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Sexual Difference in Maturation of Northeast Arctic Cod

by

Adnan Ajiad, Tore Jakobsen and Odd Nakken
Institute of Marine Research,
P. O. Box 1870 Nordnes N–5024
Bergen Norway

ABSTRACT

Maturity at age and length of the Northeast Arctic cod was investigated based on survey data from the Barents Sea and Lofoten in 1989–1997, applying the maximum likelihood method. The growth rate of immature fish is approximately the same for both sexes, but males mature at younger age and smaller size and age and length at 50% maturity are less in males than in females. The maturity analysis indicates considerable interannual variations both in 50% maturity at age and length, percentage mature by age and in the mean length of first time spawners in both sexes. Mean length of the first time spawners increases substantially with age for both sexes, but early maturation coincides with increased length at age indicating that the maturity is influenced by both age and length. The possible link between observed variation in maturation and the consumption of capelin / cod biomass ratio is discussed.

INTRODUCTION

The relationship between spawning biomass (SSB) and recruitment is fundamental in the population dynamics of fish stocks. For management purposes minimum levels of SSB have been defined to reduce the risk of recruitment failure, and the SSB is at present probably the most important factor in management advice (Jakobsen, 1996). However a functional relationship between SSB and recruitment is generally difficult to establish and often appears to be non-existent. Myers et al., (1995) give an overview of 274 time series of SSB and recruitment with plots and analyses, demonstrating the variability in the apparent relationship and in the data and information available. Iles (1994) studied 20 flatfish stocks and found only 6 stocks which showed a functional relationship. Jakobsen (1996) analyzed 20 cod stocks and found substantial evidence of reduced recruitment at low levels of spawning stock biomass. Myers and Barrowman (1996) concluded that recruitment is a function of spawner abundance. Gilbert (1997) studied 153 marine fish stocks and 31 salmonid stocks and concluded that the dependency of SSB on previous years recruitment and the occurrence of periods of environmentally high and low recruitment in the time series could produce the appearance of a relationship between SSB and recruitment where none existed. Gilberts's results were contested by Myers (1997).

One of the reasons why a functional relationship is difficult to find is that even if recruitment is dependent on the SSB, it may also be affected by a number of other factors, e.g. climatic changes (Ottersen et al., 1994), ecology and environment (Jakobsen, 1996), production of large numbers of good quality eggs (Kjesbu et al., 1991), high total mortality from egg to recruit (Pepin and Myers, 1991) and fecundity. However, Mertz and Myers (1996) found no significant relationship between recruitment variability and fecundity in 38 marine fish species, including cod.

The factors above indicate that although SSB is important, it may not be an adequate measure for estimating the recruitment potential in a stock as demonstrated for Northeast Arctic cod by Marshall et al., (1998). The data available often limit the possibilities for exploring alternative measures. Nevertheless, considering the importance given to SSB in management advice, surprisingly little has been done to try to implement new knowledge about the recruitment processes in the measure of a stock's spawning potential (Ulltang, 1996).

The egg production is obviously an important factor in the recruitment process and Marshall et al., (1998) showed large deviations from proportionality between egg production and SSB. One logical step towards exploring the spawning potential is therefore to consider the sexes separately in the SSB. Sexual difference in growth and maturation is observed in many species, e.g. among the flatfishes. For

Northeast Arctic cod, differences in maturation have been observed (Jørgensen. 1989), but have been considered relatively unimportant and have been ignored in stock assessments.

Combination of survey data from the Barents Sea (nursery and feeding area) and from the Lofoten spawning grounds in recent years makes it possible to explore the maturation of the Northeast Arctic cod in more detail than previously. Based on survey data from the period 1989 to 1997, this study gives estimates of maturity ogives of Northeast Arctic cod for the sexes separately and discusses the results, their significance and factors which may affect the maturation process, including the cod's consumption of capelin.

MATERIALS AND METHODS

The data used in this study were collected by the Institute of Marine Research during surveys in the Barents Sea and in the Lofoten region in 1989–1997. Figure 1 shows the geographical position of trawl stations in 1996. The area covered and the number of stations have been similar in the other years, except for 1997 when the eastern part of the area was not covered. The Barents Sea survey, which gives both acoustic and bottom trawl abundance indices, is carried out in February (Jakobsen et al., 1997). The Lofoten survey (Korsbrekke, 1997) gives only acoustic abundance indices and is carried out in March, near the peak of the spawning season. The indices from the surveys are important input to the stock assessment and together the surveys cover most of the stock, although some cod, mainly young and immature, will still be in Svalbard region where the access in the winter is limited because of ice.

The raw data on cod comprise length, weight, sex, age and a coded indication of maturity stage. A five point maturity scale (Fotland et al., 1997) was used to determine maturity of each individual fish. Fish in stage 2 and 3 (maturing and spawning) were classified as mature and given a value of 1 in the analysis. Immature fish (stage 1) were given a value of 0. Fish in stage 4 (spent or resting) can be difficult to distinguish from immature fish and could comprise omission specimens. They are therefore excluded from the analysis together with fish classified as uncertain.

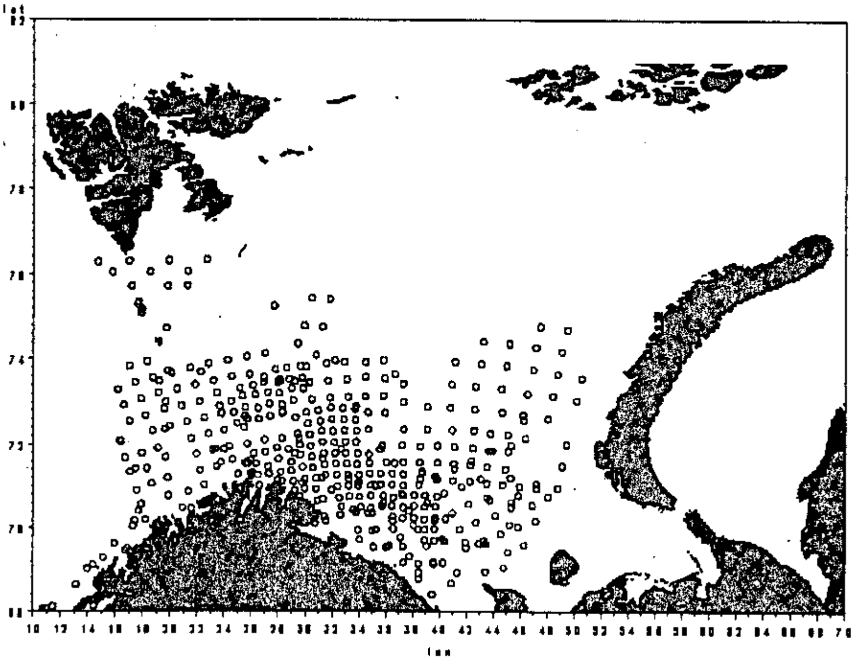

Fig. 1. Trawl stations in the 1996 survey.

