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Interim Report IR-00-024

Maturation Dynamics of Arcto-Norwegian Cod

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June 2000

Contents

Abstract

Many commercially important fish stocks are harvested with very high exploitation rates with the consequence of substantial changes in stock parameters as well as reduced harvest rates and, in the worst case, stock depletion. On a long-term the Arcto-Norwegian cod is the most productive cod stock in the world. It has a history of exploitation many hundred of years long and has been heavily exploited since about 1950. The chosen exploitation strategy might have substantial effects on the short-term production of the stock, and a serious question is if a long-term and heavy exploitation may change genetic properties of the stock and hence its reproductive and production potential.

In this paper, age and size data of spawning cod, going back to 1932, are analysed with respect to long–term changes caused by exploitation. During the studied period, average age and size at first spawning have been reduced by about three years and 20 cm. Immature growth has also increased substantially. It is shown that a lot of the variability in age and size at first spawning can be explained by the exploitation itself and, even better, by stock biomass (density dependency). Other factors, like food availability (capelin abundance) and year class strength, also seem to play a role. Due to more or less continuous trends in the data from World War II onwards, it is difficult to disentangle temporal effects (environmental forcing) from other causal agents.

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Acknowledgements

I am grateful to Terje Jørgensen for giving me access to his data, and to Åge Fotland for assistance in digging out information from the historic database. I also wish to thank Mikko Heino and Ulf Dieckmann for valuable discussions and comments and IIASA for giving me the opportunity to spend time at Laxenburg during the preparation of this manuscript.

Maturation Dynamics of Arcto-Norwegian Cod

Olav Rune Godø

Introduction

Plasticity in maturation dynamics of fish populations is well-known and in particular for commercially exploited stocks (Roff 1982, Jørgensen 1990, Rijnsdorp 1993a, Godø and Haug 1999). Changes in age and size at first spawning has been attributed to effects of fishing through e.g. density dependency or gear selectivity, as well as due to natural changes in the environment (Borisov 1978, Rijnsdorp 1993b). Potentially, fishing also may cause a genetic selection towards spawning at lower age and size with negative consequences for the productivity of the stock (Law and Grey 1989, Rijnsdorp 1993b, Heino 1998). Untangling the different effects is getting particularly complex for population living under a highly variable environment and experiencing substantial short and long-term variation in climate and fishing pressure.

The Arcto-Norwegian cod stock has a wide geographic distribution (Figure 1) with substantial geographic/environmental heterogeneity. Recruiting age groups (ages 0-3) with limited migration potential will be located at the polar front in the north and east with the potential gain of surplus access of food in this high productivity zone (Sakshaug *et al.* 1994). Environment will, however, otherwise be unfavorable with long periods of low water temperature (periodically below 0^{o} C) (see e.g. Michalsen *et al.* 1998). In contrast, more southerly and westerly recruitment may experience more favorable temperatures but less food. The potential effects on growth, survival and later maturation has been given little attention, although Jørgensen (1992) and Michalsen *et al.* (1998) indicate an east –west increase in growth for age 2-3 fish.

The Arcto-Norwegian cod stock has also been susceptible to temporal climatic changes, which are supposed to cause substantial variation in productivity of the stock (Øiestad 1994, Godø in prep). Temporal heterogeneity may work on short term i.e. 3-7 year scale in accordance with first order variation in climate cyclicity (Loeng, 1991), which again coincide roughly with the probability of rich recruitment (Sætersdal and Loeng 1987). More long-term cycles have also been suggested (Ottestad 1942, Yndestad, 1996). The productivity of the Barents Sea is totally dependent on water influx from the Atlantic drift and also on zooplankton recruitment from the Norwegian Sea to the seasonal production (Skjoldal and Rey 1989). Consequently, the total production is responsive to external forces and hence, the harvest potential for a top predator like cod, is potentially vulnerable to short and long-term variability in the environment.

Is it plausible that fish stock under such circumstances develop evolutionary traits, which are particularly robust to changes in the survival/growth conditions? Can this be depicted through studies of plasticity in e.g. growth and maturation?

The goal of this paper is to describe variation in maturation dynamics of Arcto-Norwegian cod and potential explanations. To what extent can existing data explain temporal differences in age and size at maturity? The question is pursued along two avenues: a) Maturation dynamics is dominated by exploitation, and b) density dependent factors are causal for maturation dynamics.

Material and Methods

The analysis in this paper is based on sampling of commercial catches from the period 1932 till 1998. Data from 1932 through 1984 are the same as used by Jørgensen (1992). These data consist of mean length at age of first time spawners and are from representative samples (both sexes are pooled) of otoliths and length taken from commercial long line catches at the Lofoten spawning grounds during the main spawning season (January – April, see Pedersen 1984). Procedures for sampling and otolith readings have remained virtually unchanged during the whole period (Jørgensen 1992). The time-series is updated from the later samples collected with same procedures. However, due to a more offshore distribution of the fishery and thus a more limited sampling on the traditional Lofoten spawning ground, the area of sampling was expanded to include the offshore side of the Lofoten Islands from 1985 and onwards (Figure 1).

