

**Spawner quality effects on two measures of reproductive potential: have we been
counting our eggs before they've hatched?**

by

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Abstract

Recent studies have found positive associations between recruitment and indices of spawner quality (condition) for stocks exhibiting an indeterminate relationship between recruitment and spawner biomass. This suggests that spawner biomass is insensitive to interannual variability in condition affecting total egg production. This hypothesis was tested for the Northeast Arctic (NA) cod stock using a simulation approach. Because abundance of the Barents Sea capelin stock is an important determinant of condition of NA cod, the simulations varied length-specific proportion mature, weight, and fecundity of NA cod according to capelin biomass while holding numbers at length constant. Total egg production and spawner biomass and their associated errors were estimated for levels of capelin biomass which encompassed the range observed in the Barents Sea. Increasing condition significantly increased both total egg production and spawner biomass, however, the magnitude of increase in total egg production was approximately double that in spawner biomass. Incorporating hypothesized effects of condition on atresia and skipped spawning increased the difference between total egg production and spawner biomass. Comparing simulation results for different numerical abundances and size compositions indicated that spawning stocks dominated by smaller length classes had larger differences between total egg production at the minimum and maximum capelin biomasses.

Introduction

At the stock level there is growing evidence that spawner biomass is an insensitive measure of the reproductive potential of fish stocks (Trippel et al. 1997; Solemdal 1997; Marshall et al. 1998). Positive correlations have been observed between recruitment and condition of either individual spawners (Marshall and Frank 1999) or the aggregate stock (Boyd et al. 1998). These results suggest that the effect of variation in spawner condition on the reproductive potential of a stock is not well-represented using spawner biomass as a proxy for total egg production.

Capelin (*Mallotus villosus*) is well-established as the preferred prey of cod (*Gadus morhua*) in arcto-boreal ecosystems such as the Barents Sea (Mehl and Sunnanå 1991). Since 1973 the total stock biomass of Barents Sea capelin has varied between a maximum of 7 806 000 t in 1975 and a minimum of 101 000 t in 1987 (Fig. 1a). Capelin are a rich source of lipid energy (Jangaard 1974) used to support somatic growth, gonad maturation and migration. In gadoids such as cod lipids are stored primarily in the liver (Kjesbu et al. 1991; Lambert and Dutil 1997). The close correspondence between temporal trends in capelin stock biomass (Fig. 1) and liver weights of NA cod (Nilssen et al. 1994; Yaragina and Marshall in press) suggests that the condition of NA cod is highly dependent on capelin abundance.

Food-dependent variation in condition could impact the reproductive potential of the NA cod stock in several ways. Experimental studies have shown that condition significantly affects the number of developing (vitellogenic) oocytes produced over a single spawning season (i.e., potential fecundity) of reared coastal cod (Kjesbu et al. 1991), NA cod (Kjesbu et al. 1998) and cod in the northern Gulf of St. Lawrence (Lambert and Dutil in press). Variation in condition also causes realized fecundity to deviate from potential fecundity by affecting the incidence of atresia. For example, the realized fecundity of reared coastal cod ranged between 20 and 80% of potential fecundity depending on the nutritional status of spawners (Kjesbu et al. 1991). Variation in condition could also influence the rate at which cod mature. For example, laboratory experiments using hatchery-reared cod found that a dry pellet diet having 15% of the energy from lipids resulted in 58% of the cod maturing, whereas, a higher

ration diet which included capelin and which had 70% of the energy from lipids increased the percentage maturing to greater than 90% (Lehmann et al. 1991). Furthermore, skipped spawning seasons can result when cod are in poor condition and lack the energy reserves required for normal gonad development (Burton et al. 1997; Schwalm and Chouinard 1999).

The objective of this study was to simulate the effect of variation in spawner condition on total egg production (TEP) and spawner biomass (SB) of NA cod. Statistical models predicting length-specific proportion mature, weight and fecundity as functions of capelin stock biomass were developed using empirical data for the NA cod and Barents Sea capelin stocks. Estimates of the total abundance and size composition (i.e., numbers at length) of NA cod were obtained from annual acoustic and trawl surveys of the Barents Sea and Lofoten regions conducted from 1985 to 1996 (Marshall et al. 1998). These survey-based estimates of numbers at length were combined with the predictions of m_l , w_l and f_l to simulate variation in TEP and SB with increasing capelin stock biomass. The 95% confidence intervals for both output variables were estimated by Monte Carlo simulations to test whether variation in spawner condition had a significant effect on reproductive potential of the stock as represented by either TEP or SB. The hypothesized effects of condition on atresia and skipped spawning were incorporated into estimates of TEP to approximate condition effects on realized TEP. The magnitude of the dynamic response of SB to increases in capelin stock biomass was compared to those observed in both potential and realized TEP. Simulation results using the numbers at length for different years (1985 to 1996) were compared in order to determine whether total abundance or modal length of spawners had a significant effect on the magnitude of the response to capelin stock biomass.

