

Do abiotic mechanisms determine interannual variability in length-at-age of juvenile Arcto-Norwegian cod?

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Abstract: For the large Arcto-Norwegian stock of cod (*Gadus morhua* L.) in the Barents Sea, year-to-year variability in growth is well documented. Here three hypotheses for the observed inverse relation between abundance and the mean length-at-age of juveniles (ages 1–4) are suggested and evaluated. Based on comprehensive data, we conclude that year-to-year differences in length-at-age are mainly determined by density-independent mechanisms during the pelagic first half year of the fishes' life. Enhanced inflow from the southwest leads to an abundant cohort at the 0-group stage being distributed farther east into colder water masses, causing lower postsettlement growth rates. We can not reject density-dependent growth effects related to variability in food rations, but our data do not suggest this to be the main mechanism. Another hypothesis suggests that lower growth rates during periods of high abundance are a result of density-dependent mechanisms causing the geographic range of juveniles to extend eastwards into colder water masses. This is rejected mainly because year-to-year differences in mean length are established by age 2, which is too early for movements over large distances.

Résumé : La variabilité inter-annuelle de la croissance chez l'important stock arcto-norvégien de Morues franches (*Gadus morhua* L.) de la mer de Barents est bien connue. On trouvera ici la proposition et l'évaluation de trois hypothèses pour expliquer la relation inverse observée chez les juvéniles (âges 1–4) entre la densité et la longueur moyenne à un âge donné. L'étude de données détaillées nous ont amenés à conclure que les différences inter-annuelles des longueurs à un âge donné sont déterminées principalement par des mécanismes indépendants de la densité durant la première demi-année pélagique de vie des poissons. Des influx accrus du sud-ouest entraînent le déplacement à l'âge 0 d'une cohorte importante vers l'est dans des masses d'eau plus froide, ce qui diminue les taux de croissance après l'établissement au fond. Il ne nous est pas possible de nier les effets dépendants de la densité de la variabilité des quantités de nourriture sur la croissance, mais nos données nous laissent croire que ce n'est pas là le mécanisme principal. Une autre hypothèse veut que les taux réduits de croissance durant les périodes de haute densité soient le résultat de mécanismes reliés à la densité qui amènent les juvéniles à étendre leur aire géographique vers les masses d'eau plus froide vers l'est. Cette hypothèse n'est pas retenue, car les différences inter-annuelles des longueurs moyennes sont déjà en place dès l'âge 2, âge trop précoce pour permettre des déplacements sur de grandes distances.

[Traduit par la Rédaction]

Introduction

Controlled experimental evidence has established that growth of fish is often inversely related to stock density. A change in the population size of a predator is assumed to affect intraspecific competition for food and thereby consumption and growth. An inverse relationship between growth and stock abundance is therefore indicative of density-dependent growth. Density-dependent growth in fish populations has been reported since early in the 20th century and further evi-

dence has accumulated as stocks have become overexploited (e.g., Raitt 1939; Marshall and Frank 1999). However, other studies have found no significant correlation between growth and stock abundance (e.g., Daan 1974). It should also be noted that even when such a correlation is observed in field data it could be caused by a third variable, e.g., temperature acting on both stock abundance and growth (Jørgensen 1992).

Individual growth in fish depends on density-dependent factors, such as the availability of prey. However, growth is also the integration of a series of processes (feeding, assimilation, metabolism, transformation, and excretion), the rates of which are all controlled by temperature (Michalsen et al. 1998). Brander (1995) examined 17 North Atlantic cod stocks and found that most of the variability in growth among stocks could be attributed to variation in temperature.

The Arcto-Norwegian (or Northeast Arctic) cod spawn in March–May in patchy areas off northern and mid-Norway, with spawning mainly taking place in the Lofoten region (Fig. 1). Spawning occurs at the same sites each year, but spawning depth varies considerably, following the thermocline between the cold water of the Norwegian coastal current and

Received 20 March 2001. Accepted 22 October 2001.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 14 January 2002.
J16271

