View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Brage IMR

ICES Annual Science Conference Theme Session Q Advances in Reproductive Biology – Methodology and Applications for Fisheries Science CM 2005/Q:05

Not to be cited without prior reference to the author

Systematic bias in estimates of reproductive potential of cod stocks: implications for stock/recruit theory and management

C. Tara Marshall[1], Coby L. Needle[2], Anders Thorsen[3], Olav Sigurd Kjesbu[3], and Nathalia A. Yaragina[4]

[1] University of Aberdeen, School of Biological Sciences, Zoology Bldg., Tillydrone Ave., Aberdeen, AB24 2TZ, Scotland, UK

[2] FRS Marine Laboratory, PO Box 101, 375 Victoria Rd., Aberdeen, AB11 9DB, Scotland

[3] Institute of Marine Research, P.O. Box 1870, N-5817 Bergen, Norway

[4] Polar Research Institute of Marine Fisheries and Oceanography, 6 Knipovich St., Murmansk, 1837763, Russia

Correspondence: C. Tara Marshall, University of Aberdeen, School of Biological Sciences, Zoology Bldg., Tillydrone Ave., Aberdeen, AB24 2TZ, Scotland, UK (fax +44 (0)1224 272396; email c.t.marshall@abdn.ac.uk).

Key-words: cod, population dynamics, reproductive potential, recruitment, sex ratios, reference points, management

Abstract

Stock/recruit relationships, describing the relationship between the parental population and the number of offspring produced, are a central tool in population ecology. For fish populations the stock/recruit relationship uses spawning stock biomass (SSB) to represent reproductive potential of the parental population. This assumes that the proportion of SSB comprised of females and the relative fecundity (number of eggs produced per unit mass) are both constant over time. To test these two constancy assumptions female-only spawner biomass (FSB) and total egg production (TEP) were estimated for the Northeast Arctic cod stock over a 56-year time period (1946-2001). During that time period the proportion of females (FSB/SSB) varied between 24 and 68% and the variation was systematic with length such that SSB became more female-biased as the mean length of spawners increased and more male-biased as mean length decreased. Over the same time period, relative fecundity of the stock (TEP/SSB) varied between 115 and 355 eggs g^{-1} and, like FSB/SSB, was significantly, positively correlated mean length of spawners. Because both FSB/SSB and TEP/SSB covaried with length composition, SSB is systematically biased estimate of reproductive potential. FSB and TEP were evaluated as possible replacements for SSB in stock/recruit relationship. Both indices gave a different interpretation of the recruitment response to reductions in stock size (over-compensatory) compared to that obtained using SSB (either compensatory or depensatory). The threshold level of stock size below which recruitment becomes impaired was estimated for each of the different stock/recruit relationships using piecewise linear regression. There was no difference between SSB and FSB in the assessment of stock status, however, in recent years (1980-2001) TEP fell below the threshold level more frequently than SSB fell below. This suggests that using SSB as a measure of stock reproductive potential may lead to overly optimistic assessments of stock status.

Introduction

Stock/recruit models, representing the fundamental relationship between the parental population and the number of offspring produced (recruitment), are familiar to population ecologists (Krebs 1994) and an important tool for the management of harvested populations (Ricker 1975). Empirical support for the existence of a stock/recruit relationship is notably weak (Peters 1991) making it difficult to discern the functional form of the relationship with certainty. In the case of harvested populations, the requirement for a rationale basis for management often dictates that a stock/recruit model be fit, irrespective of the degree of noise in the data. This is especially true of fisheries management that, under the precautionary approach, fits statistical models to stock/recruit data in order to define the stock size at which recruitment is impaired and then seeks to keep the stock well above that threshold level (Caddy and Mohn 1995). A high degree of variability in the stock/recruit relationship impedes the accurate estimation of that threshold level. Underestimating the threshold level is of particular concern as it will potentially lead to overly-optimistic assessments of stock status.

One potential source of variability in the stock/recruit relationship is an imprecise definition of the independent variable. In fisheries most stock/recruit relationships use spawning stock biomass (SSB) as the measure of reproductive potential thereby assuming that SSB is directly proportional to the annual total egg production by the stock. This requires firstly, that the proportion of SSB that is comprised of females is constant over time; and secondly that the relative fecundity of the stock (number of eggs produced per unit mass) is constant over time (Quinn and Deriso 1999). Intuitively, these two constancy assumptions are unlikely to be valid for fish species that exhibit strongly dimorphic growth, maturation and mortality (Ajiad et al. 1999, Lambert et al. 2003), a high degree of interannual variation in relative fecundity of individuals (Kjesbu et al. 1998; Marteinsdottir and Begg 2002) and/or

large shifts in the size/age composition of the stock (Marteinsdottir and Thorarinsson 1998). Rigorous tests of both constancy assumptions are warranted given the ubiquitous and largely uncritical use of SSB in recruitment research and fisheries management.

If the constancy assumptions are shown to be invalid then the next step is to replace SSB with an alternative index that can be reliably estimated in the current year as well as reconstructed for the historical time period depicted in the stock/recruit relationship. Many fish stocks have relatively long time series of basic demographic information including, age/size composition, maturation, and sex ratios (Tomkiewicz et al. 2003). Fecundity data are in more limited supply (Tomkiewicz et al. 2003), although contemporary fecundity data have been used to develop statistical models that can hindcast values for the historical period (Kraus et a. 2002; Blanchard, Simon and Frank 2003). Thus, by combining historical and contemporary data it is becoming increasingly feasible to estimate alternative indices of reproductive potential such as female-only spawner biomass (FSB) and total egg production (TEP). Cod (*Gadus morhua*) stocks are at the forefront of these efforts (Marshall et al. 1998, Köster et al. 2001), stimulated by research quantifying the sources and magnitude of variability in individual fecundity (Kjesbu et al. 1998, Marteinsdottir and Begg 2002) and by the growing recognition of the implications of this variability for stock management (Scott, Marteinsdottir and Wright 1999).

While alternative indices of stock reproductive potential are being actively developed they have yet to be formally incorporated into fisheries management (Marshall et al. 2003). The socio-economic implications of introducing such a fundamental change requires firstly, compelling evidence that the status quo cannot be justified, and secondly, a detailed evaluation of the consequences of replacing SSB with a new index of reproductive potential. To undertake the latter two key questions must be answered: does the alternative index fundamentally change the functional form of the recruitment response to stock depletion,

and, does the threshold level of recruitment impairment estimated for the alternative index change the classification of stock status as being inside or outside safe biological limits?

With respect to the first question, the observations near the origin of the stock/recruit relationship are of particular interest as they describe the stock as it approaches extinction. This region is critical to determining whether the functional form is classified as compensatory (recruits-per-spawner increases with increasing depletion) or depensatory (recruits-per-spawner decreases with increasing depletion) (Fig. 1a). Depensatory production dynamics potentially result from a wide variety of factors including increased *per capita* predation risk on species which continue to aggregate (or school) at low population levels (Allee et al. 1949), reduced reproductive success (Gilpin and Soulé 1986), predator saturation (Shelton and Healey 1999), and genetic deterioration and inbreeding (Taylor and Rojas-Bracho 1999). If depensation is present in the stock/recruit relationship, then the stock is prone to sudden collapse and fisheries management must be suitably cautious (Liermann and Hilborn 1997; Shelton and Healy 1999). Depensation could possibly explain the failure of collapsed cod stocks to recover despite the cessation of commercial fishing (Shelton and Healey 1999).

With respect to the second question, the precautionary approach to fisheries management, as implemented by the International Council for the Exploration of the Sea (ICES), states that: “in order for stocks and fisheries exploiting them to be within safe biological limits, there should be a high probability that 1) the spawning stock biomass is above the threshold where recruitment is impaired” (ICES ACFM 2003). Management advice for the upcoming fishing year is formulated according to the probability of staying above this threshold by a pre-specified margin of error. For highly indeterminate stock/recruit relationships estimating the level of SSB at which recruitment is impaired is more art than science. Within ICES piecewise linear regression (Barrowman and Myers

2000) is increasingly being used to objectively identify a changepoint representing the level of impaired recruitment (Fig. 1b). An evaluation of alternative indices of reproductive potential should therefore determine whether the changepoint estimated for the alternative index gives a divergent assessment of whether the stock is inside (above the changepoint) or outside (below the changepoint) safe biological limits compared to the assessment made using the conventional SSB changepoint.

These two questions represent fundamentally different approaches to representing the stock/recruit relationship. Depicting the stock/recruit relationship using a non-linear, density-dependent model (Fig. 1a) is an ecological approach that assumes a mechanistic basis for the relationship. In the piecewise linear regression model approach is entirely statistical (Fig. 1b). If the stock/recruit relationship is noisy then the changepoint is often very close to the origin and the stock/recruit relationship is horizontal for most of the range in stock size. This is nearly equivalent to the null hypothesis of no relationship between spawning stock and recruitment, a hypothesis that is categorically rejected as a basis for sustainable management. This statistical approach to describing the underlying dynamics is over-simplified compared to ecological models. While it would be preferable to use an ecological model to identify threshold levels of recruitment impairment in practice the piecewise linear regression model is used because it can be applied objectively to highly indeterminate stock/recruit relationships. Whether this is an appropriate strategy for fisheries management is beyond the scope of this study. However, the two contrasting approaches (ecological and statistical) are used here to assess both the conventional and alternative indices of reproductive potential.

In this study FSB and TEP were estimated for the Northeast Arctic cod stock using the same databases and time periods that are used to estimate SSB, thus ensuring that the two alternative indices of reproductive potential are directly comparable to the conventional index. The assumptions of constant proportion of females and constant relative fecundity of

the stock were tested by inspecting time trends in the ratios FSB/SSB and TEP/SSB. The stock/recruit relationships obtained using SSB, FSB and TEP as indices of stock reproductive potential were compared to determine whether they differed with respect to providing evidence of depensatory or compensatory production dynamics. Additionally, changepoints were estimated for the alternative stock/recruit relationships to determine whether they assessed stock status differently to or consistently with the SSB changepoint. Implications of the results for the management of Northeast Arctic cod stock, stock/recruit theory and research into maternal effects on population dynamics are discussed.

Material and methods

The Northeast Arctic cod stock inhabits the Barents Sea, an arcto-boreal shelf sea that is situated north of Norway and north-western Russia between 70 and 80°N. Both Norway and Russia have extensive long-term databases describing the biological characteristics of the Northeast Arctic cod stock. Selected age-specific data are reported annually by Russia and Norway to the ICES Arctic Fisheries Working Group (ICES AFWG). The annual report of the ICES AFWG (e.g., ICES ACFM 2002) contains time series for several demographic parameters (e.g., numbers-, proportion mature-, and weight-at-age) that have been estimated by combining the Russian and Norwegian data into a single time series. Other data (e.g., length composition, sex ratios) are only available by directly accessing the Russian and Norwegian databases.

ALTERNATIVE INDICES OF REPRODUCTIVE POTENTIAL

For Northeast Arctic cod SSB is estimated by the ICES AFWG as:

$$SSB = \sum_{a=3}^{13+} n_a \times m_a \times w_a \qquad \text{Eq. 1}$$

where n_a, m_a and w_a are the numbers-, proportion mature- and weight-at-age, respectively (Table 16 of ICES ACFM 2002). By convention, the notation 13+ indicates that all age

classes age 13 and older have been combined into a single age class. Values of n_a are determined using a version of cohort analysis known as extended survivors analysis (Shepherd 1999). The values of m_a and w_a represent arithmetic averages of the Norwegian and Russian values of m_a and w_a (ICES ACFM 2001).

To estimate FSB, Eq. 1 can be modified in several ways depending on the data that are available. One approach would be to estimate the number of mature fish at age and multiply this value by the proportion of mature fish that are female at age ($f_{a|m}$):

$$\text{FSB} = \sum_a n_a \times m_a \times f_{a|m} \times w_a \qquad \text{Eq. 2}$$

Another approach is to estimate:

$$\text{FSB} = \sum_a n_a \times s_a \times m_{a|f} \times w_a \qquad \text{Eq. 3}$$

where s_a is the sex ratio at age and $m_{a|f}$ is the proportion of females that are mature at age. This approach requires that two additional terms be estimated: sex ratios and a maturity ogive that is applicable only to females.

