Tracking the signal in year-class strength of Northeast Arctic cod through multiple survey estimates of egg, larval and juvenile abundance

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Abstract

Egg and larval abundances for Northeast Arctic cod estimated annually from 1959–1993 were combined with estimates of spawning stock biomass (SSB) and stage abundance estimates for the larvae, pelagic juveniles and demersal juveniles to determine when a correlation with recruitment could first be detected and to track how the correlation changed with increasing age/stage. The largest increase in explanatory power occurred going from SSB to the egg stage suggesting that the transition from potential to realised egg abundance is a critical stage and/or that SSB is a poor index of the potential total egg production. Egg stage abundance was significantly correlated with recruitment; however, the portion of the recruitment signal explained by this index differed from the portion explained by subsequent stages suggesting that the signal in year-class strength undergoes modification between the egg and larval stages. Contrary to the expectation that the signal in year-class strength should become stronger as the penultimate recruitment stage is approached, the significance of the correlations with recruitment decreased for the larval and juvenile stages relative to the egg stage suggesting that the measurement error for these latter stages is high. Temperatures during the post-settlement period explained a significant portion of the residual variation in stage abundance/ recruitment relationships for the larval, pelagic juvenile and demersal juvenile stages. A multivariate recruitment model was therefore developed and tested using independent data for the periods preceding and following the model calibration period. © 2003 Elsevier B.V. All rights reserved.

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1. Introduction

In fisheries science identifying when and how variability is introduced to recruitment has frequently involved testing for correlations between the abundance of different early life history stages and recruitment. For example, the widespread lack of correlation between spawner biomass and recruitment has been interpreted as evidence that mortality during the pre-recruit stage determines year-class strength (Wooster and Bailey, 1989). Correlations between recruitment and the abundance of larvae or early pelagic juveniles suggest that for some stocks year-class strength is established at very early stages (Sundby et al., 1989; Astthorsson et al., 1994; Jákupsstovu and Reinert,

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1994; Helle et al., 2000) while for other stocks significant correlations between abundance at the demersal juvenile stage and recruitment suggest that settlement is critical (Myers and Cadigan, 1993). It is also possible that the life history stage at which year-class strength is established varies due to the shifts in the relative importance of different mortality sources (Bailey, 2000).

The accuracy of such inferences is affected by the degree of error in estimating stage-specific abundance, which, in turn, depends on the availability and catchability of each stage to the survey. Both availability and catchability are influenced by survey design, sampling methodology, hydrography and/or by developmental traits that vary according to temperature and food availability. Noise introduced by these factors can obscure potentially significant reationships between stage-specific abundance and recruitment. For example, ichthyoplankton surveys of Georges Bank (1977–1987) show that the strength of correlations between stage abundance and the abundance of age-1 cod (*Gadus morhua*) increases progressively through three consecutive egg stages to a maximum at the first larval stage and thereafter decreases (Morse, 1994). The weaker correlations observed for the older larval stages have been partly attributed to noise introduced into the stage abundance estimates by gear avoidance and behaviour (ICES, 1998). Changes in survey methodology due to improved technology and/or biological knowledge are common in long survey series (Lepesevich and Shevelev, 1997; Jakobsen et al., 1997) and introduce a systematic source of variation to stage abundance estimates over time. Thus, the presence or absence of correlations may say more about the accuracy, precision and non-stationarity of the stage-specific abundance indices than it does about the stage at which year-class strength becomes established.

The Northeast Arctic (NA) cod stock has multiple survey series describing the relative abundance of egg, larval, pelagic juvenile and demersal juvenile stages (Fig. 1). Several earlier studies have examined correlations between these stage-specific abundance estimates and recruitment. Correlation analysis of data from Russian ichthyoplankton surveys of the Norwegian and Barents Seas (1959–1993) indicates that for NA cod the relative abundance of eggs and larvae is correlated with recruitment to age 3 (Mukhina, 1999).
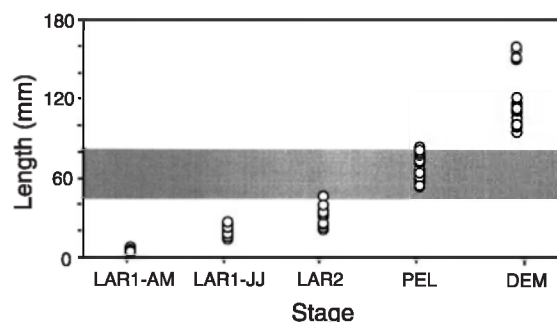

Fig. 1. Mean lengths measured for the different life history stages of Northeast Arctic cod (*x*-axis label corresponds to the label used for the different stage abundance indices). The mean lengths of larvae measured on the April/May and June/July surveys are denoted as LAR1-AM and LAR1-JJ, respectively. The shaded area indicates the approximate length range over which settlement occurs (40 and 80 mm, adapted from information in Lough and Potter, 1993; Jákupsstovu and Reinert, 1994; Hüssy and Tomkiewicz, 1995).

Data from Norwegian ichthyoplankton surveys that were conducted for a subset of these years (1977–1991) also suggest that the relative abundance of larvae (also referred to as early pelagic juveniles) is significantly correlated with recruitment (Sundby et al., 1989; Helle et al., 2000). The international 0-group survey has been conducted since 1965 (Bjørke and Sundby, 1987) and is the only survey of pre-settlement stages still being conducted. Abundance estimates for pelagic juveniles obtained from this survey show weak or insignificant correlations with recruitment (Helle et al., 2000). Trawl surveys of recently settled juveniles in the southern Barents Sea were initiated by Russia in 1946 and show significant correlations between recruitment and the relative abundance of demersal juveniles (Ponomarenko, 1984; Tretyak et al., 1995).

The Russian ichthyoplankton survey series have not previously been combined with the other survey series and subjected to a common statistical analysis. Therefore, the primary goal of this study was to use the multiple survey series for NA cod to identify the life history stage at which a significant correlation between stage abundance and recruitment could first be detected and to determine how the signal evolves through subsequent stages. The expectation was that in the absence of appreciable measurement error the signal, as reflected by the statistical significance of the correlation with recruitment, would become progres-

sively stronger with increasing stage (Van der Veer et al., 2000). The analysis used survey-based estimates of the relative abundance of egg, larval, pelagic juvenile and demersal juvenile stages available for the time period corresponding to years of the Russian ichthyoplankton surveys. Because temperature is considered to be a key environmental variable influencing recruitment of NA cod (Ponomarenko, 1984; Ottersen and Sundby, 1995; Sundby, 2000) a secondary goal was to examine the effect of temperature on residual variation in the different stage abundance/recruitment relationships using temperature indices corresponding to different time periods in the pre-recruit period. Multivariate recruitment models were then developed which included terms for both stage abundance and temperature. To assess their utility for forecasting recruitment the recruitment models were tested using independent data for the time periods preceding and following the model calibration period.

2. Spatial and temporal distribution of early life history stages

The coastal region surrounding the Lofoten islands is the primary spawning site for NA cod (Fig. 2). The date of peak spawning is often assumed to be stable at approximately April 1 (Pedersen, 1984). Eggs and larvae are transported northeastwards by the Norwe-

gian coastal current with lateral spreading taking a portion of them into the Atlantic current which runs parallel to the coastal current (Ådlandsvik and Sundby, 1994). Hatching of cod larvae begins in late April and early May (Mukhina et al., 1987). Three months after spawning, high concentrations of early pelagic juveniles are found in the southwestern Barents Sea (Bjørke and Sundby, 1987). When surveyed by the international 0-group survey (ca. 5 months after spawning) pelagic juveniles are distributed throughout the Barents Sea as well as along the narrow shelf lying to the west of Svalbard (Randa, 1982). There is considerable interannual variation in the spatial distribution of settled juveniles (Nakken and Raknes, 1987), which could be due to variability in the extent of eastward displacement during the pelagic stages (Mukhina et al., 1987). It has also been suggested that the spatial distribution of juveniles is density-dependent with abundant year-classes having a more easterly center of mass (Shevelev et al., 1987; Ottersen et al., 1998).

