Condition and size composition effects on the simulated relationship between spawner biomass and total egg production for Northeast Arctic cod (Gadus morhua L.).

by

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ABSTRACT

Spawner biomass (SB) is often assumed to be proportional to total egg production (TEP) by fish stocks. Recent studies suggest that this assumption may not be valid, particularly when the physiological condition of fish varies. This study used Monte Carlo techniques to simulate the relationship between SB and TEP for Northeast Arctic cod (Gadus morhua). In the first simulation exercise, reproductive traits reflecting condition (length-specific maturity, weight and fecundity) were varied according to food abundance (capelin biomass) while the size composition (numbers at length) was held constant. In the second exercise, the size composition, as described by the modal length of spawners, was varied and condition was held constant. In the final exercise, condition and size composition were varied simultaneously. The first exercise indicated that variation in TEP was not constant but increased as the SB increased. The second exercise showed that, for a given SB, TEP increased with increasing modal length of spawners. Comparing the results of the first and second exercise showed that food-dependent variation in condition introduced greater variability into the relationship between SB and TEP than did shifting the size composition. When condition and size composition were varied simultaneously, as would be expected in wild stocks, TEP exhibited approximately 4-fold level of variation at any given SB.

Keywords: cod, spawner biomass, egg production, condition, size composition, Monte Carlo simulations
INTRODUCTION

The cause of variability in fish recruitment has been a problem for both scientists and fisheries managers for several decades. Recruitment is most often studied in relation to the size of the spawning stock, where biomass of sexually mature individuals is assumed to represent the reproductive potential of the stock (Marteinsdottir and Thorarinsson, 1998). However, it is possible that a fish population having the same spawner biomass (SB) in different years has substantially different levels of total egg production (TEP) as well as different levels of egg survival. Therefore, SB may not be a reliable indicator of the population's ability to sustain itself (MacKenzie et al., 1997).

Interannual variation in condition of spawners is one source of variation in TEP (Marshall and Frank 1999). Condition is commonly measured by the Fulton's condition factor (K):

\[ K = 100 \times \frac{W}{L^2} \]

where W is whole body weight (in g) and L is total length (in cm). Another measure used for describing condition is the liver condition index (LCI):

\[ LCI = 100 \times \frac{LW}{BW} \]

where LW is liver weight (in g) and BW is whole body weight (in g). Studies done for a variety of species have shown that condition, at the individual level, influences the potential fecundity of females (Hislop et al. 1978; DeMartini 1991; Koslow et al. 1995; Kjesbu et al. 1998). Variation in condition also affects the realized fecundity of spawning females through atresia (Ma et al. 1998). At the stock level, mature female in poor condition can skip spawning seasons (Marshall et al. 1998; Schwalm and Chouinard, 1999).

Shifts in the size composition can also introduce variability into TEP (Kjesbu et al. 1998). Maturity in Northeast Arctic cod occurs at age 6-9, with a length of approximately 60-90 cm (Torsvik et al. 1995). Larger fish are more fecund than smaller ones (Kjesbu et al. 1991). In the last decades the fish seem to mature earlier, perhaps because of a higher fishing pressure (Trippel et al. 1997). The depletion of large fish may seriously lower a stock's egg production. Stock reproductive potential is further diminished if poorer gamete quality is exhibited by smaller compared with larger members (Trippel et al. 1997).
This study used data for the Northeast Arctic cod stock to test how varying the condition and size composition of spawners affect the simulated relationship between SB and TEP. The specific objectives were in the first exercise to vary condition according to capelin biomass and keep size composition (i.e., numbers at length) constant. In the second exercise condition was held constant and the size composition was varied. The final exercise varied condition and size composition simultaneously to see how this affected the relationship between SB and TEP.

METHODS

The goal of the first exercise was to simulate how varying the condition of cod while keeping the size composition constant affected the relationship between TEP and SB. Field data from combined acoustic/trawl surveys of Barents Sea and Lofoten region were used to describe the size composition (numbers at length or n_l) and sex ratio (s_l) of Northeast Arctic cod (Marshall et al. 1998). Values of n_l and s_l were both estimated for 5 cm length classes for the period 1985 to 1996. The s_l generally increases with length, but a large degree of interannual variability occurs (Marshall et al. 1999). To remove the effect of this source of variability on the analysis the mean value of s_l for each length class from the twelve years (s_l) was used to partition the stock into males and females. Length-specific weight (w_l), fecundity (f_l) and maturity (m_l) were predicted using the statistical models described in Marshall et al. (1999). These models were developed using potential fecundity data collected from the Lofoten area (Kjesbu et al. 1998) and data from Norwegian surveys of the Barents Sea region (Marshall et al. 1998). Estimates of capelin stock biomass from acoustic surveys (Gjøsæter 1999) were used as the independent variable. From these data sources, the following statistical models were developed.

