Cod in fjords and coastal waters of North Norway: distribution and variation in length and maturity at age

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The distribution of cod along the Norwegian coast and in fjords from 62°N north to the Russian border was examined using data from annual trawl surveys carried out between 1995 and 2001. Based on differences in growth zones of the otoliths, cod are traditionally classified into two types: Northeast Arctic cod and coastal cod. Both types were found throughout the area investigated. The catch rate of both increased northwards and from offshore to inshore. In a statistical model of length at age, abiotic factors such as area and year of capture explained more of the variance than biotic factors such as sex, stage of maturity, and type of cod. Length at age increased in a southward direction and was higher for cod captured offshore than for those captured inshore. In a statistical model of the proportion mature at age, area, type, and year of capture explained more of the variance than sex and depth of capture. On average, coastal cod attained 50% maturity (M_{50}) more than a year younger than Northeast Arctic cod. Although there were relatively large differences in age at maturity between neighbouring areas, age at maturity was lowest in the south and inshore, and in general, lower inshore than offshore. As genetic analysis clearly indicates that cod in the study area consist of at least two genetically separated stocks, it is likely that the differences found here in age at M_{50} might have a genetic component.

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Introduction

In the North Atlantic, cod (*Gadus morhua*, L.) are commonly found in open oceans, over coastal banks, in open fjords, and in semi-enclosed bays at depths from 0 to 600 m. The Norwegian coast includes all these marine habitats, and in addition the coast spans a large part of the latitudinal distribution of the species. Thus, off Norway, cod are found within a range of different environmental conditions, which in turn may influence population parameters and, hence, the sustainable level of the commercial catch. In most regions where cod are found, they are targeted by the commercial fishing fleet. The species has therefore been a major focus for stock assessment, and in the North Atlantic, some 20 cod stocks are assessed and managed as separate units. To manage cod in the Northeast Arctic, quotas are set for three different stocks: Northeast Arctic cod, Norwegian coastal cod, and Murman cod.

Identification of the two types of cod found along the coast of North Norway, Northeast Arctic cod and Norwegian coastal cod, is based on differences in the structure of growth zones in the otoliths (Rollefsen, 1933). Otoliths have been successfully used to separate stocks of other species, such as king mackerel (DeVries *et al.*, 2002). Other methods used to identify the stock structure of cod in Norwegian coastal areas include differences in the number of vertebrae (Løken *et al.*, 1994; Noreide and Pettersen, 1998) and hemoglobin and genetic investigations (Møller, 1968, 1969; Mork *et al.*, 1984; Jørstad and Nævdal, 1989; Dahle and Jørstad, 1993; Fevolden and Pogson, 1995, 1997; Árnason and Pálsson, 1996; Noreide and Pettersen, 1998; Mork and Giæver, 1999). Most of these investigations found differences between Northeast Arctic cod and coastal cod, although some did not, and the results from Fevolden and Pogson (1997) indicate that coastal cod probably comprises of several more or less discrete stocks. This is also in accordance with the inferred stock structure of cod in the Northwest Atlantic (Smedbol and Stephenson, 2001; Smedbol and Wroblewski, 2002). However, it is difficult to draw firm conclusions on the basis of these investigations because neither methodology nor interpretation fully agree.

Still, the two types of cod do seem to differ with respect to life history. Northeast Arctic cod migrate over a long distance, from their feeding area in the Barents Sea to spawning areas that are mainly around Lofoten, and also migrate along the coast, north of approximately 62°N (Bergstad *et al.*, 1987). Tagging experiments on coastal cod, on the other hand, indicate only local migrations (Jakobsen, 1987; Godø, 1995; Nøstvik and Pedersen, 1999b; Skreslet *et al.*, 1999). The spawning grounds used by coastal cod are at numerous locations inside fjords and in the same coastal areas used by Northeast Arctic cod (Jakobsen, 1987). Coastal cod utilize the same spawning grounds repeatedly from year to year (Jakobsen, 1987).

Good management of cod within the heterogeneous environment of the Norwegian coastal zone relies on knowledge of spatial patterns in the biological parameters. Failure to account for possible isolation of stocks violates the precautionary principle of contemporary natural living resource management (Smedbol and Wroblewski, 2002).

This study investigates the distribution, abundance, length at age, and the age and size at sexual maturity of cod along the Norwegian coast between 62°N and the Russian border. Differences among geographical area, year, and type of cod are discussed. The results are also discussed by way of comparison with corresponding data from Northeast Arctic cod in the Barents Sea.

Material and methods

Sampling and type separation

The sampling area consists of numerous fjords and offshore banks between 62°N and the Russian border (Figure 1). The whole area was divided into three regions (northern, middle, and southern), and these regions were divided into 26 smaller areas. The 26 areas were stratified from distribution of the trawl stations, the density of cod, and the environmental heterogeneity (depth, fjord system). Fjords north of 68°N are mainly shallower than 300 m, while those farther south are generally deeper. The coastal banks outside the fjords range in depth from 50 to 400 m.