The fish were grouped in 5 cm length intervals. The fraction mature at age and length by year and sex was calculated and a curve fitted to the observed values using logistic procedure with a logit link function by the method of maximum likelihood estimation using Fisher-scoring algorithm (SAS Institute Inc. 1996) where the number of mature individuals represents the number of events and the total number represents the number of trials. This method was selected as it is often more appropriate than ordinary least squares regression when the dependent variable is dichotomous, typically if the two outcomes are mature and immature (Stokes et al., 1995). The model used is:

$$logit(p) \equiv log\left(\frac{p}{1-p}\right) = \alpha + \beta x \qquad (1)$$

where p = predicted probability of the mature fraction, x is age or length, α and β are coefficients. The length and age at 50% maturity is estimated as (— α/β).

Data on cod biomass and capelin consumption are taken from the Arctic Fisheries Working Group report (ICES, 1998).

RESULTS

Geographical distribution of mature cod

Figure 2 shows how the fraction of mature cod varied with geographical area in the Barents Sea in the winter 1989–1997. Mature cod were dominating in the southwestern part of the area, reflecting the seasonal migration towards the spawning grounds farther south along the Norwegian coast. However, in 1994 and 1995 high fractions of mature fish are also observed between 35° and 45° E, close to the Murman coast.

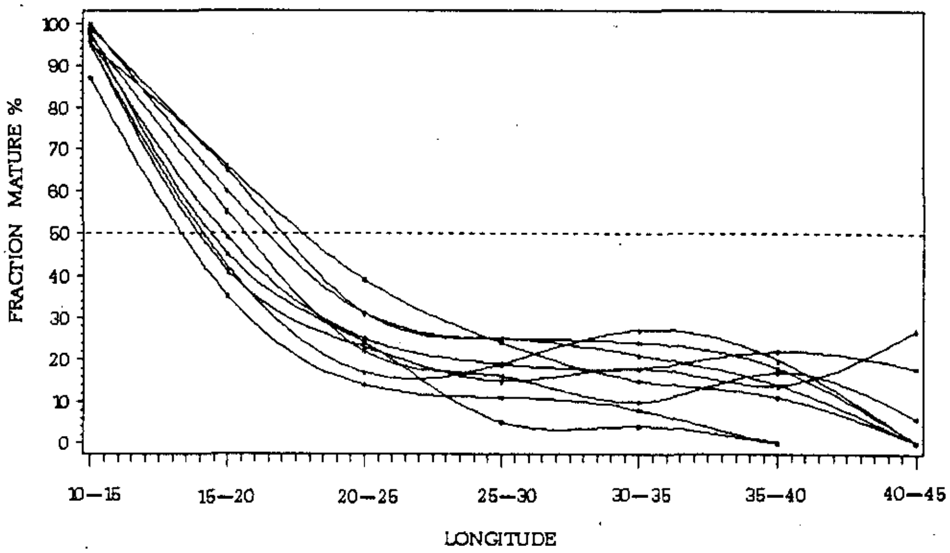

Fig. 3 Fraction mature versus longitude in 1989–1997.

Fig. 3 demonstrates how the percentage mature (including only cod >50cm) varies with longitude. In the westernmost part, at 10°E-15°E, between 90 and 100% were mature, but the percentage is decreasing rapidly eastward. East of 30°E it does not exceed 30% and is mostly in the range of 10–30%.

Time trends

Tables 1– 4 summarise the fraction mature and the total number of females and males sampled annually 1989–1997 by age and 5 cm length interval. There is a fairly consistent difference between the sexes with males on average reaching maturity at an earlier age and smaller length than the females. During these years the main changes have been for age 6 where the fraction mature for both sexes was considerably higher in 1992–1995 than in the years before and after (Tables 1 and 2). Thus, a temporary shift towards earlier maturation in 1992–1995 is indicated. This shift is only partly reflected at other ages and is difficult to see in the length data (Tables 3 and 4), probably because it is obscured by overlapping in length between age groups and variation in year class strength.

Results of the model fit are given in Tables 5 and 6. They are tabulated for each year and sex and show the parameter estimates with the associated standard error and the estimated age (Table 5) and length (Table 6) at 50% maturity. The shift towards earlier maturation in 1992–1995 is reflected in the age data, but not in the length data.

Figure 4 is a plot of age at 50% maturity against length at 50% maturity. This plot seems to indicate that there is a strong linear correlation between age and length at 50% maturity. However, the apparent correlation is to a large extent caused by the fact that the ratio between age and length at 50% maturity is similar for females and males, and is not so strong if the sexes are considered separately.

