regression based on an assumption of independent residuals. Table 6, here called the *D*-table, shows the relative amounts of information contributed by each fleet to the estimate of each parameter in model #10, based on the number of observations and the fleet weightings, i.e. *D* in Equation. (4) of Cotter and Buckland (2004). Also shown in Table 6 are the parameters and standard errors on the log scale estimated after 3 iterative re-weightings, the absolute fleet weights (i.e. not constrained to add to 1, as they are in table 4), and the numbers of observations. Table 6 may be used to indicate how much confidence to place on the standard errors of estimates. As examples, the 1976 – 1978, and 2002 year-classes and a selectivity factor were all estimated solely by BTS Isis and, since residuals appeared reasonably independent for this survey (Figure 3), the standard errors could be considered to be reasonable. The coefficient of *age* (i.e.  $\log Z'$  in Table 6) was estimated with substantial contributions of information from BTS Tridens and SNS, both of which showed correlated residuals (Figure 3); the standard error of +/- 0.090 is therefore likely to be under-estimated. The standard errors for the *fleet* and *selectivity* factors estimated solely by, and for SNS are likely to be substantially under-estimated because of the correlated residuals for that fleet (Figure 3). Unfortunately, a link between the degree of under-estimation of the standard error and the degree of correlation among the residuals-at-age is not available due to lack of statistical theory. The *D* values for model #4, not shown, did not differ substantially from those for model #10 in Table 6, except for  $\log Z'$  for which each fleet contributed a separate estimate.

Figure 4 is a graphic presentation of the correlations between estimated parameters for model #4. That for model #10 was similar. In both cases, estimated year-class parameters were highly correlated positively. This is consistent with the two models estimating similar relative recruitments but with different elevations for, if one estimate is high, all are high when positively correlated. With model #4 (Figure 4), all year-class estimates were positively correlated with the coefficient of *age* estimated for BTS Isis. This is consistent with BTS Isis contributing the longest data series and the most age groups to the analysis. With model #10 (not illustrated) year-class estimates were most positively correlated with the coefficient of *age* which was common to all fleets. The year-class estimates in Figure 4 were negatively correlated with the coefficient of *selectivity* estimated for BTS Isis because a large value depresses the estimated numbers of young fish in each year-class. It may be helpful to note that the correlations among parameters,  $\theta$ , are computed from  $\text{cov}(\theta) = \hat{\sigma}_e^2 \cdot (\mathbf{X}'\mathbf{X})^{-1}$  where  $\mathbf{X}$  is the predictor matrix of the model. The patterns in Figure 4 therefore depend on the choice of parameters in the model, and of years, ages, and fleets over which cpue were observed, and not on the observed values themselves. Other strong relationships, both positive and negative, among estimated parameters are also evident in Figure 4 and may be worthy of further investigations but will not be commented upon here.

Year-class curves obtained by fitting model #10 are shown in Figure 5a, b, c. Those for Isis are concave upwards while those for BTS Tridens show the opposite effect reflecting the different signs of *S* (Table 6). The negative value for BTS Isis implies that old plaice were less well caught than younger fish, as is consistent with migrations by older fish out of the survey area. The SNS curves showed a tendency to over-estimate older fish in the more recent years but, considering the shortness of the age series, this is not surprising. Plots of residuals over *year*, *year-class*, and *age* were also examined for all surveys (not shown). Patterns over *year* were evident but were not cured by adding polynomial terms. BTS Isis and, to a lesser extent, BTS Tridens showed waves in residuals over *age*. The presence of patterns was not ideal but was not generally improved by other candidate models. The patterns were accepted because of other favourable properties of model #10 noted above, and a reluctance to further complicate the set of candidate models on an *ad hoc* basis.

An analysis of relative residual variance (Cotter, 2001) was also carried out to see whether the residual variance exhibited by any one fleet was significantly higher than the residual variance of all the others, as judged by an  $F$  test. Tridens showed the highest fleet weightings with either model #4 or #10 (Table 4), and correspondingly the lowest fleet-specific residual variances (Table 7). The comparison of residual variances is somewhat different from that foreseen when this method was presented (Cotter, 2001) because the interest now is in whether one survey is significantly better, not worse than two others. Here we tested ratios of fleet-specific residual variances as  $F$  for Isis/Tridens and SNS/Tridens. The data and calculations for model #10 are shown in table 7. The residual variances of BTS Isis and SNS were significantly higher than for BTS Tridens ( $p < 0.05$ ), suggesting that BTS Tridens was achieving better precision. This result is expected given that BTS Tridens covers a much larger survey area (Figure 2) but, bearing in mind dependence among some of the residuals and the short time-series for Tridens, the result should be treated with caution. Results for model #4, not shown, were similar.

To summarise, models #4 and #10 were selected on prior biological grounds, competitive predictive abilities, and low  $AIC_c$ . Exclusion of polynomials in *year* was preferred for both models because the extra terms did not notably improve prediction variance, mean bias, or homogeneity of residuals. This exclusion implies that  $Z$  did not change detectably over the survey period, from 1982 to 2003. A final choice between the two models was not possible but may not be particularly important for an assessment of the stock since both gave comparable estimates of relative recruitments, and the trend in  $-Z$  was clearly SNS < BTS Isis < BTS Tridens with both models (Table 5). This is consistent with the increasing geographic spreads of the three surveys and the loss of plaice offshore with age. Heincke (1905, p17) notes that for the North Sea: “*the occurrence of the young plaice, from the coast to the open sea, is arranged like the steps of a ladder . . . the smallest and youngest quite close to land, the largest and oldest the furthest out*”. See also Metcalfe et al.(2006) and Rijnsdorp et al. (2006).

