

# Reconstructing the stock–recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential

C. Tara Marshall, Nathalia A. Yaragina, Bjørn Ådlandsvik, and Andrey V. Dolgov

**Abstract:** Correlation and simulation analyses suggest that, for the Northeast Arctic (NA) cod stock, the total lipid energy (TLE (kJ)) contained in the livers of mature females is proportional to total egg production, making TLE a potential predictor of recruitment. Accordingly, the TLE of NA cod was estimated for a 51-year time period (1946–1996), using estimates of numbers at length derived from virtual population analysis, modelled values of proportion mature and weight at length, and observed values of the liver-condition index. A significant linear relationship between TLE and recruitment to age 3 was observed. The temporal trend in TLE suggests that the reproductive potential of the NA cod stock has been in decline since the mid-1970s. A multiple-regression model that included TLE, mean temperature, and mean alongshore wind stress as independent variables explained approximately 43% of the variation in recruitment. Reconstructing stock–recruit relationships using more sensitive measures of reproductive potential is the first step in resolving environmental effects on recruitment and in developing biological reference points that are more effective in stock conservation.

**Résumé :** Des analyses de corrélation et de simulation suggèrent que l'énergie lipidique totale (TLE (kJ)) contenue dans le foie des femelles à maturité de la population de morues du nord-est de l'Arctique (NA) est proportionnelle à la production totale d'oeufs; la TLE est donc un critère potentiel de prédiction du recrutement. C'est pourquoi nous avons calculé les TLE de la population NA de morues pour une période de 51 ans (1946–1996) en nous servant d'estimations tirées de populations virtuelles des nombres de poissons dans les différentes classes de longueurs, d'estimations par modélisation des proportions d'individus matures et des masses à chacune des longueurs et d'observations des coefficients de condition du foie. Il existe une relation linéaire statistiquement significative entre les TLE et le recrutement jusqu'à l'âge 3. L'évolution au cours des ans de la TLE laisse croire que le potentiel reproducteur de la population NA décline depuis le milieu des années 1970. Une analyse de régression multiple, qui utilise la TLE, la température moyenne et le stress éolien moyen le long des côtes comme variables indépendantes, explique environ 43% de la variation du recrutement. L'établissement de meilleures corrélations entre les stocks et le recrutement à l'aide d'indicateurs plus sensibles du potentiel reproducteur est un premier pas vers l'évaluation des effets de l'environnement sur le recrutement et vers l'établissement de repères biologiques plus efficaces pour la conservation des stocks.

[Traduit par la Rédaction]

## Introduction

As in many other stocks of marine fish, the relationship between spawner biomass and recruitment for Northeast Arctic (NA) cod (*Gadus morhua*) is indeterminate. However, recent research suggests that spawner biomass is a poor proxy for total egg production for NA cod (Marshall et al. 1998, 1999) and possibly for other stocks (Lowerre-Barbieri et al. 1998; Scott et al. 1999; Kraus et al. 2000). Furthermore, variables that could influence total egg production (e.g., age diversity of the stock, condition of spawners) have shown positive associations with recruitment (Boyd et al. 1998;

Marteinsdottir and Thorarinsson 1998; Marshall and Frank 1999). These convergent findings point to the need to re-evaluate the stock effect on recruitment, using more accurate measures of reproductive potential (Solemdal 1997; Trippel et al. 1997; Cardinale and Arrhenius 2000).

From a bioenergetic viewpoint, the reproductive potential of individual spawners reflects the balance between food intake and energy expenditures, i.e., surplus energy. Relevant data for reconstructing the reproductive potential of a stock therefore include time series describing the quality and quantity of food and the condition of spawners. Time series of absolute abundance and demographic composition (size, sex, proportion mature) of the stock are also required, to estimate the abundance and size composition of spawning females.

The NA cod stock has a comparatively rich collection of such data. Of particular value to this study are liver-weight observations for cod in the southern Barents Sea that have been recorded monthly since 1927 by the Russian Federation (Yaragina and Marshall 2000). These data are archived as the liver-condition index (LCI), which expresses liver weight as a percentage of total body weight. Because the

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liver is the primary storage site of lipid energy in gadoids (Kjesbu et al. 1991), the database constitutes a highly resolved record of seasonal and interannual changes in surplus energy. Given that the lipid fraction of the liver is nonlinearly related to the LCI (Lambert and Dutil 1997a; Audunsson 1999), the LCI database can also be used to estimate the energy content of cod livers (Marshall et al. 1999).

To take advantage of both the temporal scope and bioenergetic import of the LCI database, the total lipid energy (TLE (kJ)) contained in the livers of mature females was estimated annually for a 51-year time period (1946–1996). Correlation and simulation analyses have previously suggested that, for the NA cod stock, TLE is proportional to total egg production and exhibits a similar dynamic response to varying food abundance (Marshall et al. 1999). In this study, the relationship between TLE and virtual population analysis (VPA) estimates of spawner biomass was examined. A linear relationship would be expected if both variables were directly proportional to total egg production. The stock–recruit (S–R) relationship was reconstructed using TLE as a proxy for total egg production by the NA cod stock, and this relationship was compared with that of the biomass-based S–R relationship. A multivariate analysis of the recruitment variation was performed, using estimates of environmental and demographic variables representing plausible recruitment mechanisms for NA cod. The implications of the results for management are discussed, with particular reference to the biological reference points currently used for the stock.