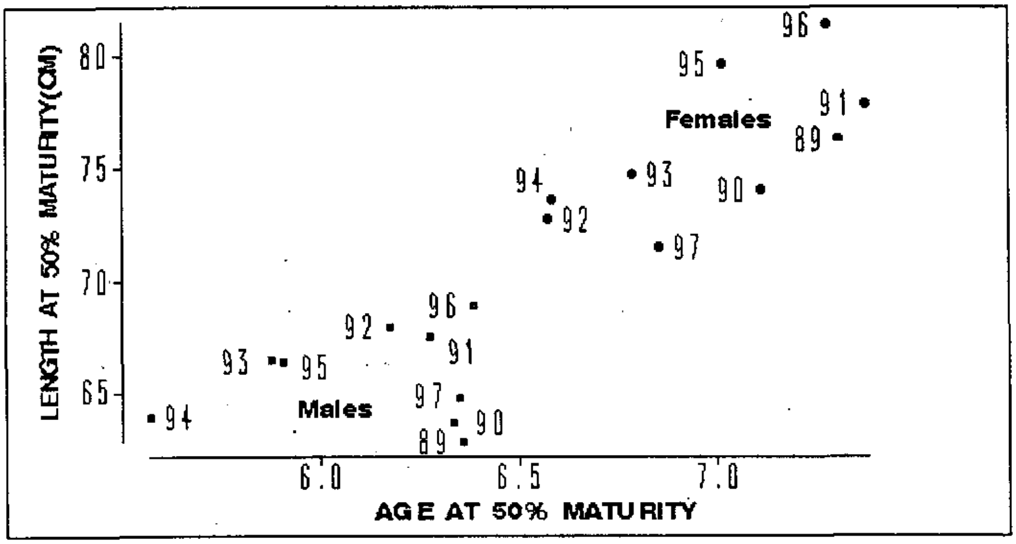

Fig. 4. Length (cm) versus age (year) at 50% maturity in 1989–1997.

Sexual differences in maturation

The curve fitted to the maturity data from 1989–1997 gives maturity ogives by sex and year according to age (Figure 5) and length (Figure 6). In general they show the same consistent difference between males and females as indicated by Tables 1–4. In age at 50% maturity the difference is close to 1 year, with an average of 6.99 years for females and 6.14 years for males. The difference in length is close to 10 cm with an average of 76.0 cm for females and 64.9 cm for males. The observed ranges are 6.59–7.31 years and 71.6–81.5 cm for females and 5.57–6.39 years and 62.7–69.0 cm for males.

Figure 7 is a plot of mean length at age in each year 1989–1997 for females versus males. The value used are for immature fish at age 5 and 6 and mature fish at ages 6–9. The value for the age 5 immature fish are close to the 1/1 reference line, but at age 6 the points are mostly above the line and there is little difference between mature and immature fish. The distance from the reference line tends to increase with age. Thus there appears to be little sexual diversity in length at age up to age 5, whereas females seem to be longer than males at older ages.

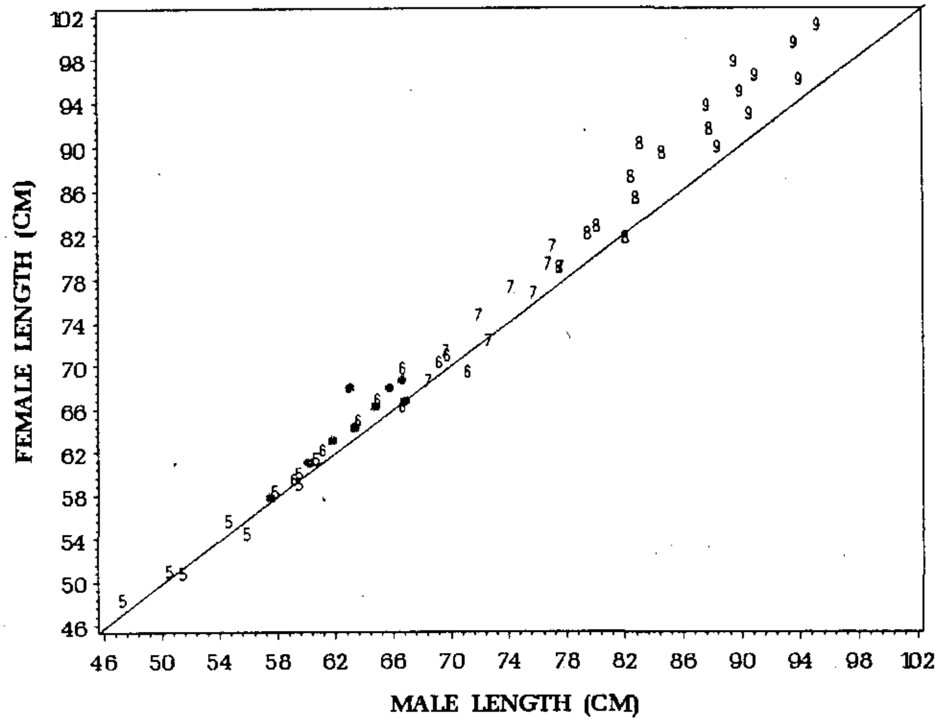

Fig. 7 Mean length (cm) at age of males versus females in 1989–1997 (-immature fish at age 6).*

Table 7 shows the mean length at age for the first time spawners by year and sex for age 6–8. A period of high values at age 6 in 1992–1995 coincides with the early maturation in those years and can be followed as a shift of one year with increasing age, except for age 8 in 1997 which shows a decrease. The values reflect the same trend as seen in Figure 7, i.e. that the females gradually attain a larger length at age than the males. This also reflected in the results of a two-way ANOVA for length of the first time spawners at age in 1989–1997 with respect to sex and year which is presented in the table below. The mean square values indicate that interannual variation in length of the first time spawners is larger than the difference in length between males and females at age 6 and 7 whereas at age 8 both year and sex are important factors.

AGE	SOURCE OF VARIATION	df	MEAN SQUARE	F
6	YEAR	8	2060.85	58.68 **
	SEX	1	249.73	7.11 **
	YEAR*SEX	8	31.64	0.90
	ERROR	961	35.12	
7	YEAR	8	1935.45	47.70 **
	SEX	1	545.16	13.44 **
	YEAR*SEX	8	44.65	1.10
	ERROR	1011	40.57	
8	YEAR	8	780.76	16.82 **
	SEX	1	893.55	19.25 **
	YEAR*SEX	8	62.29	1.34
	ERROR	461	46.41	
				**-1% level

Consumption of capelin and cod maturation

In order to study the effects capelin as a major prey species has on maturity, the consumption of capelin / cod biomass (C/B) ratio was calculated, subtracting 25% of the spawning stock biomass from the cod stock biomass at January 1 to account for the fact that the spawning stock is outside the Barents Sea for three months (Mehl, per. comm.). The C/B ratios for 1989–1996 are given below, showing the highest values in 1990–1993.