## Discussion

Year-class curves have several desirable features not all of which are available with other, more elaborate methods of stock assessment:

- They are based on statistical theory for least squares and AIC.
- They are equally applicable to cpue results from surveys or commercial fishing.
- They use continuous rather than categorical variables for all variables except *year-class* and *fleet*, thereby reducing the numbers of parameters to be estimated and allowing best precision with the available observations.
- They generate illustrated output which can be discussed with fishers and other, non-mathematical stakeholders, e.g. when selecting the best approximating model.
- They allow fleets to be ranked for precision using their fitted weights and relative residual variances. Results are model-dependent but may, nevertheless, be useful for assigning priorities to different sources of data.
- They are quickly fitted.
- They are compatible with a range of candidate models from which one may be selected so as best to capture the biological and fishery-related factors affecting cpue.

In addition, the inclusion of polynomials in *year* allows year-class curves to vary gradually over time, a feature that was not suggested when they were previously described as a method for intercalibrating groundfish surveys (Cotter, 2001). Allowing only a conservative estimate of variability in  $Z$  gives fewer opportunities for erroneously interpreting sampling variance or random year effects as trends in time. The possibility of model-related bias arising from including or excluding polynomials can be checked by seeing whether predictive abilities are improved as seen by forward validation. A weakness of year-class curves is that they are totally dependent on catchabilities remaining constant over time. However, few, if any, cpue-based stock assessment methods are immune to this problem.

The large range of candidate models available for year-class curves opens up the problem of how to select the “best approximating” model. Some other methods for estimating stock parameters offer a more limited range of candidate models. For example the XSA method offers only two, concerning whether or not abundances of the youngest age-classes are proportional to eventual year-class strength (Darby and Flatman, 1994; Shepherd, 1999). The small number of options simplifies the analyst’s task but may mean that model-related bias is being overlooked. The several candidate models together with the visual means of examining them offered by year-class curves encourage thorough consideration of the biological relevance of each model to the species and locations of interest, as in Table 3. This would surely represent valuable use of a working group’s time, particularly if commercial fishers were invited to take part in the discussions and perhaps help to choose the best model. Smith and Punt (1998) report involving fishers in a (Bayesian) assessment of gemfish in eastern Australia, leading to better acceptance by the fishing industry of the science and management process.

Selecting the best model is, however, not easy. The results of the analysis of plaice in the North Sea showed that the various indicators of fit may favour different models. For example, the  $AIC_c$  implied that polynomials in *year* would be beneficial in some of the models even though the MSPE was not improved, or only slightly, and none of the models listed in Table 3 provided neat horizontal bands of residuals over *year*, *year-class*, and *age* as is usually considered important for a good fit. Priority was given to the MSPE criterion here because of the importance of prediction for stock assessments and because forward validation is based on repeated use of the model with successively lengthening data series, as it would be applied in reality from year to year. The  $AIC_c$ , on the other hand, relates only to the model fitted once to the complete set of data. It is also compromised by dependence of data across ages within years and fleets, as well as by possible inadequacy of the constant variance, normal distribution model of residual errors. The conflict among indicators of fit underlines the importance of biological considerations and the principle of parsimony of parameters when choosing the model to go forward with. Elaboration of the candidate models with extra terms or different functions designed to deal with patterned residuals is always an option but could amount to little more than an *ad hoc* exercise with no lasting explanatory power unless there are clear prior justifications based on ‘thoughtful science’.

Year-class curves do not allow absolute stock numbers or fishing mortality,  $F$ , to be estimated but, as has been pointed out (Rivard, 1989; Cotter *et al.*, 2004), other methods can only do this if the coefficient of natural mortality,  $M$ , is accurately known which is not usually the case (Vetter, 1988; Hewitt and Hoenig, 2005). Statistical inferences from year-class curves are compromised somewhat by dependence among observed data but so too are other assessment methods unless a covariance matrix of errors is an estimated component of the method. The practical relevance of dependence is that precision is generally over-estimated. Analysts are consequently encouraged to add too many terms to models, and to have false confidence in the estimated parameters. This lends further support for preferring parsimonious models.

Year-class curve models could be augmented by inclusion of commercial fishing effort,  $E$ , being applied to the stock (Beverton and Holt, 1957, section 14.3). This could be achieved by disaggregating the  $Z_{age}$  term in the model equations:

$$Z_{age} = (F + M)_{age} = q' \cdot E_{age} + M_{age}$$

where  $F$  and  $M$  are the coefficients of fishing and natural mortality respectively, and  $q'$  is a catchability coefficient.  $E$  is total commercial fishing effort, or an index of it. Adding an annual estimate (multiplied by *age*) to the predictor matrix for each cpue-at-age could remove the need to use polynomials in *year* to allow  $Z$  to vary over time. Alternatively, if polynomials were still found necessary in the model, they would indicate changes in  $M$  over time. However, note that if effort does not vary much from year to year (as in the North Sea for example, Jennings *et al.*, 1999) the two factors  $E_{age}$  and  $age$  would be nearly collinear, meaning that estimates of  $q'$  and  $M$  would be highly correlated. Another problem is that a

reliable index of total fishing effort is often not readily obtainable, particularly when different fishing gears are in use commercially and their effort measures cannot be readily added. For these reasons, we did not attempt to include effort in our analyses.