3. Russian ichthyoplankton surveys

The sampling design and methodology used for the Russian ichthyoplankton surveys are described in detail here. Because the same methods were used to sample egg and larval stages throughout the 35-year time series, the indices have the virtue of consistency. At present, there are only several abundance indices that have been computed for the full time series and these are presented here. The original data are currently being entered into a database so that in future it will be possible to compute alternative abundance indices, e.g., daily egg production.

3.1. Survey design and sampling methodology

The Russian ichthyoplankton surveys were conducted from 1959 to 1993. The spatial distribution of the sampling stations extended from the Lofoten islands to a northeastern boundary located at approximately 33°30′E and 74°30′N (Fig. 2). The surveys did not include the inner part of Lofoten where there are dense aggregations of spawning cod in March and April. Two surveys were conducted each year: the April/May (AM) survey and the June/July (JJ) survey
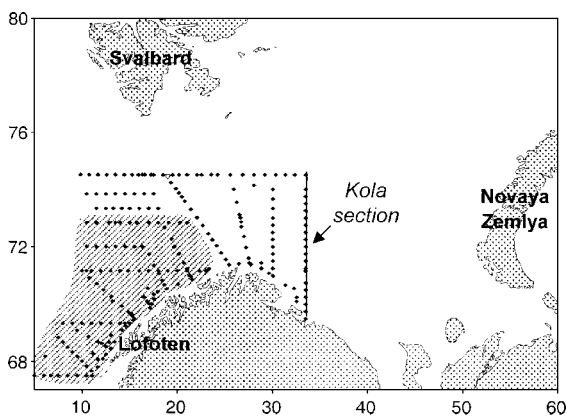

Fig. 2. The survey coverage of the Russian ichthyoplankton surveys. The shaded region encloses the stations that are used to calculate the index of relative egg abundance. The vertical line indicates the location of the Kola hydrographic section.

(Table 1). The starting dates of the AM survey varied considerably between 30 March and 4 May while the starting dates for the June/July (JJ) survey varied between 31 May and 1 July. There was no long-term trend in the starting dates (Fig. 3a). The modal starting dates of the AM and JJ surveys were the third week in April and the first week in June, respectively (Fig. 3b). There was no significant correlation between the

Table 1

Information on Russian ichthyoplankton surveys conducted in the Norwegian and Barents Seas

Year	Dates		No. of stations	No. of samples	
	April/May	June/July		IKS-80	RT
1959	17/04 – 22/05	05/06 – 15/07	401	783	363
1960	20/04 – 24/05	29/05 – 27/06	329	753	202
1961	18/04 – 21/05	03/06 – 06/07	355	1189	505
1962	12/04 – 21/05	06/06 – 15/07	459	1218	499
1963	21/04 – 18/05	10/06 – 07/07	350	1056	362
1964	01/04 – 29/05	05/06 – 11/07	275	895	257
1965	21/04 – 28/05	09/06 – 27/07	334	1242	163
1966	27/04 – 06/06	01/07 – 27/07	222	620	0
1967		02/06 – 09/07	174	1005	281
1968	17/04 – 25/05	04/06 – 11/07	498	1269	381
1969	24/04 – 23/05	03/06 – 08/07	407	833	411
1970	12/04 – 22/05	05/06 – 13/07	465	1267	441
1971	03/05 – 27/05	13/06 – 12/07	384	998	366
1972	15/04 – 28/05	07/06 – 11/07	504	1279	396
1973	20/04 – 26/05	11/06 – 12/07	384	1163	379
1974	22/04 – 24/05	09/06 – 17/07	407	1587	393
1975	16/04 – 28/05	25/06 – 06/07	311	996	154
1976	15/04 – 03/06	02/06 – 18/07	481	1340	451
1977	11/04 – 30/05	04/06 – 15/07	463	1395	486
1978	15/04 – 26/05	04/06 – 15/07	469	1275	386
1979	19/04 – 20/05	28/05 – 03/07	423	1129	446
1980	02/04 – 26/05	02/06 – 11/07	437	1188	365
1981	03/04 – 24/05	03/06 – 16/07	422	1193	401
1982	14/04 – 30/05	07/06 – 16/07	400	934	196
1983	14/04 – 24/05	02/06 – 14/07	397	939	419
1984	15/04 – 27/05	31/05 – 10/07	429	1261	441
1985	04/05 – 30/05	31/05 – 13/07	375	1025	398
1986	12/04 – 28/05	06/06 – 15/07	347	1193	0
1987	14/04 – 28/05	10/06 – 11/07	416	1129	178
1988	03/04 – 27/05	05/06 – 12/07	392	985	176
1989	30/03 – 24/05	01/06 – 13/07	408	1098	358
1990	04/04 – 27/05	05/06 – 12/07	502	992	329
1991	14/04 – 25/05	03/06 – 01/07	296	954	209
1992	19/04 – 25/05	11/06 – 13/07	308	528	59
1993	14/04 – 29/05	08/06 – 12/07	332	948	0

The number of stations sampled is the combined total for both the April/May and June/July surveys. The number of samples is the combined total for both vertical hauls and horizontal tows in both surveys. A survey was not conducted in April/May 1967.
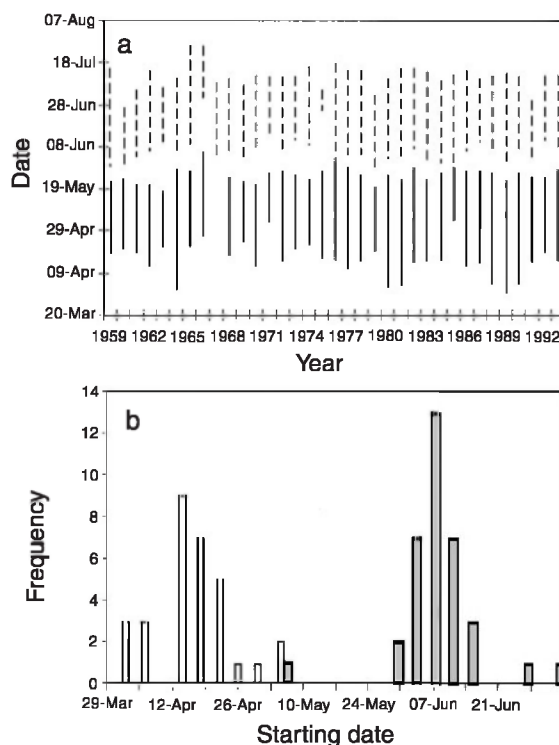

Fig. 3. (a) The temporal coverage of the Russian ichthyoplankton surveys. The duration of the April/May and June/July surveys are indicated as solid and dashed lines, respectively. (b) The frequency distribution of starting dates for the April/May (open bars) and June/July (shaded bars).

starting date of the AM survey and either the proportion of stage I eggs ($r^2 = 0.05$, $p = 0.22$, n = 34) or the proportion of stage I + II eggs ($r^2 = 0.02$, $p = 0.40$, n = 34).

During the AM surveys, an egg net (IKS-80) having a diameter of 80 cm, a height of 1.5 m and a mesh size of 0.505 mm was used. At each station one vertical haul was taken, either from the bottom or from a maximum depth of 500 m. Horizontal tows of ten-minute duration were also taken at 0 and 25 m depths using the IKS-80. While taking horizontal tows, the vessel circled the station location at a speed of 2.5 knots. Corrections for the observed cable angles were applied to obtain the desired depths. During the JJ surveys, two types of sampling gear were used: the IKS-80, configured as for the AM surveys, and a ring-trawl (RT) having a diameter of 1.6 m, a height of 3.0 m and a mesh size of 3 mm. At

each station vertical hauls were taken using both the IKS-80 and RT. Ten-minute horizontal tows were taken at 0 and 25 m using the IKS-80 and at 50 m using the RT.

The total number of IKS-80 and RT hauls + tows taken in the AM and JJ surveys combined is given in Table 1 by year. As described above, there were generally three IKS-80 hauls + tows at each station for both the AM and JJ surveys and two RT hauls + tows for the JJ survey. However, variation in the actual number of hauls + tows taken at each station resulted because of faulty equipment operation or rough weather. Sampling at several stations was skipped during the AM survey in 1964. However, these stations were located outside of the area considered to represent the distributional area of cod eggs (Fig. 2) and therefore did not affect the calculation of the egg abundance index for that year. The AM cruise was not conducted in 1967 for technical reasons. All information for the AM survey in 1974 was inadvertently lost. Because the larval abundance index was calculated using observations from both the AM and JJ survey (as described below) the values for 1964, 1967 and 1974 were compromised by missing data for the AM survey in those years (Table 1). In 1966, 1986 and 1993, no RT samples were collected and there was an anomalously low number of samples in the JJ survey for 1992. Due to these technical considerations, indices for the relative abundance of eggs in 1967 and 1974 and indices for the relative abundance of larvae in 1964, 1966, 1967, 1974, 1986, 1992 and 1993 were considered either to be missing or biased relative to the other values in the time series and were excluded from the subsequent analyses.