1988	1989	1990	1991	1992	1993	1994	1995	1996
0.43	0.67	1.86	2.21	1.52	1.41	0.56	0.37	0.28

The C/B ratio in each year was then related to the fraction mature of males and females at ages 6–8 in the following year. The text table below displays the correlation matrix. There is a significant increase in the fraction mature in both sexes with increasing C/B ratio, but the relationship becomes less pronounced with increasing age.

Sex	6 yr	7 yr	8 yr
Females	0.6269	0.4141	0.3521
Males	0.6730	0.4302	0.2220

DISCUSSION

The Northeast Arctic cod is at the limit of the species' geographical distribution and is clearly under influence of the environmental changes in the area which tend to be periodical. Thus, growth can vary considerably, both between individuals and on the population level. Variations in maturity also occur, but are more difficult to relate to environmental conditions, partly because maturity is more difficult to record than growth. The results presented use length as the parameter which indicate changes in the growth. In general, the weight is closely linked to the length, but in some periods. especially when capelin stock is low, a marked reduction in the condition of the cod has been observed. In some cases, using weights may therefore qualify some of the results, but will not change the general conclusions of the study.

The occurrence of mature cod in the easternmost part of the area in some years (Figure 2) may be linked to environmental conditions, but could also reflect changes in the feeding migrations. Spawning of Northeast Arctic cod is not considered to occur normally east of 25 °E, but the cod would still have time to move westwards to the known spawning grounds during 1–2 moths before the spawning season ends. Another possibility is that they do not spawn at all. Thus, Oganesyan (1995) reported a high proportion of females with spawning omission, indicating that the assumption that cod spawn annually after first spawning is not valid. Spawning omission could be an energy saving or fecundity gaining strategy. Specimens with spawning omission fall under code 4 on the maturity scale, but are according to Kjesbu (1991) difficult to distinguish from immature, recovering or spent individuals based on visual inspection. Burton et al., (1997) showed that inspection of the ovarian walls can solve this problem, but such procedures are time consuming and are not integrated in the routine sampling.

The annual maturity ogive used in the assessment of Northeast Arctic cod has historically been based on different data sources. In recent years data from the main Russian survey (Lepesevich and Shevelev, 1997) have been used. The unertainty with these data has been that it can be difficult to decide the maturity stage in late autumn when the Russian survey is conducted. The present estimates from the Norwegian survey, however, do not differ much from the Russian results and confirm that the maturity ogives used in recent years are realistic, if not accurate.

Changes in both size and age at maturity where the population size is small could be an indicator that cod stocks are under stress (Trippel, 1995). Jørgensen (1989) found a reduction in age at maturity, probably as a response to the increased mortality. Myers et al., (1996) showed that age at maturity appears to be dependant on ambient temperature. Saborido and Junquera (1997) stated that female cod at

Flemish Cap appeared to have reached the limit of density-dependent response with maturity fixed at about age 3 in recent years.

Mean length at age of the first time spawners increased nearly proportionally with age (Table 7). If the onset of maturity in Northeast Arctic cod is mainly triggered by size, the mean length of the first time spawner would be expected to be fairly stable and the approximate proportionality with age indicate that maturation is little influenced by length. This is apparently supported by the plot in Figure 4 which for both sexes indicates a linear relationship between age and length at 50% maturity. However, the linearity is not so clear if the sexes are considered separately. Some years (1989, 1990 and 1997) appear as outliers, and it can be argued that slow growth may have delayed the maturation in these years. Furthermore, the period of early maturation in 1992–1995 coincided with high length and weight at age 6 (ICES, 1998). Thus, length appears to have some effect on maturation, but the nature of the relationship is obscure.

The capelin is the most important prey for cod and in years of low capelin abundance the cod will increase the consumption of prey like amphipods with lower caloric content (Bogstad and Mehl, 1997). According to Bogstad (1997) one of the minimum requirement for a multispecies risk analysis is a model for how cod maturation depends on consumption of capelin. The consumption of capelin to cod biomass ratio shows a correlation of 0.63 for females and 0.67 for males with fraction mature at age 6. The correlation decreases with age, probably because the observed variation in maturity is most pronounced at age 6. This result indicates that the fraction mature at age 6, mainly first time spawners, to some extent is dependent on capelin abundance during the feeding season prior to spawning. Although the weight at age was high for 6 year old in these years, the growth rate from age 5 to age 6 was relatively low (ICES, 1998). The energy obtained from consumption of capelin therefore appears to have been used more for maturation than for growth during the year prior to the first spawning.

The earlier maturationin in 1992–1995 coincided with a substantial reduction in the number of old cod (>7 years) in the spawning stock which started to increase again in 1996 (ICES, 1998). Also, in 1996 the strong 1990 year class was 6 years old. Density dependent effects of stock size on maturity may therefore exist, but it is difficult to distinguish between these and effects of growth and consumption of capelin because they are to some extent related.

The sexual difference in age at 50% maturity during the period investigated is consistent and amounts to approximately one year, with males maturing first. This is a larger difference than reported by Jørgensen (1989) who, based on otoliths from commercial samples 1950–1975, found less than half a year difference in median age at maturity. There is a possibility that the results based on surveys may be biased, mainly because the maturity stages for females and males could be interpreted differently by those taking the samples. The results therefore need verification through investigation of other data sources, but both the results of Jørgensen (1989) and the age and sex composition from commercial landings in the Lofoten spawning fishery confirm that there is a significant difference between the sexes.

The data from the surveys do not indicate any large difference in growth between the sexes before maturity, but show slightly higher weights at age for the females after maturity. This could reflect higher individual growth, but could also be an effect of increased mortality when the fish enter the spawning stock. The difference in mean length at age are, however, relatively small (0–8% at age 8) and are negligible in the stock assessment.

The survey data indicate that the sexes are approximately equal in numbers in the age groups prior to maturity. Thus, the earlier maturation of males will tend to give a predominance of males in the spawning stock. A preliminary analysis of survey data and commercial landings in Lofoten indicate that the sex ratio (males:females) in the mature part of the cod population during 1989–1997 is more than 2:1 in many cases

In the Northeast Arctic cod stock, maximum fishing mortality has in recent years not been reached until age 7 or 8 (ICES, 1998). This is to a large extent an effect of the Norwegian coastal spawning fishery which for these age groups comes in addition to the trawl fishery. Hence, when the cod reaches maturity it will be subject to a higher exploitation rate than immatures at the same age. The sex difference in maturity will therefore result in a higher fishing mortality on males than on females for ages where the proportion mature is different. This effect will be seen mainly in the ages 5–8. As a result of this, the ratio males:females in the stock is reduced with age and from approximately age 9, females are predominant (Tables 1 and 2).