In general, the water temperature increases from north to south. Although there are large temperature differences between the fjords, fjords in general are cooler than the coast in winter and warmer than the coast in summer (Hegseth *et al.*, 1995).

Sampling of fish was carried out on annual combined trawl and acoustic surveys conducted in autumn of the years 1995–2001. The bottom trawls were not randomized because the seabed in fjords and over the shelf zones is generally too rough to permit trawling. Therefore, trawling was carried out whenever the seabed conditions allowed, and catches are considered reasonably representative of seabeds suitable for trawling. Each survey lasted for approximately 30 days, and on each survey, approximately 250 hauls were made. On average, half the hauls were

made with a pelagic trawl. The bottom-trawl hauls were conducted at more or less the same locations each year, whereas the pelagic-trawl hauls were conducted at different locations during each survey. The pelagic trawl was a 1600-mesh Harstad trawl with a 10 mm inner net in the codend. The bottom trawl was a 1800-mesh campelen shrimp trawl, also with a 10 mm inner net in the codend. For each haul, the round weight (g) and the total length (rounded down to the nearest centimetre) were recorded for all cod or for a random subsample. Sex and maturity were determined by visually inspecting the gonads, using a general maturity index (immature, maturing, running, spent). The spawning season for cod in the area peaks between mid-March and late April, but in some areas it may continue through to late June. All surveys were conducted in autumn between August and November. The periods of investigations were therefore midway between two spawning seasons, making it difficult to determine the stage of maturity. Although measures were taken to standardize the classification method, the precision of the maturity data is not known.

The sampled cod were separated into coastal cod and Northeast Arctic cod on the basis of the structure of the growth zones on the otoliths, as described by Rollefsen (1933). The otoliths were broken along their mid-axis, and read under refracted light, as described by Williams and Bedford (1974). Approximately 19 300 cod were aged, measured, and separated into type, i.e. coastal cod and Northeast Arctic cod. Coastal cod have a smaller and more circular first winter zone than Northeast Arctic cod. The shape of the first winter zone in Northeast Arctic cod otoliths is similar to the shape of the otolith and to the other winter zones. The distance between the first and the second winter zone is also larger in coastal cod otoliths. This pattern is established at an age of 2 years, and error in differentiating between the two types does not increase with age. The accuracy of this classification technique is difficult to estimate, partly because, as far as we know, no relevant investigations have been conducted, and partly because the true answer is unknown, because other methods do not agree fully about either method or interpretation of the result. However, the otolith method of separating the two types of cod is to some extent supported by other investigations, such as haemoglobin variation (Dahle and Jørstad, 1993), DNA (Fevolden and Pogson, 1995), and number of vertebrae (Løken *et al.*, 1994). In the stock assessments of Norwegian coastal cod and Northeast Arctic cod at ICES, the otolith method is used to separate both commercial catch and scientific survey data to type. In large-scale investigations, the method is convenient because it is possible to type numerous cod within a relatively short time.

Statistical analyses

Initially, generalized linear models (GLMs) of length at age were used to find appropriate expressions of the age effect.
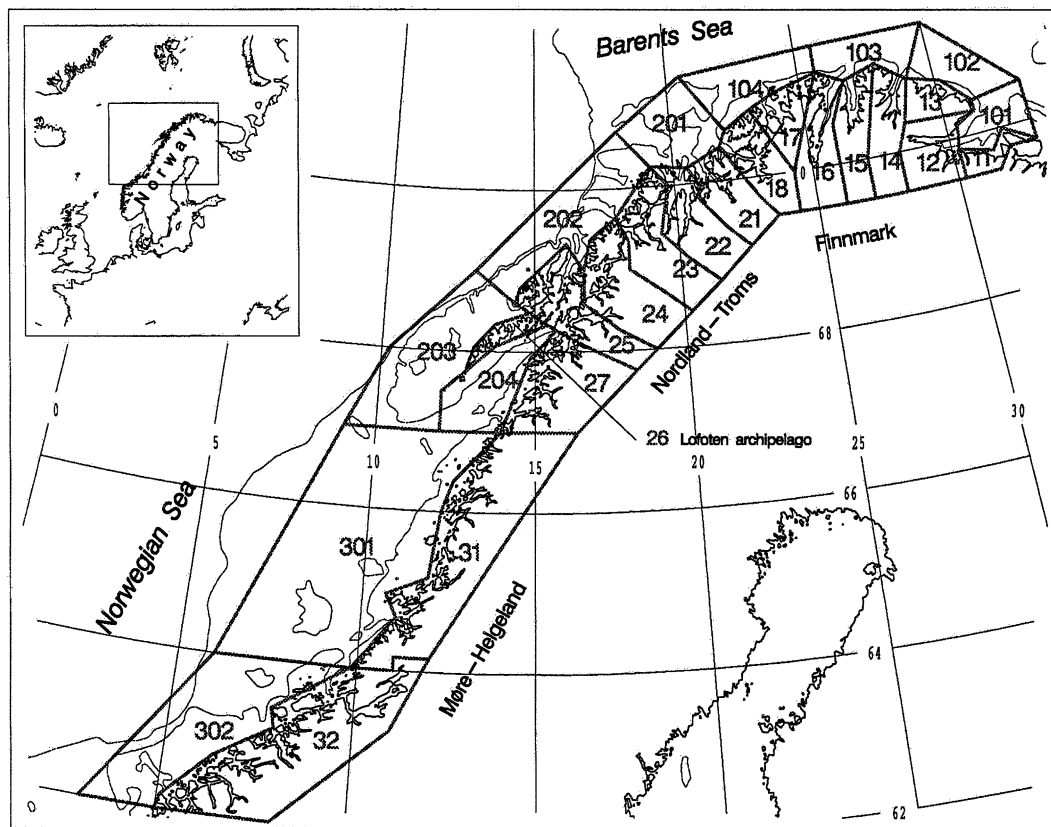
Figure 1. Map of the sampling area. The different areas correspond to areas used in the model for estimation of length at age and proportion mature at age.