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## Annex: Prediction using a Taylor series

Taylor's theorem states that a function of  $x$  may be predicted at a point  $(x + h)$  with

$$f(x + h) = f(x) + hf'(x) + \frac{h^2}{2!} f''(x) + \frac{h^3}{3!} f'''(x) + \frac{h^4}{4!} f^{(4)}(x) + \dots$$

The primes indicate successive differential coefficients. Denote the date of the final observation of any forward validation step as  $Y_0$ , and let a small fraction of a year be  $\delta$ . Let  $Y_1 = Y_0 - \delta$ ,  $Y_2 = Y_0 - 2\delta$ , etc.. Backward differences are used so as to keep estimation within the fitted domain, and so that the differential coefficients are estimated as close as possible to the value to be predicted for forward validation. Then the coefficients are approximated by

$$f'(Y_0) = (f(Y_0) - f(Y_1))/\delta, \quad f'(Y_1) = (f(Y_1) - f(Y_2))/\delta, \text{ etc.}$$

$$f''(Y_0) = (f'(Y_0) - f'(Y_1))/\delta, \text{ etc.}$$

$$f'''(Y_0) = (f''(Y_0) - f''(Y_1))/\delta, \text{ etc.}$$

$$f^{(4)}(Y_0) = (f'''(Y_0) - f'''(Y_1))/\delta.$$

$\delta$  is set to a value, say 0.01, which is not too large for estimating the differentials accurately, and not so small as to cause significant rounding errors in the calculations. Finally, the Taylor series is evaluated with  $x = Y_0$ , and  $h = 1$  year.

Table 1. Summary of the principal varying features of 5 stock simulations used to test the YCC method. Based on table 5.1 of NRC (1998).

NRC set #	Population trend	Age at selectivity	50% Survey catchability ( $q$ )	Mean Yield/Biomass
1	Depletion	Lower later	Constant	0.19
2	Depletion	Lower later	Constant	0.12
3	Depletion	Lower later	Higher from year 16	0.12
4	Depletion	Constant	Constant	0.21
5	Recovery	Constant	Constant	0.07



Table 2. Brief details of YCC models preferred for fitting the 5 stock simulations prepared by NRC (1998). 10 years of forward validation were used for all sets except #3 which used 25 years. Abbreviations: MPB = mean prediction bias factor; MSPE = mean square (log) prediction error; FPE = forward prediction errors;  $Z$  = estimated total mortality for age range in subscripts and for years (yr) shown; 'f' in model terms means 'having nested within it'. Parameters corresponding to (=) model terms:  $fleet = V_f$  for all  $f$ ;  $yclass = \log U_{0,c}$  for all  $c$ ;  $age = Z$  or  $Z'$ ;  $selectivity = S$ ;  $fleet/age = Z_f$  for all  $f$ ;  $fleet/yclass = \log U_{0,c,f}$  for all  $c, f$ ;  $fleet/selectivity = S_f$  for all  $f$ ;  $age*year = 1^{st}$  degree polynomial in year, etc.

NRC set #	Model terms and ages used in fit	N parameters	MPB/age class	Trend in $Z$	Reasons for preference and reservations
1	$selectivity + yclass + age + age.year + age*year^2$ Ages: 2 – 10	43	0.982	$Z_{5-10}$ : yr1: 0.48 yr30: 0.95	<ul style="list-style-type: none"> <li>• 2<sup>nd</sup> lowest MSPE/age class, lowest <math>AIC_c</math></li> <li>• FPE plots show fewest trends and shapes</li> </ul>
2	$yclass + age + age*year$ Ages: 3 - 14	46	0.932	$Z_{6-14}$ : yr1: 0.27 yr30: 0.66	<ul style="list-style-type: none"> <li>• Lowest MSPE/age class; parsimonious; <math>AIC_c</math> second lowest</li> <li>• Trends seen in residuals and FPE on <math>age</math> but not worse than for other models</li> </ul>
3	$yclass + fleet/selectivity + age + age*year + age*year^2$ Ages: 1 – 14	49	.972	$Z_{6-14}$ : yr1: 0.31 yr11: 0.23 yr30: 0.69	<ul style="list-style-type: none"> <li>• Low MSPE, low <math>AIC_c</math>.</li> <li>• FPE and residuals evenly banded</li> <li>• <math>V_f</math> estimated more precisely than from models with more parameters nested within fleet</li> </ul>
4	$selectivity + yclass + age + age*year$ Ages: 1 – 14	46	1.084	$Z_{6-14}$ : yr1: 0.37 yr30: 0.77	<ul style="list-style-type: none"> <li>• MSPE lowest, <math>AIC_c</math> low but not lowest; parsimonious</li> <li>• FPE convex upwards on <math>age</math> but not worse than for other models</li> <li>• Residuals evenly banded</li> </ul>
5	$selectivity + yclass + age$ Ages: 1 – 14	43	1.123	$Z_{6-14}$ : yr1: 0.28 yr30: 0.31	<ul style="list-style-type: none"> <li>• Lowest MSPE; low but not lowest <math>AIC_c</math>; parsimonious</li> <li>• Residuals evenly banded but FPE trend down on <math>yclass</math>.</li> </ul>

Table 3. Plaice in the North Sea. Preliminary, subjective assessment of candidate models for fitting year-class curves to cpue data from 3 beam trawl surveys carried out by IMARES. See Table 2 for explanation of model terms.