Gear efficiency has changed substantially during the period, mainly connected to mechanization and introduction of new materials and hooks. The possible effect on the selective properties of the longline is unknown, but supposed to be negligible in this analysis. Data from gillnets and Danish seine catches from the same area and season from the period 1985-1998 are used to study potential selectivity. An overview of the material is shown in Tables 1 and 2.

The otoliths were broken through the nucleus and age was determined from counting the annual rings. Rollefsen(1933) found that zones changed character when cod reach maturity, and thus number of spawning zone are given as a separate information. First time spawners are here defined as fish with ripe or ripening gonads with no spawning zones. Further, the otolith zonation, particularly in the nucleus, are traditionally used to distinguish between Norwegian coastal cod and Arcto-Norwegian cod. In this paper data from only the last has been analyzed. Background and methodology of the otolith readings are described in more details by Rollefsen 1933 and Godø and Haug 1999).

All calculation of age and size at spawning are based on first time spawners only, and not on maturity ogives. Consequently, they will be relative measures for the applied gear and sampling procedures and are used to track changes over time and variation in exploitation. Calculations are done by year and year class. Average age at first spawning for a given year (WSA_y) is a weighted mean of the sampled fish:

$$WSA_y = \frac{1}{ntot_y} \sum_{a=\min}^{\max} a \cdot n_{ay},$$

where $ntot_y$ is total number sampled in a given year (y), a is age in years, and n_{ay} is the number sampled at age a in year y. *Min* and *max* represent maximum and minimum ages at first spawning. The same procedure was used for calculating weighted mean length by year (WSL_a). An average fishing mortality for ages 4-8 is used a measure of exploitation pressure for a given year, and fishing mortalities (F) by age and year were obtained from (Anon 1999) for the period 1946 – 1998.

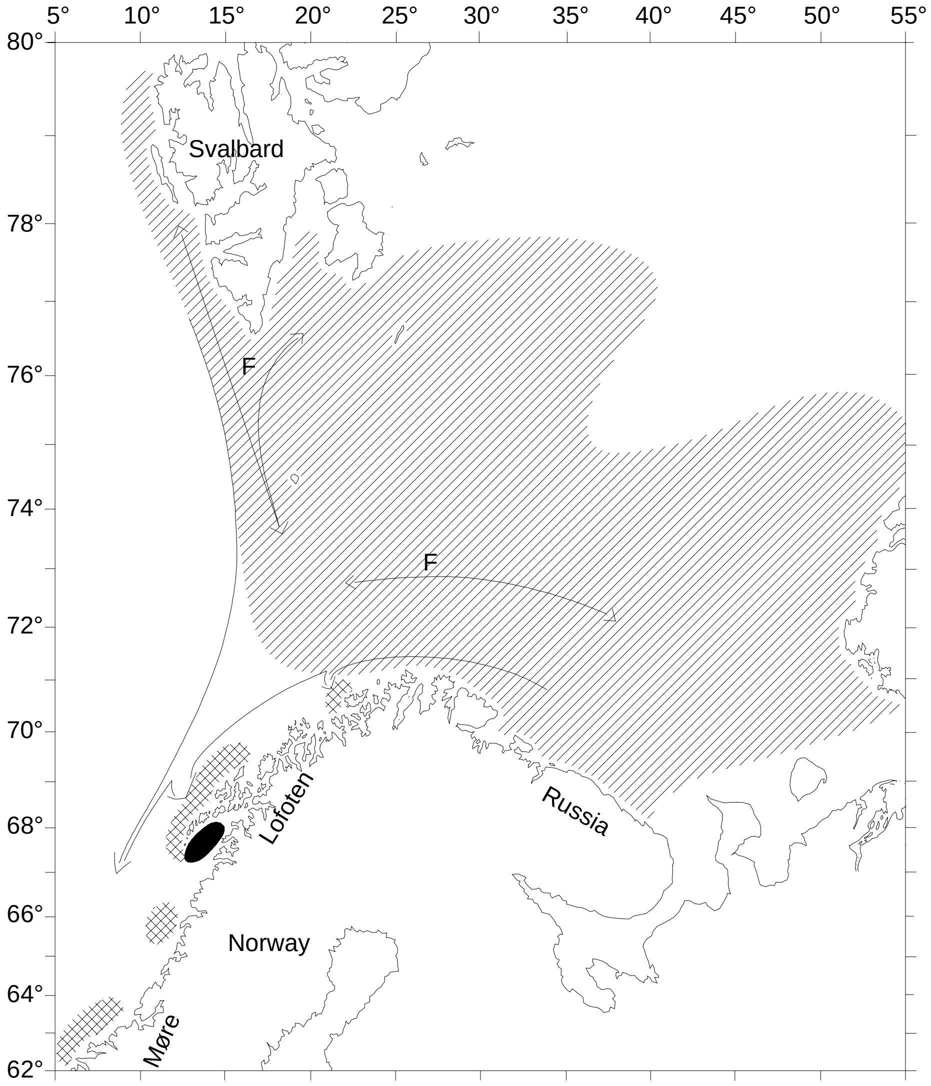

Figure 1. Area of distribution and major migrations of Arcto-Norwegian cod. Spawning areas are double hatched or solid. The solid area indicates the traditional sampling area in Lofoten. The adjoined double hatched area was included in the sampling from 1985 and onwards.