For slow-growing stocks such as Northeast Arctic cod reproductive traits such as fecundity are length- rather than age-dependent. A length-based estimate of SSB (len-SSB) would be estimated as:

$$\text{len-SSB} = \sum_l n_l \times m_l \times w_l \qquad \text{Eq. 4}$$

where n_l, m_l and w_l are the numbers-, proportion mature- and weight-at-length, respectively. A length-based estimate of FSB (len-FSB) would be obtained using:

$$\text{len-FSB} = \sum_l n_l \times s_l \times m_{l|f} \times w_l \qquad \text{Eq. 5}$$

where s_l is the proportion of females at length and $m_{l|f}$ is the proportion of females that are mature at length. Length-based total egg production (len-TEP) could be estimated using:

$$\text{len-TEP} = \sum_{l} n_l \times s_l \times m_{l|f} \times e_l \qquad \text{Eq. 6}$$

where e_l is the number of eggs produced by mature females of a given length.

Female-only spawner biomass

To estimate len-FSB for the years 1946 to 2001 using Eq. 5 length-based equivalents for n_a, w_a and m_a were derived as is described below.

(a) Numbers-at-length (n_l)

Estimates of n_a (ICES ACFM 2002) were transformed to n_l using the combined (Russian and Norwegian) age/length keys (ALK) that are described in detail in Marshall et al. (2004). These combined ALK were estimated for each year in the time period (1946-2001) using Russian and Norwegian data and describe the aggregate stock (immature and mature combined, males and females combined). They were constructed for 5-cm length groups ranging from 0 to 140+ cm and ages 3 to 13+ and each element in the matrix gives the proportion of fish at that age and length combination. The vector representing the values of n_a (ages 3-13+, from Table 3.23 of ICES ACFM 2002) for a given year was then multiplied by the ALK for that year to obtain a vector of n_l values for that year.

(b) Proportion female at length (s_l)

Only Norwegian data were used to estimate the s_l for each 5-cm length class. The observed values of s_l for all years (excluding 1980-1984 which had data quality problems) are shown in Fig. 2a. At lengths greater than 80 cm the data show a clear trend towards increasing values of s_l with increasing length, reflecting the differential longevity of females relative to males. At lengths less than 60 cm values of s_l fluctuate about 0.5 with values of 0 and 1 being observed when the sample size used to estimate the proportion is low. Between

60 and 80 cm there is some suggestion of values of s_l being less than 0.5. However, this tendency is likely an artefact resulting from the differential behaviour and/or distribution of mature males (Brawn 1962) that could predispose them to capture.

The values of s_l that were used for estimating len-FSB (Eq. 5) and len-TEP (Eq. 6) assumed that the proportion of females was constant and equal to 0.5 for cod less than 80 cm. For lengths greater than 80 cm, the data were re-expressed as the total count of females (p_l) and males (q_l) with the response variable of the model (z_l) being equal to the odds (i.e., p_l/q_l). The model:

$$z_l = \exp(a + b\,L) \qquad \text{Eq. 7}$$

was fit to data for each year using a logit link function and assuming a binomial error distribution with L being the midpoint of the 5 cm length class. The response variable was back-transformed from logits to proportions ($s_l = p_l/p_l+q_l$) by:

$$s_l = 1/(1 + 1/e^{z_l}) \qquad \text{Eq. 8}$$

The predicted proportions show that above 80 cm the proportions of females increases with increasing length, however, there is a considerable amount of interannual variability in sex ratios (Fig. 2b). Modelled values for s_l (Fig. 2b) were used to estimate the len-FSB (Eq. 5) and len-TEP (Eq. 6). For the years 1980 to 1984 the average of the modelled values for 1979 and 1985 were used.

(c) Proportion mature at length (m_l)

The ALK described above were also used to estimate m_l as follows. For each year the numbers of mature ($n_{a,mat}$) and immature ($n_{a,imm}$) cod at age vectors were estimated by multiplying the VPA numbers at age vector (n_a) by the m_a and $1 - m_a$ vectors, respectively. The resulting vectors of $n_{a,mat}$ and $n_{a,imm}$ were then multiplied by the corresponding year-specific ALK to give the numbers of mature and immature cod at length ($n_{l,mat}$ and $n_{l,imm}$,

respectively). The proportion mature at length (m_l) was therefore estimated as $n_{l,mat} / (n_{l,mat} + n_{l,imm})$.

There were several years for which observations for the 127.5, 132.5 and 137.5 cm length classes were equal to 0. Such observations could be valid, i.e., created by a single individual that was skipping spawning. However, given that these observations were based on relatively few observations, a value of 1.0 was assumed instead. The resulting values of m_l show a high degree of variation across the entire 56 year time period (Fig. 3a). For, example the values of m_l for 72.5 cm range from 0.01 to 0.67. The estimated values of m_l were used to estimate len-SSB, len-FSB, and len-TEP.

(d) Proportion of females that are mature at length ($m_{l|f}$)

The approach taken to estimating $m_{l|f}$ was to correct the m_l values described above, which were estimated for males and females combined, to account for the slower maturation of females compared to males (Lambert et al. 2003). To develop a correction factor, only Norwegian data for 1985 and onwards were available. For each of these years logistic models were fit to data for males and females combined and to data for females-only using generalised linear models and assuming a binomial error distribution. The difference between the two ogives at the mid-point of each 5-cm length class (Δm_l) was then estimated. Values of Δm_l consistently peak at length classes having midpoints of 62.5 or 67.5 cm (Fig. 4) indicating that in the intermediate length range the values of m_l for male and female combined are consistently greater than values for female-only.

For each year in the time period 1985 to 2001 the value of $m_{l|f}$ was estimated as m_l minus the estimated value of Δm_l for that year. Values of $m_{l|f}$ were assumed to be zero if m_l minus Δm_l was negative. No correction was applied for lengths greater than 100 cm. For years prior to 1985 a two-step approach was taken. Firstly, a polynomial model was fit to

values of Δm_l pooled for 1985 to 2001 using non-linear regression in SPLUS (Fig. 4). The resulting model is given by:

$$\ln(\Delta m_l) = -318.81 + 154.28*\ln(L) - 18.79*(\ln(L)^2) \qquad \text{Eq. 9}$$

where L is the midpoint of the 5 cm length class. The fitted quadratic model was used to give a standard value of Δm_l for each midpoint in the range from 42.5 to 97.5 cm (outside of that length range Δm_l was assumed to be 0). The $m_{l|f}$ was estimated as the year-specific value of m_l for males and females combined minus the model value of Δm_l.

(e) Weight-at-length (w_l)

This study used the year-specific weight/length relationships that were derived from the weight-at-age time series that are provided annually to the ICES AFWG by Norway and Russia. These are described in detail in Marshall et al. (2004). The weight/length relationships show considerable interannual variation (Fig. 5) and for cod that are larger than 70 cm there has been a distinct longterm trend towards higher values of w_l (Fig. 3b).

Total egg production

Estimating len-TEP required values of individual fecundity (e_l) for each year in the 56-year time period. Given that fecundity determinations were made for only a small number of those years, it was necessary to develop a statistical model that could hindcast e_l for the full time period using available information. During the full time period there has been considerable variation in condition (*sensu* energy reserves) of cod that resulting from fluctuations in the abundance of capelin (Yaragina and Marshall 2000). Consequently, model development included testing whether relative condition explained a significant portion of the residual variation in the fecundity/length relationship.

Fecundity-at-length (e_l)

A dataset was available of fecundity determinations made for Northeast Arctic cod in the years 1986-1989, 1991, 1999 and 2000 (see Kjesbu et al. 1998 for sampling details). The

subset of this dataset that was used here omitted observations if they were from coastal cod (distinguished by otolith type), from cod having oocyte diameters less than 400 μm or from cod that were assessed visually as having begun spawning. Using this subset of observations, the following steps were taken as part of model development.

(a) Estimation of condition of pre-spawning females in the fecundity dataset

The pre-spawning females exhibited a temporal trend in condition that mirrored that observed in the stock generally (Fig. 6). To represent the condition of the individual pre-spawning females in the fecundity dataset, relative condition (Kn) was estimated as the observed weight of the female divided by a standard weight which was estimated using a length/weight relationship developed using data for all of the pre-spawning females pooled for all seven years. This relationship is given by:

$$w = \exp(-5.472 + 3.171 \ln(L)) \qquad \text{Eq. 10}$$

which was obtained by fitting a generalized linear model (assuming a gamma error distribution with a log–link function, d.f. = 478, $p < 0.001$) to the length and weight data for the pre-spawning females pooled for all seven years. Thus, Kn expresses condition of the individual female relative to the "mean" condition of all of the females in the pooled dataset for the seven years.

Fortuitously, the seven years in which fecundity was sampled was marked by strong variation in the condition of cod (Fig. 6). Consequently, the variability observed in the length and weight data for the fecundity dataset is similar to the magnitude of variability observed in the length/weight regressions developed for the stock over the full time period (Fig. 5). The variability in condition of the pre-spawning females in the fecundity dataset was therefore considered to mimic the variability occurring at the stock-level over the full time period.

(b) Development of a fecundity model for hindcasting

For the fecundity dataset, both length and Kn of the pre-spawning females were significantly correlated with fecundity (Table 1). The resulting model for e_l (millions) was:

$$e_l = \exp(-15.090 + 3.595 (\ln(L)) + 1.578 (\ln(Kn))) \quad \text{Eq. 11}$$

The model adequately captures the range of variability in observed fecundity (Fig. 7a) and the residuals showed no pattern with either length or Kn.

(c) Estimation of Kn at the stock level

In order to apply Eq. 11 to the stock-level, year- and length-specific values of Kn were required for the full time period (1946-2001). The year-specific weight/length relationships described above (see Fig 5) were used to predict w_l ranging in five cm increments between 50 and 140 cm for each year. These model-derived values of w_l were then treated as the "observed" weights for the pre-spawning females in the stock for that year (note these values of w_l were also used to estimate len-SSB and len-FSB).

To express condition in a specific year relative to longterm (1946-2001) trends in condition the "longterm" weight was estimated by pooling all of the "observed" weights for standard lengths for all years and fitting a weight/length relationship to those data. The resulting equation was:

$$W = \exp(-4.836 + 3.014 \ln L) \quad \text{Eq. 12}$$

and was fit using a generalised linear model (assuming a gamma error distribution with a log–link function, d.f. = 1007, $p < 0.001$). For each year Kn was then estimated by the ratio of the "observed" weight to the "longterm" weight obtained from Eq. 12.

Application of the fecundity model to estimating TEP of the stock

For each year e_l was estimated for lengths ranging in five cm increments between 50 and 140 cm using Eq. 11. The degree of variability in values of e_l over the full time period

(Fig. 7b) is similar to the level of variability observed in the fecundity dataset (Fig. 7a). This indicates that the dynamic range in the hindcast values is comparable to that observed in the seven years of highly variable condition that are represented in the fecundity dataset. The hindcast values of e_l were then used to estimate len-TEP from Eq. 6.

REPRESENTING THE SIZE STRUCTURE OF THE SPAWNING STOCK

To represent the length composition of the spawning stock in a given year the mean length of the spawning stock (SS_{len}) was estimated as:

$$SS_{len} = \frac{\sum_{l=42.5}^{137.5+} l \times n_l \times m_l}{\sum_{l=42.5}^{137.5+} n_l \times m_l} \qquad \text{Eq. 13}$$

where l is the midpoint of 5-cm length classes spanning 40 to 140+ cm. This value describes mean length composition of spawners based on their numerical abundance ($n_l \times m_l$) rather than on the basis of their biomass (i.e., $n_l \times m_l \times w_l$).

