Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link

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We address the hypothesis that survival of a cohort is directly related to growth rates during the pre-recruit period for marine fish. This hypothesis is widely accepted, but supporting field evidence has been elusive. Here the connection between size and year-class strength at the early stages is examined for the commercially important Barents Sea stocks of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*). We show that there is a close link between length and year-class strength at the 0-group stage within and among the populations studied, and that the connection also holds between length at the 0-group stage and strength of recruitment at age 3. Both length and abundance are closely related to temperature. Interannual variability in the temperature conditions is concluded to be the underlying cause of the covariability between growth and year-class strength. We hypothesize that for stocks at the high latitude end of the overall range of the species the environmental signal tends to over-ride density-dependent effects on growth. High temperature will cause a high production of prey items leading to higher growth rates and higher survival through the vulnerable larval and juvenile stages. The duration of the high-mortality and vulnerable stages is also decreased by higher temperature directly increasing the development rate.

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Introduction

The concept that size-specific growth and mortality rates interact to determine survivorship in fish populations has long been a foundation of fisheries theory (Gulland, 1965; Cushing, 1974; Ware, 1975; Campana, 1996). In simple terms, the theory predicts that survival of a cohort is directly related to growth rates during the pre-recruit period (Anderson, 1988). A rapid growth rate through the larval and juvenile stages is thought to increase the probability of survival due to an enhanced ability to feed and avoid predators (Rice *et al.*, 1993; Cushing and Horwood, 1994). While widely accepted, field evidence supporting the hypothesis for marine fishes has been elusive (Campana, 1996).

The commercially important stocks of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*) in the Barents Sea display

large interannual variability in abundance. For Arcto-Norwegian cod, the amplitude, measured as the ratio between poor and strong year classes, is about 1:70 at the early juvenile stage (Sundby *et al.*, 1989) and 1:15 at the 3-year-old stage (ICES, 1996a). As for many fish stocks, stock–recruitment relationship is indeterminate, leading to a focus on the environmental conditions during the early life stages as regulatory factors of recruitment variability, as hypothesized for example by Hjort (1914).

A number of authors have found that recruitment of Barents Sea fish populations, particularly cod, appears to be influenced by sea temperature. Izhevskii (1961) showed a close connection between annual mean Barents Sea temperature and catch per hour of trawling of cod. Ponomarenko (1984) argued that the minimum temperature during the first wintering influences cod survival rates, while Ellertsen *et al.* (1987) concluded

that high temperature is a necessary but not a sufficient condition for the production of good year classes of cod. Ottersen et al. (1994) found the average abundance of cod and haddock at the 0-group stage to be 2.5–3 times as high in warm years as in cold; for herring the ratio is as high as 6. Krysov and Ergakova (1990) and Krysov et al. (1994) noted that warm waters on the spawning grounds and along the routes of larval drift and predominance of south-westerly winds determine the appearance of abundant herring year classes. Sætersdal and Loeng (1987) and Borisov and Elizarov (1989) concluded that the high incidence of temporal similarity in survival success of cod, haddock, and herring larvae is related to the inflow of Atlantic Water masses, with high temperatures acting favourably on all three stocks. Close connections have also been found between temperature and fish size at early stages by Loeng and Gjøsæter (1990) and Loeng et al. (1995).

We investigate the connection between size and year-class strength at the early stages for Arcto-Norwegian cod, haddock, and Norwegian spring-spawning herring in relation to environmental variability. All three stocks display synchrony in year-class strength and early growth variability.

Material and methods

International 0-group surveys have been carried out annually in the Barents Sea and adjacent waters since 1965 during late August/early September. Data on number, length, and geographical distribution of cod, haddock, and herring have been collected in the Barents Sea. The 0-group index (I_0) is found by determining the logarithmic mean of the catches per nautical mile in a predefined stratification of the whole survey area (Randa, 1982, 1984). Note that while I_0 is calculated from log-transformed catch data, the time series itself is untransformed; its natural log-transform is denoted by $\ln (I_0)$. Abundance indices are taken from the latest survey report (ICES, 1996a); length data are aggregated from annual survey reports. Time series on 0-group mean length (L_0) exist from 1965, 1969, and 1976 for cod, haddock, and herring, respectively. Here, 0-group abundance and length values until 1996 are used.