Multiple regression model was used to estimate w_l for a given capelin biomass (w_{1,cb}):

\[
\ln(w_{1,cb}) = -9.5 + 4.07(\ln{\text{length}}) + 0.32(\ln{\text{CapBio}}) - 0.07(\ln{\text{length}} \times \ln{\text{CapBio}})
\]  (1)

Multiple regression model was also used for estimating f_l for a given capelin biomass (f_{1,cb}):

\[
\ln(f_{1,cb}) = -15.64 + 6.36(\ln{\text{length}}) + 1.11(\ln{\text{CapBio}}) - 0.21(\ln{\text{length}} \times \ln{\text{CapBio}})
\]  (2)
A logistic model was used for estimating \( m_1 \) at each capelin biomass (\( m_{l,cb} \)):

\[
\text{logit}(m_{l,cb}) = -11.93 + 0.15(\text{length}) + 1.23 \times 10^{-7} (\text{CapBio})
\]

The value of \( m_{l,cb} \) was then estimated from:

\[
m_{l,cb} = \frac{e^{\text{logit}(m_{l,cb})}}{1+e^{\text{logit}(m_{l,cb})}}
\]

Predicted values of \( w_{l,cb}, f_{l,cb} \) and \( m_{l,cb} \) were assumed to have errors that were normally distributed with a mean of zero and a standard deviation of \( \sigma \). For \( f_{l,cb} \) and \( w_{l,cb} \), \( \sigma \) was estimated to be 0.32 and 0.17, respectively. For \( m_{l,cb} \), \( \sigma \) was assumed to be non-constant with length, with a maximum at \( m_{l,cb} = 0.5 \) and decreasing linearly to zero at 50 and 100 cm (Marshall et al. 1999).

For each simulation in exercise 1, TEP for a given capelin biomass (\( \text{TEP}_{cb} \)) was estimated as:

\[
\text{TEP}_{cb} = \sum_{l=50}^{L} n_l \times S_1 \times m_{l,cb} \times f_{l,cb}
\]

Similarly, SB for a given capelin biomass (\( \text{SB}_{cb} \)) was estimated as:

\[
\text{SB}_{cb} = \sum_{l=50}^{L} n_l \times m_{l,cb} \times w_{l,cb}
\]

In each simulation \( \text{TEP}_{cb} \) and \( \text{SB}_{cb} \) were estimated for seven levels of capelin biomass ranging from a minimum of 100 000 t to a maximum of 8 million t. Monte Carlo sampling was used to estimate the means and standard deviation (s.d.) for both \( \text{SB}_{cb} \) and \( \text{TEP}_{cb} \). Convergence (less than 1.5% change in both the mean and s.d.) was always achieved within 1500 iterations. 95% confidence intervals were approximated as the mean ± 2 s.d. Twelve separate simulations were performed using \( n_l \) values for 1985 through to 1996.

In the second exercise, the size composition of spawners (\( n_{l,sc} \)) was determined using numerical optimization techniques (Solver in Microsoft Excel for Windows, Version 7.0). Values of \( n_{l,sc} \) were determined by solving the equation:
for pre-specified values of both SB (SBsc) and the modal length. The values of m_l and w_l used were held constant and the observed values for 1991 were arbitrarily chosen as the constants. The pre-specified values of SBsc corresponded to the annual VPA estimates of SBsc for the years 1985 to 1996 (ICES 1999). These twelve values range from a minimum of 112 000 t to a maximum of 882 000 t. The pre-specified modal lengths ranged in 5-cm increments from 67.5 to 97.5 cm. This is a realistic range for the modal lengths of spawning NA cod (see Fig. 9 in Marshall et al. 1998). Figure 1 illustrates seven different length compositions which gives a SBsc corresponding to that observed for 1991 (679 000 t). Each simulation estimated the TEP for a given size composition (TEPsc) as:

$$SB_{sc} = \sum_{i=50}^{140} n_{i,sc} \times m_i \times w_i$$  \hspace{1cm} (7)

$$TEP_{sc} = \sum_{i=50}^{140} n_{i,sc} \times S_i \times m_l \times f_i$$  \hspace{1cm} (8)

Twelve different simulations were performed using SBsc values from 1985 to 1996. To be consistent, the values of m_l and f_l used corresponded to the observed values for 1991. Because each simulation held both condition and the pre-specified SBsc constant variation in TEPsc was introduced solely through variation in the size composition. Uncertainty in the resulting estimates of TEPsc was not estimated.