## Materials and methods

### Total numbers of females by length

Previously, acoustic-survey estimates of abundance were used to quantify total egg production and TLE for NA cod (Marshall et al. 1998, 1999). Here, only VPA estimates of the number at age (ages 3–15+; ICES 2000) were used so that abundance of spawners would be consistently scaled throughout the entire time series. Thus, the assumption that the VPA numbers at age accurately describe interannual variation in stock abundance is inherent in the analysis. Because the VPA estimates of numbers at age were used to estimate both spawner biomass and TLE, differences between the two variables will result from sources other than abundance.

Because the LCI database is predominantly length based (Yaragina and Marshall 2000), the approach taken to quantify the TLE of the stock was also length based. Year-specific age–length keys were required to convert VPA estimates of numbers at age to numbers at length. Age–length keys for 1946–1979 were developed, using data from the Norwegian fishery in Lofoten (Jørgensen 1990). Each record in this database consists of age and length observations for individual cod, with corresponding information on geographic area, gear type, and sampling date. The database was subsampled by selecting the records that were sampled in the first quarter of the year and for which the otolith type was classified as being that of NA cod rather than coastal cod. Age–length keys were constructed for each year, to give the proportion of each age-class observed in 5-cm length-classes having midpoints ranging from 52.5 to 137.5 cm. Cod ages 3 and 4 were infrequently captured. When observations for these age-classes were missing, it was assumed that all cod in these age-classes were in the 52.5- and 57.5-cm length-classes, respectively. This assumption will have a negligible effect on final TLE estimates, because the proportion of mature cod in these two length-classes is very low (Fig. 6 in Marshall et al. 1998). When observations for older age-classes were missing, it was assumed that all cod in that age-class fell into a single length-class (62.5,

67.5, 97.5, 102.5, 107.5, 112.5, 117.5, and 122.5 cm for ages 5, 6, 10, 11, 12, 13, 14, and 15+, respectively). Age–length keys for 1980–1996 were constructed using data from research-vessel surveys, as well as from the commercial fishery. Otherwise, the same selection criteria were used for selecting data records.

The VPA estimates of numbers at age were multiplied by the age–length key for that year, to estimate the number at length ( $n_l$ ) by year. The total number of females in each length-class was then estimated by multiplying  $n_l$  by values of the proportion “females at length” shown in Fig. 5 of Marshall et al. (1998) as a solid line. These values allow for the proportion females at length to increase with increasing length, but do not account for interannual variation in the length-specific sex ratio.

### Proportion mature and weight

VPA estimates of spawner biomass use constant values for the proportion mature at age and weight at age from 1946 until either 1981 (proportion mature) or 1982 (weight). This reflects the practical difficulties of developing historical time series that are methodologically consistent. The abundance of capelin in the Barents Sea affects the growth, condition, and maturation of NA cod (Yaragina and Marshall 2000). Consequently, the approach used here was to predict the proportion mature and weight at length using statistical models that include length and capelin-stock biomass as independent variables. No attempt was made to incorporate genetic changes (e.g., selection for faster growth – earlier maturation) that have been hypothesized for NA cod.

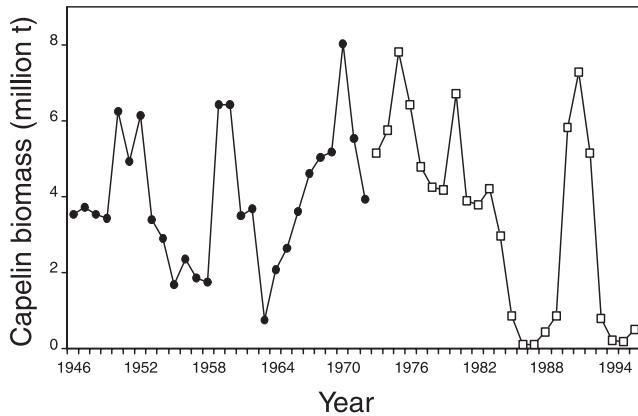
Acoustic-survey estimates of capelin-stock biomass are available from 1973 to the present (ICES 1998). To hindcast capelin-stock biomass for the time period 1946–1972, it was assumed that the intensity of cod feeding on capelin was linearly related to capelin-stock biomass, i.e., that the availability of capelin to cod was the same as the availability of capelin to the acoustic surveys. Cod-feeding observations have been collected year-round by commercial and research vessels as part of a sampling program initiated by Russia in 1947 (Ponomarenko and Yaragina 1978). The contents of non-empty cod stomachs were classified according to the following categories of prey items observed: capelin, juvenile cod, redfish, herring, shrimp, euphausiids, and other. The frequency of capelin in cod stomachs ( $F_{\text{cap}}$ ) is the percentage of non-empty cod stomachs that contain capelin (Ponomarenko and Yaragina 1984). Only data for the southern Barents Sea were used here. Values of  $F_{\text{cap}}$  in year  $t+1$  ( $F_{\text{cap},t+1}$ ) are significantly positively correlated ( $n = 24$ ,  $p < 0.001$ ,  $r^2 = 0.63$ ) with the acoustic estimates of capelin-stock biomass (thousand tonnes (t)) in September–October of year  $t$ , according to the following:

$$(1) \quad \text{capelin biomass in year } t = 159 F_{\text{cap},t+1} - 390$$

Incorporating a lag was justified as follows. The spatial overlap between the cod and capelin stocks in the Barents Sea is at its maximum in February and March. Thus, the capelin-stock biomass estimated during the September–October acoustic survey more closely approximates the biomass that will be available to cod early in the following year. Incorporating the 1-year lag between the biomass estimate and  $F_{\text{cap}}$  also gave a higher  $r^2$  value ( $r^2 = 0.63$ , compared with 0.43 for the unlagged relationship), which was advantageous for predictive purposes. Equation 1 was then used to predict capelin-stock biomass for  $t$  equal to 1946 through to 1972. The predicted values (Fig. 1) show a sudden decline in the capelin stock in the early 1960s that is consistent with the disappearance of the 1958–1960 capelin year-classes, an event that may have been triggered by the recruitment of strong herring year-classes in 1959 and 1960 (Gjøsæter 1998).