Methods

The models described in Table 1 were used to predict length-specific proportion mature (m_l), weight (w_l) and fecundity (f_l) for increasing values of capelin stock biomass. Since the simulation analysis applies to the mature portion of the stock only observations for cod greater than 50 cm in length were used in model development.

Figure 2 illustrates the predicted length-dependent variation in m_l , w_l , and f_l for capelin stock biomasses of 100 000, 1 million and 8 million t.

The effect of varying condition on TEP and SB was simulated by estimating the input variables for seven levels of capelin stock biomass ranging from 100 000 to 8 million t. Random error was incorporated into these estimates through Monte Carlo simulations. Estimates of the three input variables were assumed to have errors that were normally distributed with a mean equal to zero and a standard deviation of σ . For both w_l and f_l the value of σ was estimated from the multiple regression model (Table 1) and was constant across length and among years. In the case of m_l σ was assumed to be non-constant with length such that σ was maximum at the length at 50% maturity (l_{50}). The l_{50} was estimated from following relationship between capelin stock biomass:

$$l_{50} = 79.33 - 8.2 \times 10^{-7} (\text{capelin stock biomass})$$

which was obtained by solving the equation given in Table 1 for m_l equal to 0.5. The magnitude of σ at l_{50} was chosen to give realistic levels of uncertainty but was not empirically determined. Above and below the l_{50} it was assumed that σ decreases linearly to zero at lengths of 50 and 100 cm and was equal to zero for lengths greater than 100 cm. The length-dependent variation in σ of m_l for the minimum and maximum levels of capelin stock biomass is illustrated in Figure 3.

Separate simulations were performed using numbers at length (n_l) from research vessel surveys of the Barents Sea and Lofoten region conducted from 1985 to 1996. The term simulation year therefore refers to a year having distinct values of total numerical abundance and size composition. Values of n_l for each simulation year were estimated for 5-cm length classes by partitioning the acoustic estimates of total abundance for the Barents Sea and Lofoten surveys according to length using information from trawl samples then summing the two surveys (Marshall et al. 1998). The sex ratio (s_l) was estimated by partitioning the values of n_l by sex for the Barents Sea and Lofoten surveys separately then combining the two surveys to estimate the proportion of each sex. Values of s_l generally increase with length, however, there is a large degree of interannual variability (see Fig. 5 in Marshall et al. 1998) which could

be due to sampling artifacts and (or) differential spawning mortality. To remove this high frequency source of variation from the simulation analysis the grand mean of s_l values for each length class for 1985 to 1996 (\bar{s}_l) was used to partition n_l by sex in each simulation year.

For each simulation year the TEP for a given capelin stock biomass (csb) was estimated as:

$$TEP_{csb} = \sum_{l=50}^{140} n_l \times \bar{s}_l \times m_{l,csb} \times f_{l,csb} \quad (1)$$

where $m_{l,csb}$ and $f_{l,csb}$ were both estimated using the models in Table 1. SB was estimated as:

$$SB_{csb} = \sum_{l=50}^{140} n_l \times m_{l,csb} \times w_{l,csb} \quad (2)$$

where $m_{l,csb}$ and $w_{l,csb}$ were both estimated using the models in Table 1. Estimates of SB assume that males and females have the same values of m_l and w_l which is consistent with the standard practice in the analytical assessment of this stock (ICES 1999). Monte Carlo sampling was used to estimate the means and standard deviations (s.d.) for both output variables at each capelin stock biomass. 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 \pm 2 s.d. To compare the pattern of variation in TEP and SB on a common scale the means were divided by the mean calculated for that simulation year at the minimum capelin stock biomass of 100 000 t. The mean value for the maximum capelin stock biomass (8 million t) expressed relative to the minimum capelin stock biomass is subsequently referred to as the maximum dynamic response (MDR). A MDR of 2 indicates that the value of the output variable at the maximum capelin stock biomass is double that at the minimum capelin stock biomass.

To incorporate condition effects on realized TEP, two physiological responses were incorporated into the simulation analysis: atresia and skipped spawning in larger cod. Because the degree of interannual variation in atretic intensity for the NA cod

stock is unknown the relationship between atretic intensity and capelin stock biomass was hypothetical rather than observed. It was assumed that the maximum atretic intensity was 0.50 (i.e., 50% of the eggs were resorbed), a value that is midway between the maximum and minimum rates (80% and 20%) observed for reared coastal cod in varying condition (Kjesbu et al. 1991). It was further assumed that the maximum atretic intensity occurred at the minimum capelin stock biomass (100 000 t) and decreased linearly to a value of 0 for capelin stock biomasses equal to or greater than 1 million t. A capelin stock biomass of 1 million t was chosen as boundary between atretic and non-atretic cod because below that value the liver condition index (LCI) of NA cod decreases rapidly while above it LCI is relatively constant (Yaragina and Marshall in press). The analysis therefore assumes that reductions in lipid reserves increase atretic intensity. No length dependency was introduced to values of atretic intensity. Skipped spawning seasons have been observed in length classes of NA cod dominated by repeat spawners (Fig. 6 in Marshall et al. 1998). Repeat spawners could be more likely to skip spawning because their energy reserves have been depleted in the previous spawning season. Therefore, cod greater than 90 cm in length were assumed to skip spawning when capelin stock biomass was below 1 million t. These hypothesized responses were incorporated into estimates of TEP singly (atresia only) and in combination (atresia + skipped spawning). The resulting estimates of TEP are subsequently referred to as realized TEP.