Model #	Model terms	Biological meaning (B.M.) of model	Comments (C.)	Credibility of model
1	<i>fleet</i> + <i>yclass</i> + <i>age</i>	<ul style="list-style-type: none"> <li>• <math>Z</math> is the same for all fleets</li> <li>• Catchability is the same for all years and ages</li> <li>• No age-related migrations</li> </ul>	<ul style="list-style-type: none"> <li>• Ignores variation of trawl selectivity with age</li> <li>• Ignores possible offshore migrations</li> </ul>	LOW
2	<i>yclass</i> + <i>fleet/age</i>	<ul style="list-style-type: none"> <li>• B.M. as for #1 except</li> <li>• <math>Z</math> varies among fleets</li> </ul>	<ul style="list-style-type: none"> <li>• C. as for #1 except</li> <li>• Varying <math>Z</math> by fleet allows for age-related migrations</li> </ul>	MED
3	<i>fleet/(yclass + age)</i>	<ul style="list-style-type: none"> <li>• B.M. as for #2 plus</li> <li>• Year-class signal varies by fleet</li> </ul>	<ul style="list-style-type: none"> <li>• C. as for #2 and</li> <li>• Year-class signal unlikely to differ among fleets</li> </ul>	LOW
4	<i>yclass</i> + <i>fleet/(age + selectivity)</i>	<ul style="list-style-type: none"> <li>• B.M as for #2 plus</li> <li>• Selectivity varies by fleet</li> </ul>	<ul style="list-style-type: none"> <li>• Slope varies with fleet and age</li> <li>• Estimates of <math>Z'_f</math> and <math>S_f</math> likely to be highly correlated implying too many parameters.</li> </ul>	MED
10	<i>yclass</i> + <i>age</i> + <i>fleet/selectivity</i>	<ul style="list-style-type: none"> <li>• B.M. as for #1 plus</li> <li>• Selectivity varies by fleet</li> </ul>	<ul style="list-style-type: none"> <li>• Slope varies with fleet; young fish probably most affected</li> <li>• Fleets likely to show different selectivities</li> </ul>	HIGH
14	<i>fleet/(yclass + age + selectivity)</i>	<ul style="list-style-type: none"> <li>• All parameters vary by fleet</li> </ul>	<ul style="list-style-type: none"> <li>• Global model</li> <li>• Difficult to see why overlapping surveys should have no stock parameters in common</li> </ul>	LOW

Table 4. Plaice in the North Sea. Selected results from fitting the preferred pair of models, #4 and #10, see table 3, to cpue data from 3 beam trawl surveys (BTS Isis, BTS Tridens, SNS) carried out by IMARES. Some comments refer to results not presented. See Table 2 for explanation of abbreviations and model terms

Model #	Model terms	N parameters	Small sample AIC <sub>c</sub>	Fleet	log MSPE/age class	MPB/age class	Fleet weights	Reasons for preference + reservations
4	<i>yclass+ fleet/(age + selectivity)</i>	36	556	Isis: Tridens: SNS:	0.571 0.330 0.870	1.184 0.824 1.497	0.247 0.490 0.263	<ul style="list-style-type: none"> <li>• Good AIC<sub>c</sub>; good MSPE/Age class but</li> <li>• all fleet residuals show trends on <i>year</i>, and waves on <i>age</i>.</li> <li>• SNS year-class curves fit poorly</li> </ul>
10	<i>yclass + age + fleet/selectivity</i>	34	555	Isis: Tridens: SNS:	0.588 0.286 0.794	1.187 0.806 1.386	0.249 0.497 0.254	<ul style="list-style-type: none"> <li>• Best AIC<sub>c</sub> among non-polynomial models; good MSPE/Age class but</li> <li>• Tridens residuals slope on <i>year</i>; Isis and Tridens resids wavy on <i>age</i></li> </ul>

Table 5. Plaice in the North Sea: Coefficients of total mortality,  $Z$ , as estimated numerically at the ages shown for models #4 and 10 fitted to cpue data from 3 beam trawl surveys (BTS Isis, BTS Tridens, SNS) carried out by IMARES; see also Tables 3 and 4, and Table 2 for an explanation of model terms.

Model #	Model terms	Fleet	$Z$ <i>year</i> <sup>-1</sup>	at Age
4	<i>yclass + fleet/(age + selectivity)</i>	Isis:	-0.88	9
		Tridens:	-0.62	9
		SNS:	-1.84	3
10	<i>yclass + age + fleet/selectivity</i>	Isis:	-0.91	9
		Tridens:	-0.57	9
		SNS:	-1.34	3

Table 6. Plaice in the North Sea: *D*-table for model # 10, i.e. relative contributions of information on a 0 to 1 scale by each of 3 IMARES survey fleets to estimates of each parameter based on the numbers of observations (N) and the estimated fleet weightings ( $\hat{w}$ ). 3 iterative re-weightings. 1<sup>st</sup> column: '1976 Yclass' =  $\log(U_{0,1976})$ , etc. D.o.f.=degrees of freedom. Right 2 columns: log-transformed parameter estimates and corresponding standard errors.

Parameter	Survey fleet			D.o.f.	Log estimate	St.err.
	Isis N=167 $\hat{w} = 2.49$	Tridens N=63 $\hat{w} = 5.0$	SNS N=61 $\hat{w} = 2.52$			
1976 Yclass	1.00	0.00	0.00	1	10.078	0.783
1977 Yclass	1.00	0.00	0.00	1	9.411	0.653
1978 Yclass	1.00	0.00	0.00	1	9.573	0.608
1979 Yclass	0.73	0.00	0.27	1	9.501	0.569
1980 Yclass	0.73	0.00	0.27	1	9.040	0.553
1981 Yclass	0.73	0.00	0.27	1	10.164	0.543
1982 Yclass	0.73	0.00	0.27	1	9.719	0.539
1983 Yclass	0.73	0.00	0.27	1	9.633	0.532
1984 Yclass	0.73	0.00	0.27	1	9.626	0.520
1985 Yclass	0.73	0.00	0.27	1	11.012	0.520
1986 Yclass	0.73	0.00	0.27	1	10.215	0.520
1987 Yclass	0.73	0.35	0.18	1	9.970	0.511
1988 Yclass	0.73	0.35	0.18	1	9.362	0.511
1989 Yclass	0.47	0.35	0.18	1	9.329	0.507
1990 Yclass	0.47	0.35	0.18	1	9.251	0.508
1991 Yclass	0.47	0.35	0.18	1	9.160	0.510
1992 Yclass	0.47	0.35	0.18	1	8.905	0.510
1993 Yclass	0.47	0.35	0.18	1	8.941	0.511
1994 Yclass	0.47	0.35	0.18	1	9.258	0.505
1995 Yclass	0.47	0.35	0.18	1	9.091	0.519
1996 Yclass	0.47	0.35	0.18	1	10.543	0.522
1997 Yclass	0.47	0.35	0.18	1	9.516	0.516
1998 Yclass	0.47	0.35	0.18	1	9.203	0.516
1999 Yclass	0.47	0.35	0.18	1	9.076	0.514
2000 Yclass	0.47	0.35	0.18	1	8.941	0.515
2001 Yclass	0.47	0.35	0.18	1	10.005	0.529
2002 Yclass	1.00	0.00	0.00	1	8.426	0.738
Fleet factors, $V_f$	0.00	1.00	1.00	2	Tri.: -6.411 SNS: 5.230	0.445 0.574
$Z'$	0.47	0.35	0.18	1	-0.680	0.090
Selectivity, $S_f$	1.00	1.00	1.00	3	Isis: -2.445 Tri: 1.162 SNS: 5.230	0.534 0.623 0.482
Totals	18.36	7.67	6.97	33		