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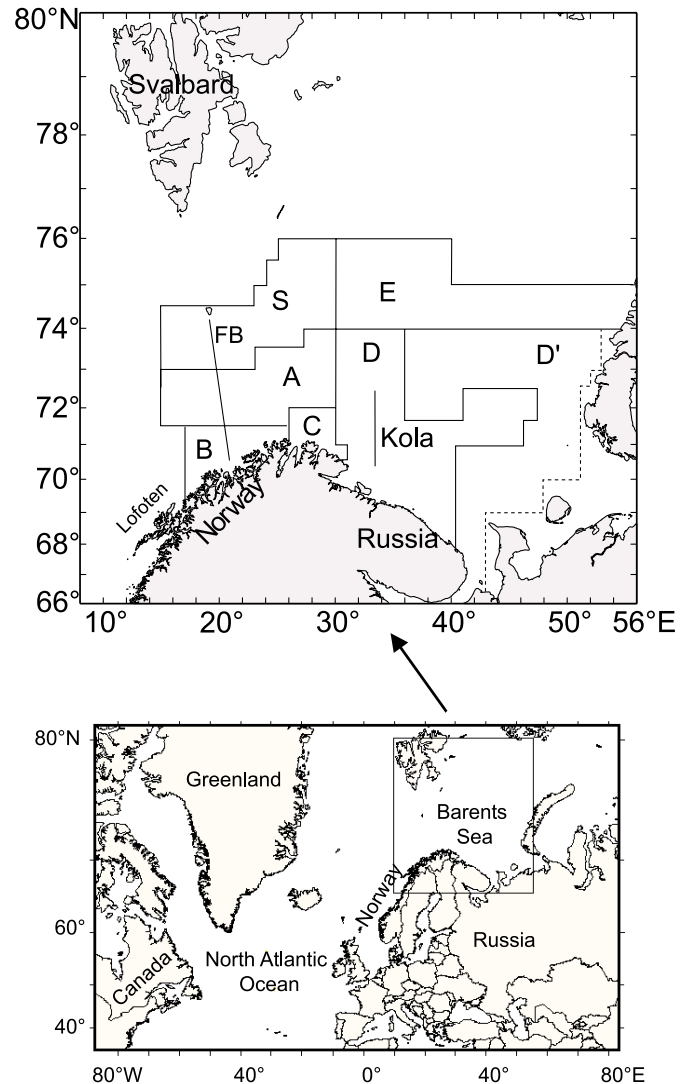
the warmer Atlantic water. Eggs and larvae are carried by the currents to the north and east into the southern Barents Sea and south and west of Svalbard (Fig. 1), 600–1200 km from their spawning ground. The spatial distribution of pelagic juveniles has substantial interannual variation. In some years, a typical westerly distribution occurs, whereas in others, an easterly distribution is observed. They settle to the bottom when they are about 5 months old. The immature cod feed at the bottom and in the midwater layers and make seasonal east–west and north–south migrations. The ranges of these migrations increase with age, and at an age of 3–4 years, when capelin (*Mallotus villosus*) become a major food item, cod follow the spawning migration of capelin to the coasts of northern Norway and Murman (Nakken 1994).

Year-to-year variability in the growth of Arcto-Norwegian cod has been observed over a long period (Nakken 1994; Michalsen et al. 1998). Several authors have suggested that this variability in growth is density dependent (e.g., Rollefson 1953; Nilssen et al. 1994). On the other hand, Jørgensen (1992) found an apparent absence of density-dependent growth because no significant relationship between length increments and stock size could be established. Nakken and Raknes (1987) noted a negative correlation between abundance and mean length of cod but concluded that density-dependent growth was unlikely. At the 0-group stage (5 months old), a positive relationship between abundance and mean length, which may be explained as size-dependent survival, was shown by Ottersen and Loeng (2000).

A number of earlier authors have observed larger mean lengths-at-age for Arcto-Norwegian cod in warmer years than in colder years and have proposed a positive connection between temperature and growth (Demytyeva and Mankevich 1965; Nakken and Raknes 1987; Michalsen et al. 1998). In the Barents Sea, the water temperature decreases from west to east. This east–west gradient is a general feature regardless of interannual variability. Year-classes with an easterly distribution will consequently experience lower ambient temperatures than those with a more westerly pattern. Ottersen et al. (1998) suggest a range expansion towards the east during periods of high density, apparently independent of the temperature conditions. Thus, high abundance leads to low ambient temperatures, which should cause reduced growth rates (Helle et al. 2000).

Temperature variability in the Barents Sea is, to a large degree, caused by fluctuations in the inflow of warm Atlantic water masses from the southwest (Ådlandsvik and Loeng 1991). A year with enhanced inflow of Atlantic water masses provides the 0-group cod with a relatively warm and prey rich environment (Helle and Pennington 1999) and carries them farther east in the Barents Sea (Ottersen et al. 1998). It is well documented that years with positive temperature anomalies tend to produce cohorts of high abundance, both as 0-group and as age-3 recruits (Sætersdal and Loeng 1987; Ottersen and Sundby 1995). Thus the distribution of cohorts with high abundance at the 0-group stage is extended farther into the colder eastern parts of the Barents Sea (Helle et al. 2000). Several Russian studies (e.g., Maslov 1960) have shown that 1-year-old cod remain close to where they settled. Thus an easterly 0-group distribution would lead to an easterly distribution of the age-1 group, which could influence the distribution of the year-class at older

Fig. 1. The Barents Sea with subareas framed. For analysis by subarea, we only use A, B, C, and D covered each year throughout the full period 1983–2000. The Fugløya – Bear Island section, where the inflow has been estimated (FB), and the Kola section, where temperatures have been measured (Kola), are shown. The general location of the region is displayed in the lower map.



ages. Furthermore, one would expect lower growth rates for these year-classes, leading to reduced juvenile length-at-age, on average.

Here we examine the possible connections, described above, between abundance and mean length-at-age of immature Arcto-Norwegian cod. To summarise, the following three hypotheses are investigated. (H1) Year-to-year differences in length-at-age of demersal, immature Arcto-Norwegian cod are determined by population size, high abundance leading to reduced growth (density-dependent growth). (H2) Year-to-year differences in mean length-at-age of demersal, immature Arcto-Norwegian cod are determined by abundance influencing growth through altering geographical distribution patterns. Lower growth rates during periods of high abundance are a result of density-dependent mechanisms causing the geographic range of the population to extend eastwards into colder water masses, causing a de-

crease in the mean ambient temperature. (H3) Year-to-year differences in mean length-at-age of demersal, immature Arcto-Norwegian cod are determined by abiotic, density-independent mechanisms during the pelagic stages. Enhanced inflow of warm, prey-rich Atlantic water masses from the southwest leads to an abundant cohort as 0-group that is distributed farther east into colder water masses, which causes lower average postsettlement growth rates.