Table 1 . Overview of data used in analysis of long term effects and some summary statistics.

Year	Mean length (cm)	Age range (years)	Sample size	Year (cont.)	Mean length (cm)	Age range (years)	Sample size
1932	89.9	6	136	1966	88.4	5	1066
1933	89.1	7	303	1967	91.0	6	1774
1934	89.1	6	459	1968	86.2	5	904
1935	90.2	8	806	1969	88.0	5	839
1936	91.3	6	767	1970	88.8	5	3026
1937	86.8	5	1129	1971	88.7	5	1876
1938	85.5	4	593	1972	86.2	4	1595
1939	87.7	5	1486	1973	84.7	4	1536
1940	86.5	5	521	1974	85.3	4	103
1941	84.1	5	346	1975	88.7	5	732
1942	86.9	6	292	1976	80.8	3	253
1943	84.8	6	633	1977	80.3	3	195
1944	83.4	6	631	1978	79.6	3	275
1945	85.6	5	418	1979	86.2	4	299
1946	84.8	4	610	1980	84.9	4	225
1947	87.0	6	558	1981	83.6	4	1214
1948	87.5	6	702	1982	78.5	3	1093
1949	90.4	6	726	1983	78.5	3	364
1950	90.6	6	1323	1984	82.3	3	487
1951	85.7	6	1952	1985	86.1	6	928
1952	91.0	6	1771	1986	77.5	5	715
1953	86.1	6	1816	1987	82.1	6	331
1954	86.4	6	1564	1988	88.8	5	27
1955	90.4	7	2087	1989	72.4	4	108
1956	89.9	7	2333	1990	71.2	4	798
1957	87.6	6	2143	1991	73.8	4	539
1958	90.8	7	2848	1992	83.9	4	235
1959	87.2	6	3122	1993	80.8	5	65
1960	89.4	7	1781	1994	87.6	6	167
1961	90.8	7	2752	1995	78.3	4	228
1962	91.3	6	2699	1996	80.4	4	493
1963	91.6	6	2149	1997	83.0	3	442
1964	87.8	5	880	1998	75.5	4	472
1965	91.7	6	1435				

Table 2. Material used to study gear and area effects on the data.

Year	Gear	Mean l	Age range	Sample (N)
1985	Danish seine	86.5	6.0	429
1985	Gillnet	86.9	5.0	1528
1985	Long line	86.1	6.0	928
1986	Danish seine	76.9	5.0	147
1986	Gillnet	84.6	5.0	860
1986	Long line	77.5	5.0	715
1987	Danish seine	80.8	4.0	95
1987	Gillnet	84.0	6.0	658
1987	Long line	82.1	6.0	331
1988	Danish seine	57.5	3.0	36
1988	Gillnet	88.5	6.0	51
1988	Long line	88.8	5.0	27
1989	Danish seine	61.1	4.0	121
1989	Gillnet	79.8	5.0	368
1989	Long line	72.4	4.0	108
1990	Danish seine	72.3	4.0	760
1990	Gillnet	78.6	4.0	633
1990	Long line	71.2	4.0	798
1991	Danish seine	73.9	4.0	213
1991	Gillnet	79.0	3.0	1055
1991	Long line	73.8	4.0	539
1992	Danish seine	71.6	5.0	142
1992	Gillnet	82.5	5.0	359
1992	Long line	83.9	4.0	235
1993	Danish seine	77.6	6.0	133
1993	Gillnet	85.9	6.0	172
1993	Long line	80.8	5.0	65
1994	Danish seine	84.9	5.0	375
1994	Gillnet	85.6	5.0	331
1994	Long line	87.6	6.0	167
1995	Danish seine	82.8	5.0	350
1995	Gillnet	87.2	6.0	570
1995	Long line	78.3	4.0	228
1996	Danish seine	80.5	4.0	361
1996	Gillnet	85.1	4.0	519
1996	Long line	80.4	4.0	493
1997	Danish seine	78.5	4.0	250
1997	Gillnet	85.9	4.0	433
1997	Long line	83.0	3.0	442
1998	Danish seine	75.2	4.0	291
1998	Gillnet	79.1	4.0	591
1998	Long line	75.5	4.0	472