Length data for early juveniles (2–3 months old), based on surveys conducted in the southwestern Barents Sea in June and July, are available for the period 1977 to 1991. A detailed description of the survey methods is given in Bjørke and Sundby (1987) and Sundby et al. (1989). Estimates of daily growth increments (G_0) are taken from Loeng et al. (1995), who calculated the difference in mean length measured during the 0-group and early juvenile surveys for each year (1977–1991), divided by the number of days between the mid-dates of
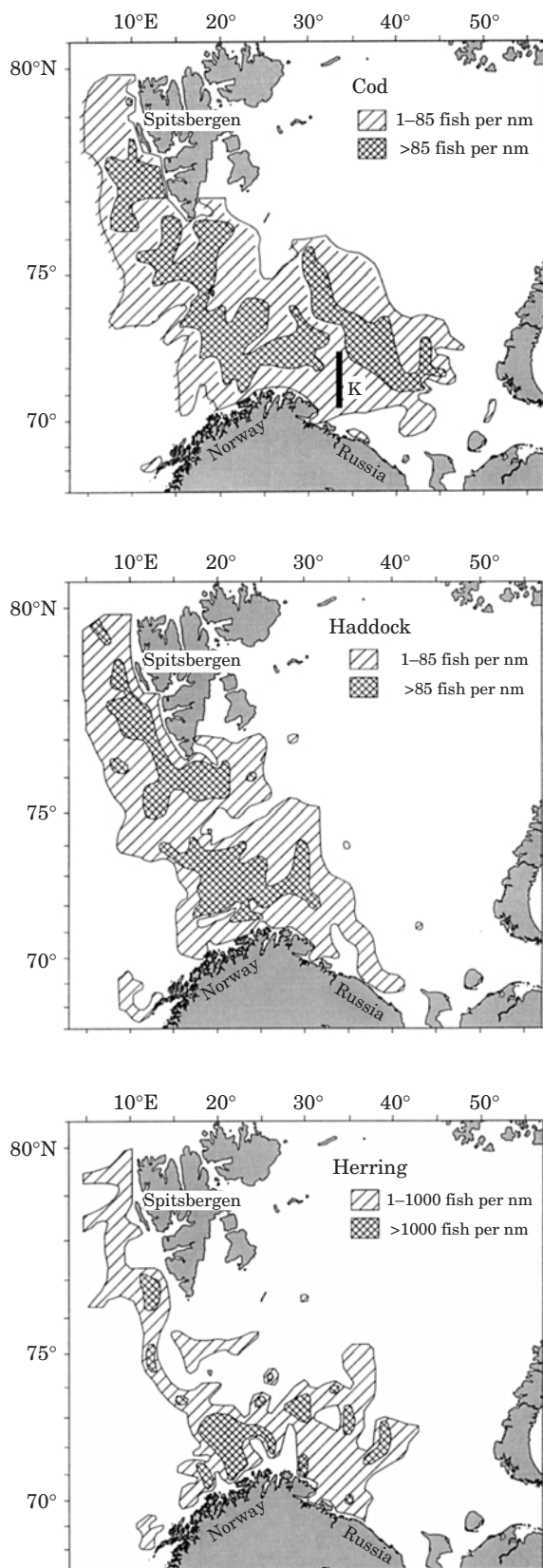
the two surveys. Virtual population analysis estimates of year-class abundance at age 3 based on commercial catch data (VPA_3) were used for the 1965 to 1994 year classes of cod and the 1966 to 1994 year classes of haddock and herring (ICES, 1996b, c). Abundance data were ln-transformed.

Annual mean temperature values for the 0–200 m depth range were derived from the Russian hydrographic section off the Kola peninsula (Bochkov, 1982; Tereshchenko, 1996; Fig. 1), 1965–1996.

Methods like correlation analysis, linear regression, and t-tests all depend on assumptions which are rarely met by time-series data. The true significance level of a test may deviate from the intended nominal level if the series are autocorrelated, non-normal, or non-stationary (Chatfield, 1989; Thompson and Page, 1989; Ottersen, 1996). The Shapiro-Wilks statistic (W) was used for testing normality, the null-hypothesis being that the data are a random sample from a normal distribution. The Durbin-Watson test statistic was calculated for detecting statistically significant first-order autocorrelations.

Spearman rank correlation was used in addition to Pearson product-moment correlation to avoid problems with non-normality. To calculate significance levels, the effective number of independent observations, adjusted for order 1 and 2 autocorrelations (N_e), were estimated using Quenouille's (1952) formula: $N_e=N/(1+2r_{a1}r_{b1}+2r_{a2}r_{b2})$, where N is the number of data points in the two series, r_{a1} and r_{b1} are the lag-one autocorrelations, and r_{a2} and r_{b2} the lag-two autocorrelations. Where appropriate, Pearson partial correlations, which measure the linear association between two stochastic variables after eliminating the effects of any third variable, were worked out (Johnsen and Wichern, 1988). In addition to Student t-tests, non-parametric median and Wilcoxon tests were employed to determine the significance in differences in length and growth rate between warm and cold years. For the t-tests, Satterthwaite's approximation was used rather than assuming equal variances between the groups. As an alternative to traditional multiple linear (ordinary least squares) regression, which assumes uncorrelated error terms, autoregressive time series models were used (Box and Jenkins, 1970; Ottersen and Sundby, 1995). Statistical calculations were done by means of the SAS package (SAS Institute, 1988, 1991).

