

LONG-TERM CHANGES IN AGE AT SEXUAL MATURITY OF THE NORTHEAST  
ARCTIC COD (GADUS MORHUA L.)

by

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ABSTRACT

Maturity ogives of the Northeast Arctic cod for the year classes 1932 to 1976 were computed based on age and number of spawning zones in otoliths of cod caught on the spawning grounds at Lofoten. A reduction in the median age at maturity of approximately 2.5 years over the period is indicated. A similar reduction in mean age of the spawning stock was found. Males generally mature at a lower age than females, but the difference has become smaller over the period studied. The decline in median age at maturity is most marked for the year classes after 1950. A compensatory response to the demographic changes could explain the decline. Genetic changes as a result of selective fishing is also possible, but cannot be evaluated from the present data.

## 1. INTRODUCTION

A marked decline in the abundance of many fish stocks has been observed as a result of intense exploitation (Gulland, 1983). This is also the case for the Northeast Arctic cod, for which a steady decline has been observed over the last 50 years (Bergstad, Jørgensen and Dragesund, 1987). Generally, an increase in the rate of mortality leads to a reduction in the median age of the stock (Baranov, 1918). For some stocks a concurrent change in size and/or age at the onset of sexual maturity has been documented (Gwahaba, 1973; Oosthuizen and Daan, 1974; Schmitt and Skud, 1978; Ricker, 1981; Beacham, 1983; Sorokin, Shestova and Lukmanov, 1986).

Age and length at sexual maturity are among the fundamental parameters determining the reproductive potential of a stock and its capacity to withstand exploitation (Stearns, 1976). A thorough understanding of the response of these parameters to fishing is therefore important to the management of the stock. Changes in growth rate caused by density-dependent factors or environmental perturbations (Nikolsky, 1963; Weatherley, 1972) and genetic changes due to selective fishing (see Nelson and Soulé, 1987, for a review) are believed to lead to alterations in age and/or size at maturity.

A number of maturity ogives for the Northeast Arctic cod has been published (Rollefsen, 1953; Garrod, 1967; Hysten and Dragesund, 1973; Ponomarenko, Ponomarenko and Yaragina, 1980; Ponomarenko and Yaragina, 1981; Hysten and Nakken, 1982, 1983; Hysten and Rørvik, 1983; Hysten and Nakken, 1984, 1985). When combined, they suggest a gradually decreasing age at maturity from 1941 to 1985. However, since a variety of methods has been used to calculate the ogives, it is difficult to assess to what extent the observed change is real.

The estimation of maturity ogives for the Northeast Arctic cod is not straightforward due to the differences in geographical distribution of immature and mature fish of the same age. Consequently the ogive is to a large extent dependent on where

and when the samples were collected. Maturity ogives based on samples from the eastern Barents Sea in the first quarter of the year will most likely underestimate the proportion of matures as the majority of spawners are on their way to or already at the spawning grounds, while samples taken at or near the spawning grounds will give a too high percentage of mature fish. In summer the distribution of mature and immature will to a large extent overlap, but at this time of the year immature and recovering fish are difficult to separate based on visual inspection of the gonads (O. Kjesbu, pers. comm.)

With the exception of data from the spawning fishery at Lofoten, samples of Northeast Arctic cod, especially before 1975, are relatively few. Moreover they do not cover the area of distribution well, and time of sampling varies from one year to another. Information on maturity stage is often lacking. Given these limitations, a study of long-term changes in age at maturity based on these data was likely to be futile. An attempt was therefore made to estimate maturity ogives from samples from the spawning area at Lofoten.

The objective of this study was to analyze changes in age at maturity of the Northeast Arctic cod, both the absolute extent of the change and whether there has been an abrupt or a gradual alteration. It is based on an analysis of a comprehensive time-series of data collected at the spawning grounds at Lofoten from 1932 onwards. Possible explanations for and consequences of the changes are discussed.

## 2. MATERIAL AND METHODS

For some species age at first spawning may be determined from the patterns of the otolith described as spawning zones (Williams and Bedford, 1973). Rollefson (1933) was the first to describe this feature for the cod otolith. By following a year class through the spawning fishery, a table with the proportion of first time and repeat spawners at each age may thus be constructed. From this table a maturity ogive can be calculated

by the method described below, originally proposed by Gulland (1964). Let

- $k$  be the age at which all fish of a year class are mature  
 $R_i$  be the proportion of first time spawners among mature fish of age  $i$   
 $M_i$  be the proportion of mature fish of the same age and year class

At age  $k$  the proportion of first time spawners then equals the proportion of immatures of the same year class as  $k-1$  year old fish. The proportion of the year class mature when  $k-1$  years old is consequently given as

$$M_{k-1} = 1 - R_k \quad (1)$$

The mature  $k-2$  year-old fish of the same year class are those spawning for the second or later time at age  $k-1$ , their proportion of the spawners at this age being  $1 - R_{k-1}$ . As the spawners at age  $k-1$  make up a proportion  $1 - R_k$  of the year-class, the proportion of mature fish at age  $k-2$  is consequently

$$M_{k-2} = (1 - R_{k-1}) (1 - R_k) \quad (2)$$

By similar reasoning the proportion of the year class mature at age  $j$  ( $j < k-2$ ) is given as the product of the proportion of first time spawners at the ages  $j+1, \dots, k$

$$M_j = \prod_{i=j+1}^k (1 - R_i) \quad (3)$$

An assumption underlying this method is that mature and immature fish of a year class suffer the same mortality at the same age. However, the fishing mortality for spawners are higher than for immature fish (Garrod, 1967). A higher natural mortality for spawners caused by migration and spawning stress is also probable, but difficult to detect and quantify. With a

higher mortality for mature fish, the proportion of first time spawners at each age will be overestimated.

Therefore, an attempt was made to correct for different fishing mortality ( $F$ ) among mature and immature fish of the same age of a year class. At each age the spawners were grouped according to number of past spawnings and the proportion of each group was calculated. This proportion was then adjusted by multiplying by the inverse of the survival rate of this group relative to that of the first time spawners. This is equivalent to multiplying by the exponent of the absolute value of the difference in cumulative fishing mortality of the two groups. In a given year immature fish were assumed to suffer the fishing mortality of the oldest age group without mature individuals that year, while  $F$  for the mature fish was set equal to the mean  $F$  for the 9 to 12 year olds. Thus, second and first time spawners have had different fishing mortality for one year (the year prior to when they were caught) and therefore the proportion of second time spawners is multiplied by  $\exp(|F_m - F_i|)$ ,  $F_m$  and  $F_i$  being the fishing mortality that year of mature and immature respectively. Third time spawners are multiplied by  $\exp(|{}_aF_m + {}_bF_m - {}_aF_i - {}_bF_a|)$ , as they have suffered a mortality differing from first time spawners for two years preceding the one in which they were caught, indexed  $a$  and  $b$  respectively. A similar procedure was followed for the remaining groups of repeat spawners. Finally the proportions were normalized and proportion mature at age was calculated using equation 3.

Furthermore, central assumptions are that i) number of annuli and number of spawning zones are correctly determined, ii) the spawning population at Lofoten is not qualitatively different (regarding age/length distribution, sex ratio, percentage first time spawners etc) from the spawning population of Northeast Arctic cod as a whole and iii) the samples from the catches reflect the composition of the spawning population at Lofoten.

Data from from commercial and research catches from the

spawning grounds at Lofoten in the period 1932-1987 were made available by the Institute of Marine Research, Bergen. The gears used and the time series available are given in Table 1. Total fish length (cm) and sex were recorded, and pairs of sagittal otoliths collected for subsequent determination of age, age at first spawning and the stock component to which the fish belonged (Rollefsen, 1933; Trout, 1957). Fish classified as coastal cod (Rollefsen, 1933; Bergstad et al., 1987) have been excluded from the analysis. F-values used for the corrections of unequal fishing mortality of mature and immature fish are based on Virtual Population Analysis estimates (Anon., 1986).

To compute the maturity ogives all samples by all gears for each year were pooled to increase the number of measurements, especially for the older age groups. Computations based on a large number of samples were assumed to give a better picture of characteristics of the spawning population in Lofoten as a whole. Since the method uses the frequency distribution of number of spawnings within an age group, grouping of data from gears with different selective properties is justified if the length distributions of fish with a different number of past spawnings, but of the same age, do not differ. If so, the frequency distribution of number of spawnings will be the same in any length interval and different size selectivity of the various gears will not bias the estimated distribution. To test this, age groups and years were chosen at random among the purse seine data with sufficiently large number of measurements (minimum 10 in any subgroup). The purse seine is the only gear not selective for length. The hypothesis that the length frequency distribution for an age group is independent of number of past spawnings could not be rejected at the 5% level (Table 2).