To compare the results for the twelve simulation years two descriptors of stock demography were used. The modal length corresponds to the midpoint of the 5-cm length class having the highest number of mature females. Numerical abundance is simply n_i integrated across length. The two descriptors therefore represent two distinct aspects of stock demographics: the most frequently occurring size of spawning females and the total abundance of cod larger than 50 cm.

Results

In all twelve simulation years the mean values of TEP at high capelin stock biomasses are significantly higher than those at the minimum capelin stock biomass (Fig. 4). The differences become significant at capelin stock biomasses between 1 and 4 million t.

Variability in estimates of TEP, as indicated by the width of confidence intervals, increases with increasing mean value of TEP. However, if the variation is expressed as the coefficient of variation ($c.v. = (s.d./mean) \times 100$) then the variation is relatively constant with increasing capelin stock biomass (Table 2). Across all levels of capelin stock biomass the c.v.'s range between a minimum of 9.4% and a maximum of 13.2% (Table 2).

In three of the twelve simulation years (1991 to 1993) the mean values of SB at the maximum capelin stock biomass are not significantly different from those at the minimum capelin stock biomass (Fig. 5). Otherwise, the differences become significant between 4 and 6 million t. Minimum and maximum c.v.'s for SB are given for each capelin stock biomass in Table 2. The values are lower than those observed in TEP, ranging between a minimum of 5.4% and a maximum of 7.4%.

The MDR of TEP ranges between approximately 2.4 and 3.7 (Fig. 6a) which indicates that as capelin stock biomass increases from the minimum to the maximum value there is between a two- and four-fold increase in TEP for a fixed quantity of spawners. The MDR of SB is approximately half that observed in TEP, ranging between approximately 1.3 and 1.8 (Fig. 6b).

The MDR of the TEP corrected for hypothesized condition effects on atresia ranges between 4.8 and 7.3 (Fig. 7a), while the MDR of the TEP corrected for hypothesized condition effects on atresia and skipped spawning ranges between 7.6 and 11.7 (Fig. 7b). The precise magnitude of these effects is highly speculative due to the paucity of field data which could be used to develop statistical models for atresia or skipped spawning similar to those used to predict m_1 , w_1 and f_1 (Table 1).

The midpoint of the modal length class of mature females ranged from 62.5 cm in 1989 to 92.5 cm in 1993. There were significant ($p \leq 0.001$) negative correlations between the MDR and the midpoint of the modal length class of mature females for both TEP and SB (Table 3). During the survey time period the numerical abundance of cod larger than 50 cm ranged from a minimum of 55 million in 1988 to

a maximum of 833 million in 1993. No significant relationship with numerical abundance and the MDR was detected (Table 3).

Discussion

Variation in condition has a significant effect on TEP for a fixed number of spawners (Fig. 4), resulting in a two- to four-fold level of increase. When hypothesized effects of condition are included the level of variation in realized TEP approaches one order of magnitude (Fig. 7). These estimates do not account for condition effects on egg size and mortality (Solemdal et al. 1993) and are therefore likely to be conservative estimates of condition effects on reproductive potential. This could explain why positive correlations have been observed between recruitment and condition in both demersal (Marshall and Frank 1999; Marshall et al. submitted ms.) and pelagic (Boyd et al. 1998) stocks.

The observation that the range of variation observed in SB is smaller than the range observed in recruitment has often been interpreted as indicating that recruitment is determined primarily by factors other than SB (Shepherd et al. 1984; Wooster and Bailey 1989; Rijnsdorp et al. 1991). Our analysis, isolating condition effects on TEP from abundance effects, shows that this conventional interpretation of stock effects on recruitment is incorrect. Condition-dependent variation in total body weight does not capture the dynamics that condition-dependent variation in fecundity (Fig. 2). Consequently, SB lacks the dynamic range of more direct measures of the reproductive potential of the stock (e.g., TEP).

High fishing mortality has shifted the length composition of the NA cod stock towards smaller spawners (Nilssen et al. 1994). Over the same time period, the Barents Sea capelin stock has begun to fluctuate more widely (Fig. 1). Our analysis (Table 3) suggests that this combination of factors will cause the variation in TEP to be more extreme. This could potentially result in more extreme recruitment variation.