Statistical tests for normality (Shapiro-Wilks) showed that none of the length, growth, or VPA_3 distributions departed with statistical significance (5%) from a normal distribution. For cod and haddock I_0 was significantly non-normal. Durbin-Watson tests revealed a statistically significant order 1 autocorrelation for most of the series. Adjustment of degrees of freedom, Box-Jenkins modelling, and non-parametric tests as described earlier, were therefore applied.

Figure 1. Typical distribution of cod, haddock, and herring during the 0-group surveys (data for 1991; ICES, 1991). The position of the hydrographic section along the Kola meridian (K) is indicated.

Results

Figure 2 provides an update of the mean length of 0-group cod, haddock, and herring given by Loeng *et al.* (1995) for 1965–1992. The overall picture shows a large degree of synchrony in length variability from the start until the early 1990s. During the latest years, L_0 of haddock has been stable far above the long-term mean and median (Table 1), while cod L_0 fell towards the long-term mean from 1995 to 1996 and herring L_0 has declined each year since 1992. Spearman/Pearson correlation coefficients between length of cod and haddock are 0.78/0.82, between cod and herring 0.66/0.66, and between haddock and herring 0.59/0.60 (all $p<0.01$, see also Fig. 3). Variability in 0-group length between years has been highest for herring, while the length of cod has been the most stable (Table 1).

There is also a connection between length and abundance index at the 0-group stage for all three stocks (Table 2, Fig. 4). The 11 years with highest cod I_0 also had a L_0 above the overall mean. The same applies to the 8 years with highest haddock I_0 and the 4 years with highest herring I_0. Furthermore, the connection is just as clear between L_0 and VPA_3 (Fig. 5, Table 2). Higher than average L_0 was found for the 7, 4, and 6 most abundant year classes of cod, haddock, and herring, respectively.

Temporal development of cod L_0 shows a clear synchrony with I_0, VPA_3, and annual mean sea temperature along the Kola section (Fig. 6). However, in some years the discrepancies between the four variables are considerable, particularly during 1965–1967. Spearman rank correlation coefficients between $\ln(I_0)$ and $\ln(VPA_3)$ were 0.43 for cod ($p<0.10$), 0.53 for haddock ($p<0.05$), and 0.79 for herring ($p<0.01$). The two abundance estimates thus show an intermediate degree of covariation for cod and haddock, while the herring values seem to be more closely connected.

While G_0 was not strongly correlated with I_0, high cod and haddock VPA_3 were connected with a high G_0 (Table 2). First-order autoregressive models for VPA_3 with I_0 and L_0 or G_0 as independent variables explain on average about two-thirds of the total variability, even though the explanatory power of each variable varies (Table 3).

Ottersen *et al.* (1994) classified years as being warm or cold according to the annual mean temperature in the Kola section being above or below the long time mean. They used the resulting dichotomous time series to show the difference in cod recruitment between warm and cold
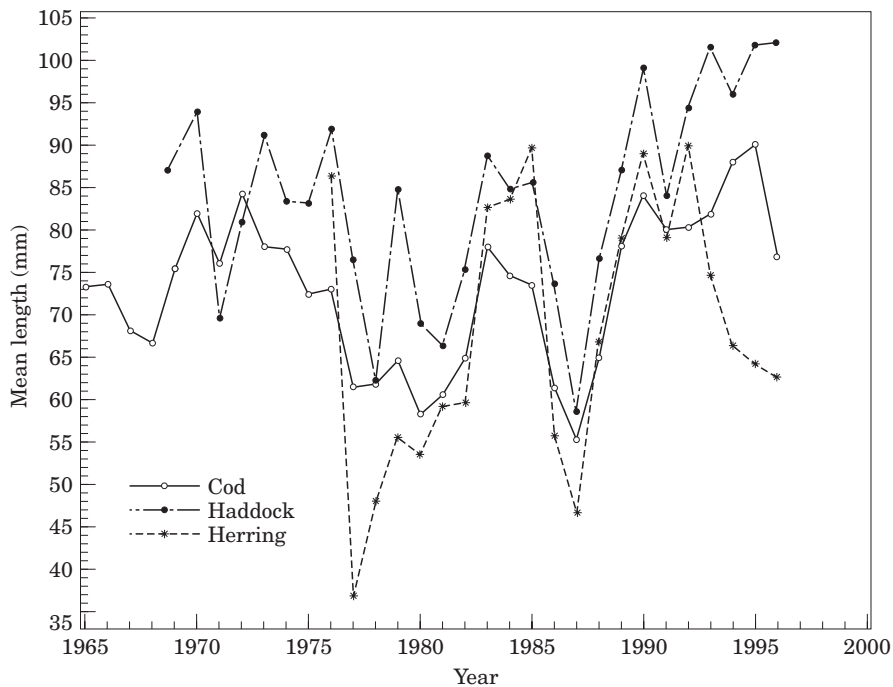
Figure 2. Mean length of 0-group cod, haddock, and herring in August–September, 1965–1996.