Material and methods

The data on length and abundance (ages 1–4) of Arcto-Norwegian cod are from the Institute of Marine Research bottom trawl surveys conducted in the Barents Sea each January–March since 1981 (abundance data for 1981 are considered unreliable and not used). For a detailed description of the survey and its history, see Jakobsen et al. (1997).

A Campelen 1800 shrimp trawl with mesh size of 80-mm in front was used until 1993, with a codend of 35- to 40-mm stretched mesh size. Because this mesh can cause considerable size selection of 1-year-old cod, the mesh size was reduced to 22 mm in 1994. The survey indices have not been corrected for this change.

The surveys followed a stratified random design until 1990 and a stratified systematic design from 1991 onwards. Until 1992, the area covered by the survey was limited to the ABCD region (Fig. 1). The number of trawl stations varied, but the entire ABCD area was always reasonably well covered. We have used established area definitions, where the subareas are based on the observed fish distribution, the important fishing grounds, and the statistical areas for recording commercial catches. The estimates of mean length and swept area estimates of abundance for the whole Barents Sea are taken from ICES (2001), with slight adjustments for age 3 and for 1981–1982, which are based on recent recalculations.

We examine data on length and abundance by age for the entire Barents Sea and for each of the subareas A, B, C, and D (numerical values available from the authors). Because area-specific data are scanty for the younger age classes in 1981 and 1982, the analysis is based on 1983 and onwards. Abundance and mean length estimates by area are in the annual survey reports, but those estimates differ somewhat from the recalculated values (consistent with the values for the entire area) given here. Typical values of the standard deviation of length-at-age for the total area are 2 cm for age 1, 3 cm for age 2, and 4 cm for ages 3 and 4. The estimation procedure for age-based abundance indices and mean lengths-at-age is given in Appendix A.

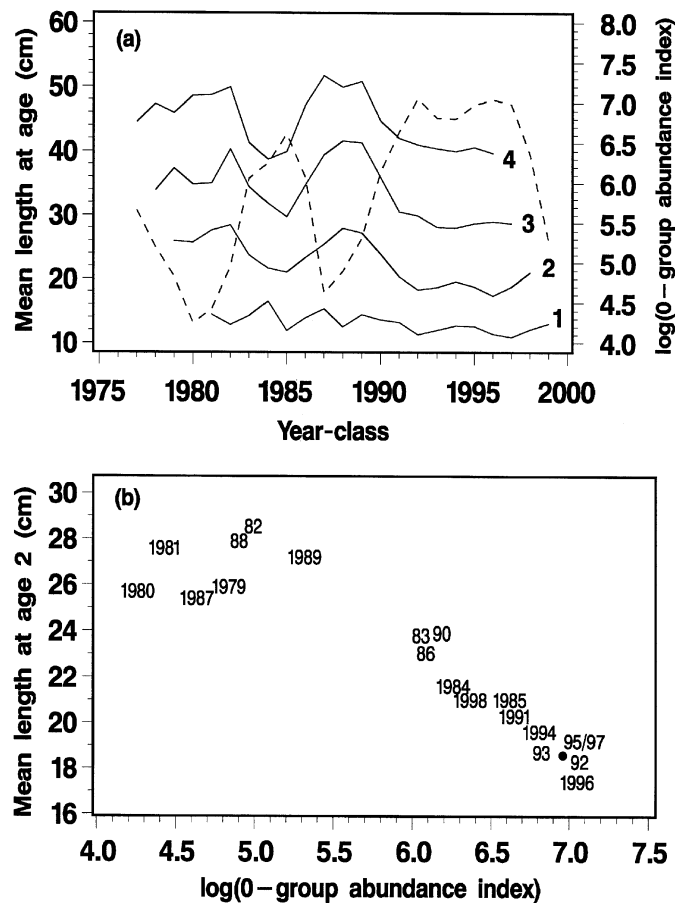
The time series was revised to account for several changes in methodology (Jakobsen et al. 1997). However, no correction has been made for the introduction of an inner net in 1994. This mainly affects the abundance and mean length estimates of age-1 fish, whose abundance index before 1994 will be underestimated and mean length before 1994 will be overestimated. For this reason, the results for ages 2 and 3 are more reliable than those for age 1. Furthermore, the mean length-at-age estimates for 1988 and earlier years are slight overestimates, which is due to a change from bobbins to rock-hopper gear in 1989 being accounted for in the calculation of abundance-at-age but not in the calculation of

Table 1. Correlations between abundance at ages 0–4 (logarithmically transformed) and mean length at ages 1–4 for the 1978–2000 year-classes of Arcto-Norwegian cod.

Abundance-at-age	Length-at-age			
	1	2	3	4
0-group	-0.54*	-0.93***	-0.81***	-0.87***
1	-0.57**	-0.71**	-0.64**	-0.71**
2		-0.62**	-0.50**	-0.73**
3			-0.51*	-0.68**
4				-0.41

Note: The 1978 year-class was age 4 in 1982, the first year with reliable abundance estimates. Significance levels: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.