REPRESENTING THE STOCK/RECRUIT RELATIONSHIP

Separate stock/recruit relationships were developed using SSB, len-FSB and len-TEP as indices of reproductive potential. In all cases, the recruitment index used was the number at age 3 (ICES ACFM 2002) corresponding to the 1946 to 1998 year-classes. Depensation cannot be resolved using the standard two-parameter Beverton-Holt nor Ricker models (Quinn and Deriso 1999). Therefore, the functional form of the stock/recruit relationships was described by fitting a three-parameter Saila-Lorda model (Needle 2002) that is formulated as:

$$R = \alpha S^{\gamma} e^{-\beta S} \qquad \text{Eq. 14}$$

where S denotes the index of reproductive potential (here SSB, len-FSB, or len-TEP) and R denotes recruitment. In the Saila-Lorda model α measures density-independence as

modulated by depensation, β measures density-dependent factors, and γ is a scale-independent shape parameter (Fig. 1a). The γ parameter in the Saila-Lorda model is a direct measure of depensation that is independent of the scale of the datasets, a property that facilitates comparisons among the different datasets. When $\gamma > 1$ the relationship between R and S is depensatory. For the special case where $\gamma = 1$ the relationship is perfectly compensatory and equivalent to the standard Ricker curve. When $\gamma < 1$ the relationship is considered to be over-compensatory. The Saila-Lorda model has several other convenient analytical properties, as summarized in Table 2. For example, a unique maximum (R_p and S_p) occurs at:

$$\left(R_p, S_p\right) = \left(\alpha\left(\frac{\gamma}{\beta}\right)^{\gamma} e^{-\gamma}, \frac{\gamma}{\beta} \right) \qquad \text{Eq. 15}$$

(Table 2). Conceptually, this point can be considered as the level of S below which R decreases in either a depensatory or compensatory fashion (Fig. 1a).

In this study, the Saila-Lorda model was fit through a lognormal transformation of Eq. 14 to:

$$\ln R = a + b\,S + c \ln S \qquad \text{Eq. 16}$$

where α is equal to exp (a), β is equal to – b and γ is equal to c. The model was fit in SPLUS as a linear model and 95% confidence intervals were approximated as ± 2 × standard error of the prediction.

Depensation in a stock can only be tested for properly if there are observations in the stock/recruit scatterplot that are sufficiently close to the origin. To ensure that was the case here, the following criteria were applied. For fits that were deemed to potentially be depensatory ($\gamma > 1$), the lower inflection point of the Saila-Lorda curve (Table 2) was

compared to the S_{min}. If the lower inflection point was greater than S_{min} then the fit was accepted as being depensatory.

ESTIMATION OF CHANGEPOINTS

Piecewise linear regression (Barrowman and Myers 2000) was used to estimate changepoints for the stock/recruit relationships developed using the two alternative indices of reproductive potential (len-FSB and len-TEP) as well as the conventional index (SSB). The piecewise linear regression model is given as:

$$R = \begin{vmatrix} \alpha_1 + \beta_1 S & 0 \le S \le \delta \\ \alpha_2 + \beta_2 S & \delta \le S \end{vmatrix} \qquad \text{Eq. 17}$$

where δ represents the changepoint value. For stock and recruitment data, the model is constrained to pass through the origin (i.e., $\alpha_1 = 0$) and beyond the changepoint (δ) the line is horizontal (i.e., $\beta_2 = 0$). Thus, Eq. 17 simplifies to:

$$R = \begin{vmatrix} \beta_1 S & 0 \le S \le \delta \\ \alpha_2 & \delta \le S \end{vmatrix} \qquad \text{Eq. 18}$$

which can be re-expressed on a lognormal scale as:

$$\ln R = \begin{vmatrix} \ln\beta_1 + \ln S & 0 \le S \le \delta \\ \ln\alpha_2 & \delta \le S \end{vmatrix} \qquad \text{Eq. 19}$$

All possible two-line models were fit iteratively (i.e., values of α_2 and β_1 were assumed) and their intersection point (δ) was then estimated. The algorithm of Julious (2001) for fitting a model with one unknown changepoint was used. The model that minimized the residual sum of squares was selected to give a final value of δ and the associated value of α_2 indicating the level at which R plateaus for values of S that are greater than δ.

Results

COMPARISON OF SSB AND LEN-SSB

To confirm that the conversion from age- to length-based descriptors of the stock did not result in significant distortion the values of SSB (Eq. 1) and len-SSB (Eq. 4) were compared. The two values are close (average difference between len-SSB and SSB expressed as a percentage of SSB: 1.8%) and the mean of the difference between them was not significantly different from 0 (paired t-test, df = 55, p-value = 0.13).

TIME TRENDS IN THE PROPORTION OF FEMALES

The proportion of SSB consisting of females (i.e., len-FSB/SSB) is not constant and equal to 0.5 (Fig. 8a). Instead, len-FSB/SSB ranges between a maximum of 0.68 in 1948 and a minimum of 0.24 in 1987. Values of len-FSB/SSB were below 0.5 in approximately 57% of the years, indicating that the spawning stock has been dominated by males for a majority of the full time period. In extreme years (e.g., the late 1980's), males comprise approximately three-quarters of the SSB. Over the full time period there have also been dramatic changes in the size composition of the spawning stock. Values of SS_{len} were generally high (> 75 cm) until the mid-1970s when they decreased by more than 30 cm, from a maximum of 91.7 cm in 1974 to a minimum of 60.9 cm in 1988 (Fig. 8a). There is a statistically significant, positive correlation between SS_{len} and len-FSB/SSB ($r = 0.71$, d.f. = 55, $p < 0.001$) indicating that SSB becomes progressively male-biased as the length composition shifts towards smaller-sized fish.

TIME TRENDS IN RELATIVE FECUNDITY OF THE STOCK

The relative fecundity of the stock was estimated as len-TEP/SSB. Relative fecundity of the stock exhibits a three-fold level of variation, ranging from a maximum of 355 eggs g^{-1} in 1974 to a minimum of 115 eggs g^{-1} in 1987 (Fig. 8b). Because SSB includes non-contributing males these values of relative fecundity of the stock are lower than values of

relative fecundity estimated for an individual female. As was the case for len-FSB/SSB, interannual variation in relative fecundity of the stock is being driven by variation in size composition of the spawning stock, as represented by SS_{len} (Fig. 8b) and there is a significant, positive correlation between them ($r = 0.70$, d.f. = 55, $p < 0.001$). Since 1980, a majority of years (15 out of 22) have been below the longterm (1946-2001) mean relative fecundity of 235 eggs g^{-1}.

DEPENSATORY VS. COMPENSATORY PRODUCTION DYNAMICS

Using SSB as an index of reproductive potential for the 1946 to 1998 year-classes, the fitted Saila-Lorda model had a value of γ of 1.044 (Table 3) which is very close to 1 suggesting that the functional form of the relationship between R and SSB for the full time period is approximately compensatory (Fig. 9a). The Saila-Lorda models for both len-FSB (Fig. 9b) and len-TEP (Fig. 9c) gave values of γ that were less than 1 (Table 3) suggesting that there was over-compensation in the stock/recruit relationship. The values of S_p for SSB, len-FSB and len-TEP were 705,000 t, 563,000 t, and 2.93E+14, respectively. There were only small differences between the three indices in values of R_p, which ranged from 7.19E+8 to 7.41E+8 (Table 3).

In approximately 1980 the spawning stock shifted towards a smaller-sized stock having reduced relative fecundity (Fig. 8). This reduction in productivity could have repercussions for the stock/recruit relationship. Accordingly, the stock/recruit relationships for the recent time period (representing the year-classes spawned in 1980-1998) were examined separately. There is clearer evidence of a non-linear stock/recruit relationship for the recent time period (Fig. 9d-f) and, unlike the full time period (Fig. 9a-c), the scatterplots do not feature as many observations having high values of R and low values of stock reproductive potential. Using SSB as the index of reproductive potential the value of γ was estimated to be 1.689 which is suggestive of depensation (Fig. 9d). Because the lower

inflection point (123,000 t) exceeds the value of S_{min} (108,000 t), there was sufficient data near the origin to support the conclusion of depensation. The stock/recruit relationships that used len-FSB and len-TEP as indices of reproductive potential had values of γ that are consistently less than 1 (Table 3), once again suggesting over-compensation (Fig. 9e,f). There were relatively small differences between R_p values (6.82E+8, 6.63E+8, and 6.47E+8 for SSB, len-FSB and len-TEP, respectively; Table 3). However, these R_p values are consistently lower than for the full time period, suggesting that there has been a decline in the maximum level of recruitment.

CHANGEPOINTS

Changepoint values (δ) were determined for the same six sets of stock/recruit data that were used to fit Saila-Lorda models. For the full time period the values of δ for SSB, len-FSB and len-TEP are 186570 t, 61679 t and 3.26E+13 eggs, respectively (Table 4). Visually, the piecewise linear regression models for the full time period are relatively indistinguishable from each other in terms of the relative position of δ (Fig. 10a-c). The recruitment (R) values associated with the horizontal line segment (i.e., α_2 in Eq. 18) range between 5.07E+8 and 5.27E+8 which amounts to a small difference (ca. 4%) between them (Table 4). The three different indices of reproductive potential gave similar assessments of the proportion of years in the 56-year time series when the stock was above or below δ. Agreement between SSB and len-FSB about whether stock status was inside (above δ) or outside (below δ) safe biological limits was achieved in 48 (85.7%) of the 56 years (Table 5). Similarly, there was agreement between SSB and len-TEP in 49 (87.5%) of the 56 years (Table 5).

The value of δ for SSB in the recent time period (1980 – 1998 year-classes) was very close (within 3.8%) to the value of δ estimated for the full time period (Table 4). For len-FSB, the values of δ for the full and recent time periods were exactly equivalent (Table 4). This was because for both the full and recent time periods the same assumed values of α_2 and

β_1 were used to iteratively fit piecewise linear regression models. The value of δ for len-TEP in the recent time period (6.33E+13) is nearly double the value estimated for the full time period (3.26E+13) and the R value associated with the horizontal line segment in the recent time period was 6.17E+8 compared to 5.14E+8 for the full time period (Table 4). As was the case for the full time period, there was considerable agreement between SSB and len-FSB in assessing stock status: the two changepoints gave the same assessment of stock status in 20 (90.9%) of the 22 years (Table 5). The greatest difference between the full and recent time periods was a lower level of agreement between SSB and len-TEP about whether stock status was inside or outside safe biological limits. There was disagreement between the two indices of reproductive potential in 50% of the years in the recent time period (Table 5). In 5 (22.7%) of the 22 years stock status was inside safe biological limits according to the changepoint for SSB, whereas, using the changepoint for len-TEP the stock was judged to be outside safe biological limits. Thus, in over twenty percent of the years in the recent time period len-TEP gives a more pessimistic view of stock status than did SSB.

Discussion

This study has clearly shown that the dimorphic growth, maturation and mortality that is characteristic of cod (Lambert et al. 2003) combined with size-dependent harvesting causes sex ratios to become increasingly female-biased when the stock has a high proportion of large individuals and increasingly male-biased when the size composition is shifted towards smaller sizes. Skewed sex ratios are likely to occur in other commercially harvested fish stocks given that size dimorphism (either females or males being larger at maturity) is widespread and often indicative of the reproductive strategy of the species (Henderson et al. 2003). This result is consistent with other studies indicating that at the population-level sex ratios fluctuate to a considerable degree (Caswell and Weeks 1986; Lindström and Kokko 1998; Pettersson et al. 2004). In some populations variability in sex ratios is an adaptive

response that matches the proportional abundance of males and females to current and expected fitness payoffs (Trivers and Willard 1973; Clutton-Brock 1986). For other populations, sex ratios are modified by externally applied selection pressures that are gender-specific and variable in time and(or) space. For example, female-biased sex ratios have been noted for species that experience sport hunting for male trophy animals (Milner-Gulland et al. 2003; Whitman et al. 2004) and gender-specific mortality (Dyson and Hurst 2004).

IMPLICATIONS FOR CONSERVATION OF COD STOCKS

There are several implications of skewed sex ratios for fisheries management. Systematic variation in both the proportion of mature females contributes to variation in the relative fecundity of the stock (i.e., TEP/SSB). Consequently, the constancy assumptions which underlie the use of SSB in stock/recruit relationships are invalid. As a result, SSB underestimates reproductive potential when the stock is dominated by large cod and overestimates reproductive potential when the stock is dominated by small cod. Because stocks dominated by smaller-sized individuals often result from sustained high fishing mortality the efficacy of management protocols is impacted by a systematic bias and the magnitude of that bias is partly determined by the intensity and duration of fishing mortality. For example, in 1987 the mean length of the spawning stock declined to 62.9 cm, just slightly higher than the minimum for the full time period (60.9 cm in 1988). This decline was largely due to the high levels of fishing mortality sustained by the stock: from 1946 to 1988 the average fishing mortality on cod ages 5-10 increased steadily from 0.18 to 0.98 (ICES ACFM 2002). In 1987 approximately one-quarter of the SSB was female and the relative fecundity of the stock was 115 eggs g^{-1} which is approximately one-half of the longterm mean value (235 eggs g^{-1}). Russian and Norwegian authorities sharply reduced fishing mortality from 0.98 in 1989 to 0.27 in 1990 (ICES ACFM 2002). As a result, the relatively strong 1983 year-class of cod was protected and allowed to develop into a year-class that

sustained high total egg production by the stock for five years starting in 1990 (Marshall et al. 1998). This stock recovery was fortuitous because it is clear from this study that management was unaware of the true magnitude of the decline that had occurred because the index that was used (SSB) fails to accurately account for the effect that variation in length composition has on reproductive potential.