Table 1. Overall mean, standard deviation (s.d.), and median length at the 0-group stage (L_0).

Species	Mean L_0	s.d.	Median
Cod	73.0	9.0	74.1
Haddock	83.7	11.8	84.8
Herring	67.9	15.5	66.0

years. Using the same approach on L_0 and G_0 of cod, haddock, and herring, average lengths and growth increments in warm years were higher than in cold years for all three species (Table 4). Three independent tests show that the differences in length were all significant ($p<0.05$), while the differences in growth increments were only significant for herring. The standard deviations indicate that the variability in length is higher in cold than in warm years for all three species.

To investigate whether temperature variability may explain any of the covariation between length and abundance, Pearson partial correlations are calculated. The partial correlation coefficients between L_0 and $\ln(I_0)$ accounting for mean annual temperature in the Kola section were 0.29 for cod, 0.26 for haddock, and 0.63 for herring, while those between L_0 and $\ln(VPA_3)$ were 0.38, 0.26, and 0.12, respectively. These values are much lower than the Spearman and Pearson correlations (Table 2), only the two highest values being significant ($p<0.05$), even without taking autocorrelations into account. This

indicates that a large part of the covariability between size and abundance is mediated through temperature.

Discussion

The empirical results based on field data for Barents Sea cod, haddock, and herring generally support the established theory of a positive connection between growth and survival during early life stages for marine fish (Gulland, 1965; Cushing, 1974; Anderson, 1988; Meekan and Fortier, 1996). They also confirm the hypothesis of Houde (1989, 1990) that the larvae of species inhabiting a cold environment should be more exposed to environmental fluctuations than species that inhabit warmer waters as a consequence of longer development times.