When studying changes in other biological parameters (e.g. age composition and length at age), gear selectivity cannot be disregarded as a major source of bias. Here the data from the long line catches have been used since the time-series for long line is comprehensive and number of samples and geographical

coverage are usually better than for the other gears. For each year all samples were pooled. Even though long line is size selective (Sætersdal, 1963; Ralston, 1982), its selectivity is assumed to have changed relatively little over the period.

### 3. RESULTS

#### 3.1. Changes in age at maturity

Percentage mature by age was calculated for each of the year classes 1923 to 1976, initially without adjusting for unequal fishing mortalities (Table 3). A trend towards maturation at younger ages is seen. Median age at maturity ( $A_{50}$ ), as read from ogives fitted by eye, has declined by approximately 2.5 years over the year classes 1923 to 1976 (Fig. 1), from 10.5 to 8 years ( $p < 0.001$ ,  $n = 54$ ; Mann trend test (Lehman, 1975)). For the year classes 1923 to 1950,  $A_{50}$  varied between 9.2 and 10.9 years, with an average of 10.2 years. No marked overall trend in  $A_{50}$  is apparent for these year classes, but comparatively large short-term fluctuations are seen, the more conspicuous being the low values for the 1926 and 1927 year classes. The long-term reduction has consequently primarily affected the year classes 1950 and later, the decline over the year classes from 1958 to 1970 being almost monotonous.

Parallel to the reduction in median age at maturity, a decrease was observed in the interquartile range ( $A_{75} - A_{25}$ ) of the fitted maturity ogives, the overall reduction being of the order 1 year (Fig. 2). This significant trend ( $p < 0.001$ ,  $n = 54$ ; Mann trend test) indicates that the transition from immature to mature state happened over a progressively shorter age range. A reduction in the total age range over which fishes mature has also been observed, primarily because no fish matured for the first time at old ages in more recent years (Table 3).

The estimation of maturity ogives for each sex separately showed that males generally mature at younger ages than females (Table 4, Fig. 3). The difference became smaller over the

period studied (Fig. 4), the decline in the difference between median age at maturity being significant ( $p < 0.001$ ,  $n = 33$ , Mann trend test). Ogives for some year classes have not been computed because the number of observations for each sex is too small.

Calculations based on data adjusted for unequal fishing mortalities show trends similar to those described above (Table 5, Figs. 5 and 6). However, the results now indicate maturation at younger ages, the  $A_{50}$ -values generally being 0.5 to 1 year lower. The overall change in age at maturity is still 2.5 years. Some short-term trends are different, notably the increasing median age at maturity at for the 1965-1968 year classes. Moreover, the declining trend in the interquartile range is less pronounced, but still significant ( $p < 0.01$ ,  $n = 39$ , Mann trend test ).

### 3.2. Changes in other biological parameters

Mean age in the spawning population decreased notably from 1930 to 1987 (Fig. 7A). The overall reduction is approximately equal to the change in median age at maturity. The larger part of the reduction took place between 1950 and 1970. In the 1970- and 1980-ies large year-to-year variations were observed, but there was no apparent trend. Mean length increased slightly up to 1960 (Fig. 7B), then decreased, but with year to year variations being comparatively large. The overall reduction from 1932 to 1987 was, however, no more than 5 cm.

The proportion of first time spawners has increased markedly over the period 1932 to 1987 (Fig. 8), the trend being highly significant ( $p < 0.001$ ,  $n = 56$ , Mann trend test ). Between 1932 and 1955 approximately half of the spawners caught by long line were first time spawners. By the end of the 1960's this proportion had increased to 90%. From 1960 onwards the average percentage first time spawners has been around 80, but with marked year-to-year variations.



The time-series of mean length at age of first time spawners shows a trend towards increased length at age over the period 1932-1987, the trend being more pronounced for the older age groups (Fig. 9). Between 1935 and 1944/1945 a marked reduction in length at age of approximately 10 cm was observed for all age groups. The 1938 year class had by far the smallest mean length at age observed over the period. From 1945 to 1950 mean length at age increased again, back to its 1935 level. For the period 1950 to 1980 an overall increase of 5-7 cm is seen for the 9 and 10 year old fish, while no clear tendency is evident for the 6-8 year old first time spawners. An increased length at age of 10-15 cm is seen for all age groups in the 1980's and affects the year classes 1977 and later.

#### 4. DISCUSSION

##### 4.1 Evaluation of method and data

The central underlying assumptions of the analysis are that age and number of spawnings are correctly determined from the otoliths. Age determinations of Northeast Arctic cod using otolith readings were initiated by Rollefsen (1933). The readings have been validated by tracking of particularly strong year classes over a series of years. No estimates of the precision or the accuracy of the age determinations are available, but incorrect ageing of the cod is not considered a major source of error.

The calculation of age at first spawning is based on the identification of spawning zones in the otolith (Rollefsen, 1933; Williams and Bedford, 1973). According to Williams and Bedford (1973) the identification of first time spawners caught at the time of spawning or soon after generally presents problems. For the Lofoten fishery however, only mature specimens of the Northeast Arctic cod are caught and fish without spawning zones are classified as first time spawners. Fish spawning for the first time as young and small are those which present the greatest difficulty in reading the number of

spawning zones in subsequent years, while those spawning for the first time at an old age can more easily be determined (Williams and Bedford, 1973). Thus, the determination of age at first spawning might become less accurate as a consequence of the reduction in age and size at maturity.

Hence, the interpretation of the zonation of the otolith is no doubt to some extent subjective. With an experienced reader, however, consistency in the interpretation of zones is probably achieved. For the cod data from Lofoten, otoliths have been read on a routine basis by experienced technicians. Specifically, the same person read the data over a period of 30 years from 1950 until 1980. Even if absolute values of age and number of spawning zones are biased, long-term trends should thus be reliable.

The method used for backcalculation is based on information on percentage of first time spawners at each age. For the older age groups the number of fish are sometimes low and the percentages not well defined. Moreover, fish maturing for the first time at a low age were often totally missing in the older age groups. Consequently no correction for a higher mortality rate could be applied to these groups. This may have caused overestimation of the proportion of first time spawners for the older age groups. The computed percentage of mature fish at each age will therefore probably be underestimates.

#### 4.2 Evaluation of the results

A summary of the maturity ogives for the Northeast Arctic cod by other authors show a trend similar to that found in this study (Fig. 10). However, the estimated percentages mature at age usually differ. The ogive by Garrod (1967) for the years 1941 to 1953 is based on a subset of the data used in this analysis. Unfortunately, no details of the method of computation is given, but the estimated percentages mature at age are somewhat lower compared to those presented in Tables 3 and 5 of this paper, especially for the older ages. The ogives

based on trawl surveys (Ponomarenko et al., 1980; Ponomarenko and Yaragina, 1981) generally indicate a higher percentage mature for the younger ages and a lower percentage for the older ages, relative to those found here. This discrepancy is probably partly a result of using pooled but unweighed data from geographical areas with different percentages mature at age. Also, the values for the oldest age groups are based on a small number of specimens. The modified mesh assessment model (Hysten and Rørvik, 1983) indicate maturation at older ages, probably a consequence of the selection curve used.

A marked change towards maturation at younger ages in the 1980-ies is indicated in Fig. 10 by the ogives calculated by combining acoustic estimates of abundance and data on maturation from trawl surveys (Hysten and Nakken, 1982, 1983, 1984, 1985). This rapid change is also reflected in the present results, although a comparison for the younger ages is possible for 1982 only. The major discrepancy is the much higher percentages mature for the age groups 4-7 compared to the results based on data from the spawning area. The age composition in the spawning stock estimated from the 1985 ogive (Hysten and Nakken, 1985) and stock numbers by VPA (Anon., 1986), is not reflected in the catches by any of the gears used at Lofoten (Table 6). Tagging experiments (Sætersdal and Hysten, 1959; Godø, 1984) and examination of the otolith structure (Trout, 1957) indicate that fish from the Spitzbergen-Bear Island area mainly spawn south of the Lofoten area. According to Ponomarenko et al. (1980) cod from these waters mature at a younger age than cod from the Barents Sea, but this component of the Northeast Arctic cod stock is small compared to that in the Barents Sea (Hysten and Nakken, 1982, 1983, 1984, 1985). A considerable spawning has however taken place on the grounds between Lofoten and Sørøy in recent years (Sundby and Bratland, 1986). Thus, either the percentages mature for the youngest age groups are overestimated by Hysten and Nakken (1982, 1983, 1984, 1985) or these age groups spawn mainly outside the Lofoten grounds.