Modelling condition effects on realized TEP is difficult because data on atresia and egg viability are not routinely collected at the stock level. Even the fecundity data

required to reconstruct a time series of potential TEP are lacking for many stocks. In the absence of either historical or contemporary fecundity data, it is possible to construct alternative proxies of reproductive potential which exhibit a dynamic range approaching that observed in TEP (Marshall et al. submitted ms.). Modelling approaches which partition variation in TEP into constituent elements (Mackenzie et al. 1998) are useful starting points to quantifying the true stock effect on recruitment.

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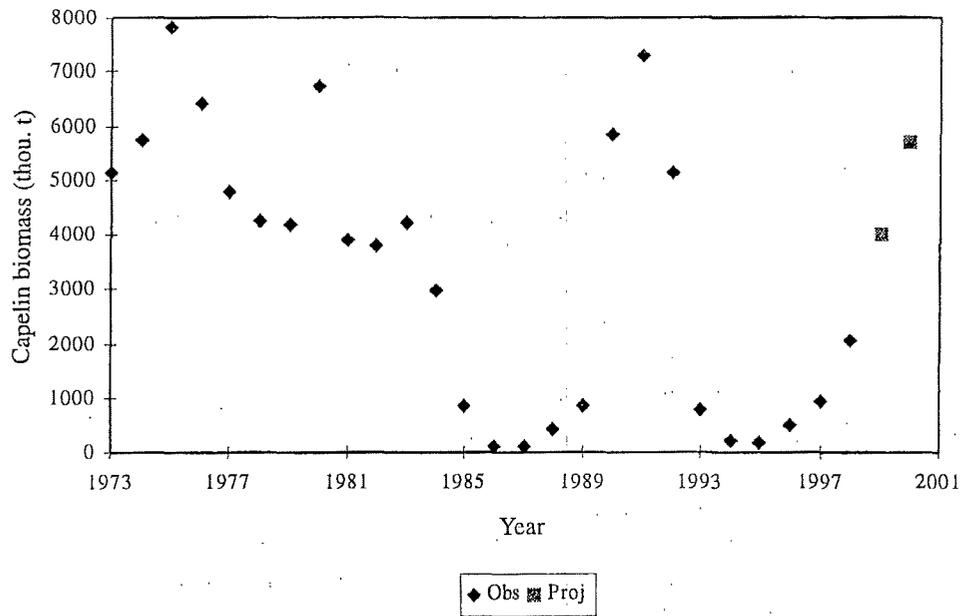


Figure 1: Time series of total stock biomass of Barents Sea capelin (ICES 1997) with projected values for the years 1999 and 2000 (Gjøsæter 1999).

