

Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock–recruit theory and management

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Abstract: Stock–recruit relationships that use spawning stock biomass (SSB) to represent reproductive potential assume that the proportion of SSB composed of females and the relative fecundity (number of eggs produced per unit mass) are both constant over time. To test these two assumptions, female-only spawner biomass (FSB) and total egg production (TEP) were estimated for the Northeast Arctic stock of Atlantic cod (*Gadus morhua*) over a 56-year 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. Relative fecundity of the stock (TEP/SSB) varied between 115 and 355 eggs·g⁻¹ and was significantly, positively correlated with mean length of spawners. Both FSB and TEP gave a different interpretation of the recruitment response to reductions in stock size (overcompensatory) compared with that obtained using SSB (either compensatory or depensatory). 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 at which recruitment becomes impaired more frequently than did SSB. This suggests that using SSB as a measure of stock reproductive potential could lead to overly optimistic assessments of stock status.

Résumé : Les relations stock–recrues qui utilisent la biomasse du stock reproducteur (SSB) pour représenter le potentiel reproductif présupposent que la proportion de SSB représentée par les femelles et que la fécondité relative (nombre d'oeufs produits par unité de masse) sont toutes deux invariables dans le temps. Afin d'évaluer ces deux présuppositions, nous avons estimé la biomasse des reproducteurs femelles seuls (FSB) et la production totale d'oeufs (TEP) chez un stock de morues franches (*Gadus morhua*) de l'Arctique sur une période de 56 ans. La proportion de femelles (FSB/SSB) varie de 24 à 68 % et elle change systématiquement en fonction de la longueur de telle manière que SSB favorise de plus en plus les femelles à mesure que la longueur moyenne des reproducteurs augmente. La fécondité relative du stock (TEP/SSB) varie de 115 à 355 oeufs·g⁻¹ et elle est en corrélation positive significative avec la longueur moyenne des reproducteurs. FSB et TEP fournissent toutes deux une interprétation différente de la réaction du recrutement à la réduction de la taille du stock (surcompensation) par comparaison à la réaction du recrutement obtenue à partir de SSB (compensation ou bien effet d'Allee). Il n'y a pas de différence entre SSB et FSB pour ce qui est de l'évaluation du statut du stock; cependant, ces dernières années (1980–2001), TEP est tombée sous le seuil sous lequel le recrutement se détériore plus fréquemment que SSB. Cela laisse croire que l'utilisation de SSB comme mesure du potentiel reproductif du stock pourrait mener à des évaluations trop optimistes du statut du stock.

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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 are 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

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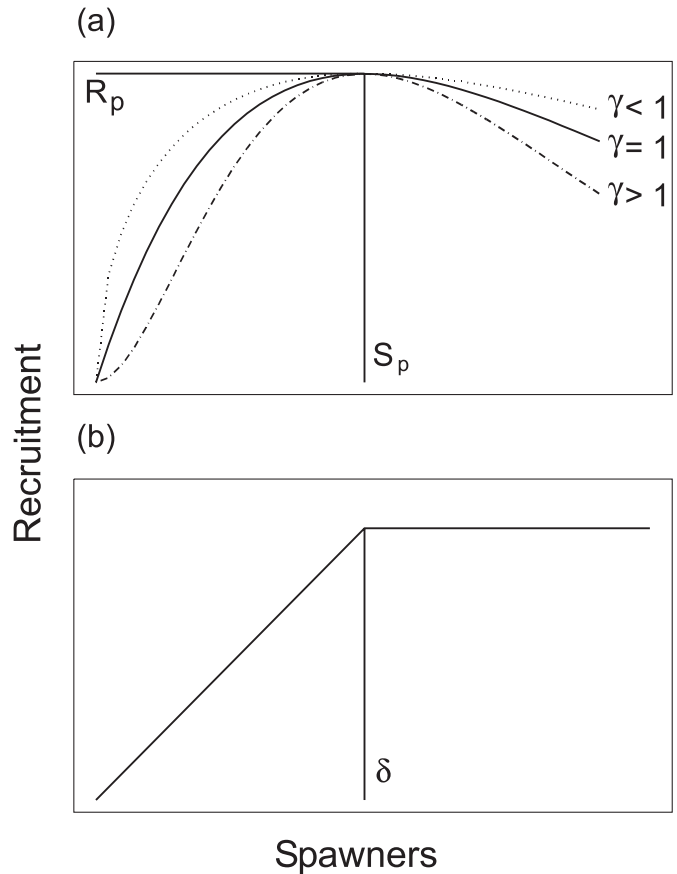
model be fit, irrespective of the degree of noise in the data. This is especially true of fisheries management that, under the precautionary approach, fits statistical models to stock–recruit data to define the stock size at which recruitment is impaired and then seeks to keep the stock well above that 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 composed 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 strong dimorphism in 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 age–size composition of the stock (Marteinsdottir and Thorarinnsson 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 time period depicted in the stock–recruit relationship used by management. 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 al. 2002; Blanchard et al. 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). Atlantic 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 et al. 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 (i) compelling evidence that the status quo cannot be justified and (ii) 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. (i) Does the alternative index funda-

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 overcompensation ($\gamma < 1$). 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 change point (δ) indicated.



mentally change the functional form of the recruitment response to stock depletion? (ii) 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 that continue to aggregate 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 Healey 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 Advisory Committee on Fishery Management 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 change point representing the level of impaired recruitment (Fig. 1*b*). An evaluation of alternative indices of reproductive potential should therefore determine whether the change point estimated for the alternative index gives a divergent assessment of whether the stock is inside (above the change point) or outside (below the change point) safe biological limits compared with the assessment made using the conventional SSB change point.

These two questions represent fundamentally different approaches to representing the stock–recruit relationship. Depicting the stock–recruit relationship using a nonlinear, density-dependent model (Fig. 1*a*) is an ecological approach that assumes a mechanistic basis for the relationship. The piecewise linear regression model approach is entirely statistical (Fig. 1*b*). If the stock–recruit relationship is noisy, then the change point 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. Clearly, the piecewise linear regression model approach is oversimplified compared with 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 the alternative indices of reproductive potential (FSB and TEP) relative to the conventional one (SSB) that is used by management.