Loeng *et al.* (1995) observed a relatively high degree of covariability between length of the three species at the 0-group stage. The extended time series still give an overall picture of synchrony in length variability (Figs 2, 3), although there are periods with marked divergences, notably during the last half of the 1970s and from 1991 onwards. In the absence of any explanation in environmental data, these discrepancies are more likely related to peculiarities in the population dynamics of the different species. The great variability in herring length (Table 1, Fig. 2) may be connected with the small stock size throughout most of the period. However, the recent sharp decrease in herring size might be explained by a
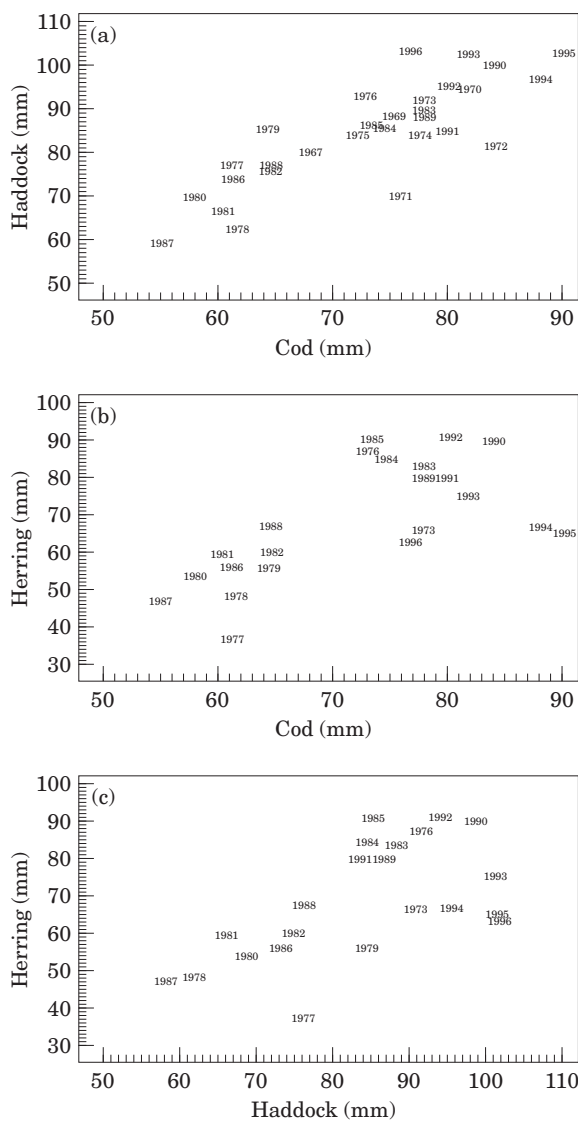
Figure 3. Relationship between mean length of 0-group of the different species: (a) haddock *vs* cod; (b) herring *vs* cod; (c) herring *vs* haddock.
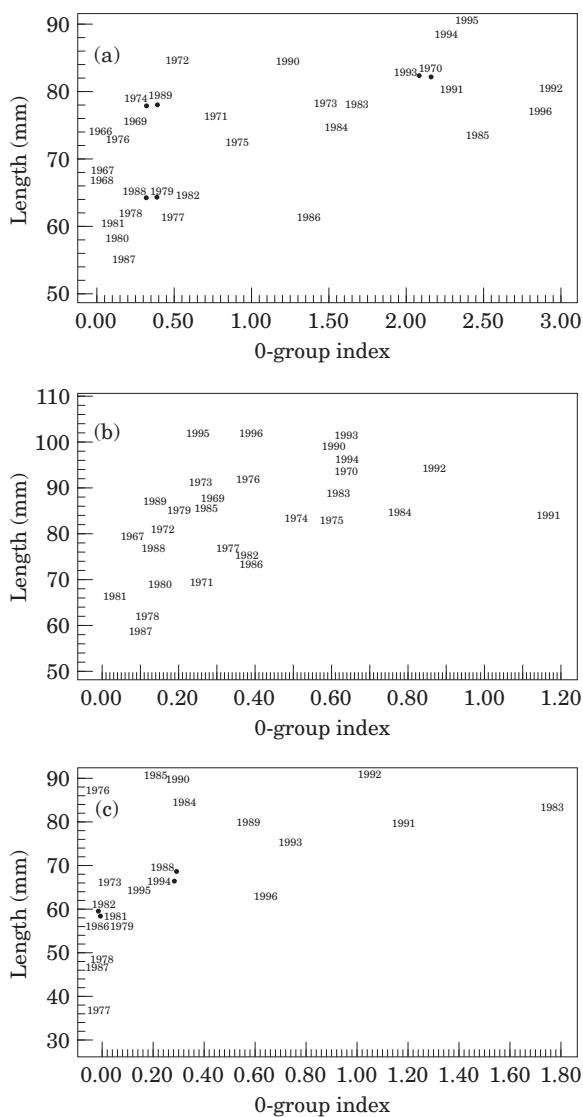
Figure 4. Relationship between mean length and abundance of 0-group: (a) cod; (b) haddock; (c) herring. Values are indicated by dots when otherwise difficult to distinguish between years.

Table 2. Spearman rank (r_s) and Pearson product-moment correlations (r_p) between length as 0-group (L_0), daily growth increments from the early juvenile to the 0-group stage (G_0), and log-transformed recruitment indices for 0-group (I_0) and 3-year-old fish (VPA_3; n: number of observations; n_e: effective number of observations, adjusted for order 1 and 2 autocorrelations).