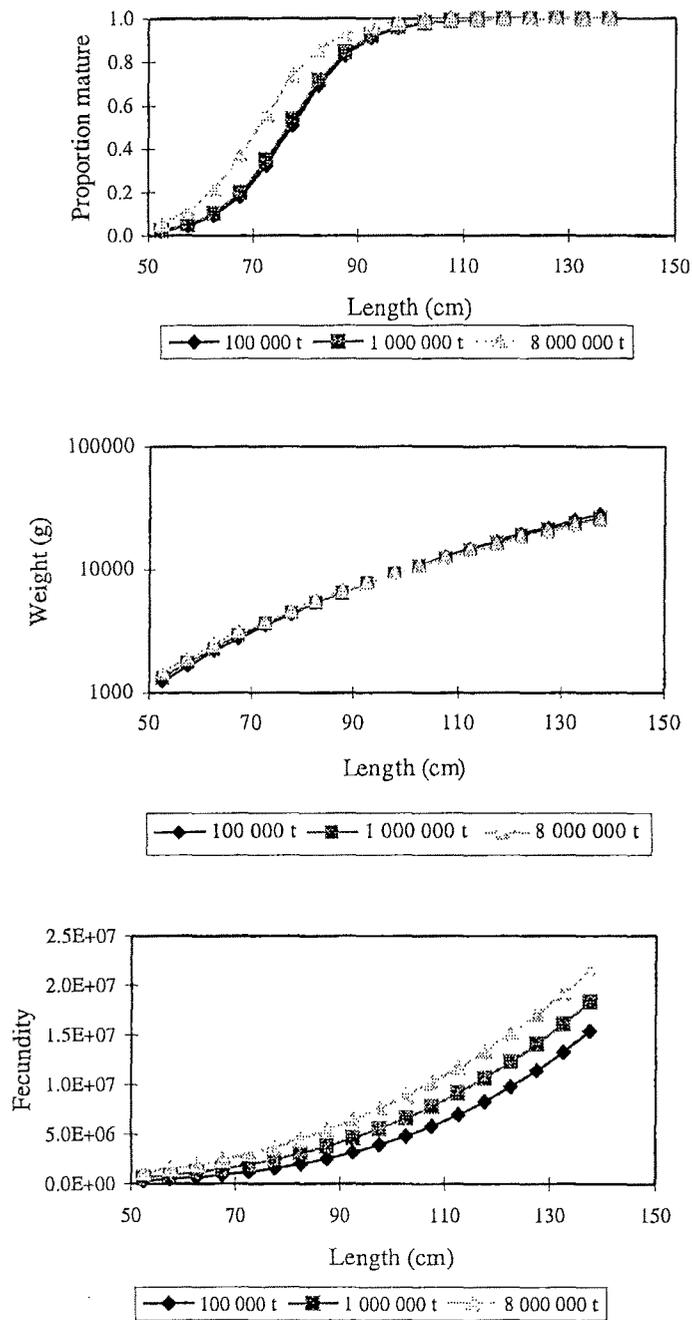


Figure 2: Models used in the simulation analysis to predict the three input variables for three different levels of capelin stock biomass. a) Proportion mature at length; b) weight at length (weight is plotted on a logarithmic scale); and c) fecundity at length.

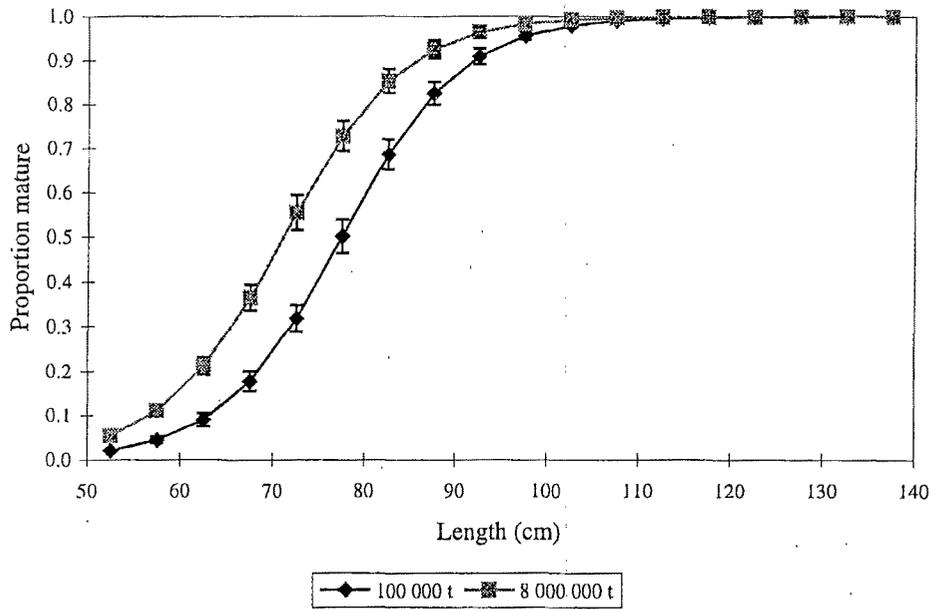


Figure 3: Modelled length-dependent standard deviations for the proportion mature at length for the minimum and maximum capelin stock biomasses used in the simulation analysis.