Flow meters were unavailable at the inception of the survey and were never incorporated into the sampling methodology. Consequently, the data cannot be corrected for variation in filtering efficiency of sampling gear. However, in the AM surveys conducted between 1987 and 1990 the nets were visually examined following sample collection and nets that appeared to be coated with organic material were noted. In most cases the material was composed of phytoplankton and/or protozoans associated with the spring bloom. In the four years of the study, a small proportion of the nets had some degree of coating and the frequency of occurrence was highest (between 9 and 18%) for horizontal tows taken at the surface (Table 2). Coating was less frequent for vertical hauls (between 1 and 11%) and for horizontal tows collected at 25 m (between 3 and 15%). Thus, coating was not observed in a large majority ($\geq 80\%$). On this basis, it was concluded that variation in filtering efficiency was not introducing a large or systematic bias to the estimates of stage abundance.

3.2. Sample processing

Plankton samples were initially fixed in 10% formaldehyde. Eggs and larvae were picked out of the bulk sample within 12 h and preserved in 4% formaldehyde for long-term storage. Identification and enumeration of eggs and larvae were made using the preserved material. Plankton samples were sorted according to species using techniques described by Baranenkova (1961). Eggs were sub-divided into four developmental stages based on the developmental stages shown in Fig. 1 of Russell (1976). Eggs in Russell's stages $1-10$ were classified as stage I, eggs in stages $11-20$ were stage II, eggs in stages $21-25$ were stage III and eggs in stages $26-30$ were stage IV. The stage definitions used for the Barents Sea ich-

Table 2
Qualitative observations on the frequency of nets coated with organic matter for the April/May surveys

	1987			1988			1989			1990		
	Total	No. coat	% coat	Total	No. coat	% coat	Total	No. coat	% coat	Total	No. coat	% coat
Tows (0 m)	232	22	9	190	8	4	150	27	18	149	26	17
Tows (25 m)	232	8	3	190	5	3	148	17	11	149	23	15
Vertical hauls	168	3	2	212	1	0.5	144	9	6	145	11	7

Totals indicate the total number of stations having samples.

thyoplankton surveys were also used for ichthyo-plankton surveys of the Baltic Sea because the methodology used in both surveys had the same origin (Baranenkova, 1961). Cod and haddock eggs in stages II to IV were distinguished from each other as follows: eggs having pigment cells which were grouped into two distinct rows on the dorsal side were counted as haddock eggs, whereas eggs having pigment cells which were uniformly distributed over the body were counted as cod eggs. Visual identification has been found to correctly differentiate between cod and haddock eggs as compared to biochemical methods (Sundby and Solemdal, 1984). Stage I cod and haddock eggs could not be differentiated visually. Therefore, at each station the proportions of each species at stage I were assumed to be equal to the proportions observed in stages II–IV combined.

The proportion of eggs having abnormal patterns of development was noted for each station. This value was generally near or equal to zero, but in some years the proportions were considerably higher. For example, in 1990 and 1991 the overall proportions of abnormal cod eggs were 8% and 8.4%, respectively (Mukhina et al., 1996). In coastal areas of Norway, approximately 20% of the eggs are abnormal is in March but this percentage decreases steadily throughout April and May as early egg stages become less abundant (Kjørsvik et al., 1984). No correction for abnormal development was applied to the egg abundance index used for this analysis.

4. Data and analyses

4.1. Stage-specific indices

4.1.1. Stock reproductive potential

For the purposes of comparison, the stock/recruit relationship that uses spawning stock biomass (SSB) as an index of potential total egg production was included in the analysis. Prior to 2001 SSB for the pre-survey time period was estimated using knife-edge values for maturity-at-age (until 1982) and constant values of weight-at-age (until 1983). This is the SSB time series that has been used in most previously published work on NA cod (e.g., Ottersen and Sundby, 1995). In 2001 the time series for SSB was

substantially revised by replacing these constant values of maturity- and weight-at-age with observed values (males and females combined) that were reconstructed from historical Russian and Norwegian sources (ICES ACFM, 2001). In most years this led to a downward revision of the SSB estimate. The revised time series was used here.

4.1.2. Egg stage

To estimate the relative abundance of cod eggs only data from the AM surveys were used. Furthermore, only stations located in the shaded region shown in Fig. 2 were included in the calculation. This excluded stations outside of the area where cod eggs could reasonably be expected given the timing of the AM survey. Otherwise, null values were included as valid observations in the calculation. The average abundance of cod eggs at station x (e_x) was calculated as the average of the number of cod eggs in the vertical haul and horizontal tows and combined all four egg stages. The annual index of relative egg abundance (EGG) for year t was then calculated as:

$$\text{EGG} = \sum_{x=a} e_x / a \tag{1}$$

where a is the number of stations in the AM survey belonging to the sub-set of stations assumed to represent the distributional area of cod eggs (Fig. 2).

The EGG time series was characterised by anomalously high values for 1992 and 1993, whereas, the next highest value in the time series (1959) was approximately one order of magnitude less than the value in 1992 (Fig. 4a). Despite this, values of recruitment in 1992 and 1993 were only 36 and 24%, respectively, of the maximum value observed in the 1959–1993 time period (1.8×10^9 recruits produced by the 1970 year-class). In both 1992 and 1993 very high values of e_x were observed at a majority of the stations rather than in localised hot spots. Stage I and II eggs usually constituted between 60 and 100% of the total eggs captured (Fig. 4a), but in both 1992 and 1993 the proportions of the two earliest egg stages dropped to below 60%. Thus, both the absolute and relative abundances of stages III and IV were anomalously high. In these years, the spawning stock was dominated by large spawners (Marshall et al., 1998) and this could have
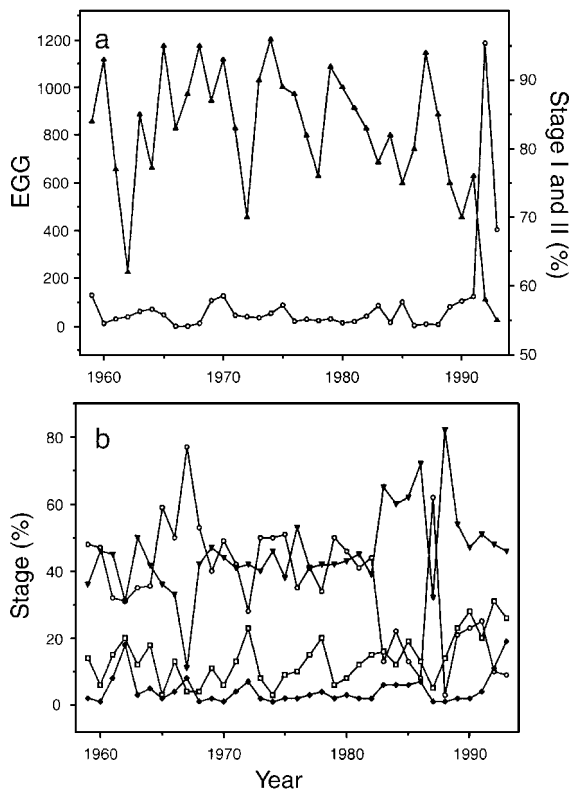
Fig. 4. (a) time series of EGG (open circles) and the percentages of stage I and II eggs combined (filled triangles); and (b) time series of the percentages of stage I (open circles), stage II (filled triangles), stage III (open squares) and stage IV (filled diamonds) eggs.

resulted in an earlier starting date of spawning (Marteinsdottir and Steinarsson, 1998). Because the values of EGG for 1992 and 1993 were such extreme outliers in the stage abundance/recruitment relationships they were omitted from the subsequent statistical analysis.