A change in age at maturity has been observed for other cod stocks as well. Both size and age at maturity declined in the

West Greenland stock from 1917 to 1936 (Hansen, 1949). In the North Sea, maturity was reached at smaller sizes in the 1970-ies than in 1893 and 1924 (Oosthuizen and Daan, 1974). No indications of growth changes have been found since the prewar years (Daan, 1974), and there has consequently also been a reduction in age at maturity. On the Scotian Shelf, median age at maturity declined by 50% (2-3 years) between 1959 and 1979 for most of the cod stocks (Beacham, 1983). Maturation at younger ages and smaller sizes for males than for females is reported for the Northeast Arctic cod (Rollefsen, 1938; Ponomarenko et al., 1980) and cod in other regions (e.g. Gulf of St. Lawrence, Powles, 1958; Scotian Shelf, Beacham, 1983; North Sea, Oosthuizen and Daan, 1974; Baltic, Thurov, 1970). A shorter age range for the transition from immature to mature state and smaller differences in age at maturity in more recent years were noted in the cod stocks on the Scotian Shelf (Beacham, 1983).

The long-term decline in age at maturity observed for the Northeast Arctic cod is thus similar to that observed for other stocks, and also in other studies on Northeast Arctic cod. The accuracy of the estimated percentages mature at age is difficult to assess. Generally, correcting for unequal fishing mortality of mature and immature results in a better agreement between the maturation ogives deduced from the data from the Lofoten spawning fishery and those based on trawl surveys.

#### 4.3. Possible causes and consequences

The Northeast Arctic cod has been intensively fished, especially since the 1950-ies, and the biomass of the stock has declined markedly (Bergstad et al., 1987). Simultaneously an overall reduction in the mean age of the spawning population has been observed, probably as a direct consequence of the increased rate of exploitation. However, this change cannot account for the decline in median age at maturity. An increased mortality will reduce the abundance of old fish, but not lead to a lower percentage of immatures for these age groups. If

mortality is higher for matures than for immatures, an increased proportion of first time spawners at age would be expected as survival decreases.

Length at age has increased for both juvenile and mature cod over the period 1932-1987 (Borisov, 1978; Ponomarenko *et al.*, 1980; Fig. 9). For the mature individuals the change is most marked for the old fish. The increased growth may be caused by less competition for food as a consequence of the reduced abundance. This would also explain the larger change for the old fish, as these are the more strongly decimated age groups. An increased growth rate is usually associated with maturation at a lower age (Molander, 1925; Alm, 1959; Donaldson, 1970) and is considered the mechanism whereby increased mortality is compensated for without any mediation of genetic changes (Nikolsky, 1963; Weatherley, 1972). No study has documented that the growth of Northeast Arctic cod is density-dependent, nevertheless it seems reasonable to assume that the the reduction of the recruited stock by more than 75% over 30 years has affected the availability of food.

The short-term variation in median age at maturity is not well reflected in length at age of first time spawners, except for the marked increase of length at age in the 1980-ies. Variations in length at age is probably not an accurate measure of changes in growth rate, and on a finer scale, several factors affect the maturation process. Thus, year-to-year variations in age at maturity cannot be explained adequately by variations in length at age.

According to Allendorf, Ryman and Utter (1987), exploitation affects the genetic composition of fish populations. Moreover, observed changes in age and length at maturity in some cod stocks have been attributed to genetic selection by harvesting (Borisov 1978; Beacham 1983). If selective fishing leads to an increase of the relative reproductive contribution of individuals with a genetic makeup for maturation at a low age, then this can cause a reduced median age at maturity. The few heritability estimates available for fish species, are gen-

erally much lower than for other vertebrates (Allendorf et al., 1987). The phenotypic variation is however larger (Allendorf et al., 1987). The environmental component of phenotypic variation thus seems to be more important than the genetic component.

The prediction of genetic change due to fishing requires knowledge of the genetic basis for the trait selected, and also of how fish with this trait are differentially harvested. The response to selection is dependent on the selective properties of the gear and a number of interrelated biological parameters, e.g. growth rate, fecundity, age and size at maturity and mortality rates (Nelson and Soulé, 1987). If age at maturity is heritable, and the harvest differential is the time fished before maturation, then other factors being equal, early maturing fish will be at a selective advantage, with a higher probability to reproduce before being caught and having a shorter generation time. However, age at maturity is usually correlated with growth rate, so that the early maturing fish is vulnerable to fishing earlier. For cod, individuals maturing at a higher age are larger and have higher fecundity since fecundity is a function of size and not age (Kjesbu, 1988a). The fact that cod is iteroparous further complicates the picture. As long as the gain in fecundity by postponing maturation balances a longer generation time and a decreased probability of reproducing, fish with a genetic makeup for late maturation will not be selected against.

Borisov (1978) demonstrated by simulation that for a low fishing intensity (survival rate 0.65), the ratio of reproductive output from early (6-7 years old), medium (8-10 years old) and late maturing (11 years and older) subgroups of Northeast Arctic cod remained constant over time. With increasing mortality, the contribution of late maturing, and to a lesser extent medium age maturing fish, was rapidly reduced. With a total annual mortality of 70%, fish maturing late made an insignificant contribution to reproduction.

Since the changes predicted by life-history theory as a result of intensified exploitation and reduced abundance are exactly

the same as expected from phenotypic compensatory mechanisms, observed changes in length and/or age at maturity per se are no proof of genetic changes (Nelson and Soulé, 1987). Moreover, with the lack of knowledge of heritability in cod and the large impact of the environment on the phenotypic variation, a hypothesis of genetic changes cannot be substantiated. This conclusion is furthermore supported by the observation that percentage mature at length has changed little between 1930 and 1978-1980 (Ponomarenko and Yaragina, 1981).

Concern has been expressed that the rejuvenation of the spawning population may have adverse consequences on the reproductive fitness of the Northeast Arctic stock of cod (Borisov, 1978). Small fish have a lower relative fecundity than bigger individuals and fecundity is a function of length rather than age (Kjesbu, 1988a). In addition, egg size has been shown to increase with size of the female in farmed cod (Kjesbu, 1988b) and larval size and survival are positively correlated with egg size in Northeast Arctic cod (Knutsen and Tilseth, 1985). Consequently, for a given spawning stock biomass, the one with the higher mean length of spawners must be assumed to be more valuable. However, the long line catches indicate that the age structure, rather than the size distribution of the spawning stock has changed. Thus, the relative fecundity per unit of stock biomass has increased as a result of a shorter generation time without survival of eggs and larvae being negatively affected by the reduction in age at maturity. The response of the stock is therefore probably an adaptation to the increased mortality.

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Table 1 . Number of fishes aged in the samples collected from the spawning fishery at Lofoten in the period 1932-1987 for the various gears used. The purse seine data from 1956 onwards are from research catches, otherwise all data have been sampled from commercial catches. Only samples collected between 1 January and 30 April have been included

Sampling gear	Sampling year													
	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945
Long line	397	866	1096	1401	1323	2401	1346	2771	1177	694	701	1127	1282	714
Gill nets	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hand lines	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Danish seine	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Purse seine	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Long line	1019	1074	1512	1854	2508	3255	3152	3198	2632	3883	3520	3151	3846	3967
Gill nets	0	0	134	54	95	372	870	1535	530	124	404	0	282	282
Hand lines	0	0	0	0	0	307	31	0	0	168	0	0	44	0
Danish seine	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Purse seine	0	0	0	0	0	849	1904	0	637	822	1148	74	0	274
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Long line	2709	4330	3699	2896	1083	2019	1293	2031	949	890	3114	2049	1797	2130
Gill nets	508	225	866	834	573	322	1106	831	384	194	625	1514	585	870
Hand lines	0	0	0	0	0	0	27	135	30	122	183	235	93	190
Danish seine	0	0	0	49	174	6	47	0	163	199	295	365	200	220
Purse seine	0	684	380	428	413	187	77	244	351	220	574	1145	593	1042
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Long line	167	892	297	204	354	502	318	1398	1243	490	725	546	294	224
Gill nets	1372	432	787	807	240	894	584	1960	1422	1324	881	680	620	505
Hand lines	134	171	351	188	424	61	172	878	1014	705	558	172	32	237
Danish seine	165	236	309	0	250	148	219	606	1020	650	568	512	140	119
Purse seine	1136	908	996	561	295	300	545	1339	360	1045	310	593	450	0

Table 2. Comparison of length frequency distributions of fish with a different age at first maturity, but of the same age. The null hypothesis of no difference between the length distributions was tested using a Kolmogorov-Smirnov test (Lehman 1975). YEAR and AGE refer to year and age when caught, SPG is the spawning groups (i.e. fishes spawning for the first time, second time etc) and N is the number of observations in each spawning group (as defined above).