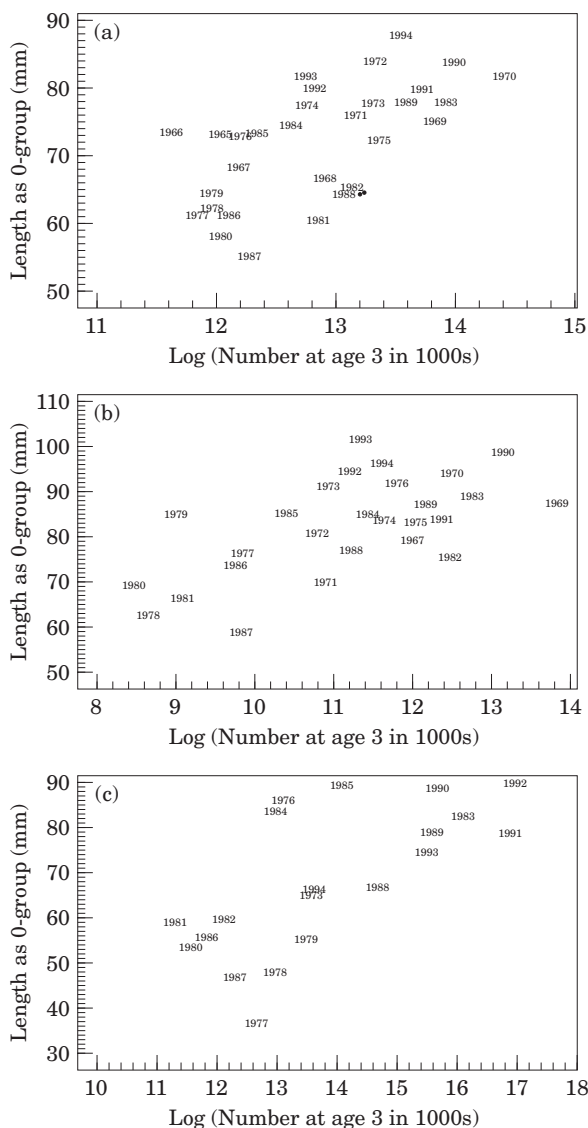| Species		$\ln(I_0)$					$\ln(VPA_3)$				
		r_s	r_p	n	n_e	p	r_s	r_p	n	n_e	p
Cod	L_0	0.62	0.55	31	17	<0.01	0.65	0.63	29	14	<0.05
	G_0	0.43	0.43	15	10	>0.1	0.71	0.65	15	9	<0.05
Haddock	L_0	0.56	0.60	29	21	<0.01	0.57	0.63	29	18	<0.05
	G_0	0.44	0.45	15	14	>0.1	0.62	0.62	15	13	<0.05
Herring	L_0	0.62	0.78	16	10	<0.1	0.72	0.68	20	13	<0.01
	G_0	0.28	0.59	9	6	>0.1	0.54	0.54	14	10	>0.1

Figure 5. Relationship between mean length of 0-group and log-transformed number at age 3 from VPA: (a) cod; (b) haddock; (c) herring. Values are indicated by dots when otherwise difficult to distinguish between years.
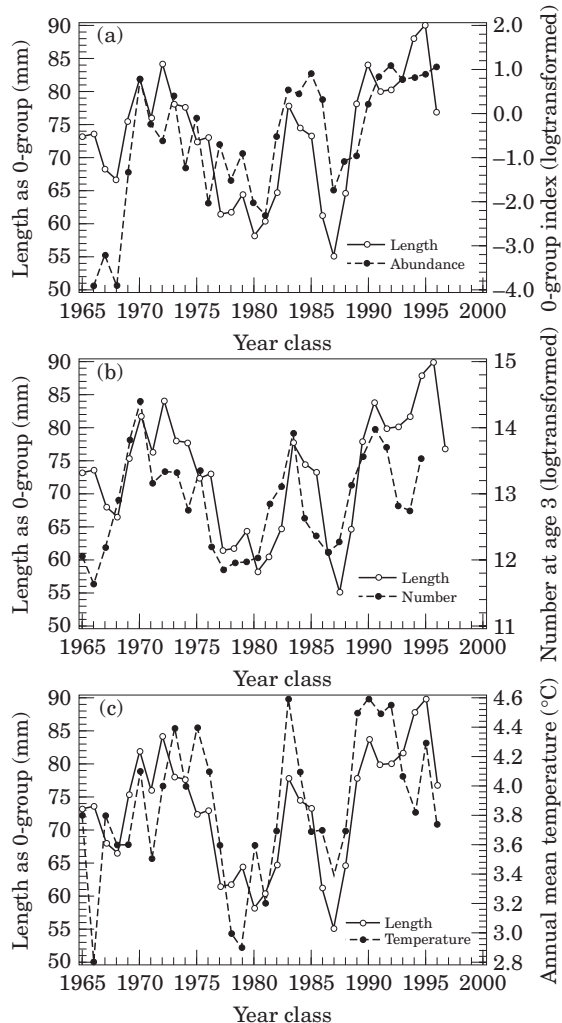

Figure 6. Temporal development in length of 0-group cod in comparison with (a) cod abundance of 0-group, (b) recruitment at age 3, and (c) annual mean temperature in the Kola section.

reduction in food availability. Hassel *et al.* (1996) showed a reduction in Barents Sea plankton biomass from 1994 to 1996 by almost 50%. This does not, however, explain the small size of the herring 0-group in 1994.

Figures 4 and 5 indicate that a relatively large length as 0-group is a necessary but not a sufficient condition for a high abundance of 0-group or successful recruitment at age 3. This is parallel to the finding by Ellertsen *et al.* (1987) of high temperature being a necessary but not a sufficient condition for the production of good year classes of cod.