Linear, polynomial, and other relationships were tried, but analyses of residuals showed trends with respect to age, indicating inappropriate model specification. Therefore, a relative measure of length at age was used to facilitate comparisons across age groups. Relative length at age (RL) was expressed as the length of each fish divided by the mean length of the respective age group. A relative length of 1 was therefore the same as the mean length of the same age group.

A GLM was applied to the RL data, and recommended procedures of model selection, model fitting, and checking of the available explanatory variables were followed (Aitken *et al.*, 1989; McCullagh and Nelder, 1989). The model selected as full (see below) described the data adequately in the sense that residuals showed constant variance and no trend with either fitted values or any explanatory variable. For comparison of the effects of areas, two variables were established to account for the main geographical variability. A two-level factor was used to separate offshore (areas 101–302 in Figure 1) from inshore areas (areas 11–32). In addition, the longshore distance from Stadt, far south in the survey area, was calculated for each haul.

A GLM with a logistic link function for the response probabilities was applied to data on maturity at age. For this model, the recommended procedures of model selection, model fitting, and checking of the available explanatory variables were those documented by Collett (1991). The model selected as the full model included those biologically relevant variables most likely to influence the probability of being mature. This model (see below) described the data adequately in the sense that the link function was valid, the form of the linear predictor was adequate, and the standardized deviance residuals revealed no unexpected features or patterns.

For both models, the formal procedure of model simplification by way of F-tests was complicated because the large number of degrees of freedom (some 20 000 and 16 000, respectively) made even very small and probably biologically insignificant effects statistically significant. Therefore, model terms that contributed the least to the explained variance ($<1\%$) were eliminated even if they were statistically significant. Reduced models were also checked for residual distribution and patterns. Further, individual factor levels were combined selectively to reduce the complexity of the models. The combination was

based both on the estimates and their standard errors, and on the logical relationship between the levels. Thus, areas with similar estimates (within 95% confidence limits) were combined only if they also were geographical neighbours.

Full model describing RL:

$$RL = \alpha + Type + Sex + Maturity + Area + Year$$
$$+ Depth + Type \times Year + Type \times Area$$
$$+ Maturity \times Sex + Maturity \times Area$$

Full model describing the probability of being mature:

$$p = \alpha + Age + Length + Area + Depth + Type$$
$$+ Sex + Year + Type \times Year + Type \times Area$$
$$+ Type \times Sex + Type \times Depth + Sex \times Year$$
$$+ Sex \times Area$$

In both models, α denotes the intercept, Type is a two-level factor for otolith type (Northeast Arctic or coastal cod), Sex and Maturity are two-level factors for sex and stage of maturity (immature or mature), Area is a factorial variable representing the areas shown in Figure 1, Year is a factor for year of capture, Depth is a covariate given in metres, and p is the linear predictor, where probability factor $= \exp(p)/(1 + \exp(p))$.

Results

Distribution of cod

Cod were found in all parts of the area surveyed, both offshore and well inside the fjords (Figure 2). However, >75% of the catches of cod by number were from the northern part of the area, 67°N and northwards (Figures 1 and 2). In the southern part surveyed, catch rates were generally low, except for a few locations far inside some fjords in shallow water (<150 m). Inshore areas had better catch rates than offshore ones, and likewise, shallow areas had better catch rates than deeper ones (Figure 3). The same pattern was found throughout the survey period. The catch rate decreased steadily from 1995 to 2001.

The length composition of both types of cod combined was bimodal inshore (Figure 4), but only the larger mode was found offshore. Cod between 35 and 70 cm long (3–6 years) were most numerous in the catches. Northeast Arctic cod were larger than coastal cod both inshore and offshore (Table 1), and both types of cod were larger offshore than inshore. Throughout the areas and the survey period, cod younger than 2 years or older than 10 years were rarely caught.