YEAR	AGE	SPG	N		Spawning groups compared					
					1,2	1,3	1,4	2,3	2,4	3,4
1961	11	1	78	statistic	0.113	0.111	-	0.086	-	-
		2	105	p-value	0.224	0.258	-	0.296	-	-
		3	61							
1972	9	1	100	statistic	0.221	-	-	-	-	-
		2	86	p-value	0.067	-	-	-	-	-
1973	10	1	86	statistic	0.139	0.263	0.270	0.142	0.167	0.157
		2	105	p-value	0.170	0.075	0.149	0.210	0.257	0.286
		3	46							
		4	18							
1974	11	2	57	statistic	-	-	-	0.094	0.123	0.085
		3	68	p-value	-	-	-	0.301	0.237	0.300
		4	84							
1980	10	1	38	statistic	0.153	0.140	0.184	0.192	0.105	0.246
		2	54	p-value	0.235	0.268	0.256	0.168	0.347	0.182
		3	47							
		4	19							

TABLE 3. Percentage mature fish by age for the year-classes 1923 to 1976. No percentages less than one are given.

YEAR-CLASS	AGE									
	6	7	8	9	10	11	12	13	14	15
1923			2	10	37	59	84	100	100	100
1924			3	20	50	85	98	100	100	100
1925			3	18	45	71	86	93	100	100
1926		1	13	41	77	93	96	100	100	100
1927		5	20	48	69	83	96	100	100	100
1928		4	19	39	57	79	92	96	100	100
1929		4	14	30	59	79	92	98	100	100
1930		2	6	23	48	79	88	100	100	100
1931		1	6	14	32	54	70	90	100	100
1932			3	14	32	55	75	86	96	100
1933			2	12	33	60	93	98	100	100
1934			2	13	27	59	87	97	100	100
1935			5	16	39	66	92	99	100	100
1936			3	15	40	71	92	98	100	100
1937			2	13	36	70	89	99	100	100
1938			2	11	45	81	98	99	100	100
1939			3	17	48	74	86	100	100	100
1940			4	21	46	71	95	100	100	100
1941			6	22	47	78	97	98	100	100
1942		2	9	28	55	83	95	100	100	100
1943		2	10	29	58	85	93	98	100	100
1944		2	10	29	61	82	93	100	100	100
1945		1	6	22	39	59	83	100	100	100
1946			4	14	31	55	87	100	100	100
1947		1	2	9	22	52	82	100	100	100
1948		1	4	13	35	70	97	100	100	100
1949			1	8	34	73	95	100	100	100
1950			3	19	56	93	97	99	100	100
1951			6	27	74	92	96	100	100	100
1952		1	7	36	73	93	97	100	100	100
1953			6	32	59	85	94	100	100	100
1954		1	9	34	72	95	98	100	100	100
1955		1	10	38	70	85	100	100	100	100
1956		1	8	36	67	100	100	100	100	100
1957			6	24	60	100	100	100	100	100
1958			2	13	51	76	94	100	100	100
1959				11	60	98	100	100	100	100
1960			1	29	85	100	100	100	100	100
1961			7	55	87	94	98	100	100	100
1962			8	52	80	95	100	100	100	100
1963		2	20	60	93	99	100	100	100	100
1964		2	20	63	88	98	100	100	100	100
1965		5	36	70	98	100	100	100	100	100
1966		5	23	59	100	100	100	100	100	100
1967		2	12	40	79	95	100	100	100	100
1968		5	24	55	95	100	100	100	100	100
1969		5	25	69	95	100	100	100	100	100
1970		6	32	71	97	100	100	100	100	100
1971		6	27	68	98	100	100	100	100	100
1972		5	29	84	100	100	100	100	100	100
1973		8	46	96	100	100	100	100	100	-
1974		11	59	88	99	100	100	100	-	-
1975	3	31	65	96	100	100	100	-	-	-
1976	7	25	65	97	100	100	-	-	-	-

TABLE 4. Percentage mature fish by age and sex for the year-classes 1923 to 1976. Some year-classes have been left out because of insufficient data. No percentages less than one are given. (M= males, F= females).

YEAR-CLASS	SEX	AGE									
		6	7	8	9	10	11	12	13	14	15
1927	M		8	25	56	75	87	100	100	100	100
	F		3	16	44	67	82	95	100	100	100
1928	M		8	32	55	72	93	100	100	100	100
	F		3	13	32	51	73	89	93	100	100
1929	M		5	18	35	63	84	91	100	100	100
	F		2	11	28	57	76	92	97	100	100
1930	M		3	10	33	59	86	97	100	100	100
	F		1	4	18	44	75	84	100	100	100
1931	M		2	11	24	54	84	94	100	100	100
	F			4	10	24	45	61	88	100	100
1932	M		1	5	19	42	67	87	100	100	100
	F			2	10	27	48	67	78	94	100
1933	M			4	18	45	76	100	100	100	100
	F			1	8	26	52	87	98	100	100
1934	M			3	17	36	65	86	95	100	100
	F				10	21	52	86	96	100	100
1935	M		1	8	20	43	70	86	92	100	100
	F			3	13	34	60	92	98	100	100
1936	M			5	22	58	85	95	97	100	100
	F			1	11	30	64	89	99	100	100
1937	M			4	22	52	84	94	100	100	100
	F			1	8	29	62	87	99	100	100
1938	M			6	22	57	89	98	100	100	100
	F				6	39	77	97	97	100	100
1939	M			7	25	56	78	85	100	100	100
	F			2	12	43	72	88	100	100	100
1940	M			5	26	54	76	97	100	100	100
	F			3	18	41	68	92	100	100	100
1941	M		1	10	34	57	82	100	100	100	100
	F			4	16	40	75	95	98	100	100
1942	M			4	17	40	71	91	100	100	100
	F			6	20	45	78	93	100	100	100
1943	M		4	17	41	66	92	100	100	100	100
	F			6	22	53	83	91	97	100	100
1944	M		4	13	38	69	84	100	100	100	100
	F		1	8	24	57	80	90	100	100	100
1945	M		3	13	43	66	81	100	100	100	100
	F			4	16	34	56	82	100	100	100
1947	M		2	6	14	30	62	100	100	100	100
	F			2	7	21	50	78	100	100	100
1948	M		2	6	15	35	79	97	100	100	100
	F			3	12	34	68	97	100	100	100
1949	M			2	10	40	78	100	100	100	100
	F			1	7	31	72	94	100	100	100
1950	M		1	5	25	63	94	100	100	100	100
	F			3	18	55	95	98	100	100	100
1951	M			8	34	78	100	100	100	100	100
	F			5	25	75	92	97	100	100	100
1952	M		2	8	43	81	96	100	100	100	100
	F			6	34	70	92	97	100	100	100
1954	M		1	14	43	86	100	100	100	100	100
	F			8	33	72	97	97	100	100	100
1959	M			1	18	82	93	100	100	100	100
	F				9	53	100	100	100	100	100

Table 4. Continued.

YEAR-CLASS	SEX	AGE									
		6	7	8	9	10	11	12	13	14	15
1960	M			1	35	82	100	100	100	100	100
	F			2	26	85	100	100	100	100	100
1962	M			11	57	82	87	100	100	100	100
	F			7	51	79	97	100	100	100	100
1963	M		3	23	59	88	95	100	100	100	100
	F		2	19	59	95	99	100	100	100	100
1964	M		2	20	61	84	90	100	100	100	100
	F		1	19	63	90	100	100	100	100	100
1965	M		6	37	69	100	100	100	100	100	100
	F		4	34	70	96	100	100	100	100	100
1969	M	1	8	34	71	91	100	100	100	100	100
	F		4	21	67	96	100	100	100	100	100
1970	M		7	34	71	95	100	100	100	100	100
	F		4	26	65	88	90	100	100	100	100
1971	M		7	28	66	100	100	100	100	100	100
	F		4	26	68	97	100	100	100	100	100
1972	M		5	29	85	100	100	100	100	100	100
	F		3	29	82	100	100	100	100	100	100
1973	M		10	48	92	100	100	100	100	100	100
	F		6	42	97	100	100	100	100	100	100
1974	M		15	69	92	100	100	100	100	100	100
	F		8	54	87	99	100	100	100	100	100
1975	M		5	38	71	97	100	100	100	100	-
	F		2	25	62	96	100	100	100	-	-
1976	M		9	29	63	97	100	100	-	-	-
	F		5	20	65	97	100	-	-	-	-



TABLE 5. Percentage mature fish by age for the year-classes 1938 to 1976. Correction for unequal fishing mortality for mature and immature fish has been applied (see text for details).