Since the late 1980s there have been substantial increases in knowledge pertaining to the reproductive potential of individual cod (Kjesbu et al. 1998) and stocks (Köster et al. 2001; Marteinsdottir and Begg 2002). Incorporating a higher degree of biological information into fisheries management is therefore regarded as imperative (Marteinsdottir and Begg 2002; Köster et al. 2003; Berkeley, Chapman and Sogard 2004). This study illustrates that there are no technical impediments to incorporating alternative indices of reproductive potential into the framework of the precautionary approach, e.g., changepoints. Fisheries management places a premium on using management protocols that can be universally applied which makes it difficult to implement change. However, failing to use the best available knowledge disadvantages data-rich stocks by constraining them to approaches that are suitable for data-poor stocks. Furthermore, the data on sex ratios and maturity required for estimating FSB are readily available for many stocks and species (Tomkiewicz et al. 2003). Fecundity data are considerably more scarce (Tomkiewicz et al. 2003). The approach taken in this study was to use a statistical model developed using relatively recent (post 1980) data to hindcast e_l. In future, improved methods for measuring the fecundity of wild stocks have been developed (Murua et al. 2003) and should encourage the acquisition of new data on this key life history parameter.

For some species a more biological approach to representing reproductive potential in management has already been adopted. In the Northwest Atlantic FSB is being used to estimate threshold levels for spiny dogfish (*Squalus acanthias*) and fecundity data, in terms

of number of pups per female at length, has been used in population projections (Northeast Fisheries Science Center 2003). Because small females produce smaller pups that may have a lower survival rate the population projections account for differential survival rates (Northeast Fisheries Science Center 2003). Stock projections for this depleted stock indicate that it will take considerably longer to rebuild FSB compared to rebuilding SSB because the former requires substantial increases in the proportional representation of large individuals (Northeast Fisheries Science Center 2003). While stock rebuilding times are necessarily long for K-selected species such as the ovoviviparous spiny dogfish, it would be of considerable interest to determine whether there would be substantial differences between SSB and FSB (or between SSB and TEP) in stock rebuilding times for an r-selected species such as cod.

IMPLICATIONS FOR STOCK/RECRUIT THEORY

Cod stocks that approach (e.g., Northeast Arctic cod in 1987/1988) or reach (e.g., northern cod in the early 1990s) a state of collapse provide valuable opportunities to delineate the origin of the stock/recruit relationship more clearly and determine whether the underlying production dynamics are compensatory or depensatory. Using SSB as the index of reproductive potential for Northeast Arctic cod, the recent time period suggested depensation, whereas, the full time period suggested compensation. However, if either len-FSB or len-TEP are used as indices of reproductive potential then both the full or recent time periods exhibited over-compensation. Other studies have found compensatory production dynamics to be the norm among marine groundfish stocks (Myers et al. 1995; Liermann and Hilborn 1997). All other factors being equal, over-compensation should promote a faster stock recovery given that production rate of recruits is highest at the lowest levels of stock reproductive potential.

The behaviour near the origin of the stock/recruit relationship is also important for determining changepoint values that, under the precautionary approach, indicate the level at

which recruitment becomes impaired. Comparing changepoints for both the full and recent time periods showed that the assessments of stock status (in the sense of being inside or outside safe biological limits) did not differ substantially using either SSB or len-FSB as the index of reproductive potential. However, the changepoint for len-TEP was more conservative than the changepoint for SSB in the recent time period when the stock was dominated by smaller-sized spawners: in 22.7% of the years the len-TEP changepoint classified the stock as being outside safe biological limits and the SSB changepoint classified the stock as being inside safe biological limits. The precautionary approach, which advocates using a more risk-averse approach where knowledge is limiting, should therefore consider using len-TEP to assess whether the reproductive potential of the Northeast Arctic cod stock is inside or outside safe biological limits. Given the magnitude of the systematic bias in SSB that has been detected in this study as well as the possibility that in some years SSB assesses the stock as being within safe biological limits when len-TEP indicates that it is not, it is difficult to justify not using the alternative indices in management. Both FSB and TEP are quantifiable, simple, logical, tractable, faithful, comparable and cost-effective, all of which are desirable attributes for any measure that is used to indicate overall stock status (Hall and Mainprize 2004).

The alternative indices of reproductive potential did not substantially increase or decrease the explanatory power of the stock/recruit relationship when compared to SSB (Table 3). This result contrasts with that for the Baltic cod stock which showed incremental improvements in the amount of recruitment variation explained as increasing levels of biological detail were incorporated into the alternative estimates of reproductive potential (Köster et al. 2001; Marshall et al. 2003). The customary explanation of the weakness of the stock/recruit relationship for fish stocks generally is that there is a high degree of interannual variability in mortality during early life history stages (Wooster and Bailey 1989). For

Northeast Arctic cod year-class strength is frequently established during the egg and larval stages (Sundby et al. 1989; Mukhina, Marshall and Yaragina 2003) when mortality rates are at a maximum. Indices describing the abundance of settled juveniles show a higher degree of correlation with subsequent recruitment, indicating that the periods that are critical for establishing year-class strength occur prior to settlement (Mukhina et al. 2003).

Given the importance of mortality during early life stages for recruitment it would be inappropriate to require the alternative indices of reproductive potential to explain a substantially higher degree of recruitment variability than SSB (notwithstanding that they do so for Baltic cod). They should not, however, explain substantially less recruitment variation. For both the full and recent time periods the r^2 values obtained using the two alternative indices of reproductive potential were slightly lower than that obtained using SSB (Table 3). However, given that the formulations of both FSB (Eq. 5) and TEP (Eq. 6) both include four terms rather than the three terms that are used to estimate SSB (Eq. 1), the reductions in r^2 are small. The slight reduction in explanatory power that would accompany replacing SSB with either of the two alternatives is a cost that must be judged against the benefit of correcting for a systematic source of bias and eliminating the need for the two constancy assumptions which underlie the use of SSB.

A larger improvement in the explanatory power of the stock/recruit relationship occurred when the time series for Northeast Arctic cod was restricted to the recent time period only (1980-1998 year-classes) and a clearer density-dependent signal emerged. This observation is consistent with the splitting of the stock/recruit relationship for Baltic cod at 1980 to differentiate between the period when oxygen conditions were favourable to egg and larval survival (1966-1980) and the period when oxygen conditions were unfavourable (1981-present) (ICES ACFM 1998). Given that discontinuities in the stock/recruit dynamics for both cod stocks occurred circa 1980 it is possible that large-scale changes in climate are

responsible. In the case of the Baltic Sea, a reduction in major inflow events occurred in the early 1980s which has been attributed to high indices of the NAO which, in turn, give rise to strong westerly winds, above normal rainfall and increased freshwater runoff (Hänninen et al. 2000).

While it remains to be shown if climate may have contributed to a shift in the recruitment dynamics of Northeast Arctic cod circa 1980 several fundamental demographic changes took place in the stock at the same time. Comparing the pre- and post-1980 periods it is evident that the spawning stock in the former time period was both larger and older compared to the more recent time period when the stock was dominated by smaller/younger individuals. However, a large and relatively abrupt increase in length-at- age and weight-at-length (Marshall et al. 2004) and in the proportion mature-at-length (Fig. 3a) occurred near 1980. Thus, the negative effect of a decline in the proportional abundance of large fish on reproductive potential was partially compensated for by the positive effect of higher growth and maturation rates of smaller fish.

MATERNAL EFFECTS ON POPULATION DYNAMICS

The advances being made in quantifying the reproductive potential of marine fish stocks are occurring simultaneously with a proliferation of experimental studies investigating maternal effects in a wide range of vertebrate and invertebrate species. This research shows that maternal provisioning fluctuates in response to environmental conditions (Mousseau and Fox 1998a) and influences offspring fitness (Mousseau and Fox 1998a,b; LaMontagne and McCauley 2001). It is possible that maternal effects on offspring fitness persist through several generations (Mousseau and Fox 1998b, Metcalfe and Monaghan 2001; Beckermann et al. 2002; Gorman and Nager 2004), setting up so-called downstream effects (Lummaa 2003). In fish populations, maternal effects on offspring can be amplified because, instead of being traded off against each other, both the number and quality of eggs can vary positively

with maternal size and condition (Kjesbu et al. 1991; Lambert and Dutil 2000; Marteinsdottir and Begg 2002). For iteropareous species such as cod smaller females produce fewer batches of eggs over shorter time spans (Kjesbu et al. 1996). Stocks having a relatively broad size structure produce eggs over a longer time period potentially increasing the probability of eggs hatching into favourable environmental conditions (Lambert 1990; Secor 2000; Wright and Gibb 2005). Stocks that are dominated by small females spawn over a narrower time window that could increase the likelihood of recruitment failure if egg production does not coincide with favourable environmental conditions (Kjesbu et al. 1996). Identifying and quantifying the maternal characteristics that impact the probability of survival during early life stages (Lambert et al. 2003) would allow estimates of potential total egg production to be prorated so as to estimate realised total egg production.

CONCLUSION

In the past, the exceptionally high fecundity of many marine fish species engendered a belief in their inexhaustibility that was used to justify excessive rates of exploitation (Kurlansky 1999). A trace of this belief persists in our current approach to quantifying the reproductive potential of fish stocks that assumes that relative fecundity of the stock is constant over time. This study is one of several recent investigations that have illustrated the fallibility of over-simplified assumptions about reproductive potential of cod stocks. The factors contributing to bias in SSB (excessive fishing mortality, variable size composition, variable fecundity, dimorphic growth) apply to other cod stocks and possibly many other species. For many stocks sufficient data are available to correct for the bias and there are no technical impediments to using the alternative indices of reproductive potential within the framework of the precautionary approach (Morgan and Brattey 2004). Thus, the continued use of a flawed estimator of stock reproductive potential is not scientifically defensible. Incorporating greater biological realism into the metrics that are used by cod stock

management to assess stock status will enhance our ability to measure the true effect of fishing on reproductive potential.

Acknowledgements

X. Lambin and B. Bogstad are thanked for their comments on an earlier draft. A. MacLay facilitated the collaboration between CTM and CLN. CTM was partially supported by funding from the Norwegian Research Council (Project No. 130197/130). AT and OSK were partially supported by funding from the European Union (Q5RS-2002-01825).

References

Ajiad, A., Jakobsen, T., and Nakken, O. 1999. Sexual difference in maturation of Northeast Arctic cod. Journal of the Northwest Atlantic Fishery Science **25:**1-15.

Allee, W.C., Emerson, A.E., Park, O., Park, T., and Schmidt, K.P. 1949. Principles of animal ecology. W.B. Saunders Co., Philadelphia.

Barrowman, N.J., and Myers, R.A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences **57**:665-676.

Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V., and Lundberg, P. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology and Evolution **17**:263-269.

Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology **85**:1258-1264.

Blanchard J.L., Frank K.T., and Simon J.E. 2003. Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock (*Melanogrammus aeglefinus*). Canadian Journal of Fisheries and Aquatic Sciences **60**:321-332.

Brawn, V.M. 1962. Reproductive behaviour of the cod (*Gadus callarias* L.). Behaviour **18**:177-198.

Caddy, J.F., and Mahon, R. .1995. Reference points for fisheries management. FAO Fisheries Technical Paper. No. 347. Rome, FAO.

Caswell, H., and Weeks, D.E. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. American Naturalist **128**:707-735.

Clutton-Brock, T.H. 1986. Sex ratio variation in birds. Ibis **128**:317-329.

Dyson, E.A., and Hurst, G.D.D. 2004. Persistence of an extreme sex-ratio bias in a natural population. Proceedings of the National Academy of Sciences **101**:6520-6523.

Gilpin, M., and Soulé, M. 1986. Minimum viable populations: processes of species extinctions. Conservation Biology: the science of scarcity and diversity. (ed M. Soulé), pp. 19-35. Sinauer Associatiates Inc., Sunderland, Mass.