Fig. 2. (a) Temporal development of length (in cm) for ages 1 to 4 (solid lines) and abundance as 0-group (natural logarithmic transform of the index corrected for trend by Nakken and Raknes (1996), broken line) of Arcto-Norwegian cod year-classes from 1977 to 1999 (but note that year-classes covered necessarily varies with age). (b) Scatter plot showing abundance as 0-group (log-transformed) versus mean length at age 2 for Arcto-Norwegian cod year-classes 1979–1998. When it is difficult to distinguish between different years, only the last two digits are shown in the graph; when the values for 2 years coincide, a dot is used.



mean length-at-age. See Jakobsen et al. (1997) for a more thorough description and references.

To examine interannual fluctuations within each of the

subareas A, B, C, and D relative to the entire region, we defined relative abundance for a specific age group and year as the number within a particular area divided by the total number of this age group within ABCD. This allows for examination of possible shifts in abundance among areas and their relationship to overall abundance. A direct comparison between abundance within the whole of ABCD and that within each area would be misleading because most of the fish studied are typically found in area D. Thus fluctuations in area D would dominate the total variability.

In addition to bottom trawling, the winter survey also acoustically measures fish density and records temperature (conductivity–temperature–depth (CTD)/Rosette) profiles. We use the centre of mass of the spatial distribution (in degrees longitude) by age based on the acoustic measurements for the years 1988–1995 as a supplementary measure of horizontal location (Ottersen et al. 1998).

Ambient (fish-density weighted) winter temperature means for each age group for the years 1985–1999 were calculated from bottom temperatures and the swept area data described above. To extend our time series backwards, we also use ambient winter temperatures for the years 1978–1984 from Nakken and Raknes (1987), although these were based on acoustic densities. However, Ottersen et al. (1998) compared the variation of cod density in space and time from swept area and acoustic density estimates and concluded that the main developments were similar.

Abundance indices for pelagic 0-group cod have been worked out from material gathered during the International Barents Sea 0-group surveys, which are conducted in late August to early September. The 1974–1999 indices of abundance used in this paper were adjusted to take into account trends in catchability (Nakken and Raknes 1996), with post-1995 values taken from ICES (2001). Estimates for the years 1989–1996 of ambient temperature for 0-group cod are from Stensholt and Nakken (1998).

Estimates of monthly atmospherically driven water flux through the Fugløya–Bear Island section (FB, Fig. 1) for the period 1970–1999 are based on a numerical hydrodynamic model (Ådlandsvik and Loeng 1991; Loeng et al. 1992; B. Ådlandsvik, Institute of Marine Research (IMR), Bergen, Norway, personal communication). We used winter (January–April) means (F_{FB}) in this paper. Density-driven (baroclinic) currents are not included in the model; hence these flux measurements only reflect the variability in atmospheric forcing (barotropic component). The mean F_{FB} for the period studied is small compared with estimates of total transport, but the variability in total inflow is mainly due to year-to-year differences in barotropic conditions, as reflected in F_{FB} (Ottersen and Stenseth 2001).

Observations of the sea temperature in the Kola meridian transect (33°30'E, 70°30'N to 72°30'N), which intersects the Murman Current in the south central Barents Sea (Fig. 1), are considered good indicators of thermal conditions in the entire Barents Sea region.

Monthly means have been calculated by averaging along the transect and vertically from water depths of 0 to 200 m. We used 1975–1999 winter (December previous year – February) means, T_{Kola} , with the pre-1995 data taken from Bochkov (1982) and Tereshchenko (1996), whereas PINRO, Murmansk, provided the 1995–1999 values.

Table 2. Correlations between abundance (logarithmically transformed) and centre of mass of winter distribution (in east–west direction, degrees longitude) in 1988–1995 for Arcto-Norwegian cod at ages 0–3.

Abundance-at-age	Centre of mass of distribution at age		
	1	2	3
0-group	0.66	0.79*	0.41
1	0.43	0.77**	0.50
2		0.91**	0.63
3			0.79*
4			

Note: Significance levels: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$. No correlations involving age 4 were statistically significant.

Standard Pearson product-moment correlations were used to study linear covariation. However, correlation analysis depends on assumptions that are rarely met by time series data. In our case, as often occurs in biology, we have short, positively autocorrelated time series. This violates the assumption of statistical independence of the points in the time series used in estimating standard significance levels. As a result, the significance levels calculated by standard statistics packages are inflated compared with the true significance level. To deal with this, we estimated the effective number of independent observations (N_e), adjusted for order 1 and order 2 autocorrelations, using the formula of Quenouille (1952): $N_e = N/(1 + 2r_{a1}r_{b1} + 2r_{a2}r_{b2})$. Here N is the number of data points common to the two series, r_{a1} and r_{b1} are the lag-one autocorrelations, and r_{a2} and r_{b2} the lag-two autocorrelations for the time series a and b .

Results

Mean lengths of Arcto-Norwegian cod at ages 1–4 are negatively correlated with the total abundance of the cohort at the same and earlier ages (Table 1, Fig. 2). For the years 1988–1995, the abundance of a cohort and centre of mass of the spatial distribution at ages 1–4 are positively correlated; high abundance at age a is linked to an easterly displacement at age a and at age $a + 1$ (Table 2). Fish in area A were on average 1.2 cm longer than in area D at age 2, 2.5 cm longer at age 3, and 1.7 cm longer at age 4. The east–west differences in length were not significantly correlated (at the 5% level) with abundance of the age group within ABCD.