In this study, FSB and TEP were estimated for the Northeast Arctic stock of Atlantic cod 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 with 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 dynam-

ics. Additionally, change points were estimated for the alternative stock–recruit relationships to determine whether they assessed stock status differently from or consistently with the SSB change point. Implications of the results for the management of the Northeast Arctic stock of Atlantic cod, stock–recruit theory, and research into maternal effects on population dynamics are discussed.

Material and methods

The Northeast Arctic stock of Atlantic cod inhabits the Barents Sea, an arcto-boreal shelf sea that is situated north of Norway and northwestern Russia between 70°N and 80°N. Both Norway and Russia have extensive long-term databases describing the biological characteristics of the Northeast Arctic stock of Atlantic cod. 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-at-age, proportion mature-at-age, 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 the Northeast Arctic stock of Atlantic cod, SSB is estimated by the ICES AFWG as

$$(1) \quad \text{SSB} = \sum_{a=3}^{13+} n_a \cdot m_a \cdot w_a$$

where n_a , m_a , and w_a are the numbers-at-age, proportion mature-at-age, and weight-at-age, respectively (table 16 of ICES Advisory Committee on Fishery Management 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 Advisory Committee on Fishery Management 2001).

For slow-growing stocks such as the Northeast Arctic stock of Atlantic cod, reproductive traits such as fecundity are primarily length-dependent, and the substantial variation in length-at-age that has occurred over the study period (Marshall et al. 2004) would invalidate an exclusively age-based approach to estimating reproductive potential. A length-based estimate of SSB (len-SSB) would be estimated as

$$(2) \quad \text{len-SSB} = \sum_l n_l \cdot m_l \cdot w_l$$

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

$$(3) \quad \text{len-FSB} = \sum_l n_l \cdot s_l \cdot m_{lf} \cdot w_l$$

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

$$(4) \quad \text{len-TEP} = \sum_l n_l \cdot s_l \cdot m_{lf} \cdot e_l$$

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. 3, length-based equivalents for n_a , w_a , and m_a were derived as described below.

Numbers-at-length (n_l)

Estimates of n_a (ICES Advisory Committee on Fishery Management 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 described 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 to 13+, from table 3.23 of ICES Advisory Committee on Fishery Management 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.

Proportion females 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 are shown (Fig. 2a, excluding 1980–1984, which had data quality problems). At lengths >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 <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 possibly 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. 3) and len-TEP (eq. 4) assumed that the proportion of females was constant and equal to 0.5 for cod <80 cm. For lengths >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

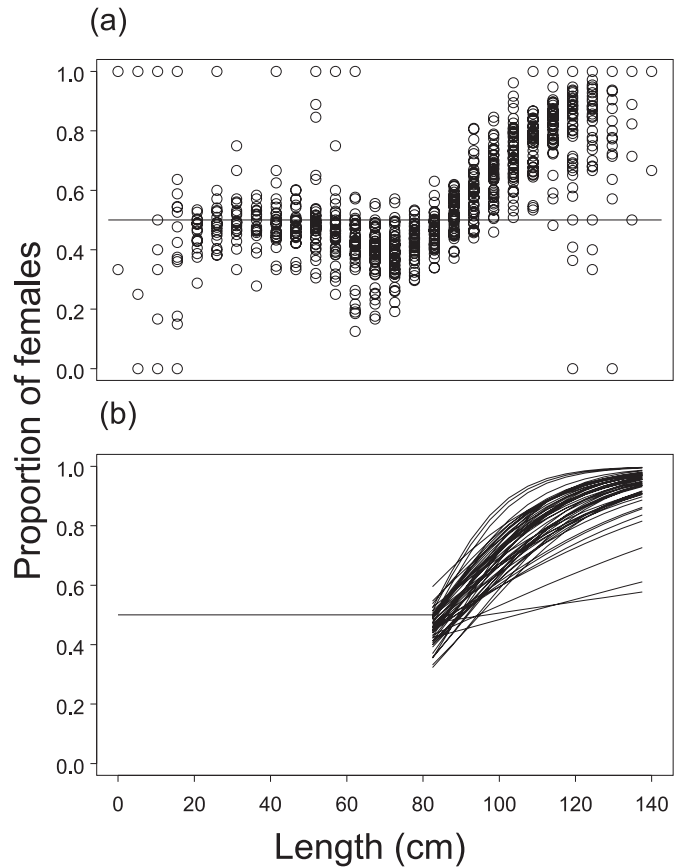
$$(5) \quad z_l = \exp(a + bL)$$

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

$$(6) \quad s_l = 1/[1 + 1/\exp(z_l)]$$

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. 2. The proportion of females in each 5 cm length class plotted against the midpoint of that length class. (a) Estimated values for 1946–2001. (b) Models used to estimate female-only spawner biomass and total egg production for all 56 years in the time period.



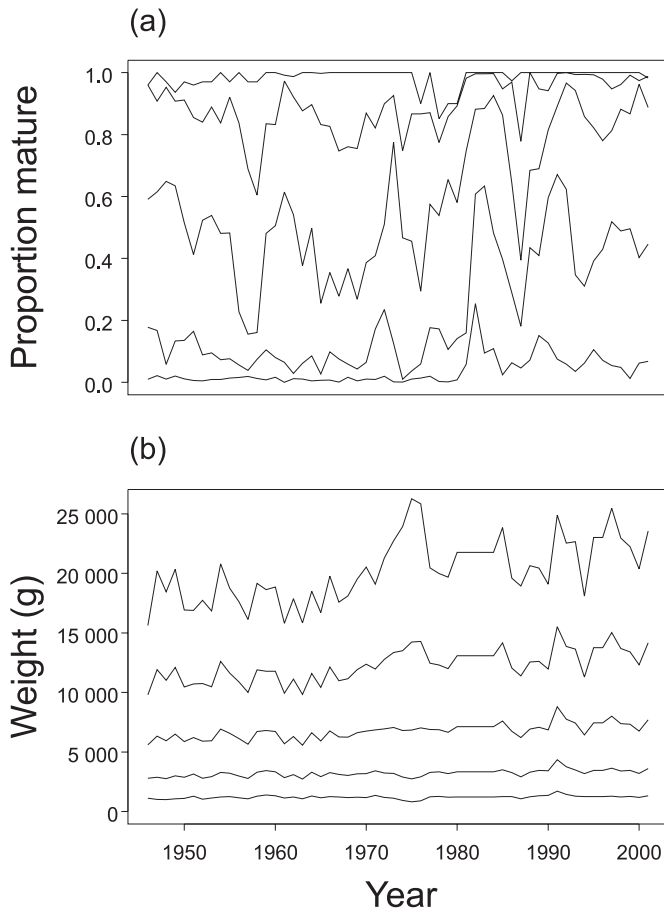
(Fig. 2b) were used to estimate the len-FSB (eq. 3) and len-TEP (eq. 4). For the years 1980–1984, the average of the modelled values for 1979 and 1985 were used.