Approximately 15 000 (78%) of the cod were classified as coastal and 4300 (22%) as Northeast Arctic (Table 1). The catches from each area contained both types (Figure 5). The portion of coastal cod increased southwards and

was higher inshore than offshore. Offshore in the northeast (areas 101–103), the proportion of coastal cod was almost 50%, and in the south (areas 32 and 302), almost all cod were classified as coastal. The proportion of Northeast Arctic cod increased with size, few cod <40 cm being classified as Northeast Arctic in any area or year. This pattern was stable throughout the study period. However, the proportion of Northeast Arctic cod increased from about 15–20% in 1995 to about 30% in 2001, this observation being widespread across all areas.

Length at age

Mean length at age from age 4 was near linear (Figure 6). However, the length of individual cod varied extensively within a single age group, the range being almost the same magnitude as the mean length for an age group. Coastal cod had a slightly larger mean length at age than Northeast Arctic cod. However, because the percentage of cod classified as coastal varied between areas, interpretations must be based on the statistical model.

The full GLM model of RL included 68 parameter estimates and still explained only 19% of the variance in the data. By comparison, a similar model of length at age, including a linear age effect, explained 70% of the variance. However, age is a trivial explanation of length and the low R^2 of the RL model only reflects the high variability inherent in length-at-age data. This variability is largely independent of the spatial, temporal, and biological variables normally included in a fish survey program.

The reduced model of RL included 25 parameter estimates, retaining 17% of the total variance (89% of the variance explained in the full model). Most of the explained variance was due to the geographical component and year of sampling, whereas biological variables were of minor importance (Table 2). Mature females were on average larger than mature males and coastal cod were somewhat larger than Northeast Arctic cod of the same age.

The parameter estimates for the four combined offshore areas (areas 101–302) clearly indicate a trend of decreasing RL from south to northeast in the survey area (Table 2). There appears to be a clear linear reduction ($R^2 = 0.80$, $p \ll 0.01$) in RL offshore along the coast from Stadt to East Finnmark (Figure 7). Inshore, RL was more variable, with only a weak linear trend along the coast ($R^2 = 0.39$, $p \ll 0.01$). Further, RL was significantly lower inshore than offshore, and the difference decreased in a northward direction. Average RL was 15% higher offshore in the south than offshore in the north, and 20% higher than inshore in the north. Most (76%) of the variance explained by the 25-parameter area-based model could be explained by a 12-parameter model replacing the area effect, with a two-level factor for inshore–offshore (representing areas 11–32 and 101–302, respectively), and a covariable representing longshore distance from Stadt.
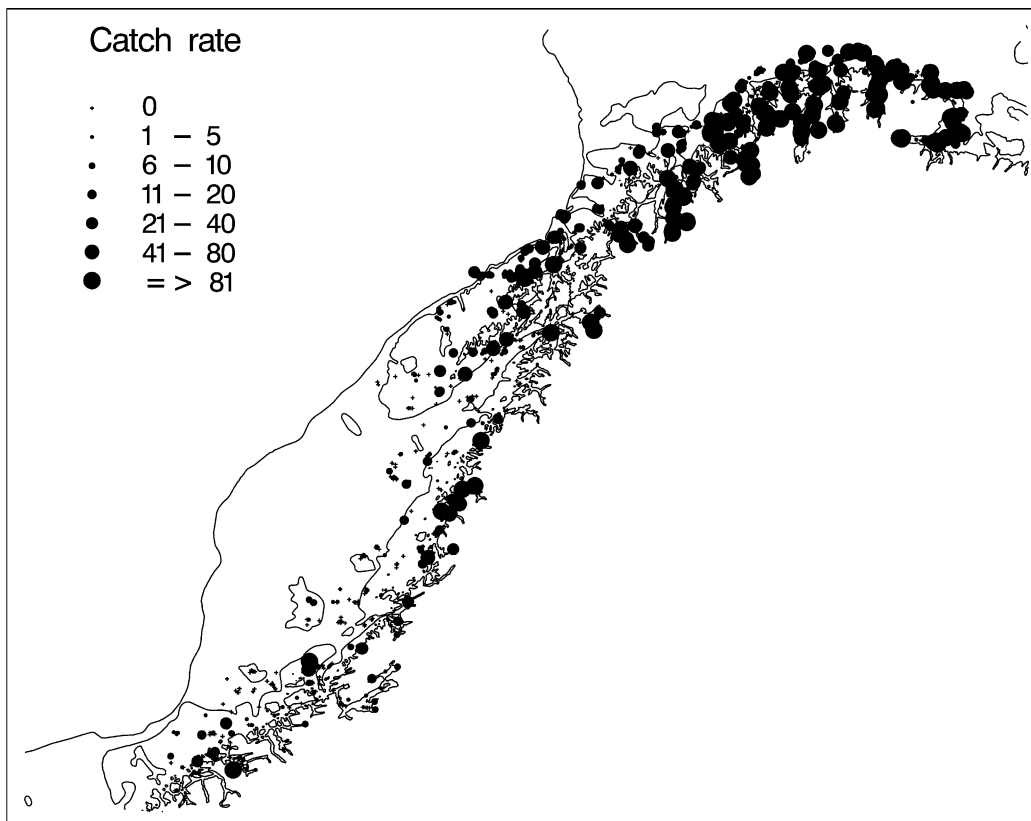
Figure 2. Mean catch rate of cod (number per nautical mile) stratified by region (data from all surveys combined, 1995–2001).