YEAR-CLASS	AGE									
	6	7	8	9	10	11	12	13	14	15
1938			3	15	55	86	98	100	100	100
1939			6	25	60	86	92	100	100	100
1940			7	31	61	82	98	100	100	100
1941		1	11	36	61	88	99	99	100	100
1942		4	19	43	73	92	98	100	100	100
1943		5	21	48	74	93	97	99	100	100
1944		6	22	47	78	92	98	100	100	100
1945		4	15	43	64	81	95	100	100	100
1946		2	14	33	57	79	95	100	100	100
1947		4	11	25	47	74	91	100	100	100
1948		3	12	30	52	88	98	100	100	100
1949			4	13	41	81	98	100	100	100
1950		1	5	23	62	93	95	96	100	100
1951		1	8	35	83	95	98	100	100	100
1952		1	10	47	80	96	99	100	100	100
1953		1	10	39	67	90	98	100	100	100
1954		1	13	45	85	99	99	100	100	100
1955		3	17	53	76	83	100	100	100	100
1956		3	19	53	81	100	100	100	100	100
1957		2	14	42	82	100	100	100	100	100
1958			2	10	70	87	94	100	100	100
1959			2	20	72	99	100	100	100	100
1960			3	40	90	100	100	100	100	100
1961			12	63	91	94	95	100	100	100
1962		1	13	68	92	98	100	100	100	100
1963		4	33	78	97	100	100	100	100	100
1964		4	37	76	94	98	100	100	100	100
1965		12	48	82	99	100	100	100	100	100
1966	1	11	40	76	100	100	100	100	100	100
1967		7	30	66	83	97	100	100	100	100
1968		10	30	58	98	100	100	100	100	100
1969	1	8	31	84	99	100	100	100	100	100
1970	1	10	55	86	96	97	100	100	100	100
1971	1	20	53	84	98	100	100	100	100	100
1972	3	14	50	93	100	100	100	100	100	100
1973	2	20	65	98	100	100	100	100	100	-
1974	2	23	74	94	99	100	100	100	-	-
1975	8	46	77	98	100	100	100	-	-	-
1976	15	39	76	99	100	100	-	-	-	-

Table 6. Estimated age composition in the spawning stock in 1985 based on the maturity ogive given by Hysten and Nakken (1985) and VPA-estimates of stock size in numbers (Anon. 1987) compared with age composition in catches by trawl (survey data), long line, gill net and purse seine from the Lofoten. All fish of the age 10 and older have been pooled.

age	estimated	trawl	long line	gill net	purse seine
4	0.0	2.9	0.4	0.0	0.2
5	14.7	8.6	0.4	0.4	0.2
6	42.3	28.6	19.9	10.0	5.2
7	27.4	37.1	37.8	38.5	13.4
8	8.4	8.6	21.5	29.5	11.2
9	3.7	11.4	11.5	12.8	12.9
10+	3.6	2.9	8.6	8.7	57.0

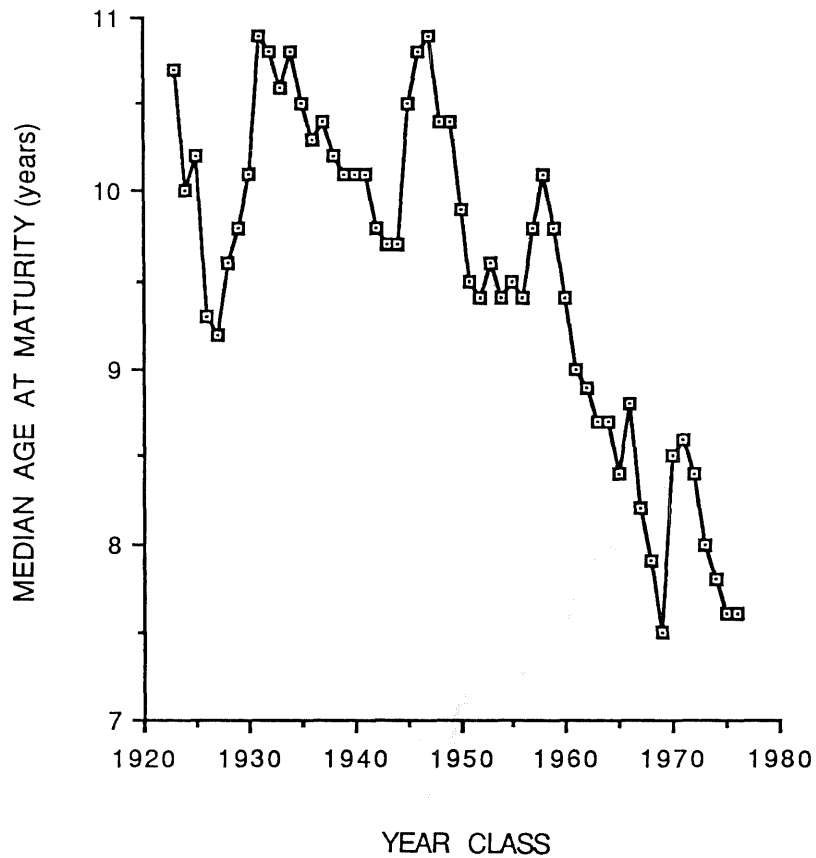


Fig. 1. Median age at maturity for the year classes 1923-1976.

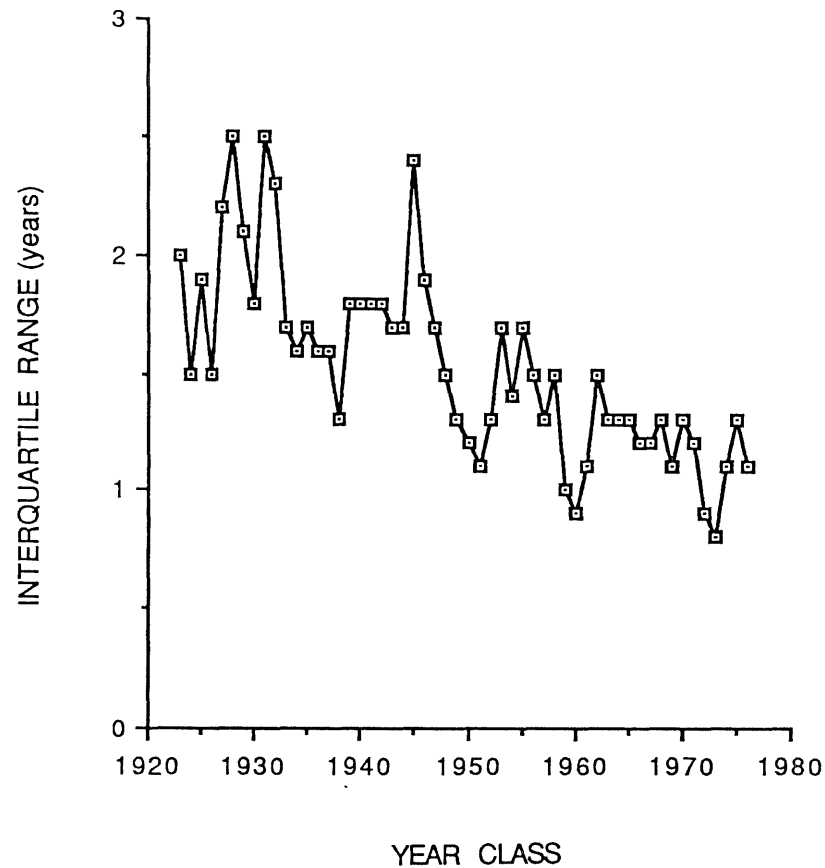


Fig. 2. Interquartile range ( $A_{75}-A_{25}$ ) of the maturity ogives for each of the year classes 1923-1976.  $A_{25}$  and  $A_{75}$  are the first and third quartile respectively.