It might be argued that the covariation between 0-group indices and mean lengths is biased owing to the information being based on the same material. Assuming that there actually is an underlying connection, temporal changes in sampling procedures, timing and geographical coverage could influence the values in a similar manner, artificially strengthening the correlations. It is therefore reassuring that the connection between mean length and recruitment according to VPA is equally strong, as is also the relation between growth during the early juvenile to 0-group phase and recruitment (Table 2). Estimates from the early juvenile and 0-group cruises and VPA must be regarded as independent.

Despite the positive relation between 0-group abundance and recruitment of cod and haddock at

Table 3. Results of autoregressive modelling, where $\ln(VPA_3)$ is the dependent variable and the first-order autoregressive parameter (AR1), $\ln(I_0)$, and L_0 or G_0 are the explanatory variables (B: parameter of the explanatory variables; p corresponding significance level; R^2_{tot}: percentage variance explained by the full model; R^2_{reg}: percentage explained by $\ln(I_0)$ and L_0 or G_0).

	AR1		$\ln(I_0)$		L_0			
Species	B	p	B	p	B	p	R^2_{tot}	R^2_{reg}
Cod	0.55	0.01	0.18	0.06	0.04	0.04	0.60	0.39
Haddock	0.69	0.00	0.46	0.08	0.04	0.06	0.65	0.37
Herring	0.39	0.29	0.79	0.02	0.01	0.87	0.75	0.65
					G_0			
Cod	0.58	0.14	0.15	0.53	1.27	0.34	0.55	0.17
Haddock	0.71	0.02	0.59	0.07	1.59	0.09	0.75	0.52
Herring	0.31	0.64	0.92	0.05	− 0.63	0.82	0.70	0.66

Table 4. Statistics for length at the 0-group stage (L_0) and daily growth increments from early juvenile to 0-group stages (G_0) within warm and cold years (n: number of years; s.d. standard deviation; p_{stud}, p_{med}, p_{wil}: probability levels for Student's t test, median, and Wilcoxon tests).

		Warm years			Cold years					
Species	Variable	n	Mean	s.d.	n	Mean	s.d.	p_{stud}	p_{med}	p_{wil}
Cod	L_0	16	79.2	4.5	16	66.9	8.2	0.00	0.00	0.00
Haddock	L_0	16	89.8	9.0	13	76.3	10.7	0.00	0.03	0.00
Herring	L_0	11	77.9	9.9	11	57.9	13.7	0.00	0.04	0.00
Cod	G_0	5	0.9	0.1	10	0.7	0.1	0.05	0.08	0.03
Haddock	G_0	5	1.2	0.3	10	0.9	0.2	0.12	0.08	0.10
Herring	G_0	5	0.8	0.1	9	0.5	0.2	0.02	0.01	0.03

age 3, the correlations are so low that the predictive value of the 0-group indices to estimate abundance at a later stage is limited. The finding of a closer connection between 0-group length and recruitment is important, because inclusion of both L_0 and I_0 in the regression should enhance the precision of the predictions. Although the determination coefficients are reasonably large (Table 3), the confidence limits of these regressions must be evaluated more thoroughly before they can be applied effectively.

Mean length and daily growth increments from early juvenile to 0-group were distinctly larger in warm than in cold years (Table 4) for the three species. The detailed information for cod (Fig. 6) shows clearly that length follows the same pattern of variability as sea temperature, in accordance with Nakken (1994). The similarity in variability patterns among the stocks and also with temperature strengthens the conclusion of others (Dragesund, 1971; Sætersdal and Loeng, 1987; Loeng et al., 1995; Ottersen, 1996) that they are strongly and similarly influenced by large-scale environmental processes. These oceanographic and atmospheric processes supposedly act on the fish through regulating the heat interchange between the Barents Sea and surrounding
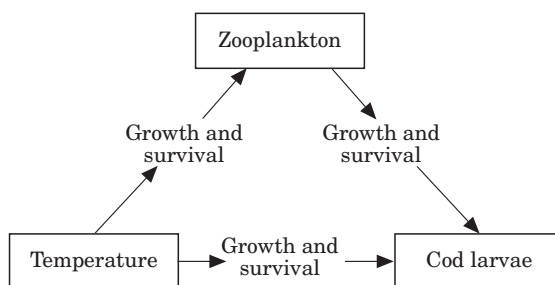

Figure 7. Mechanisms linking temperature to growth and survival.

areas, particularly through regulating the volume flux and thus the heat transport of Atlantic water masses entering the Barents Sea.