4.1.3. Larval stage

Data from both the AM and JJ surveys were used to estimate annual indices of the relative abundance of cod larvae. In this case, data for all of the stations shown in Fig. 2 were included. For both the AM and JJ surveys the number of cod larvae caught at station x using the IKS-80 ($l_{AM,x,IKS-80}$ and $l_{JJ,x,IKS-80}$, respectively) was estimated as the arithmetic average of the number of larvae for the vertical haul and the number of larvae for the horizontal tows at 0 and 25 m. For the JJ survey the number of cod larvae caught at station x

using the RT ($l_{JJ,x,RT}$) was the average of the number of larvae for the vertical haul and the number of larvae for the horizontal tow at 50 m. The annual index of relative larval abundance for year t (LAR1) was calculated as:

$$LAR1 = \left(\sum_{x=b} l_{AM,x,IKS-80} + \sum_{x=c} l_{JJ,x,IKS-80} + \sum_{x=d} l_{JJ,x,RT} \right) \bigg/ (b + c + d) \qquad (2)$$

where b is the number of stations sampled in the AM survey using the IKS-80 and c and d are the total number of stations sampled in the JJ survey using the IKS-80 and RT, respectively. The sum of b, c, and d is given in Table 1.

Norwegian surveys of the coast of northern Norway and the western Barents Sea provide a second index of the relative larval abundance (LAR2) for a shorter time period (1977–1991). In the Norwegian ichthyoplankton surveys larvae were sampled using a 29×29 m mid-water trawl having a codend with a 4 m long liner with a 5 mm mesh size. At each sampling station the trawl was towed for 15 min at two depths (20 and 40 m) and for 30 min at the surface. In the literature related to the Norwegian ichthyoplankton survey, this stage has been variously referred to as the post-larvae or early pelagic juvenile stage. In this study it is referred to as a larval stage simply to be consistent with Russian terminology. The spatial coverage of the Norwegian ichthyoplankton survey was similar to that of the Russian surveys (Helle and Pennington, 1999). However, the LAR2 does not constitute a replicate of LAR1 because the latter was calculated using data from both the AM and JJ surveys (Eq. (2)) and therefore integrates information over a longer time period. The differences in mean length (Fig. 1) indicate that LAR2 represents a population that is at a later developmental stage than the population represented by LAR1.

4.1.4. Pelagic juvenile stage

The international 0-group survey of the Barents Sea and adjacent waters has been conducted annually by Norway, Russia and the UK (the latter participating up to 1976) since 1965 (Bjørke and Sundby, 1987). The survey takes place from late August to September

and the spatial coverage of the survey includes both the western and eastern Barents Sea and the west coast of Svalbard (Fig. 2). The gear and sampling methodology used for the 0-group survey was the same as used for the Norwegian ichthyoplankton surveys. Both an areal index and a logarithmic index are calculated from the data. The areal index corrected for interannual variation in the width of the trawl opening (Nakken and Raknes, 1996) was used here (PEL).

4.1.5. Demersal juvenile stage

Russian surveys of recently settled cod and haddock juveniles began in 1946 and covered the southern Barents Sea eastward to Novaya Zemlya. In 1957 the spatial coverage of the survey was expanded to include the region west of Svalbard. The surveys have generally been conducted between October and December. One-hour hauls were made at standard stations with a trawl having a 14 m kapron liner (8 mm mesh size) in the codend. The abundance index (DEM) was calculated by dividing the total number of individuals of that age-class caught in the survey by the total number of trawling hours. In 1982 the survey design was modified to sample adult stages. Because of this change the formulation of DEM was modified (DEM_{mod}). However, the original formulation of DEM (DEM_{orig}) was calculated up until 1995 (Ozhigin et al., 1995). The period of overlap for the two indices (1982–1995) shows that they are in reasonable agreement except in 1984 and 1992 (Fig. 5).
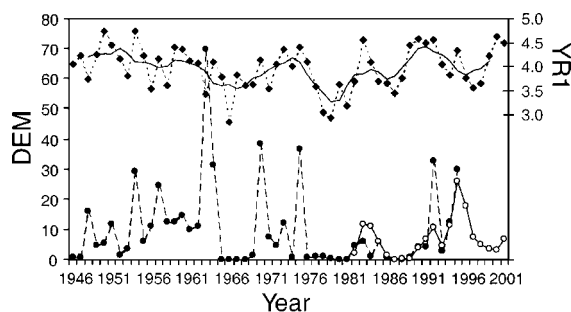

Fig. 5. The time series of DEM_{orig} (closed circles, dashed line), DEM_{mod} (open circles, solid line) and YR1 (closed diamonds, dotted line). A five-year running average for YR1 is indicated by the solid line.

4.2. Recruitment

From 1984 onwards cod cannibalism has been incorporated into the analytical assessment as an additional source of natural mortality (Bogstad and Mehl, 1997). Prior to 1984, natural mortality was assumed to be equal to 0.2. This has introduced a non-stationarity into the recruitment time series. Consequently, two versions of the recruitment indices were used here: recruitment to age 3 including cannibalism mortality from 1984 (REC_{can}) and recruitment to age 3 assuming no cannibalism mortality for the full time period (REC_{nocan}). Recruitment values for the period preceding the incorporation of cannibalism in 1984 are nearly identical. Both REC_{can} and REC_{nocan} were obtained from the same assessment (ICES ACFM, 2001).

4.3. Temperature

Monthly temperatures reported for the Kola hydrographic section (Fig. 2) represent the average temperatures over a depth range of 0–200 m (Tereshchenko, 1996). Logically, residual variation in the stage abundance/recruitment relationships should only be compared to temperature indices describing environmental conditions subsequent to the stage because the stage abundance index should already have corrected for any temperature effects on mortality incurred prior to the stage. Therefore, the Kola section data were used to estimate the following: the annual average temperature in spawning year t (YR1; Fig. 5); the average temperature during the seven months (April in year t to October in year t) covering the pelagic period (APROCT); the average temperature during the seven months (October in year t to April in year $t+1$) representing the first overwintering period (OCTAPR); and the average temperature during the first two calendar years (January in year $t+1$ to December of year $t+2$) of demersal habitat (YR23).

4.4. Statistical methods

Bivariate scatterplots suggested that the relationships between stage abundance and recruitment were characterised by non-constant variance. To accommodate this feature of the data, generalised linear models were used to fit models describing the relationship

between stage abundance and recruitment. Models were fitted assuming a gamma distributed response variable and using a log-link function (S-PLUS 6.0, Insightful Corp.). The 95% confidence intervals were estimated as twice the standard error of the prediction. The goodness of fit was determined by assuming that the distribution of the residual deviance could be approximated by a χ^2 statistic having N-p degrees of freedom where N is the total degrees of freedom and p is the number of parameters included in the model (Venables and Ripley, 1999). The proportion of explained deviance (PED) for a model was estimated the difference between the null deviance (the deviance associated with a model having no predictors) and residual deviance for the fitted model expressed as a proportion of the null deviance. Influential values were identified as those observations satisfying two criteria: (i) the leverage exceeded 2*(p/N); and (ii) the leverage was more than twice as high as the next highest leverage value in the series.

The importance of temperature was assessed firstly using scatterplot matrices showing the relationship between deviance residuals from the stage abundance/recruitment models described above and the different temperature variables. The general trends in each bivariate plot were represented using a LOWESS scatterplot smoother. For life history stages that showed significant correlations between stage abundance and recruitment, multivariate generalised linear models were fitted with both the main effects terms for stage abundance and temperature and the interaction term. Influential observations were removed prior to model fitting. Goodness of fit was assessed using tests of significance based on the χ^2 statistic and the PED. Where possible the multivariate models were tested by comparing the predicted recruitment to age 3 to the observed values for an independent time period (1946 to 1958). Similarly, DEM_{mod} (Fig. 5) was used to develop a comparable recruitment model for the most recent time period (1982–1997). Recruitment predictions for two upcoming year-classes (1998 and 1999) were then compared to the predictions that are currently used in the assessment which are generated using the RCT3 model (ICES ACFM, 2001). For NA cod this model combines several different survey indices of abundance, including DEM_{mod}, but does not include temperature information.