Gorman, H.E., and Nager, R.G. 2004. Prenatal developmental conditions have long-term effects on offspring fecundity. Proceedings of the Royal Society, London, B, **271**:1923-1928.

Hall, S.J., and Mainprize, B. 2004. Towards ecosystem-based fisheries management. Fish and Fisheries **5**:1-20.

Henderson, B.A., Collins, N., Morgan, G.E. and Vaillancourt, A. 2003. Sexual size dimorphism of walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences **60**:1345-1352.

Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnology and Oceanography **45**:703-710.

International Council for the Exploration of the Sea Advisory Committee on Fishery Management. 1998. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1998/ACFM 16.

International Council for the Exploration of the Sea Advisory Committee on Fishery Management. 2001. Report of the Arctic Fisheries Working Group. ICES C. M. 2001/ACFM:19.

International Council for the Exploration of the Sea Advisory Committee on Fishery Management 2002. Report of the Arctic Fisheries Working Group. ICES C. M. 2002/ACFM 18.

International Council for the Exploration of the Sea Advisory Committee on Fishery Management 2003. Report of the Study Group on biological reference points for Northeast Arctic cod. ICES C. M. 2003/ACFM 11.

Julious, S.A. 2001. Inference and estimation in a changepoint regression problem. The Statistician **50**:51-61.

Kjesbu, O.S., Klungsøyr, J., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences **48**:2333-2343.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*) Canadian Journal of Fisheries and Aquatic Sciences **53**:610-620.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Greer Walker, M. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. Journal of Sea Research **40**:303-321.

Kraus, G., Tomkiewicz, J., and Köster, F.W. 2002. Egg production of Baltic cod in relation to variable sex ratio, maturity and fecundity. Canadian Journal of Fisheries and Aquatic Sciences **59**:1908-1920.

Krebs, C.J. 1994. Ecology: the experimental analysis of distribution and abundance. 4th edition. HarperCollins College Publishers. New York.

Kurlansky, M. 1999. Cod: a biography of the fish that changed the world. Vintage, Denmark.

Köster, F.W., Hinrichsen, H.-H., St. John, M.A., Schnack, D., MacKenzie, B.R., Tomkiewicz, J., and Plikshs, M. 2001. Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences **58**:1534-1566.

Köster, F.W., Schnak, D., and Möllmann, C. 2003. Scientific knowledge of biological processes that are potentially useful in fish stock predictions. Scientia Marina **67(Suppl. 1)**:101-127.

Lambert, T.C. 1990. The effect of population structure on recruitment in herring. Journal du Conseil. Conseil Permanent International pour L'exploration de la Mer **47**:249-255.

Lambert, Y., and Dutil, J.-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences **57**:815-825.

Lambert, Y., Yaragina, N.A., Kraus, G., Marteinsdottir, G., and Wright, P.J. 2003. Using environmental and biological indices as proxies for egg and larval production of marine fish. Journal of the Northwest Atlantic Fishery Science **33**:115-159.

LaMontagne, J.M. and McCauley, E. 2001. Maternal effects in Daphnia: what mothers are telling their offspring and do the listen? Ecology Letters **4**:64-71.

Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences **54**:1976-1984.

Lindström, J., and Kokko, H. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. Proceedings of the Royal Society, London B, **265**:483-488.

Lummaa, V. 2003. Early developmental conditions and reproductive success in humans: downstream effects of prenatal famine, birthweight, and timing of birth. American Journal of Human Biology **15**:370-379.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Canadian Journal of Fisheries and Aquatic Sciences **55**:1766-1783.

Marshall, C.T., O'Brien, L., Tomkiewicz, J., Marteinsdóttir, G., Morgan, M.J., Saborido-Rey, F., Köster, F.W., Blanchard, J.L., Secor, D.H., Kraus, F., Wright, P., Mukhina, N.V., and Björnsson,. H. 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. Journal of the Northwest Atlantic Fishery Science **33**:161-190.

Marshall, C.T., Needle, C.L., Yaragina, N.A., Ajiad, A.M., and Gusev, E. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Canadian Journal of Fisheries and Aquatic Sciences **61**:1900-1917.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Canadian Journal of Fisheries and Aquatic Sciences **55**:1372-1377.

Marteinsdottir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Marine Ecology Progress Series **235**:235-256.

Metcalfe, N.B., and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution, **16**:254-260.

Millner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B., and Grachev, I.A. 2003. Reproductive collapse in saiga antelope harems. Nature **422**:135.

Morgan, M.J., and Brattey, J. 2004. The use of indices of reproductive potential in the setting of reference points and stock projections. Northwest Atlantic Fisheries Organization Scientific Research Document. 04/39.

Mousseau, T.A., and Fox, C.W. 1998a. The adaptive significance of maternal effects. Trends in Ecology and Evolution **13**:403-407.

Mousseau, T.A., and Fox, C.W. 1998b. Maternal effects as adaptations. Oxford University Press.

Mukhina, N.V., Marshall, C.T., and Yaragina, N.A. 2003. Tracking the signal in year-class strength of Northeast Arctic cod through multiple survey estimates of egg, larval and juvenile abundance. Journal of Sea Research **50**:57-75.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P.R., Thorsen, A., and Junquera, S. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. Journal of the Northwest Atlantic Fishery Science **33**:33-54.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science **269**:1106-1108.

Needle, C.L. 2002. Recruitment models: diagnosis and prognosis. Reviews in Fish Biology and Fisheries **11**:95-111.

Northeast Fisheries Science Center. 2003. Report of the 36th Northeast Regional Stock Assessment Workshop (37th SAW): advisory report. Northeast Fisheries Science Center Reference Document 03-17. (available from http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0317/)

Peters, R.H. 1991. A critique for ecology. Cambridge University Press.

Pettersson, L.B., Ramnarine, I.W., Becher, S.A., Mahabir, R., and Magurran, A.E. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulate*. Behavioral Ecology and Sociobiology **55**:461-468.

Quinn II, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.

Scott, B., Marteinsdottir, G., and Wright, P. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Canadian Journal of Fisheries and Aquatic Sciences **56**:1882-1890.

Secor, D.H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake By striped bass. ICES Journal of Marine Science **57**:403-411.

Shelton, P.A., and Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? Canadian Journal of Fisheries and Aquatic Sciences **56**:1521-1524.

Shepherd, J.G. 1999. Extended survivors analysis: An improved method for the analysis of catch-at-age data and abundance indices. ICES Journal of Marine Science **56**:584-591.

Sundby, S., Bjørke, H., Soldal, A.V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of Northeast Arctic cod (*Gadus morhua* L.). Rapport et Procès -verbaux des Reunions, Conseil international pour l'Exploration de la Mer **191**:351-358.

Taylor, B., and Rojas-Bracho, L. 1999. Examining the risk of inbreeding depression in a naturally rare cetacean, the vaquita (*Phoceana sinus*). Marine Mammal Science **15**:1004-1028.

Tomkiewicz, J., Morgan, M.J., Burnett, J., and Saborido-Rey, F. 2003. Available information for estimating reproductive potential of northwest Atlantic groundfish stocks. Journal of the Northwest Atlantic Fishery Science **33**:1-21.

Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science **191**:249-263.

Whitman, K., Starfield, A.M., Quadling, H.S., and Packer, C. 2004. Sustainable trophy hunting of African lions. Nature **428**:175-178.

Wooster, W.S., and Bailey, K.M. 1989. Recruitment of marine fishes revisited. Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment (eds R.J. Beamish and G.A. McFarlane), pp 153-159. Can. Spec. Publ. Fish. Aquat. Sci. Vol. 108.

Wright, P.J., and Gibb, F.M. 2005. Selection for birth date in North Sea haddock and its relation to maternal age. Journal of Animal Ecology **74**:303-312.

Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod. ICES Journal of Marine Science **57**:42-55.

Table 1: Summary statistics to a generalized linear model fit (family = gamma, link =log) to fecundity data for Northeast Arctic cod. Data are from Kjesbu et al. 1998 and O.S. Kjesbu and A. Thorsen (Institute of Marine Research, Bergen).

	d.f.	**Deviance Residual**	**Resid. d.f.**	**Resid. Dev.**	**F**	**Pr(F)**
Null			479	272.2433		
ln(Length)	1	232.8794	478	39.3639	4562.342	<0.0001
ln(Kn)	1	14.8693	477	24.4946	291.305	<0.0001

Table 2: Properties of the Saila-Lorda model. S, R, and F denote stock, recruitment and fishing mortality, respectively. The value of ρ corresponds to the slope of the replacement line for F_{med} and, as can be derived from information given below, equals the median value of R divided by the median value of S.

Value	**Formulation**
Maximum recruitment	$R_{max} = \alpha\left(\frac{\gamma}{\beta}\right)^{\gamma} e^{-\gamma}$
S at R_{max}	$S_{max} = \frac{\gamma}{\beta}$
S at points of inflexion	$S_{inf} = \frac{\gamma \pm \sqrt{\gamma}}{\beta}$
Threshold for recruitment overfishing (S_{thr})	Numerical solution to: $\frac{\alpha}{2}\left(\frac{\gamma}{\beta}\right)^{\gamma} e^{-\gamma} - \alpha S_{thr}^{\gamma} e^{-\beta S_{thr}} = 0$
Slope	$\frac{dR}{dS} = \alpha S^{\gamma} e^{-\beta S}\left(\frac{\gamma}{S} - \beta\right)$
Slope at the origin	$\left.\frac{dR}{dS}\right\|_{S=0} = \begin{cases} 0 & \gamma > 1 \\ 1 & \gamma = 1 \\ \infty & \gamma < 1 \end{cases}$
Yield (Y)	$Y = \alpha S^{\gamma} e^{-\beta S} - \rho S$
SSB giving Maximum Sustainable Y at F_{med} (S_{MSY})	Numerical solution to: $\alpha S_{MSY}^{\gamma} e^{-\beta S_{MSY}}\left(\frac{\gamma}{S_{MSY}} - \beta\right) - \rho = 0$
SSB at replacement for F_{med} (S_{med})	Numerical solution to: $\alpha S_{med}^{\gamma - 1} e^{-\beta S_{med}} - \rho = 0$
Recruitment at replacement for F_{med}	$R_{med} = \rho\, S_{med}$

Table 3: Summary statistics for Saila-Lorda model fit to data from the full time period (year-classes 1943 to 1998) and the recent time period (year-classes 1980 to 1998). RSS denotes residual sum of squares. Standard errors for parameter estimates are given in parentheses.

		Full			**Recent**	
	SSB	**FSB**	**TEP**	**SSB**	**FSB**	**TEP**
α	1.61	4.78E2	1.01E-2	7.82E-4	97.38	5.33E-5
	(7.95)	(1.57E3)	(9.70E-2)	(5.18E-3)	(447.46)	(6.78E-4)
β	1.48E-6	1.07E-6	1.91E-15	3.17E-6	1.87E-6	4.10E-15
	(1.03E-6)	(1.40E-6)	(3.09E-15)	(1.58E-6)	(2.75E-6)	(5.42E-15)
γ	1.04	0.60	0.56	1.68	0.74	0.73
	(0.42)	(0.30)	(0.31)	(0.56)	(0.43)	(0.41)
d.f.	50	50	50	16	16	16
RSS	19.44	20.43	20.80	2.49	3.31	3.54
r^2	0.22	0.18	0.16	0.56	0.41	0.38
p	0.002	0.007	0.011	0.001	0.014	0.023
R_p	7.19E8	7.39E8	7.41E8	6.82E8	6.63E8	6.47E8
S_p (t or no. eggs)	705440	562730	2.93E14	533180	396990	1.78E14

Table 4: Parameter estimates and summary statistics for the different changepoint models. Note that δ and α_2 correspond to the S* and R*, respectively, as used in Barrowman and Myers (2000). The value –2 ln L, where L is the likelihood, is analogous to a measure of residual deviance and is included here as a measurement of goodness of fit.

	Full			**Recent**		
	SSB	**FSB**	**TEP**	**SSB**	**FSB**	**TEP**
δ (t or no. eggs)	186570	61679	3.26E13	193794	61679	6.33E13
α_2 (thou.)	527009	507432	514433	496655	483921	617226
-2 ln L	100.52	106.09	104.42	24.58	28.67	24.47

Table 5: A summary of the percentage agreement between the two alternative indices of reproductive potential and SSB about whether stock status is inside safe biological limits (value of S greater than changepoint value) or outside safe biological limits (value of S less than changepoint value).