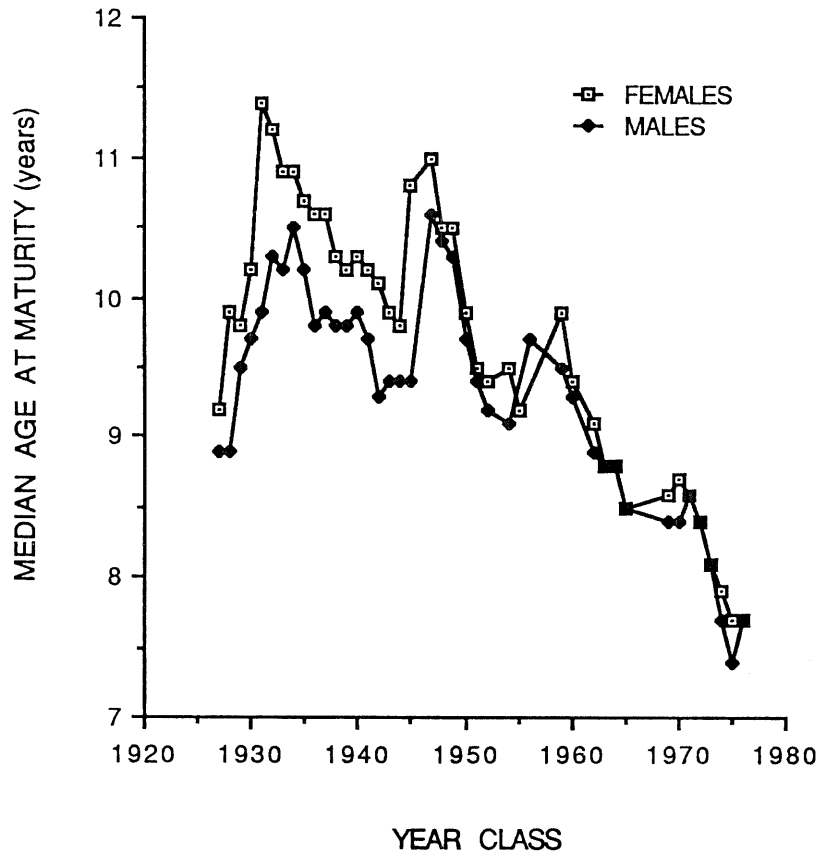


Fig. 3. Median age at maturity for males and females for the year classes 1927-1976.

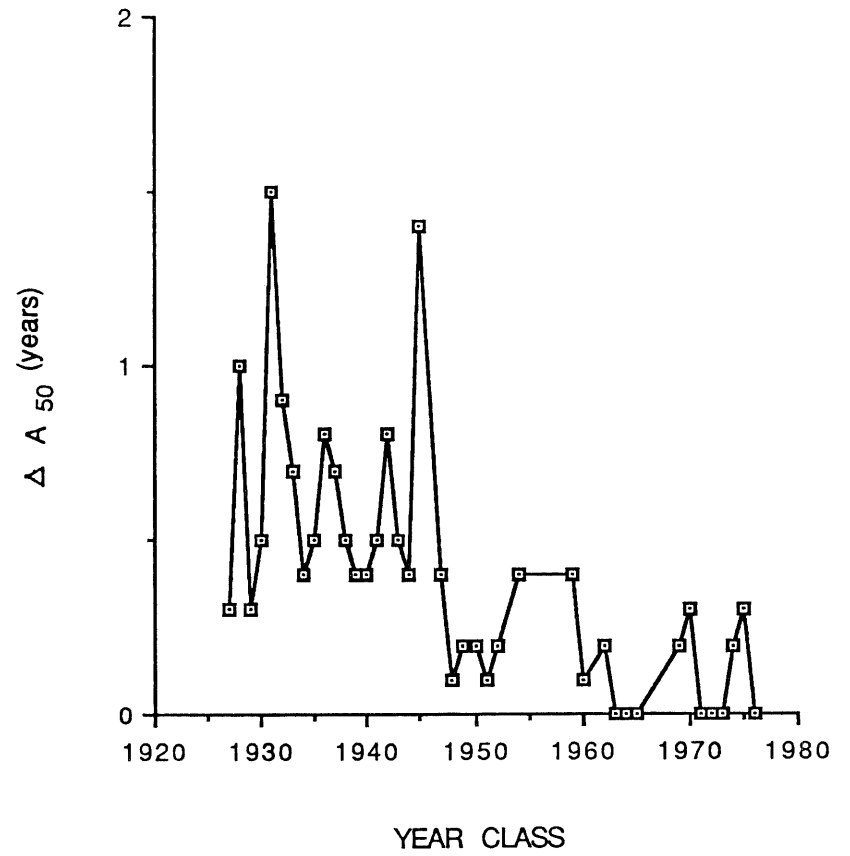


Fig. 4. Trend in difference between median age at maturity of males and females ( $\Delta A_{50}$ ) for the year classes 1927-1976.

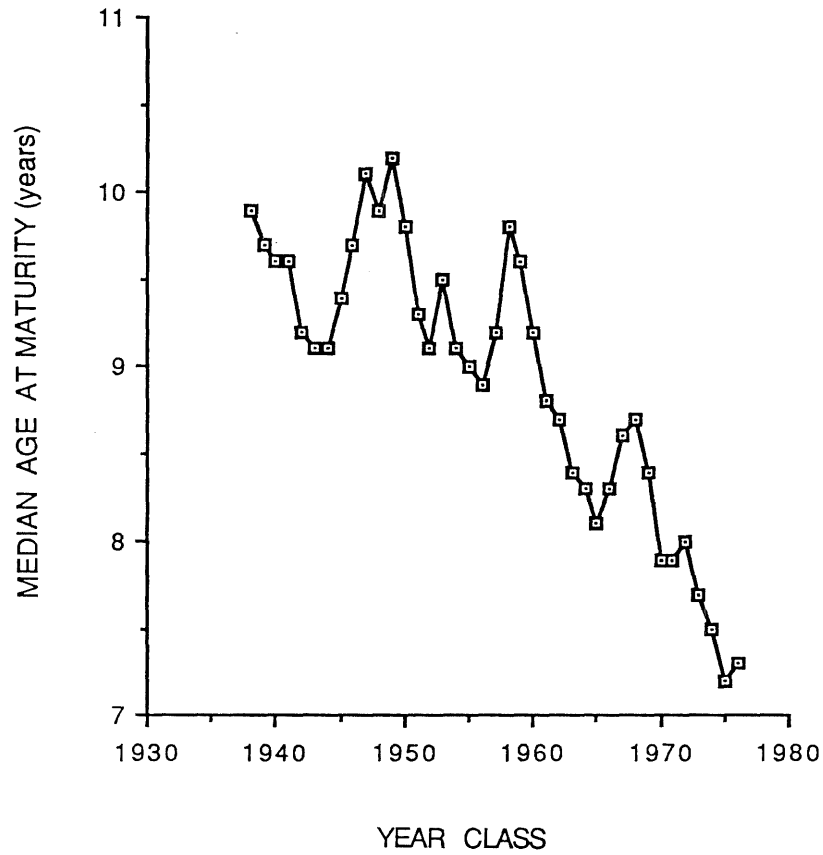


Fig. 5. Median age at maturity for the year classes 1938-1976 after adjusting for different fishing mortality for mature and immature fish.