The effect that maturity and mortality have on the female age composition in the spawning stock might be important in view of the results presented by Solemdal et al., (1993). They found that repeat spawners of Northeast Arctic cod had larger eggs than first time spawners and that egg size was more important on this factor than on fish length. Larval survival is probably related to egg size and both the size and the age structure of the females spawning stock might therefore represent a more relevant measure of the spawning potential than the traditional SSB.

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Table 1. Fraction of females mature by age group and numbers sampled in 1989–1997 (f —fraction mature and t —total number).

Age		1989	1990	1991	1992	1993	1994	1995	1996	1997
4	f	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	t	93	62	91	69	198	204	259	175	83
5	f	0.02	0.01	0.04	0.04	0.01	0.21	0.04	0.01	0.00
	t	83	91	81	23	125	225	371	226	109
6	f	0.17	0.11	0.14	0.46	0.28	0.31	0.33	0.12	0.12
	t	369	71	114	13	60	156	284	348	161
7	f	0.42	0.47	0.42	0.60	0.59	0.49	0.38	0.40	0.59
	t	136	135	66	15	27	65	124	217	236
8	f	0.61	0.79	0.68	0.91	0.94	0.85	0.71	0.72	0.92
	t	33	14	112	22	51	34	28	53	100
9	f	1.0	0.67	0.9	0.99	0.96	0.98	0.88	1.0	1.0
	t	9	3	10	86	55	51	17	12	28
10	f	1.0		1.0	1.0	0.98	1.0	0.93	1.0	1.0
	t	4		3	10	116	31	15	6	4
11	f		1.0	1.0	1.0	1.0	0.99	1.0	1.0	1.0
	t		1	1	4	19	90	13	6	1
12	f	1.0				1.0	1.0	1.0	1.0	1.0
	t	1				3	25	46	6	3
13	f				1.0	1.0	1.0	1.0	1.0	1.0
	t				1	3	4	3	8	1

Table 2. Fraction of males mature by age group and numbers sampled in 1989–1997 (f —fraction mature and t —total number).

Age		1989	1990	1991	1992	1993	1994	1995	1996	1997
4	f	0.01	0.01	0.01	0.02	0.02	0.01	0.00	0.00	0.00
	t	102	71	91	45	158	231	265	194	87
5	f	0.06	0.07	0.11	0.00	0.29	0.49	0.19	0.06	0.07
	t	85	83	83	19	117	287	402	239	115
6	f	0.39	0.21	0.51	0.75	0.59	0.62	0.62	0.40	0.4
	t	402	71	103	12	75	204	375	297	178
7	f	0.69	0.82	0.71	0.83	0.81	0.72	0.70	0.73	0.74
	t	124	184	106	18	57	68	124	253	280
8	f	0.91	1.0	0.91	0.96	0.91	0.89	0.80	0.84	0.96
	t	32	36	169	24	42	48	20	62	93
9	f	1.0	1.0	1.0	0.97	0.98	0.97	1.0	1.0	1.0
	t	3	9	25	60	50	30	12	12	21
10	f		1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.67
	t		3	5	9	97	15	10	7	3
11	f			1.0		1.0	0.98	1.0	1.0	1.0
	t			1		9	60	10	8	1
12	f		1.0			1.0	1.0	1.0	1.0	1.0
	t		1			2	11	20	3	1
13	f					1.0		1.0	1.0	
	n					1		2	5	

Table 3. Fraction of females mature by length interval and numbers sampled in 1989–1997.

L.I-cm	1989	1990	1991	1992	1993	1994	1995	1996	1997
45-49	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	60	44	80	34	74	81	114	91	56
50-54	0.12	0.00	0.00	0.00	0.00	0.03	0.01	0.03	0.00
	102	45	67	36	83	79	110	103	50
55-59	0.15	0.11	0.02	0.00	0.00	0.14	0.07	0.03	0.04
	143	67	51	23	81	77	136	104	68
60-64	0.20	0.24	0.14	0.05	0.02	0.25	0.15	0.08	0.13
	117	51	74	20	62	93	130	134	82
65-69	0.23	0.33	0.16	0.38	0.14	0.31	0.29	0.16	0.39
	80	58	70	8	37	91	109	123	82
70-74	0.50	0.45	0.38	0.55	0.47	0.35	0.31	0.28	0.53
	48	62	66	11	36	68	103	97	89
75-79	0.54	0.48	0.43	0.83	0.79	0.50	0.43	0.31	0.69
	24	27	44	12	24	40	75	85	77
80-84	0.50	0.38	0.58	0.85	0.82	0.65	0.39	0.50	0.87
	14	8	45	20	33	34	54	54	46
85-89	0.39	1.0	0.79	0.96	0.89	0.90	0.50	0.60	0.94
	13	1	29	23	44	39	32	25	34
90-94	1.0	0.00	0.83	0.97	0.98	0.98	0.91	0.76	1.0
	4	1	12	29	51	51	34	29	21
95-99	1.0	0.5	1.0	1.0	1.0	0.98	0.85	0.80	1.0
	4	2	6	23	55	49	13	20	20
100-104	1.0	1.0	0.67	0.95	0.97	1.0	0.96	1.0	0.95
	5	1	3	19	34	46	28	15	20
105-109	1.0			1.0	0.93	0.96	0.92	1.0	1.0
	2			3	14	24	12	10	8
110-114		0.00		1.0	1.0	1.0	1.0	1.0	1.0
		1		3	8	16	7	4	3
115-119			1.0	1.0	1.0	1.0	1.0	1.0	1.0
			3	1	3	5	8	5	1
120-124					1.0	1.0	1.0	1.0	
					3	1	6	4	

Table 4. Fraction of males mature by length interval and numbers sampled during 1989–1997.