	Full		**Recent**	
	SSB and len-FSB	**SSB and len-TEP**	**SSB and len-FSB**	**SSB and len-TEP**
Both agree inside	42 (75.0%)	42 (75.0%)	16 (72.7%)	11 (50%)
Both agree outside	6 (10.7%)	7 (12.5%)	4 (18.2%)	6 (27.3%)
SSB inside, alternative outside	1 (1.8%)	1 (1.8%)	0 (0%)	5 (22.7%)
SSB outside, alternative inside	7 (12.5%)	6 (10.7%)	2 (9.1%)	0 (0%)

Figure headings

Fig. 1 Schematic diagrams illustrating the two different models that were used to describe the stock/recruit relationship. (a) depensation ($\gamma > 1$), compensation ($\gamma = 1$), and over-compensation ($\gamma < 1$). The unique maximum, occurring at (S_p, R_p), is indicated. Below this point recruitment decreases in either a depensatory or compensatory fashion. (b) Piecewise regression model with the changepoint (δ) indicated.

Fig. 2 The proportion of females in each 5-cm length-class plotted against the mid-point of that length class. (a) estimated values for 1946-2001. (b) models used to estimate len-FSB and len-TEP for all 56 years in the time period.

Fig. 3 Time series for (a) proportion mature at length (m_l) and (b) weight at length (w_l). The length classes shown in each panel have midpoints 52.5, 72.5, 92.5, 112.5 and 132.5 cm with the lowest and highest values belonging to the smallest (52.5 cm) and largest (132.5 cm) length class, respectively.

Fig. 4 the difference between length-based maturity ogives for males+females and females-only (Δm_l) plotted by length class for the years 1985 to 2001. These were the values used to convert m_l to $m_{l|f}$ in those years. The solid line shows the polynomial model (Eq. 9) that was used to estimate values for the years 1946 to 1984.

Fig. 5 The year-specific length/weight regressions (dashed lines) used to generate values for weight at length for the stock (w_l; see also Fig. 3b) through the time period 1946 to 2001. The observed values of weight and length for the pre-spawning females (circles) used to develop the fecundity/length model are shown for comparison.

Fig. 6 (a) monthly values of the liver condition index (LCI = liver weight/total body weight × 100) for 51-60 (open circles), 61-70 (open triangles) and 71-80 (crosses) cm cod from 1986 to 2001. (b) boxplots showing the range of values of Fulton's K condition index for the pre-spawning females used in the fecundity study, plotted by year.

Fig. 7 (a) the observed fecundity of pre-spawning females (open circles) and fecundity predicted using Eq. 11 for the minimum (0.5), unity (1.0) and maximum (1.4) values of Kn. (b) the values of fecundity at length (e_l) predicted for all midpoints for the time period 1946 to 2001 using Eq. 11.

Fig. 8 (a) time series of mean length of the spawning stock (solid line) and the estimate of the ratio of female-only spawner biomass to total spawning stock biomass (dashed line). (b) time series of mean length of the spawning stock (solid line) and the estimate of the ratio of total egg production to total spawning stock biomass (dashed line).

Fig. 9 Stock/recruit relationships using different indices of reproductive potential and different time periods. (a) SSB and full time period. (b) FSB and full time period. (c) TEP and full time period. (d) SSB and recent time period. (e) FSB and recent time period. (f) TEP and recent time period. The Saila-Lorda model fit is shown (solid line) with 95% confidence intervals (dashed lines). The solid vertical lines indicate S_p (Eq. 15).

Fig. 10 Stock/recruit relationships using different indices of reproductive potential and different time periods. (a) SSB and full time period. (b) FSB and full time period. (c) TEP and full time period. (d) SSB and recent time period. (e) FSB and recent time period. (f) TEP and recent time period. The piecewise linear regression model fit is shown (solid line).

Fig. 1

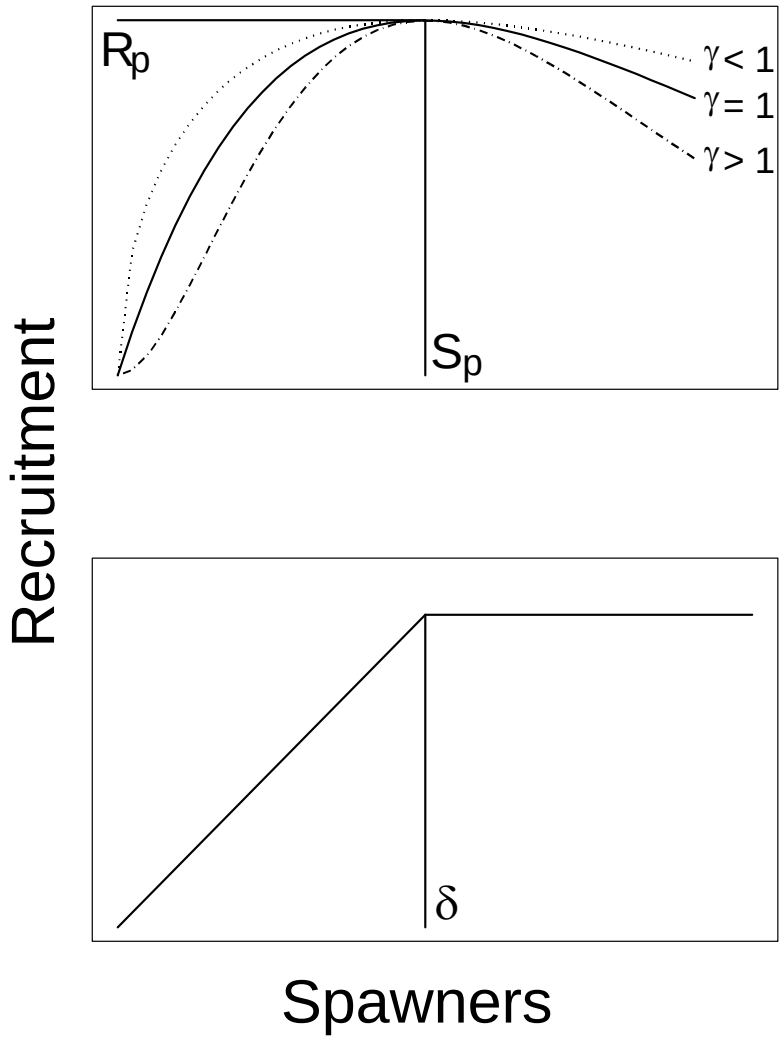


Fig. 2

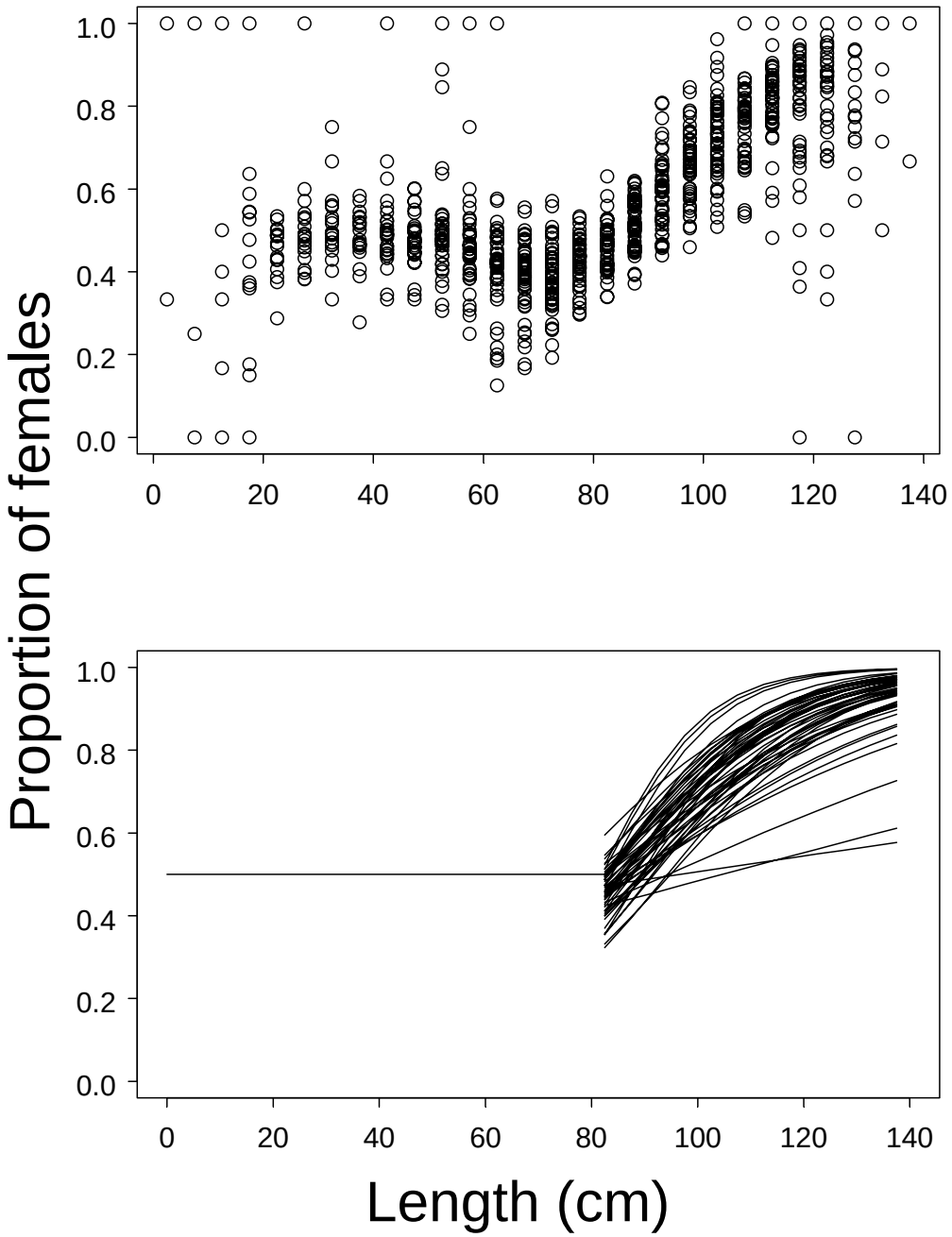

Proportion of females
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
140
Length (cm)