Table 7. Plaice in the North Sea: F tests of which of three IMARES beam trawl survey was most precise with one model. See Table 2 for an explanation of model terms.

Model #	Model terms	Fleet-specific residual variances	Fleet-specific d.o.f.	F statistic	Probability
10	<i>Yclass</i> + <i>Age</i> + <i>Fleet/selectivity</i>	Isis: 0.402	148	Isis/Tri: 2.01	0.012
		Tridens: 0.200	54	SNS/Tri: 1.99	0.032
		SNS: 0.397	53		

Figure 1. Comparison between NRC simulations for stocks 1 to 5 (National Research Council, 1998) and blind estimates made with preferred models of year-class curves (see text). Ordinates normalised to standard deviations from the mean for each series. For set 3, data were analysed as two surveys changing at year 16. a) Total biomass estimated for ages 2-14. b) Recruits aged 1.

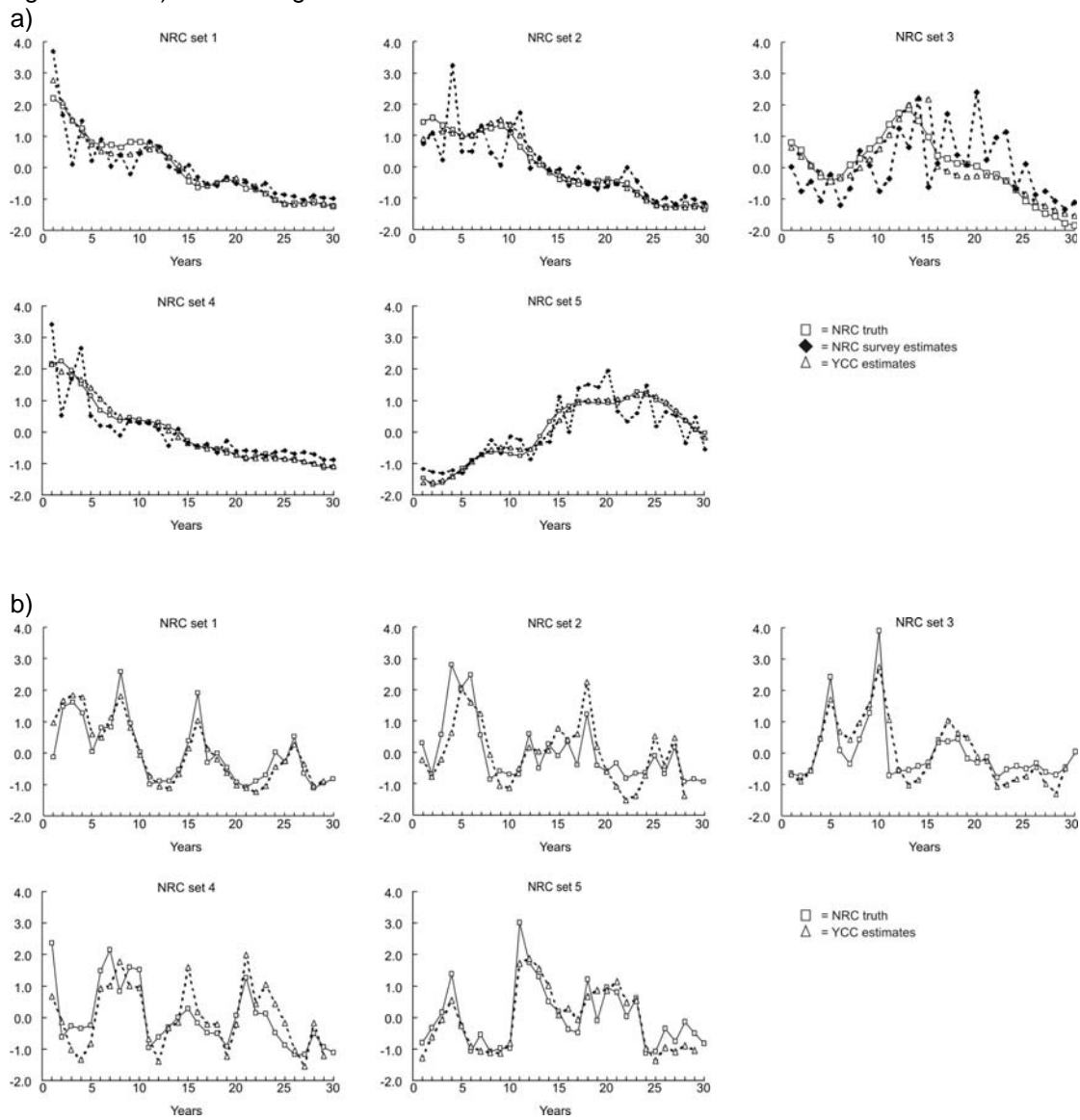


Figure 2. Coverage of three beam trawl surveys carried out by IMARES as used for the YCC analysis of cpue abundance indices-at-age for plaice.