The proportion mature at length ( $m_l$ ) and weight at length ( $w_l$  (g)) were predicted for the midpoints of the 5-cm length-classes using statistical models that included capelin-stock biomass (Fig. 1) as an independent variable (Table 1). These models were developed

**Fig. 1.** Time series of capelin-stock biomass in the Barents Sea. Open squares and filled circles indicate observed and predicted values, respectively.



using data for females only from Norwegian surveys of both the Barents Sea and Lofoten conducted between 1985 and 1996. While this is a relatively short calibration period, it includes a dramatic signal in the growth of NA cod resulting from the collapse and recovery of the Barents Sea capelin stock (Fig. 1). Thus, the dynamic range of the data used to develop the statistical models should be sufficient to hindcast the proportion mature and weight back to 1946. Predicted values of  $m_l$  and  $w_l$  were used for the full time period (1946–1996), so that the scaling would be consistent.

**Liver-condition index**

Prior to 1967, only annual averages of LCI are available. From 1927 to 1950, LCI values were aggregated into three weight-classes: small (0.5–1.5 kg), medium (1.5–3.0 kg), and large (>3.0 kg). These values were assigned to the different length-classes on the basis of the predicted values of  $w_l$ . Missing values for 1951–1953 were interpolated from adjacent years. For 1954–1966, only observations for two 10-cm length-classes were available (51–60 and 61–70 cm). For these years, larger length-classes were assumed to have the same values as the 61–70 cm length-class. Since 1967, liver weights have been recorded monthly for 10-cm length-classes (51–60 to 91–100 cm). Larger length-classes were assumed to have the same values as the 91–100 cm length-class. Values for each 10-cm length-class were applied to the corresponding 5-cm length-classes.

**Liver energy content**

The liver energy content (LEC (kJ·g<sup>-1</sup>)) indicates the amount of energy (primarily lipid) contained in a known weight of liver tissue. It can be estimated from the LCI using the nonlinear regression model ( $n = 407, p < 0.001, r^2 = 0.64$ ):

$$(2) \quad \text{LEC} = 24.77 (1 - \exp^{-0.52(\text{LCI}-0.48)})$$

Equation 2 was developed for northern Gulf of St. Lawrence cod having a LCI between approximately 1 and 8% (see Lambert and Dutil (1997a) for further details) and has been applied to NA cod (Marshall et al. 1999). In contrast with the equation given in Lambert and Dutil (1997a), eq. 2 has been reformulated using values of LCI that have total body weight as the denominator rather than somatic weight. This asymptotic equation indicates that the increase in LEC is negligible beyond a LCI value of approximately 5%, while below that value the LEC decreases rapidly.

**Total lipid energy**

The TLE in year  $t$  (TLE <sub>$t$</sub> ) was calculated as

$$(3) \quad \text{TLE}_t = \sum_{l=52.5}^{137.5} n_{l,t} \times \bar{s}_l \times m_{l,t} \times w_{l,t} \times (\text{LCI}_{l,t} \times 0.01) \times \text{LEC}_{l,t}$$

where  $l$  is the midpoint of 5-cm length-classes,  $\bar{s}_l$  is the standard value of the proportion females at length and  $\text{LEC}_{l,t}$  is the value predicted from  $\text{LCI}_{l,t}$  using eq. 2. The factor 0.01 converts the LCI values from a percentage to a proportion of total body weight. Values of  $n_{l,t}$  are time-referenced to 1 January of year  $t$ , whereas values of  $\text{LCI}_{l,t}$  (and hence  $\text{LEC}_{l,t}$ ) represent annual averages. Conceptually,  $\text{TLE}_t$  can be considered as an annual average of the stored energy acquired by mature cod throughout year  $t$ .

**Timing considerations**

In a simplified description of the seasonal cycle of energy expenditure–acquisition for NA cod, migration and spawning take place in the first 4 months of the year followed by a feeding period during which cod rebuild energy reserves for use in the next cycle of gonadal maturation that begins in the fall. Therefore, approximately two-thirds of the monthly values used to estimate  $\text{LCI}_{l,t}$  are from the period following spawning in year  $t$  and preceding spawning in year  $t+1$ . Values of  $\text{TLE}_t$  were assumed to approximate the surplus energy acquired by spawners throughout year  $t$  for expenditure in spawning year  $t+1$ . Consequently, the relationship between  $\text{TLE}_t$  and spawner biomass in spawning year  $t+1$  was examined. Likewise, the reconstructed S–R relationship was assumed to be the relationship between  $\text{TLE}_t$  and recruitment for spawning year  $t+1$ . This approach is consistent with that of Marshall and Frank (1999), who lagged recruitment by 1 year relative to an index reflecting the condition of haddock in the second half of the calendar year.

**Recruitment index**

The recruitment index used was the abundance of age-3 cod backshifted by 3 years to correspond to the spawning year. Estimates of recruitment were obtained from the most recent assessment (ICES 2000). Estimates in the uncovered portion of the VPA numbers-at-age matrix were used, despite having relatively larger errors. The most recent estimate of the abundance at age 3 was for 1998, i.e., the 1995 year-class.