L.I-cm	1989	1990	1991	1992	1993	1994	1995	1996	1997
45-49	0.05	0.02	0.00	0.00	0.02	0.01	0.01	0.00	0.02
	79	47	67	46	69	84	121	114	53
50-54	0.22	0.06	0.00	0.00	0.08	0.10	0.04	0.07	0.05
	106	50	68	28	60	87	147	100	60
55-59	0.42	0.20	0.08	0.14	0.24	0.36	0.25	0.18	0.27
	132	56	53	14	68	103	145	112	84
60-64	0.46	0.46	0.42	0.15	0.39	0.55	0.47	0.41	0.50
	144	93	60	13	64	121	162	111	99
65-69	0.61	0.69	0.55	0.50	0.53	0.67	0.61	0.56	0.65
	89	75	92	8	47	121	153	122	107
70-74	0.71	0.81	0.70	0.84	0.75	0.64	0.67	0.59	0.74
	38	70	93	19	40	105	110	103	106
75-79	0.75	0.86	0.80	0.91	0.77	0.82	0.79	0.69	0.78
	17	28	76	11	44	62	96	89	88
80-84	0.86	0.93	0.88	0.84	0.86	0.93	0.64	0.79	0.93
	14	14	57	19	43	42	47	56	53
85-89	1.0	1.0	0.93	1.0	0.93	1.0	0.85	0.85	0.94
	10	10	30	18	42	42	27	48	33
90-94	1.0	1.0	0.92	1.0	0.98	0.91	0.95	0.82	0.88
	1	3	26	17	47	33	19	27	17
95-99	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.90	1.0
	4	2	8	9	40	25	18	20	8
100-104		1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
		1	3	2	16	18	10	9	5
105-109		1.0	1.0		1.0	1.0	1.0	1.0	1.0
		2	2		7	6	6	5	1
110-114			1.0			1.0	1.0	1.0	
			1			1	1	2	
115-119				1.0		1.0			
				1		2			
120-124					1.0				
					2				

Table 5. Estimated age at 50% maturity in 1989–1997 by sex.

Year	Sex	α *(standard error)*	β (standard error)	Age at 50% maturity
1989	F	-9.3834 (0.825)	1.2845 (0.127)	7.31
	M	-9.7088 (0.823)	1.5274 (0.134)	6.36
1990	F	-13.0806 (1.643)	1.8379 (0.241)	7.12
	M	-11.8938 (1.084)	1.8764 (0.166)	6.34
1991	F	-9.3218 (0.76)	1.2636 (0.107)	7.38
	M	-9.1460 (0.628)	1.4554 (0.097)	6.28
1992	F	-12.0324 (1.516)	1.828 (0.224)	6.58
	M	-10.7435 (1.288)	1.7391 (0.208)	6.18
1993	F	-11.3805 (0.844)	1.6768 (0.129)	6.79
	M	-9.1462 (0.626)	1.5552 (0.112)	5.88
1994	F	-7.9677 (0.491)	1.209 (0.081)	6.59
	M	-7.0899 (0.436)	1.2727 (0.081)	5.57
1995	F	-9.0441 (0.546)	1.2889 (0.088)	7.02
	M	-9.6518 (0.531)	1.6321 (0.093)	5.91
1996	F	-12.008 (0.837)	1.6504 (0.125)	7.28
	M	-10.8962 (0.638)	1.7050 (0.102)	6.39
1997	F	-15.3879 (1.228)	2.2445 (0.179)	6.86
	M	-10.6281 (0.744)	1.6746 (0.114)	6.35

Table 6. Estimated length at 50% maturity in 1989–1997 by sex.

Year	Sex	α (standard error)	β (standard error)	Length at 50% maturity
1989	F	-7.6674 (0.639)	0.1003 (0.009)	76.44
	M	-8.4818 (0.670)	0.1352 (0.011)	62.74
1990	F	-8.6182 (0.947)	0.1133 (0.014)	74.07
	M	-12.477 (1.102)	0.1960 (0.017)	63.66
1991	F	-10.9418 (0.894)	0.1402 (0.012)	78.04
	M	-11.4503 (0.811)	0.1694 (0.011)	67.59
1992	F	-15.1422 (1.824)	0.2079 (0.024)	72.83
	M	-14.8945 (1.931)	0.2188 (0.028)	68.07
1993	F	-16.5109 (1.327)	0.2208 (0.017)	74.78
	M	-10.4407 (0.710)	0.1568 (0.010)	66.59
1994	F	-10.3937 (0.648)	0.1411 (0.009)	73.66
	M	-9.5568 (0.594)	0.1495 (0.009)	63.93
1995	F	-9.0149 (0.516)	0.1131 (0.007)	79.71
	M	-9.5548 (0.517)	0.1437 (0.008)	66.49
1996	F	-10.4478 (0.669)	0.1282 (0.009)	81.50
	M	-8.8514 (0.503)	0.1283 (0.007)	68.99
1997	F	-13.6106 (1.035)	0.1902 (0.014)	71.56
	M	-9.7004 (0.668)	0.1495 (0.010)	64.89

Table 7. Mean length of the first time spawners in 1989–1997 by sex.

Year	Sex	AGE 6(stdr.err)	AGE 7(stdr.err)	AGE 8(stdr.err)
1989	F	59.1 (6.5)	72.2 (5.2)	84.2 (9.2)
	M	59.4 (4.2)	69.9 (7.9)	81.8 (5.9)
1990	F	62.0 (4.8)	69.2 (4.6)	78.7 (4.9)
	M	60.8 (4.5)	68.8 (5.0)	78.4 (5.4)
1991	F	66.5 (4.1)	72.1 (5.5)	82.7 (5.7)
	M	66.6 (4.4)	73.1 (4.9)	80.6 (6.8)
1992	F	69.7 (4.3)	77.4 (4.5)	83.5 (5.8)
	M	71.2 (3.3)	74.1 (7.9)	81.1 (5.6)
1993	F	70.0 (3.9)	77.5 (3.4)	86.0 (5.1)
	M	66.6 (5.9)	75.8 (6.3)	85.0 (6.6)
1994	F	71.1 (7.6)	82.1 (8.5)	93.0 (5.3)
	M	70.5 (6.5)	79.2 (8.5)	86.2 (8.3)
1995	F	70.9 (6.7)	79.7 (7.5)	94.5 (6.4)
	M	69.8 (6.6)	80.0 (5.4)	85.0 (8.9)
1996	F	68.7 (4.8)	80.5 (7.7)	91.9 (8.3)
	M	65.7 (5.8)	78.4 (7.3)	89.2 (6.7)
1997	F	65.3 (7.6)	75.3 (6.3)	88.7 (9.0)
	M	63.7 (5.7)	72.7 (6.2)	83.3 (6.6)