Changes in reproductive traits by year-class might be more relevant than by year. This, however demand a sampling regime giving comparable measures of density by year. In the above the samples are considered representative of the fish population available to longline. The applied sampling have varied in intensity and diversity from year to year and the available material is therefore difficult to apply by year class. The percentage of occurrence in the samples of a year-class in a given year is used as a rough relative proxy for density. It is assumed that following this percentage by age gives a fair representation of maturation trajectory by year-class. A weighted spawning age by year-class (WSA_{ycl}) can thus be calculated as

$$WSA_{ycl} = \sum_{y=first}^{last} (a_y \cdot pct_y) / \sum_{y=first}^{last} pct_y ,$$

where *y* denote the year of observation, *ycl* the year of birth, and *first* and *last* gives years of appearance and disappearance of first time spawners. Similar approach was also used to calculate the weighted average length at first spawning for a year-class (WSL). Again an average fishing mortality (*F*) for ages 4-8 is used a measure of exploitation pressure for a given year-class (Anon 1999). Average *F* for a year class thus emerges from

$$F = \frac{1}{first - last} \cdot \sum_{y=first}^{last} F_y$$

Capelin is a factor of great importance for growth of cod (Mehl and Sunnanå 1991, Ohzigin *et al.* 1995, Nakken 1994). In these analysis the relationship between capelin and cod biomasses (from Gjøsæter (1999) and ICES (1999) respectively) is used as a proxy for the growth potential in the cod stock. Due to the lack capelin biomass data before 1973, occurrence of capelin in cod stomachs from 1947 to 1977 from Ozhigin *et al.* (1996) was used in backward facing of the existing time-series to the 1940s from comparable observations from the overlapping years.

Size divided by age at first spawning is used as a proxy for immature growth. If growth is important for the onset of maturation, it is plausible that a density dependency effect may play an important role in maturation dynamics, as also suggested by e.g. and Saborido-Ray *et al.* (1998) and Godø and Haug (1999). Biomass estimates for studying density dependency are obtained from VPA (ICES 1999).

Due to possible confusion of the material by insufficient sampling and uncertainties in VPA measures of exploitation on individual ages and years, the material is first approached through presentation of decadal means of spawning size and age and growth to reveal broad scale developments and relationships. Simple averaging of annual mean values are used for the decadal overview.

Simple and multiple linear regressions and analysis of variance models of the type below were used to quantity effects of length, F, stock size etc. on age at maturity

$$\text{Dep. Var.} = \beta_0 + \beta_1 \text{(indep.1)} + \beta_2 \text{(indep.2)} + ..+ \beta_n \text{(indep.n)} + \varepsilon$$

where β_0 to β_2 are regression coefficients and ε the error term. Two different avenues were pursued. In the first the maturation is governed by density dependency. The hypothesis to be tested is that internal stock dynamics driven by stock biomass is tightly related to onset of maturation, i.e. available food resources for the maturation and migration will be less at high densities than at low. In the second avenue it is hypothesized that variation in exploitation dominates the dynamics of maturation through size selective removals of individuals. The extraction of the older and larger individuals of the population will truncate the size distribution and reduce the probability of slow growing and late maturing individuals to reach maturity. In both avenues modulation of the relationships are allowed for by the level of capelin and the year class strength. Capelin is the major food item of cod and its availability significantly affects directly individual growth (Bogstad and Mehl 1997, Ohzegin *et al.* 1995) and indirectly maturation (Godø and Haug 1999). Year-class strength is included because it might cover short-term variability at the youngest stages that are not included in the variation of the biomass. Finally, to study interaction of the two main avenues models combining any of the available variables were tested.

Results

The data

The effect of expanding the area after 1984 was studies by comparing average age and size of first time spawners with old and new sampling area. Weighted average spawning ages (WSA) and lengths (WSL) by year were according to a t-test not significantly different as it appears from the text table below.

Comparison	Old area	New area	Pr>t
WSL	75.63	74.45	0.61
WSA	6.90	6.82	0.78

Selectivity of long line might cause artifacts in long-term relationships. Recent data from longline and other fishing gears used in the area at the same time were therefore compared for the period 1985-1998. Longline data were similar to Danish seine in both composition and size distribution but differed significantly from gillnet catches (Figure 2). A t-test (see text-table below) indicated that WSL and WSA from longline (LL) differed significantly from those for gillnet (GN). The comparison between longline and Danish seine (DS) means indicated no difference.

Comparison	LL mean	GN mean	Pr>t	DS mean	Pr>t
WSL	74.45	81.01	0.0016	71.97	0.32
WSA	6.82	7.26	0.0625	6.82	0.43

Long term development

Long-term changes in length at maturity related to growth were explored from mean decadal values per age group (Figure 3). With increasing growth both length and age atmaturity are reduced. It should particularly be noted that the line for the 1940s lies to left of the 1930s and the 1990s line is positioned to the left of the 1980s. The remaining lines move progressively from left to right with time.