**Environmental and demographic variables**

Temperature has previously been associated with recruitment of NA cod (Ottersen and Sundby 1995). It can influence recruitment directly, via survival during egg and (or) larval stages, or indirectly, via its effects on productivity at lower trophic levels. For example, the intrusion of Atlantic water on the shelf increases the temperature and provides more prey for cod larvae. Water temperatures along the Kola hydrographic transect, located in the central part of the Barents Sea (33°30'E between 70°30' and 72°30'N), have been monitored since 1921 (Tereshchenko 1996). Mean temperatures for the 0–200 m layer in April, May, June, and July were used here to represent temperature conditions during the pelagic stages.

Wind-induced flux of water from the Norwegian Sea into the Barents Sea may influence the growth and survival of larvae by affecting temperature and (or) the availability of zooplankton (Ottersen and Sundby 1995). It has also been suggested that interannual variation in wind speed and direction influences the horizontal dispersion of eggs and larvae of NA cod, which could, in turn, affect the location of settlement and the overwintering survival of juveniles. Monthly means of the wind-stress components  $\tau_x$  (going to the east (N·m<sup>-2</sup>)) and  $\tau_y$  (going to the north) were downloaded from the National Centers for Environmental Prediction – National Center for Atmospheric Research Global Reanalysis Project (Kalnay et al. 1996). For this analysis, the wind-stress components from a location

**Table 1.** Statistical models used to estimate proportion mature at length ( $m_l$ ) and weight at length ( $w_l$ ) for female Northeast Arctic cod.

Variable	Calibration period	Model type	Independent variables	Regression coefficient	$r^2$	$p$
$m_l$	1985–1996	Logistic regression	Intercept	-11.9	na	na
			Length	0.15		na
			Capelin biomass	$1.2 \times 10^{-7}$		na
$\ln(w_l)$	1985–1996	Multiple regression	Intercept	-9.5	0.93	<0.0001
			$\ln(\text{length})$	4.07		<0.0001
			$\ln(\text{capelin biomass})$	0.32		<0.0001
			Interaction term	-0.07		<0.0001

**Note:** Length refers to the midpoint of 5-cm length-classes. Estimates of capelin biomass were obtained from annual acoustic surveys. Variables that were transformed to natural logarithms are identified as  $\ln(\text{variable name})$ . The interaction term is the product of  $\ln(\text{length})$  and  $\ln(\text{capelin biomass})$ . Unavailable data are indicated by na.

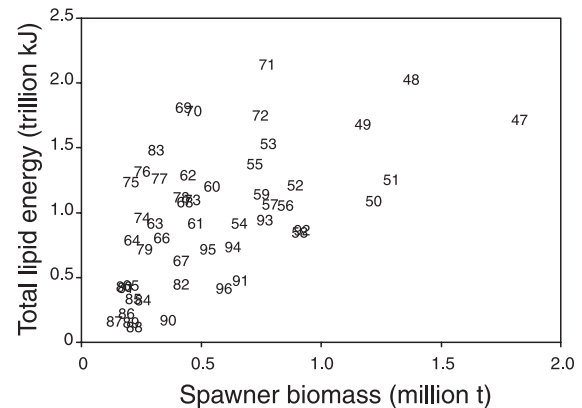
(13°7.5'E and 67°37'N) in the vicinity of the spawning grounds at Lofoten were selected. Monthly means were available back to 1948 only. To facilitate comparisons with the results of Ottersen and Sundby (1995),  $\tau_x$  and  $\tau_y$  values for April and the average of monthly  $\tau_x$  and  $\tau_y$  values for April through October were used to represent the wind stress at the time of spawning and from spawning through to settlement, respectively.

Both total egg production and prerecruit mortality could potentially be affected by demographic characteristics of the spawning stock. For example, maternal size influences egg quality (Solemdal et al. 1993; Marteinsdottir and Steinarsson 1998) and larval viability (Marteinsdottir and Steinarsson 1998; Nissling et al. 1998). Eggs produced by repeat spawners have a lower mortality rate than those produced by first-time spawners (Solemdal et al. 1995). To assess the influence of these demographic characteristics, the following variables were included in the multivariate analysis: (1) the mean length of spawners and (2) the percentage of repeat spawners. Both indices were calculated using females only. The percentage of repeat spawners was calculated by assuming that the percentage of repeat spawners increased with increasing length (table 8 of Marshall et al. 1998) and that these length-specific percentages were constant over time.

### Statistical analysis

Multiple-regression analysis was used to develop statistical models predicting recruitment to age 3 as a function of the stock, environmental, and demographic factors described above. Stepwise variable selection was used, with the  $p$  value to enter the model and the  $p$  value to remain in the model being 0.10 and 0.05, respectively (SAS Institute Inc. 1989). The potential for collinearity among the independent variables was examined using the COLLIN and COLLINOINT options in the REG procedure in SAS. These options produce the proportion of the variance in each variable accounted for by each of the principal components of the  $\mathbf{X}\mathbf{X}$  matrix and a condition factor for each component. Collinearity is indicated when a component having a large condition value also explains a high proportion of the variance in two or more variables.