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 virtual population analysis 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, with a abrupt shift to higher values occurring around 1980. The estimated values

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.



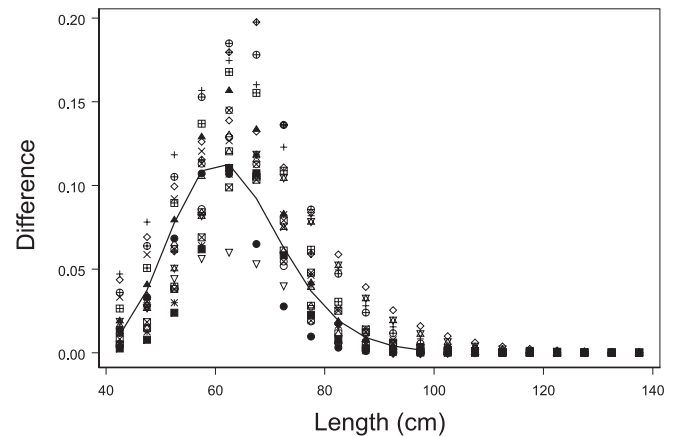
of m_l were used to estimate len-SSB, len-FSB, and len-TEP instead of modelled values to be consistent with the approach used by the ICES AFWG to estimate SSB.

Proportion of females that are mature-at-length (m_{lf})

The approach taken to estimating m_{lf} 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 with 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 generalized linear models and assuming a binomial error distribution. The difference between the two ogives at the midpoint of each 5 cm length class (Δm_l) was then estimated. Values of Δm_l consistently peaked 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 1985–2001, the value of m_{lf} was estimated as m_l minus the estimated value of Δm_l for that year. Values of m_{lf} were assumed to be zero if m_l

Fig. 4. The difference between length-based maturity ogives for males + females and females only (Δm_l) plotted by length class for the years 1985–2001. These observed values were used to convert m_l to m_{lf} in those years. The solid line shows the polynomial model (eq. 9) that was used to estimate values for the years 1946 to 1984. Different symbols correspond to different years (1985–2001).



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 nonlinear regression in SPLUS. The resulting model is given by

$$(7) \quad \ln(\Delta m_l) = -318.81 + 154.28 \cdot \ln(L) - 18.79 \cdot \ln(L)^2$$

where L is the midpoint of the 5 cm length class. The fitted quadratic model (Fig. 4) was used to give a standard value of Δm_l for each midpoint in the range 42.5–97.5 cm (outside of that length range Δm_l was assumed to be 0). The m_{lf} was estimated as the year-specific value of m_l for males and females combined minus the model value of Δm_l .

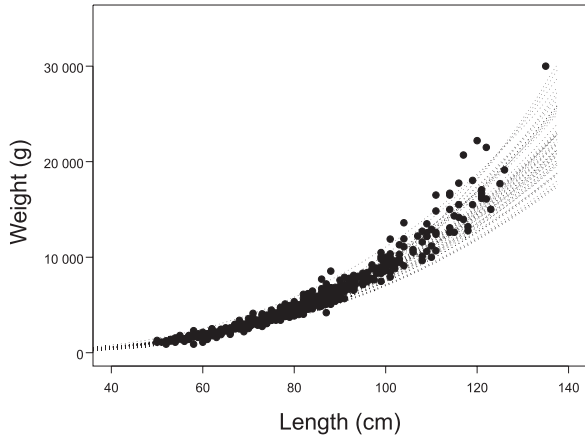
Weight-at-length (w_l)

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

Total egg production

Given that fecundity determinations were made for only a small number of years, it was necessary to develop a statistical model that could hindcast e_l for the full time period. During the full time period, there has been considerable variation in condition (sensu energy reserves) of cod that resulted 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 length–fecundity relationship.

Fig. 5. The year-specific length–weight regressions (dotted lines) used to generate values for weight-at-length for the stock (w_l) through the time period 1946–2001. The observed values of weight and length for the prespawning females (circles) used to develop the length–fecundity model are shown for comparison.



Fecundity-at-length (e_l)

A data set was available for fecundity determinations made for the Northeast Arctic stock of Atlantic cod in the years 1986–1989, 1991, 1999, and 2000 (see Kjesbu et al. 1998 for sampling details). The subset of this data set that was used here omitted observations if they were from coastal cod (distinguished by otolith type), from cod having oocyte diameters <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.