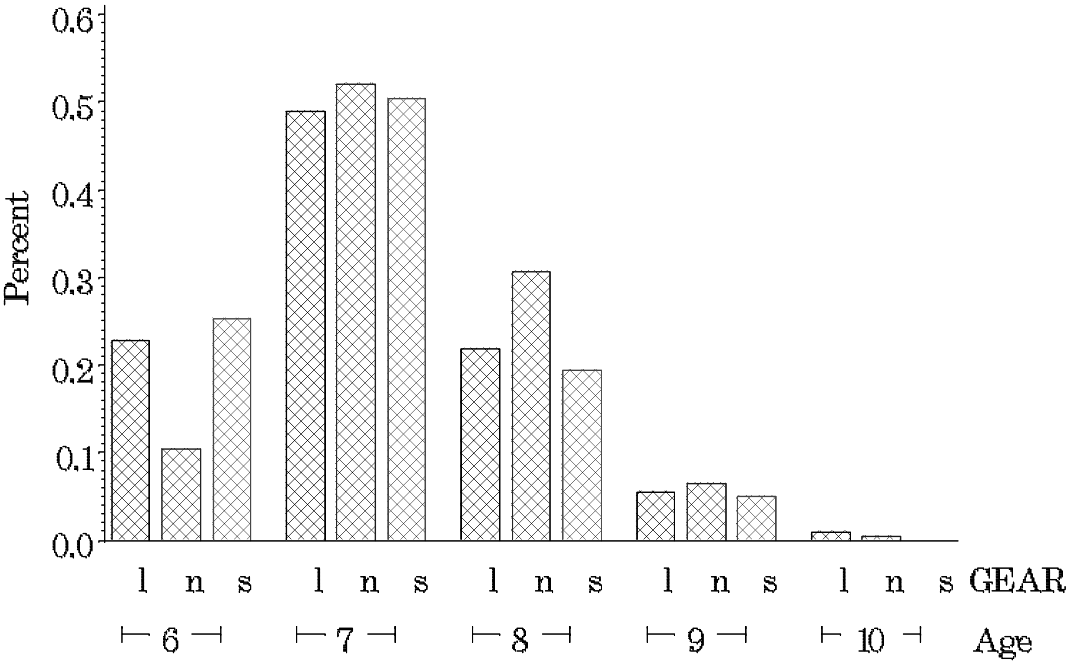

Figure 2. Comparison among gears used in Lofoten (longline (l), gilnet (n), Danish seine (s)).

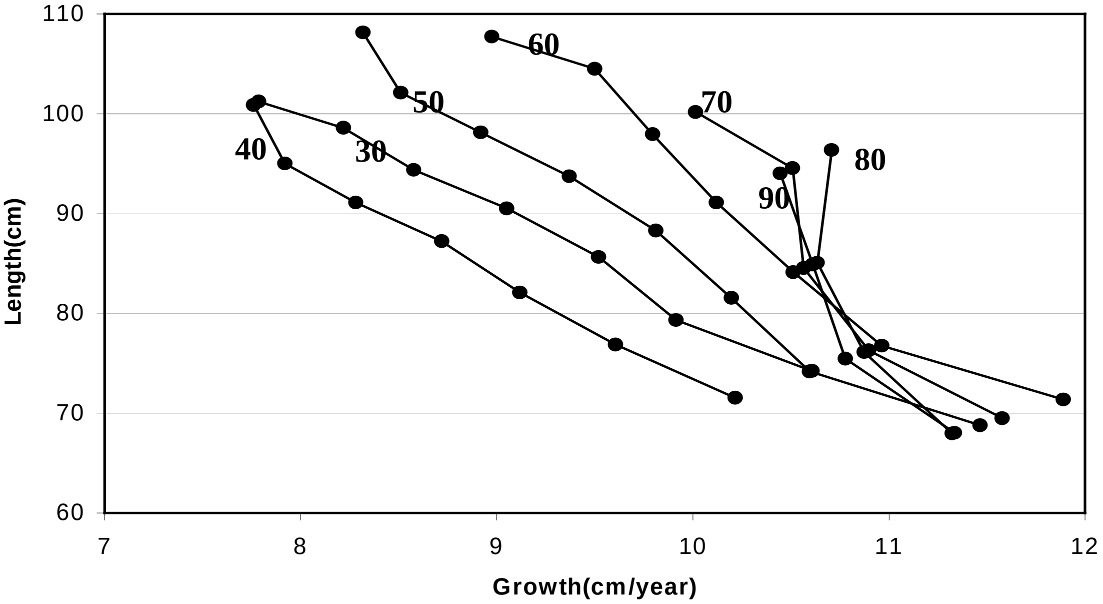

Figure 3. Trends in the growth – length relationship by decade. The individual data points are mean lengths by age at maturity with age progressively increasing from left to right in the individual curves. Each curve is tagged with decade (40 is the 1940s etc.)

For the period when analytical assessment is available (1946-1998), WSA and WSL has steadily moved towards lower values with intermediate maxima and minima. The minima seem to roughly be coordinated with the appearance of rich year-class in the spawning stock (Figure 4A). Time (or year class) explains 87% and 72% of the variability of WSA and WSL respectively for the year-class time-series (Table 3). When comparing WSA and WSL from the time-series based on years and year class, similar length and a slightly higher age appears (see text table below). The time-series by year classes is truncated in both ends of the time scale to include only those with a complete maturation history. It should be noted that the standard deviation of the average values from the time-series by years is higher than the corresponding from year classes.