In the final exercise, condition and size composition were varied simultaneously. The values of n_l used corresponded to the values of n_{i,sc} for the minimum and maximum modal lengths (67.5 and 97.5 cm) at each of the SB values used in exercise 2. Only the minimum and maximum levels of capelin stock biomass (100 000 and 8 million t) were used to estimate w_{l,cb}, f_{l,cb} and m_{l,cb} using equations 1, 2 and 4. TEP_{cb,sc} and SB_{cb,sc} were estimated from n_{i,sc} and the predicted values of w_{l,cb}, f_{l,cb} and m_{l,cb} using equations 5 and 6. Monte Carlo simulations were run to estimate the s.d. of the TEP_{cb,sc} and SB_{cb,sc}.

These three exercises each generated a bivariate relationship between TEP and SB. Error bars (± 2 s.d.) were put on both TEP and SB for exercises 1 and 3.
RESULTS

Results for exercise 1 illustrate that variation in TEP was not constant but increased as the SB increased (Fig. 2). To look more in detail at the magnitude of variation, one specific simulation (1993) was chosen. The possible range in values of TEP and SB is indicated by the lowest to the highest extremes in error bars in the y- and x-axes respectively. In 1993 SB ranged from about 700 000 to 1200 000, and TEP ranged from about $120 \times 10^{12}$ to $480 \times 10^{12}$. Thus, a fixed quantity of spawners subject to food-dependent variation in condition exhibits nearly 2-fold variation in SB and 4-fold variation in TEP.

In the second exercise there was a linear relationship between TEP and SB (Fig. 3) when data for all simulations was combined. Looking at the results of each simulation separately the difference between lowest modal length (67.5 cm) and highest modal length (97.5 cm) increased with increasing SB. In 1993 the values for TEP ranged from approximately $250 \times 10^{12}$ to $350 \times 10^{12}$ i.e. less than 2-fold. Comparing the magnitude of variation in Fig. 2 and Fig. 3, which are plotted on the same scale, suggests that condition-dependent variation in reproductive traits introduced greater variability into the relationship between SB and TEP than did shifting the size composition.

Varying condition and size composition simultaneously (exercise 3) revealed how far the simulated relationship between TEP and SB deviates from simple proportionality, i.e., linearity. TEP shows approximately 4-fold level of variation for any given level of SB (Fig. 4). For any given SB large spawners in good condition will have highest TEP while small spawners in poor condition has the lowest. More interestingly, TEP by small spawners in good condition is higher than TEP for large spawners in poor condition. Variation in this plot can also be examined by comparing the slopes of the relationship between TEP and SB for the different combinations of condition/modal length. Figure 4 shows that the slopes of the high condition/high modal length and high condition/low modal length combination are higher than the slopes of the low condition/high modal length and low condition/low modal length combinations. This indicates that variation in condition introduces more scatter into the simulated relationship between TEP and SB than does variation in size composition.
DISCUSSION

For all three exercises, varying the condition and size composition affected the simulated relationship between TEP and SB, but varying the condition seemed to introduce more variation into the relationship between TEP and SB than did varying the size composition of the stock.

The condition of the cod stock is influenced by food supply. The main food item for the cod is the Barents Sea capelin (Kjesbu et al., 1998). And as the size of the capelin stock varies, this will also affect the cod stock. In this study the capelin biomass were varied from a low level to a high level (Gjøsæter, 1999) and the resulting variation in TEP was approximately 4-fold.

We have not included condition effects on realised TEP and egg quality. Egg quantity are neither included, but are expected to increase the variability in TEP.

In future we plan to use the simulated relationship between TEP and SB (Fig. 2, 3 and 4) as the starting point in an investigation into how variation is introduced to the relationship between recruitment and SB. Two additional sources of variation which will be included in this analysis are variation in pre-recruit mortality and variation between the estimated values of SB (e.g. from virtual population analysis) and the «true» SB.

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REFERENCES


Figure 1: Seven different size compositions giving modal lengths and constant SB.

Figure 2: The simulated relationship between SB and TEP when varying the condition of the spawners while holding the size composition (numbers at length) of the stock constant. Results for 12 simulations using observed size composition for 1985 to 1996 are shown.
Figure 3: The simulated relationship between SB and TEP when varying size composition/modal length of the stock and holding condition of the spawners constant. Results for 12 simulations using observed SB for 1985 to 1996 are shown.

Figure 4: The simulated relationship between SB and TEP when varying size composition and condition simultaneously.