Estimation of condition of prespawning females in the fecundity data set

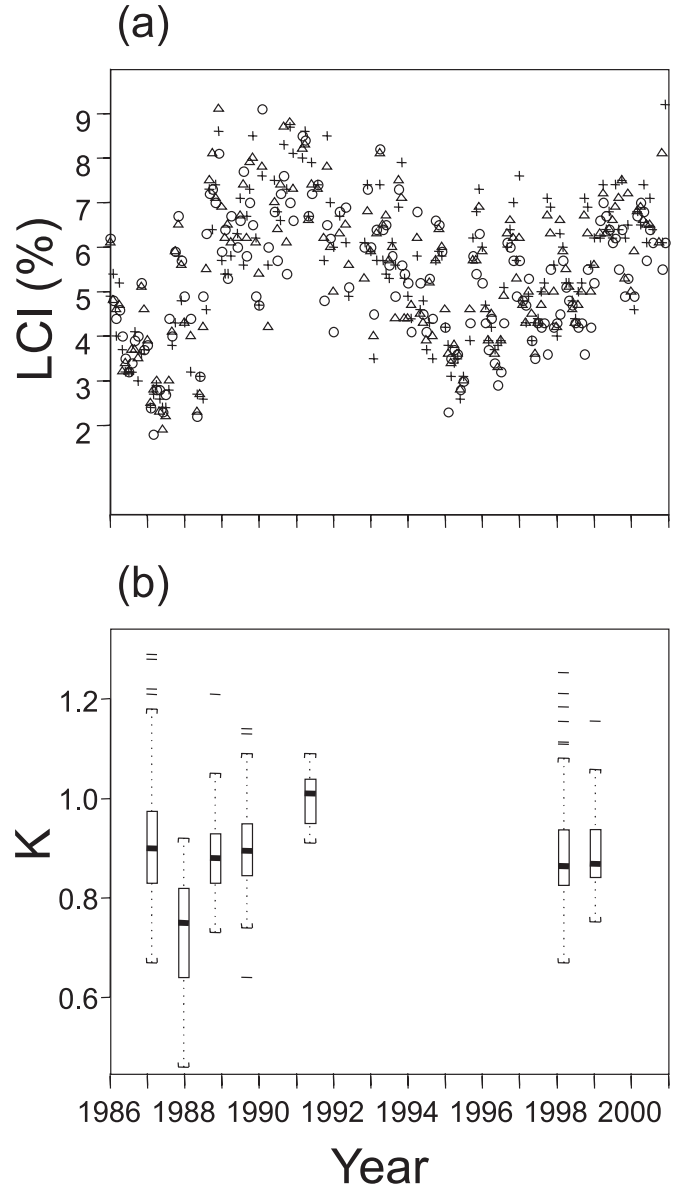
The prespawning females exhibited a temporal trend in condition that mirrored that observed in the stock generally (Fig. 6). To represent the condition of the individual prespawning females in the fecundity data set, relative condition (Kn) was estimated as the observed weight of the female divided by a standard weight, which was estimated using a length–weight relationship developed using data for all of the prespawning females pooled for all 7 years. This relationship is given by

$$(8) \quad w = \exp[-5.472 + 3.171 \cdot \ln(L)]$$

which was obtained by fitting a generalized linear model (assuming a gamma error distribution with a log–link function, $df = 478$, $p < 0.001$) to the length and weight data for the prespawning females pooled for all 7 years. Thus, Kn expresses condition of the individual female relative to the mean condition of all of the females in the pooled data set for the 7 years.

Fortuitously, the 7 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 data set 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 prespawning fe-

Fig. 6. (a) Monthly values of the liver condition index (LCI = liver weight/total body weight \times 100) for 51–60 (open circles), 61–70 (open triangles), and 71–80 (crosses) cm Atlantic cod (*Gadus morhua*) from 1986 to 2001. (b) Boxplots showing the range of values of Fulton’s K condition index for the prespawning females used in the fecundity study, plotted by year.



males in the fecundity data set was therefore considered to mimic, to a reasonable degree, the variability occurring at the stock level over the full time period.

Development of a fecundity model for hindcasting

For the fecundity data set, both length and Kn of the prespawning females were significantly correlated with fecundity (Table 1). The resulting model for e_l (in millions) was

$$(9) \quad e_l = \exp\{-15.090 + 3.595 [\ln(L)] + 1.578 [\ln(\text{Kn})]\}$$

Table 1. Summary statistics to a generalized linear model fit (family = gamma, link = log) to fecundity data for the Northeast Arctic stock of Atlantic cod (*Gadus morhua*).

	df	Deviance residual	Residual df	Residual deviance	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

Note: Data are from Kjesbu et al. (1998) and O.S. Kjesbu and A. Thorsen (unpublished data).

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

Estimation of Kn at the stock level

To apply eq. 9 to the stock level, year- and length-specific values of *Kn* were required for the full time period (1946–2001). The year-specific length–weight relationships described above (see Fig. 5) were used to predict *w_l* ranging in 5 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 prespawning 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 long-term (1946–2001) trends in condition, the long-term weight was estimated by pooling all of the observed weights for standard lengths for all years and fitting a length–weight relationship to those data. The resulting equation was

$$(10) \quad W = \exp(-4.836 + 3.014 \cdot \ln L)$$

and was fit using a generalized linear model (assuming a gamma error distribution with a log–link function, df = 1007, *p* < 0.001). For each year, *Kn* was then estimated by the ratio of the observed weight to the long-term weight obtained from eq. 10.

Application of the fecundity model to estimating TEP of the stock

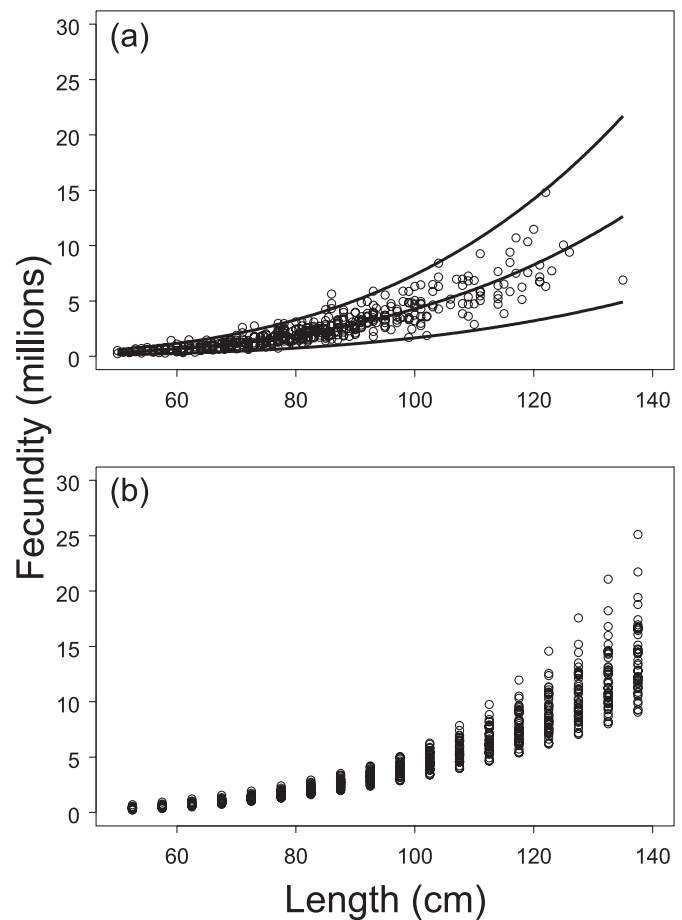
For each year, *e_l* was estimated for lengths ranging in 5 cm increments between 50 and 140 cm using eq. 9. The degree of variability in values of *e_l* over the full time period (Fig. 7b) was similar to the level of variability observed in the fecundity data set (Fig. 7a). This indicated that the dynamic range in the hindcast values is comparable with that observed in the 7 years of highly variable condition that were represented in the fecundity data set. The hindcast values of *e_l* were then used to estimate len-TEP from eq. 4.