The observed size-at-age is generally lower in the period 1994–2000 (when an inner net was used) than in the earlier years. To determine whether this is due to a smaller mean size-at-age or to possible differences introduced by the gear change, we compared the size-at-age from the Russian bottom trawl survey in autumn (data given in ICES (2001)) with the Norwegian data for the periods 1985–1993 and 1994–2000. The results of this comparison are shown in Table 3. The size-at-age is larger in the first period in both surveys, confirming that the difference was not an artifact introduced by changes in Norwegian survey methodology.

The correlations between the relative abundance of age-2 cod in each subarea and in ABCD are given in Table 4. The temporal development of abundance of age-2 fish in ABCD is compared with the fractions in A and D (Fig. 3). The relative abundance in area A fluctuates out of phase with the

Table 3. Mean length-at-age (cm) for the periods 1985–1993 and 1994–2000 for the Norwegian (Nor) and Russian (Rus) surveys.

Period	Age 1		Age 2		Age 3		Age 4	
	Nor	Rus	Nor	Rus	Nor	Rus	Nor	Rus
1985–1993	13.3	13.7	23.8	21.3	36.4	29.8	46.4	41.2
1994–2000	12.1	11.3	18.9	19.2	29.0	28.0	41.2	36.8

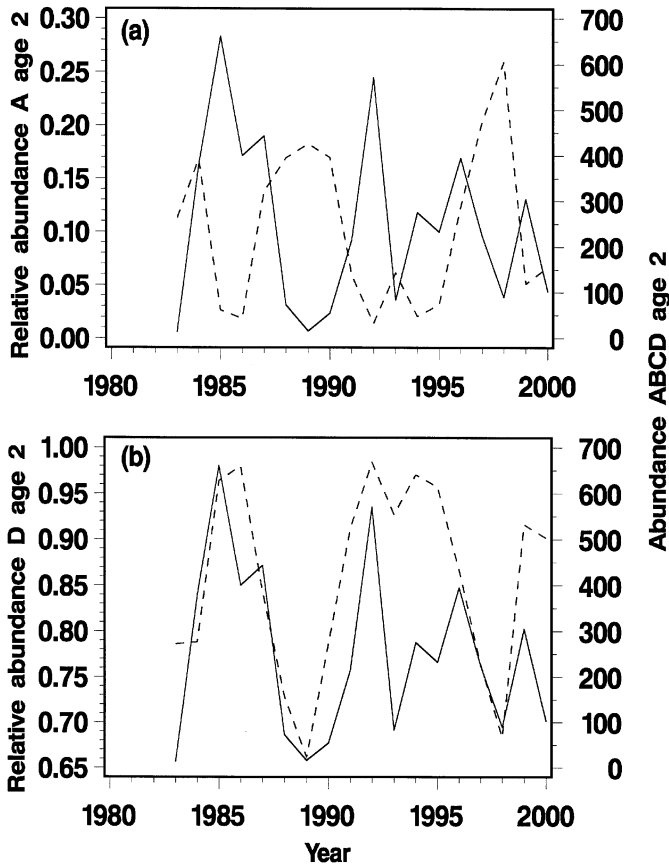
Note: Russian surveys, which are conducted in late autumn, are shifted 1 year and 1 age for comparative purposes. Age 1 in 1988 and 1990 are omitted from the calculation because there are no Russian data available.

Table 4. Correlations between abundance of Arcto-Norwegian cod at age 2 in the ABCD region (logarithmically transformed) and relative abundances in the subareas as well as between the subareas for the years 1983–2000.

	Abundance in ABCD	Fraction in B	Fraction in C	Fraction in D
Fraction in A	−0.45*	0.50**	0.56**	−0.95***
Fraction in B	−0.73***		0.71***	−0.70***
Fraction in C	−0.79***			−0.79***
Fraction in D	0.65***			

Note: Significance levels: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.

Fig. 3. Temporal development in 1983–2000 of abundance of age-2 Arcto-Norwegian cod in the ABCD area (numbers in millions, solid line) compared with relative abundance (fraction) in (a) area A and (b) area D, broken lines.



overall abundance, which is in synchrony with the fraction in area D.

T_{Kola} has fluctuated more or less in accordance with F_{FB} during the study period (Fig. 4). F_{FB} in the winter preceding spawning is positively correlated with cod abundance at the

0-group stage and with an easterly distribution. Furthermore, enhanced winter inflow preceding spawning is negatively correlated with ambient temperatures and length-at-age for ages 1–4 (Table 5; Fig. 5).

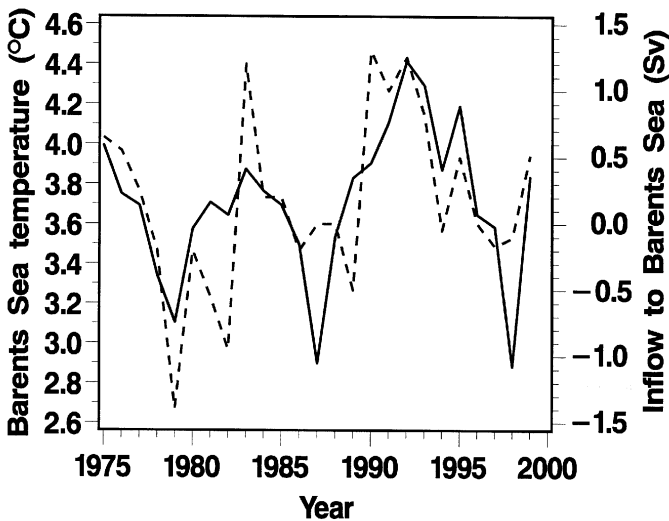
Discussion

This study demonstrates that the mean length of 1- to 4-year-old Arcto-Norwegian cod tends to be small when the abundance of the same cohort and (or) neighbouring cohorts is high. Three hypotheses are put forth, each giving an alternative explanation to the observed pattern. The main focus of the discussion is to disentangle the evidence available from our own and earlier studies and to draw a conclusion regarding the validity of the suggested mechanisms.