	N	WSL	Std.	WSA	Std.
Year	73	82.6	6.31	7.9	1.17
Year class	50	82.8	5.57	8.3	0.90

Potential causal factors to the time correlated reduction are explored in Figure 4. There are significant correlation between WSA and WSL, and stock abundance (BIO), indicating density dependency, and these are further negatively correlated to fishing mortality (FBAR) (significance levels are given in Table 3). Immature growth, a potential important factor for the maturation (Figure 3), exhibits a density dependency as well as a positive relationship to the level of capelin compared to cod. It should be noted that several of the year classes in the 1980s diverge from the general patterns. Particularly, it is interesting to see that a reduction of the fishing mortalities in the end of the 1980s did not move those year classes upward on the WSA axis.

Table 3. Simple linear regression between WSA, WSL, growth and various potential causal variables. Year classes 1940-1989 are included in all regressions except for capelin which includes year classes from 1969.

Dependent var1	WSA r^2	WSL r^2	Growth r^2
WSL	0.85* (+)		
Year class (time)	0.87 (-)	0.72	0.72*(+)
Stock abundance	0.72 (+)	0.63 (+)	0.52 (-)
Average F	0.32 (-)	0.27 (-)	0.21 (+)
Year class strength	0.03 (+)	0.03 (+)	0.12 (-)
Capelin	0.07 (-)	0.00	0.23 (+)

*) Invalid regression as the variables are not independent.

Given the various relationships in Table 3, it is obvious that maturation dynamics of cod is related both to endogenous and environmental variables.

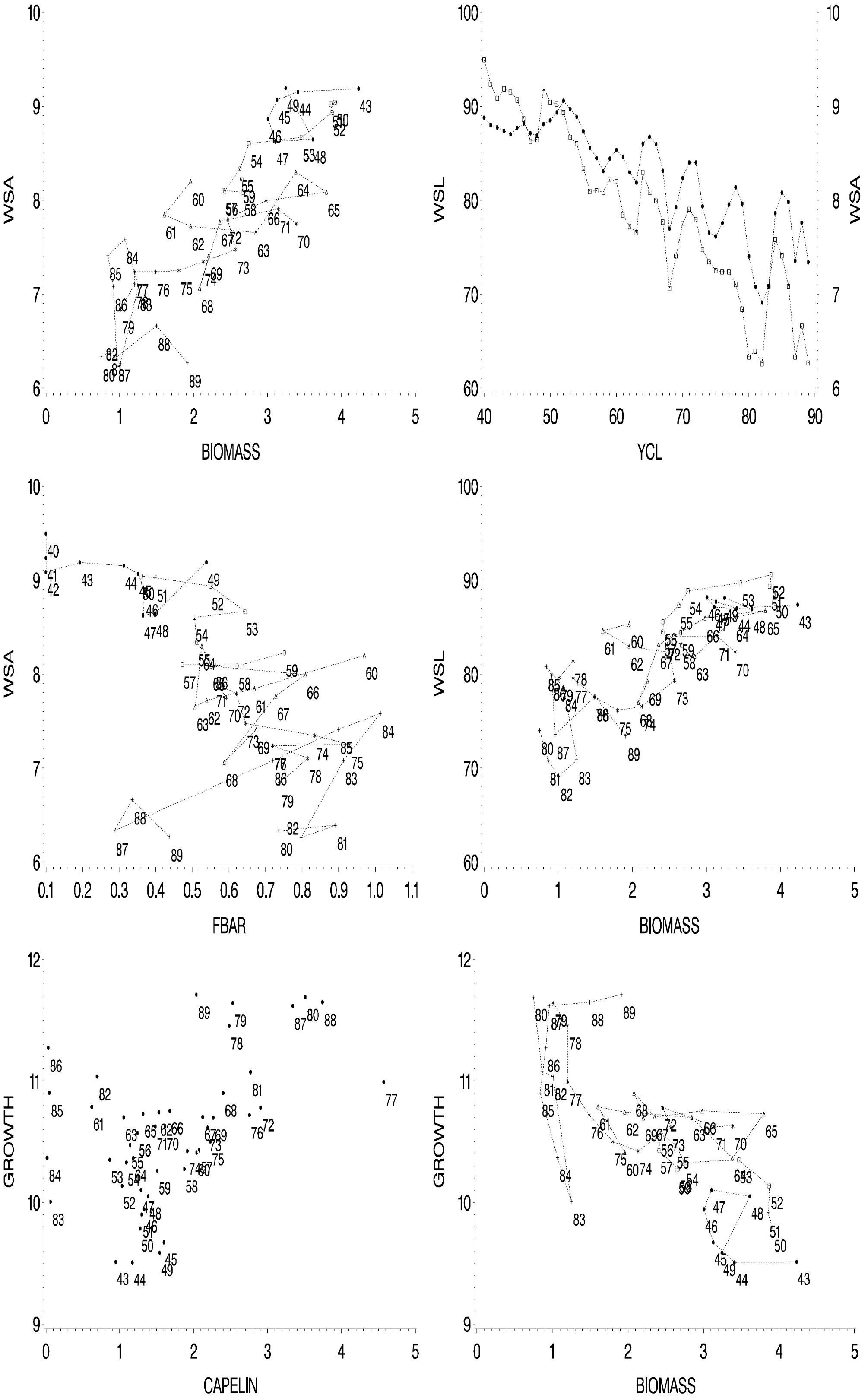

Figure 4. Various relationships of significance to age (WSA) and size (WSL) at maturity. YCL is year class strength and FBAR is average fishing mortality.