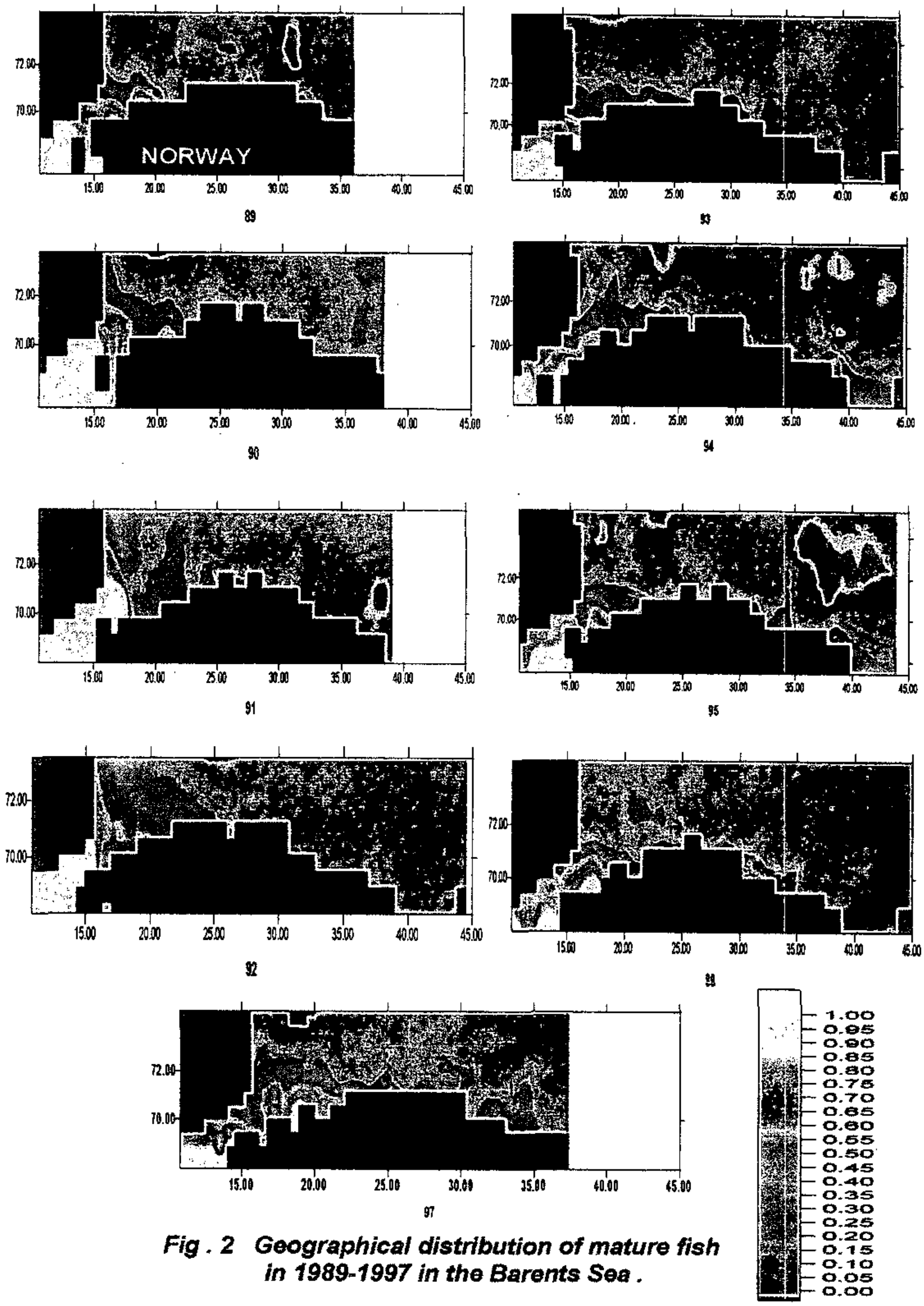

Fig . 2 Geographical distribution of mature fish in 1989-1997 in the Barents Sea .