Temperature influences growth and survival at the early life stages in two ways (Fig. 7): it affects the development rate of the fish larvae directly, but also indirectly through regulating the production of prey. Nesterova (1990) showed that zooplankton biomass in the Norwegian and Barents Seas is generally larger when temperature is high. High food availability for larval

and juvenile fish results in higher growth rates and greater survival through the vulnerable stages when year-class strength is determined. Temperature also affects the development rate of the fish larvae directly and, consequently, the duration of the high-mortality and vulnerable stages decreases with higher temperature (Ottersen and Sundby, 1995).

Loeng and Gjøsæter (1990), studying relations between temperature conditions and growth of 0-group fish in the Barents Sea, stated that temperature effects linked to the availability of food might be as important as direct temperature effects. Rey et al. (1987) reported that climatic variations have a pronounced impact on the development in time of the Barents Sea spring bloom, the primary production accessible for zooplankton being larger in warmer years. Ellertsen et al. (1989), investigating the influence of temperature on the feeding conditions for cod larvae, concluded that the temperature-dependent spawning of the copepod *Calanus finmarchicus* may be the most important process causing variability in cod larval survival. The largest early juveniles of Arcto-Norwegian cod are as a rule found in the western part of the distribution area where the larvae experience the highest temperatures. The higher growth rate in this region is probably caused by a combination of higher temperature and higher food concentrations (Suthers and Sundby, 1993), because higher temperatures not accompanied by sufficiently high food abundance may have detrimental effects on larval survival (Sundby, 1994).

Given the multiplicative nature of factors affecting growth and survival, it is biologically reasonable to consider the interactions on a log-linear scale (Stenseth et al., 1996; Forchhammer et al., 1998). Logarithmic transformation of fish recruitment series has further been argued for by pointing to the frequency distribution of such series being approximately lognormal (Hennemuth et al., 1980; Thompsen and Page, 1989). Log-transforming a time series may in addition be useful for purely methodical reasons, because it tends to make the variance constant (Chatfield, 1989; SAS Institute, 1992).

Annual averages integrated along the Kola section and vertically from 0 to 200 m were chosen for sea temperature. The values obtained may not seem to be representative for the ambient temperature conditions of the larvae as they drift northwards in the upper 60 m from the spawning grounds along the Norwegian coast and into the Barents Sea. However, Ottersen et al. (1994) compared six different temperature series from the region, including spatially integrated data from the 0-group cruises as well as the Kola series. Some of the series were highly correlated, but the Kola series was the one found to explain most of the variability in log-transformed 0-group abundance indices of both cod and haddock. Ottersen and Sundby (1995) point to

variation in sea temperature in the Barents sea being a large-scale phenomenon, while Loeng et al. (1995) observed that results based on 0–60 m mean temperatures from June and the 0-group survey to be similar to those from the North Cape-Bear Island section in August. Even if the temperature from the Kola section is not the most representative for the water masses, which the larvae have experienced, this time series has been shown to reflect the relative large-scale interannual variations very well.

The assumption of a linear relation between larval length and age (Loeng et al., 1995) used to calculate the growth increments may seem to be a crude simplification. Simple linear regression of length on age is, however, not uncommon in growth prediction models for larval gadoids (e.g. Anderson, 1982; Yin and Blaxter, 1986). Campana and Hurley (1989) noted that the degree of sophistication of predictive growth models is inversely related to the level of the experimenter's control. They pointed to complex models not easily being parameterized in field situations like ours.

The temperature-growth-survival links observed for populations close to the northern edge of the distribution range of the species are not necessarily present in populations in other environments. Pepin (1991) concluded in a comprehensive review that variations in temperature do not appear to have any significant net effect on early life history survival. Although temperature had a significant influence on almost all the estimated daily development and mortality rates, the effects at different stages tended to cancel each other out. Campana (1996) studied larval and juvenile year-class strength and growth rate of Georges Bank cod. Temperature was a significant, but not necessarily a primary, source of within-year and between-year variations in growth. Suthers et al. (1989), on examining spatial variability in cod growth during the early stages off southwest Nova Scotia, concluded that the growth index was significantly lower in the nearshore habitat than offshore. Biomass of zooplankton >308 m was the principal factor accounting for regional growth differences, while no conclusive link with sea surface temperature was found. The connection between ambient temperature and mean length of North Icelandic cod also seems to be weak (Astthorsson et al., 1994), because no significant differences were observed between cold and warm hydrographic regimes.

We conclude that the synchrony found in year-class strength and early growth of three Barents Sea populations is a result of a mutual response to temperature fluctuations. This further leads us to hypothesize more generally that for stocks at the high latitude end of the overall range of the species the environmental signal tends to over-ride density-dependent effects on growth.

Acknowledgements

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