The year of catch was the variable that explained the secondmost variance in RL. The parameter estimate indicates a continuous increase in RL after 1997 (Table 2).

Maturity at age

Some male cod were already mature at an age of 2 years, and at an age of 10 years almost all cod were mature. A
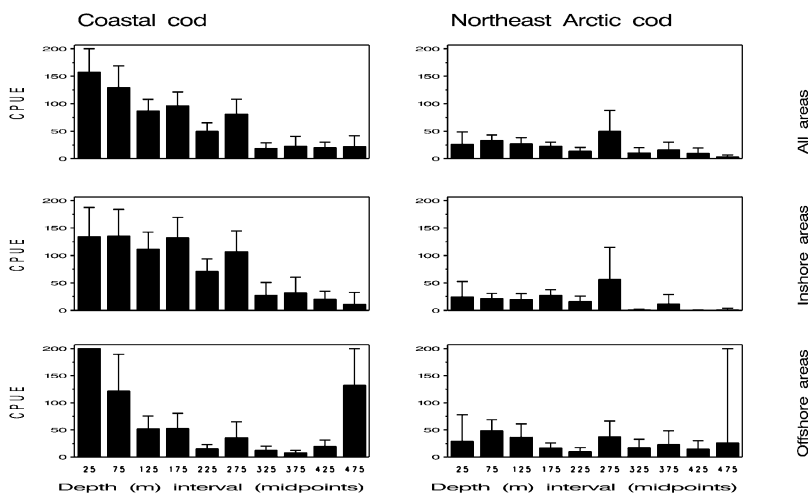

Figure 3. Mean cpue (kg per hour trawling) of cod by type, catch area, and catch depth interval (data from all surveys combined, 1995–2001).
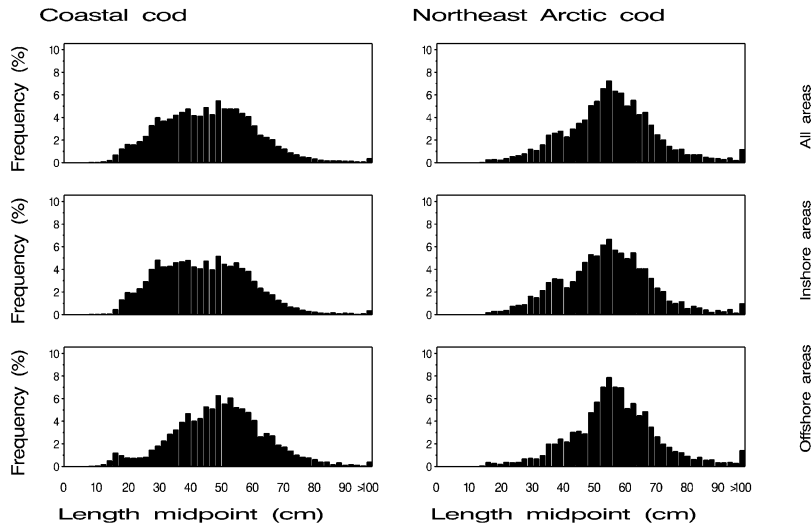
Figure 4. Length distribution of the two types of cod by area (data from all surveys combined, 1995–2001).

GLM model was applied to the data for examination of possible differences between geographic area, type of cod, sex, depth, and year of capture. The full GLM model of the probability of being mature included 70 parameter estimates and explained approximately 57% of the variance in the data. The reduced model included 27 parameter estimates, retaining 55% of the total variance in the data (Table 3). Most of the remaining 45% of variation in the data can probably be explained by natural individual variation. All parameters in the reduced model were statistically significant (p < 0.05). Not surprisingly, age and length were the two parameters explaining most variance in the probability of being mature. Of the balance of explained variance, the parameters area of catch and year of catch contributed most, followed by type of cod. Sex and depth of catch were the two parameters that explained the least variance in the model.

In general, the parameter estimates for the four outer areas combined (areas 101–302) indicated increasing age at M_{50} from south to northeast (Table 3). The parameter estimate for area 202 is, however, much lower than the estimates for all other areas. For the 14 inshore areas (areas 12–32), the variation between neighbouring areas was rather high, and there was no obvious north–south trend.

The very low parameter estimate in area 24 (−1.45) was due to low numbers (s.e. = 0.97). However, as for the outer areas, M_{50} was lowest in the south (area 32; Table 3, Figure 8). Although the age at maturity differed extensively between neighbouring areas, cod caught inshore (areas 12–32) matured younger than cod caught offshore (areas 101–302; Figure 8). The average M_{50} for coastal and Northeast Arctic cod was 5.7 and 6.9 years, respectively. The geographical difference was much larger for coastal than for Northeast Arctic cod. The fitted values from the model for Northeast Arctic cod in the south (areas 32 and 302) are rather uncertain as a result of the low numbers (Table 3, Figure 8). The difference in age at maturity between the two types of cod was notable throughout the area surveyed, and it increased in a southward direction (almost 3 years in area 32). The year effect indicated a lower age at M_{50} in the period 1995–1997 than subsequently (Table 3).