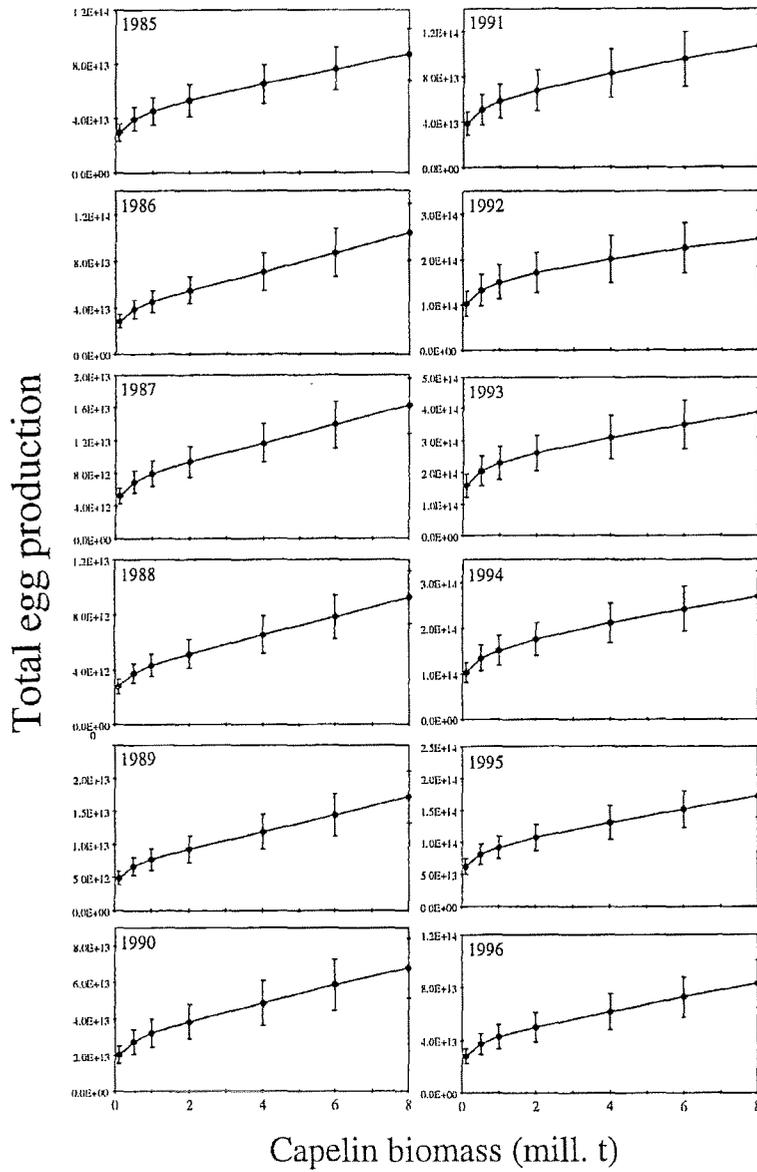


Figure 4: Simulated mean values of total egg production for seven different capelin stock biomasses and twelve simulation years (1985-1996). The 95% confidence intervals estimated using Monte Carlo simulations are shown for each mean value. Note that the panels differ in the scale of the y-axis.

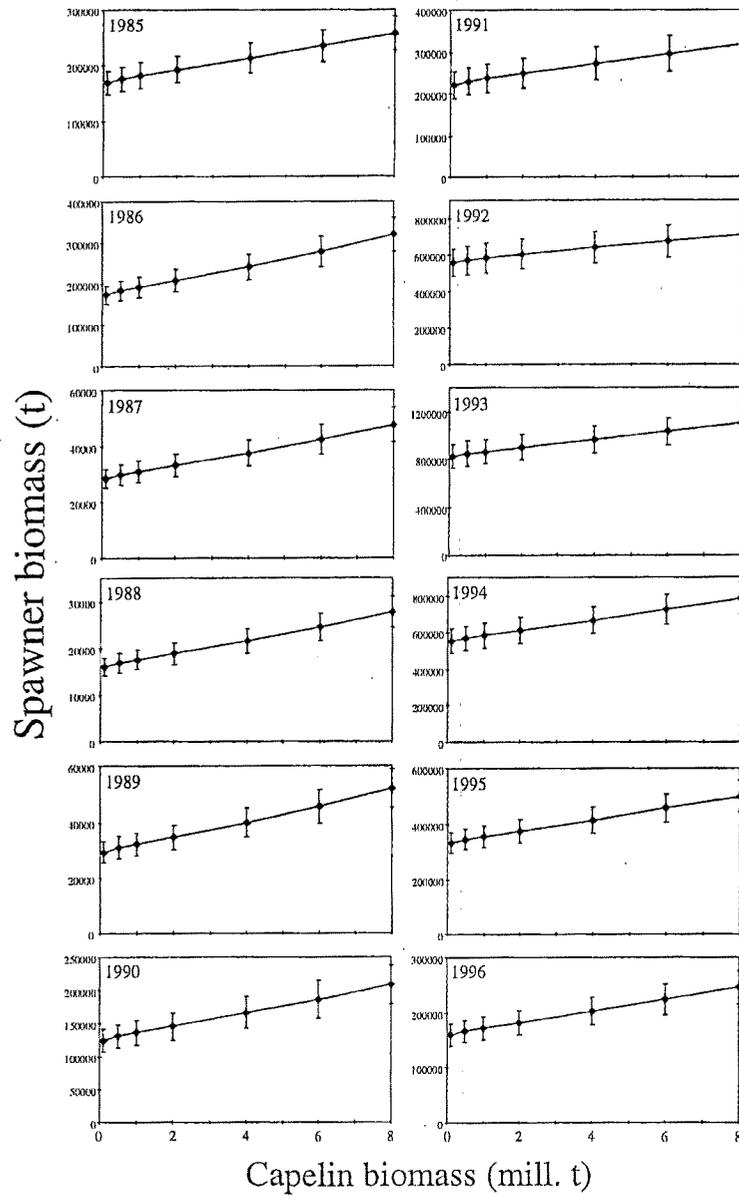


Figure 5: Simulated mean values of spawner biomass for seven different capelin stock biomasses and twelve simulation years (1985-1996). The 95% confidence intervals estimated using Monte Carlo simulations are shown for each mean value. Note that the panels differ in the scale of the y-axis.