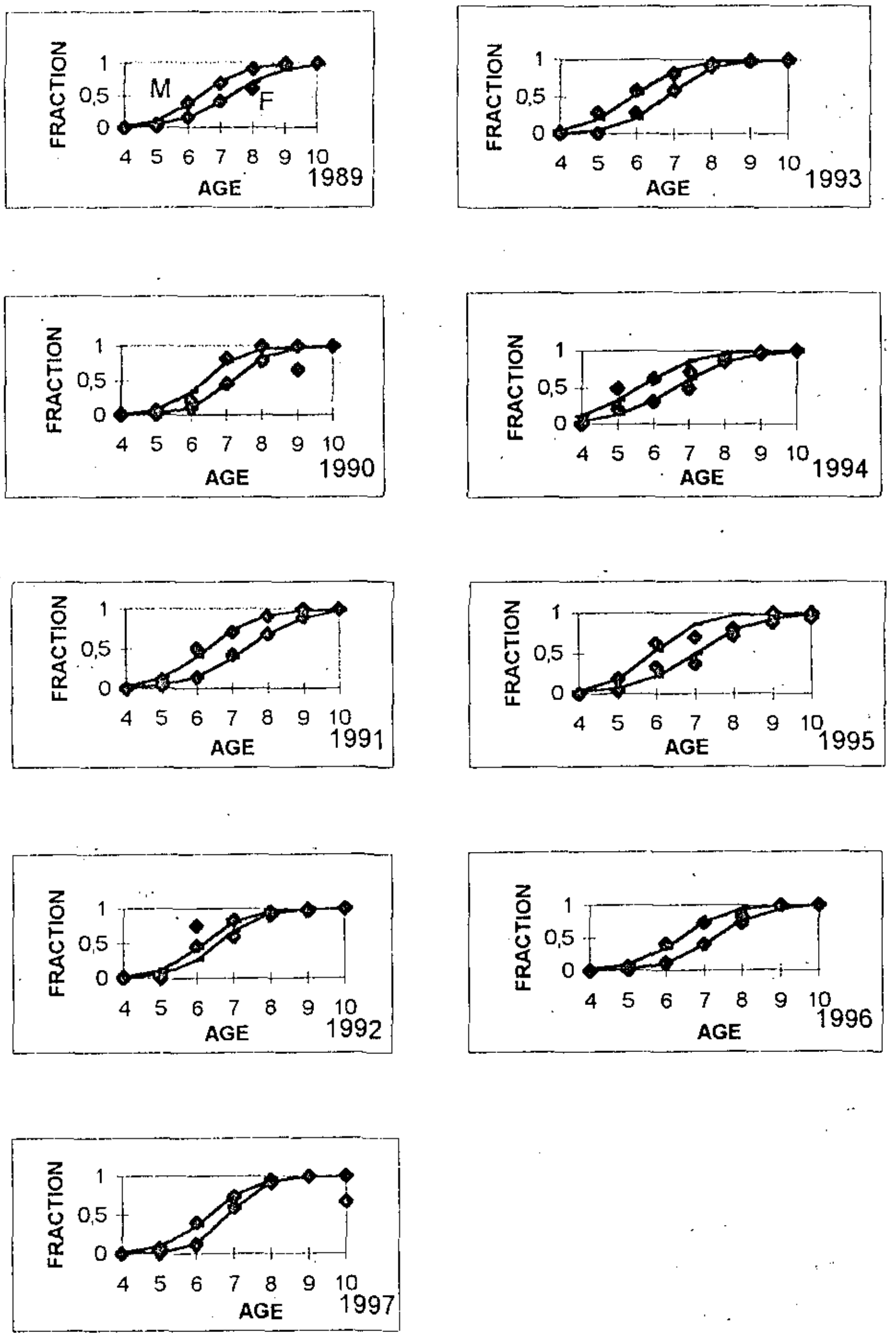

Figure 5. Maturity curves (solid line) fitted to the fraction mature (♦) of females (F) and males (M) in 1989-1997.

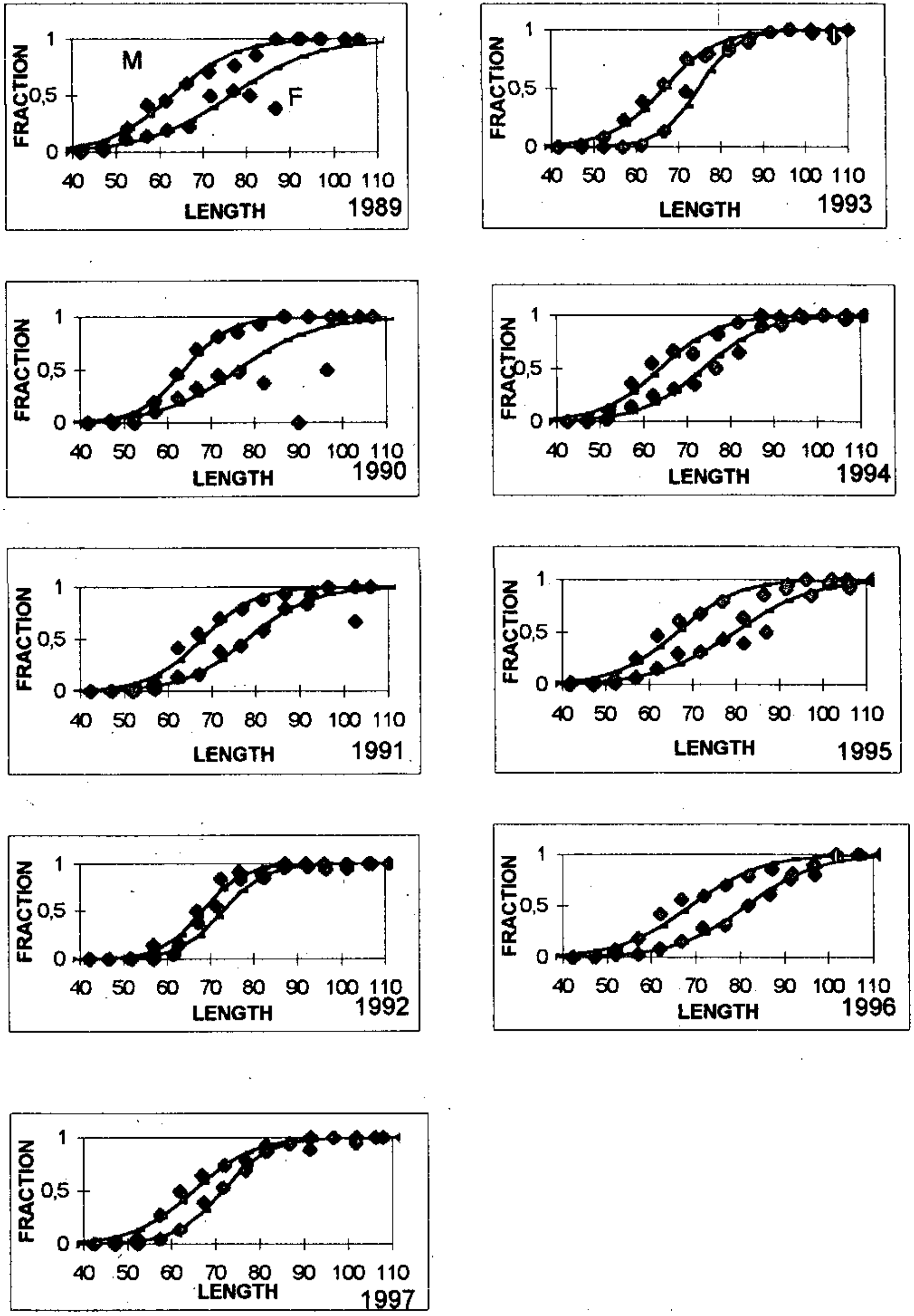

Figure 6. Maturity curves (solid line) fitted to the fraction mature at length (•) of females (F) and males (M) in 1989-1997.