Discussion

All surveys were conducted in autumn (September–November), at least 1–2 months before the spawning migration of Northeast Arctic cod towards the Norwegian coast starts (Bergstad *et al.*, 1987). The observed distribution pattern of the two types of cod would therefore have been quite different if the surveys had been conducted during the first quarter of the year. However, the differences in length at age and age at maturity would most likely have been the same because the growth rate and the age at maturity observed for Northeast Arctic cod is the same as observed in the Barents Sea (ICES, 2002).

Between 62 and 67°N, both inshore and offshore, the abundance of cod was much lower than farther north. This may partly be related to the bathymetry in the different regions, because cod density was greatest shallower than

Table 1. Average length and number of cod aged and typed from inshore and offshore areas, 1995–2001 combined.

	Inshore		Offshore	
Type of cod	Average length (cm)	Number	Average length (cm)	Number
Coastal cod	44.9	10 187	50.0	4794
Northeast Arctic cod	55.3	2260	58.4	2059

Figure 5. Proportion of coastal (black) and Northeast Arctic cod (white) caught in different areas (data from all surveys combined, 1995–2001).

300 m in all areas. The fjords in the south are generally deeper than 300 m, while those in the north tend to be shallower than 300 m, and therefore more suitable for cod.

The bathymetry of the southern coastal banks (depth 100–500 m) is also different from that of banks farther north. In the south, some 75% of the banks are deeper than 300 m, and cod (and haddock *Melanogrammus aeglifinus*) abundance at all depths was much lower than in the north. There has never been large-scale fishing activity for cod and haddock on these southern banks, where catches are dominated by blue whiting (*Micromesistius poutassou*), greater silver smelt (*Argentina silus*), Norway pout (*Trisopterus esmarkii*), and Norway redfish (*Sebastes viviparus*). Other pelagic and demersal fish species preferred as prey by cod (Bergstad *et al.*, 1987) are seldom found in the south.

Very few cod smaller than 25 cm were caught in pelagic or bottom trawls. Engås and Godø (1989) suggested that small cod may escape under the groundrope of bottom trawls, but because small cod are frequently caught in the Barents Sea with the same trawl, the absence of small cod in this study indicates that they are actually not very abundant on the trawling grounds. Small cod in the fjords and coastal areas are in shallow water close to shore, where trawling is impossible (Løken *et al.*, 1994; Johansen *et al.*, 1999; Nøstvik and Pedersen, 1999a; Berg and Pedersen,

2001). Løken *et al.* (1994) discussed settling strategies for coastal cod and suggested that in fjords and at the coast it may be advantageous for young cod to settle in the sublittoral. The macroalgae belt there may provide refuge for juvenile cod from the large cannibalistic cod that live in deeper waters. The lesser density of cod in fjords in the south may therefore also be associated with the absence of suitable areas for small cod to inhabit. Such a settling strategy is very different from that of juvenile Northeast Arctic cod in the Barents Sea, which settle in deeper water. Therefore, if eggs and larvae of Northeast Arctic cod drift into fjords, they are likely to settle in deep water, where they would probably be exposed to a higher rate of predation (Løken *et al.*, 1994). The suggested difference in settling strategy between the two types of cod might be important in maintaining the stock structure between them.

Other than food availability, temperature is the most important influence on growth rate of cod (Suthers and Sundby, 1996). The optimum temperature for large cod is 9–12°C and for small cod it is 11–15°C (Pedersen and Jobling, 1989). The bottom temperature in the investigation area seldom exceeds this. Cod living in areas with the highest temperature therefore have the fastest growth (Brander, 1995). During winter, the water, temperature is higher offshore, whereas in summer it is higher in the fjords
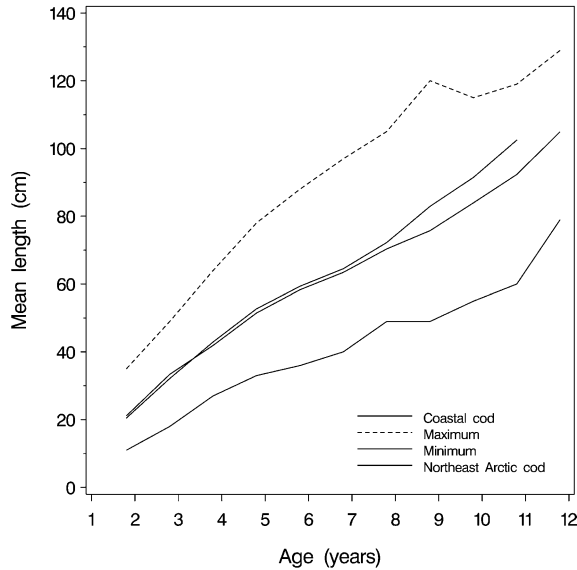
Figure 6. Mean, minimum, and maximum length at age for coastal cod and Northeast Arctic cod, 1995–2001 combined. Only data points with at least 10 observations were used to draw the lines.