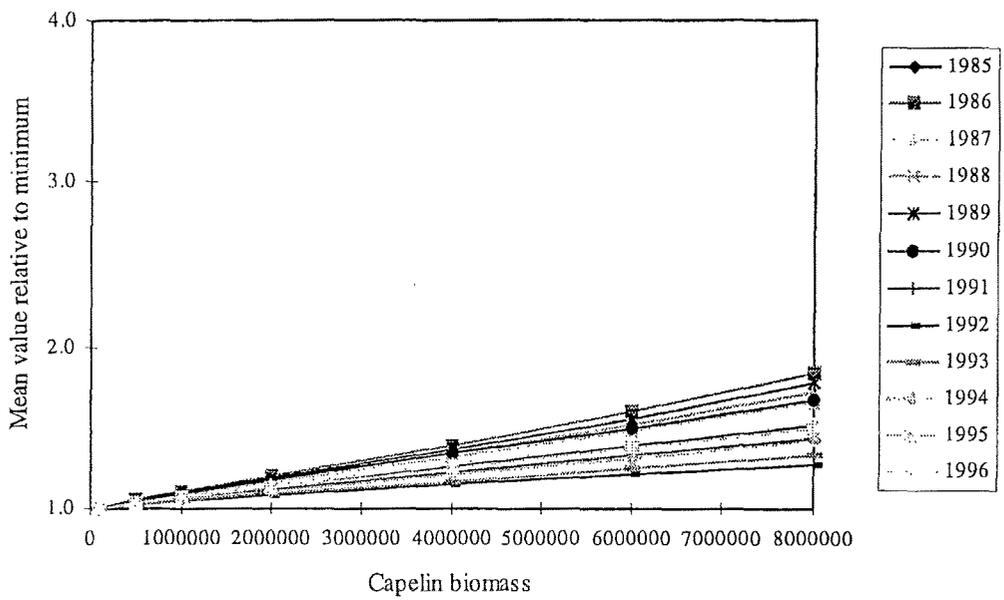
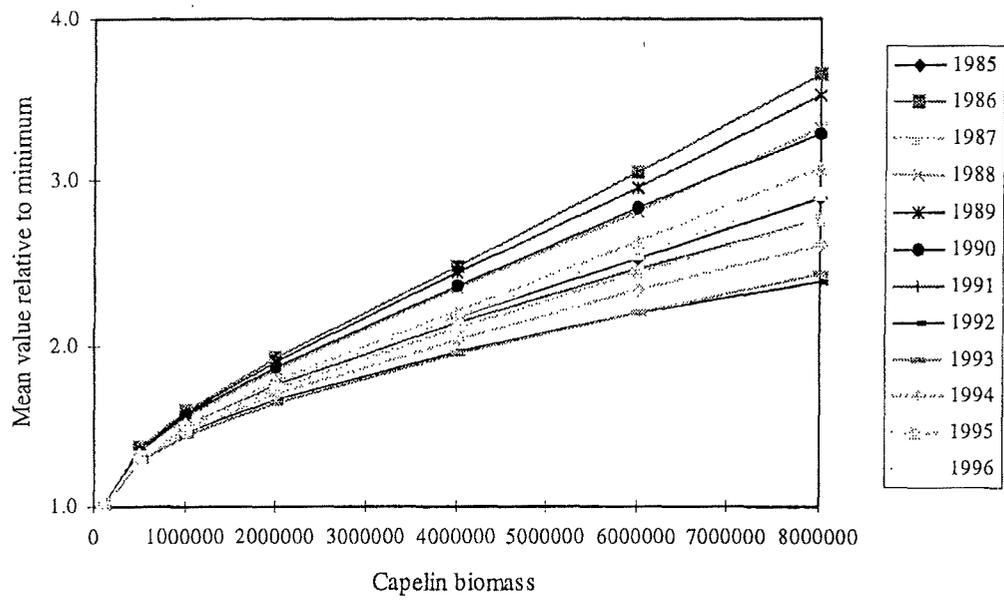


Figure 6: Standardized mean values for the twelve simulation years. A) total egg production; b) spawner biomass.