Modeling age and length at first spawning

Of the two avenues chosen to test in this paper, the best fits were obtained from the density dependent models. This concerns both the models using WSA and WSL as dependent variable. The age (WSA) density dependent model shows the best fit ($r^2 = 0.77$) where biomass is the dominant factor, although the level of capelin is also significant. Capelin comes out as a significant effect in all cases except in the density model for WSL. This is the only model where year-class strength appears significant.

Discussion

The data

The general quality of the data is discussed by Jørgensen (1990) and will not be repeated here. According to his evaluation the data have the proper consistency and quality for long term analysis. Two additional questions have to be examined in more detail related to the expanded use of the data in the present analysis. Firstly, the area expansion for the period 1995-1998 might have biased the time series, a concern which is emphasized by the fact that the data from this period appear in many instances to depart from the general trend of the time-series (see Figure 4). Analysis without the additional data shows similar exceptionalities, indicating that the information is not artifacts of area expansion. Further, the general expansion of fishing effort to offshore areas in recent decades might reflect a displacement which is part of the distributional dynamics of the stock. Consequently, inclusion of these data gives thus probably a more representative picture of the stock then excluding them. Finally, in some years with limited data from the traditional spawning grounds, the new data filled gaps in the time-series which otherwise might have prevented adequate analysis on year-class basis.

This leads to the next crucial point: To what extent do the rough assumptions related to the analysis by year-class corrupt the validity of presented analysis? Annual average length in the spawning population will be strongly influenced when rich year classes mature. The youngest first time spawners will reduce WSA and WSL and in successive years the annual means will increase according to the development of this year-class by age (see e.g. Figure 3). If the applied method for calculating means by year-class produce realistic results, the residual temporal variation must be caused by short term environmental effects, e.g. temperature fluctuation as described by Loeng (1992). The less variable values from the year-class time-series is an indication that the year-class averaging is effective. To what extent the residual variation is driven by the averaging procedure or by environment is difficult to evaluate. Nakken and Raknes (1987) and Jørgensen (1992) show that temporal variation in growth can be substantial and effects of temperature are supposed to be important. Although the year-class data still may contain some residual noise, the observed reduction in variability compared to the time-series by year is promising. The data must be expected to be somewhat biased due to both short term and long term changes in F. Under evaluation of reliability of the year-class models the negative effects of such residual noise should be kept in mind.

Table 4. ANOVA results from the 'density dependent' and ‘exploitation' governed models**.**

Model	Dependent variable	R^2	Source	Type III Sum of squares	F	Pr>F
Density	WSA	0.77	Biomass	18.23	99.25	0.0000
Dependent			Capelin	1.290	7.024	0.0112
			Year class strength	0.459	2.496	0.1215
Exploitation		0.42	Fishing mortality	6.404	13.96	0.0005
			Capelin	5.627	12.26	0.0011
			Year class strength	0.169	0.367	0.5477

Model	Dependent variable	R^2	Source	Type III Sum of squares	F	Pr>F
Density	WSL	0.69	Biomass	813.089	78.85	0.0001
Dependent			Capelin	18.1641	1.76	0.1914
			Year class strength	64.8089	6.29	0.0160
Exploitation		0.42	Fishing mortality	305.6362	13.82	0.0006
			Capelin	157.1425	7.11	0.0108
			Year class strength	1.3233	0.06	0.8079