(Hegseth *et al.*, 1995). The winter temperature is the most crucial because the temperature can approach 0°C in some fjords, and growth rate increases exponentially from this low level (Pedersen and Jobling, 1989; Brander, 1995). The temperature also decreases in a northward direction (Hegseth *et al.*, 1995). The different temperature regimes are probably the main reason why the average length at age of cod increases from north to south and from inshore to offshore.

There was only a small difference in length at age between coastal cod and Northeast Arctic cod when immature, confirming the results of laboratory experiments that revealed the same under identical conditions (Godø and Moksness, 1987; Svåsand *et al.*, 1996). However, we found that, following maturity, length at age was slightly higher for coastal than for Northeast Arctic cod, and the difference increased with age.

The average age at M_{50} for coastal cod (5.7 years) calculated here is similar to earlier estimates from a fjord system in the northern part of the area (Berg and Pedersen, 2001). The low age at M_{50} inshore in the south is the same as found in earlier studies in the same region

Table 2. Parameter estimates from the reduced GLM of RL ($R^2 = 0.17$).

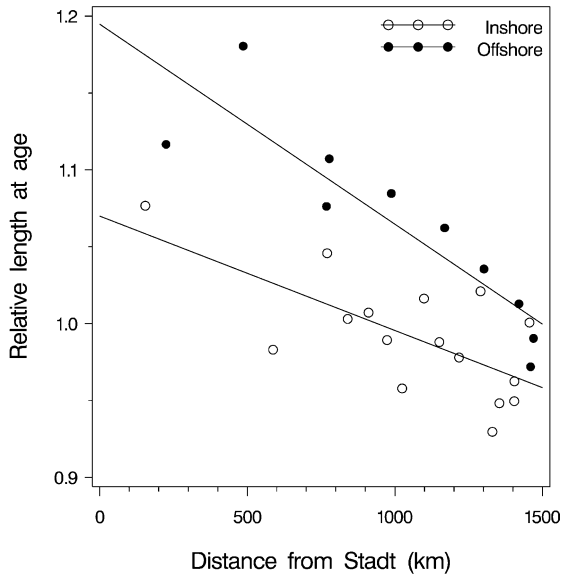| Explanatory variable	Number of parameter estimates	Percentage of total variance explained	Level	Parameter estimate	Standard error
Intercept				1.1268	0.0070
Type of cod	1	1.3	Coastal	0.0246	0.0023
			NE Arctic	0	
Sex	1	2.4	Female	0.0350	0.0032
			Male	0	
Maturity	1	3.7	Immature	−0.0119	0.0027
			Mature	0	
Female × immature	1	1.3		−0.0270	0.0038
Area	15	70.6	12	−0.1701	0.0074
			13	−0.1205	0.0089
			14	−0.1621	0.0071
			15 + 16	−0.1913	0.0067
			17	−0.1062	0.0070
			18 + 21	−0.1592	0.0067
			22	−0.1262	0.0070
			23	−0.1981	0.0074
			24	−0.1350	0.0288
			25	−0.0995	0.0081
			26 + 27	−0.1403	0.0069
			31 + 32	−0.0317	0.0093
			101 + 102	−0.1366	0.0070
			103 + 104 + 201	−0.0915	0.0066
			202 + 203 + 204	−0.0429	0.0067
			301 + 302	0	
Year	4	18.5	1995 + 1996	−0.0542	0.0029
			1997	−0.0812	0.0040
			1998	−0.0294	0.0033
			1999 + 2000	−0.0125	0.0027
			2001	0	
Depth	1	2.2		7.6×10^{-5}	9.7×10^{-6}

Figure 7. RL for cod caught inshore and offshore. The horizontal axis expresses distance in kilometres from Stadt (data from all surveys combined, 1995–2001).

(Godø and Moksness, 1987). The calculated M_{50} for Northeast Arctic cod (6.9 years) was more than a year higher than for coastal cod, and is the same as in the Barents Sea, the main feeding area of Northeast Arctic cod (ICES, 2002). This indicates that the cod determined as Northeast Arctic by the otoliths in this investigation are probably of the same origin as the same type of cod in the Barents Sea. This is also in line with life history theory, which predicts that migratory fish should mature later and at larger size than non-migrants (Roff, 1988).

When reared under similar environmental conditions, the field-observed differences in growth rate and age at maturity between coastal cod and Northeast Arctic cod seemed to be eliminated (Godø and Moksness, 1987). Those authors also indicated that the differences found in the field were probably not of genetic origin. However, in laboratory experiments, fish do not have the chance to select for temperature and prey, so the results from such experiments should not automatically be applied to natural conditions. Fish from different cod stocks can, for instance, inhabit the same areas but prefer different prey and/or different ambient temperatures, resulting in different growth rates.