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

$$(11) \quad SS_{len} = \frac{\sum_{l=42.5}^{137.5+} l \cdot n_l \cdot m_l}{\sum_{l=42.5}^{137.5+} n_l \cdot m_l}$$

Fig. 7. (a) The observed fecundity of prespawning 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 1946–2001 using eq. 11.



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·m_l*) rather than on the basis of their biomass (i.e., *n_l·m_l·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 Advisory Committee on Fishery Management 2002) corresponding to the 1946–1998 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

$$(12) \quad R = \alpha \cdot S^\gamma \exp(-\beta S)$$

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 data sets, a property that facilitates comparisons among the different data sets. 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 overcompensatory. For the Saila–Lorda model, a unique maximum (R_p and S_p) occurs at

$$(13) \quad (R_p, S_p) = \left(\alpha \left(\frac{\gamma}{\beta} \right)^\gamma \exp(-\gamma), \frac{\gamma}{\beta} \right)$$

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. 12 to

$$(14) \quad \ln R = a + b \cdot S + c \cdot \ln S$$

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 errors 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 ($S_{inf} = (\gamma - \sqrt{\gamma})/\beta$) was compared with the minimum observed value (S_{min}). If S_{inf} was greater than the minimum S_{min} , then the fit was accepted as being depensatory.

Estimation of change points

Piecewise linear regression (Barrowman and Myers 2000) was used to estimate change points 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

$$(15) \quad R = \begin{cases} \alpha_1 + \beta_1 \cdot S, & 0 \leq S \leq \delta \\ \alpha_2 + \beta_2 \cdot S, & \delta \leq S \end{cases}$$

where δ represents the change-point value. For stock and recruitment data, the model is constrained to pass through the origin (i.e., $\alpha_1 = 0$) and beyond δ , the line is horizontal (i.e., $\beta_2 = 0$). Thus, eq. 15 simplifies to

$$(16) \quad R = \begin{cases} \beta_1 \cdot S, & 0 \leq S \leq \delta \\ \alpha_2, & \delta \leq S \end{cases}$$

which can be re-expressed on a lognormal scale as

$$(17) \quad \ln R = \begin{cases} \ln \beta_1 + \ln S, & 0 \leq S \leq \delta \\ \ln \alpha_2, & \delta \leq S \end{cases}$$

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 change point 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 major distortion, the values of SSB (eq. 1) and len-SSB (eq. 2) were compared. The two values were 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, $df = 55$, $p = 0.13$).

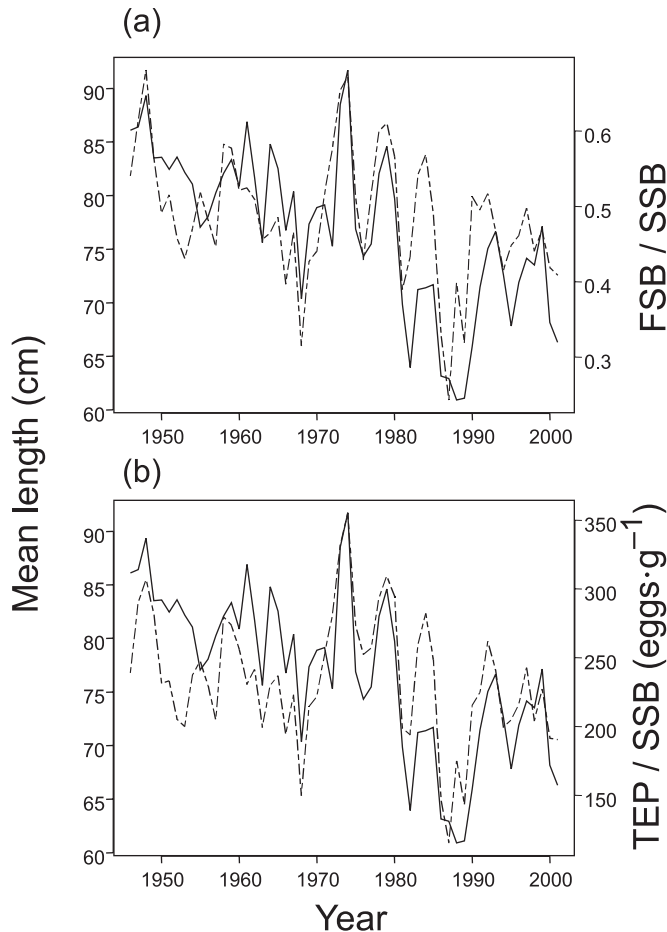
Time trends in the proportion of females

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 1980s), 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 ($r = 0.71$, $df = 55$, $p < 0.001$), indicating that SSB becomes progressively male-biased as the length composition shifts towards smaller-sized fish.