To test whether the independent variables were normally distributed, the Shapiro–Wilk's test statistic was computed for each variable using the UNIVARIATE procedure in SAS. This procedure computes a test statistic and probability for the null hypothesis that the distribution is not normal. The null hypothesis was rejected ( $p > 0.05$ ) for all variables included in the analysis, except for the mean length of spawners and the percentage of repeat spawners. Both had distributions that were skewed by the observation for 1982. This year had an unusually high abundance of 7-year-olds (table 3.15 in ICES 2000), which increased the mean length of spawners and the percentage of repeat spawners. The distributions of both variables were normal if this observation was deleted.

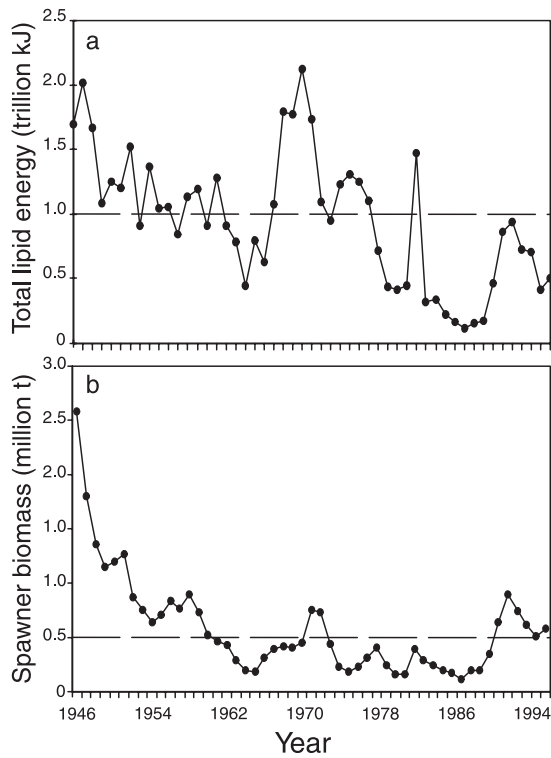
**Fig. 2.** The relationship between spawner biomass in spawning year  $t+1$  and total lipid energy in year  $t$ . Lables denote the spawning year.

### Results

If TLE and spawner biomass are both proportional to total egg production and thus to each other, then the relationship between them should be linear. This is not the case (Fig. 2). The relationship between TLE<sub>*t*</sub> and spawner biomass in spawning year  $t+1$  shows a distinct triangular pattern. Years at the beginning of the time series (1947–1951) show high values of both spawner biomass and TLE, suggesting that the cod stock in the post-war period was abundant and had a large amount of surplus energy. Spawner biomass and TLE were both low during a time period associated with a collapse of the capelin stock (1984–1989; Fig. 1). Outside of these two time periods the relationship between spawner biomass and TLE is highly variable. For example, spawner biomasses for the years 1970 and 1990 differ only by a factor of 1.3, while TLE values differ by a factor of 10.4 (Fig. 2). Thus, years having comparatively small differences in spawner biomass can have order of magnitude differences in TLE.

When the two variables are plotted as time series, other differences emerge. The TLE time series suggests that, with the exception of 1982, the reproductive potential of the stock has been below 1 trillion kJ since the mid-1970s (Fig. 3a). The high TLE value in 1982 (Fig. 3a) resulted from the large number of 7-year-olds in that year (ICES 2000). The 1983 year-class was relatively strong, which provides support for assuming that the TLE in year  $t$  will affect year-

**Fig. 3.** (a) Time series of total lipid energy. Broken horizontal line indicates a reference level of 1 trillion kJ. (b) Time series of spawner biomass. Broken horizontal line indicates a reference level of 500 000 t.



class strength in spawning year  $t+1$ . The TLE shows an increase in the early 1990s to a level that was approximately half that of the early 1970s (Fig. 3a). The temporal trend is quite different if the reproductive potential of stock is expressed as spawner biomass (Fig. 3b). For example, spawner biomass declined dramatically in the post-war period and thereafter fluctuated around 500 000 t. Spawner biomass in the early 1990s was comparable to biomasses observed in the early 1970s (Fig. 3b).

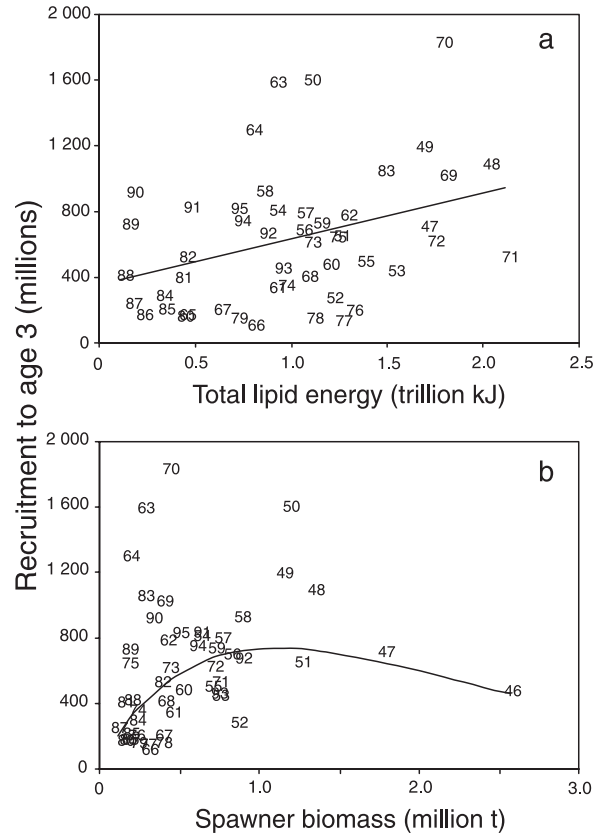
There is a significant ( $n = 49$ ,  $p = 0.013$ ,  $r^2 = 0.12$ ) positive correlation between recruitment and TLE (Fig. 4a) that can be described by the equation:

$$(4) \quad \text{recruitment to age 3} = 3.5 \times 10^5 + 2.8 \times 10^{-7} \text{TLE}$$

where recruitment to age 3 is in units of thousands. By comparison, the biomass-based S–R relationship is indeterminate (Fig. 4b). Spawner biomasses above or below 500 000 t show no tendency to result in good or poor recruitment, respectively. When both variables are ln-transformed (e.g., Ottersen and Sundby 1995), the relationship is significant ( $n = 50$ ,  $p = 0.001$ ,  $r^2 = 0.19$ ); however, the linear relationship between them is not ( $n = 50$ ,  $p = 0.09$ ,  $r^2 = 0.06$ ).

The strength of the correlation between recruitment and TLE is similar in magnitude to the correlation between recruitment and Kola temperature (Table 2). None of the four wind-stress variables were significantly ( $p > 0.05$ ) correlated with recruitment (Table 2). Both the mean length of spawning females and the percentage of repeat spawners were significantly positively correlated ( $p < 0.05$ ; Table 2), suggesting

**Fig. 4.** (a) The relationship between total lipid energy in year  $t$  and recruitment to age 3 for spawning year  $t+1$ . Equation 4 is indicated as a solid line. (b) The relationship between spawner biomass and recruitment to age 3. The fitted Ricker curve ( $\alpha = 1.81$  and  $\beta = 9.23 \times 10^{-7}$ ) is indicated by the solid line. Labels denote the spawning year.



that years having a high proportion of large fish or repeat spawners are associated with good recruitment. However, the results were affected by two anomalous observations. Bivariate plots of the relationship between recruitment and Kola temperature revealed that the observation for 1963 had higher than expected recruitment relative to temperature conditions. If the observation is deleted from the correlation analysis, then the temperature effect on recruitment becomes stronger than the effect of TLE (Table 2). Deleting the observation for 1982 normalised the distributions of both the mean length of spawners and the percentage of repeat spawners and increased the significance levels of these variables (Table 2).

**Multivariate analysis**

Data for the full time period yielded a multiple-regression model that included TLE and Kola temperature and that explained approximately one-quarter of the variation in recruitment (Table 3). Deleting the observation for 1963 increased the total amount of variation explained to approximately 43%. It also heightened the temperature effect, as indicated by the order in which the variables entered the model, and caused the alongshore wind stress term ( $\tau$ , April–October) to become significant. Deleting the observations for both 1963

**Table 2.** Correlation coefficients (*r*) for relationships between recruitment to age 3 in spawning year *t*+1 and for several stock, environmental, and demographic variables; significance levels (*p*) and number of observations (*n*) are also given.

Variable	All years			Without 1963			Without 1963 + 1982		
	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>
Total lipid energy	0.35	0.01	49	0.38	<0.01	48	0.38	<0.01	47
Kola temperature in April–July	0.35	0.01	50	0.45	<0.01	49	0.46	<0.01	48
$\tau_x$ April	-0.02	0.88	48	-0.01	0.95	47	0.01	0.93	46
$\tau_y$ April	0.06	0.69	48	0.04	0.79	47	0.04	0.78	46
$\tau_x$ April–October	-0.10	0.50	48	-0.02	0.89	47	0.01	0.90	46
$\tau_y$ April–October	0.19	0.19	48	0.22	0.13	47	0.23	0.13	46
Mean length of spawners	0.32	0.02	50	0.33	0.02	49	0.40	<0.01	48
Repeat spawners	0.30	0.03	50	0.30	0.03	49	0.39	<0.01	48

**Note:** Values of total lipid energy in livers of mature females are for the year *t*. All other variables refer to values for spawning year *t*+1.

**Table 3.** Statistical models predicting recruitment to age 3 for spawning year *t*+1.

Model	Independent variable	Regression coefficient	<i>p</i>	<i>r</i> <sup>2</sup>	<i>n</i>
All years	Intercept	-551 621	0.12	0.25	48
	TLE	$2.8 \times 10^{-7}$	<0.01		
	Kola temperature	262 377	<0.01		
Without 1963	Intercept	-870 754	<0.01	0.43	47
	Kola temperature	309 186	<0.01		
	TLE	$3.4 \times 10^{-7}$	<0.01		
	$\tau_y$ April–October	$8.3 \times 10^6$	0.02		
Without 1963 + 1982	Intercept	-4 929 291	<0.01	0.41	46
	Kola temperature	332 915	<0.01		
	Repeat spawners	58 525	<0.01		

**Note:** Values of total lipid energy in livers of mature females (TLE) are for year *t*. Values for all other variables refer to spawning year *t*+1. For each model, the independent variables are listed in the order in which they entered the model. Unit for recruitment is thousands.

and 1982 caused the percentage of repeat spawners to enter the model after the Kola temperature, giving a model that explained approximately 41% of the variation in recruitment. None of the wind-stress terms were significant in this model. Collinearity was judged not to affect the models reported here, because the greatest proportion of the variance in each of the independent variables could be attributed to a single principal component. This suggests that the independent variables are approximately orthogonal to each other.