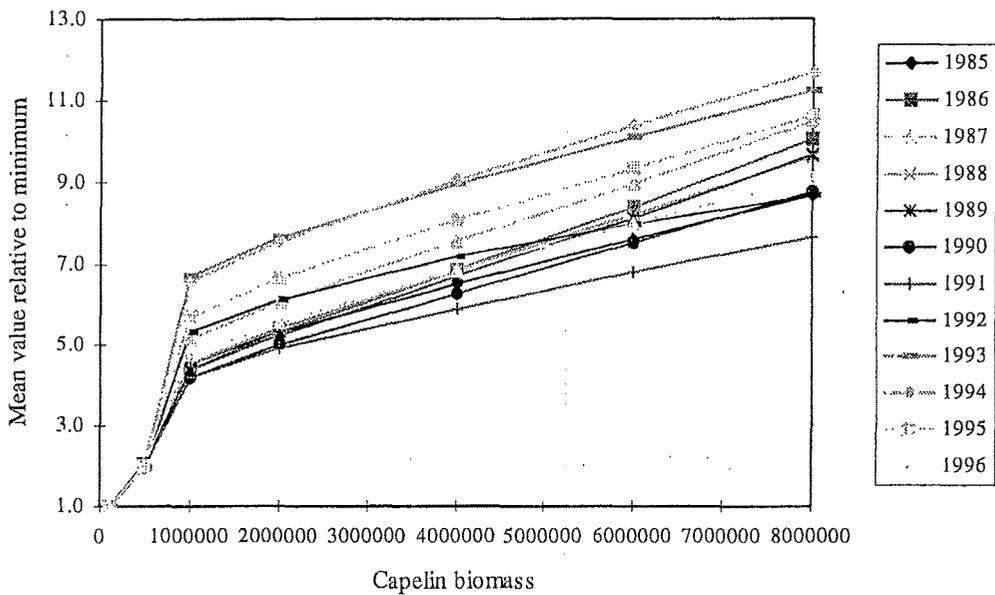
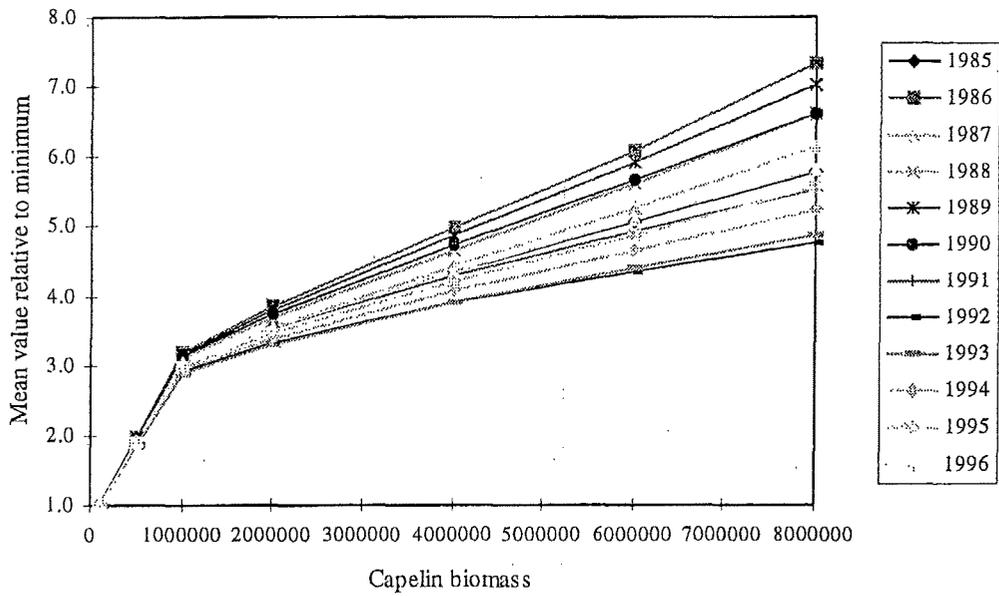


Figure 7: Standardized mean values for the twelve simulation years. A) total egg production corrected for hypothesized condition effects on atresia; b) total egg production corrected for hypothesized condition effects on atresia plus skipped spawning.

Table 1: Models used to estimate the three input variables in the simulation analysis. Length refers to the mid-point of 5 cm length classes ranging from 50 through to 140 cm. Estimates of capelin stock biomass were obtained from annual acoustic surveys (ICES 1997). Errors were normally distributed with a mean of 0 and standard deviations (σ) described below. All terms in the multiple regression models were significant ($p < 0.05$).

Input var.	Calibration period	Region	Model type	Indep. Variables	σ	r^2	Reference
m_l	1985-1996	Barents Sea and Lofoten	logit	intercept length	maximum at $m_l=0.5$ decreasing linearly to 0 at 50 and 100 cm	NA	Marshall et al. 1998
w_l	1985-1996	Barents Sea and Lofoten	multiple regression	intercept ln length ln capelin biomass interaction	0.17	0.93	Marshall et al. 1998
f_l	1986-1991, exc. 1990	Vesterålen	multiple regression	intercept ln length ln capelin biomass interaction	0.32	0.90	Kjesbu et al. 1998

Table 2: Range (minimum and maximum) in coefficients of variation (c.v.) for total egg production (TEP) and spawner biomass (SB) at different levels of capelin stock biomass.

Capelin biomass (t)	TEP		SB	
	Minimum c.v.	Maximum c.v.	Minimum c.v.	Maximum c.v.
100 000	9.4	13.2	5.6	7.2
500 000	9.6	13.0	5.4	6.9
1 000 000	9.5	12.7	5.5	7.2
2 000 000	9.5	13.1	5.6	7.3
4 000 000	10.0	13.0	5.6	7.2
6 000 000	9.4	12.8	5.6	7.4
8 000 000	9.8	13.0	5.4	7.1

Table 3: Correlations between descriptors of stock demographic composition and output variables. The correlation coefficient and level of significance (in brackets) are indicated.

	Modal length of mature females	Numerical abundance
TEP	-0.79 (0.002)	0.35 (0.27)
SB	-0.82 (0.001)	0.34 (0.28)