Time trends in relative fecundity of the stock

Relative fecundity of the stock exhibits a threefold 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). Note that because SSB includes noncontributing males, these values of relative fecundity of the stock are much 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 ($r = 0.70$, $df = 55$, $p < 0.001$). Since 1980, a majority of years (15 out of 22) have been be-

Fig. 8. (a) Time series of mean length of the spawning stock (solid line) and the estimate of the ratio of female-only spawning stock biomass (FSB) to total spawning stock biomass (SSB) (broken line). (b) Time series of mean length of the spawning stock (solid line) and the estimate of the ratio of total egg production (TEP) to total spawning stock biomass (SSB) (broken line).



low the long-term (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 1946–1998 year classes, the fitted Sella–Lords model had a γ value of 1.044 (Table 2), which is very close to 1 and suggests that the functional form of the relationship between R and SSB for the full time period is approximately compensatory (Fig. 9a). The Sella–Lords models for both len-FSB (Fig. 9b) and len-TEP (Fig. 9c) gave values of γ that were less than 1 (Table 2), suggesting that there was overcompensation 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 2.93×10^{14} eggs, respectively. There were only small differences among the three indices in values of R_p , which ranged from 7.19×10^8 to 7.41×10^8 (Table 2).

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 (re-

presenting the year classes spawned in 1980–1998) were examined separately. There was clearer evidence of a nonlinear stock–recruit relationship for the recent time period (Figs. 9d–9f), and unlike the full time period (Figs. 9a–9c), the scatterplots did not feature as many observations having high values of R and low values of stock reproductive potential. The fundamental changes to the stock dynamics (e.g., size composition, growth, and maturation) that took place around 1980 in combination with the distinct improvement to the fit of the stock–recruit relationship for the recent time period prompted the ICES AFWG to consider using only the recent time period for estimating biological reference points (ICES Advisory Committee on Fishery Management 2003). However, it was decided to base the estimation of the biological reference points on the full time period. Recognizing that this debate is not likely ended, results for both the full and recent time periods are presented here. Using SSB as the index of reproductive potential, the value of γ for the recent time period 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 were consistently less than 1 (Table 2), once again suggesting overcompensation (Figs. 9e, 9f). There were relatively small differences among R_p values (6.82×10^8 , 6.63×10^8 , and 6.47×10^8 for SSB, len-FSB and len-TEP, respectively; Table 2). However, these R_p values were consistently lower than those for the full time period, suggesting that there has been a decline in the maximum level of recruitment.

Change points

δ values were determined for the same six sets of stock–recruit data that were used to fit Sella–Lords models. For the full time period, the values of δ for SSB, len-FSB, and len-TEP were 186 570 t, 61 679 t, and 3.26×10^{13} eggs, respectively (Table 3). Visually, the piecewise linear regression models for the full time period were indistinguishable from each other in terms of the relative position of δ (Figs. 10a–10c). The R values associated with the horizontal line segment (i.e., α_2 in eq. 16) ranged between 5.07×10^8 and 5.27×10^8 , which amounts to a small difference (~4%) between them (Table 3). 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 4). Similarly, there was agreement between SSB and len-TEP in 49 (87.5%) of the 56 years (Table 4).

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 3). For len-FSB, the values of δ for the full and recent time periods were exactly equivalent (Table 3). This was because for both the full and recent time periods, the model-fitting procedures used the same assumed values of α_2 and β_1 to iteratively fit piecewise linear regression models. The value of δ for len-TEP in the recent time period (6.33×10^{13}) was nearly dou-

Table 2. Summary statistics for the Saitla–Lorda model fit to data from the full time period (year classes 1943–1998) and the recent time period (year classes 1980–1998).

	Full time			Recent time		
	SSB	FSB	TEP	SSB	FSB	TEP
α	1.61 (7.95)	4.78×10^2 (1.57×10^3)	1.01×10^{-2} (9.70×10^{-2})	7.82×10^{-4} (5.18×10^{-3})	97.38 (447.46)	5.33×10^{-5} (6.78×10^{-4})
β	1.48×10^{-6} (1.03×10^{-6})	1.07×10^{-6} (1.40×10^{-6})	1.91×10^{-15} (3.09×10^{-15})	3.17×10^{-6} (1.58×10^{-6})	1.87×10^{-6} (2.75×10^{-6})	4.10×10^{-15} (5.42×10^{-15})
γ	1.04 (0.42)	0.60 (0.30)	0.56 (0.31)	1.68 (0.56)	0.74 (0.43)	0.73 (0.41)
df	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	7.19×10^8	7.39×10^8	7.41×10^8	6.82×10^8	6.63×10^8	6.47×10^8
S_p (t or no. eggs)	705 440	562 730	2.93×10^{14}	533 180	396 990	1.78×10^{14}

Note: Spawning stock biomass (SSB), female-only SSB (FSB), and total egg production (TEP) were used as the independent variable in the model. RSS denotes residual sum of squares. Standard errors for parameter estimates are given in parentheses.

ble the value estimated for the full time period (3.26×10^{13}), and the R value associated with the horizontal line segment in the recent time period was 6.17×10^8 compared with 5.14×10^8 for the full time period (Table 3). As was the case for the full time period, there was considerable agreement between SSB and len-FSB in assessing stock status; the two change points gave the same assessment of stock status in 20 (90.9%) of the 22 years (Table 4). 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. In 5 (22.7%) of the 22 years, stock status was inside safe biological limits according to the change point for SSB, whereas using the change point for len-TEP, the stock was judged to be outside safe biological limits (Table 4). Thus, in over 20% of the years in the recent time period, len-TEP gives a more pessimistic view of stock status than did SSB. There were no years for which SSB judged stock status to be outside safe biological limits and len-TEP inside safe biological limits.

Discussion

This study has clearly shown that the dimorphic growth and maturation 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. By being selective with respect to size, fishing mortality is changing the demographic composition with respect to sex. 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 that 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. The efficacy of

Fig. 9. Stock–recruit relationships using different indices of reproductive potential and different time periods. (a) Spawning stock biomass (SSB) and full time period. (b) Female-only spawning stock biomass (FSB) and full time period. (c) Total egg production (TEP) and full time period. (d) SSB and recent time period. (e) FSB and recent time period. (f) TEP and recent time period. The Sella–Lords model fit is shown (solid line) with 95% confidence intervals (dotted lines). The solid vertical lines indicate S_p (eq. 15).