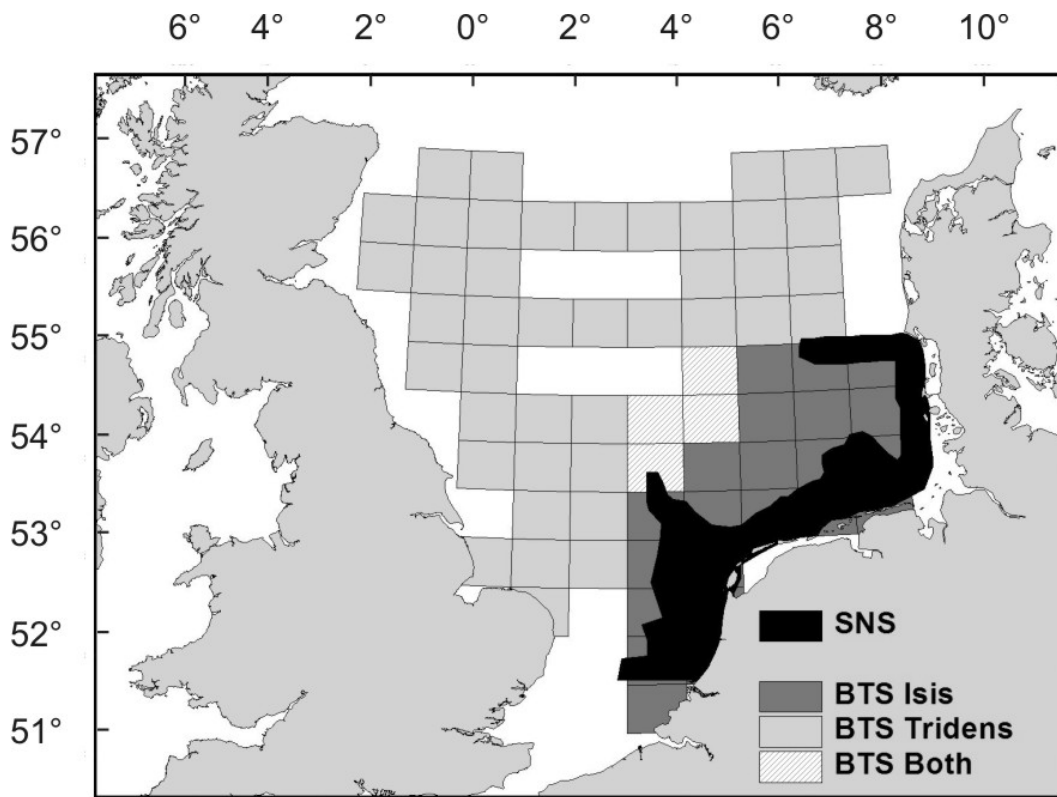
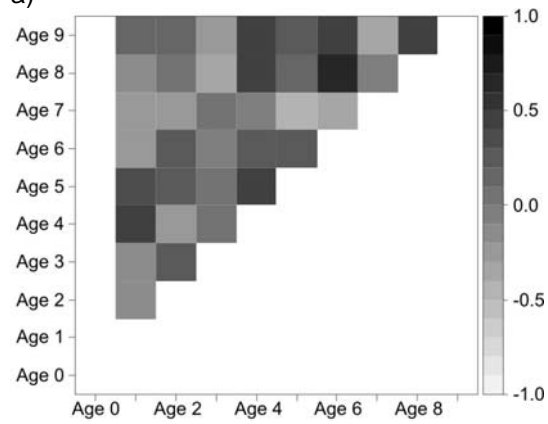


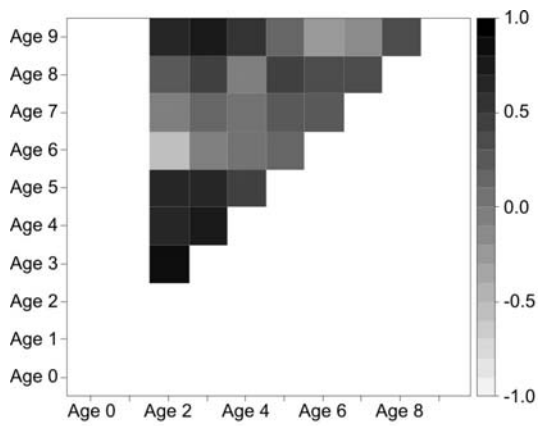


Figure 3. Plaice in North Sea: Grey scale representations of correlations of log residual errors across ages with model (#10) for 3 beam trawl surveys carried out by IMARES. a) BTS Isis; b) BTS Tridens; c) SNS.

a)



b)



c)

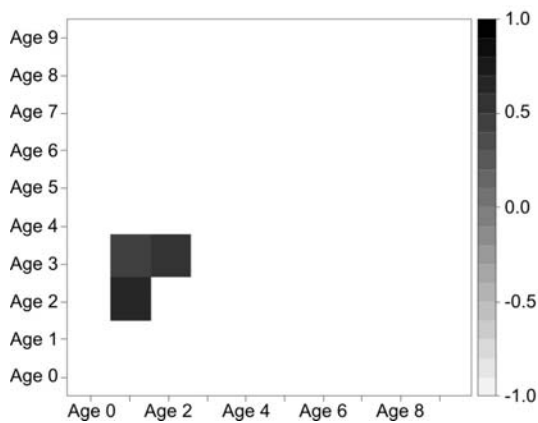


Figure 4. Plaice in North Sea: Grey scale representations of correlations of parameters estimated with model #4 from data for 3 beam trawl surveys carried out by IMARES . See Table 2 for parameters corresponding to model terms; year-classes are labelled by birth year.