5. Results

5.1. Relationships between stage abundance and recruitment

The relationship between SSB and recruitment was not significant for either REC_{can} or REC_{nocan} and the PED was negligible (Table 3). Given that the highest variability in recruitment was observed at low values of SSB (Figs. 6a and 7a) the gamma model, which assumes that the variance of the response increases with increasing value of predictor variable, appeared to be inappropriate for these data. The EGG was significantly correlated with both REC_{can} and REC_{nocan} ($p < 0.01$) (Table 3). Low values of EGG (<40) were consistently associated with low recruitment and variance in recruitment increased with increasing EGG (Figs. 6b and 7b). The relationship between LAR1 and recruitment was at or near the level of significance ($p = 0.06$ and $p = 0.05$ for REC_{can} and REC_{nocan}, respectively), but the observation for 1962 was deemed to be highly influential (Figs. 6c and 7c). Excluding this observation increased both the significance of the relationship and the PED for both REC_{can} and REC_{nocan} (Table 3). The relationship between LAR2 and recruitment (Figs. 6d and 7d) was not significant ($p > 0.05$; Table 3) for either REC_{can} and

Table 3
Degrees of freedom (N), significance levels (p), and proportion of explained deviance (PED) and for gamma models (log-link function) describing the relationship between various predictor variables and recruitment to age-3, including cannibalism mortality for 1984 to 1993 (REC_{can}) or without cannibalism mortality for the full time period (REC_{nocan})

Response	Predictor	N	p	PED
REC_{can}	SSB	34	0.49	0.03
	EGG	30	<0.01	0.44
	LAR1	27(26)	0.06(0.04)	0.25(0.32)
	LAR2	14	0.09	0.40
	PEL	28	0.04	0.27
	DEM	34(33)	<0.01(0.02)	0.37(0.33)
REC_{nocan}	SSB	34	0.92	<0.01
	EGG	30	<0.01	0.40
	LAR1	27(26)	0.05(0.03)	0.28(0.35)
	LAR2	14	0.18	0.30
	PEL	28	0.10	0.18
	DEM	34(33)	<0.01(0.02)	0.38(0.32)

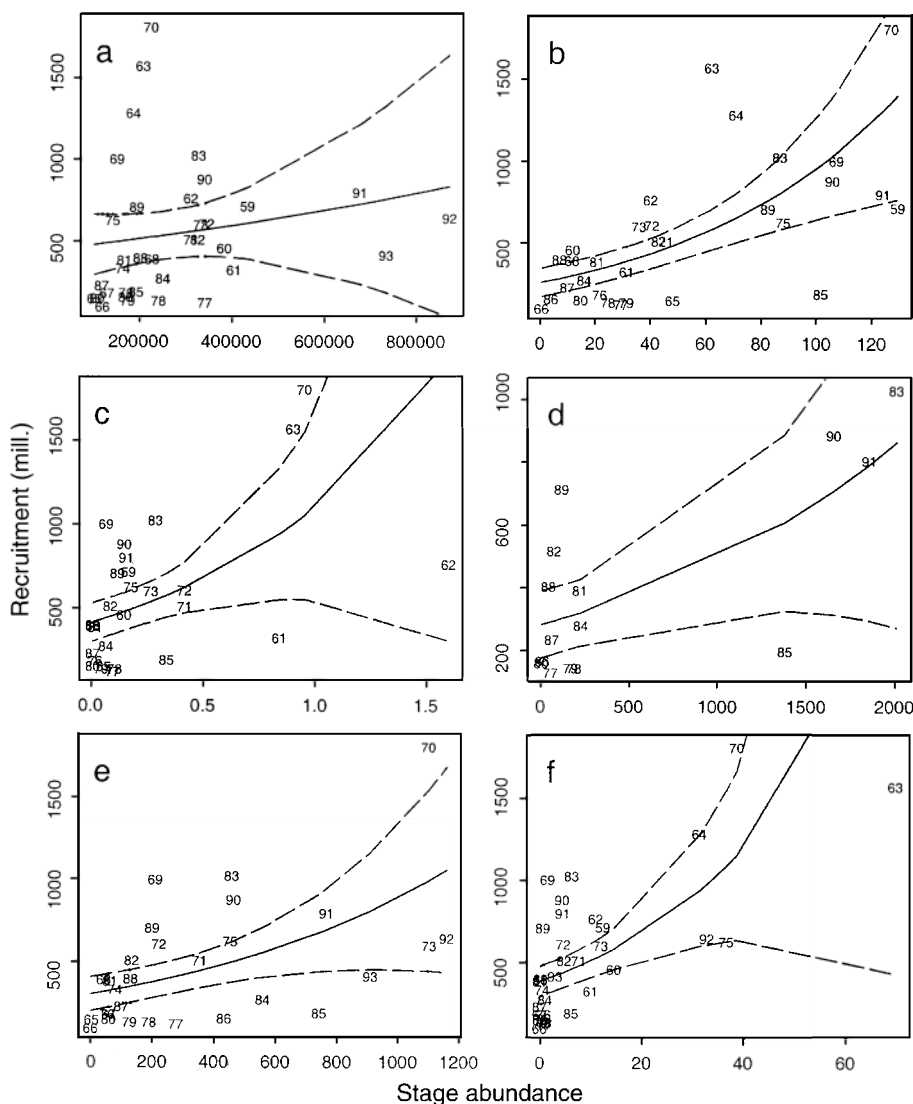Values in brackets are for models fit excluding one influential observation.

Fig. 6. Bivariate plots showing the relationship between recruitment to age-3 including cannibalism (REC_{can}) and different indices of abundance. (a) SSB (tonnes); (b) EGG; (c) LAR1; (d) LAR2; (e) PEL; and (f) DEM. The fit of the gamma model is shown as a solid line with 95% confidence intervals (dashed line). The observations are labelled by year-class.

REC_{nocan}. The relationship between recruitment and PEL (Figs. 6e and 7e) was significant for REC_{can} ($p = 0.04$) but not for REC_{nocan} ($p = 0.10$) (Table 3). Lastly, the relationship between recruitment and DEM was significant ($p < 0.05$) for both REC_{can} and REC_{nocan} (Table 3). Excluding the highly influential observation for 1963 (Figs. 6f and 7f) had little effect on the significance of the model but decreased the PED slightly (Table 3).

5.2. Effect of temperature

A scatterplot matrix was constructed using the deviance residuals from the stage abundance/recruitment relationships described above and the different temperature variables. Both SSB and LAR2 were omitted from this because neither was correlated with recruitment (Table 3). The scatterplot matrix (Fig. 8) can be sub-divided into three regions: (i) deviance
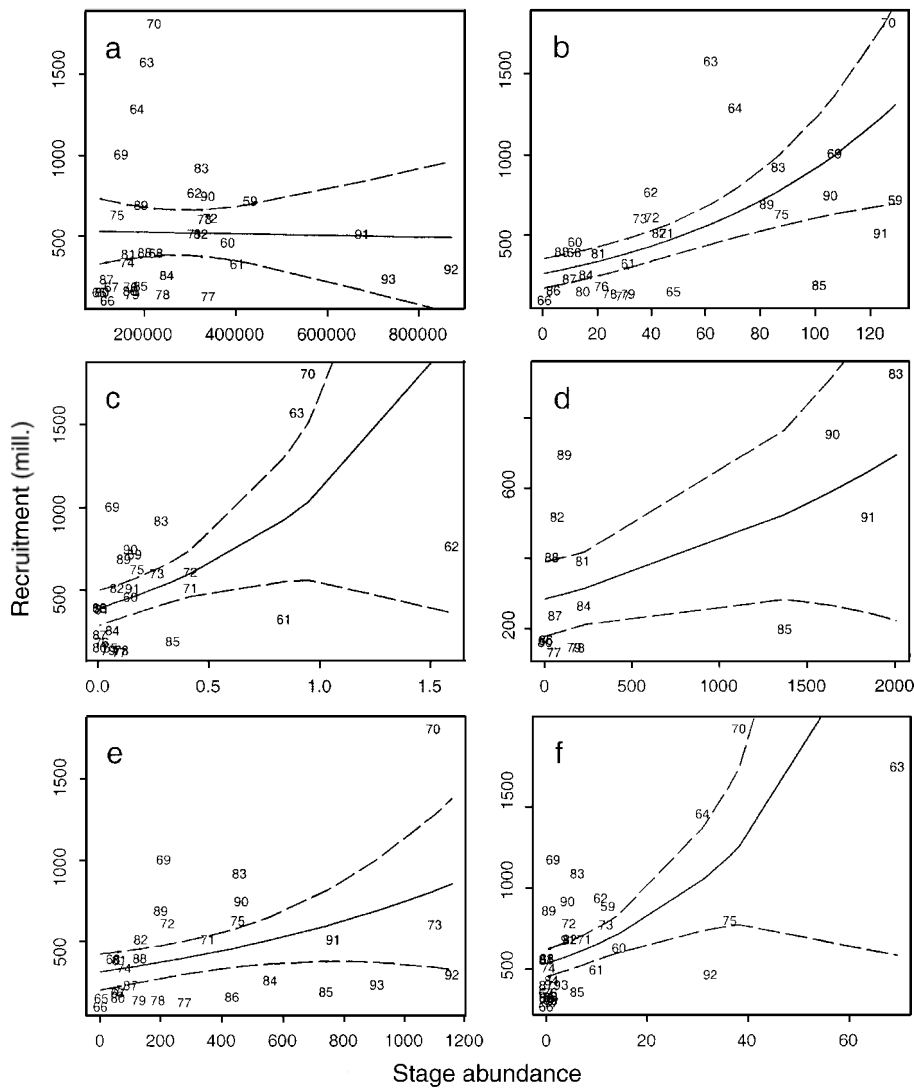
Fig. 7. Bivariate plots showing the relationship between recruitment to age-3 not including cannibalism (REC_{nocan}) and different indices of abundance. (a) SSB (tonnes); (b) EGG; (c) LAR1; (d) LAR2; (e) PEL; and (f) DEM. The fit of the gamma model is shown as a solid line with 95% confidence intervals (dashed line). The observations are labelled by year-class.