Nilssen et al. (1994) analysed weight-related specific growth rates and abundance-at-age data for Arcto-Norwegian cod during the period 1951–1991. They found a negative correlation and concluded that density-dependent growth was clearly demonstrated. On the other hand, Jørgensen (1992), based on data for nearly the same period (1953–1989), was not able to detect density-dependent growth for ages 1 through 8. Nakken and Raknes (1987) noted a negative relationship between abundance and mean length of 4- to 6-year-old cod for the period 1978–1984. However, because of the stock size in this period amounting to only a minor fraction of the long-term average, they found it hard to accept that density-dependent growth occurred in those years. The main difference between the study of Nilssen et al. (1994) and the other two is that the former studied weight rather than length. We use length-at-age data because weight data for 1981–1984 and 1987 are missing from our time series, and the older weight data are generally considered less reliable than the data on length.

Density-dependent growth is typically assumed to be related to high stock abundance leading to a reduction in individual growth rates (H1) as a consequence of reduced food rations. Therefore, data on prey abundance should be taken into account in a discussion of density-dependent growth. The main prey species of age-1 cod are krill, amphipods,

Fig. 4. Winter inflow to the Barents Sea from the southwest (solid line, modelled atmospherically driven water volume flux through the Fugløya – Bear Island section) and Barents Sea winter temperature (broken line, 0- to 200-m depth mean values from the Kola meridian transect) in 1974–1999.



and capelin; capelin increases in importance with increasing predator age (Bogstad and Mehl 1997). The abundance of capelin has varied greatly during the period of this study (Gjøsæter 1997) as has the abundance of zooplankton, such as amphipods and krill (Dalpadado et al. 2002). A more detailed study involving the abundance of zooplankton in the sea as well as in cod stomachs is needed to determine whether growth of 1-year-old cod is density dependent.

Our data show clear negative correlations between abundance and length-at-age. However, neither this nor earlier studies give us sufficient evidence to conclude that density dependence (H1) is the dominant mechanism regulating the growth of Barents Sea cod.

This led us to pursue the idea that abundance affects growth through altering geographical distribution patterns and ambient temperatures of 1- to 4-year-old fish (H2). Myers and Stokes (1989) identified three ways in which the geographical distribution of a fish population may change in response to changes in overall population size: (i) a proportional increase throughout its range; (ii) a range extension in which the population increases relatively more in marginal habitats; or (iii) a relatively greater increase in the prime habitat, i.e., increased population density leads to higher concentrations. A fourth possible response is a shift in the region of greatest density.

Positive correlations between abundance and easterly centre of mass of spatial distribution indicates that at high abundances the juvenile cod either extend their distribution farther east or the region of greatest density is shifted eastwards. This is further supported by the total abundance in ABCD being positively correlated with the fraction of age-2 cod in the easterly area D, while being negatively correlated with the fractions in A, B, and C. The relative abundance seems to fluctuate in phase in these three areas and out of phase with area D.

In principle, slight movements could result in significant differences in the number of fish in one area versus another

Table 5. Correlations between atmospherically driven winter inflow to the southwestern Barents Sea (F_{FB}) and sea temperature (T_{Kola}), abundance of 0-group cod ($N_{0\text{-group}}$), geographical distribution (east–west displacement, Lon_i), ambient temperatures (T_i), and average length-at-age ($Length_i$), respectively, all for age groups 1–4.

	<i>r</i>	<i>n</i>
T_{Kola}	0.63***	26
$N_{0\text{-group}}$	0.43*	26
Lon_1	0.57	8
Lon_2	0.84*	8
Lon_3	0.75	8
Lon_4	0.38	8
T_0	-0.50	8
T_1	-0.57**	22
T_2	-0.47*	23
T_3	-0.56**	23
T_4	-0.74***	23
$Length_1$	-0.21	19
$Length_2$	-0.41	20
$Length_3$	-0.53**	20
$Length_4$	-0.60**	20

Note: The time series are for winter except 0-group data which are autumn. All correlations are for inflow in the year spawned. Data from 1974 (first year-class with any data on juvenile fish) or whenever available. Significance levels: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.