## Discussion

### The stock effect on recruitment

Using a bioenergetic index to represent the reproductive potential of the NA cod stock provides evidence of a stock effect on recruitment over long time scales. This suggests that the growth, condition, and abundance of spawners act in combination to affect the reproductive and recruitment potential of the stock. The reconstructed relationship differs from the biomass-based S–R relationship in that there is a statistically significant positive correlation on a linear scale. There are also differences between TLE and spawner biomass in the timing and relative magnitude of peak values. Given that the VPA estimates of numbers at age are common to both TLE and spawner biomass, differences between the

two variables result from incorporating interannual variation in the LCI (to estimate both total liver biomass in the stock and the energy content of that biomass), as well as year-specific values for proportion mature and weight.

Both the mean length of spawners and the percentage of repeat spawners explained a level of recruitment variation that was comparable with TLE when the outlying observation for 1982 was deleted. This suggests that demographic characteristics affecting egg quality are important determinants of reproductive and recruitment potential. Logically, the correlation between total egg production (or its proxy) and recruitment must be stronger than correlations between indices of spawner quality and recruitment, because the effects of spawner quantity are not negligible. If this is not the case, then measurement error and (or) errors in the formulation of the proxy are introducing noise into the stock signal. There are several sources of error in estimates of TLE. Prior to 1973, the terms representing weight and maturity were predicted from values of capelin-stock biomass that were themselves predictions. The LCI for larger length-classes could be underestimated by the extrapolation scheme that was used. The age–length keys used to length-distribute the VPA estimates of the number at age could be improved so that they are more representative of the stock. These caveats illustrate the many assumptions that are required to hindcast

reproductive potential on an absolute scale, using historical-data sources that are impressive relative to other stocks but still less than ideal.

The fit of the S–R relationship for the central Baltic cod stock was also improved by replacing spawner biomass with estimates of total egg production (Jarre-Teichmann et al. 2000). However, many gadoid stocks lack contemporary and (or) historical fecundity data. This necessitates the construction of proxies for reproductive potential (e.g., TLE, age diversity, condition, percentage of repeat spawners). A sensitive proxy for the reproductive potential of a stock should include terms for both the quantity and quality of spawners weighted in proportion to their effect on total egg production. The formulation of TLE differs from that of spawner biomass by incorporating spawner quality (i.e., condition) twice: once to estimate liver biomass and once to estimate liver energy content of that biomass. This amplifies the condition signal relative to the spawner-quantity signal. Many cod stocks exhibit a high degree of interannual variation in condition (e.g., Lilly 1997; Lambert and Dutil 1997*b*) that affects both the fecundity (Kjesbu et al. 1991) and egg quality (Solemdal et al. 1993; Lambert and Dutil 2000) of individual cod. Furthermore, measures of condition show positive correlation with recruitment for cod (Marshall et al. 1999), haddock (Marshall and Frank 1999), and pelagic species (Boyd et al. 1998).

In contrast to the classic non-linear S–R models, the reconstructed S–R relationship appears linear. Non-linear, density-dependent S–R models are intuitively appealing when the independent variable is an index of spawner abundance. For example, there is a highly significant, positive correlation between spawner biomass and the numerical abundance of cod age 7 and older ( $n = 51$ ,  $p < 0.001$ ,  $r^2 = 0.77$ ) for NA cod. If total egg production (or its proxy) is determined by an interaction between spawner quantity and spawner quality, then fitting a density-dependent model may not be appropriate. There is no obvious mechanism for total egg production to self-regulate their numbers (in the sense of a feedback control mechanism) in the way that spawners can potentially self-regulate their numbers via density-dependent effects on terms such as proportion mature, weight, and fecundity that reflect per-capita food abundance (Cardinale and Modin 1999; Gillooly et al. 2000). Using total egg production to represent the stock effect on recruitment could mask the density effect by combining terms that may be inversely related to abundance (proportion mature, weight, fecundity) with terms that are, by definition, positively related to abundance ( $n_t$ ). Density-dependent survival of prerecruit stages could also introduce non-linearity to the S–R relationship between total egg production and recruitment. Our failure to observe this could result from the estimation errors associated with TLE. Alternatively, the functional form of the S–R relationship may deviate from what is traditionally assumed.

The reconstructed S–R relationship, as well as the correlations between demographic characteristics and recruitment, represent incremental steps towards an improved S–R relationship. Estimates of total egg production have become feasible as cod fecundity data have become more readily available (Kjesbu et al. 1998; Kraus et al. 2000). Characteristics of the spawning stock that are likely to affect hatching success and larval survival could be used to estimate total vi-

able egg production (e.g., Scott et al. 1999; Jarre-Teichmann et al. 2000).

### Multivariate recruitment models

Results of the multivariate modelling show that both stock and environmental factors influence the recruitment of NA cod. This conclusion is consistent with that of Ottersen and Sundby (1995), who noted the “fruitlessness of the old simplistic discussion of whether recruitment variability is environmentally driven or driven by the spawning stock biomass.” The variables that were found in this analysis to affect recruitment were qualitatively similar to those identified by the Ottersen and Sundby (1995) study. In their model, the stock and environmental effects were represented by terms for ln-transformed spawner biomass and Kola temperature, respectively. The Ottersen and Sundby (1995) study found that  $\tau_y$ , April–October was significantly correlated with the ln-transformed recruitment to age 3 (see Table 6 in Ottersen and Sundby (1995)); however, it was not included in the multivariate recruitment model (see model A in Table 9 in Ottersen and Sundby (1995)), owing to collinearity with temperature.