residuals of the different stage abundance/recruitment relationships plotted against each other (triangle of six plots on the lower left of the matrix); (ii) temperature indices plotted against each other (triangle of six plots on the upper right of the matrix); and (iii) deviance residuals of the different stage abundance/recruitment relationships plotted against the different temperature indices (rectangle of 16 plots on the lower right of the matrix).

In region (i) of Fig. 8 the deviance residuals for the LAR1, PEL and DEM stages show a high degree of linear association with each other suggesting that the abundance indices for these stages are explaining a similar portion of the recruitment signal, thus giving a high degree of association in the unexplained portion of the signal (the deviance residuals). In contrast, the deviance residuals for the EGG stage show curve-linear relationships with the deviance residuals for the
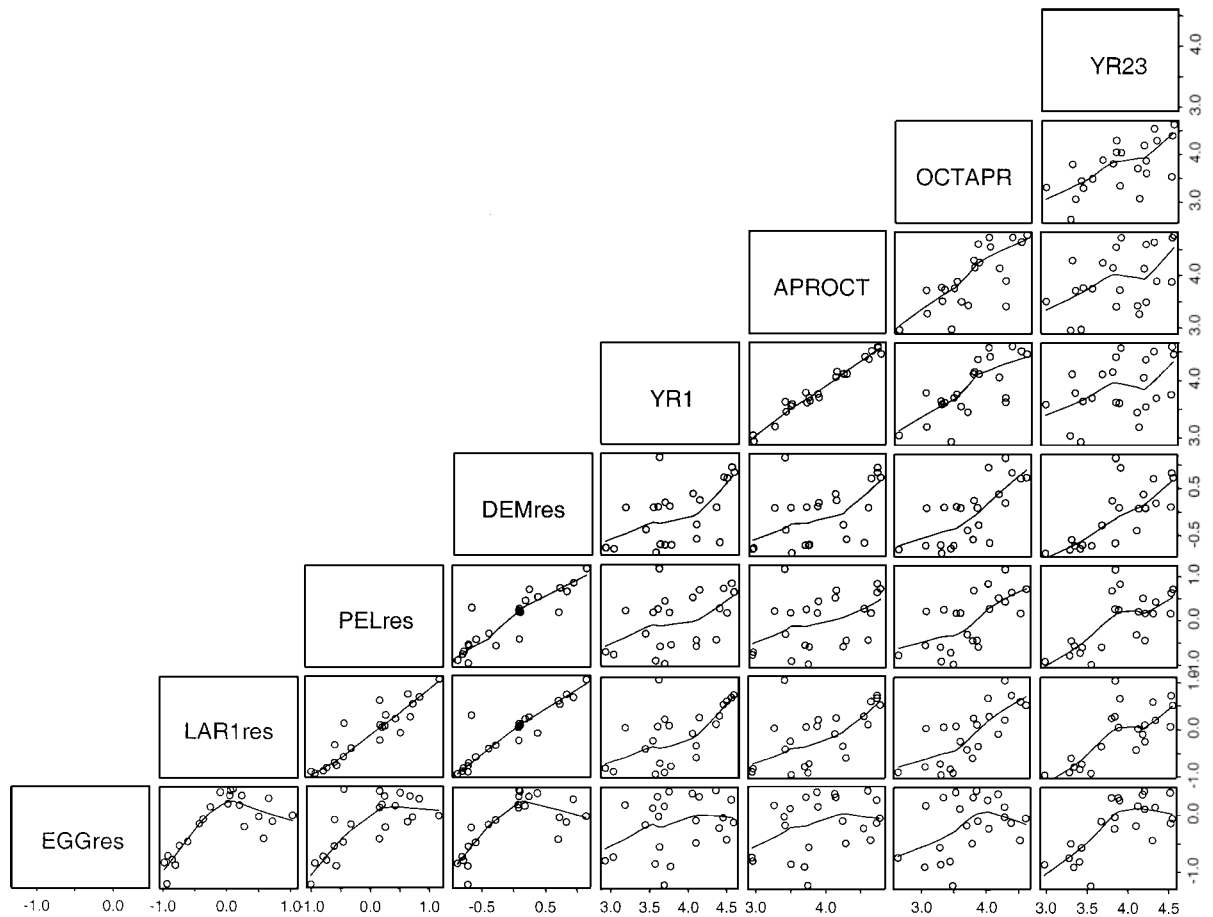
Fig. 8. Scatterplot matrix showing bivariate relationships between deviance residuals from gamma models (fit using REC_{can} as the response variable and EGG, LAR1, PEL and DEM as the predictor variables) and four different temperature indices. Lines represent the LOWESS smoothers. In the cases of LAR1 and DEM highly influential observations for 1962 and 1963, respectively, were omitted.

latter stages suggesting that there are differences between EGG and the other indices in the portion of the recruitment signal that is being explained. This distinction between the deviance residuals for EGG and the deviance residuals for the subsequent stages suggests that the recruitment signal is modified between the egg and larval stages, i.e., that there is a critical stage.

Inspection of the plots for the different temperature indices (region (ii) in Fig. 8) shows that the degree of association between YR1 and APROCT is high, a result which is expected given that the seven monthly temperature values used to estimate APROCT are included in YR1. There is a lower degree of association between YR1 and OCTAPR because only three

of twelve months in YR1 overlap with OCTAPR (viz., Oct–Dec). There is no temporal overlap between YR1 and YR23 and, hence, there is a low degree of association between them.

Several clear trends in the relationships between the deviance residuals for the stage abundance/recruitment relationships and the different temperature variables (region (iii) in Fig. 8) were noted. The YR1 and APROCT temperatures were not strongly associated with deviance residuals for any of the stage abundance indices. The deviance residuals for EGG were not strongly associated with any of the temperature variables although a curve-linear trend was suggested with both OCTAPR and YR23. The deviance residuals for the LAR1, PEL and DEM stages were all

linearly associated with OCTAPR and YR23. Thus, the temperature effect on recruitment became stronger for life history stages that followed the EGG stage. Temperature indices which represented conditions during the first overwintering period (OCTAPR) and the two post-settlement years (YR23) were more strongly associated with the deviance residuals compared to temperature conditions during the pelagic period (YR1 or APROCT).