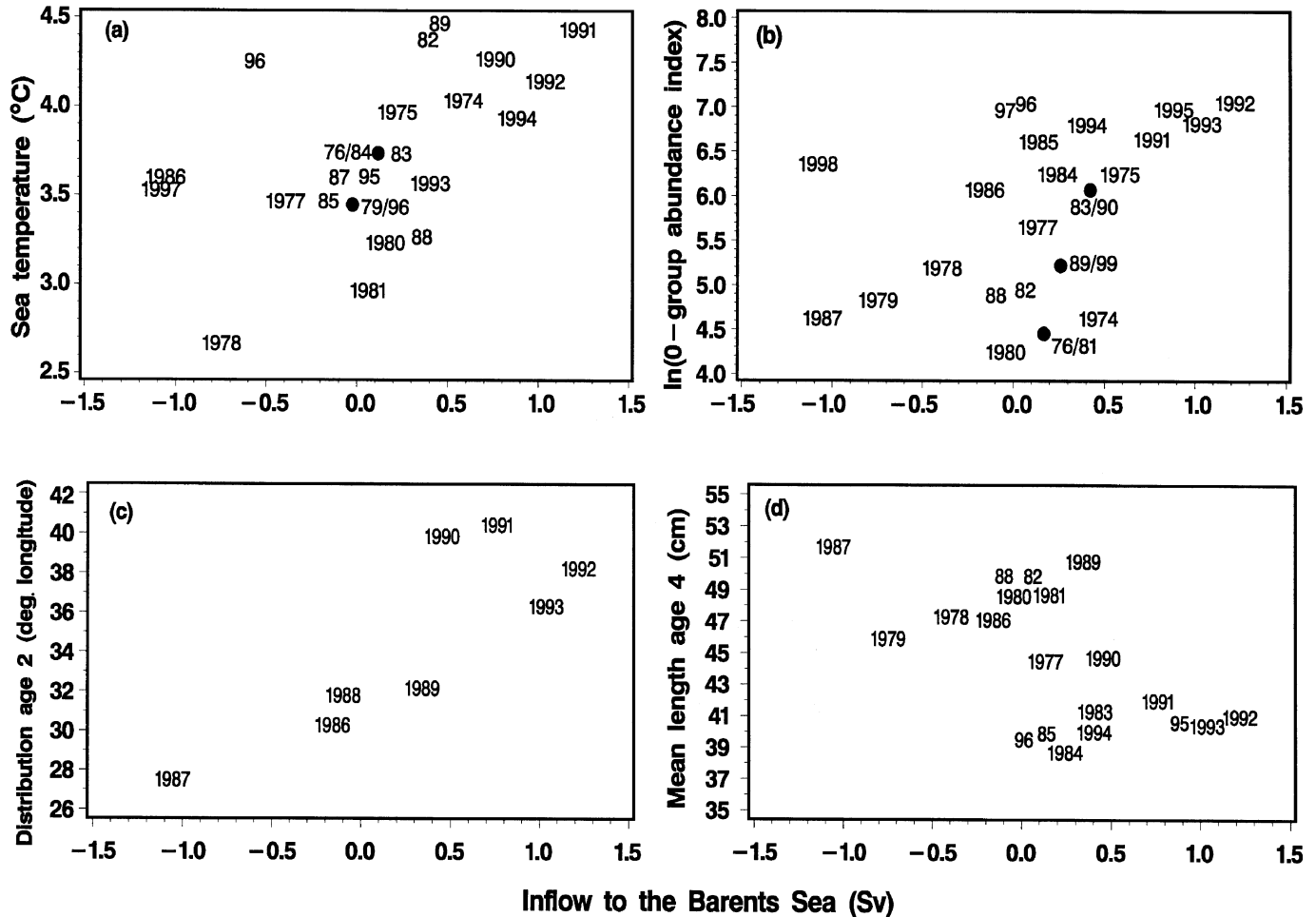
if there are many fish distributed in the vicinity of the border between two areas. However, although the fish are not evenly distributed, there is no evidence for such an effect being important. Interannual differences in the centre of mass of spatial distribution are pronounced, particularly for ages 1–3, and the shifts are far larger than those that would be caused by fish simply crossing a border. Furthermore, distribution maps of cod density during the winter surveys give no indication of higher than average concentrations along the borders between areas (maps for 1990 and 1994 given in Ottersen et al. (1998), other unpublished maps available from the authors).

Bioenergetic considerations suggest that temperature selection by fish should be density dependent. When rations are limited, the temperature yielding the highest growth rate decreases as ration size decreases (Elliott 1975). Therefore, if fish select the habitat that maximises their growth rate, preferred temperatures should decrease as food supply decreases (Elliott 1975; Swain and Kramer 1995). If food is a limiting factor, then the proportion of the population occupying habitats of lower temperature should increase with population size (Swain and Kramer 1995).

Because a more easterly distribution in the Barents Sea implies lower ambient temperatures (Ottersen et al. 1998), the observed spatial shifts could be taken as field support for the above argument. That is, a density-dependent decrease in food availability for individual fish should result in increased preference for habitats with lower density-independent costs, in this case lower temperatures.

The mechanisms suggested above imply that fish actively move in response to variation in population density. Al-

Fig. 5. Winter inflow to the Barents Sea from the southwest (modelled atmospherically driven water volume flux through the Fugløya – Bear Island section) plotted against (a) Barents Sea (Kola section) temperature, (b) abundance of Arcto-Norwegian cod as 0-group (natural logarithmic transform of the index corrected for trend by Nakken and Raknes 1996), (c) centre of distribution of cod age 2 (degrees longitude), and (d) mean length of cod age 4. Note that in (c) and (d), year-class, not year, is shown so that all variables are related to inflow in the winter preceding spawning. Data from 1974 (first year-class with any data on juvenile fish, i.e., ambient temperature at age 4) or whenever available. When it is difficult to distinguish between different years, only the last two digits are shown in the graph; when the values for 2 years coincide, a dot is used.



though our results (and those of Kristiansen et al. 2001) indicate easterly shifts in periods of high abundance, we are not able to rule out other causes for the apparent movement. Spatial variation in natural mortality, e.g., cannibalism, may shift the centre of mass without any active habitat selection being involved (Bogstad et al. 1994). The variability in the mortality rates of Arcto-Norwegian cod of ages 0–3 caused by cannibalism is large, as indicated by ICES (2001).