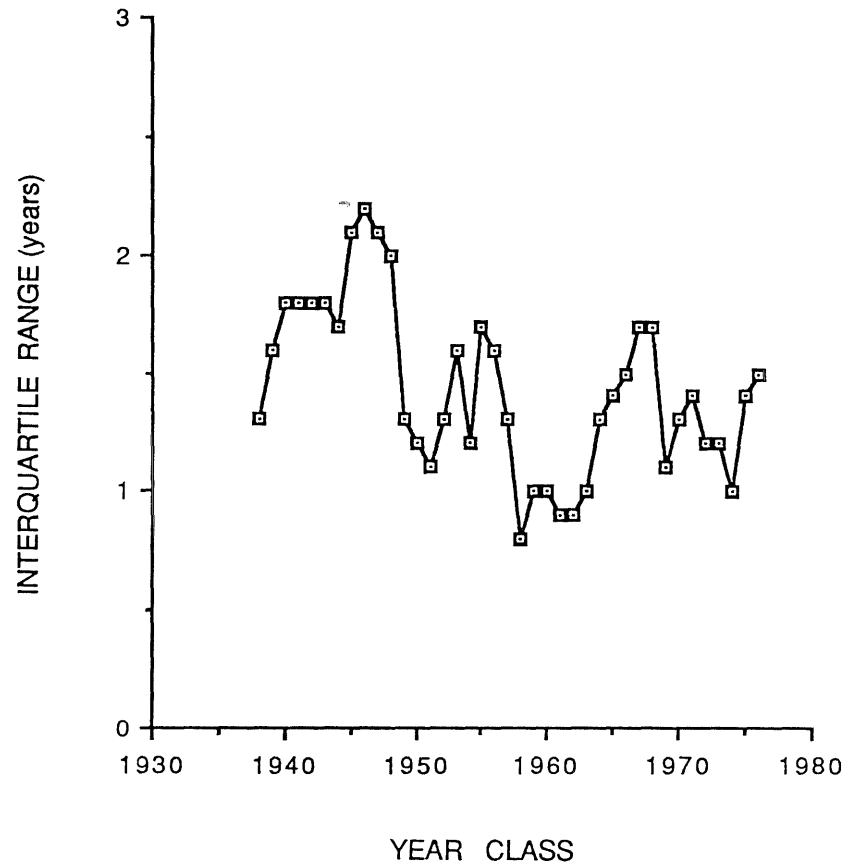


Fig. 6. Interquartile range of the maturity ogives for the year classes 1938-1976 after adjusting for different fishing mortality for mature and immature fish.

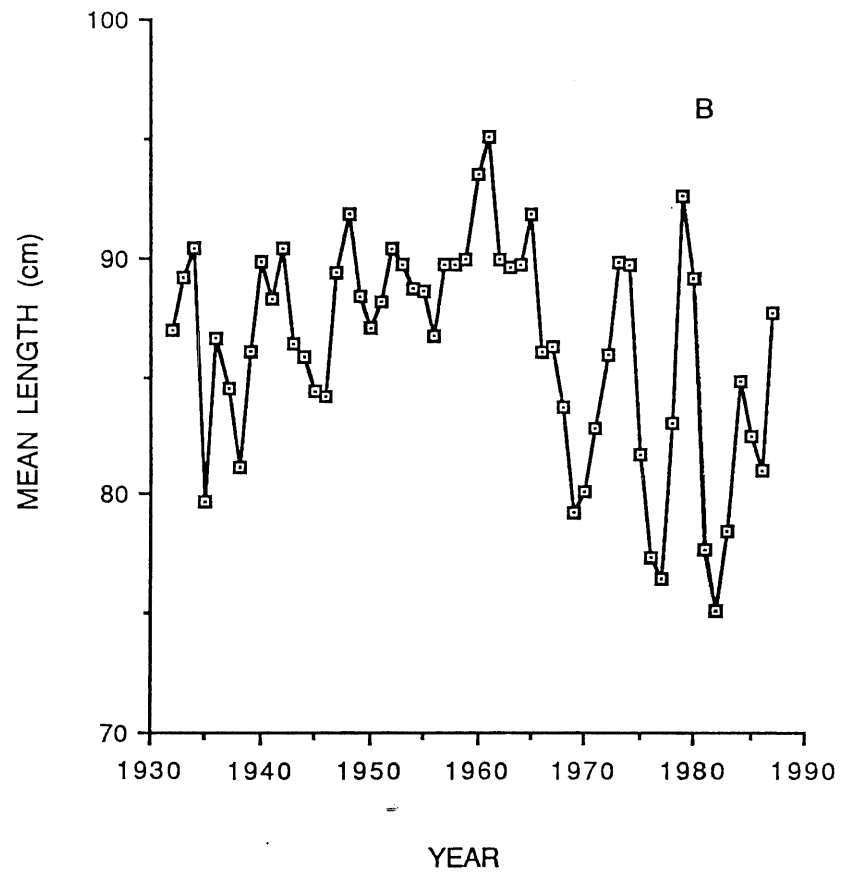
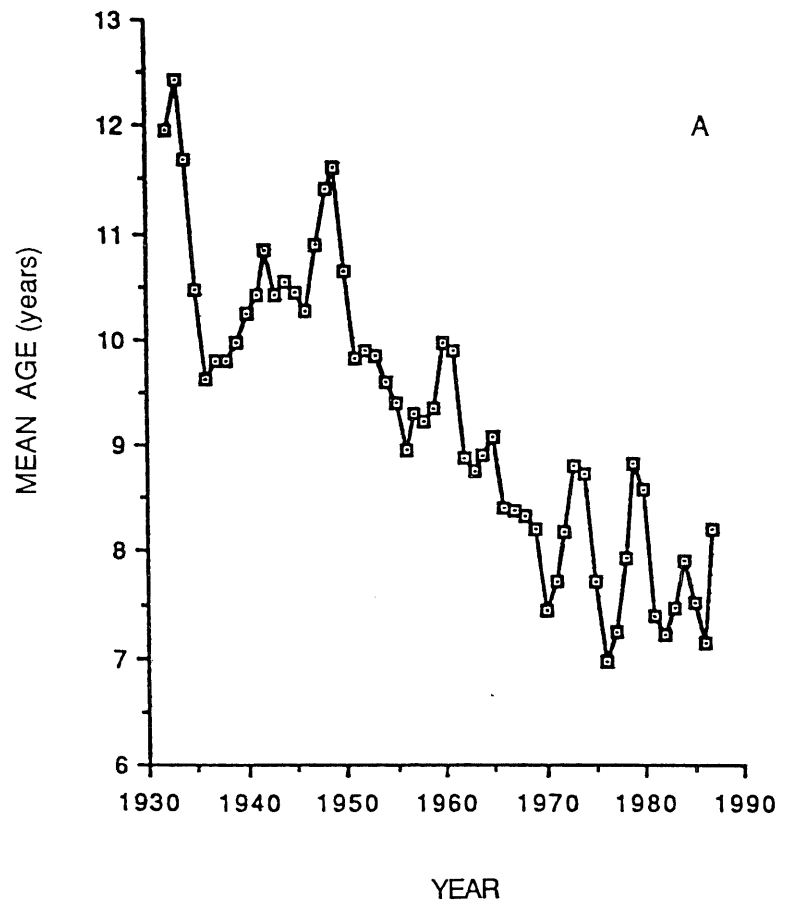


Fig. 7. Mean age (A) and mean length (B) of cod caught by long line in Lofoten during the spawning fishery.

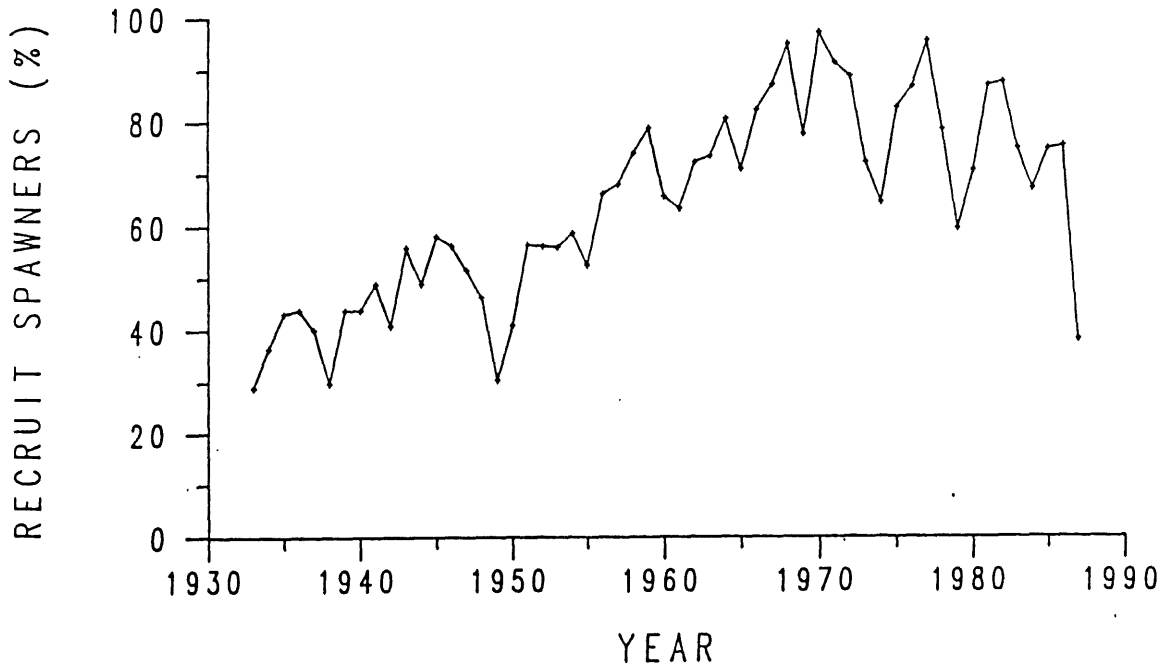


Fig. 8. Percentage first time spawners of cod in the catches by long line at Lofoten for the years 1932 to 1987.