Fig. 3

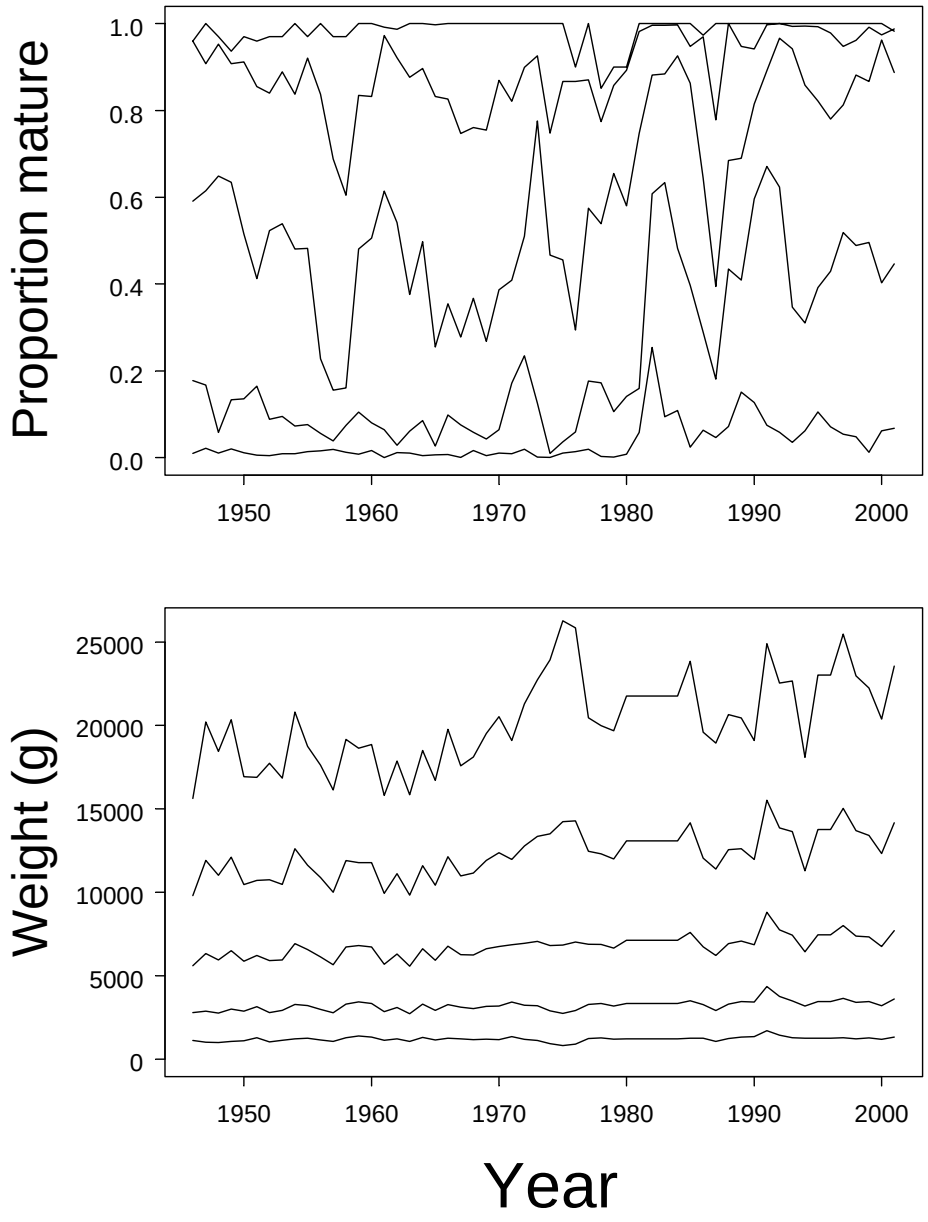

Proportion mature
1.0
0.8
0.6
0.4
0.2
0.0
1950
1960
1970
1980
1990
2000
Weight (g)
25000
20000
15000
10000
5000
0
1950
1960
1970
1980
1990
2000
Year

Fig. 4

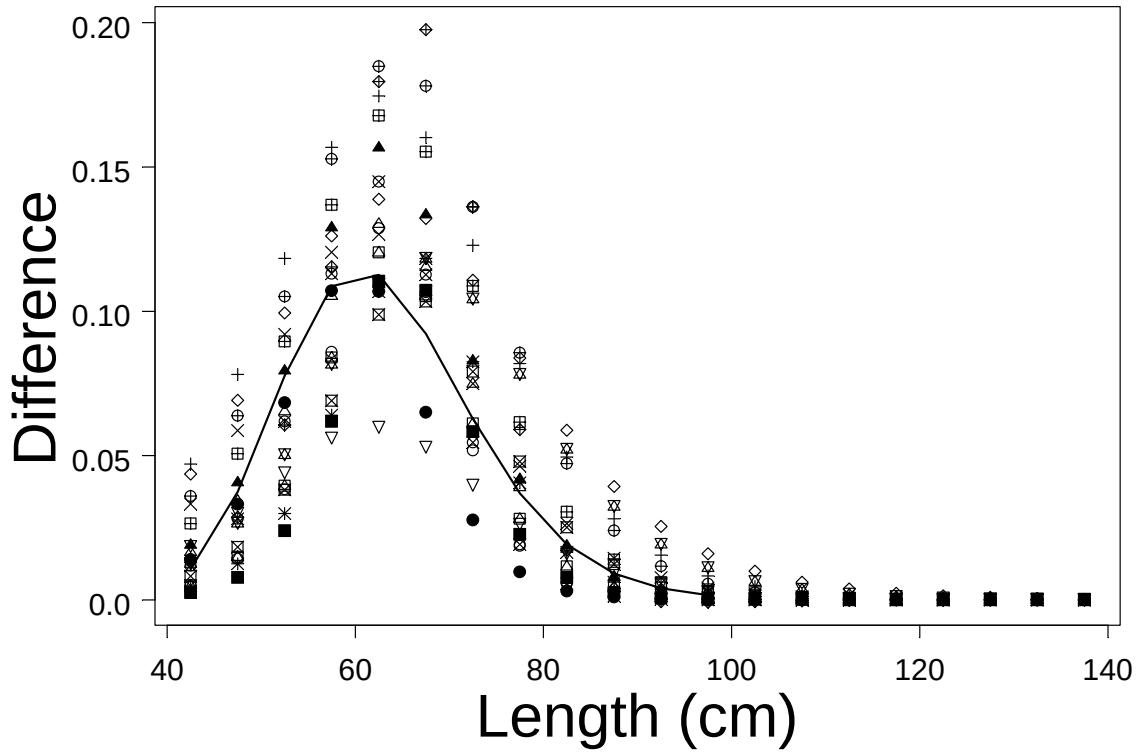


Fig. 5

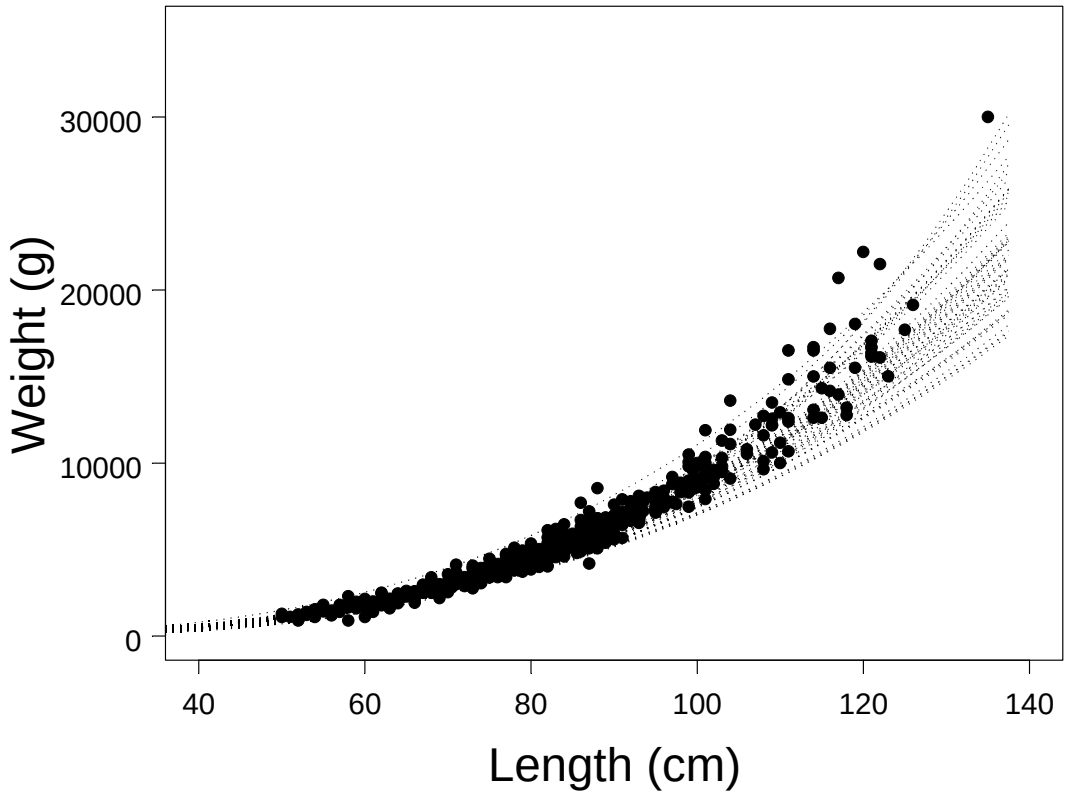


Fig. 6

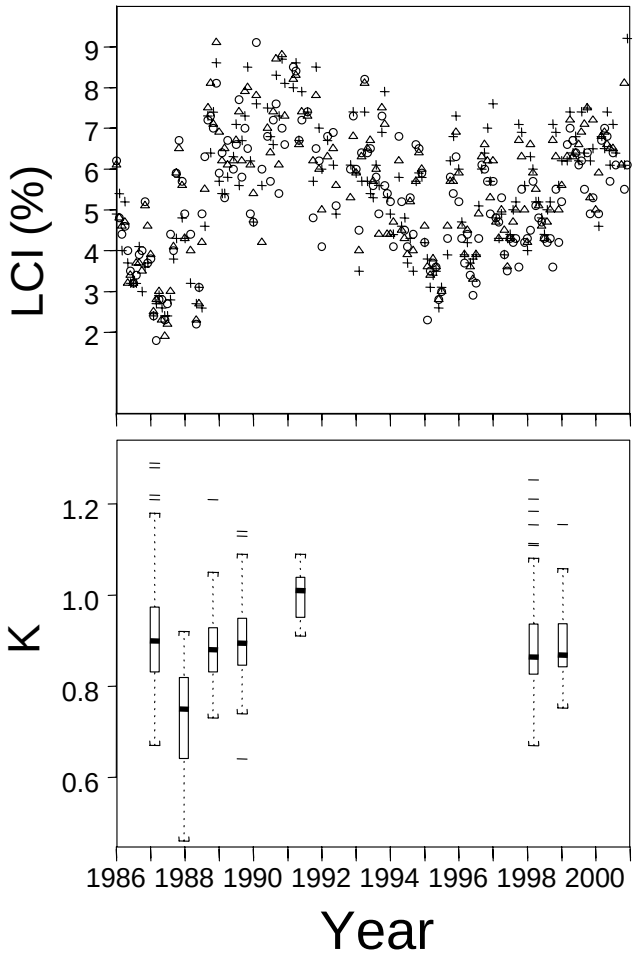

LCI (%)
9
8
7
6
5
4
3
2
K
1.2
1.0
0.8
0.6
1986 1988 1990 1992 1994 1996 1998 2000
Year