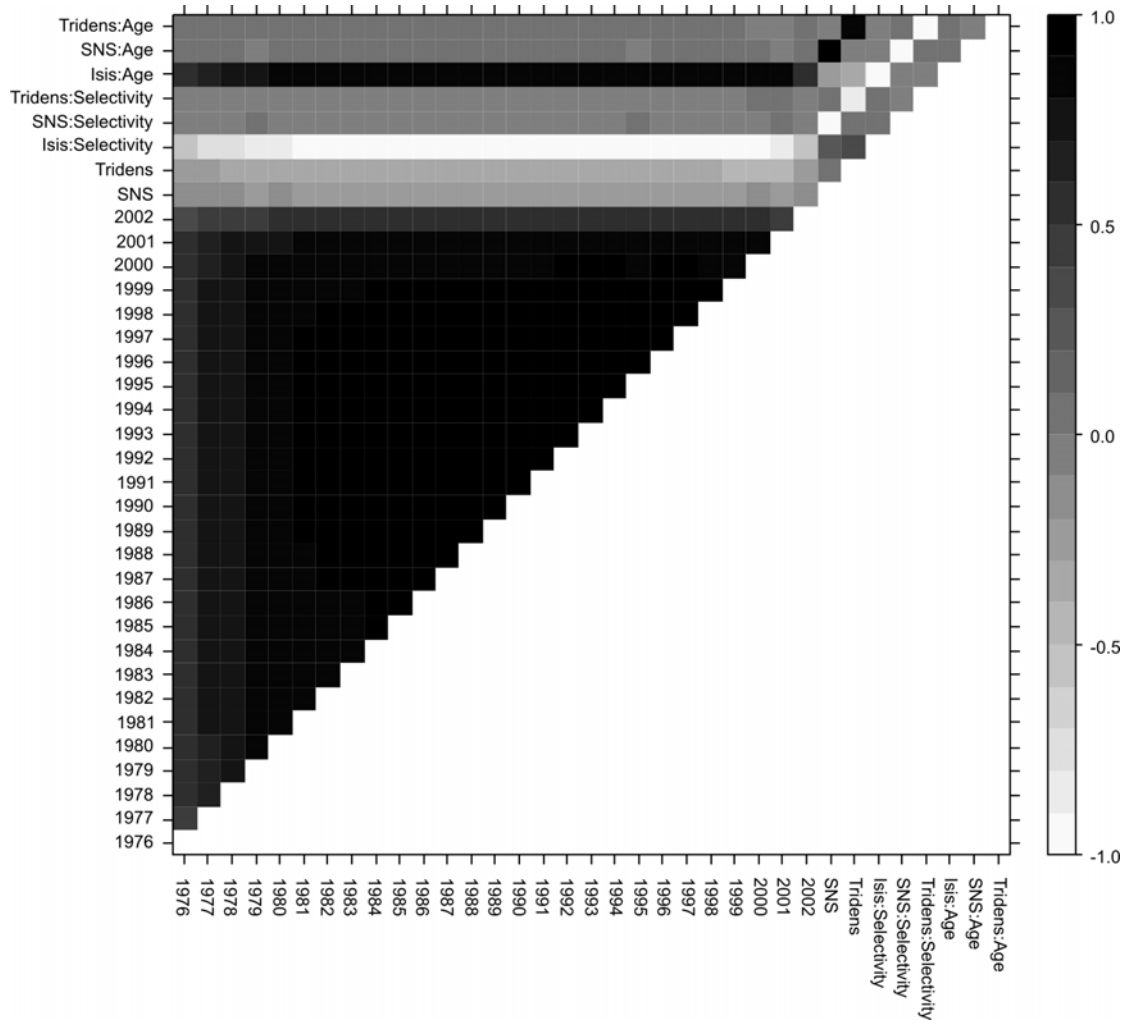


Figure 5. Plaice in North Sea: Year-class curves fitted with the YCC package to log cpue obtained from three beam trawl surveys using model #10; see Tables 3 and 4. a) BTS Isis, 1985-2003; b) BTS Tridens, 1996-2003; c) SNS, 1982-2002. Panel labels show year-classes. Surveys carried out by IMARES.