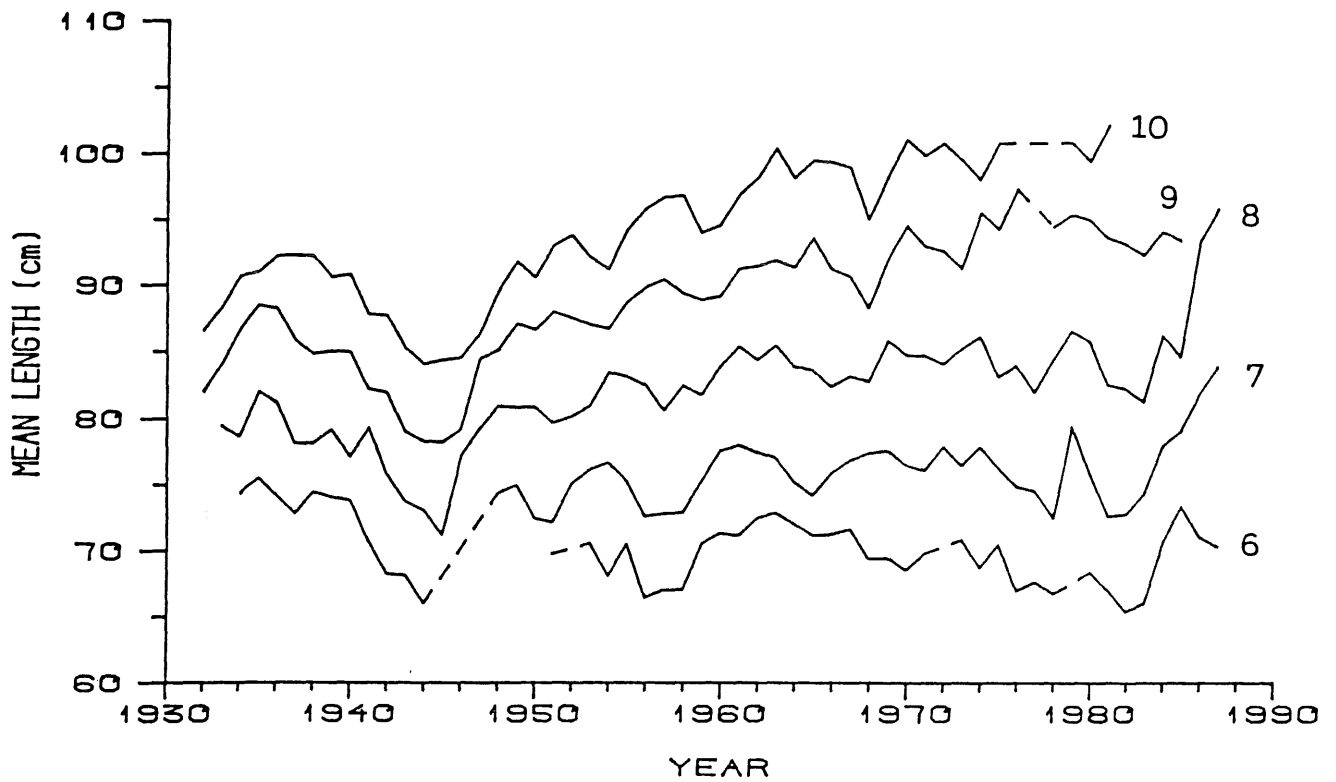


Fig. 9. Mean length at age of first time spawners of ages 6 through 10 caught by long line at Lofoten. All means are based on minimum 10 observations.

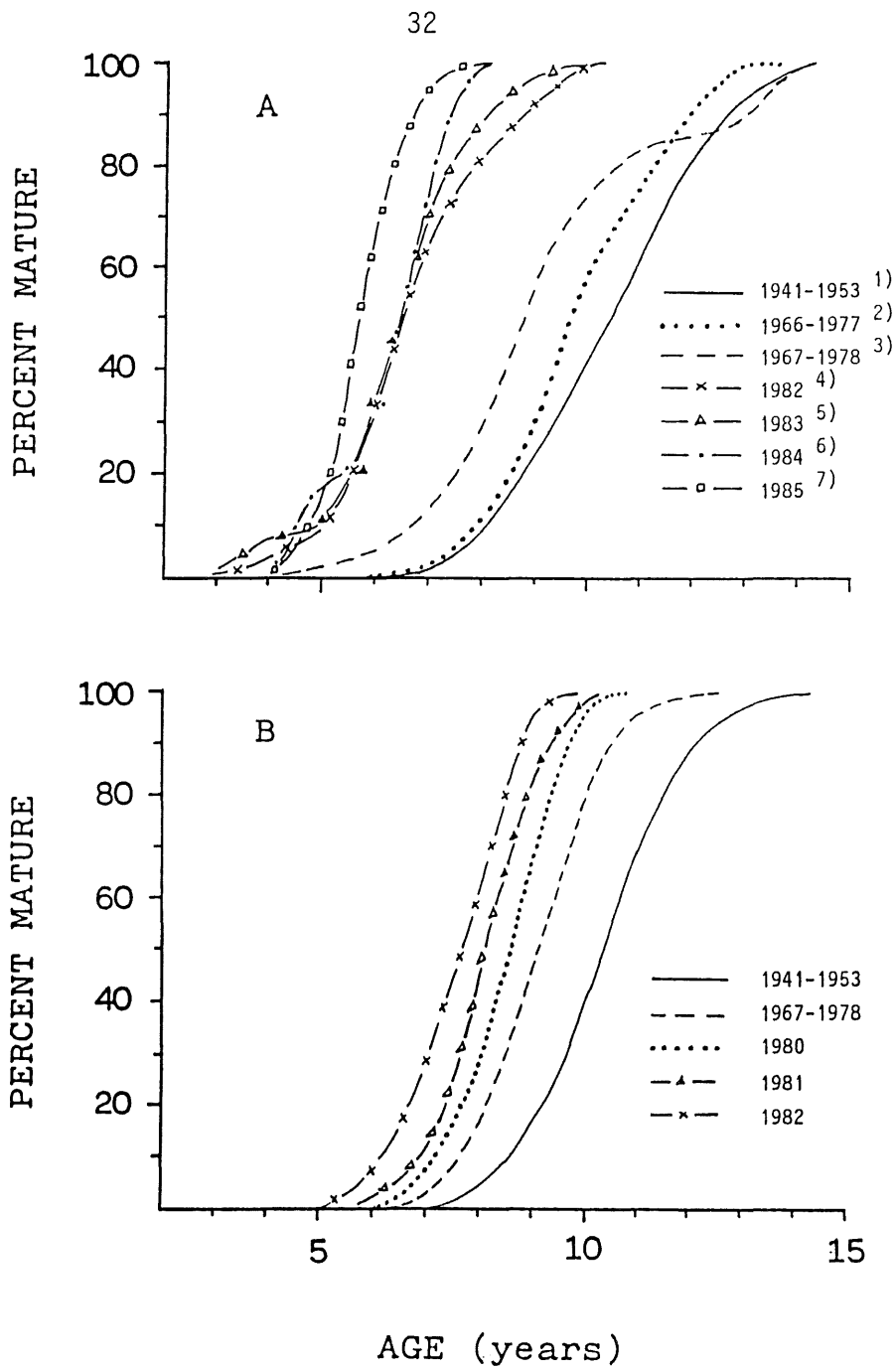


Fig. 10. Maturity ogives for Northeast Arctic cod for different years. A: From literature data, B: From Table 3. Legend for A: 1): Garrod(1967), 2): Hysten and Rørvik (1983), 3): Ponomarenko et al. (1980), 4): Hysten and Nakken (1982), 5): Hysten and Nakken (1983), 6): Hysten and Nakken (1984), 7): Hysten and Nakken (1985).