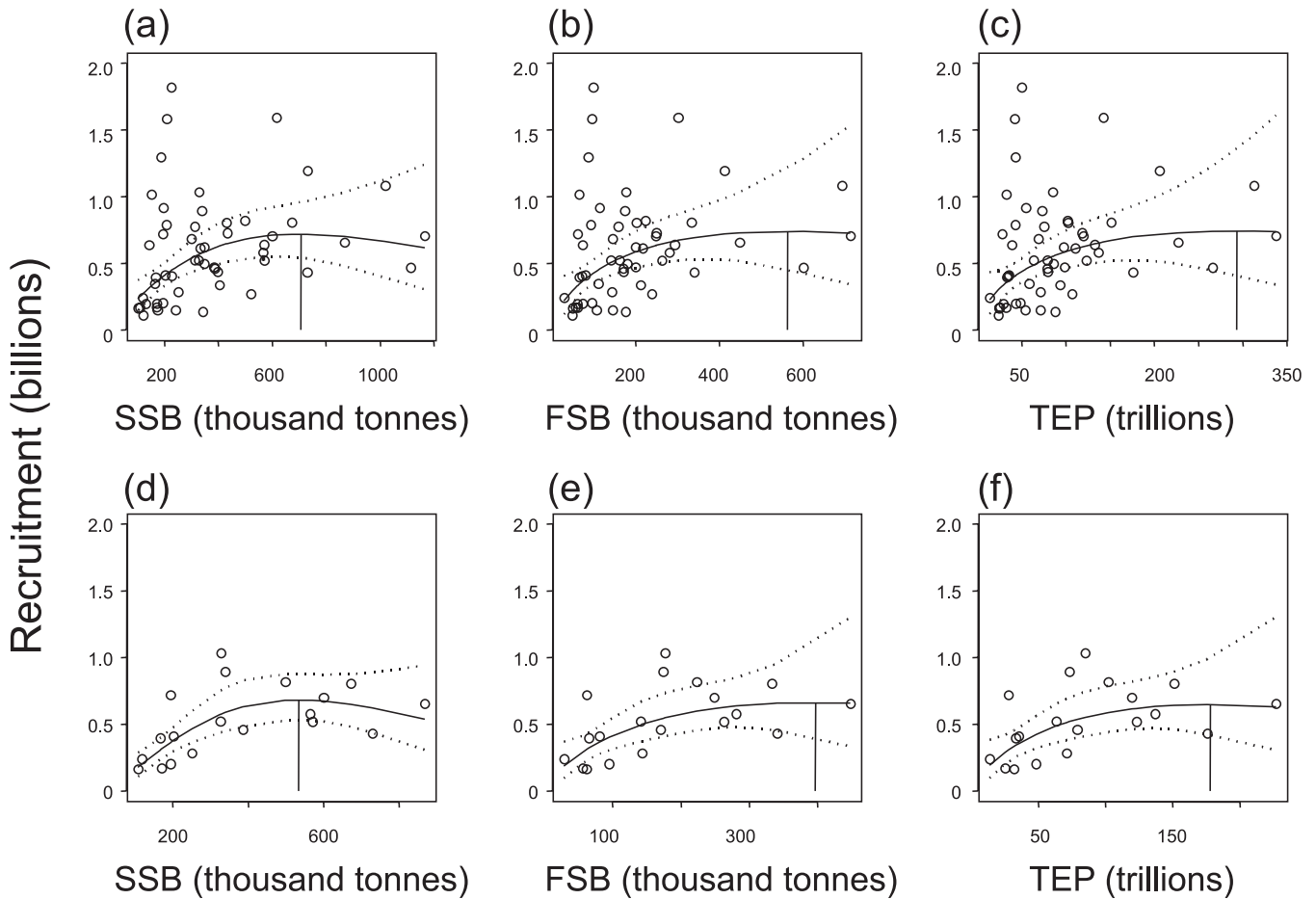


Table 3. Parameter estimates and summary statistics for the different change-point models.

	Full time			Recent time		
	SSB	FSB	TEP	SSB	FSB	TEP
δ (t or no. eggs)	186 570	61 679	3.26×10^{13}	193 794	61 679	6.33×10^{13}
α_2 (thousands)	527 009	507 432	514 433	496 655	483 921	617 226
$-2 \ln$ likelihood	100.52	106.09	104.42	24.58	28.67	24.47

Note: Spawning stock biomass (SSB), female-only SSB (FSB), and total egg production (TEP) were used as the independent variable in the model. Note that δ and α_2 correspond to the S^* and R^* , respectively, as used in Barrowman and Myers (2000). The value $-2 \ln$ likelihood is analogous to a measure of residual deviance and is included here as a measurement of goodness of fit.

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, because stocks dominated by smaller-sized individuals often result from sustained high 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 Advisory Commit-

tee on Fishery Management 2002). In 1987, approximately one-quarter of the SSB was female, and the relative fecundity of the stock was $115 \text{ eggs} \cdot \text{g}^{-1}$, which is approximately one-half of the long-term mean value ($235 \text{ eggs} \cdot \text{g}^{-1}$). Russian and Norwegian authorities sharply reduced fishing mortality from 0.98 in 1989 to 0.27 in 1990 (ICES Advisory Committee on Fishery Management 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 5 years starting in 1990 (Marshall et al. 1998). This stock recovery was fortuitous

Fig. 10. Stock–recruit relationships using different indices of reproductive potential and different time periods. (a) Spawning stock biomass (SSB) and full time period. (b) Female-only spawning stock biomass (FSB) and full time period. (c) Total egg production (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).