The qualitative trends noted in the scatterplot matrices (Fig. 8) were supported by the results of the multivariate modelling (Table 4). Using $p = 0.05$ as an arbitrary cut-off value for significance, neither YR1 nor APROCT were significant in any of the multivariate models and the EGG was not significantly correlated with any of the temperature variables. None of the interaction terms were significant. The main effect terms for OCTAPR or YR23 were significant or near significance in models that included LAR1, PEL and DEM as stage abundance indices. There was little appreciable difference between the results obtained using either REC_{can} or REC_{nocan} as the recruitment index. For both REC_{can} and REC_{nocan} the multivariate model giving the highest PED included LAR1 and YR23 as the stage abundance and temperature main effects terms, respectively (Table 5). The PED was nearly as high for the multivariate models that included DEM_{orig} as the stage abundance term and either OCTAPR or YR23 as the temperature term. The difference in PED values for models using either OCTAPR or YR23 as the temperature term was minimal.

Table 5
Multivariate models fit with just the main effects terms

Time period	Model	d.f.	PED
1959–1993	$REC_{can} = \exp(9.71 + 1.32LAR1 + 0.82OCTAPR)$	26	0.60
	$REC_{can} = \exp(8.51 + 1.45LAR1 + 1.09YR23)$	26	0.63
	$REC_{can} = \exp(9.59 + 0.00078PEL + 0.82OCTAPR)$	28	0.55
	$REC_{can} = \exp(8.67 + 0.001PEL + 1.01YR23)$	28	0.55
	$REC_{can} = \exp(9.84 + 0.029DEM_{orig} + 0.78OCTAPR)$	33	0.58
	$REC_{can} = \exp(9.01 + 0.042DEM_{orig} + 0.96YR23)$	33	0.59
	$REC_{nocan} = \exp(9.95 + 1.36LAR1 + 0.74OCTAPR)$	26	0.59
	$REC_{nocan} = \exp(8.76 + 1.47LAR1 + 1.02YR23)$	26	0.63
	$REC_{nocan} = \exp(10.039 + 0.029DEM_{orig} + 0.72OCTAPR)$	33	0.54
	$REC_{nocan} = \exp(9.34 + 0.040DEM_{orig} + 0.86YR23)$	33	0.54
1982–1997	$REC_{can} = \exp(9.49 + 0.037DEM_{new} + 0.87OCTAPR)$	15	0.55
	$REC_{can} = \exp(6.27 + 0.079DEM_{new} + 1.56YR23)$	15	0.77
	$REC_{nocan} = \exp(9.93 + 0.023DEM_{new} + 0.74OCTAPR)$	15	0.37
	$REC_{nocan} = \exp(7.14 + 0.058DEM_{new} + 1.34YR23)$	15	0.58

The EGG was not included here because the main effects for temperature were not significant (see Table 4). Also shown are the models developed for a more recent time period (1982–1997) using the modified DEM index (DEM_{mod}).

Table 4
Significance levels (p) for main effects and interaction terms in a gamma model fit for observations (1959–1993)

Response	Stage abundance	YR1		APROCT		OCTAPR		YR23	
		Main	Interaction	Main	Interaction	Main	Interaction	Main	Interaction
REC_{can}	EGG	0.47	0.27	0.50	0.24	0.28	0.41	0.26	0.15
	LAR1	0.14	0.65	0.18	0.76	0.05	0.44	0.04	0.88
	PEL	0.11	0.91	0.19	0.70	0.04	0.97	0.04	0.62
	DEM	0.08	0.27	0.13	0.24	0.04	0.38	0.04	0.34
REC_{nocan}	EGG	0.53	0.21	0.55	0.19	0.31	0.31	0.29	0.11
	LAR1	0.22	0.68	0.26	0.79	0.07	0.43	0.05	0.90
	DEM	0.16	0.15	0.23	0.15	0.06	0.32	0.06	0.30

The response variable is recruitment to age-3 either including cannibalism mortality for 1984 to 1993 (REC_{can}) or without cannibalism mortality for the full time period (REC_{nocan}). Because the multivariate models were fit in a stepwise fashion with the stage abundance entering first, the significance levels of the main effect for stage abundance correspond to those given in Table 3. The SSB, LAR2, and PEL (REC_{nocan} only) were excluded here because the main effects were not significant (see Table 3).

Compared to LAR1, DEM estimates have the advantage of being available both before and after the model calibration period. A wireframe representation of the multivariate model (from Table 5)

$$REC_{can} = \exp(9.01 + 0.0.042DEM_{orig} + 0.96YR23) \quad (3)$$

illustrates the rate of increase in REC_{can} for the temperature term relative to the rate of increase in REC_{can} for the stage abundance term (Fig. 9a). The same model can also be shown in the form of a bivariate plot for fixed values of YR23 corresponding to the minimum,

Fig. 9. (a) Wireframe representation of a multivariate recruitment model (Eq. (3)) which includes DEM_{orig} and YR23 as the stage abundance and temperature terms, respectively; and (b) the same model showing the relationship between DEM and REC_{can} for the mean YR23 (solid line) and the minimum and maximum observed values of YR23 (dashed lines). Observed values of REC_{can} for the time period 1959–1993 are also shown (open circles).
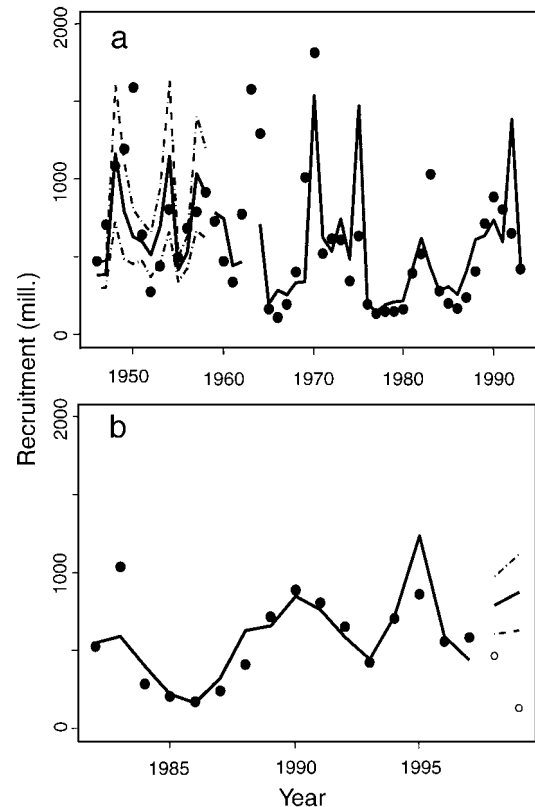
Fig. 10. (a) Time series of a multivariate recruitment model (Eq. (3)) which includes DEM_{orig} and YR23 as the stage abundance and temperature terms, respectively. Model predictions and 95% confidence intervals for 1946–1958 are indicated by the solid and dashed lines, respectively. Observed recruitment is indicated by closed circles. (b) Time series of a multivariate recruitment model (Eq. (4)) which includes DEM_{mod} and YR23 as the stage abundance and temperature terms, respectively. The model predictions and 95% confidence intervals for 1998 and 1999 are indicated by the solid and dashed lines, respectively. Observed recruitment is indicated by closed circles. Recruitment values predicted by RCT3 (from ICES ACFM, 2001) are shown as open circles.

average and maximum values (Fig. 9b). The observed recruitment values used for the model calibration period (1959–1993) fall within or near the boundaries specified by the minimum and maximum YR23 values in most years.

5.3. Model testing

Because DEM_{orig} survey series was estimated continuously from 1946 to 1995 (Fig. 5) Eq. (3) could

be used to predict recruitment for the time period 1946 to 1958 (Fig. 10a). The observed recruitment values fall within the 95% confidence intervals of the predictions in ten of the 13 years. The exceptions were the years 1947 and 1950 when recruitment is underestimated and 1952 when recruitment is overestimated (Fig. 10a).

Multivariate models developed for the 1982–1997 time period using DEM_{mod} show that for both REC_{can} and REC_{nocan} the PED for models which used YR23 as the temperature term were notably higher than the models which used OCTAPR as the temperature term (Table 5). This suggests that for the recent time period temperature during the two post-settlement years is having a stronger effect on recruitment than is temperature during the first overwintering period. Recruitment predictions for 1998 and 1999 made using the multivariate model (from Table 5)

$$REC_{can} = \exp(6.27 + 0.0.079 DEM_{mod} + 1.56 YR23) \quad (4)$$

suggest that there will be an increase in recruitment. In contrast, recruitment predictions generated by RCT3 are outside the 95% confidence intervals of the predictions made using Eq. (4) and show a decrease (Fig. 10b). The higher temperatures of recent years (Fig. 5) are causing the recruitment predictions from Eq. (4) to be higher than those obtained on the basis of survey information alone.