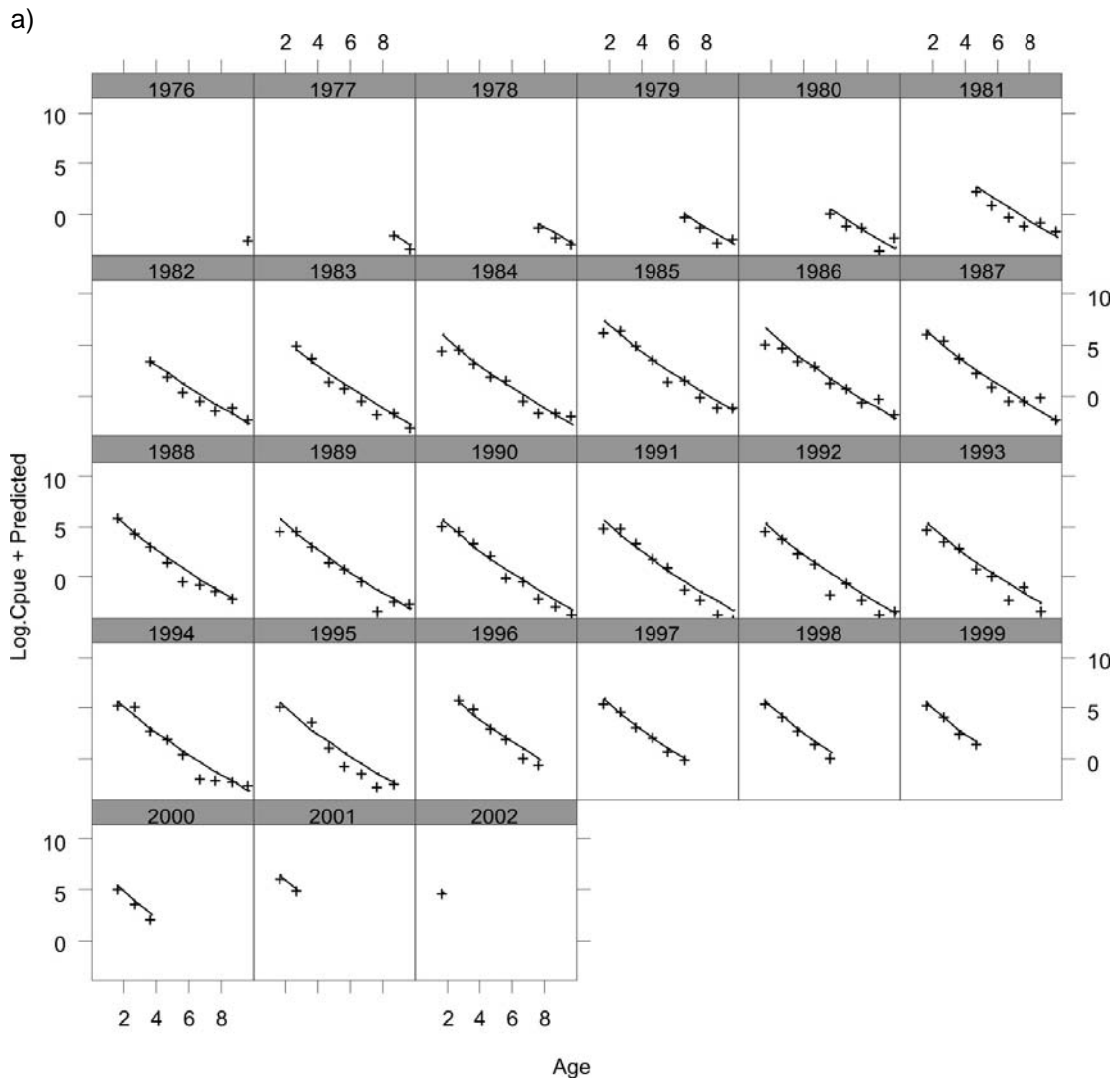


Figure 5 continued. Plaice in North Sea: year-class curves.  
b)

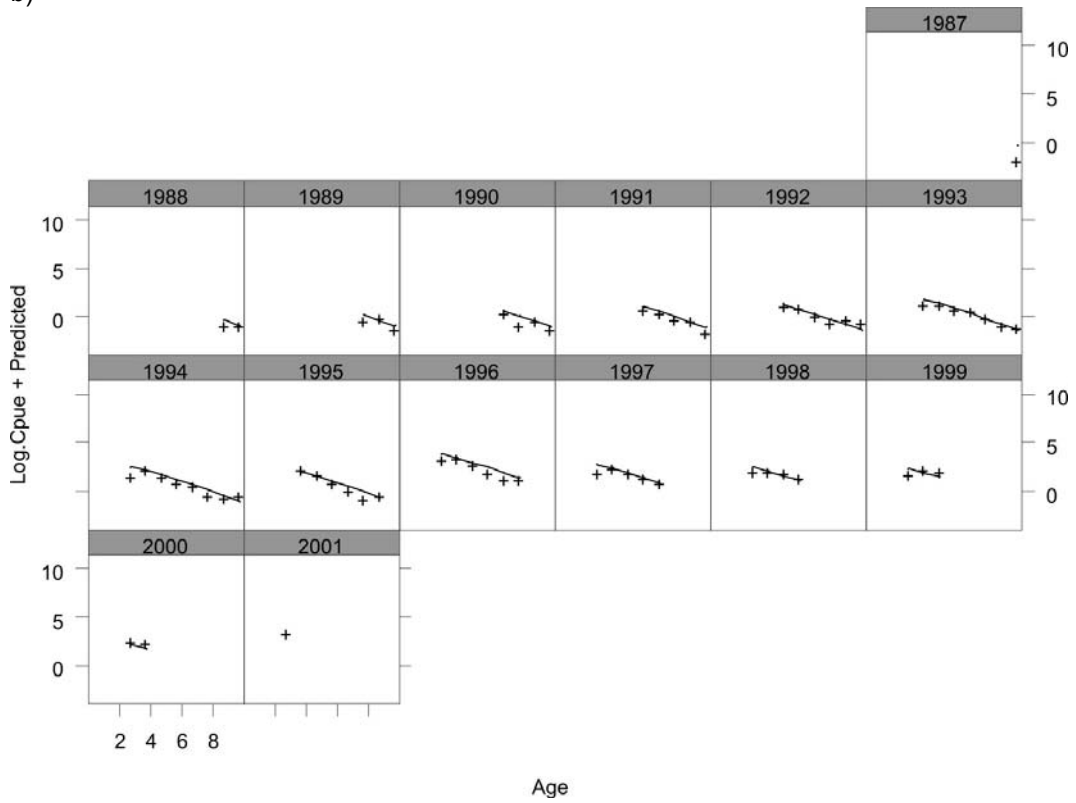


Figure 5 continued. Plaice in North Sea: year-class curves.

c)