The fact that undermines much of the foundation for H2 is, however, that year-to-year differences in length seem to be established by age 2 (as demonstrated also by Jørgensen (1992) and Michalsen et al. (1998)). The large spatial movements necessary by these young cod if H2 is true seriously questions the validity of this hypothesis. This is especially the case as age-1 cod tend to remain in the area where they settled during autumn as 0-group (Maslov 1960) and seasonal migrations by 2-year-old cod seem to be small (Ottersen et al. 1998).

We therefore considered mechanisms occurring during the first 1–2 years of life that may affect year-to-year differences

in length-at-age. It is natural to look to the environment to find sources for variability established at an early age (see Introduction). Thus, seemingly density-dependent growth may be caused by density-independent environmental effects during the early life stages, which determine the distribution patterns and indirectly, growth, as proposed in H3.

The following shows how our new results, supported by earlier authors, give evidence in support of H3. The fact that F_{FB} and T_{Kola} fluctuate in synchrony indicates that enhanced inflow of Atlantic water masses from the southwest is related to generally higher Barents Sea temperatures as earlier suggested by Ådlandsvik and Loeng (1991). We have shown that there is a positive correlation between inflow and the abundance of 0-group cod, a similar relationship between sea temperature and year-class strength at the 0-group stage has been described earlier by Ottersen and Sundby (1995) and others. The positive correlation between F_{FB} and easterly centre of mass at ages 1–4, and the negative correlation with ambient temperature at ages 0–4, shows that cod are distributed farther into the colder water masses of the eastern

Barents Sea during years with high inflow. Finally, F_{FB} is negatively correlated with lengths-at-age, indicating that the above mechanisms lead to lower postsettlement growth rates. We conclude that this chain of events, summarised in H3, gives the most consistent explanation of our observations.

Acknowledgements

This work has been financially supported by the Norwegian Research Council (NFR; Project no. 130197/130) and by the EU project "Developing structurally testable models of marine populations" (QLK5-CT1999-01609). The work was done within the framework of the international GLOBEC (GLOBAL ocean ECosystems dynamics) program. We thank C. Tara Marshall, Kathrine Michalsen, Michael Pennington, Nils Chr. Stenseth, and Doug Swain for good discussions and helpful comments on the manuscript. We further thank Bjørn Ådlandsvik (IMR, Bergen, Norway) for kindly providing the modelled flux values and PINRO (Murmansk, Russia) for generously giving us the temperature data from the Kola section. We also thank two anonymous referees for their constructive comments to an earlier version of the manuscript.

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Appendix A

Length-based abundance indices by area are estimated as follows. For each trawl station and 1-cm length group, a point observation of fish density is calculated as

$$\rho_{s,i} = \frac{f_{s,i}}{a_{s,i}}$$

where $\rho_{s,i}$ represents the density of fish of length i observed at station s , $f_{s,i}$ is the raised length frequency, and $a_{s,i}$ is the swept area ($d_s EW_i$, where d_s is the towed distance and EW_i is the length-dependent effective fishing width).

Point estimates of density at length are summed up to 5-cm length groups $\rho_{s,l}$, where l denotes 5-cm length groups. Stratified indices of abundance by length groups and strata $N_{p,l}$ are calculated as

$$N_{p,l} = \frac{A_p}{S_p} \sum_{s=1}^{S_p} \rho_{s,l}$$

where A_p is the area of stratum p (or the part covered by the survey) and S_p is the number of stations in stratum p (23 strata presently used).

Before 1984, a representative subsample of 100 fish per station was age determined at two stations per strata. From

1984, a stratified sample design was used, with samples of five fish per 5-cm length group at each station. In 1993–1995, two fish were sampled per 5-cm length group, and the number of stations sampled per stratum was increased from two to four. Before 1996, the strata structures used were different from the present 23-strata system. Since 1996, one fish is sampled per 5-cm length group at all predetermined bottom trawl stations with more than 10 specimens of cod in the catch. For each 5-cm length group, age–length keys are used to estimate the proportions at age. All age samples from the same stratum and length group are given equal weight:

$$w_{p,l} = \frac{N_{p,l}}{n_{p,l}}$$

where $n_{p,l}$ is the number of age samples in stratum p and length group l and the proportions of fish of various ages in a given length group are estimated by

$$P_a^{(l)} = \frac{\sum_p n_{p,a,l} w_{p,l}}{\sum_p n_{p,l} w_{p,l}}$$

where $P_a^{(l)}$ is the weighted proportion of age a in length group l and stratum p and $n_{p,a,l}$ is the number of age samples of age a in length group l and stratum p .

The numbers-at-age are then calculated as

$$N_a = \sum_p \sum_l N_{p,l} P_a^{(l)}$$

and the mean length-at-age is calculated as

$$L_a = \frac{\sum_p \sum_l \sum_j L_{a,p,l,j} w_{p,l}}{\sum_p \sum_l \sum_j w_{p,l}}$$

where $L_{a,p,l,j}$ is the mean length of sample j in length group l , stratum p , and age a .