Table 3. Parameter estimates (linear predictor) from the reduced GLM of probability of being mature (maximum rescaled $R^2 = 0.55$).

| Explanatory variable	Number of parameter estimates	Level	Parameter estimate	Standard error
Intercept	1		−7.8946	0.1281
Age	1		0.7379	0.0258
Length	1		0.0591	0.0030
Area	18	12	−0.3511	0.1121
		13	0.4229	0.1392
		14	0.0237	0.0934
		15	0.3328	0.1059
		16	0.0953	0.0887
		17 + 18	0.4181	0.0736
		21	0.0368	0.1307
		22	0.4061	0.0962
		23	0.6869	0.0988
		24	−1.4504	0.9706
		25	−0.1547	0.1196
		26 + 27	−0.4961	0.1978
		31	0.0725	0.0948
		32	1.1424	0.1382
		101 + 102 + 103	−0.3599	0.0788
		104 + 201	−0.1151	0.0859
		202	−0.6305	0.1044
		203 + 204	−0.0742	0.1029
		301 + 302	0	
Depth	1		−0.0005	0.0002
Type of cod	1	Coastal	0.4652	0.0260
Sex	1	Female	−0.1737	0.0192
Year	4	1995 + 1996	0.3971	0.0358
		1997	0.7760	0.0580
		1998	−0.0863	0.0473
		1999 + 2000	−0.7679	0.0350
		2001	0	
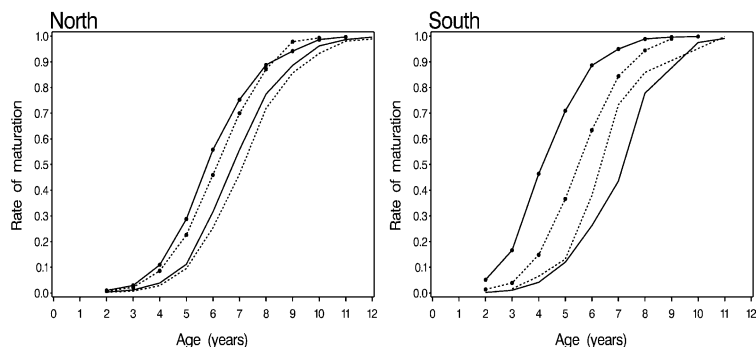
Figure 8. Rate of maturation of cod (both sexes) by age, type, and area of catch (data from all surveys combined, 1995–2001). Solid lines represent inshore areas, dotted lines offshore areas, curves with symbols plotted coastal cod, and curves with no symbols plotted Northeast Arctic cod.

An increased growth rate for a stock is usually associated with maturation at a younger age (Jørgensen, 1990). Our results showed only a small difference in length at age between coastal cod and Northeast Arctic cod, especially before maturation, whereas the difference in age at M_{50} was more than 1 year. Northeast Arctic cod were therefore 6 cm (10%) longer than coastal cod at M_{50}. This finding counters the results of earlier investigations, which showed that the two types matured at the same length (Godø and Moksness, 1987). The difference in age at maturity cannot be explained by errors in age determination or in specifying maturity stage because any such error would be the same for both types of cod.

Other possible sources of difference in these parameters between the two types of cod could be environmental, direct or indirect consequences of selection by fishing, or genetic. Environmental differences experienced early in the life of cod have been suggested as an explanation for differences in growth and maturity (Godø and Moksness, 1987). However, this is not likely because the difference in age at maturity between the two types in this investigation was demonstrated also offshore in the north, where the environment is similar to that in the open ocean. Differences in fishing mortality alone cannot explain the observed pattern because they would only change the abundance of old fish and not lead to a change in the percentage of immature cod in these age groups (Jørgensen, 1990). However, possible differences in exploitation pattern together with an inherited component in age at maturity might explain the differences.

There was nothing in the data to indicate a difference in the condition of cod that could have caused earlier or delayed maturation of the two types. If Northeast Arctic cod had been feeding in other areas, such as the Barents Sea, for most of their life prior to capture, it would still be remarkable that the two types had approximately the same length at age but large differences in age at maturity. Besides, the pattern was found throughout the whole period of investigation.

Most coastal cod spawning takes place inside fjords and close to shore (Jakobsen, 1987), so it is isolated from the spawning of Northeast Arctic cod. Investigations on the main spawning ground of Northeast Arctic cod revealed that the two types cluster in separated groups in the survey area (Dahle and Jørstad, 1993; Noreide and Pettersen, 1998). Samples taken for analysis of stock structure when cod were spawning revealed homogenous groups of the two types. Therefore, Northeast Arctic cod and coastal cod might be sufficiently isolated during spawning to maintain the stock structure revealed by all the investigations. As genetic analysis clearly indicates that cod in the study area comprise at least two genetically separated stocks (Fevolden and Pogson, 1995, 1997), it seems reasonable to assume that the differences we found in age at M_{50} might have a genetic component.

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