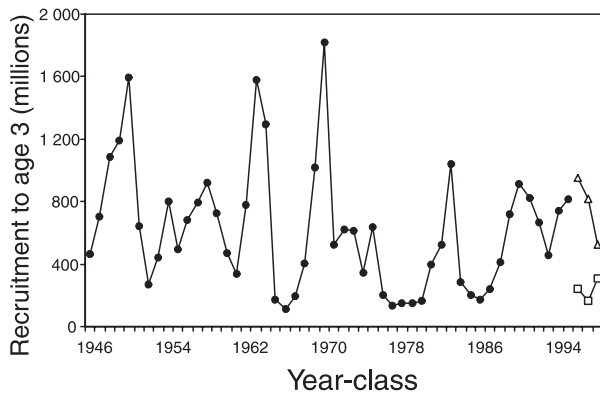
Presently, the assessment for NA cod forecasts recruitment to age 3 using a statistical model (RCT3) that includes survey estimates of abundance at the 0-group, age-1, and age-2 stages (Shepherd 1997). An alternative approach is to utilize process-oriented models, such as those developed by Ottersen and Sundby (1995) and this study, to predict recruitment. To illustrate their potential utility, the model given in Table 3 (excluding the observation for the 1963 year-class) was used to predict the recruitment to age 3 for the 1996, 1997, and 1998 year-classes. The process-oriented estimates of recruitment are consistently lower than the RCT3 estimates and are similar in magnitude to the low levels observed in the late 1960s, 1970s, and mid-1980s (Fig. 5). Thus, the short-term projections of recruitment used by the assessment are more optimistic than those based on stock and environmental conditions.

The multivariate models in Table 3 could potentially be refined by using more precise estimates of the terms that are already present or by including new variables. For example, circulation models of the Norwegian and Barents Sea (Ådlandsvik and Hansen 1998) could be used to provide a more precise description of the physical environment experienced during the pelagic stage. Variability in growth during early life-history stages was not included in our analysis. However, a multiple-regression model developed using data from ichthyoplankton surveys of the Norwegian and Barents Sea (1959–1993) predicted recruitment to age 3 from relative egg abundance, mean annual Kola temperature, and mean larval length (Mukhina 1999). Models that are hybrids of process-oriented and survey-based (e.g., RCT3) models may, in future, prove to have the greatest predictive capability.

### Implications for management

Fishing mortality rates ( $F$ ) for NA cod have, with the exception of a period in the early 1990s, increased to levels that are at or near historical highs (1.0 in 1997 and 0.9 in 1998; Table 3.21 in ICES 2000) and well above the precautionary reference level of  $F = 0.42$ . Given the strong retrospective patterns noted in recent assessments (ICES 2000),

**Fig. 5.** Time series of recruitment to age 3. Solid circles indicate estimates from the virtual population analysis (ICES 2000). Open triangles indicate estimates predicted by RCT3 (Table 3.7 in ICES 2000). Open squares indicate estimates predicted by the model in Table 3 that excludes the observation for 1963.



upward revisions to current  $F$  values are a distinct possibility. Developing strategies for stock rebuilding is an important task for the scientists involved in the management of NA cod. This study suggests that rebuilding strategies based on spawner biomass will be inefficient, because spawner biomass is a poor indicator of reproductive and recruitment potential. The reconstructed S–R relationship suggests that the probability of good recruitment is higher when TLE is above 1 trillion kJ. With the exception of 1982, the TLE has been below this value since the mid 1970s. Values for 1997, 1998, and 1999 were 0.49, 0.37, and 0.29 trillion kJ, respectively. Increasing recruitment would therefore require a large increase in the TLE. This can be achieved through reductions in  $F$  and (or) increases in recruitment to the spawning stock. However, if the process-oriented recruitment forecasts made here are correct, then recruitment to the spawning stock will be low over the short term. This increases the need for immediate and large reductions in  $F$ . Such management strategies have been implemented in the recent past: a large and rapid reduction in  $F$  was initiated in 1990 in response to the collapse of the Barents Sea capelin stock and low cod abundance. This protected the relatively strong 1983 year-class of NA cod as it recruited to the spawning stock. Consequently, TLE values approached 1 trillion kJ by 1992.

Incorporating reproductive potential into the standard assessment methodology for NA cod is easily achieved, particularly as many of the required elements are already in place. For example, matrices of age-specific proportion mature and weight are already used to estimate spawner biomass. The age-specific sex ratio is not used but the information required to estimate it is routinely collected. Maturity information could be partitioned by sex for species such as Atlantic cod that show differential maturation (Tomkiewicz et al. 1997; Jakobsen and Ajiad 1999). Age–length keys, which are essential for adding in length-based information (e.g., LCI or fecundity) to age-structured databases, are usually available. For many stocks, developing matrices describing temporal and size- or age-based variation in condition and (or) fecundity present the greatest immediate challenge.

Viewed objectively, traditional biomass-based S–R theory is poorly supported by empirical data (Peters 1991). This hinders the effectiveness of biological reference points that are derived from it in conserving heavily exploited species such as Atlantic cod. Our analysis has illustrated how a bioenergetic proxy for total egg production can be used to resolve the stock effect on recruitment. In essence, the proxy prorates spawner quantity by spawner quality. This approach has a precedent in fisheries science: correcting abundance indices for variation in condition has also been proposed to study the population dynamics of larval stages (Frank and McRuer 1989). The approach is also consistent with emerging insights into aquatic productivity that stress the importance of lipids in determining the reproductive potential of individuals and populations (Adams 1999; Shulman and Love 1999; Müller-Navarra et al. 2000). Viewing ecosystems as a bioenergetic continuum from primary production through to the reproduction and recruitment of vertebrates offers a useful conceptual framework for both the academic and applied branches of fisheries science.

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