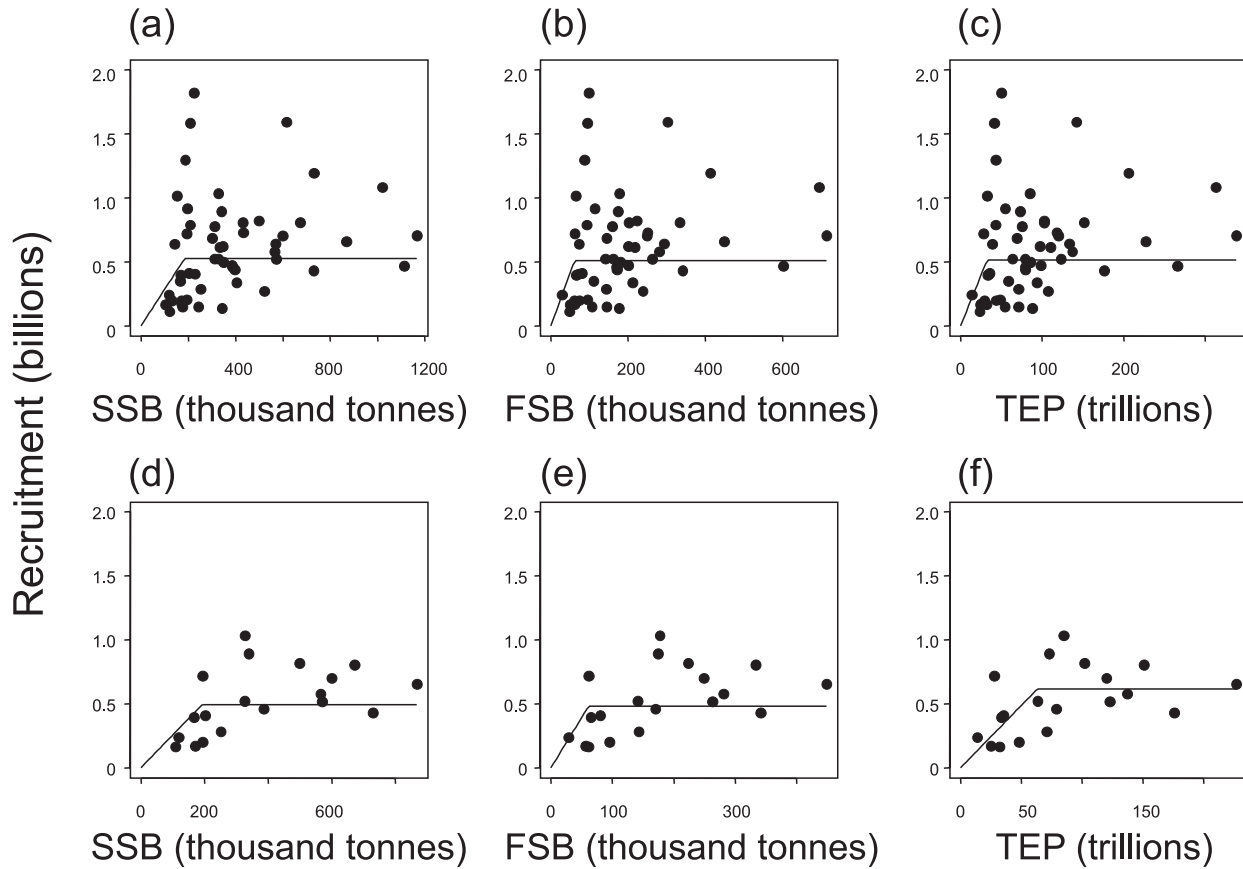


Table 4. A summary of the agreement between the two alternative indices of reproductive potential (female-only spawning stock biomass (FSB) and total egg production (TEP)) and spawning stock biomass (SSB) about whether stock status is inside safe biological limits (value of S greater than change-point value) or outside safe biological limits (value of S less than change-point value).

	Full time		Recent time	
	SSB and FSB	SSB and TEP	SSB and FSB	SSB and 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%)

Note: Data correspond to the total number of years in the time period; data in parentheses correspond to the percentage of years in the time period.

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) failed to accurately account for the effect that variation in length composition had on the reproductive potential of the stock.

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 essential (Marteinsdottir and Begg

2002; Köster et al. 2003; Berkeley et al. 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., change points). However, fisheries management places a premium on using management protocols that can be universally applied, which makes it difficult to implement change. Failing to use the best available knowledge puts data-rich stocks at a disadvantage 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 avail-

able 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_t . Improved methods for measuring the fecundity of wild stocks have been developed (Murua et al. 2003) and in the future 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 with rebuilding SSB, because the former requires substantial increases in the proportional representation of large individuals (Northeast Fisheries Science Center 2003).

Implications for stock–recruit theory

Cod stocks that approach (e.g., Northeast Arctic stock of Atlantic 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 the Northeast Arctic stock of Atlantic cod, the recent time period suggested depensation, whereas the full time period suggested compensation. However, if either len-FSB or len-TEP was used as an index of reproductive potential, then both the full or recent time periods exhibited overcompensation. 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, overcompensation should promote a faster stock recovery given that production rate of recruits is highest at the lowest levels of stock reproductive potential.

The trend near the origin of the stock–recruit relationship is also important for determining change-point values that, under the precautionary approach, indicate the level at which recruitment becomes impaired. Comparing change points 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. Accounting for both the considerable degree of interannual variation in the sex ratios and the differential maturation rates for males and females had relatively little impact on the overall assessment of stock status. However, the change point for len-TEP was more conservative than the change point 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 change point classified the stock as being outside safe biological limits and the SSB change point classified the stock as being inside safe biological limits. This

result indicates that replacing a weight term (w_t ; eq. 3) with a fecundity term (e_t ; eq. 4) that was sensitive to interannual variation in relative condition (eq. 9) caused the change point to behave more conservatively. To support the precautionary approach, which advocates using a more risk-averse approach where knowledge is limiting, a detailed sensitivity analysis is required to estimate the relative effects the individual components of reproductive potential have on the assessment of stock status.

The alternative indices of reproductive potential did not substantially increase or decrease the explanatory power of the stock–recruit relationship when compared with SSB. This result contrasts with that for the Baltic stock of Atlantic cod, 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 the Northeast Arctic stock of Atlantic cod, year-class strength is frequently established during the egg and larval stages (Sundby et al. 1989; Mukhina et al. 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 the Baltic stock of Atlantic 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. However, given that the formulations of both FSB (eq. 3) and TEP (eq. 4) 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 that underlie the use of SSB.

A larger improvement in the explanatory power of the stock–recruit relationship occurred when the time series for the Northeast Arctic stock of Atlantic 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 the Baltic stock of Atlantic 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 Advisory Committee on Fishery Management 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 were responsible.

While it remains to be shown if climate may have contributed to a shift in the recruitment dynamics of the Northeast Arctic stock of Atlantic 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 with the more recent time period, when the stock was dominated by smaller and 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 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.

In conclusion, 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 naive 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 oversimplified 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 quantify the true effect of fishing on reproductive potential.

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