Fig. 7

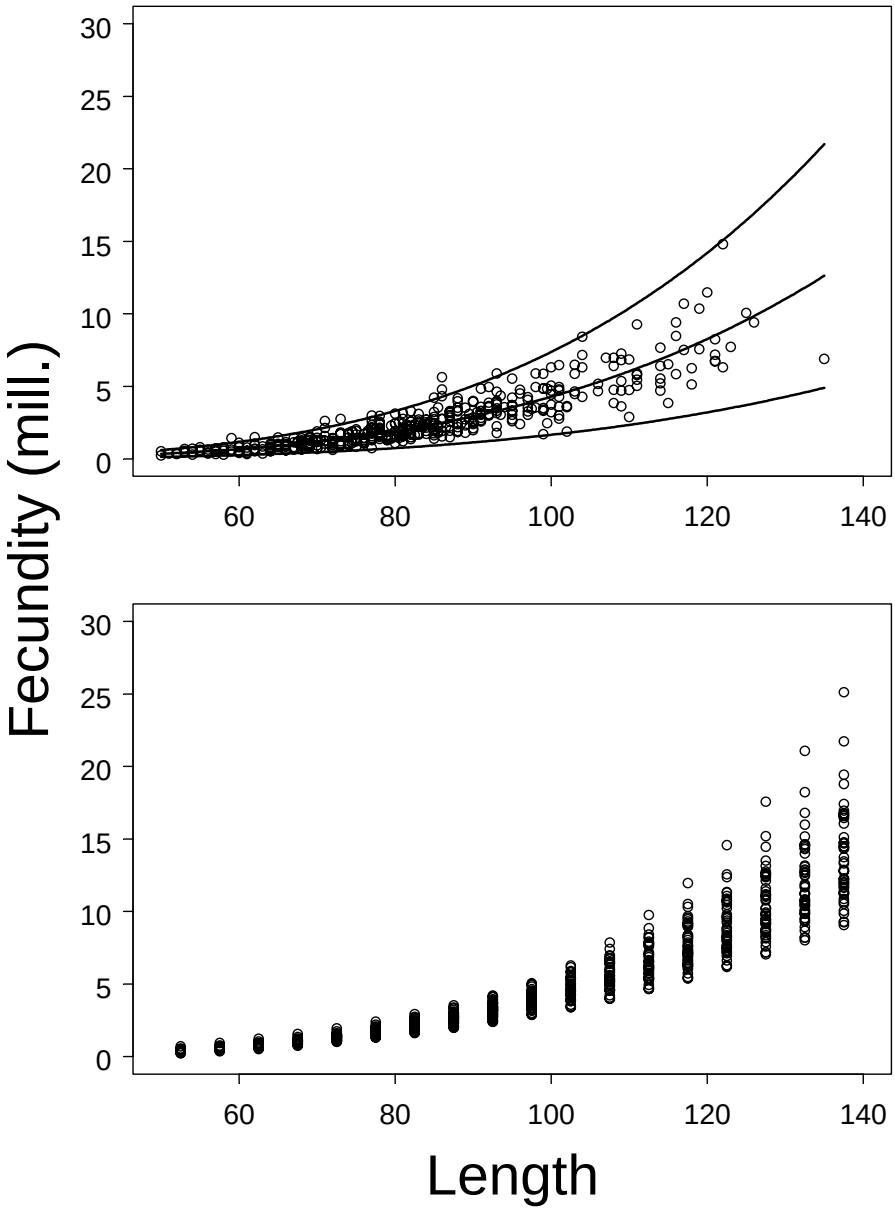


Fig. 8

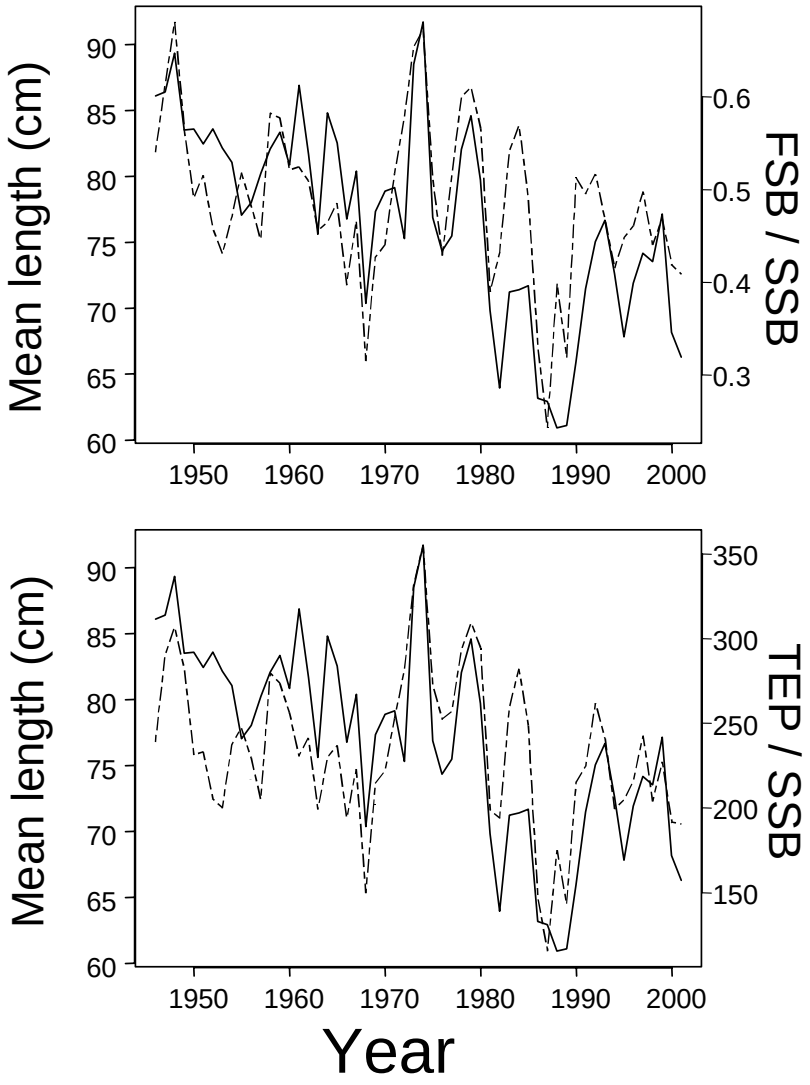

Mean length (cm)
90
85
80
75
70
65
60
1950
1960
1970
1980
1990
2000
0.6
0.5
0.4
0.3
FSB / SSB
Mean length (cm)
350
300
250
200
150
TEP / SSB
Year

Fig. 9

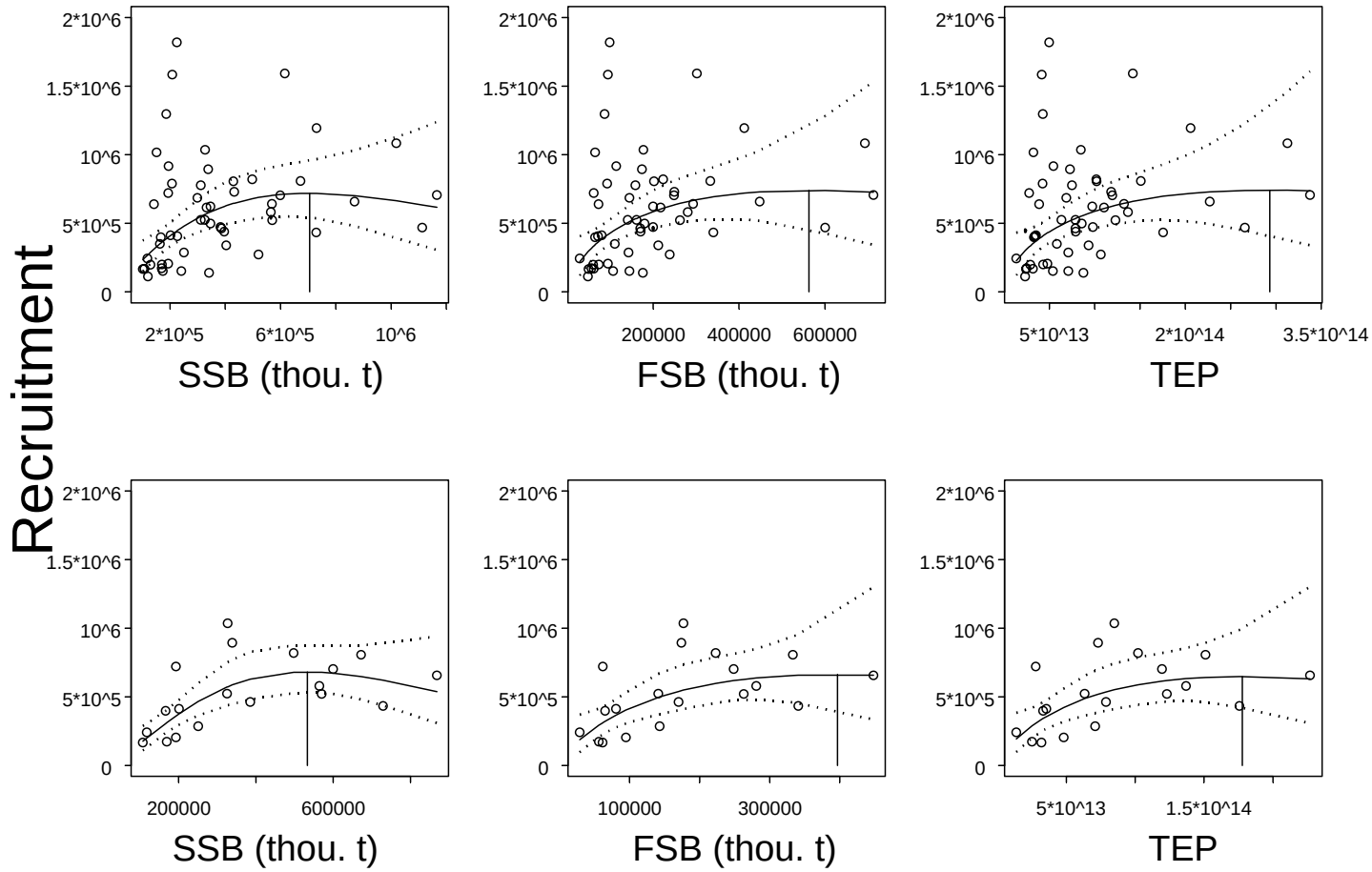
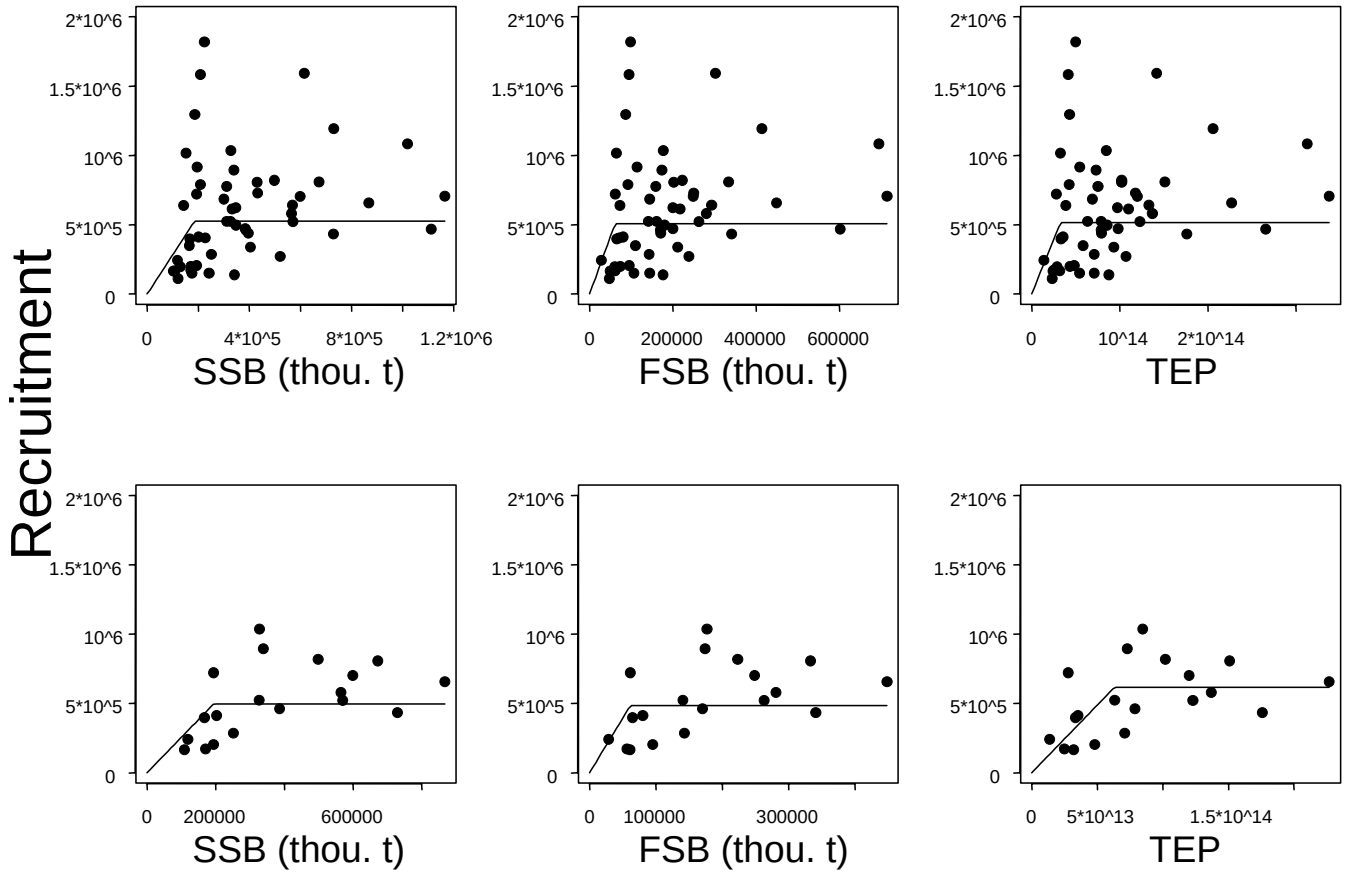

Recruitment
2*10^6
1.5*10^6
10^6
5*10^5
0
2*10^5
6*10^5
10^6
SSB (thou. t)
200000
400000
600000
FSB (thou. t)
5*10^13
2*10^14
3.5*10^14
TEP
200000
600000
SSB (thou. t)
100000
300000
FSB (thou. t)
5*10^13
1.5*10^14
TEP

Fig. 10


Recruitment
2*10^6
1.5*10^6
10^6
5*10^5
0
0
4*10^5
8*10^5
1.2*10^6
SSB (thou. t)
0
200000
400000
600000
FSB (thou. t)
0
10^14
2*10^14
TEP
0
200000
600000
SSB (thou. t)
0
100000
300000
FSB (thou. t)
0
5*10^13
1.5*10^14
TEP