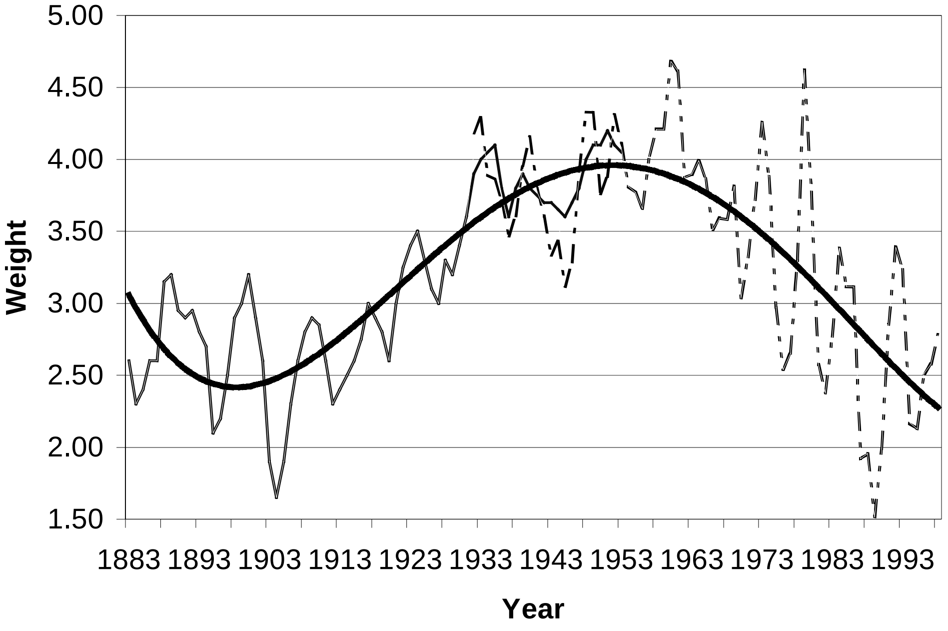

Figure 5. Long term changes in average weight in the spawning stock as presented by Godø (2000). Continuous line represent average weight data from the Lofoten fishery as presented by Rollefsen (1954). Broken lines are based on the average length data from this paper converted to weight.

The models

The continuous time trend for several of the involved variables creates difficulties in the establishment of models describing causal effects of the maturation dynamics of the Arcto-Norwegian cod. The independency of the different variables can be questioned in many cases. The obvious connection between increasing harvest level (F) and reduced biomass has been taken into consideration by using the two avenues. The used capelin level will depend on the cod biomass in addition to the capelin abundance. Further, the capelin biomass may be significantly affected by the size of the cod stock through predation (see e.g. Bogstad and Mehl 1997).

The results from the two groups of models were supposed to give insight in relative importance of the two studied factors. The superiority of the density dependent model could be due to higher sensitivity of the maturation dynamics towards changes in biomass than to changes in F. It is thus suggested that the effect of exploitation on the long-term trend in WSA has rather been to reduce density of the stock than effects caused by truncating the size composition. Although the exploitation model did not improve when average F values were allocated to year-class by using different time lags, it might well be that more refined procedures for calculating a relevant exploitation by year-class will help. In the time scale of the time series it appears clear that stock size which to a large extent is determined by exploitation determines much of the maturation dynamics. The capelin level is coming out as significant in the density dependent model, probably related to its positive effect on growth of cod (Bogstad and Mehl 1997). On the long term it might be difficult to properly exploit this dynamics because a threshold effect is expected, i.e. when the capelin level is above the threshold, there will be no forage limitation.

Maturation dynamics and biology

Cod in the Barents Sea is a long migrating – high age spawning fish. Migrations back and forth between the polar front and the spawning grounds may represent a distance of several thousand km which in itself demand substantial resources in addition to those needed for gonad development. Historically, age at spawning have normally varied between 6 and 13 years (Bergstad *et al.* 1987), but a more or less continuous reduction has occurred during the current studied period (see also Jørgensen 1990). Plasticity of age at first spawning is high as shown in this paper, but particularly as demonstrated by laboratory experiments showing that the fish from this stock potentially might spawn at age 2 when living conditions are optimized (Godø and Moksness 1987, Svaasand*et al.* 1996). The movements of the curves in Figure 2 between decades at the beginning and end of the time series demonstrate short-term plasticity. World War II stopped virtually all oceanic exploitation of immatures leaving only a marginal harvest of older immatures and spawning cod to be taken at the Norwegian (Godø in prep.). In the end of the 1980s a dramatic reduction of the cod stock compared to expectation led to strong regulation reducing the F from a level of 1.01 in 1997 to 0.29 in 1992 (Anon 1999). Both these two drastic reductions gave the same shift of length – growth relationship. Opposite reaction in the spawning dynamics with an abrupt increase in F have been clearly demonstrated for cod in other areas on similar time scales (Saborido-Ray *et al.* 1998). It is reasonable to believe that a species living towards its limits of tolerance are particularly susceptible to natural variability in the environment and has developed strategies to tackle it variable surroundings. Such variability probably lays behind large scale – long-term changes in productivity of the stock (Øiestad 1994), and might also affect the stock composition and maturation dynamics. Godø (in prep.) composed a continuous time series of individual size of fish in the Lofoten spawning population back to 1884 and indicate long term changes in the data which presumably must be environmentally driven and not caused by fishing (Figure 5). Temperature observation from this century indicates a maximum around 1960 and a cooling thereafter. What effects this might have had on an unexploited stock can only be guessed, but an interaction between the effects studied here and long term environmental changes is plausible. The suggestion by Gilbert (1996) that marine stock moves among different environmentally driven stages of reproductivity through time might be interesting also in relation to understanding of long term changes in maturation dynamics.

The conclusion so far*:* Based on the available material from recent 50-60 years it is possible to set up rather efficient maturation dynamic models. Their ability to uncover the real driving forces is still limited mainly due to the continuous trends in many of the involved variables and the problem of disentangling long term environmental effects.

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