6. Discussion

6.1. Identifying critical stages

The primary goal of this study was to use the available stage abundance estimates for NA cod to identify the stage at which the signal in year-class strength could first be detected and to track how the signal evolved. The largest increase in explanatory power, as reflected by improvements in statistical significance and explained deviance, occurred going from SSB to EGG. This result has two possible interpretations. The transition from potential to realised total egg production could constitute a true critical stage in the evolution of year-class strength if the combined influence of atresia, non-fertilisation and

early-stage egg mortality is sufficiently large. Alternatively, SSB could be a poor measure of potential total egg production by the stock (Marshall et al., 1998, 1999). Similar investigations for Baltic cod illustrate that these two possibilities are not mutually exclusive. The egg stage appears to be a true critical stage in that survey-based indices of realised egg production are more highly correlated with recruitment than the stock-based index of potential total egg production (Köster et al., 2001). Additionally, SSB is an inaccurate measure of reproductive potential for Baltic cod because it does not account for year-, area- and/or gender-specific maturities or interannual variation in relative fecundity (Köster et al., 2001).

The portion of the recruitment signal explained by EGG differed from the portion explained by subsequent life history stages (Fig. 8). This implies that a critical period occurs between the egg and larval stages. Instantaneous daily mortality rates of cod eggs in Lofoten are high and result in the removal of ca. 90% of the egg production prior to hatching (Fossum, 1988). Field estimates of endogenous egg mortality in Lofoten and the surrounding coastal regions have been estimated as ca. 25% (Kjørsvik et al., 1984; Makhotin and Solemdal, 2001) and these are almost certainly underestimates given that dead eggs are underrepresented in field samples. Exogenous sources of egg mortality in Lofoten include predation by herring, ctenophores and jellyfish (Melle, 1985), but the cumulative mortality from these sources is difficult to quantify. The stage information provided by ichthyoplankton surveys is useful for detecting when mortality rates are high. For Baltic cod, the abundance of stage I eggs was more highly correlated with stock-based estimate of potential total egg production than was stage III abundance (Köster et al., 2001) indicating that significant mortality occurred between these two egg stages. Predation by sprat on cod eggs has been identified as a major source of endogenous mortality for this stock (Köster and Möllmann, 2000).

Following the critical stage(s), the correlations between stage abundance and recruitment should, in theory, progressively strengthen as the penultimate recruitment stage is approached (Van der Veer et al., 2000). For NA cod the explanatory power of the stage abundance/recruitment relationships decreased after the egg stage rather than increased. The most parsimonious explanation for this result is that measurement

error is adding substantial noise to the stage abundance estimates. Because of the broad spatial and temporal scales at which the surveys for NA cod are conducted it is not possible to estimate measurement error for each of the survey series directly through replication. There are several obvious sources of measurement error. Larvae are notoriously difficult to sample efficiently (Heath, 1992), and therefore stage abundance/recruitment correlations that appear at an early stage may disappear at a subsequent larval stage (ICES, 1998). In the case of LAR1, pooling information across a broad temporal window (data from both AM and JJ surveys were combined to estimate LAR1) may have introduced substantial error. Abundance indices for pelagic juveniles often show highly significant correlations with recruitment, particularly when sampled at developmental stages that are available to both the survey design and sampling gear (Astthorsson et al., 1994; Jákupsstovu and Reinert, 1994). Given that the mean lengths measured during the international 0-group survey overlap with or exceed the lengths at which juveniles begin to settle (Fig. 1) pelagic juveniles may not be fully available to this survey. There is also likely to be considerable error in sampling the newly settled juveniles given that the capture efficiency for cod under 200 mm (see Fig. 1) is less than 40% (Engås and Godø, 1989; Walsh, 1992) due to escapement and/or settlement in areas that are inaccessible to the gear.

6.2. Temperature effects on recruitment

Annual temperature or temperature during the pelagic period has previously been found to explain a significant portion of the residual variation in the SSB/recruitment relationship (Ottersen and Sundby, 1995). In this study, SSB was not used in the multivariate modelling because it was not significantly correlated with recruitment. Residual variation in the EGG/recruitment relationship was not correlated with average temperatures for either the pelagic or demersal periods. However, temperatures during the post-settlement period were significantly correlated with residual variation in the stage abundance/recruitment relationships for larval and juvenile stages. The effect of post-settlement temperatures on recruitment of NA cod has previously been suggested (Ponomarenko, 1984). Cannibalism is also an important source of

mortality for NA cod, particularly for years when the biomass of their preferred prey (capelin) is reduced (Bogstad and Mehl, 1997). Provided that food is not limiting, high temperatures during the post-settlement period would enhance the growth rates of age 1 and 2 cod, thereby reducing the risk of mortality due to predation and cannibalism.

6.3. Survey-based recruitment models

Recruitment models are a critical element of the stock projections used to formulate management advice (Needle, 2002). Increasingly, these relationships are being modified to include environmental information. For example, a recruitment model has been developed for Baltic cod that includes potential total egg production, predation on cod eggs by sprat and larval transport as independent variables (Köster et al., 2001). An environmentally sensitive recruitment model has also been developed for Icelandic cod which includes SSB and an index representing the strength of the coastal current which affects the transport of eggs and larvae from the spawning grounds towards the nursery grounds (Begg and Marteinsdottir, 2002). A comparable recruitment model for NA cod includes SSB, temperature during the pelagic period and wind stress anomalies (Ottersen and Sundby, 1995). Each of these models uses a stock-based index of reproductive potential (either potential total egg production or SSB) and then incorporates processes influencing survival through the critical egg and larval stages. The approach taken to recruitment modelling here was to replace the term representing the reproductive potential of the spawning stock with a term representing the abundance at a life history stage that follows the critical stage(s) and then incorporate environmental information. Although the recruitment model developed here predicted recruitment fairly well for a historical period (Fig. 10a) its ability to forecast future recruitment remains to be evaluated more thoroughly.

6.4. Other applications of ichthyoplankton data

Temporal trends in the percentages of the four egg stages (Fig. 4b) indicate that from1983 onwards stage II eggs started to dominate over stage I eggs, whereas prior to 1983 the proportions of stage I and II eggs

were quite similar or stage I was higher than stage II. At approximately the same time the proportions of stage III eggs also began to increase. Given that there was no abrupt change in the timing of the survey (Fig. 3) it is possible that from 1983 onwards the cod spawned earlier. The shift in timing occurred simultaneously with an abrupt shift towards higher growth, as reflected in larger values of proportion mature and weight for most age classes (ICES ACFM, 2001). The factors responsible for this change in growth dynamics have yet to be identified. It should also be noted that the only exception to the trend towards earlier spawning occurred in 1987 when the proportion of stage I eggs was the second highest in the entire time series. In this year the spawners were in exceptionally poor condition (Marshall et al., 1998; Kjesbu et al., 1998) and poor condition spawners start spawning later (Kjesbu, 1994). Furthermore, there were anomalously low values of proportions mature in larger length classes (Marshall et al., 1998) that may have shifted the size composition of spawners towards smaller length classes that spawn later (Marteinsdottir and Steinarsson, 1998). While speculative, these points serve to illustrate how the biological information contained in ichthyoplankton databases can be used to examine a wide variety of aspects related to growth and reproduction at the stock-level.

7. Conclusion

The analysis presented here, using the longest continuous time series of egg and larval abundance estimates currently available for NA cod, suggests that the transition from potential to realised egg abundance is a critical stage in the evolution of year-class strength of NA cod and/or that SSB is a poor index of the potential total egg production. The signal in year-class strength undergoes modification between the egg and larval stages. These results are consistent with the conclusion that the signal in year-class strength of NA cod is determined in the earliest life history stages (Sundby et al., 1989; Anderson and Gregory, 2000). Ichthyoplankton surveys are essential for identifying the factors influencing mortality rates during these critical stages (Bailey et al., 1996; Nash, 1998; Köster et al., 2001). In the case of NA cod, standardised surveys of egg and larval stages have been discontinued by both Russia and Norway. One recourse is to use historical data more effectively and efforts are currently underway to improve data accessibility so as to facilitate such analyses.

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